Disparity in the occurrence of *Fucus vesiculosus* in two adjacent areas of the Baltic Sea — current status and outlook for the future

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Snickars, M., Rinne, H., Salovius-Laurén, S., Arponen, H. & O'Brien, K. 2014: Disparity in the occurrence of *Fucus vesiculosus* in two adjacent areas of the Baltic Sea — current status and outlook for the future. *Boreal Env. Res.* 19: 441–451.

The occurrence of the habitat-forming macroalgae *Fucus vesiculosus* has generally decreased in many Baltic Sea areas. Parallel to eutrophication, water temperature has increased, enhancing pelagic primary production, light absorption and sedimentation, affecting phytobenthic communities. We studied the occurrence of *F. vesiculosus* (> 3400 drop-video observations) and long-term environmental changes in two adjacent areas (Archipelago Sea, Bothnian Sea). *Fucus vesiculosus* has not recovered from its disappearance from the outer Archipelago Sea that was reported in the late 1970s. In the Bothnian Sea, it was six times more common and grew deeper and denser. Temperature, total phosphorus concentration and chlorophyll *a* have increased since the 1970s in both areas but from lower initial levels in the Bothnian Sea. We suggest that if the trends of these variables continue, the water quality of the Bothnian Sea will deteriorate within two to three decades and reach levels that may lead to major losses of *F. vesiculosus*.

Introduction

The bladderwrack, *Fucus vesiculosus* (henceforth Fucus), is the key habitat-forming brown algae on rocky coastal bottoms of the Baltic Sea (e.g. Kautsky *et al*. 1992). Its distribution and abundance is affected by a range of abiotic and biotic factors (e.g. Rosemarin and Notini 1996, Korpinen *et al*. 2007, Wahl *et al*. 2011) of which salinity is the most important affecting the distribution at large scale (e.g. Wærn 1952, Bergström and Bergström 1999). Exposure also plays a role with Fucus generally penetrating deeper in more exposed areas (Kiirikki 1996a, Ruuskanen

et al. 1999, Rinne *et al*. 2011). Furthermore, ice-scouring in shallow waters sets the upper limit of the vertical distribution (Waern 1952, Kiirikki 1996a). Eutrophication of the Baltic Sea has caused changes in the Fucus occurrence, e.g. increased turbidity has led to decreased depth penetration (Kautsky *et al*. 1986, Eriksson *et al*. 1998, Torn *et al*. 2006). The recruitment of Fucus is disturbed by eutrophication via increased competition for space from filamentous algae (e.g. Berger *et al*. 2003). Also the higher sedimentation rate, due to increased pelagic primary production, disturbs germling settlement (Berger *et al*. 2003, Eriksson and Johansson 2003, Eriks-

son and Bergström 2005). In addition, increased amounts of nutrients may have direct negative effects on Fucus attachment (Bergström *et al.* 2003) and grazing may increase due to higher nutritional quality of the algal tissues (Hemmi and Jormalainen 2002). Herbivory may also cause fluctuations in the occurrence as well as local loss of Fucus (Kangas *et al.* 1982, Engkvist *et al.* 2000, Korpinen *et al.* 2007).

During the late 1970s, Fucus declined rapidly in many parts of the northern Baltic Sea, including the Archipelago Sea and the Gulf of Finland (Kangas *et al.* 1982, Haahtela 1984, Rönnberg *et al.* 1985). The occurrence of Fucus is related to multiple abiotic and biotic factors (e.g. Wahl *et al.* 2011, Alexandridis *et al.* 2012) and the reason behind the decline was most likely an array of effects affecting both early and adult life-stages (Haahtela 1984, Berger *et al.* 2004). These effects were related to the influx of saline water into the Baltic Sea (Kangas *et al.* 1982 and references therein) that mobilized large amounts of nutrients from deeper waters of the Baltic Proper, further enhancing several of the ongoing eutrophication processes (Kangas *et al.* 1982, Haahtela 1984). In addition, increased abundance of herbivores coincided with this period (Haahtela 1984).

Temporal and spatial changes in the occurrence of Fucus populations are less studied farther north in the Bothnian Sea, which has a history of less severe eutrophication (Lundberg *et al.* 2009). Häyren (1950a, 1950b) reported frequent occurrence of Fucus in the outer and middle archipelago of the Bothnian Sea and no changes equivalent to the ones detected in the Archipelago Sea in the late 1970s (Keskitalo and Ilus 1987), suggesting little changes in Fucus occurrence over time in this area. However, studies from the last ten years suggest that the signs of eutrophication are getting stronger in the Bothnian Sea (Lundberg *et al.* 2009), which imply that the coastal ecosystem of the area may be negatively affected.

During the last four decades, water temperature in the Baltic Sea showed a rising trend (Alheit *et al.* 2007, Suikkanen *et al.* 2013). During the same period eutrophication was severe (e.g. Bonsdorff *et al.* 1997). Thus, the effects of climate change on eutrophication may

be substantial as rising temperature may enhance e.g. pelagic primary production (e.g. Meier *et al.* 2012). In coastal ecosystems, an increase in temperature may affect the depth limit and the occurrence of macroalgae as increasing amounts of phytoplankton absorb more light (Suikkanen *et al.* 2007, Paerl and Huisman 2008, Alexandridis *et al.* 2012). Increasing amounts of phytoplankton also results in enhanced sedimentation that further deteriorates the light conditions and increases the risk of physical smothering of macroalgae (Berger *et al.* 2003, Eriksson and Johansson 2003). Increased water temperature may also trigger an earlier maturation of receptacles in Fucus (Kraufvelin *et al.* 2012) with potential implications for the reproduction cycle.

Although the disappearance of Fucus in the late 1970s and early 1980s was both rapid and severe in the Archipelago Sea, there are few studies on the possible return and current distribution of the species. However, ongoing field surveys conducted by the Metsähallitus Natural Heritage Services within the Finnish Inventory Program for the Marine Underwater Nature (VELMU) provide data to assess the present status of Fucus in the Archipelago Sea, and also enable a comparison with the situation in the Bothnian Sea.

The aim of this study was to compare the occurrence and depth distribution of Fucus between two adjacent sea areas with similar prerequisites for Fucus growth but with different history of eutrophication. Specifically we ask whether Fucus in the Archipelago Sea has recovered from the reported decline in the late 1970s and use the less eutrophied Bothnian Sea as a reference. Furthermore, the aim was to evaluate the potential future effects of changing environment on the status of the species in these two areas.

Material and methods

The two study areas, the Archipelago Sea and the Bothnian Sea, are located in the northern Baltic Sea approximately 100 km apart (Fig. 1). The Archipelago Sea is characterised by a large archipelago area, and the study sites were situated in the outer parts where wave exposed small rocky islands and skerries dominate. The

water depth is usually < 40 m and the bottom consists of a mixture of soft and hard substrates. The study area in the Bothnian Sea is similar, but generally shallower, has fewer islands and is therefore more wind exposed. The mean depth of the potential Fucus sites (*see* below for definition) in the two areas was 5.3 ± 0.1 m and 4.8 ± 0.1 m (mean ± 95%CI) for Archipelago Sea and Bothnian Sea, respectively.

The surveys were conducted from July to September in 2005–2012 in the Archipelago Sea and in 2009–2012 in the Bothnian Sea using a hand-held video system that recorded ca. 15 m^2 of the bottom for up to 60 seconds and was operated from a boat. The system was comprised a waterproof camera (standard security camera, SD/550 TVL) with 30 metres of cable, a recording system and lights. To record video footage onboard, the camera cable was connected to a Sony Handycam camera and footage stored onto a digital video (DV) tape. Samples were recorded following a grid-based sampling design where samples were taken at every corner of the grid with a side length of 100 m or following a stratified random design based on depth and wave exposure conditions. At each site, coordinates and depth to nearest 0.1 m were noted. Video recordings were stored for later analyses of substrate and species coverage (macroscopic vegetation such as Fucus and epibenthic fauna, mainly *Mytilus edulis*). During the video analyses, the percentage coverage of all visible macroscopic species was noted. This method is well suited for detection of large macroalgae such as Fucus. The percentage coverage of hard substrate was the sum of rock, boulders and stones larger than 10 cm in diameter, and other substrate as the sum of stones smaller than 10 cm in diameter and smaller grain size, including sand and mud.

Only hard substrates were used in the analyses. A potential site for Fucus growth was a site with > 10% hard substrate located in the photic zone, which was defined as the depth with 1% left of the photosynthetically active radiation (PAR) at surface (Tett 1990). A site was defined as being in the photic zone if the depth of the site was less than the photic depth, measured from a GIS raster with 100 m resolution holding information of interpolated photic depth in the two
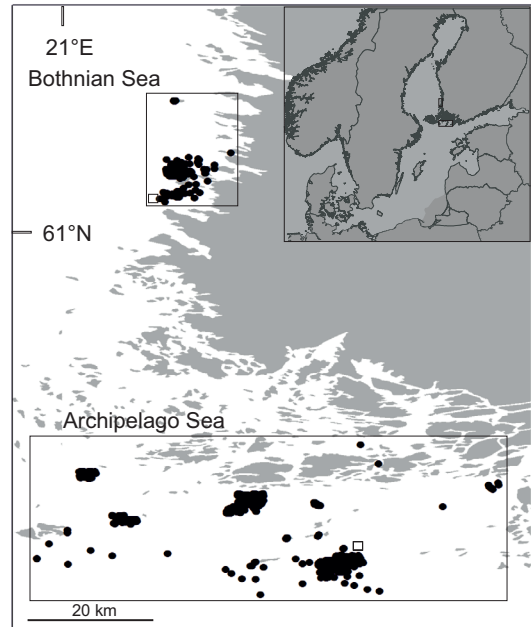

Fig. 1. The two study areas in the southern outer Archipelago Sea and the Bothnian Sea. Circles show the distribution of hard photic sites (> 10% hard substrate), squares show the position of the two long-term monitoring sites for environmental variables.

study areas. A potential site with > 1% of Fucus coverage was regarded as a realised Fucus site.

Long-term values (1975–2011) for the environmental variables, surface (1 m) water temperature (°C), as well as salinity (psu), total concentration of nitrogen (N_{tot}, µg l^{-1}), total concentration of phosphorus (P_{tot}, µg l^{-1}), total concentration of chlorophyll *a* (Chl-*a*, µg l^{-1}) and Secchi depth (m), were taken from one water quality monitoring station in each area (Archipelago Sea 59°52´N, 21°53´E, Bothnian Sea 61°8´N, 21°18´E, Fig. 1). Pooled values for 1–10 m depth from August measurements were used to verify how the data from the monitoring stations extrapolate to the study areas.

The long-term changes in the environmental variables were analysed as five year moving averages. An average value was used instead of year-to-year comparisons in order to reduce the annual variation in variables and achieve gross trends in the temporal change in variables. A five-year period was deemed sufficient to represent the general trends without loosing information inherent to year-to-year develop-

ment (*see* e.g. Zwanenburg 2000, Perry *et al.* 2005). Non-parametric Spearman's rank correlation was used to analyse associations between selected variables. In order to ensure the generality and ability of the two long-term monitoring sites to represent the whole study areas, average values covering a representative period of time of the environmental variables were compared with interpolated rasters produced within the EU LIFE+ FINMARINET-project covering the same period. Values from each raster representing each of the environmental variables were extracted for every surveyed site with hard substrate and averaged for each of the two areas and compared with the values from the monitoring station in each area. The rasters were interpolated based on the monitoring data from the national water quality monitoring database (Hertta) using average values (1–10 m depth pooled) from years 1999 to 2008 (late July–August observations). The numbers of stations used in the interpolations are listed in Table 1.

Results

Potential Fucus sites, i.e. photic hard substrates, were available in similar quantities in the two study areas. In the Archipelago Sea, 2197 (72%) of the studied sites in the photic zone had hard substrate, while in the Bothnian Sea their number was 1350 (70%). In the Bothnian Sea, Fucus (> 1% coverage) occurred at 61.7% of the potential sites, but only at 9.6% in the Archipelago Sea; i.e. Fucus was noted more than six times

more often at the potential sites in the Bothnian Sea than in the outer Archipelago Sea.

As with Fucus occurrence, the percentage coverage of Fucus was higher at all depths in the Bothnian Sea (mean ± 95%CI = 23.9% ± 1.7%) than in the Archipelago Sea (15.6% ± 3.0%) (except for the 0–1 m interval). The largest difference in depth penetration and coverage between the two areas was found in the 2–8 m depth interval with clear separation of the CIs. In the Bothnian Sea, Fucus was present at > 60% of the potential sites down to 6–7 m, then decreased steadily and was present at only < 10% of the sites at 9–10 m depth (Fig. 2). In the Archipelago Sea, Fucus occurred at > 30% of the potential sites at the shallowest (0–1 m) depth interval and declined to < 10% at 4 m depth. In the Bothnian Sea, the percentage coverage of Fucus peaked at the 2–3 m interval and was > 10% coverage down to 6–7 m depth. In comparison, Fucus in the Archipelago Sea had a steady decline in coverage and decreased under 10% coverage already at 4 m depth.

The maximum depth of Fucus in the Archipelago (mean ± 95%CI: 7.1 ± 0.8 m) was highly variable during the period (Fig. 3), mainly illustrating differences in depth penetration of Fucus in the sub-areas studied. Overall, in the Archipelago Sea Fucus was limited to more shallow areas as compared with the Bothnian Sea (mean ± 95%CI: 9.1 ± 0.2 m, Fig. 3).

The comparison between the two long-term monitoring sites and the interpolated rasters matched well, and the match was generally better in the Archipelago Sea despite the larger

Table 1. Comparison between the environmental variables from the two monitoring stations (Station) and the average value of the interpolated raster (Raster) of corresponding variable extracted for every photic hard substrate (> 10% hard substrates) site. Numbers in parentheses denote the number of sites that the interpolation is based on in each area. Pooled values from 1–10 m depth from August each year (average values of the period 1999–2008).

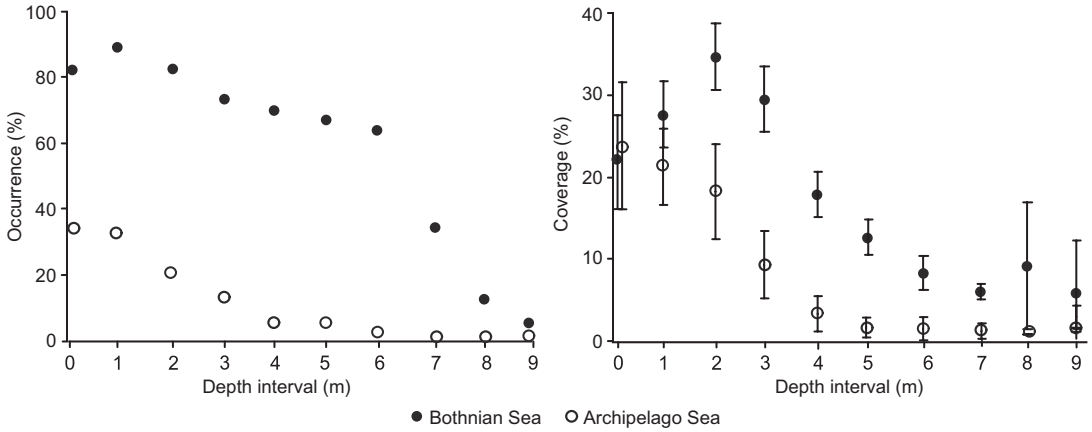| Variable	Archipelago Sea		Similarity (%)	Bothnian Sea		Similarity (%)
	Station	Raster		Station	Raster	
Chl-*a* (μg l^{-1})	4.1	4.2	98 (181)	1.7	2.0	88 (26)
P$_{tot}$ (μg l^{-1})	21.2	21.4	99 (183)	14.0	12.5	88 (26)
N$_{tot}$ (μg l^{-1})	327	327	100 (150)	256	272	94 (25)
Temperature (°C)	17.9	17.8	100 (179)	15.3	15.4	99 (48)
Salinity (psu)	6.2	6.1	99 (15)	5.6	5.6	100 (4)
Secchi depth (m)	4.1	4.1	100 (168)	4.7	4.0	82 (26)

Fig. 2. The percentage occurrence of Fucus at potential (photic hard substrate) sites, and the mean percentage cover (±95%CI) of Fucus in the depth interval 0–10 m.

geographical extent of the study area. In the Bothnian Sea, the monitoring site had a somewhat lower Chl-*a* but higher P_{tot} and Secchi depth values than the rasters (Table 1). Salinity, with the smallest number of interpolated stations, had good agreement between the sites and the raster in both areas.

As compared with the Bothnian Sea, the Archipelago Sea had clearly higher Chl-*a*, nutrients (P_{tot} and N_{tot}), temperature, and salinity levels, but similar Secchi depth (Table 2). Since the 1970s, there has been a general increase in Chl-*a*, P_{tot}, temperature, and a decrease in salinity and Secchi depth in both areas, but the changes were not always similar over the period (Fig. 4). For example, Chl-*a* and temperature showed opposite trends in the late 1970s and early 1980s in the Archipelago Sea and the Bothnian Sea, followed by a decline and further an increase in the later part of the study period in
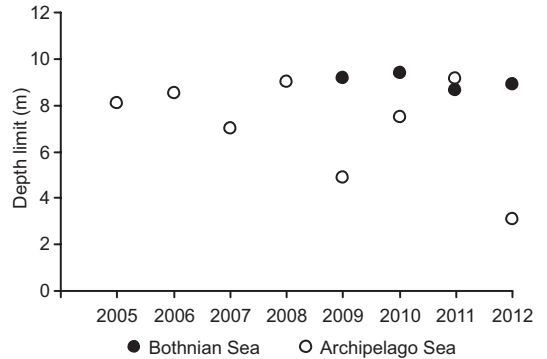

Fig. 3. Maximum depth of Fucus (> 1% coverage) at photic hard sites (> 10% hard substrate).

both areas. The relative increase over the years has been most pronounced for Chl-*a* and P_{tot}, and more so in the Bothnian Sea. N_{tot} varied in time.

In both areas Chl-*a* correlated strongly with the surface water temperature (Table 3 and Fig. 4).

Table 2. Mean ± 95%CI values of the environmental variables in the two areas during 1977–2011; in parentheses Archipelago Sea years 2005–2012 and Bothnian Sea years 2009–2012. Values are pooled data from 1–10 m depth from August each year (water quality monitoring station: Archipelago Sea 59°52´N, 21°53´E, Bothnian Sea 61°8´N, 21°18´E).

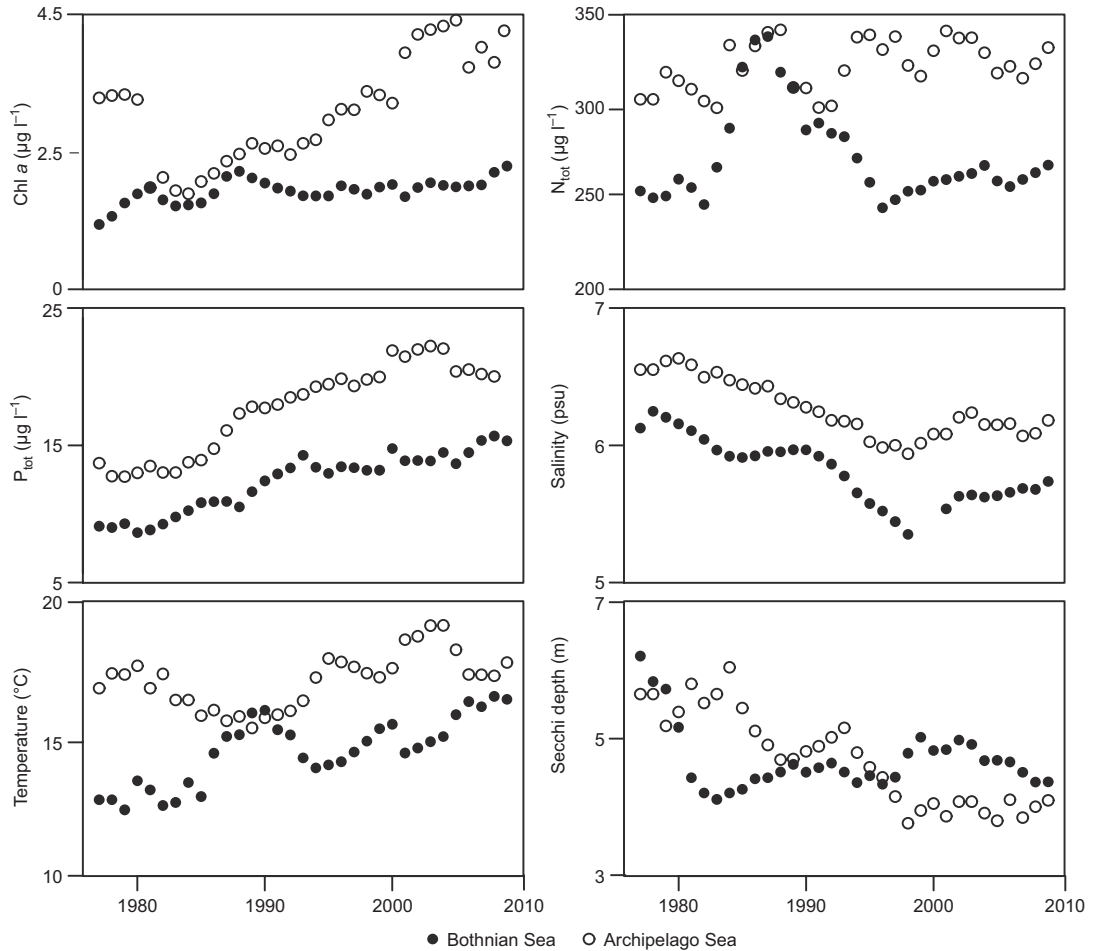| Variable	Archipelago Sea	Bothnian Sea
Chl-*a* (μg l^{-1})	3.2 ± 0.5 (4.4 ±1.0)	1.7 ± 0.2 (2.4 ± 1.0)
P_{tot} (μg l^{-1})	17.4 ± 1.6 (21.1 ± 1.8)	12.1 ± 1.0 (15.3 ± 1.9)
N_{tot} (μg l^{-1})	327 ± 17.9 (339 ± 25.6)	271 ± 16.3 (271 ± 43)
Temperature (°C)	17.1 ± 0.6 (18.2 ± 1.4)	14.5 ± 0.9 (15.7 ± 3.7)
Salinity (psu)	6.3 ± 0.1 (6.2 ± 0.2)	5.8 ± 0.1 (5.7 ± 0.2)
Secchi depth (m)	4.8 ± 0.4 (3.9 ± 0.5)	4.7 ± 0.3 (4.4 ± 0.5)

Fig. 4. Temporal development of the environmental variables during the period 1975–2011. Values are five-year means, each point represents the median year.

In the Archipelago Sea, Chl-*a* also strongly correlated with P_{tot}, but less so in the Bothnian Sea, whereas the correlation between Chl-*a* and Secchi depth differed between the two areas. N_{tot} correlated weakly with the other variables.

Discussion

The results of this study show that there is a large difference in the occurrence, depth penetration and percentage coverage of Fucus, as

Table 3. Spearman correlations (r_S) between environmental variables in the Archipelago Sea (upper right part of the matrix: ArcSea) and in the Bothnian Sea (lower left part of the matrix: BotSea), $n = 33$, five-year moving average of pooled values from 1–10 m depth from August each year. *p* values in parentheses, ns = correlation does not exist.

	Chl-*a*	N_{tot}	P_{tot}	Secchi depth	Temperature	Salinity
Chl-*a*	**BotSea**	ns	0.78 (< 0.01)	−0.84 (< 0.01)	0.77 (< 0.01)	−0.62 (< 0.01)
N_{tot}	ns	–	0.45 (0.02)	−0.40 (0.03)	ns	−0.40 (0.03)
P_{tot}	0.53 (< 0.01)	ns	–	−0.86 (< 0.01)	0.53 (< 0.01)	−0.81 (< 0.01)
Secchi depth	ns	ns	ns	–	−0.51 (< 0.01)	0.83 (< 0.01)
Temperature	0.83 (< 0.01)	ns	0.69 (< 0.01)	ns	–	−0.40 (0.02)
Salinity	ns	ns	−0.73 (< 0.01)	ns	−0.40 (0.03)	**ArcSea**

well as in the environmental conditions in the two adjacent areas of the northern Baltic Sea. Fucus was present at potential sites up to six times more often in the Bothnian Sea than in the Archipelago Sea. The overall ecosystem effects of such a large difference in the occurrence of the key habitat-forming species are likely pronounced (e.g. Kautsky *et al.* 1992) but outside the scope of this study. The observed differences are likely due to the differences in water quality of the two areas since the mid-1970s.

During the past decades, the status of Fucus populations along the Finnish side of the Bothnian Sea remained largely unrecorded. However, the high proportional occurrence, the deep depth limit and the high percentage coverage of Fucus in the area suggest that no or little change has taken place over the decades (cf. Häyren 1950a, 1950b, Keskitalo and Ilus 1987). In the Archipelago Sea, no apparent improvement has been recorded from the drastic decline in Fucus occurrence recorded in the late 1970s (Kangas *et al.* 1982, Rönnberg *et al.* 1985). In the inner and middle Archipelago Sea, the disappearance of Fucus in the 1970s was affected by many factors acting simultaneously, such as increased nutrient concentrations leading to deteriorated light conditions, outburst of filamentous algae, severe ice-conditions and a mass occurrence of the herbivorous isopod *Idotea balthica* (Haahtela 1984). However, the decline in the outer archipelago area was less pronounced (Rönnberg *et al.* 1985). Since then, few follow-up studies on the status of the species have been carried out in the area (Vahteri *et al.* 2003). Our results show that currently the occurrence of Fucus populations is very low in the outer Archipelago Sea, as a clear majority of the potential sites were devoid of Fucus. In general, the algae occurred on much shallower bottoms and grew sparse as compared with the Fucus populations in the Bothnian Sea. This is most likely because there has been no apparent improvement in the water quality in the outer Archipelago Sea. Instead chlorophyll *a* concentrations have been increasing since the mid-1970s, and especially total phosphorous has increased strongly since the 1980s although it seems to have leveled off at high values during the most recent time. In addition to deteriorated light conditions, the poor water quality has likely

contributed to increased sedimentation affecting Fucus settlement and growth, as well as competition from filamentous algae (Berger *et al.* 2003). Thus, it seems that a clear change in water quality needs to happen before Fucus will recover.

Overall, the values of examined environmental variables, except for Secchi depth, were smaller in the Bothnian Sea as compared with those in the Archipelago Sea. The Secchi depth also correlated in different ways with the other environmental variables in the two areas, suggesting that the Secchi depth as a measure may be insensitive to regional differences in underlying causes to the light attenuation (e.g. differences in bottom substrate, wind conditions, sediment composition and nutrient levels derived from catchment areas, water colour). The correlation between chlorophyll *a* and total phosphorous was stronger in both areas than that with total nitrogen, which is in line with Andersson *et al.* (1996) stating that phosphorous is a limiting factor for pelagic primary production in coastal waters. With the predicted increase in rainfall (and run-off from rivers) due to climate change, an increased inflow of freshwater is expected to increase nutrient levels from land run-off (Meier *et al.* 2012). The results of the present study support this scenario showing a close correlation between increasing total phosphorous and decreasing salinity.

An increase in temperature over the recent decades can be seen in the open Baltic Sea (Alheit *et al.* 2007, Suikkanen *et al.* 2013) and also in the two coastal study areas, especially during the last two decades. The indirect role of rising temperature may be important for phytobenthos (Wahl *et al.* 2011, Alexandridis *et al.* 2012), as it enhances the negative effects of eutrophication. In the present study, the increase in temperature was accompanied by higher levels of total phosphorous and chlorophyll *a* resulting from enhanced pelagic primary production. This is in line with Meier *et al.* (2012) who predicted that increasing water temperature may accelerate eutrophication by strengthening the so-called "vicious circle", an internal feedback mechanisms releasing phosphorous from the sediment as a consequence of eutrophication-induced low oxygen levels in the bottom water layer, further reinforcing the eutrophication process (Vahtera

et al. 2007, Meier *et al.* 2012). Although phosphorous is important for the pelagic primary production, the results of the present study suggest that chlorophyll *a* may be more closely linked to temperature than to phosphorous, implying that temperature rather than nutrient limitation currently regulates the level of pelagic primary production in the coastal waters. For example, the increase in total phosphorous has levelled off and even showed a declining trend in one of the areas during the most recent time, however, chlorophyll *a* has continued to increase and follow temperature despite the dissimilar pattern in temporal development of temperature in the two areas.

As a result, when the predicted increase in temperature is added to high (not limiting) nutrient concentrations, it is likely that the Bothnian Sea is changing towards a more eutrophic state (Lundberg *et al.* 2009). With the current rate of environmental change, similar conditions to those reported in the Archipelago Sea may be reached already within a couple of decades. Water transparency (coupled to increasing pelagic primary production) is a key factor regulating Fucus depth penetration (Kautsky *et al.* 1986, Torn *et al.* 2006, Rinne *et al.* 2011). Thus, projections of increasing temperature and pelagic production imply that the depth penetration of Fucus in the Bothnian Sea may be negatively affected by increased shading, while pelagic primary production enhances sedimentation (Berger *et al.* 2003). If restricted to shallower waters, Fucus is more susceptible to ice-scraping (Kiirikki 1996a) that can be severe in the Bothnian Sea where most of the rocky shores are exposed. Thus, a reduction in the vertical distribution would seriously reduce the potential growth areas for Fucus, although, the effect of ice-scraping may also decrease due to less ice cover with a warmer climate.

The year-to-year variation in the maximum depth limit was rather high in the Archipelago Sea, which may reflect differences in the status of Fucus and conditions among the sub-areas studied. Although the conditions for Fucus seem to vary within the Archipelago Sea, the overall difference in depth limit was still large as compared with that in the Bothnian Sea and confirms its poor status in the Archipelago Sea.

The declining trend in maximum depth that was observed between the sampling years in both study areas could be due to differences among the sub-areas studied, or give some indications on the ongoing negative change in Fucus depth penetration.

Although the reported predictions imply a future decline in Fucus occurrence in the Bothnian Sea, there are some regional differences that may alter this scenario. First, the hydrographic conditions in the Bothnian Sea are different as compared with those in the northern Baltic Proper, and the potential role of the internal feedback mechanism (Vahtera *et al.* 2007, Meier *et al.* 2012) is considered less important due to lower ambient nutrient loads and better oxygen conditions in the bottom water layer than in the northern Baltic Proper (Raateoja 2012). However, increased precipitation, leading to increased run-off from rivers, may increase nutrient loads (Meier *et al.* 2012), which is potentially equally important as the internal feedback mechanism. Further, the Bothnian Sea coast is more exposed than that of the Archipelago Sea and thus likely less affected by the negative effects of sedimentation in the photic zone as the wave-induced water movements are stronger. The high exposure and potentially also the physical whiplash effect reduces the growth of the filamentous algae (Kiirikki 1996b) and thus the competition for space. In general, shading and space allocation are recognised as critical issues that may impair Fucus growth and its maximum depth limit (e.g. Rohde *et al.* 2008). However, despite high coverage, the amount of filamentous algae is not a likely factor explaining the difference in Fucus occurrence between the two areas as the amount of filamentous algae seems to be similar in the two areas (ca. 30% mean percentage coverage in both areas, authors' unpubl. data). Also competition for space from other species may be less severe in the Bothnian Sea than in the Archipelago Sea. For example, *Mytilus edulis*, occupying a lot of the hard bottom areas in the Archipelago Sea, is less abundant and restricted to deeper waters in the Bothnian Sea due to lower salinity (e.g. Mathiesen 1974, Bonsdorff 2006). Furthermore, although the role of grazing in controlling Fucus growth and population maintenance may be important and further

enhanced with eutrophication and a warming climate (e.g. Hemmi and Jormalainen 2002, Wahl *et al* 2012), the potential role of grazing by the main herbivore *Idotea* is probably less important in the Bothnian Sea due to lower abundance of the species in the less saline north (Råberg and Kautsky 2007).

The fact that Fucus is more common and grows more densely in the Bothnian Sea may also be important from the population maintenance and recruitment perspective. Eriksson *et al*. (1998) found that Fucus belts with high percentage coverage, reflecting maximum development, had healthy algae with lower epiphytic growth than low coverage belts. Dense algal belts physically reduce sedimentation and growth of the opportunistic filamentous algae, resulting in positive effects on internal recruitment (Kiirikki 1996b, Berger *et al*. 2003) and long-term maintenance of the algal belts. In a large-scale disappearance event (e.g. Archipelago Sea in the 1970s) such beneficial effects of living in a dense formation are lost. Furthermore, low occurrence or a large-scale loss affects the connectivity among patches (e.g. Bologna and Heck 2000), which may be detrimental to species such as Fucus whose gamete dispersion is limited to tens of metres (Serrão *et al*. 1997). Thus, the reduction in connectivity reduces the success of sexual reproduction and potential for re-establishment. In addition, in the outer Archipelago Sea, Fucus is restricted to shallow hard substrates near small islands and skerries (e.g. Rönnberg *et al*. 1985) surrounded by deep waters with soft substrates. In the generally shallower Bothnian Sea, potential sites for Fucus are better connected across areas of shallow water.

Conclusions

Increasing temperature and nutrient levels seem to be strongly affecting higher pelagic production having severe effects on phytobenthic species. The results of this study suggest that the status of Fucus will remain poor in the Archipelago Sea unless the negative trends in water quality can be reversed. Even more alarming is that the good status of the Bothnian Sea is at risk as several critical factors describing the status of the sea area have already reached and others are reaching levels similar to those that were associated to the sudden and major loss of Fucus populations in the Arhchipelago Sea. If the current development continues, we may face a dramatic decline in Fucus occurrence, a shift that will likely influence the phytobenthic community and the whole coastal ecosystem.

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