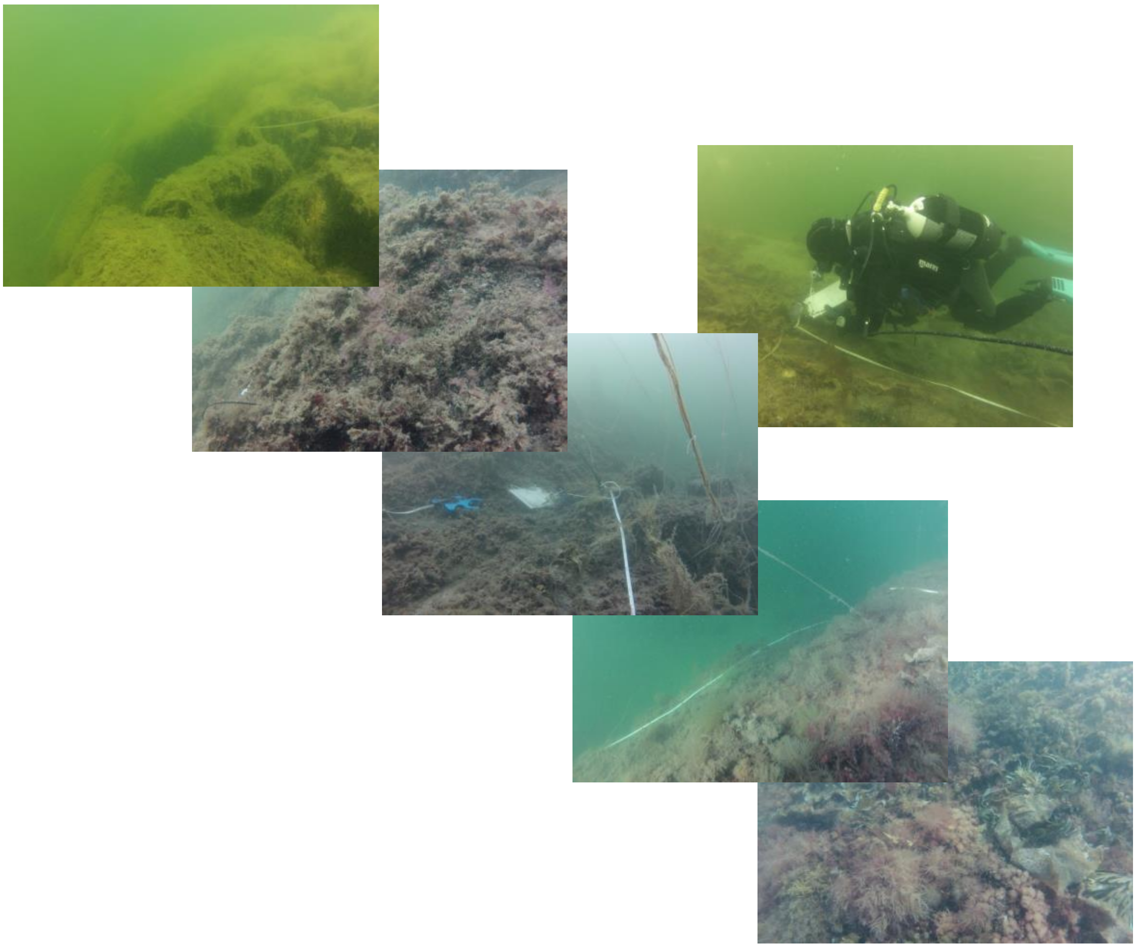

RESPONSE OF MACROPHYTE INDICATORS TO NATURAL AND ANTHROPOGENIC GRADIENTS IN TWO COASTAL AREAS OF SWEDEN

Sofia A. Wikström, Mats Blomqvist, Susanne Qvarfordt and Antonia Nyström Sandman

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Response of macrophyte indicators to natural and anthropogenic gradients in two coastal areas of Sweden

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Cover photo: Vegetation in the five west coast gradient study areas in 2013, upper left Byfjorden to lower right Marstrandsfjorden, diver surveying in the middle area Askeröfjorden. Photo: Sandra Andersson.

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http://waters.gu.se/resultat/WATERS-leveranser

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. In the report a number of candidate indicators are tested against pressure gradients in two coastal areas of Sweden. The result will serve as input to the establishment of new monitoring programs as well as for recommendations on new indicators for the WFD.

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

Contents

Summary

Benthic macrophytes are known to be affected by anthropogenic activity, and therefore these communities are suitable for the assessment of ecological status according to the WFD. The existing assessment method for benthic macrophytes is based on the depth distribution of a few selected species, which only represents one aspect of potential changes in macrophyte communities in response to stress. Moreover, the present method performs poorly in shallow areas and areas dominated by soft substrate. There is therefore a need for new macrophyte indicators for the assessment of ecological status. The aim of the study was to test and evaluate a number of potential macrophyte indicators on a homogenous data set from well-described pressure gradients on both the west and east coast of Sweden.

On the west coast, the study was conducted in five areas along the gradient in the fjord areas inside the islands of Orust and Tjörn. In the Baltic Sea (Swedish east coast), sampling took place in seven areas in three parallel gradients in the county of Östergötland. Surveys of large squares (5x5 m) using SCUBA-technique was chosen as the main method of the studies. To reduce the variation between sampling squares, the squares were sampled on either hard or soft substrate within a limited depth range. On soft bottoms communities on the west coast, depth range of eelgrass (*Zostera marina*) was surveyed using video. Environmental data such as salinity, Secchi depth, total nitrogen and total phosphorus were sampled at three stations in each of the five and seven areas.

For hard substrate communities, the results show that species richness in macroalgal communities is a promising indicator as it increased with increasing Secchi depth. Cumulative cover and community complexity (the ratio between cumulative and total cover) were also positively related to Secchi depth. The proportion of opportunistic and late-succesional macroalgal species was only related to Secchi depth on the west coast.

For soft substrate communities on the west coast, the depth distribution of *Zostera marina* responded strongly in the study gradient and is a promising indicator. In the more species-rich soft bottom communities on the east coast, the areas with high nutrient concentrations and small Secchi depth had low species richness and dominance of tolerant species. However, this was likely at least in part due to low salinity in these areas. Overall, the tested indicators for soft substrate on the east coast showed a large variation within areas and a large sampling effort is required to reduce uncertainty.

Svensk sammanfattning

Bottenlevande växters utbredning och sammansättning påverkas av mänsklig aktivitet och dess effekter. Det gör att dessa samhällen är lämpliga att använda för bedömning av ekologisk status i enlighet med EU:s Vattendirektiv. Den nuvarande bedömningsgrunden för bentiska makrofyter baseras på djuputbredningen av ett fåtal utvalda arter. Djuputbredning representerar endast en aspekt av flera när det gäller potentiella förändringar i makrofytsamhällena till följd av miljöpåverkan. Den nuvarande metoden har också visat sig ge svag respons i grunda områden och i områden där mjukbotten dominerar och det finns därför ett behov av nya makrofytindikatorer för statusbedömning. Syftet med studien har varit att testa ett antal potentiella indikatorer och utvärdera dessa på ett homogent dataset från väl beskrivna påverkansgradienter på såväl ost- som västkust.

På västkusten utfördes studien längs med gradienten i fjordsystemet innanför Orust och Tjörn. På ostkusten provtogs tre parallella gradienter i Östergötland (Bråviken, Slätbaken och Kaggebofjärden). Som huvudsaklig provtagningsmetod för undersökningarna valdes dykundersökning av 5x5-metersrutor. För att reducera variationen mellan rutor provtogs hård- respektive mjukbotten i separata rutor inom ett begränsat djupintervall. På mjukbottnar på västkusten undersöktes djuputbredningen av ålgräs (*Zostera marina*) med hjälp av video. Salthalt, siktdjup, totalkväve och totalfosfor provtogs i samma gradienter.

Studien visade att artrikedom är en lovande indikator för hårdbottensamhällen, då den ökar med ökat siktdjup och/eller minskande näringskoncentration. Kumulativ täckningsgrad och samhällskomplexitet (kvoten mellan kumulativ och total täckningsgrad) var också positivt korrelerade med siktdjup. Proportionen av arter med olika livshistoriestrategi (opportunister och sen-successionsarter) var korrelerade med siktdjup på västkusten men inte på ostkusten.

Djuputbredningen av ålgräs på västkusten svarade starkt i den undersökta gradienten på västkusten och är därför också en lovande indikator. I de mer artrika mjukbottensamhällena på ostkusten hade områden med höga närsaltshalter och lågt siktdjup också låg artrikedom och högre inslag av toleranta arter. Dock kan en del av det mönstret förklaras av att dessa områden också har låg salthalt. Överlag var variationen inom områden stor för mjukbottenindikatorerna på ostkusten, vilket innebär att det krävs en omfattande provtagningsansträngning för att reducera osäkerheten.

1. Introduction

One major pressure on coastal vegetation is nutrient enrichment from anthropogenic or natural sources, e.g. favoring the growth of phytoplankton (references in Krause-Jensen et al. 2008) and opportunistic macrophytes (e.g. Wallentinus 1984; Pedersen and Borum 1996). Increased pelagic phytoplankton biomass reduces light availability for benthic primary producers. Increased nutrient concentrations in the water and/or water turbidity can thereby negatively affect lower depth limits as well as the biomass, cover or species composition of macrophytes at certain depths (reviewed by Krause-Jensen et al. 2008).

Since benthic macrophytes are known to be affected by anthropogenic activity these communities are suitable for the assessment of ecological status. The existing assessment method for benthic macrophytes is based on the depth distribution of a few (3-9) selected species (e.g. Blomqvist et al. 2012). However, this method has proved to perform poorly in recent tests (Blomqvist et al. 2014), especially in shallow areas and areas dominated by soft substrate, which are common along the entire Swedish coast. These problems have resulted in the need for new indicators for the assessment of ecological status.

In the report 'Potential Eutrophication Indicators Based on Swedish Coastal Macrophytes' (Blomqvist et al. 2012), we suggested a set of candidate vegetation indicators for assessing the ecological status of Swedish coastal waters. The suggested indicators represented the distribution, abundance, diversity and composition of macroalgal communities on rocky shores as well as of soft-substrate communities of vascular plants and charophytes along the Swedish coastline. The candidate indicators fulfilled fundamental criteria for good indicators, i.e. they had a sound scientific basis, had ecosystem relevance, were supported by existing/ongoing monitoring data and thus relatively cost-efficient, and they were concrete and measurable.

Several of the candidate indicators have subsequently been tested against additional central quality criteria, namely responsiveness to pressures and variability associated with the indicators, using a large dataset compiled from Swedish environmental monitoring (Blomqvist et al. 2014). This allowed us to identify indicators that showed a clear response to eutrophication (cover of macroalgae, and species richness of macroalgae) and indicators that showed a response but also large variability (cover of soft-substrate macrophytes and proportion of opportunistic algae relative to the total algal cover). The large variability seen for some indicators may reflect a natural variability in the vegetation communities and the effect of natural gradients (e.g. the strong salinity gradient along the Swedish coastline), but may also be an effect of methodological uncertainty. The monitoring data used in the study was collected over a long time period by different experts. The survey method, diving transects according to the standard method for vegetation surveys in Sweden (Kautsky 1992), operates with a variable monitoring effort (variable seabed surface area that is surveyed), which can be expected to increase uncertainty in estimation of indicators based on species number or diversity. Also, sampling is not stratified with regard to substrate type, which can be expected to increase uncertainty since substrate is one of the most important determinants of macrophyte abundance and composition.

Some of the candidate indicators were not possible to test with available monitoring data. These included indicators based on the distribution and abundance of the seagrass *Zostera marina*, which are used in several other countries in the region as indicators for ecological status (Marba et al. 2013). *Z. marina* is poorly covered by existing monitoring programs in Sweden, resulting in too little data on the abundance and distribution of this species to allow testing of the suggested indicators. As mentioned above, the variable monitoring effort also made the existing data suboptimal for testing indicators based on the number of species.

1.1 Aim

The aim of this study was to further test the most promising candidate indicators identified by Blomqvist et al. (2012) for their response in coastal gradients and the variability associated with the indicators, using data sets collected specifically for the purpose in pressure gradients on the west and east coasts of Sweden. The study thus complements our previous report 'Response of Coastal Macrophytes to pressures' (Blomqvist et al. 2014), where the indicators were evaluated based on existing monitoring data. Specifically, we test (1) indicators that could not be tested with existing monitoring data (e.g. depth distribution of *Zostera marina*) and (2) if a decreased methodological uncertainty can give a clearer response of vegetation indicators to anthropogenic pressures.

This study is part of the joint WATERS gradient study where all WFD quality elements were sampled together with physical and chemical data in the same areas. A more detailed account of the sampling of vegetation data and methods to reduce sampling uncertainty will be given in a coming report on monitoring methods for macrophyte indicators.

2. Material and methods

2.1 Study areas

WATERS gradient study areas were selected to allow for sampling of all WFD quality elements (phytoplankton, macroalgae and angiosperms, benthic invertebrate fauna and fish) and at the same time cover gradients in eutrophication. The resulting areas (Figure 1) cover five fjord areas in one gradient inside the islands of Orust and Tjörn on the west coast of Sweden and seven archipelago areas in Östergötland on the east coast of Sweden.

The west coast areas are heavily influenced by weather conditions, and wind direction determines in- and outflows of the basins (Hansson et al. 2013). The inner area is influenced by the river Bäveån and the city Uddevalla. The middle area is influenced by the city Stenungsund.

The seven east coast areas are situated in three different inner to outer archipelago gradients: Bråviken, Slätbaken and Kaggebofjärden (north to south). Bråviken is a rather narrow bay with a fault steep northern shore and a flat southern shore. The inner part, with a large city and industries, has a strong freshwater inflow from the river Motala Ström resulting in comparatively large salinity fluctuations. Bråviken has no shallow sills or narrow straits, which allows for a large wind-driven water exchange.

Slätbaken inner parts are surrounded by agricultural plains with nutritious soils and have large inflows of fresh water, as well as heavy loads of nitrogen and phosphorous, mainly from the river Söderköpingsån. The Slätbaken gradient has limited water exchange due to several narrow straits and shallow sills. Kaggebofjärden inner part is less influenced by freshwater than the inner parts of the two northern gradients but also has limited water exchange due to straits and sills similar to the Slätbaken gradient. Kärrfjärden is the outer area, situated east of the middle gradient Slätbaken. It is a relatively open large archipelago area.

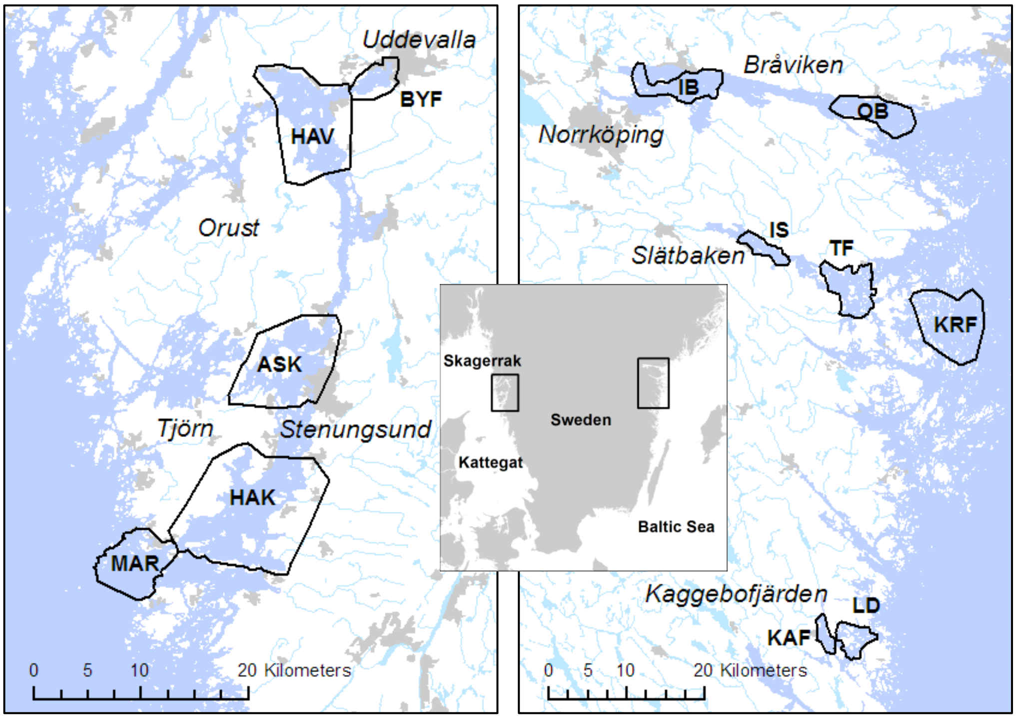

Figure 1. WATERS gradient study areas on the Swedish west coast (left) and east coast (right). The small map in the middle shows the outline of the gradient study area maps on a larger scale. The gradient study areas in the west coast were BYF Byfjorden, HAV Havstensfjord, ASK Askerö-/Halsefjorden, HAK Hake fjord and MAR Marstrandsfjorden. The gradient study areas on the east coast were IB Inner Bråviken, OB Outer Bråviken, IS Inner Slätbaken, TF Trännöfjärden, KRF Kärrfjärden, KAF Kaggebofjärden and LD Lindödjupet.

2.2 Physical and chemical data

Data on physical and chemical parameters were jointly sampled in the WATERS gradient studies in cooperation with and extending regular monitoring programmes and research programmes. On the west coast WATERS cooperated with the regional monitoring program run by Bohuskustens vattenvårdsförbund (http://www.bvvf.se/) in Byfjorden funded by the Swedish EPA (www.marsys.se). On the east coast WATERS cooperated with the regional monitoring program run by Motala Ströms vattenvårdsförbund (www.motalastrom.org).

Data was sampled at least monthly (Table 1) in the summer (June-August) period of 2012 and 2013 mainly on three stations regarded to be representative for each study area (Figure 2).

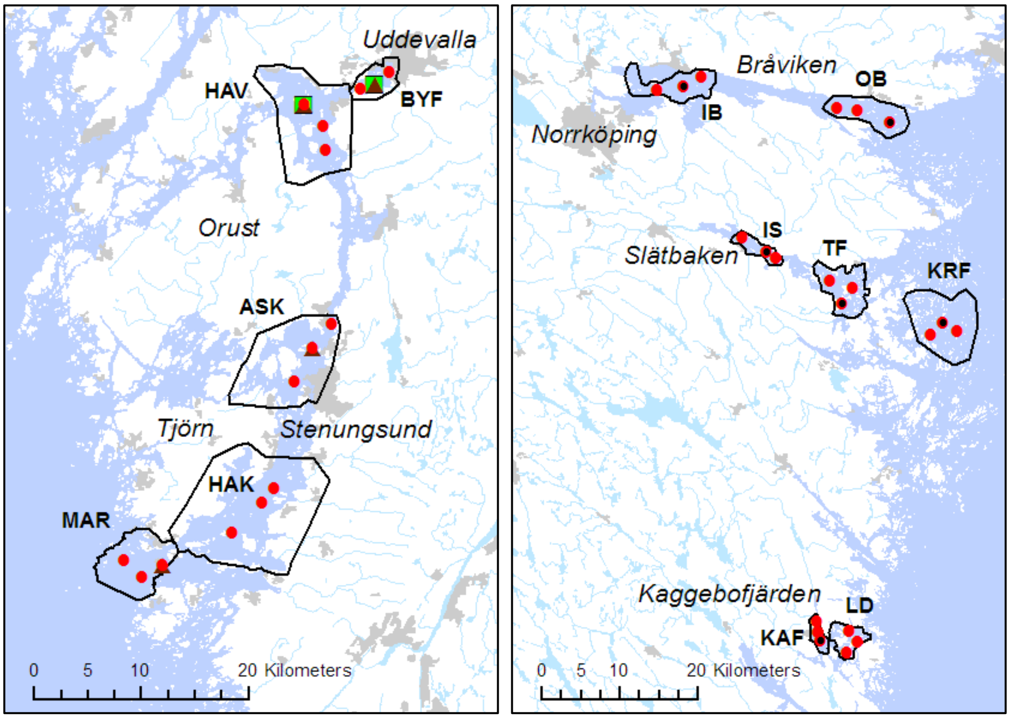

Figure 2. Sampling stations for physical and chemical data. Red circles represents stations sampled by the WATERS project, green squares were sampled by the BOX project, brown triangles were sampled by Bohuskustens vattenvårdsförbund and small black dots indicate stations sampled by Motala Ströms vattenvårdsförbund.

We used Secchi depth and surface values of salinity, total phosphorus and total nitrogen from these physical and chemical stations as predictors for vegetation indicators in our tests. Secchi depth was used as a proxy for the attenuation of light in the water column. Measurements of the optical components chlorophyll a, coloured dissolved organic matter (CDOM), suspended particulate matter (SPM) and its organic (SPOM) and inorganic (SPIM) fractions were also made in order to evaluate the relative importance of the factors explaining the Secchi depth, CDOM, SPM and chlorophyll a, within each study area. Physical and chemical analysis methods are described in Appendix 1.

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 sampling sites were assigned the SWM value from the closest grid cell.

The gradients in physical and chemical data in the study areas are shown in Figures 3 and 4. The west coast study areas had a clear gradient in Secchi depth with generally lower values in BYF, comparable values in HAV, ASK and HAK and higher values in MAR

(Figure 3). This can mainly be explained by corresponding gradients in Chlorophyll a and CDOM which explained 31 and 25 % of the variation in Secchi depth (Figure 5). There was no clear gradient in salinity between the areas. The innermost area BYF had higher values of total nitrogen and the outermost area MAR lower values of total phosphorus, remaining areas had only small differences without clear gradients in the respective nutrient concentrations. More significant was the considerable variation in physical and chemical values between years, especially in salinity. This large year to year variation might be explained by difference in rain during summer with higher values in 2012 (276 mm in 2012 and 173 mm in 2013, SMHI Henån weather station on Orust) which could also explain the generally lower Secchi depth values, higher nutrient concentrations, higher chlorophyll a and higher CDOM values in 2012.

In the more complex east coast study areas no such clear differences between years could be seen (Figure 4). Salinity seemed to be generally higher in several areas in 2012 but the freshwater influenced IB showed no clear difference between the years. A similar pattern in precipitation as on the west coast, with higher amounts of rain in summer 2012 (272 mm in 2012 and 188 mm in 2013, SMHI Börrum weather station), was found indicating that other factors than precipitation were important for salinity since salinity generally was higher in 2012 despite higher precipitation. Salinity was lowest in the inner areas IS and IB and highest in KRF. The outer part of Bråviken had surprisingly low salinity, approximately one PSU lower than TF, KAF, LD and KRF but still approximately one PSU higher than IB and IS indicating a strong transport of water from inner to outer parts of Bråviken. Secchi depth was highest in the outer area KRF and lowest in IS and IB and again surprisingly also in OB, indicating large water exchange from inner to outer Bråviken. CDOM was by far highest in IS whereas SPM, with low organic content, was highest in IB and OB. SPM was also comparatively high in IS but here organic content was much higher. Lowest SPM but highest organic content in SPM was found in the outer region KRF. Chlorophyll a was highest in IS followed by IB. TF, KAF, LD and KRF had comparable values of chlorophyll a whereas OB was a bit higher but still lower than IB. Total nitrogen followed the chlorophyll a values indicating that chlorophyll a relate well to total nitrogen in these areas ($r^2 = 0.62$, $p<0.01$). Total phosphorus showed a strong difference between the years with higher values in 2012. This might be explained by higher rates of phosphorus rich upwelling in 2012 rather than precipitation, since the relationship between salinity and total phosphorus was weak (Figure 5).

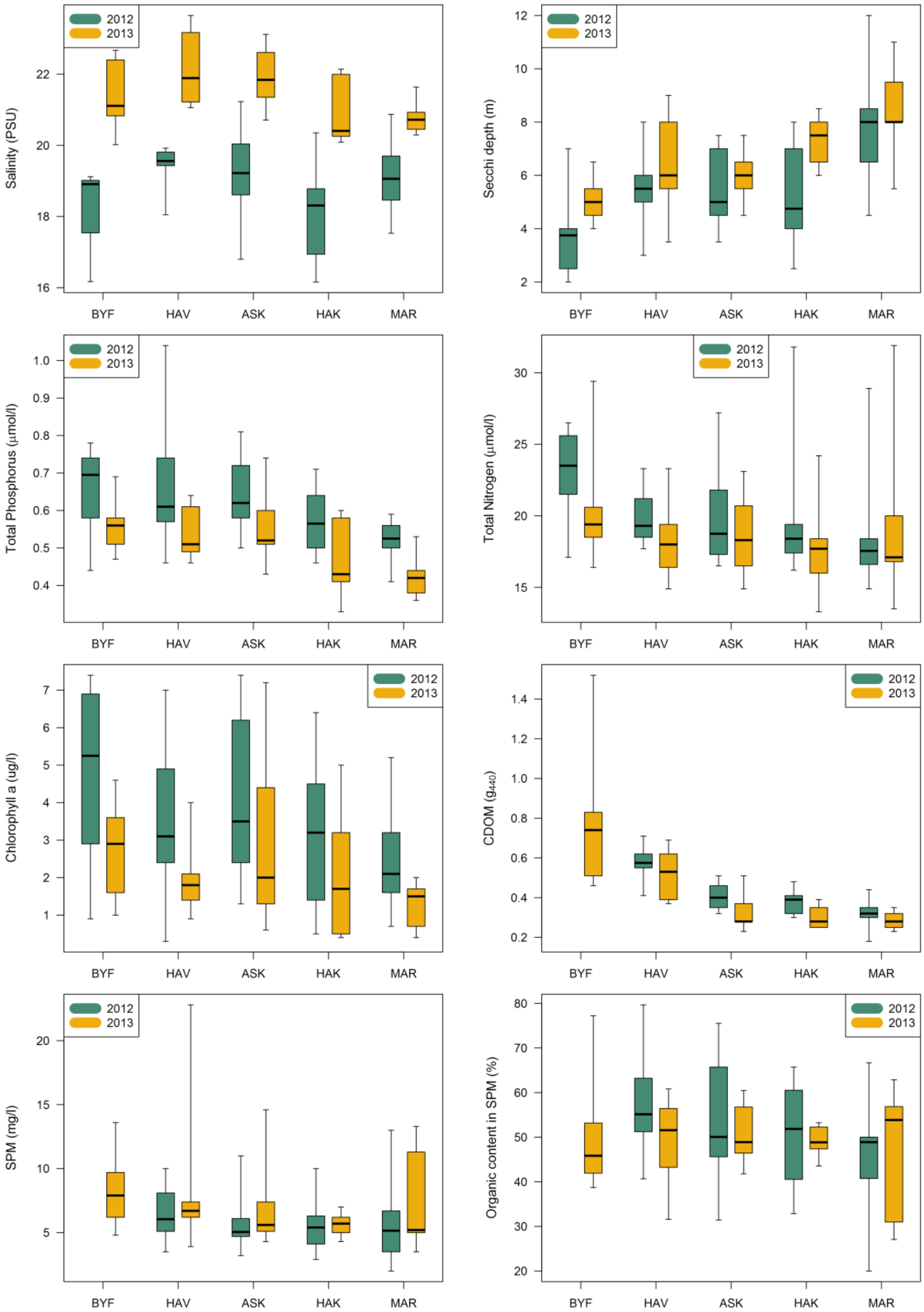

Figure 3. Physical and chemical surface data from the summer months (June-August) of two years in the west coast study areas. Each box shows the first and third quartile with a horizontal line at the second quartile (median). The whiskers represent minimum and maximum values. CDOM and SPM were not measured in BYF in 2012. The number of measurements in each area and year are listed in Table 1.

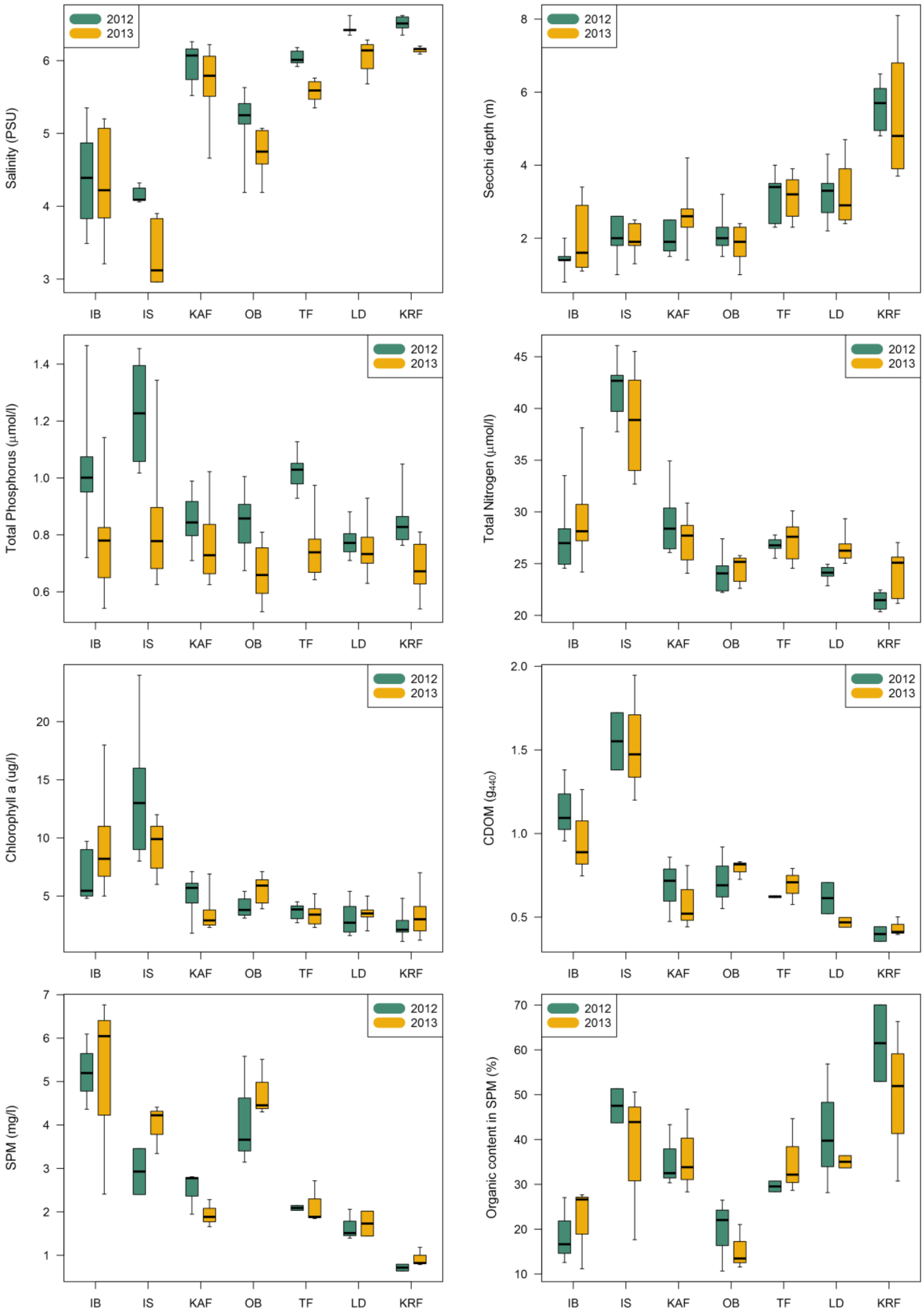

Figure 4. Physical and chemical surface data from the summer months (June-August) of two years in the east coast study areas. Each box shows the first and third quartile with a horizontal line at the second quartile (median). The whiskers represent minimum and maximum values. The number of measurements in each area and year are listed in Table 1.

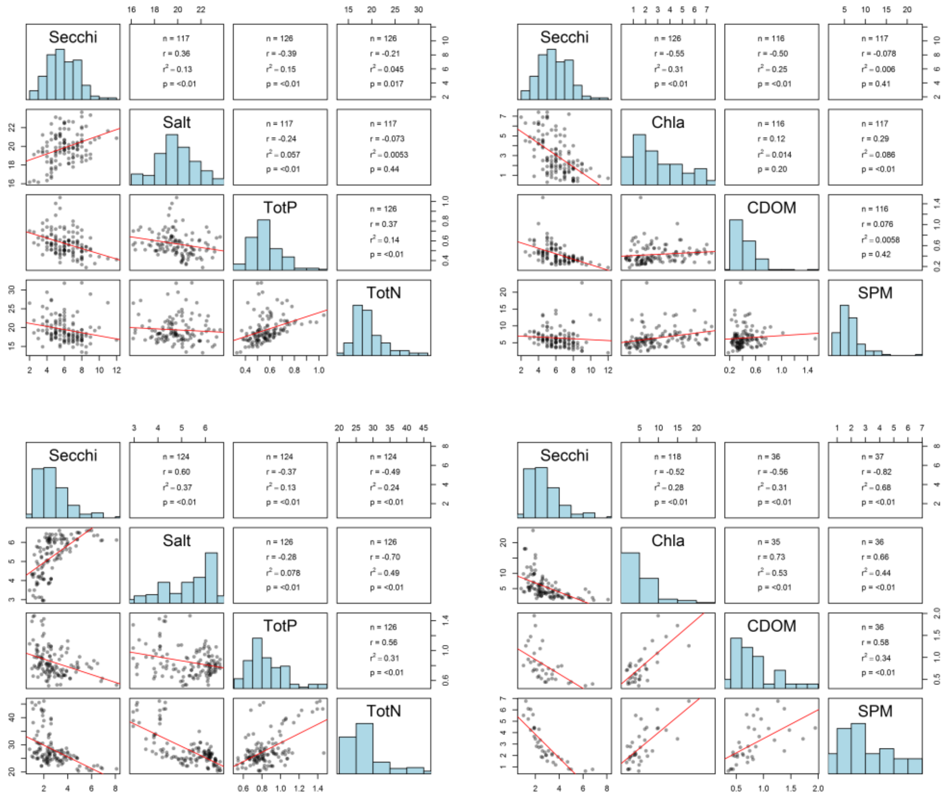

Figure 5. Relationships between physical and chemical data in the west (upper matrix plots) and east (lower matrix plots) coast study areas. Left matrix plots shows correlations between predictors used in this report and right matrix plots shows correlations between optical components affecting Secchi depth. Transparency makes overlapping dots darker. Linear regression lines are shown in red in the lower panels and n, r, r^2 and p for the regressions are shown in the upper panels in each matrix plot.

Table 1. Number of physical and chemical surface summer data values in each study area.

Coast	Area	Year	Salinity	Secchi	TotP	TotN	Chla	CDOM	SPM
West	BYF	2012	3	6	6	6	6	0	0
West	BYF	2013	9	9	9	9	9	9	9
West	HAV	2012	18	21	21	21	21	18	18
West	HAV	2013	9	9	9	9	9	9	9
West	ASK	2012	17	18	18	18	18	18	18
West	ASK	2013	9	9	9	9	9	9	9
West	HAK	2012	18	18	18	18	18	18	18
West	HAK	2013	8	9	9	9	9	9	9
West	MAR	2012	17	18	18	18	18	17	18
West	MAR	2013	9	9	9	9	9	9	9
East	IB	2012	9	9	9	9	6	3	3
East	IB	2013	9	9	9	9	9	3	3
East	OB	2012	9	9	9	9	7	3	3
East	OB	2013	9	9	9	9	9	3	3
East	IS	2012	9	9	9	9	9	2	2
East	IS	2013	9	9	9	9	9	3	3
East	TF	2012	9	9	9	9	8	2	2
East	TF	2013	9	9	9	9	9	3	3
East	KAF	2012	9	8	9	9	9	3	3
East	KAF	2013	9	9	9	9	9	3	3
East	LD	2012	9	9	9	9	9	2	3
East	LD	2013	9	9	9	9	9	2	2
East	KRF	2012	9	8	9	9	9	2	2
East	KRF	2013	9	9	9	9	9	3	3

Wave exposure at the vegetation sites differed most between study areas in the gradient on the west coast, with MAR having by far the highest values and BYF the lowest (Figure 6). On the east coast the highest values were generally found in Bråviken, areas IB and OB, and the lowest values were generally found in LD. The differences between areas outside Bråviken were generally small.

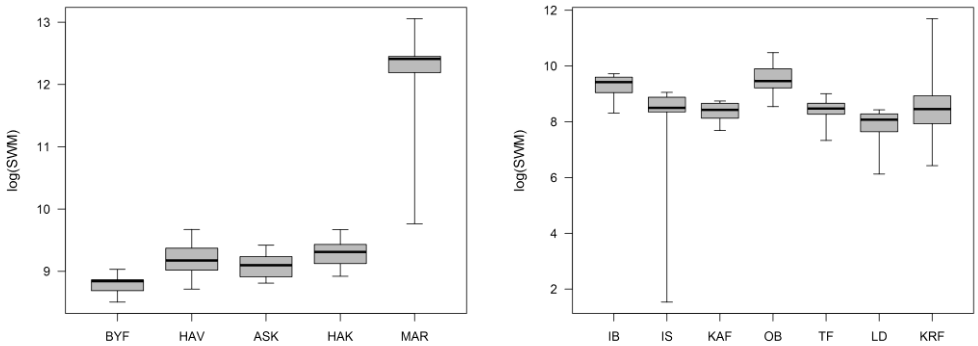

Figure 6. Wave exposure at vegetation sampling sites investigated by diving in west (left) and east (right) coast areas. Values of SWM (Isaeus 2004) were log-tranformed before analyses. As SWM were calculated as a static parameter the values did not differ between years. Each box shows the first and third quartile with a horizontal line at the second quartile (median). The whiskers represent minimum and maximum values.

To conclude, the west coast areas had large variation within and especially between years and there were more or less clear gradients between areas in all parameters apart from salinity and SPM. The east coast areas had smaller variation between years and often stronger gradients between areas in all parameters including salinity and SPM.

2.2.1 Spatial variation within each study area

At each vegetation site the salinity and temperature near the seafloor were measured by the diver in the field. Close to these sites Secchi depth was also measured. Secchi depth was also measured at each eelgrass site within the study areas on the west coast. The salinity and Secchi depth data from each vegetation sampling site were not used in the analyses of the vegetation indicators since we wanted to relate the indicators to the general conditions measured at the three physical and chemical stations within each study area. However, conditions vary spatially within the study areas and physical and chemical data from the vegetation sites can be used to evaluate if systematic differences could be seen between the vegetation sites and the three dedicated physical and chemical stations located more centrally within each study area. Sampling was not done at the same time as the physical and chemical stations were sampled at least three times per year in June to August whereas the vegetation sites were sampled once a year mainly in August to September. Hence, vegetation site data reflects only spatial variation while data from physical and chemical stations reflects temporal variation and to a smaller extent spatial variation within each year and study area.

Comparing Secchi depth measured close to vegetation sites with values from physical and chemical stations revealed no consistent systematic differences (Figure 7). Higher Secchi depth were observed at the more shallow vegetation sites closer to shore compared to the deeper and centrally placed physical and chemical sites in the innermost west coast area BYF both in 2012 and 2013. This contradicts the expectation that resuspension would reduce Secchi depth closer to the shore in this area. Similar patterns were seen in a few other areas: HAK and MAR but only in 2012, OB both years and KAF in 2012. The expected pattern with higher Secchi depth in deeper central parts was only seen in the outermost east coast area KRF and only in 2013. One explanation for higher Secchi depths close to the shore could be that vegetation stabilize sediment and reduce resuspension. There was in many cases much larger variation in Secchi depths measured close to vegetation sites, especially on the west coast.

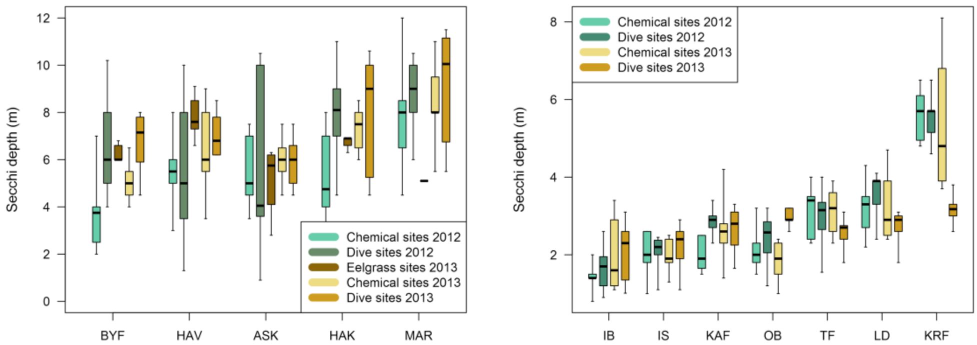

Figure 7. Secchi depth from physical and chemical stations and vegetation sites compared in west (left) and east (right) coast areas. Each box shows the first and third quartile with a horizontal line at the second quartile (median). The whiskers represent minimum and maximum values.

Making the same comparison with salinity did not show any consistent systematic differences. Similar patterns as for Secchi depth with higher values at vegetation sites was observed in all areas on the west coast apart from ASK both years and HAV in 2012 (Figure 8). This could indicate that there were different water masses at the different sampling periods which could be another explanation of the contradictory Secchi depth results from the west coast. On the east coast there were in some instances lower salinity values at the vegetation sites which indicates that it also here was likely that a change in water masses occurred between the different sampling periods.

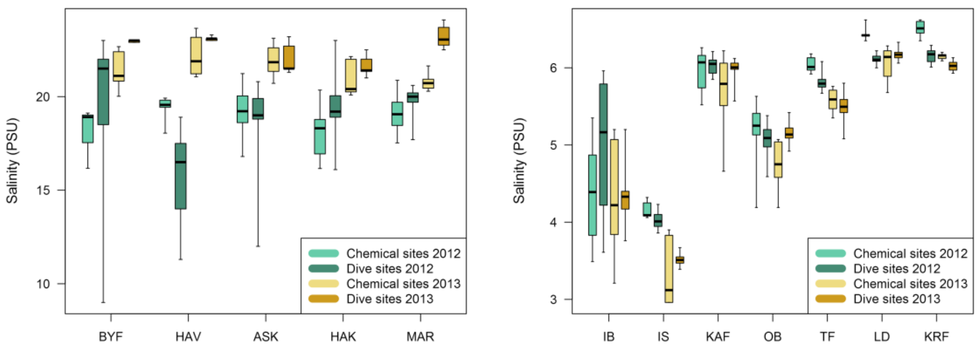

Figure 8. Salinity from physical and chemical stations and vegetation sites compared in west (left) and east (right) coast areas. Salinity at the vegetation sites was measured at the seafloor (ca 3 – 5 m depth) by the diver. Each box shows the first and third quartile with a horizontal line at the second quartile (median). The whiskers represent minimum and maximum values.

To conclude we believe that the physical and chemical stations are likely to represent a valid general view of the situation within the study areas.

2.3 Vegetation data

Composition of coastal vegetation is to a large extent determined by seafloor substrate and depth with a dominance of algal communities on hard substrates and vascular plants on soft and sandy substrates. In order to reduce variation and increase the possibility of finding correlations between vegetation indicators and pressures, sampling of vegetation was stratified into one depth interval (circa 3 – 5 m depth) on either stable hard substrates or soft substrates. To further reduce variation between sites we used a fixed sampling effort of a 5x5 m square at each sampling site. On the west coast, soft substrates are strongly dominated by eelgrass and here we used video sledge transects to measure the depth range of eelgrass meadows instead of 5x5 m squares.

2.3.1 Vegetation sampling sites

A large number (20 – 40) of potential sampling sites within each study area were identified based on previous surveys, local knowledge, sea charts, aerial photographs and depth curves. From these potential sites ten sites of each substrate type (hard or soft) were randomly selected for field sampling. If any of these did not meet the criteria listed in Table 2 another potential site was used. Sites for eelgrass transects in the west coast study areas were randomly selected in areas with high probability of eelgrass based on a multivariate classification of satellite registrations by the geo satellite SPOT-5 (Envall 2012).

Most of the hard substrate sites were sampled in both 2012 and 2013 but data from soft substrates were, in this study, used only from 2012 on the west coast and only from 2013 on the east coast. In total 8 – 10 hard substrate sites and 5 – 10 soft substrate sites were sampled each year in each study area (Figure 9 and Table 3).

Table 2. Criteria for selection of vegetation sampling sites for 5x5 m squares. In several cases different criteria were applied for hard and soft substrate types.

Factor	Criteria	Hard	Soft
Depth	3-5 m	X	
Depth	2-4 m		X
Cover of substrate type in square	> 80 %	X	X
Slope	< 45 °	X	
Slope	Gentle slope (not depressions)		X
Shape of square	5x5 m	X	X
Distance between sites	> 100 m water	X	X
Exposure	Sheltered from waves, but good water circulation		X
Surroundings	Not below cliffs/rock faces		X
Surroundings	Existing vascular plants (>25% cover) on adjacent shallow bottoms		X

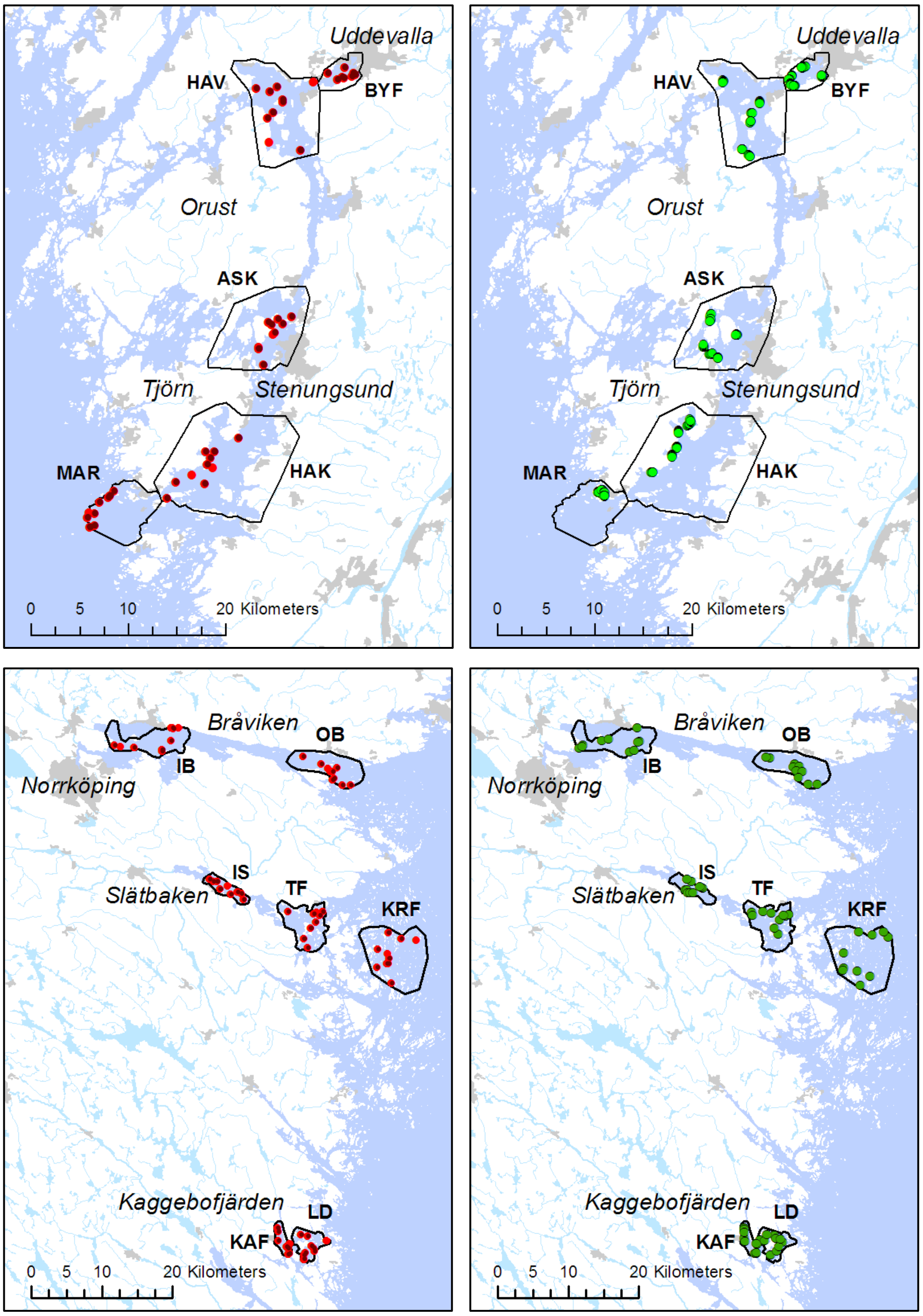

Figure 9. Vegetation sampling sites in the west coast areas (upper two maps) and east coast areas (lower two maps), hard substrate sites (left) and soft substrate sites (right). Lighter color and larger symbols represents sampling in 2012 and darker color and smaller symbols in top layer represents sampling in 2013.

Table 3. The number of vegetation sites sampled each year in each study area. The sampling period is also shown.

WEST COAST		**Hard substrates**		**Soft substrates**
		2012	**2013**	**2012**
Area	Code	5x5 m	5x5 m	transects
Byfjorden	BYF	8	8	7
Havsstenfjorden	HAV	10	8	7
Askeröfjorden	ASK	10	8	6
Hake fjord	HAK	10	8	6
Marstrandsfjorden	MAR	9	8	5
Total number of sites		47	40	31
Sampling period		20/8 - 25/9	13/8 - 20/9	8/10 - 16/10

EAST COAST		**Hard substrates**		**Soft substrates**
		2012	**2013**	**2013**
Area	Code	5x5 m	5x5 m	5x5 m
Inner Bråviken	IB	10	8	10
Inner Slätbaken	IS	10	8	10
Kaggebofjärden	KAF	10	8	10
Outer Bråviken	OB	10	8	10
Trännöfjärden	TF	9	8	10
Lindödjupet	LD	10	8	10
Kärrfjärden	KRF	10	8	10
Total number of sites		69	56	70
Sampling period		20/8 - 7/9	29/7 - 5/8	29/7 - 5/8

2.3.2 Vegetation sampling methods

Sampling squares were placed on either a hard or soft substrate type seafloor. The hard substrate type consisted primarily of rock and boulders, but stones, assessed as stable substrate, were also included. The soft substrate type was defined as sand and more fine-grained sediments, but not hard clay (Table 4).

The squares were sampled by divers to ensure sampling of all vegetation layers, to enhance correct species determinations and to facilitate collection of specimens for later species determination of species hard to identify in field (Figure 10). Depth was measured by the diver in the four corners of the square as well as in the middle.

Figure 10. A diver surveying a hard substrate type 5x5 m square in Marstrandsfjorden (MAR) on the west coast of Sweden. Photo: David Börjesson.

Cover estimates, projected from above, of vegetation and substrate were made within the respective substrate type according to a continuous scale from 0-100%. In practice, the diver first determined how much (%) of the substrate in the square that belonged to either the hard or soft substrate type and then the percentage of any remaining substrate. The diver then estimated the individual cover of respective substrates and species within the square's substrate type. For example, a hard substrate type square was determined to consist of 90% hard substrate and 10% other substrate. The cover of rock and boulders within the hard substrate type was estimated at 60 and 40% respectively. Definitions of different substrates and substrate types are shown in Table 4.

Table 4. Definition of substrates based on existing methods (e.g. Blomqvist 2009). The table also shows which substrate type each substrate belongs to.

Substrate	Definition	Substrate type
Rock	Solid rock	Hard
Boulders	> 20 cm	Hard
Stones	ca 3 cm – 20 cm	Hard/Other
Gravel	2 mm – ca 3 cm	Other
Sand	0,5 mm – 2 mm	Soft
Fine-grained sediments	< 0,5 mm	Soft

All kinds of vegetation coverage was, as already mentioned, estimated in relation to the substrate type in question (hard or soft). Cover was estimated individually for each occurring species, including crust forming species. Total vegetation coverage including all the macrophytes (not crust-forming species) was estimated separately and gives an overall picture of the percentage of the substrate type that is covered by vegetation (0-100%).

Free-living species, i.e. species that grow and thrive loose-lying on the substrate, were included as regular cover estimates and included in the analyses. They were thus separated from dead or dying, loose algae, which have been torn loose from the substrate and drifts around before they decompose. Surface coverage of dead/dying, loose algae was only estimated as a group and not included in the analyses.

Epiphytes, plants attached to other plants, were separated from those that grow attached to the substrate. The cover was estimated individually for each epiphyte in relation to the substrate type in the square. Epiphytes were included in the analyses.

A video transect method was employed to assess the depth distribution of eelgrass on the west coast soft substrate type. The method included filming the seagrass meadows along transects randomly placed in areas with high probability of eelgrass. Transects were filmed perpendicular to the depth curves from about 1 m depth down to the last eelgrass plant and then 0.5-2 meters deeper. The transects ended with a zigzagging stretch parallel with the depth curves in order to get an additional 7-10 replicate observations of the deepest part of the eelgrass meadow. The camera was mounted on a sledge pulled by a boat (Figure 11). The sledge held the camera 0.9 m above the substrate with an angle towards the seafloor of 30 degrees. Field notes were made of position (GPS) and depth at transect start and end (before zigzagging part), as well as of the observations of the deepest parts of the meadow. The distance between the GPS and camera during filming was also noted. The films were analysed in the laboratory.

Figure 11. Video sledge used for filming of eelgrass depth distribution. Photo: David Börjesson.

2.4 Indicators

The indicators tested in this study are taken from Blomqvist et al. (2012) where we identified promising indicators for status assessment based on macrophytes. An overview of the indicators is presented in Table 5.

High values of the indicator community complexity indicate more layers in the community. The layers in soft substrate vegetation communities on the east coast of Sweden can be composed of free-living macroalgae on the substrate among charophytes and short (isoetids) and long (elodeids) vascular plants. Epiphytic macroalgae can create an additional "layer".

The characterisation of macroalgal taxa into "opportunistic" and "late-successional" was based on literature. Tables listing the recorded species and their functional morphology group, longevity and sensitivity to eutrophication classifications are presented in Appendix 2. Opportunists and late-successionals were defined using a combination of functional morphology groups and longevity. Macroalgae with opportunistic strategies, i.e. fast growth and short life span, were defined as those with simple tissues (functional morphology groups 2, 2.5 and 3) classified as annual or perennial by overwintering parts. Late-successional were defined as those with complex tissues (functional morphology groups 3.5, 4. 4.5, 5 and 6) belonging to the longevity groups perennial by overwintering parts, persistent perennial or perennial.

The indicator depth distribution of eelgrass was calculated per transect as the mean of the 7 – 10 replicate values of the deepest part of the meadow.

Table 5. Description of indicators used in this study. Further information is given in the text below the table.

Indicator	Description	Hard	Soft
Species richness	Number of taxa. Crust-forming taxa were excluded.	X	X
Cumulative cover	Sum of cover of individual taxa including epiphytes and free-living taxa. Crust-forming taxa were excluded. Can exceed 100% as species can grow in different layers.	X	X
Community complexity	Cumulative cover divided by total cover. Higher complexity indicates more layers.	X	X
Proportion of opportunistic macroalgae	Cumulative cover of opportunistic taxa divided by the cumulative cover.	X	
Proportion of late-successional macroalgae	Cumulative cover of late-successional taxa divided by the cumulative cover.	X	
Depth distribution of eelgrass	Deepest recording of eelgrass meadows		X
MI_c	Macrophyte sensitivity index, species counts, based on Hansen (2012), see Equation 1		X
MI_a	Macrophyte sensitivity index, species abundance (cover), based on Hansen (2012), see Equation 2		X

The macrophyte index (MI) was calculated according to Hansen (2012), using the equations:

$$MI_c = \frac{N_s - N_t}{N} \times 100 \qquad \text{Equation 1}$$

$$MI_a = \frac{\sum_{i=1}^{N_s} A_i - \sum_{j=1}^{N_t} A_j}{\sum_{k=1}^{N} A_k} \times 100 \qquad \text{Equation 2}$$

where N_S is the number of sensitive species, N_t is the number of tolerant species, and N is the total number of species (including species without sensitivity classification), and A is a measure of cover. Both versions of the index produce values from -100 (all species tolerant) to +100 (all species sensitive).

Classification of sensitivity to eutrophication was based on literature and is given in Appendix 2. We used this classification in calculation of the indexes MI_c and MI_a and not the classification used by Hansen (2012) as the latter included fewer taxa and was based on sensitivity to a number of anthropogenic pressures. Before calculation of MI_c and MI_a our sensitivity groups very sensitive (S+) and sensitive (S) were combined as sensitive taxa and groups tolerant (T), slightly favored (T+) and favored (T++) as tolerant taxa since the indexes MI_c and MI_a are based on a classification of species as either sensitive or tolerant.

2.5 Statistical analyses

We analysed differences in the indicators between study areas as well as the correlation between the indicators and a number of physical and chemical gradient variables. In the correlation analyses, the indicators and the gradient were aggregated to a common denominator, mean by area and year for each study area, since the variables had different spatial and temporal resolution.

The hard substrate data that was collected in two different years was analysed with linear mixed models. When comparing the different study areas, year and the interaction between year and study area were included as random factors in the models. In the correlation analyses, year was included as random and r^2-values (marginal + conditional) were calculated according to Nakagawa and Schielzeth (2013) and Johnson (2014). The soft substrate data was from one year and was analysed with ordinary linear models. All models were run in R (R Core Team 2014), the linear mixed models using package nlme (Pinhero et al. 2015).

3. Results

3.1 Macrophytes on hard substrate

3.1.1 Description of communities

In the hard substrate communities on the West coast a total of 52 macroalgal taxa (crustose species not included) were recorded (Appendix 2). The proportion of filamentous algal cover was generally around 60% of the cumulative cover in the sampling squares. The epiphytic flora was species rich including 27 species, most of which also occurred growing attached to the substrate. Only two taxa, *Cladophora* and *Ectocarpus*/*Pylaiella*, occurred also in free-living forms.

In the species-poor hard substrate communities on the east coast 23 taxa (crustose species not included) were observed (Appendix 2). The communities were dominated by filamentous algae, which generally accounted for ca 80% of the cumulative vegetation cover in the sampling squares. The annual brown algae *Ectocarpus siliqulosus*/*Pylaiella littoralis* were the most common filamentous algal taxa in all but one of the seven investigated areas. In Inner Slätbaken, the most freshwater influenced area, the green algae *Cladophora glomerata* and *Aegagropila linnaei* were equally common. Most species grew attached to the hard substrate but the communities also included a few epiphytes and free-living macroalgae. The six epiphytes were mainly annual filamentous taxa of which *Ectocarpus*/*Pylaiella* were the most common. The seven free-living macroalgae included species such as *Monostroma balticum* and *Cladophora fracta* as well as free-living forms of algae that generally grow attached to the substrate such as *Fucus vesiculosus*.

3.1.2 Differences in the tested indicators between areas

All the tested indicators differed significantly between study areas, both at the west coast and east coast (Table 6). There was no significant difference between years, except for the proportion of late-successional macroalgae on the west coast and species richness on the east coast, where there was a significant interaction between study area and year.

Table 6 Mixed models of the tested hard substrate indicators (species richness, cumulative cover, community complexity and proportion of opportunists and late-successional species) on the west and east coast.

WEST COAST	**Df**	**F values**				
		Sp. richness	**Cum. cover**	**Com. compl.**	**Prop. opp.**	**Prop. late**
Area	4	**36.396*** **	**67.369*** **	**21.929*** **	**36.958*** **	**36.100*** **
Year	1	1.421 ns	0.183 ns	0.391 ns	2.516 ns	0.686 ns
Area*Year	4	1.322 ns	1.054 ns	1.202 ns	0.927 ns	**3.247***
Residuals	77					

EAST COAST	**Df**	**F values**				
		Sp. richness	**Cum. cover**	**Com. compl.**	**Prop. opp.**	**Prop. late**
Area	6	**19.060*** **	**9.98*** **	**6.093*** **	**4.436*** **	**7.89*** **
Year	1	**5.834***	3.122 ns	2.23 ns	0.301 ns	0.08 ns
Area*Year	6	**2.561***	1.268 ns	0.614 ns	2.158 ns	1.441 ns
Residuals	111					

*** p<0.001, * 0.01<p<0.05, ns p>0.05

On the west coast, the innermost study area in the gradient (Byfjorden, BYF) differed almost consistently from all other areas, having lower species richness, cumulative cover, community complexity and proportion of late-successional species and a higher proportion of opportunistic species (Figure 12). Also the outermost area (Marstrandsfjorden, MAR) differed in most cases from all other areas, with the highest species richness, cumulative cover, community complexity and proportion of late-successional species and the lowest proportion of opportunistic species. The areas between Byfjorden and Marstrandsfjorden had intermediate values and only differed from each other in cumulative cover and community complexity (where Hakefjorden had higher values than the other two) and the proportion of opportunistic species (where all areas differed significantly).

On the east coast, the patterns differed more between the tested indicators (Figure 13). For the proportion of late-successional species, two of the innermost areas (Inner Slätbaken, IS and Inner Bråviken, IB) had lower values compared to all or almost all of the other areas while there was no difference between the other areas. Species richness showed a similar pattern, although there was large variation between years in some of the outer areas. Also for community complexity the same two inner areas had lower values than the rest, but in addition the outer area (Kärrfjärden, KRF) differed from all other areas with higher community complexity. Cumulative cover showed a different pattern with low values in all inner and one of the intermediate areas, while the fraction of opportunistic species showed a weak pattern with large variation and few differences between the areas.

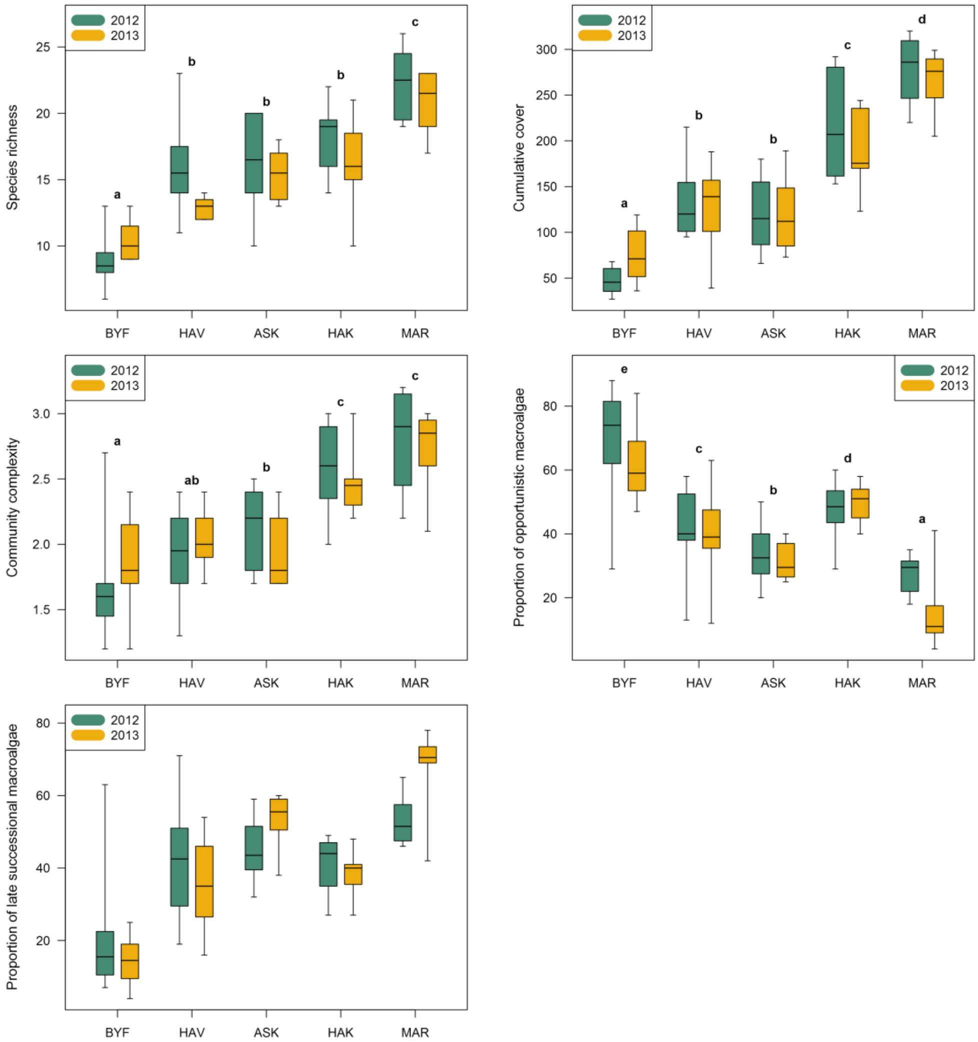

Figure 12 Hard substrate indicators in the west coast study areas. Each box shows the first and third quartile with a horizontal line at the second quartile (median). The whiskers represent minimum and maximum values. Letters show the results from the mixed models analysis of differences between areas: areas sharing the same letter did not differ significantly (α=0.05). For proportion of late-successional macroalgae there was a significant interaction between area and year; BYF had a lower proportion than all other areas both years but MAR only had a higher proportion than the other areas in 2013.

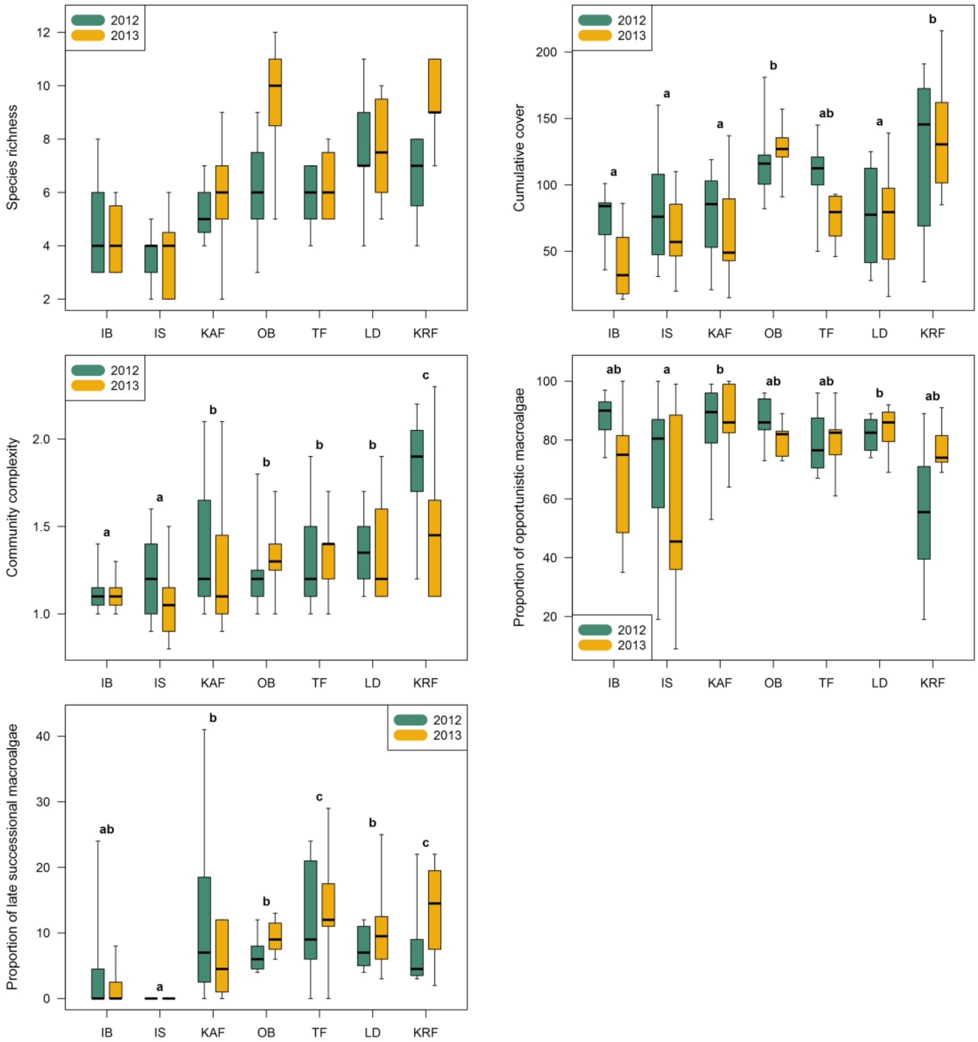

Figure 13 Hard substrate indicators in the east coast study areas. Each box shows the first and third quartile with a horizontal line at the second quartile (median). The whiskers represent minimum and maximum values. Letters show the results from the mixed models analysis of differences between areas: areas sharing the same letter did not differ significantly (α=0.05). For species richness there was a significant interaction between area and year; the only difference that was consistent between years was a lower species richness in IS and IB compared to LD and KRF.

3.1.3 Correlation between indicators and environmental gradients

In the west coast gradient, all indicators were significantly related to the mean Secchi depth in the study areas (Table 7). The proportion of opportunistic species decreased and all the other indicators increased with increasing Secchi depth (Figure 14). Cumulative cover was also positively correlated with mean wave exposure (SWM) at the vegetation sites. A number of indicators were also significantly correlated with nutrient concentrations, while the relationship to salinity was weak and not significant.

On the east coast, species richness, cumulative cover and community complexity were all significantly related to Secchi depth (Table 7, Figure 15). Species richness, community complexity and proportion of late-successional species were significantly correlated to nutrient concentrations as well as salinity.

Table 7 Relationship between hard substrate indicators and physical and chemical parameters. The table show r^2-values and significance level.

a. West Coast

Indicator	Salinity		Secchi		Total N		Total P		SWM (log)	
Species Richness	0.00		0.66	***	0.39	*	0.41	**	0.58	+
Cumulative cover	0.01		0.68	***	0.33	+	0.51	***	0.63	*
Community Complexity	0.03		0.59	**	0.29	+	0.49	***	0.50	+
Proportion of Opportunists	0.05		0.60	**	0.34	+	0.23		0.46	
Proportion of Late-successionals	0.01		0.57	**	0.27		0.33	+	0.47	

b. East Coast

Indicator	Salinity		Secchi		Total N		Total P		SWM (log)	
Species Richness	0.43	**	0.35	*	0.54	**	0.43	*	0.00	
Cumulative cover	0.21	+	0.31	*	0.25	+	0.10		0.05	
Community Complexity	0.67	***	0.68	***	0.42	*	0.23	*	0.02	
Proportion of Opportunists	0.21	+	0.02		0.19		0.03		0.03	
Proportion of Late-successionals	0.59	**	0.24	+	0.45	**	0.25	+	0.00	

*** p<0.001, ** 0.001<p<0.01, * 0.01<p<0.05, + 0.05<p<0.1

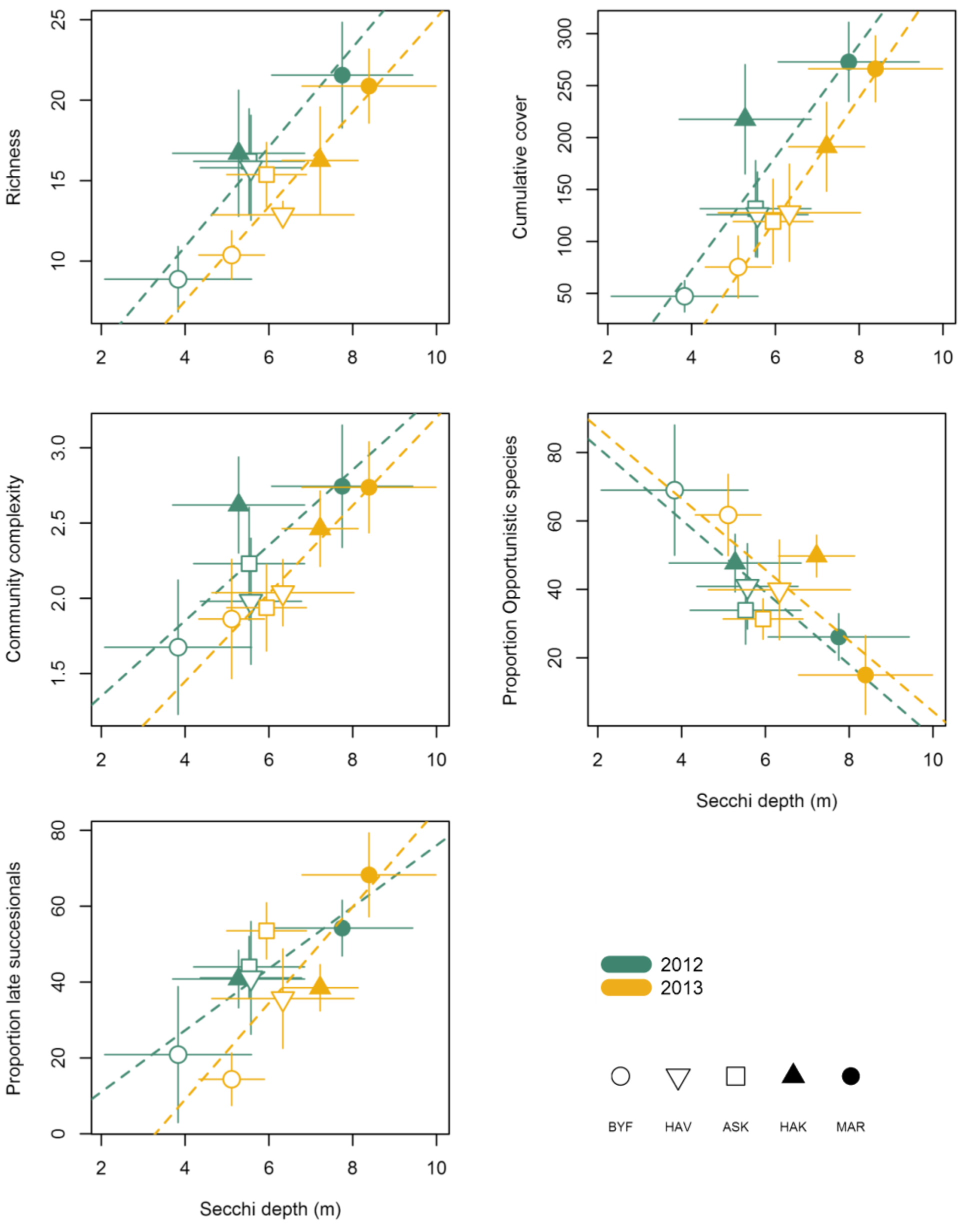

Figure 14 Correlation between the hard substrate indicators and Secchi depth in the west coast study areas. The graphs show average values per area and year ± one standard deviation, with regression lines for averages per year where the regression was significant ($p<0.05$).

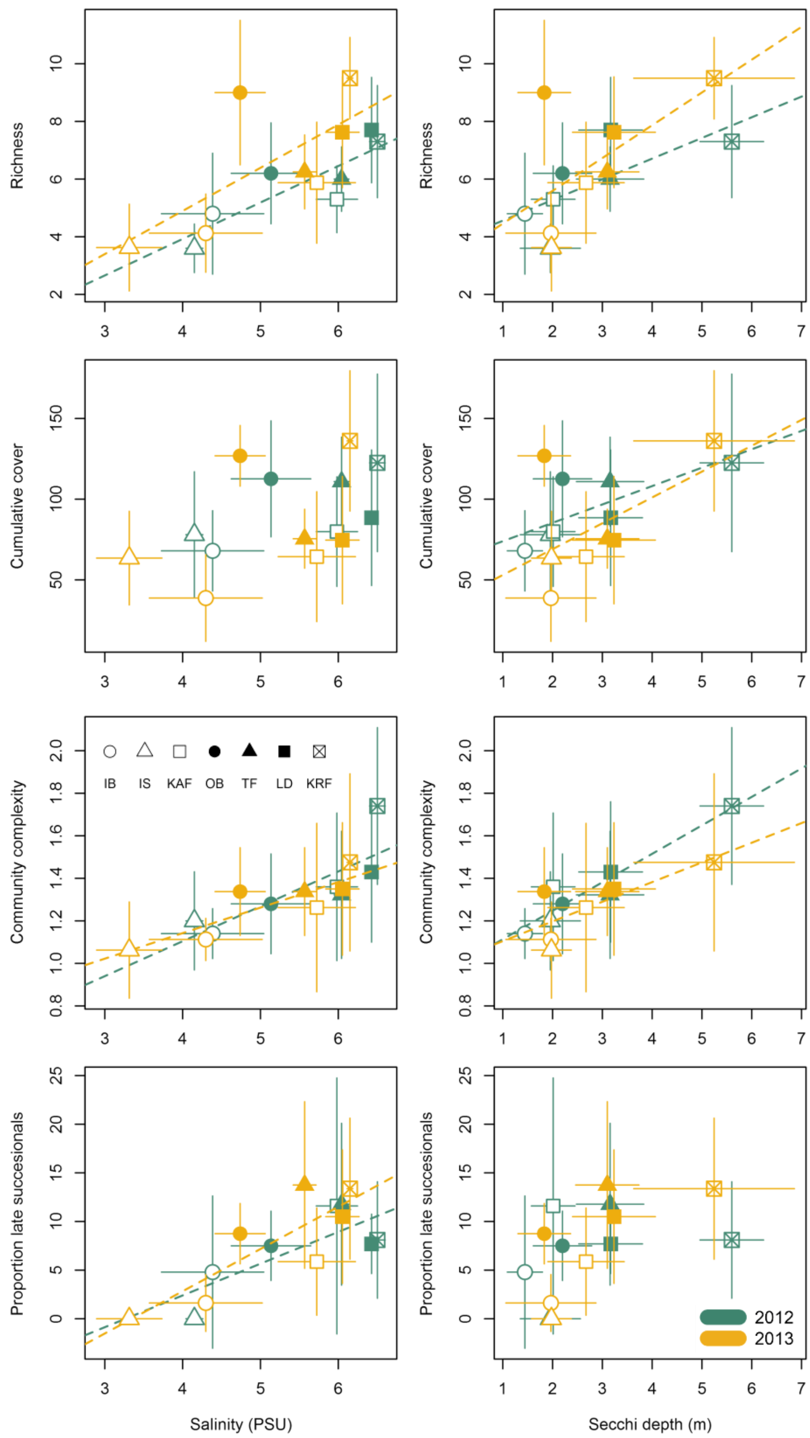

Figure 15 Correlation between the hard substrate indicators and Secchi depth and salinity in the east coast study areas. The graphs show average values per area and year ± one standard deviation, with regression lines for averages per year when the regression was significant (p<0.05).

3.2 Soft substrate communities

3.2.1 Description of communities

On the west coast the study of soft substrate vegetation was confined to eelgrass meadows, more or less monospecific stands of *Zostera marina*. On the east coast, the macrophyte communities on soft substrate were more species rich than the communities on hard substrates. A total of 34 macrophyte taxa were recorded on soft substrate on the east coast, compared to 23 taxa in the hard substrate communities (Appendix 2). The species rich soft substrate communities included vascular plants, charophytes and macroalgae, including epiphytic and free-living macroalgae. The vascular plants were represented by 13 taxa whereas the charophytes were relatively rare in the investigated communities. The macroalgae included the coarse brown alga *Chorda filum*, seven epiphytic taxa and eight free-living macroalgal taxa.

In Inner Slätbaken (IS), seven of the eight recorded taxa are classified as having a positive response (T+ or T++in Appendix 2) to eutrophication. Of these the most distinguishing features for the macrophyte communities in this area was the free-living green alga *Chaetomorpha linum*. *C. linum* was the most common alga in IS, occurring in half of the sampling squares and often covering 80-100% of the substrate, but was not observed in any of the other six areas. A similar species composition, i.e. almost exclusively species classified as having a positive response to eutrophication, was recorded in Inner Bråviken (IB). The other areas had more species classified as sensitive to eutrophication. In these five areas 30-43% of the total number of observed species was classified as sensitive compared to 11 and 13% in the two inner areas IB and IS.

3.2.2 Differences in the tested indicators between areas

The depth distribution of *Zostera marina* differed significantly between the west coast study areas (ANOVA $F_{4, 26}$=12.073, p<0.001). The depth distribution was smaller in the innermost area (Byfjorden, BYF) compared to all areas except Askeröfjorden (ASK) and larger in Marstrandsfjorden (MAR) compared to two of the inner areas (Figure 16).

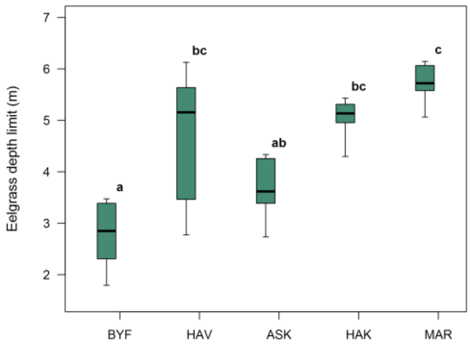

Figure 16 Eelgrass depth limit in the west coast study areas in 2012. Each box shows the first and third quartile with a horizontal line at the second quartile (median). The whiskers represent minimum and maximum values. Letters show the results from the Anova of differences between areas: areas sharing the same letter did not differ significantly (α=0.05).

On the east coast, four of the tested indicators differed significantly between areas. These included species richness (ANOVA $F_{6, 63}$=9.451, p<0.001), cumulative cover (ANOVA $F_{6, 63}$=3.265, p<0.01), MI_c (ANOVA $F_{6, 63}$=14.486, p<0.001) and MI_a (ANOVA $F_{6, 63}$=5.474, p<0.001). Both species richness and the two macrophyte indices were significantly lower in two of the inner areas (IS and IB) compared to all or almost all outer parts of the gradients and the outermost KRF. For the MI_c (based on presence/absence of species), the third inner area (KAF) was also significantly lower than three of the outer areas. For cumulative cover, the only difference was a lower cover in IB compared to two of the outer areas. Community complexity did not differ between the study areas (ANOVA $F_{6, 63}$= 0.7537, p=0.61).

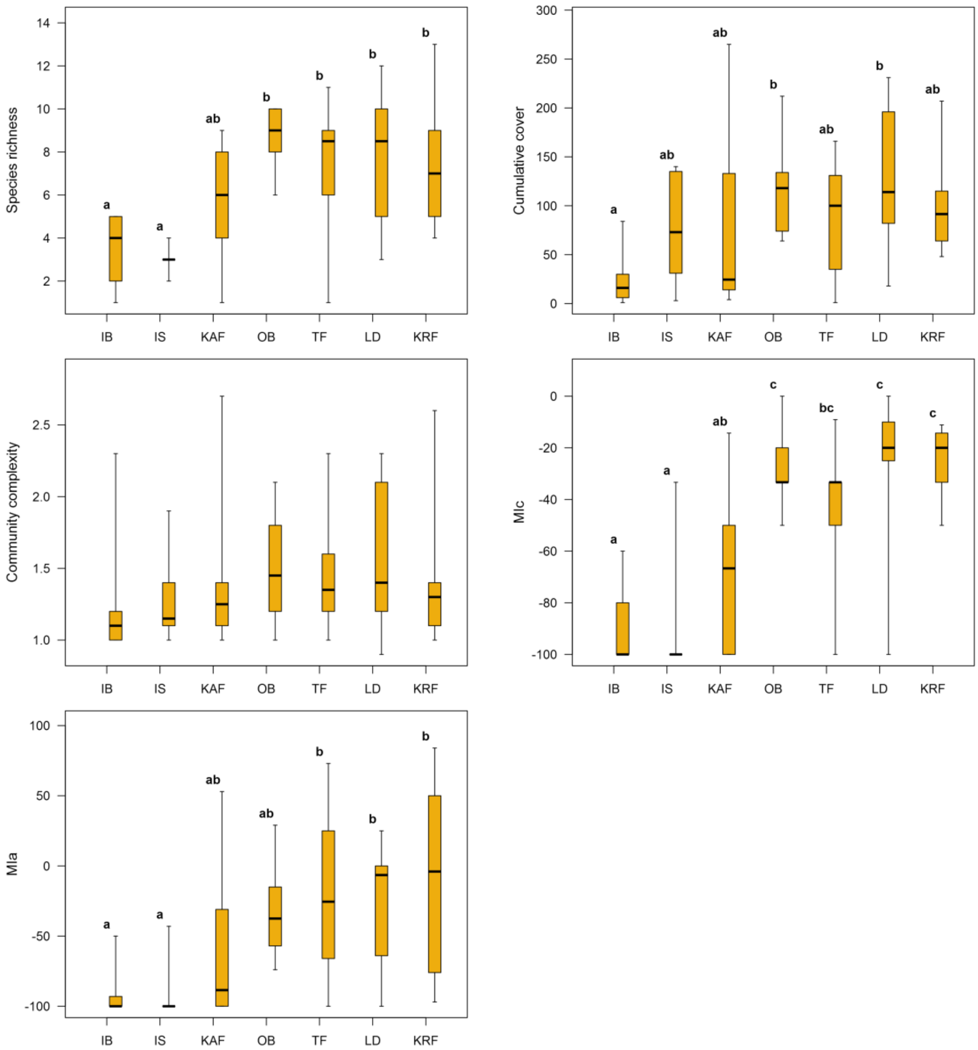

Figure 17 Soft substrate indicators in the east coast study areas in 2013. Each box shows the first and third quartile with a horizontal line at the second quartile (median). The whiskers represent minimum and maximum values. Letters show the results from the Anova of differences between areas: areas sharing the same letter did not differ significantly (α=0.05). For community complexity there was no differences between any of the areas.

3.2.3 Correlation between indicators and environmental gradients

The depth distribution of eelgrass was correlated with both the Secchi depth and total nitrogen in the west coast gradient, although the correlation with Secchi depth was not significant due to the small number of data points (Table 8, Figure 18). On the east coast there were few significant relationships between indicators and environmental variables (Table 8, Figure 19).

Table 8 Relationship between soft substrate indicators and physical and chemical parameters. The table show r^2-values and significance levels.

a. West Coast

Indicator	Salinity		Secchi		Total N		Total P		SWM(log)	
Max depth of eelgrass	0.10		0.73	+	0.78	*	0.63		0.61	+

b. East Coast

Indicator	Salinity		Secchi		Total N		Total P		SWM(log)	
Species richness	0.48	+	0.14		0.63	*	0.68	*	0.02	
Cumulative Cover	0.22		0.13		0.13		0.24		0.06	
Community Complexity	0.46	+	0.08		0.38		0.34		0.01	
MI_c	0.53	+	0.34		0.53	+	0.62	*	0.00	
MI_a	0.67	*	0.53	+	0.55	+	0.57	+	0.00	

*** p<0.001, ** 0.001<p<0.01, * 0.01<p<0.05, + 0.05<p<0.1

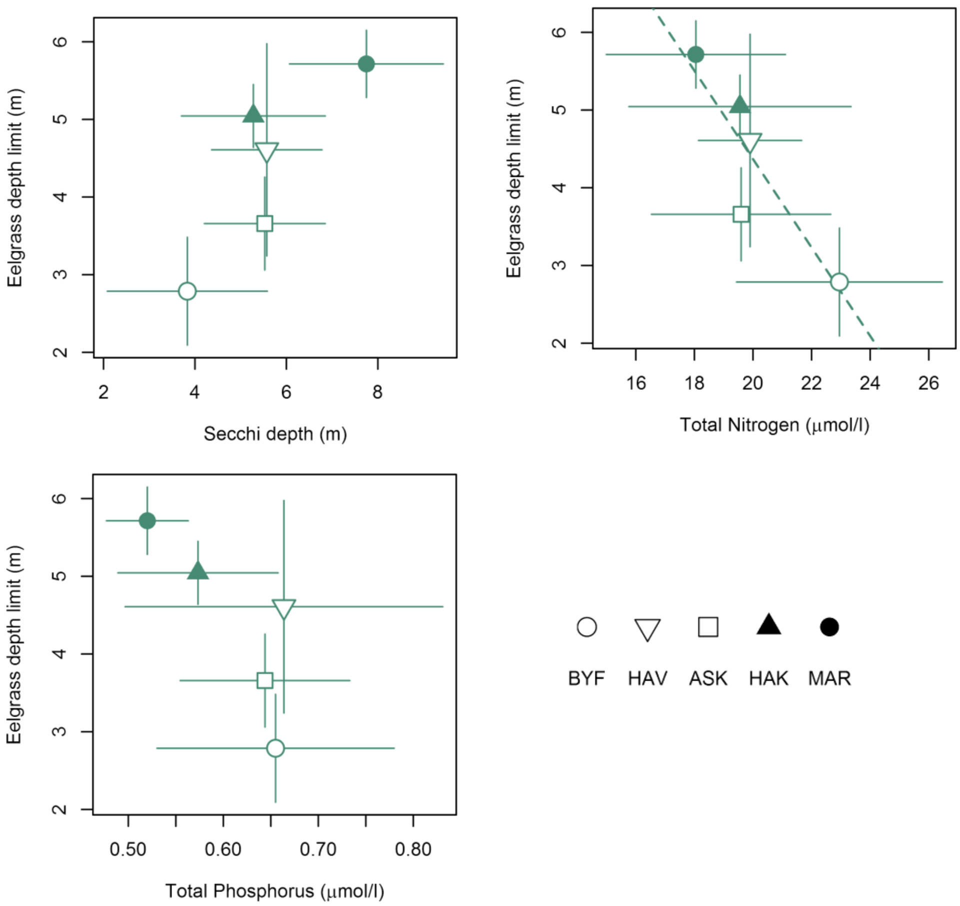

Figure 18 Correlation between the lower depth limit of eelgrass and Secchi depth and nutrient concentrations in the west coast study areas. The graph shows average values per area and year ± one standard deviation, with regression lines for averages per year when the regression was significant ($p<0.05$).

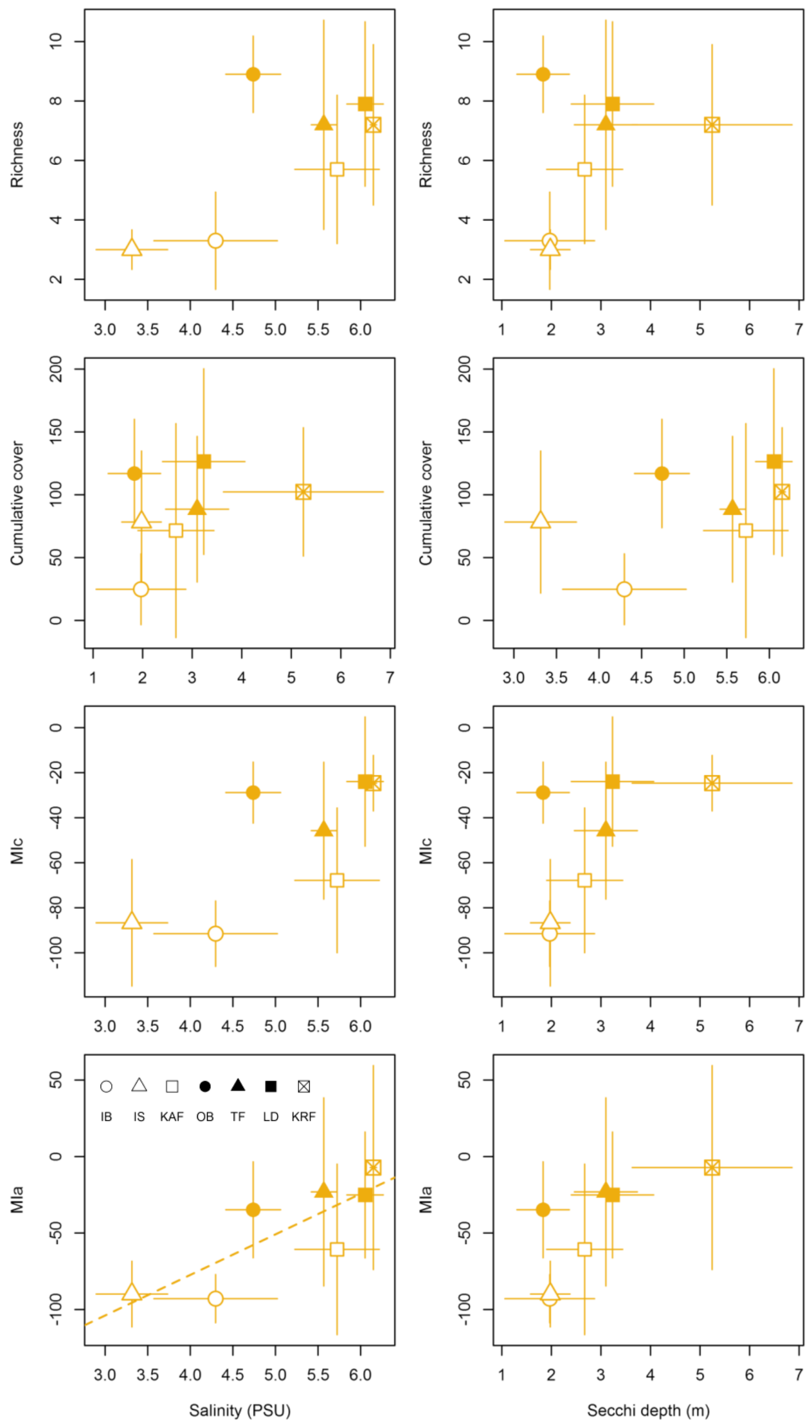

Figure 19 Correlation between the soft substrate indicators and Secchi depth and salinity in the east coast study areas. The graphs show average values per area and year ± one standard deviation, with regression lines for averages per year when the regression was significant ($p<0.05$).

4. Discussion

4.1 The coastal gradients

In the study areas on the west coast the macroalgal vegetation on hard substrate changed dramatically along the gradient from the open sea to the innermost area Byfjorden. The change included a shift from diverse, multi-layered communities and high cumulative cover to communities with fewer species and lower cumulative cover and community complexity. The species composition also changed, with a decreasing fraction of late-successional species and increasing fraction of opportunists. On soft substrate, the depth distribution of *Zostera marina* decreased from the open sea to the innermost fjord. These changes in the vegetation are in accordance with what is predicted in a gradient of increasing eutrophication (e.g. Cloern 2001, Krause-Jensen et al. 2008). Increased nutrient concentrations stimulate growth of phytoplankton, decreasing light penetration in the water and increasing sedimentation leading to a decrease in cover and depth penetration of sea-floor vegetation. Also, opportunistic macroalgae are favoured by increased nutrient concentrations at the expense of large, late-successional species.

The change in the vegetation coincided with a strong decrease in Secchi depth from the open sea to the innermost area, driven by an increase in chlorophyll concentrations and CDOM. All the tested indicators were also significantly correlated with Secchi depth. However, it is important to keep in mind that vegetation communities also respond to a number of natural gradients, particularly salinity and wave exposure, which often change from the outer to inner parts of coastal areas. In the west coast gradient the salinity was highly variable over time in all the study areas and not consistently lower in the inner parts, which means that it likely has a relatively low importance in explaining the observed vegetation patterns. However, wave exposure was clearly higher in the outermost area compared to the inner areas. Wave exposure has previously been shown to increase both the cover of macroalgal vegetation at a certain depth and the species richness of macroalgae (Blomqvist et al. 2014). For instance, Blomqvist at al. (2014) showed that over the entire Swedish coastline an increase in wave exposure corresponding to the difference between the outer Marstrandsfjord and the inner study areas resulted in a doubling of the cumulative cover at 7 m depth. This suggests that the high wave exposure at the diving stations in the outermost area may contribute to explain the high macroalgal cover but cannot explain the entire difference from the inner areas.

Also on the east coast there were clear differences in vegetation communities between the study areas. In two of the three investigated gradients (Bråviken and Slätbaken) the innermost areas had fewer species on both hard and soft substrate, lower community complexity on hard substrate and a lower proportion of late-successional macroalgae on hard substrate and of sensitive species on soft substrate compared to the outer parts of the gradients. In the third gradient (Kaggebofjärden) only the cumulative cover and community complexity on hard substrate and only the macrophyte index on soft substrate was lower compared to one or a few outer areas.

Similarly to the west coast, the differences in vegetation between inner and outer east coast areas are in accordance with the prediction for a gradient in eutrophication. However, the two innermost areas where the vegetation is most distinctly different did not only have high concentrations of TN and chlorophyll and low Secchi depth, they also had the lowest salinity. Such intertwining of eutrophication and salinity is common in coastal areas since nutrients from land to a large extent enter the sea with fresh water inflow, which makes it difficult to separate eutrophication effects from the effect of salinity.

For species diversity and species composition, it is obvious that salinity can explain at least part of the differences between areas. The low species richness on hard substrate in inner Bråviken and Slätbaken is to a large degree driven by the loss of red algae and the brown alga *Fucus vesiculosus*, all species that are suggested to have a limit to their salinity tolerance around 4 based on their large-scale distribution in the Baltic Sea (Nielsen et al. 1995). Since these species include the dominating late-successional macroalgal species in the Baltic Sea (i.e. *Furcellaria lumbricalis* and *F. vesiculocus*), the loss is also reflected in the fraction of late-successional species and community complexity. Similarly, the low species richness on soft substrate can to a large extent be explained by loss of species with marine origin (macroalgae and the vascular plants *Zostera marina* and *Ruppia cirrhosa*), which also include many of the species that are classified as sensitive to eutrophication. It is likely that also the high nutrient concentrations and turbidity in the inner parts of Bråviken and Slätbaken contribute to the low abundance of late-successional macroalgae and soft-substrate species classified as sensitive, but the results clearly shows the importance of controlling for the effect of salinity for indicators based on species richness or community composition.

In contrast, cumulative cover of macroalgae can be predicted to respond less strongly to salinity. When analysing data from the entire Swedish coast (Blomqvist et al. 2014), there was only a few percent change in cumulative cover of macroalgae at 7 m depth over the small salinity interval from 3 or 4 to 6 that was documented in the east coast study areas. This suggests that salinity is of minor importance for the documented differences in cumulative cover between the study areas. This is supported by the fact that the cumulative cover was low in all inner areas compared to the outermost area, not only in the gradients that were most strongly influenced by salinity.

4.2 Hard substrate indicators

Cumulative cover of hard substrate vegetation turned out to be one of the most promising indicators for eutrophication when analysing monitoring data from the entire Swedish coast (Blomqvist et al. 2014). A clear connection between water quality and cumulative cover has also been documented from other coastal areas (reviewed by Krause-Jensen et al. 2008). The cover of macroalgae at a certain depth can be expected to respond directly to the amount of light reaching the sea bed, which depends on the Secchi depth. High amounts of sedimentation can also have a negative effect on macroalgal cover by decreasing algal growth and impairing recruitment. The present study in two smaller parts of the Swedish coast confirms that cumulative cover at 3-5 m depth changes in coastal gradients of Secchi depth. The correlation with Secchi depth was very clear on the west coast but weaker on the east coast, indicating that also other factors affect cumulative cover.

The cumulative cover of vegetation is the summed cover of all species in the sampling plot, which means that it is affected both by the total area covered by vegetation and the number of vegetation layers. By dividing the cumulative cover with the total cover of vegetation we could also analyse the community complexity. The indicator responded clearly to the west coast gradient, from on average 1.7 in the innermost to 2.8 in the outermost area. The community complexity can be expected to reflect the species richness and also the presence of large, canopy-forming species as these increase the cumulative cover by adding a canopy layer but also by providing substrate for epiphytes thus further increasing the cumulative cover. It is therefore not surprising that community complexity seemed to respond strongly to salinity in the east coast areas, where the areas with low salinity were strongly dominated by small, filamentous algae. This means that salinity has to be accounted for when using it as indicator for eutrophication and that the indicator is most promising for the more species-rich west coast communities.

The proportion of opportunistic and late-successional species showed a weaker response to Secchi depth. Ecological theory predicts that late-successional macroalgal species will decline and opportunistic species increase in response to many types of disturbance, including eutrophication (Littler and Littler 1980, Steneck and Dethiers 1994, Pedersen 1995). Indices of community composition based on opportunistic and late-successional species are also used as indicators in other coastal areas (e.g. Orfanidis et al. 2001, Wells et al. 2007, Sfriso et al. 2009). However, in our analyses of the entire Swedish coastline the relationship between relative abundance of these functional groups and eutrophication was weak (Blomqvist et al. 2014). We interpreted this as an effect of the strong influence of salinity on the presence of late-successional species in the Baltic Sea. As mentioned above there are only a few late-successional species in the Baltic proper and Gulf of Bothnia and they do not occur at salinities below approximately 4. Moreover, Krause-Jensen et al. (2007) showed that salinity was the best predictor for the relative abundance of opportunistic species in Danish coastal waters. This suggests that indicators based on macroalgal functional groups, for instance the fraction of late-successional and opportunistic species, are difficult to apply in areas with strong salinity gradients such as the Swedish coast.

Species richness of macroalgal communities was identified as a promising indicator in the study of the entire Swedish coast (Blomqvist et al. 2014). This indicator is also supported by theory: disturbance, including strong eutrophication effects, typically result in the loss of many sensitive species and dominance of a few opportunistic or stress-tolerant species. The decline in diversity can be predicted to be strengthened by the fact that large and complex macroalgal species, which form multi-layered communities that can support high species diversity (e.g. Kautsky et al. 1992), often are sensitive to disturbance and are lost in areas affected by eutrophication. However, as other composition indicators, species richness responds strongly to the long salinity gradient in the Baltic Sea. In the study of the entire Swedish coast a significant relationship between macroalgal species richness and eutrophication only appeared when accounting for the even stronger relationship to salinity. In the present study, the pattern in species richness in the west coast areas (with a weak salinity gradient) could be related to eutrophication, while salinity was probably the most important factor explaining species richness in the east coast areas. Together, this shows that if macroalgal species richness should be used as indicator for ecological status, salinity needs to be monitored parallel to the vegetation and accounted for in the indicator value.

4.3 Soft substrate indicators

Previous studies of eelgrass distribution have established that the depth distribution is primarily regulated by light (Duarte 1991, Duarte et al. 2007). Accordingly, the depth distribution of *Zostera marina* increased strongly from the inner to the outer part of the west coast gradient. Eelgrass has not been included in Swedish west coast vegetation monitoring, but our results suggest that the depth distribution of defined eelgrass meadows is a promising indicator on the Swedish west coast (mainly county of Västra Götaland). Ideally, the depth distribution of *Z. marina* is combined with other indicators describing for instance abundance or cover of eelgrass, but these have not been evaluated in this study.

Along with the depth distribution of seagrass, cover of seagrass vegetation belongs to the most commonly used seagrass indicators in Europe (Marba et al. 2013). However, in the mixed soft-substrate communities in the east coast study areas cumulative cover varied strongly within study areas and did not show any clear relationship with the eutrophication gradient. Large variability in the cover of soft-substrate vegetation was seen also in the study including data from the entire Swedish coastline (Blomqvist et al. 2014). In that study, cumulative cover of soft-substrate vegetation was significantly correlated with Secchi depth, but the relationship was much weaker than for cumulative cover of hard-substrate vegetation. Together, this indicates that cover in these mixed-species communities is variable and probably partly regulated by factors that were not included in the analyses.

Community complexity, i.e. the ratio between cumulative and total cover, was also not significantly related to any of the tested pressure variables. This is somewhat surprising as the high diversity in plant types, vascular plants, charophytes and macroalgae from both marine and freshwater, might be expected to allow for a gradient in community complexity. Higher complexity indicates more layers in the community, i.e. species growing under canopy species which function as substrate to epiphytic species. Although, there are certainly jungle-like communities composed of several layers of different length vascular plants, short charophytes and free-living macroalgae, there is often a patchiness created by dominance of single species. For example, the free-living form of *Fucus vesiculosus* often forms dense populations that totally cover the substrate. As *F. vesiculosus* also is a perennial species this effectively hinders other species from colonizing. This patchiness likely contributes to the large variation seen for this indicator.

Of the tested indicators, species richness and the macrophyte index were the only two that showed a significant relationship to any of the pressure variables in the east coast study areas. The pattern was to a large extent driven by the low species richness and macrophyte index in the two innermost areas with highest nutrient concentrations (Inner Slätbaken and Bråviken). The low diversity in Inner Slätbaken and Bråviken was to a large extent driven by very low occurrence of species classified as sensitive according to literature. The few species that occurred in Inner Slätbaken and Bråviken were almost exclusively species classified as tolerant, which was reflected by the low macrophyte index, both calculated on presence/absence and abundance of sensitive and tolerant species. This indicates that the response of the vegetation to eutrophication included a loss of sensitive species and strong dominance of a few tolerant species that are favoured by eutrophication. However, as discussed above the sensitive species that were absent from these inner areas included a number of species with marine origin, which may be limited by salinity in addition to poor water quality (including the vascular plants *Zostera marina* and *Ruppia cirrhosa* and the macroalgae *Chorda filum*, *Fucus vesiculosus* and *Furcellaria lumbricalis*). Since the salinity and eutrophication gradients were correlated in our study we are not able to conclude how important the salinity gradient is for the observed patterns in the soft substrate vegetation. Hansen and Snickars (2014) showed that across a large number of sheltered bays, nutrient concentrations but not salinity contributed to explain variation in the macrophyte index. However, we suggest that the effect of salinity on species composition of soft substrate vegetation should be explored further to evaluate if salinity has to be accounted for if species richness or the macrophyte index should be used as indicators for water quality.

In the present study we used a fixed sampling effort, a strict method for cover estimation and attempted to choose sites with comparable conditions for vegetation, in order to reduce uncertainty in the estimation of the indicators. Still, the variation in most soft-substrate indicators was very large, which likely contributed to the lack of patterns in the soft substrate vegetation of the east coast. The large small-scale variability in the soft substrate vegetation is a challenge for the development of soft substrate indicators for the Swedish east coast. A larger sampling area (for instance by sampling more than one square per site), capturing small scale patchiness, could reduce the large variation between sites and a larger number of sites could provide a better cover estimation for a certain area.

4.4 Conclusion

Both cumulative vegetation cover and species richness of hard substrate vegetation responded clearly to the Secchi depth gradient in the west coast study areas and to the combined salinity/eutrophication on the east coast. Both these are promising indicators for water quality, but in particular for species richness it is necessary to also account for the effect of salinity. Similarly, the depth distribution of *Zostera marina* meadows responded to the Secchi depth gradient and is a promising indicator for soft-substrate on the west coast, possibly in combination with an indicator for density of the meadows (e.g. cover). *Zostera marina* is not included in current west coast monitoring programs north of the Sound, but could be a good complement to give a more complete picture of the status of coastal vegetation and allow status assessment in areas with little hard substrate.

Cumulative cover and species richness could potentially also be used as indicators for the diverse soft substrate communities on the east coast, along with the macrophyte index describing the occurrence or abundance of sensitive and tolerant species. However, our result from this and previous studies suggest that these communities are highly variable on small spatial scales, which means that a large sampling effort is required for monitoring in order to detect changes. Monitoring of soft-substrate vegetation will still be important in order to be able to assess the status in areas dominated by soft substrate and in areas with very low salinity and impoverished hard substrate vegetation.

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Appendix 1. Analysis methods for physical and chemical data in WATERS gradient studies

All west coast samples were analysed at the SMHI oceanographic laboratory in Gothenburg (accredited according to Swedac, Swedish Board for Accreditation and Conformity Assessment). Nutrients and chlorophyll a was analysed according to standard methods (HELCOM 2015). Secchi depth, SPM and CDOM were analyzed with the methods described below.

On the east coast nutrient and salinity samples were all analyzed at the Stockholm University laboratory (accredited by Swedac) by the standard methods used in the National marine monitoring. Chlorophyll a analyses were done by Alcontrol Linköping (SS028146-1, one liter of water filtered, actone extraction). As a quality check, 14-15 chlorophyll samples each year were analyzed in parallel by Laboratoriet Marin Ekologi, Dept. Ecology, Environment and Plant sciences, at Stockholm University, according to HELCOM (2015). No systematic discrepancy between the laboratories was found. Secchi depth, SPM and CDOM were analyzed at the Stockholm University laboratory with the methods described below.

To determine Suspended Particulate Matter (SPM) particulate matter was filtered onto dry, pre-weighed glass fibre filters (WHATMAN GF/F). Filters were weighed again after filtering and drying. The difference in weight was used to calculate SPM. Suspended Particulate Inorganic Matter (SPIM) was measured by weighing the filters again after removing organic matter at 450 °C. Three to four replicate samples was filtered for SPM.

Coloured Dissolved Organic Matter (CDOM) was analyzed according to Kratzer and Tett (2009). The water was filtered through 0.2-µm membrane filters and measured spectrophotometrically. The optical density (OD), i.e., absorbance, at 440 nm was corrected for the OD at 750 nm, and g440, the absorption coefficient for CDOM at 440 nm, was derived as follows:

$$g_{440} = \ln(10) * (OD_{440} - OD_{750}) \; / \; L \; (m^{-1})$$

where L is the path length of the cuvette in meters (in this case 0.1 m).

The Secchi depth was measured using a standard 30-cm white Secchi disk. A water telescope was used to avoid the influence of reflectance at the sea surface having an effect on the viewer’s reading.

Appendix 2. Taxon longevity, functional group and sensitivity classifications

The appendix lists all taxa that were recorded on hard substrate on the west and east coasts and on soft substrate on the east coast. The macroalgal taxa have been assigned to morphological functional groups mainly based on Carstensen et al. (2008) after Steneck and Dethiers (1994). However, some modifications to the classification by Carstensen et al. (2008) were 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 macroalgal taxa are thus 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.

We have also characterized the longevity of the macroalgal taxa based on information extracted from articles, floras, databases and other work (mainly Wallentinus 1979, Tolstoy and Österlund 2003, the MarLIN database online). The taxa were assigned to one of the following five groups: Annual (A), Perennial by overwintering parts (PoW), Persistent perennial (PP, whole or most of the plant overwinters), Perennial (P) and variable (V). In the group Perennial, also those perennial taxa are included which, due to lack of information, could not be further classified into either of the groups Perennial by overwintering parts or Persistent perennial. The perennial group can thus include taxa that overwinter as whole plants and taxa that have overwintering parts. The group Variable includes taxa that can be either perennial or annual, e.g. the genus *Cladophora*.

Taxa occurring on soft substrates were classified with regard to their sensitivity to eutrophication. The classification was based on literature, where references including actual experimental evidence were considered the most reliable. Our classification was done in several steps. In the first step, separate classifications were made based on freshwater (lake) references (e.g. Melzer 1999; Ecke 2007; Penning et al. 2008; Søndergaard et al. 2010) or brackish and marine water references (e.g. Wallentinus 1979; the MarLIN database). In the second step, the classifications were compared with other information on nutritional preferences (oligotrophic or eutrophic waters; e.g. Mossberg et al. 2003; Kautsky and Andersson 2005; the Swedish virtual flora).

Soft substrate taxa were then grouped, based on eutrophication response, as most sensitive (S++), very sensitive (S+), sensitive (S), tolerant (T), slightly favored (T+) and favored (T++) and coupled with confidence values. The confidence values for the combined classification generally rated references regarding Swedish coastal waters slightly higher than references regarding lakes or remote marine water.

West coast - hard substrate		
Taxon	**Longevity**	**Functional group**
EPIPHYTES		
B. hamifera/S. repens *	A	2 Filamentous algae
Bryopsis hypnoides	A	2 Filamentous algae
Callithamnion corymbosum	A	2 Filamentous algae
Ectocarpus/Pylaiella	A	2 Filamentous algae
Pterothamnion plumula	A	2 Filamentous algae
Spongomorpha aeruginosa	A	2 Filamentous algae
Griffithsia corallinoides	PoW	2 Filamentous algae
Cladophora	V	2 Filamentous algae
Aglaothamnion		2 Filamentous algae
Antithamnion cruciatum		2 Filamentous algae
Ceramium tenuicorne	A	2.5 Filamentous algae
Polysiphonia fibrillosa	A	2.5 Filamentous algae
Chaetopteris plumosa	P	2.5 Filamentous algae
Brongniartella byssoides	PoW	2.5 Filamentous algae
Polysiphonia fucoides	PoW	2.5 Filamentous algae
Polysiphonia stricta	PoW	2.5 Filamentous algae
Ceramium virgatum	PP	2.5 Filamentous algae
Plumaria plumosa	PP	2.5 Filamentous algae
Rhodomela confervoides	PP	2.5 Filamentous algae
Sphacelaria	PP	2.5 Filamentous algae
Sphacelaria cirrosa	PP	2.5 Filamentous algae
Ceramium cimbricum		2.5 Filamentous algae
Heterosiphonia japonica		2.5 Filamentous algae
Phycodrys rubens	PoW	3.5 Corticated foliose algae
Membranoptera alata	PP	3.5 Corticated foliose algae
Cystoclonium purpureum	PP	4 Corticated algae (thick, soft)
Chordaria flagelliformis	A	4.5 Corticated algae (thick, hard)
Osmundea	P	4.5 Corticated algae (thick, hard)
FREE-LIVING		
Ectocarpus/Pylaiella	A	2 Filamentous algae
Cladophora	V	2 Filamentous algae
ON HARD SUBSTRATE		
B. hamifera/S. repens *	A	2 Filamentous algae
Callithamnion corymbosum	A	2 Filamentous algae
Ectocarpus/Pylaiella	A	2 Filamentous algae
Pterothamnion plumula	A	2 Filamentous algae
Griffithsia corallinoides	PoW	2 Filamentous algae
Chaetomorpha melagonium	PP	2 Filamentous algae
Cladophora rupestris	PP	2 Filamentous algae

Cladophora	V	2 Filamentous algae
Antithamnion cruciatum		2 Filamentous algae
Ceramium tenuicorne	A	2.5 Filamentous algae
Dasya baillouviana	A	2.5 Filamentous algae
Dictyosiphon/Stictyosiphon	A	2.5 Filamentous algae
Chaetopteris plumosa	P	2.5 Filamentous algae
Polysiphonia fucoides	PoW	2.5 Filamentous algae
Polysiphonia stricta	PoW	2.5 Filamentous algae
Ceramium virgatum	PP	2.5 Filamentous algae
Plumaria plumosa	PP	2.5 Filamentous algae
Polysiphonia elongata	PP	2.5 Filamentous algae
Rhodomela confervoides	PP	2.5 Filamentous algae
Sphacelaria	PP	2.5 Filamentous algae
Ceramium	V	2.5 Filamentous algae
Heterosiphonia japonica		2.5 Filamentous algae
Polysiphonia brodiei		2.5 Filamentous algae
Ulva	A	3 Foliose algae
Ulva lactuca	A	3 Foliose algae
Delesseria sanguinea	PoW	3.5 Corticated foliose algae
Phycodrys rubens	PoW	3.5 Corticated foliose algae
Chondrus crispus	PP	3.5 Corticated foliose algae
Coccotylus/Phyllophora	PP	3.5 Corticated foliose algae
Membranoptera alata	PP	3.5 Corticated foliose algae
Dumontia contorta	PoW	4 Corticated algae (thick, soft)
Cystoclonium purpureum	PP	4 Corticated algae (thick, soft)
Chorda filum	A	4.5 Corticated algae (thick, hard)
Chordaria flagelliformis	A	4.5 Corticated algae (thick, hard)
Ahnfeltia plicata	PP	4.5 Corticated algae (thick, hard)
Codium fragile	PP	4.5 Corticated algae (thick, hard)
Furcellaria lumbricalis	PP	4.5 Corticated algae (thick, hard)
Polyides rotundus	PP	4.5 Corticated algae (thick, hard)
Laminaria digitata	PoW	5 Leathery algae
Sargassum muticum	PoW	5 Leathery algae
Fucus serratus	PP	5 Leathery algae
Halidrys siliquosa	PP	5 Leathery algae
Laminaria hyperborea	PP	5 Leathery algae
Saccharina latissima	PP	5 Leathery algae
Corallina officinalis	PP	6 Calcareous algae
Lithothamnion/Phymatolithon	PP	7 Crustose algae
Pseudolithoderma	PP	7 Crustose algae
Hildenbrandia CF		7 Crustose algae

* *B. hamifera/S. repens = Bonnemaisonia hamifera/Spermothamnion repens*

East coast – hard substrate		
Taxon	**Longevity**	**Functional group**
EPIPHYTES		
Ectocarpus/Pylaiella *	A	2 Filamentous algae
Spirogyra	A	2 Filamentous algae
Ceramium tenuicorne	A	2.5 Filamentous algae
Dictyosiphon foeniculaceus	A	2.5 Filamentous algae
Polysiphonia fucoides	PoW	2.5 Filamentous algae
Elachista		
FREE-LIVING		
Chaetomorpha linum	A	2 Filamentous algae
Cladophora fracta	A	2 Filamentous algae
Spirogyra	A	2 Filamentous algae
Stictyosiphon tortilis	PoW	2.5 Filamentous algae
Monostroma balticum	A	3 Foliose algae
Ulva	A	3 Foliose algae
Fucus vesiculosus	PP	5 Leathery algae
ON HARD SUBSTRATE		
Aglaothamnion roseum	A	2 Filamentous algae
Ectocarpus/Pylaiella *	A	2 Filamentous algae
Urospora penicilliformis CF	A	2 Filamentous algae
Cladophora glomerata	PoW	2 Filamentous algae
Aegagropila linnaei	PP	2 Filamentous algae
Ceramium tenuicorne	A	2.5 Filamentous algae
Dictyosiphon/Stictyosiphon **	A	2.5 Filamentous algae
Polysiphonia fibrillosa	A	2.5 Filamentous algae
Polysiphonia fucoides	PoW	2.5 Filamentous algae
Battersia arctica	PP	2.5 Filamentous algae
Rhodomela confervoides	PP	2.5 Filamentous algae
Ulva	A	3 Foliose algae
Coccotylus/Phyllophora ***	PP	3.5 Corticated foliose algae
Chorda filum	A	4.5 Corticated algae (thick, hard)
Furcellaria lumbricalis	PP	4.5 Corticated algae (thick, hard)
Fucus vesiculosus	PP	5 Leathery algae
Hildenbrandia CF		7 Crustose algae

* *Ectocarpus/Pylaiella = Ectocarpus siliqulosus/Pylaiella litoralis*

** *Dictyosiphon/Stictyosiphon = Dictyosiphon foeniculaceus/Stictyosiphon tortilis*

*** *Coccotylus/Phyllophora = Coccotylus truncatus/Phyllphora pseudoceranoïdes*

East coast – soft substrates		
Taxon	**Growth form**	**Sensitivity**
MACROALGAE		
Chorda filum	On seabed	Sensitive
Ceramium tenuicorne	Epiphyte	Sensitive
Dictyosiphon foeniculaceus	Epiphyte	Sensitive
*Ectocarpus/Pylaiella**	Epiphyte	Tolerant ++
Elachista	Epiphyte	-
Polysiphonia fibrillosa	Epiphyte	Sensitive
Polysiphonia fucoides	Epiphyte	Tolerant
Ulva	Epiphyte	Tolerant ++
Chaetomorpha linum	Free-living	Tolerant ++
Cladophora fracta	Free-living	Tolerant ++
*Coccotylus/Phyllophora***	Free-living	-
Fucus vesiculosus	Free-living	Sensitive
Furcellaria lumbricalis	Free-living	Tolerant
Monostroma balticum	Free-living	Tolerant
Spirogyra	Free-living	Tolerant ++
Ulva	Free-living	Tolerant ++
CHAROPHYTES		
Chara aspera	On seabed	Sensitive +
Chara baltica	On seabed	Sensitive ++
Chara globularis	On seabed	Sensitive +
Tolypella nidifica	On seabed	Sensitive +
VASCULAR PLANTS		
Callitriche hermaphroditica	On seabed	Tolerant +
Myriophyllum	On seabed	Tolerant +
Najas marina	On seabed	Tolerant +
Potamogeton crispus	On seabed	Tolerant +
Potamogeton gramineus	On seabed	Sensitive
P. gramineus × perfoliatus	On seabed	-
Potamogeton pectinatus	On seabed	Tolerant ++
Potamogeton perfoliatus	On seabed	Tolerant +
Ranunculus circinatus	On seabed	Tolerant ++
R. peltatus ssp. baudotii	On seabed	Tolerant +
Ruppia (cirrhosa)	On seabed	Sensitive
Zannichellia palustris	On seabed	Tolerant ++
Zostera marina	On seabed	Sensitive
Ceratophyllum demersum	Free-living	Tolerant +++
Lemna trisulca	Free-living	Tolerant +

* *Ectocarpus/Pylaiella = Ectocarpus siliqulosus/Pylaiella litoralis*

** *Coccotylus/Phyllophora = Coccotylus truncatus/Phyllphora pseudoceranoïdes*

RESPONSE OF MACROPHYTE INDICATORS TO NATURAL AND ANTHROPOGENIC GRADIENTS IN TWO COASTAL AREAS OF SWEDEN

Benthic macrophytes are affected by anthropogenic activity, and therefore these communities are suitable for the assessment of ecological status according to the WFD. The existing assessment method for benthic macrophytes is, however, based on the depth distribution of only a few selected species, and in shallow areas and areas dominated by soft substrate the present method performs poorly.

The aim of the present study was therefore to test and evaluate a number of potential macrophyte indicators on a homogenous data set from well-described pressure gradients on both the west and east coast of Sweden.

Our results show that species richness in macroalgal communities on hard substrate is a promising indicator as it increased with increasing Secchi depth. Cumulative cover and community complexity were also positively related to Secchi depth.

For soft substrate communities on the west coast, the depth distribution of *Zostera marina* proved to be a promising indicator since it responded strongly in the study gradient. For soft substrates on the east coast the tested indicators showed a large variation within areas and a large sampling effort is required to reduce uncertainty.

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