Factors structuring *Fucus* communities at open and complex coastlines in the Baltic Sea

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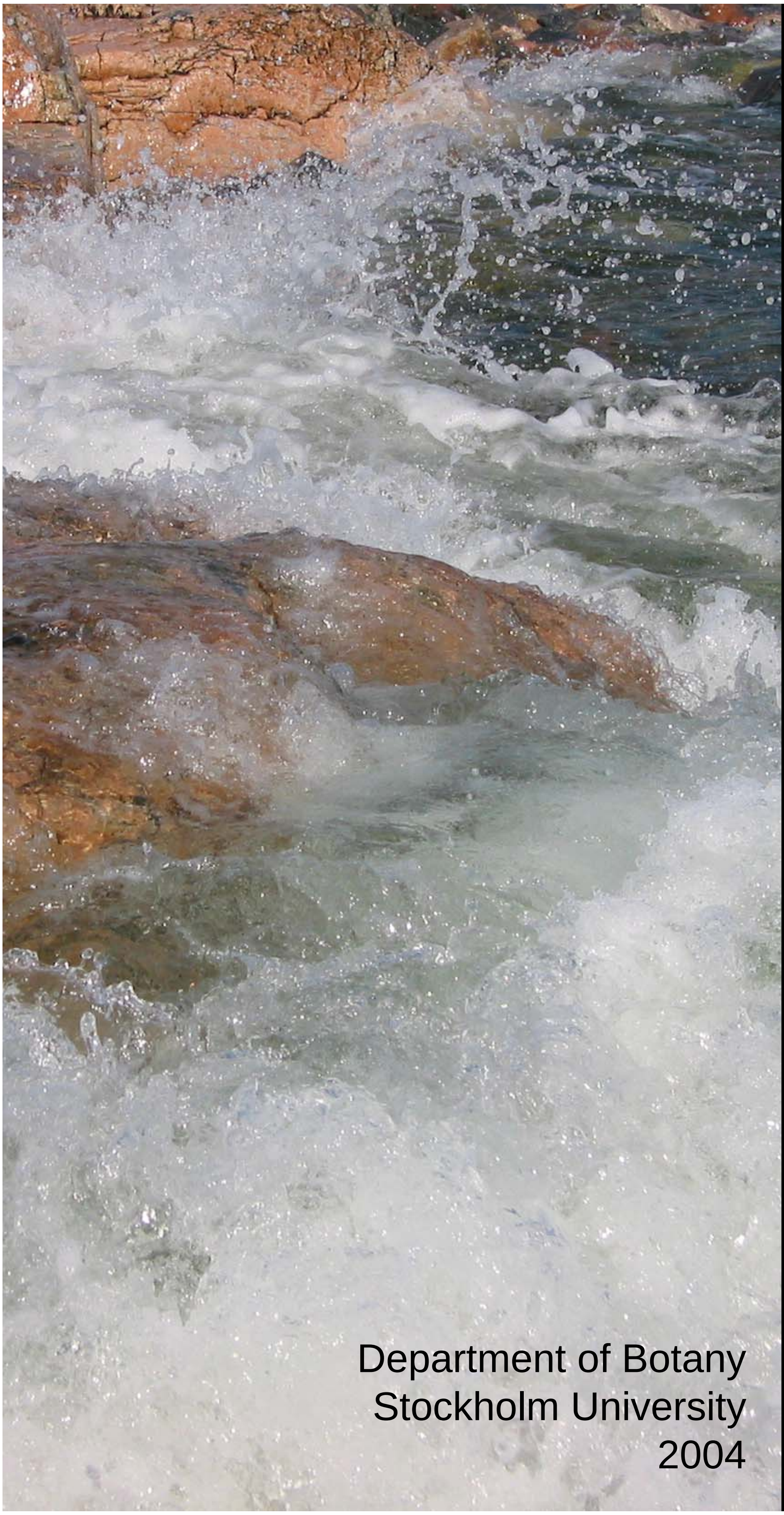

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Abstract

This thesis deals with physical factors and biological interactions affecting the distribution of two fucoid species, *Fucus vesiculosus* and *F. serratus*, in the Baltic Sea. Studies have been carried out in two quite different environments: an archipelago, and an open rocky coast. The archipelago has an extremely long coastline with a heterogeneous submerged landscape of different substrate types, slopes, water qualities, and degrees of wave exposure. The factors influencing *F. vesiculosus* distribution, morphology and epiphyte composition were studied in the Stockholm archipelago using field surveys and spatial modelling in Geographic information systems (GIS). A GIS-method to estimate wave exposure was developed and validated by comparing the result to an index based on vertical zonation of lichens. Wave exposure was considered an important factor for predicting the distribution of *F. vesiculosus* by its ability to clean hard surfaces from silt, and a predictive model was constructed based on the information of wave exposure and slope of the shore. It is suggested that the lower distribution boundary of attached *F. vesiculosus* is set by sediment in sheltered parts of the archipelago, and by light availability in highly wave exposed parts. The morphology of *F. vesiculosus* was studied over a wave exposure gradient, and several characters responded in accordance with earlier studies. However, when separating effects of wave exposure from effects of other confounding water property parameters, only thallus width was significantly different. Several water property parameters were shown to be correlated with wave exposure in the Stockholm archipelago, and the mechanism responsible for the effects on *F. vesiculosus* morphology is discussed. The composition of epiphytes on *F. vesiculosus* varied over a wave exposure gradient with a positive correlation to *Elachista fucicola*, and a negative to *Chorda filum*.

At an open coast the physical environment is much less heterogeneous compared to an archipelago. The distributions of *F. vesiculosus*, *F. serratus*, turf-forming algae, and the seafloor substrate, were surveyed along the open coasts of Öland and Gotland. Turf-forming algae dominated all hard substrates in the area, and *Polysiphonia fucoides* was most abundant. At the Gotland coast *F. vesiculosus* was less abundant than at the Öland coast, and *F. serratus* occurred only in the southern-most part. *Fucus serratus* was increasingly more common towards south which was interpreted as an effect mainly of the Baltic salinity gradient, or the variation of salinity that has occurred in the past. The effects of turf-forming algae and sediment on *F. serratus* recruitment at 7 m depth off the Öland east coast were studied in the field, and by laboratory experiments. Almost no recruits were found in the algal turf outside the *F. serratus* patches. More fine sediment was found in the turf than in the *F. serratus* patches, suggesting that the turf accumulates sediment by decreasing resuspension. Both filamentous algae and sediment decreased the attachment ability of *F. serratus* zygotes and survival of recruits, and sediment had the strongest effect. It is therefore suggested that *F. serratus* has difficulties recruiting outside its patches, and that these difficulties are enforced by the eutrophication of the Baltic Sea, which has favoured growth of filamentous algae and increased sedimentation. An overall conclusion is that *Fucus* distribution is affected by large-scale-factors, such as the eutrophication and salinity changes of the Baltic Sea, as well as by small-scale variation in wave exposure, substrate and slope, and by surface competition with neighbouring species.

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List of papers

I	**Isæus M. and Lindblad C.** A predictive GIS model using factors structuring *Fucus vesiculosus* distribution in a Baltic Sea archipelago (conditionally accepted for publication in *Estuarine, Coastal and Shelf Science*)
II	**Isæus M.** A GIS-based wave exposure model calibrated and validated from vertical distribution of littoral lichens (manuscript)
III	**Isæus M.** Morphological variation of *Fucus vesiculosus* caused by wave action, or by factors correlated to waves? (manuscript)
IV	**Malm T. and Isæus M.** Effects of salinity and geomorphology on the structure of macroalgal communities in the central Baltic Sea (manuscript submitted to *Annales Botanici Fennici*)
V	**Isæus M., Malm, T., Persson S. and Svensson A.** Effects of filamentous algae and sediment on recruitment and survival of *Fucus vesiculosus* (Phaeophyceae) juveniles in the eutrophic Baltic Sea (accepted for publication in *European Journal of Phycology*)

Introduction

Physical conditions determine the potential distribution of all species is. Plants for example, depend on light for photosynthesis. Marine plant species will therefore only thrive in the upper part of the water column that is reached by sunlight, while animals are found at all depths. On a global scale, temperature is one of the main climatic factors influencing the distribution of both terrestrial and marine species. Species occurring at a site must first have dispersed or evolved there, and then managed to withstand the abiotic and biotic environment at the site. Within the range of physically potential habitats the species is constrained by life-history characters and interactions with other organisms.

Light and water movement are considered the most important physical factors influencing macroalgal distribution and density (Sheperd & Womersley 1981). Visual light is scattered and absorbed while penetrating the water column, both by plankton and other particles as well as by the water itself (Kirk 1994). The amount of plankton in the water varies over the year. The availability of light at the bottom, which is decreased by water turbidity and depth, is considered a major factor limiting depth distribution of submersed plants (Chambers & Kalff 1985, Kiirikki 1996, Schwarz et al. 2002).

Hard substratum is a scarce resource in the marine sublittoral zone. Both sessile animals and algae compete for rock, stone or other hard surfaces. The hard surfaces may be covered by sediment, i.e. gravel, sand or finer mineral or organic particles, that may block the hard surface from colonization (Eriksson & Johansson 2003). Vascular plants lower the resuspension of sediment by their structure and inhibit erosion of sandy bottoms (Scoffin 1970, Duarte 2000), and macroalgal turfs may accumulate sediment on hard substrata by decreasing resuspension (Kendrick 1991). The interaction between plants and sediment may therefore have significant effect on the distribution of sessile algae and animals.

Effects of waves on macroalgae are both direct and indirect. Water motion affects macroalgae directly by drag force (Koehl 1984), or by increasing gas exchange when water flow over the thallus surface (Hurd 2000). As a result, there is morphological variation in shore species between sites with different degree of wave exposure. For example, macroalgal fronds are often broader, more undulated, and thinner in sheltered areas compared to more elongated and thicker in exposed areas (Koehl & Alberte 1988, Gaylord et al. 1994, Friedland & Denny 1995, Blanchette et al. 2002). Wave action may indirectly affect macroalgae by turning boulders and thereby open patches for succession (Sousa 1979). Water motion may further be an effective vector for propagule dispersal (Reed et al. 1988). There are many examples of wave effects on macroalgal communities. Storms may form gaps in macroalgal canopies causing patches of secondary succession (Lubchenco & Menge 1978), or erase whole kelp forests (Seymour et al. 1988). The amount and species composition of epiphytes may vary between sites of different wave exposure (Rönnberg & Ruokolahti 1986). However, both macroalgae and herbivore species differ in their tolerance to wave action. Wave exposure affects therefore the shore community composition at more than one trophic level (Duggins et al. 2001, Schanz et al. 2002).

The concentration of bio-available nutrients (mainly nitrogen, phosphorous and carbon) in the water may affect macroalgal growth. The growth may be nutrient limited during part of the year, usually the summer period, and limited by light during winter (Gagné et al. 1982). Algal species respond differently to increased nutrient concentrations. Generally are phytoplankton and fast-growing macroalgae superior competitors under abundant nutrient supply over seagrasses and slow-growing macroalgae (Duarte 1995). Phytoplankton decreases the water transparency, which limiting the availability of light further down in the water column (Kirk 1994). Water chemistry parameters are sometimes correlated in coastal areas (Zoppini et al. 1995), which make it difficult to separate the effects of one factor on the biota from the other. In estuaries, salinity may be correlated with water transparency (Bowers et al. 2000), or wave exposure (Connell 1972). Apart from designing manipulative experiments to break correlations between explanatory variables, no technique exists that allows researchers to infer functional relationships between response variables and individual explanatory variables (Graham 2003).

The Baltic Sea is a brackish inland sea without significant tide, but with prolonged periods of high or low water mainly caused by atmospheric fluctuations (Ericson & Wallentinus 1979). The salinity has changed several times over the 9000 years since the last glaciation, from the Baltic Ice Lake, to the Yoldia Sea, to the Ancylus Lake, and via the Littorina Sea to the brackish Baltic Sea of today (Cato & Kjellin 1992). The present salinity decreases over a gradient from about 10 ‰ S at the Danish Straits to about 3‰ S in the northernmost Gulf of Bothnia (Winsor et al. 2001). The salinity of the Baltic Sea changes now as a consequence of river runoff and the freshwater budget (Winsor et al. 2001, 2003).

The recent, human-induced eutrophication of the Baltic Sea has increased the growth of annual filamentous algae and probably enhanced sedimentation (Cederwall & Elmgren 1990). Together these factors may have a detrimental effect on the survival of perennial macroalgal populations by blocking hard surfaces from colonization. Another consequence of eutrophication is decreased water transparency due to increased plankton growth. Water transparency is often measured as the Secchi-depth, the distance at which a white disc can be seen when submersed. Secchi-depth has been described as a function of total nitrogen concentration (r^2=0.89) and total phosphorous concentration (r^2=0.51) for Himmerfjärden, south of Stockholm archipelago, Sweden (Elmgren & Larsson 2001). The decreased water transparency has been suggested as a reason for the upward movement of *F. vesiculosus* vertical distribution in the Baltic Sea between 1943/44 and 1984 (Kautsky et al. 1986), a trend that may have stopped during the last years (Eriksson et al. 1998, Kautsky 2001).

The largest archipelagos of the world are found in the Baltic Sea. The complex coastline of an archipelago is extremely long, and contains a great variety of littoral habitats due to variation of wave exposure, substrate and water chemistry. At an open coast the heterogeneity of water properties, i.e. wave exposure levels and usually seafloor substrate, are much lower compared than in archipelagos. Examples of Baltic open coasts are the extended sand beaches of the Gulf of Riga and Poland, and the rocky coasts of the large islands Gotland and Öland.

Bladderwrack *F. vesiculosus* and toothed wrack *F. serratus* are the only large perennial belt-forming brown alga in the Baltic Sea (Waern 1952, Kautsky et al. 1992). Their geographical distribution is limited by salinity in the brackish Baltic Sea. *Fucus vesiculosus* is the most tolerant species inhabiting areas as north as the Järnäs udde (63.5°N, ≥ 4 ‰ S) (Kautsky 1989), while *F. serratus* is found only south of Gryt (58°N, ≥ 7 ‰ S) (Malm 1999).

Fucus vesiculosus is a perennial and dioecious brown algae that is found submerged at 0.5 – 8 m depth in the Stockholm archipelago where the study for Paper I was made, but mainly belt-forming shallower than 6 m of depth where it is the dominating macroalgae in terms of biomass (Wallentinus 1979). It is highly variable in shape with taller plants with broader, vesiculated fronds found in sheltered areas compared to more exposed sites (Knight & Parke 1951, Bäck 1993). Skult (1977) identified 44 phytal macrofauna taxa in the *F. vesiculosus* belts outside Helsinki, and it is considered the most diverse community in the northern Baltic Proper (Wallentinus 1979), which is relatively species-poor due to its brackish water (Kautsky 1989, Lüning 1990, Kautsky et al. 1992).

Fucus serratus is also dioecious and has been much less studied in the Baltic Sea than *F. vesiculosus*. It is found mixed with *F. vesiculosus* at 1 – 2 m, but dominates at rocky bottoms deeper than 2 m where both fucoids coexist. The record of the deepest *F. serratus* found in the Baltic are from 14-15 m depth in Kalmarsund (Du Rietz 1945 in (Waern 1952)). Off the east coast of Öland, where the study site of Paper V was located, it is found in small patches or larger stands from 3.5 to 10 m depth (Malm 1999).

Both these dioecious fucoids have two reproductive periods in the Baltic Sea, whereas North Atlantic populations have only one. *Fucus vesiculosus* is releasing its gametes during May – July and September – November in the Baltic and in spring – summer in the North Atlantic (Knight & Parke 1951, Bäck 1993, Berger et al. 2001). *Fucus serratus* is releasing its gametes during June – July and October – November in the Baltic in contrast to the oceanic costs where it is reproductive from autumn to spring with one maximum in September and one in March (reviewed by (Malm et al. 2001)).

Geographic Information systems (GIS) and overlay analysis have been used for describing or predicting distributions of several marine organisms, e.g. mussels (Brinkman et al. 2002), *Zostera marina* L. (Ferguson & Korfmacher 1997), *Ulva rigida* (Runca et al. 1996), *Laminaria hyperborea* (Bekkby et al. 2002) and *Macrocystis pyrifera* (Deysher 1993, Bushing 2000), although there appears to be no studies of fucoids yet. Physical factors have been used to assess the limits of species distributions, or remote sensing for mapping distributions or habitats. In this thesis, mapped or simulated physical factors have been used to predict the distribution of *F. vesiculosus* in Stockholm archipelago in the Baltic Sea. To be able to use structuring factors for GIS modelling of species distributions the factors must be represented in a map format. The factors may for example be digitalized from aerial photographs, mapped by interpolation between locations where the factor has been measured, or modelled from other map layers. The quality of the input data is crucial for the model performance. Nautical charts are most often used as depth source as well as source for calculation of slope. Fetch-models are often used to estimate wave exposure since wind blowing over a water surface builds up waves in the wind direction, the larger fetch the larger waves. In models of coastal areas the fetch may be restricted by a maximum value, or a model based on openness, (e.g. (Baardseth 1970), may be used.

Objectives

This thesis deals with physical factors and biological interactions that affect the distribution of two fucoid species, *Fucus vesiculosus* L. and *Fucus serratus* L., in the Baltic Sea. The objectives were to:

- assess the factors most useful for modelling the distribution of *F. vesiculosus* in an archipelago area, and to predict the *F. vesiculosus* distribution in the Ornö parish located in the southern part of Stockholm archipelago using these factors in a Geographic Information System (GIS). (Paper I)

- develop and validate a method to map wave exposure in an ecologically relevant way, thereby producing a tool for basic research and coastal management. (Paper II)

- improve the *F. vesiculosus* distribution model of Paper I by using the method for wave exposure mapping of Paper II

- (a) examine if there are correlations between wave exposure and water property parameters in Stockholm archipelago, (b) study morphological variation of *F. vesiculosus* at sites over a gradient of wave exposure in the Stockholm southern archipelago, and (c) try to separate effects of wave exposure on *F. vesiculosus* morphology from effects caused by water property parameters. (Paper III)

- examine the dominant epiphytes on *F. vesiculosus* over a wave exposure gradient in Stockholm southern archipelago

- (a) estimate the abundance of *F.vesiculosus*, *F.serratus* and filamentous algae in the central Baltic Sea, an area that so far have been poorly investigated. (b) test the hypothesis that salinity (i.e., north-south gradient) and geomorphology are important factors determinants for the vegetation structure on a regional scale. (Paper IV)

- assess the factors that determine the distribution of submerged *F. serratus* at the local level off an open coast along the central Baltic Sea. Specifically we wanted to study the role of turf-forming algae and sediment in interacting with *F. serratus* colonisation. (Paper V)

Methods

Fucus vesiculosus distribution in a Baltic Sea archipelago (Paper I)

Structuring factors for the distribution of *F. vesiculosus* was studied in Ornö parish in southern Stockholm archipelago (Fig 1). A diving inventory including 30 transects was performed. Depth, dominating substrate, amount of silt, and species abundances (as percent cover) were recorded along the transects reaching from the surface to the lower boundary of vegetation. All healthy looking *F. vesiculosus* were recorded, attached as well as detached. At each diving site Secchi-depth, and the position and direction of the transect were recorded. Wave exposure calculations from a previous study were used (Lindblad et al. 1999). The wave exposure grid, which had been calculated from fetch and wind data, was manually manipulated to achieve effects

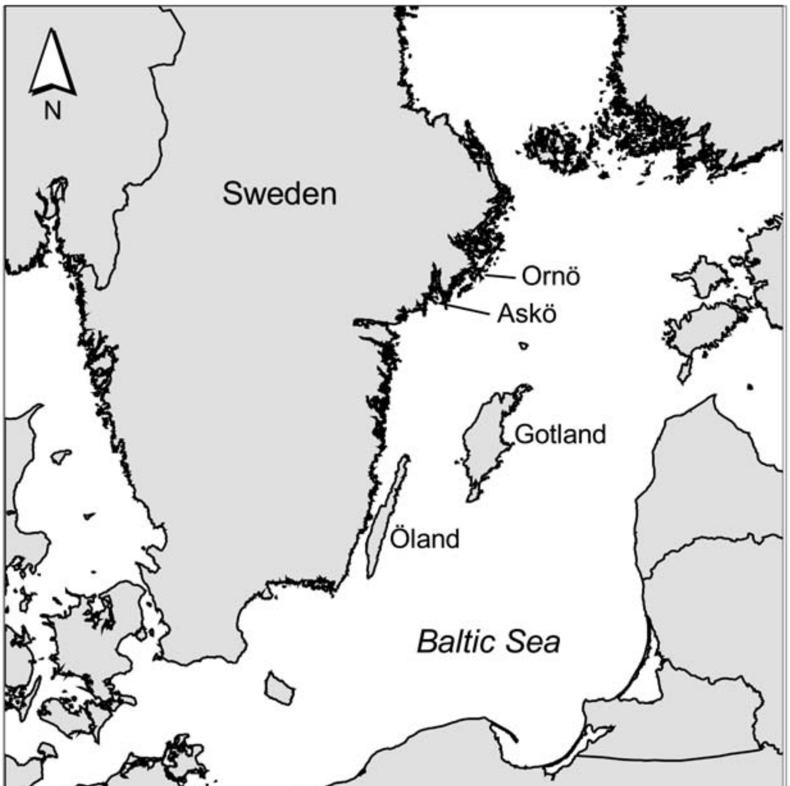

Figure 1. The study areas location in the Baltic Sea.

resembling refraction and diffraction patterns that were not included in the original study.

A GIS-based wave exposure model (Paper II)

Since wave exposure was considered such an important factor (Paper I), an improved method for calculating wave exposure including refraction and diffraction effects was developed in a new study. First, a biological wave exposure index was constructed, which was considered a measure of the true wave exposure. The biological index was based on vertical distributions of lichen growing epilithically on the shore, which was surveyed in the Askö and Lacka area in southern Stockholm archipelago (Fig. 1). This lichen zonation is generally considered affected by the wave regime (Du Rietz 1925, Lewis 1964, Johannesson 1989), although the patterns of zonation has not been quantitatively described in the study area. The biological index was derived from the upper and/or lower distribution boundary of three lichen species by using PC 1 values of a principal component analysis (PCA). Then a fetch model was constructed in GIS and calibrated by the biological index. A new software, WaveImpact 1.0, was developed to manage the grid calculations. Refraction/diffraction effects were included and coarsely calibrated by using aerial photographs of waves turning around islands. Different sets of wind data from a nearby meteorological station was combined with fetch values in order to find the formula that best correlated the fetch model values with the biological index. The fetch model was then validated in a new area using an equally derived biological index.

Improvement of the *F. vesiculosus* distribution model

The *F. vesiculosus* distribution model from (Paper I) was run again with the new wave exposure model (Paper II). Due to a slight mismatch between the grids of the old study (Paper I) and the new wave exposure grid the number of data points (n) decreased from 1272 to 1238.

Effects of wave exposure on *F. vesiculosus* morphology (Paper III)

A study was designed to separate effects of wave exposure on *F. vesiculosus* morphology from effects of water property variables. Initially possible correlations between wave exposure and water property variables were examined by comparing 173 water property measurements from the SUCOZOMA project covering the whole Stockholm archipelago to a wave exposure grid (as in Paper II but with 100 m cell size). Then nine islands in the Askö area in Stockholm southern archipelago (Fig. 1) were chosen for the *F. vesiculosus* inventory. The islands had to fulfil two criteria: free water circulating around them, and one side more exposed to the sea than the other. The salinity, Secchi-depth and temperature were measured at four sides of each island to make sure the water body surrounding each island was homogenous. Along the shore of each island *F. vesiculosus* specimens were sampled every 10-50 m. Six morphological characters that were expected to vary between sites of different wave exposure (Bäck 1993), were measured for each sampled specimen. The characters were; length, thallus width, stipe width, midrib width, distance between dichotomies, and number of vesicles. Wave exposure in the study area was calculated for each sampling site using the same method as in Paper II. The effects on the morphological characters were analysed in by using MANCOVA. An unblocked statistical design was used to examine the morphological variation over the wave exposure gradient. Another analysis was performed to separate effects of waves from effects of water property variation. In this analysis island was used as a blocking factor.

Epiphytes on *F. vesiculosus* over a wave exposure gradient

In a field study in the Askö area (Fig. 1) in July 1999 the epiphyte species on *F. vesiculosus* specimen were recorded at 16 sites over a wave exposure gradient (unpublished data). Wave exposure was calculated as in (Paper II). Epiphytes on the *F. vesiculosus* thallus were classified as absent to scarce (0), present (1), or dominating (2). Epiphyte abundances were treated as ordinal multinomial classes and analysed using a generalized linear model (GLZ) with logit as link function in Statistica 6.0. Likelihood type 3 significance tests were used. No effort was made to separate effects of waves from effects of correlated factors.

Fucus distribution at the Öland and Gotland coasts (Paper IV)

Extended inventories were performed at the east coasts of Öland and Gotland during 2001-03 (Fig. 1) in order to map the distributions of the fucoids and the environment in which they grow. Manta tow diving was used to be able to cover large distances, which included 110 km along the Öland coast at 7 m depth, and at 20 transects perpendicular to the shoreline (1-10 m depth) at Gotland. Using this technique the percent cover of *F. vesiculosus*, *F. serratus*, and turf-forming algae was surveyed, although it was not possible to detect individual turf algal species. The seafloor substrata were classified as sand, gravel, boulder or bedrock. Another survey at 2.5 m depth alongshore the southern and central Öland coast was also performed by using a small skiff with a plexiglass window in the hull. The same classifications of the vegetation and seafloor were used as in the manta tow diving inventory. Quantitative sampling was made at three sites along the Öland coast, and at four sites along Gotland coast, using five 20x20 cm frames at each site. The relative frequency of small *F. serratus* fronds in stands at northern Öland was compared to stands of southern Öland. Both island coasts were divided into three regions (north, central and south) for analysis of geographical differences.

Factors affecting the small-scale distribution at the Öland coast (Paper V)

The recruitment success of *F. serratus* was studied at a small scale at 7 m depth on the flat limestone bedrocks on the east coast of Öland, central Baltic Sea (Fig. 1). At this site extended fucoid stands occur constantly submerged at 3.5 - 10 m depth, surrounded by turf forming filamentous algae, mainly *Polysiphonia fucoides*. The density of juvenile *F. serratus* thalli (< 10 cm) and the amounts of filamentous algae and sediment were examined in the *F. serratus* patches and the surrounding filamentous turf. As a complement to the field studies, laboratory experiments were used. The ability of eggs and zygotes to settle and attach in sediment, filamentous algae or empty petri dishes was tested in the laboratory. The ability of the *F. serratus* recruits to survive under a cover of sediment, filamentous algae or without cover was also tested.

Results and discussion

Öland and Gotland macroalgal communities

The southern region of Öland had an open coast dominated by limestone bedrock, the central region had open coast dominated by moraine deposits and in north there were a relatively broken coast with sandy moraine deposits (Paper IV). The Gotland regions were geomorphologically more similar. Turf algae dominated at both islands, and the dominating species at 5 m depth was *Polysiphonia fucoides* (Huds.) Grev. everywhere except at northern Gotland where *Furcellaria lumbricalis* (Huds.) J.V.Lamour. dominated. Fucoids were sparsely distributed at the Gotland coast. *Fucus vesiculosus* was only stand-forming (>25% coverage) at shallow sites in the central region (0-2 m) and the southern region (0-6 m), but never in the northern region. *F. serratus* where found only at the most southern transect of Gotland where extended stands occurred. Fucoids were not significantly more common on boulders or bedrock on Gotland. *Fucus vesiculosus* was occasionally found in most 7 m transects of Öland, but no stands (>25% coverage) occurred. Both fucoids were equally abundant at 2.5 m depth, although *F. serratus* was more abundant on limestone bedrock.

Salinity

The salinity in the water surrounding Öland and Gotland is today on average 7.1-7.3 psu which should be sufficient for recruitment of both *Fucus* species. However, the salinity in the Baltic changes over time making species living on their salinity-tolerance limit vulnerable. During the last century the mean salinity of the Baltic Sea has fluctuated with about 1 ‰ (Winsor et al. 2001, 2003) which should be enough variation for moving the spatial distribution limits of Baltic species. The critical limit for *F. serratus* recruitment is 7 psu (Malm et al. 2001) and the boundary of successful recruitment may have moved over the area as a consequence of changes in the Baltic salinity gradient. Around 1980 the mean salinity of the Baltic Sea was about 8.2 psu. After that the salinity decreased steeply to 7.3 psu 1995 (Winsor et al. 2001, 2003), a decrease that happened during the same period as cast walls of filamentous red algae became an apparent problem along the east coast of Öland (Paper IV). The observed pattern with less *F. serratus* in the north may be caused by the condition after the latest decline 1980-95, or due to a time-lag from repeatedly limited recruitment ability in the past. The northbound dispersal-rate of *F. serratus* is probably low since *F. serratus* is a poor long-range disperser (Arrontes 2002), and the currents along the Öland east coast are mainly southbound. Perhaps lower recruitment still is the mechanism behind the significantly lower proportion of small individuals in the northern Öland *F. serratus* population compared to the southern populations.

Salinity is generally considered a major limiting factor for species large scale distribution in the brackish Baltic Sea (Kautsky & Kautsky 1989). Serrão et al. (1996a) concluded that the present range of *F. vesiculosus* distribution in the Baltic appeared to correspond with the osmotic tolerance of its gametes. Climatic factors, such as insolation and ice cover duration, covary with salinity along the north-south gradient of the Baltic Sea, making also other factors possibly limiting for macroalgal distribution. However, both *F. vesiculosus* and *F. serratus* occur event further north in the Atlantic Ocean (Lüning 1990), making declining salinity the most probable delimiting factor for the fucoids at a large scale.

In the Ornö area (Paper I), in Stockholm archipelago, salinity normally exceeds 4 ‰ (Lindblad et al. 1999) and should not affect the *F. vesiculosus* distribution. However, there are some semi-enclosed bays in the area, which have low water exchange with the surrounding water and where the salinity may be lower and nutrient concentrations high due to land run-off and accumulation of organic matter. These bays have often completely different benthic vegetation (Munsterhjelm 1997), and are a source of error in the GIS model (Paper I). In the inner part of Stockholm archipelago, the water is less saline due to the outflow from Lake Mälaren. During an inventory along this gradient *F. vesiculosus* was found at a salinity of about 5 psu and higher (Lindblad & Kautsky 1996). The water passing through central Stockholm and entering the archipelago is also polluted by oil, copper and other toxicants that may negatively affect *F. vesiculosus*, so there are other possible explanations to the distribution pattern. However, even though several other factors are correlated, salinity seems to affect the distributions of aquatic organisms at several spatial scales.

Water transparency and sediment

Secchi-depth, a measure of the water transparency to light, has been shown to set the maximum depth of submersed plants (Chambers & Kalff 1985), and available light has generally been considered one of the main factors limiting depth distribution of

F. vesiculosus in the Baltic (Waern 1952, Wallentinus 1979, Kautsky et al. 1986, Kautsky & van der Maarel 1990, Bäck & Ruuskanen 2000). Bäck and Ruuskanen (2000) concluded that light determined the maximum distribution of *F. vesiculosus* in the Gulf of Finland in the Baltic Sea. However, in the same study it was also described that the maximum depth for the *F. vesiculosus* distribution was shallower at moderately exposed sites than at exposed sites due to lack of suitable hard substrates, which is accordance with our results. In our study, the maximum depth distribution of *F. vesiculosus* at each diving transect was more clearly correlated to wave exposure than Secchi-depth (Paper I), which was explained by resuspension of silt due to water motion, and accordingly correlated estimated silt abundance negatively to wave exposure (Paper I). This result is in accordance with what Kiirikki (1996) suggested for the northern Baltic Sea, i.e. that wave exposure clears the substrate from sediment that otherwise could limit the depth distribution of *F. vesiculosus.*

Silt or other sediment blocks the hard substrate and lower the attachment success of *Fucus* eggs and zygotes, and decreases the survival by burying the *Fucus* recruits. In laboratory experiments these effects have been shown for *F. vesiculosus* (Berger et al. 2003), and for *F. serratus* (Paper V). In a 4.5 year long field study sediment was shown to significantly decrease the recruitment success of *F. vesiculosus* in the northern Baltic proper (Eriksson & Johansson 2003). Many diving sites in Ornö area (Paper I) were located in sheltered areas where silt was present at relatively shallow bottoms due to the low wave exposure. The depth distribution of *F. vesiculosus* thus seems to be limited by sediment at sheltered sites, and by available light at exposed sites. This pattern was also seen during the improvement of the GIS model (GIS-modelling section below), where a threshold effect appeared at a certain level of wave exposure, at which the depth distribution did not increase further.

The lower end of the vertical distribution of *F. vesiculosus* has moved upward since 1940's (Kautsky et al. 1986, Eriksson et al. 1998), which has generally been considered an effect of factors related to eutrophication, such as decreased water transparency and increased sedimentation (Kangas et al. 1982, Kautsky et al. 1986, Eriksson et al. 1998). Kautsky et al. (1986) concluded that no physical factor other than light was likely to have caused the decrease of the depth distribution of *F. vesiculosus*. The stations in that study were located in Öregrund archipelago Åland Sea, and were all classified as exposed, or very exposed to wave action. It is likely that silt and sediment are swept away by waves at such shores and therefore not limit the depth penetration (Kautsky et al. 1986). In Paper I the full range of wave exposure in the Baltic was investigated, from sheltered sites to the most exposed, and the depth penetration of *F. vesiculosus* was considered an effect of silt removal caused by the level of wave exposure. If a decrease of the depth penetration of *F. vesiculosus* as an effect of eutrophication has occurred in the Ornö area it is likely that this is a result of the increased siltation, except at exposed sites where light may be the limiting factor. From one study at southern Bothnian Sea (Eriksson et al. 1998), and the ongoing monitoring in southern Stockholm archipelago, northern Baltic Sea proper, it has been reported that the decrease of *F. vesiculosus* depth penetration has stopped during the last decade (Kautsky 2001). The sites in Bothnian Sea are exposed or very exposed (Eriksson et al. 1998) and the exposed monitoring sites shows a trend towards deeper vertical distribution. A possible trend of the more sheltered monitoring sites is not as apparent.

At the open east coasts of Öland and Gotland soft sediment bottoms rarely occur shallower than 10 m depth, although decaying algae sometimes accumulate close to the shore. Fine sediment is found mainly in macroalgal turfs (Paper V) where resuspension is lower (Kendrick 1991). The turfs, which mainly consist of filamentous algae, thus have a key function in blocking hard substrate from colonisation, both the algae themselves and by their ability to accumulate sediment. Both the occurrence of filamentous algae and sedimentation is seems to have increased as a consequence of the eutrophication of the Baltic Sea (Cederwall & Elmgren 1990, Schramm 1996). These factors in combination are likely to be important for explaining the decline of *F. vesiculosus*, and perhaps also *F. serratus*, during the same period.

Slope

The slope of the seafloor had a significant effect on the maximum cover of *F. vesiculosus* (Paper I). At flat or gently sloping substrates, dense as well as sparse *F. vesiculosus* stands were found, but at increasingly steeper substrates the maximum cover decreased. No *F. vesiculosus* was found at sites steeper than 38°. Slope is a scale dependent phenomenon and the effects of slope on the macroalgae may therefore be a result of how slope was measured. In Paper I the contribution of slope to the model performance was not decreased by using a coarser resolution (a 10 m grid) compared to the meter-by-meter dive inventory. Actually the performance was improved a little. The effects of slope on the macroalgal occurrence may therefore be explained by either small-scale or large-scale processes. At the small-scale the effect may be on the settling of eggs and zygotes that may easier roll off a steep than a flat substrate unless they attach to the substrate immediately. The settling ability is also dependent on water movement, and it has been shown that *F. vesiculosus* eggs are released mainly during calm conditions (Serrão et al. 1996b). We observed that blue mussel *Mytilus edulis* L. often covered steep hard surfaces. The mussel may be better adapted to these habitats and outcompete *F. vesiculosus*, which partly would explain the pattern. Shading has suggested to be the major effect of slope (Sheperd & Womersley 1981). Shading may be an effect of topography and thereby a large-scale phenomenon, but smaller objects can also shade the surface. At the flat seafloors out of Öland and Gotland east coasts (Paper IV and V) slopes caused by topography hardly occur at all. Effects of slope on macroalgae have therefore not been examined at open coasts.

Substrate stability and wave action

Both *F. vesiculosus* and *F. serratus* need to attach to a hard substrate free from sediment during recruitment (Paper I, (Berger et al. 2003, Eriksson & Johansson 2003). This substrate may be rock, stones, mussel shells or holdfasts of larger plants as long as they are stable enough to resist the prevailing wave action. When safely attached to the substrate the plant starts to grow and increase its planform area, which is considered the most important morphological character influencing the drag force from waves (Carrington 1990). If the substrate is less stable, such as a small stone or mussel shell, the plant may eventually reach the critical size when the drag force exceeds gravity and the plant will be moved together with its substrate as suggested by (Malm 1999). In Stockholm archipelago moraine remnants often form the shoreline at sheltered sites and for *F. vesiculosus* plants attached to those moraine stones this is a likely scenario. The plants that are moved to deeper places further off the shore are likely to stay there since the orbital water movements caused by waves decreases with depth (Brown et al. 1999). If this place is above the light compensation point they will continue growing and possibly reach the critical size for transportation again. Since *F. vesiculosus* has bladders, at least at sheltered sites during the vegetative period (Kiirikki & Ruuskanen 1996), its fronds are uplifted and sensible to water movements. During the late phase of reproduction, *F. vesiculosus* receptacles become swollen and gas-filled, erects the plant even more and lower its density. This further increase the effects of waves due to the uplifting force of the receptacles. A similar transport mechanism has been recorded for another macroalgae, *Colpomenia peregrina* "Oyster thief", which attaches to oysters, mussels and stones. It has a globose thalli that becomes air-filled and accordingly buoyant, and floats away with the attached oyster (Farnham 1980). The transportation mechanism described above may move the *F. vesiculosus* plants together with their substrata from shallow waters to the deeper soft bottoms that often are only a few meters away in sheltered areas. At more exposed sites the fronds may be ripped off by breakage of the stipe, or the substrate may break resulting in a loose plant with its holdfasts attached to a rock fragment (Malm 1999). These plants may then drift ashore, or end up at a shallow soft or hard bottom where they may stay healthy (Waern 1952, Wallentinus 1979), or sink to deep bottoms with insufficient light where they will slowly decay. Fucoids attached to limestone fragments are often found at the beaches of Öland and Gotland. In Paper I, *F. vesiculosus* plants were found on all substrates in the Ornö area, and significantly more on sand than on rocky or soft bottoms. However, scattered stones or other hard secondary substrates were not recorded in the survey, only the dominating substrate and boulders. Thus effects of substrate type in this study should not be interpreted occurring at a small scale (Paper I). Healthy detached plants were also included in the inventory.

In Paper IV on the other hand, substrate was inventoried as coverage classes (%) and their association with fucoids and turf-forming algae was possible to examine. In accordance with (Sousa 1979), the stability of the substrate affected the distribution of fucoids and turf-forming algae at the studied coastal regions of Öland and Gotland. Fucoids were found only at stones larger than 20 cm or on bedrock, while algal turf was abundant on all substrates except sand. *Fucus serratus* is rarely found shallower than 2 m depths in the Baltic Sea and almost exclusively growing attached to large boulders or on bedrock (Paper IV, (Malm 1999). The species may therefore seldom be transported together with its hard substrate as described for *F. vesiculosus*. *Fucus serratus* was more abundant at bedrock than on boulders which may be another sign of the preference for stable substratum. However, it may also indicate preference for the more porous limestone bedrock compared to mainly crystalline boulders, similar to the preference of *F. vesiculosus* for porous sandstone at exposed sites (Malm et al. 2003). At shallow sites, where wave action is even more evident, *F. vesiculosus* is more abundant on boulders than bedrock, and *F. serratus* more abundant on bedrock than boulders. This may be a result of *F. serratus* outcompeting *F. vesiculosus* on bedrock, which has been observed in Spain (Arrontes 2002). *Fucus vesiculosus* may, on the other hand, be better adapted to more exposed positions, or less stable substratum, by its ability to regenerate from holdfasts, which is an ability that *F. serratus* lacks (Malm

& Kautsky 2003). The fucoids probably compete with the turf-forming algae for substrate, a process that is further described and discussed below (Paper V).

The upper boundary of *F. vesiculosus* distribution is often described as an effect of desiccation, ice scraping and fluctuating water level (Waern 1952, Kiirikki 1996). *Fucus vesiculosus* was not present close to the surface at the most exposed sitesof the Ornö archipelago, although it was found deeper down (Paper I). This pattern was interpreted as an effect of wave exposure, or scraping of ice floes that is more intense at wave exposed sites. The effect was not linearly correlated to wave exposure, rather it resembled a threshold effect.

Fucus vesiculosus morphology

The morphology of *F. vesiculosus* changes over a wave exposure gradient (Paper III). The results of the analysis using an unblocked design resembled those of earlier studies (Bäck 1993, Kalvas & Kautsky 1993). Length, thallus width, distance and number of vesicles were negatively correlated to wave exposure. This analysis examined among as well as within island variation, and did not control for differences in water property between islands. In contrast, analysis using island as a blocking factor, thus controlling for differences in water properties, suggested that only thallus width was significantly negatively affected by wave exposure. However, when the design was blocked to control for differences in water properties between islands, the variation of wave exposure between islands were also neglected. It can thus not be ruled out that length, number of vesicles and distance between dichotomies also respond to wave action. If other parameters that potentially could affect *F. vesiculosus* morphology (nutrient concentrations, salinity, water transparency etc.) are measured at each sampling site, there are statistical methods for analysing the parameters contribution to the effects on the responding variable, although true casual relationships can only be examined by manipulative experiments (Graham 2003).

Epiphytes on *F. vesiculosus*

The composition of epiphytic macroalgae growing on *F. vesiculosus* changed over the wave exposure gradient in the Askö area. There was a significant negative wave effect on *Chorda filum* (L.) Stackh. (χ^2=8.32, p=0.004) and positive effect on *Elachista fucicola* (Velley) Aresch. (χ^2=6.80, p=0.009) (Fig. 2). *Chorda filum* was regularly occurring epilithically although it also grew attached to *F. vesiculosus* holdfasts or basal parts at sheltered sites and was then considered an epiphyte. *Elachista fucicola* has basal cells that penetrates into the *F. vesiculosus* cortex, and firmly attaches it to the basiphyte (Rönnberg & Ruokolahti 1986). Furthermore it has short, unbranched filaments which should cause little drag force due to wave action. Wærn (1952) used the occurrence of epiphytic growth of *E. fucicola* on *F. vesiculosus* as an indicator of an ecological district of the Öregrund archipelago he named the Elachistea district. Öregrund archipelago is located on the boarder between Åland Sea to the east, and Gulf of Bothnia to the west and north. The eastern part of Öregrund archipelago was defined as the Elachistea district, which shares much of the same species as Åland Sea, however it is also the most exposed part of the archipelago. Other authors have reported *E. fucicola* epiphytic growth from the whole wave exposure gradient, although with a higher coverage at more exposed sites (Wallentinus 1979, Rönnberg & Ruokolahti 1986), which resembles my results. However, the epiphytic species vary over the season and (Rönnberg & Ruokolahti 1986) monitoring over a year cycle found *E. fucicola* to be the dominant epiphyte at both a sheltered and an exposed site in Åland Sea.

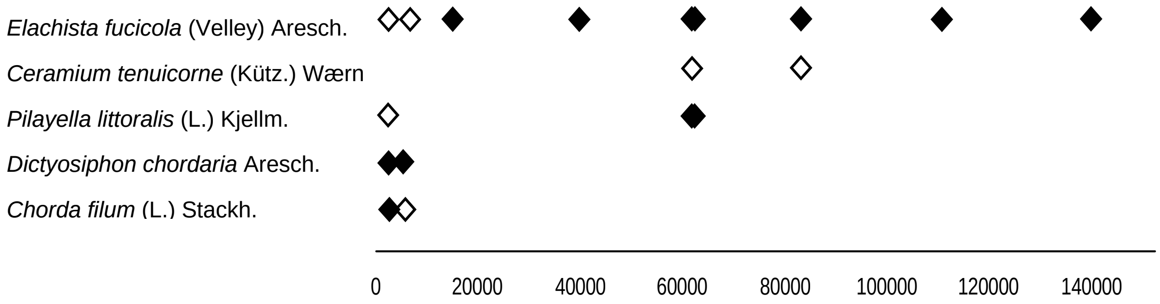

Figure 2. Epiphytes on *F. vesiculosus* over a wave exposure gradient in the Askö area, NW Baltic Sea. ◇= present, ◆ = dominant. Wave exposure in m^2s^{-1}.

Grazers may be swept away by waves, giving an indirect positive wave exposure effect on the amounts of epiphytes (Schanz et al. 2002). However, there are generally smaller amounts of epiphytes at exposed sites compared to sheltered sites in the Askö area, contrary to what could be expected from such effect. In analogy with the discussion above (Paper III) effects from factors correlated to wave exposure may affect the epiphyte composition, and such effects have not been controlled for in this study, which should be considered when interpreting the results.

Effects of turf-forming algae and sediment

Very few *F. serratus* juveniles were observed outside the sweeping radius of the adult *F. serratus* individuals, while abundant juveniles were found inside the *F. serratus* stands at 7 m depth off the Öland coast (Paper V). The amount of filamentous algae and fine (<0.25 mm) sediment were significantly larger outside the *F. serratus* stands than inside. Fine sediment was correlated with the biomass of filamentous algae, which suggests that sediment accumulates in the algal turf as described by Kendrick (1991). The fine sediment has low settling velocity (Agrawal & Pottsmith 2000), and is easily resuspended by wave action when not sheltered by a structure. The laboratory experiments showed that both filamentous algae and sediment negatively affect the settling ability of *F. serratus* eggs and zygotes and the following survival of recruits. The negative effect of filamentous algae on survival of the recruits may be interpreted as resulting from shading. Sediment was shown to both inhibit recruitment and reduce survival even more than the filamentous algal treatment. Similar effects of sediment have also been shown for *Macrocystis pyrifera* (Devinny & Volse 1978) and for *F. vesiculosus* (Berger et al. 2003). (Chapman & Fletcher 2002) concluded from laboratory experiments that light deprivation due to sediment cover was not responsible for the observed effect on *F. serratus* embryo survival, and suggested that the slow rate of diffusion resulting from compact sediment layer causes waste products to accumulate around *F. serratus* embryos resulting in high death rates.

The amounts of filamentous algae and sediment covering the seafloor during the periods of gamete release in summer and late autumn should be of great importance for its colonisation ability. The annual dynamics of filamentous algae are rather species-specific even though some general patterns occur (Kiirikki & Lehvo 1997). Preliminary data on biomass of filamentous algae from the study area (Malm, unpublished data) indicate increasing biomass during the summer, peaking in August, and followed by a decrease. In the study area, the storms in the autumn often rip off and deposit large amounts of filamentous alga at the beaches (Engkvist et al. 2001). The storm frequency is therefore important for regulating the filamentous biomass during the autumn. There are no data on how the amount of sediment on the bottom in the study area changes over the year. However, there are data on the sedimentation rate of the Baltic proper, which varies over the year with high settling rates of primary organic matter in spring, low sedimentation rates during the summer and considerable increase of resuspension in October-November (Heiskanen & Tallberg 1999). The resuspension is of great importance and represents often over 50 % of the sediment caught in sediment traps (Blomqvist & Larsson 1994).

The periods of gamete release of *F. serratus* in the Baltic Proper is May - July and October – November (Malm 1999), although autumn reproduction is more common. Summer reproducing *F. serratus* has only been found on southern Öland and on Sturkö in Blekinge (Malm 1999). Over these two periods the amount of both filamentous algae and sediment change. In May-July, the sedimentation is high and sediment should accumulate in the growing filamentous turf. In the autumn the amounts of both filamentous algae and sediment are potentially high but, as suggested above, this might be altered by storm events. It is speculative to compare the ability of *F. serratus* to colonise outside its patches during these two periods since it seems very much to depend on weather conditions. However, an early and warm summer may result in a dense cover of filamentous algae during the summer reproduction period, which should be detrimental for *F. serratus*. During the autumn there may be large amounts of filamentous algae and other of semi-decayed organic matter from the summer production. Dependent on storms and currents the turf may be less affected, or ripped off and washed ashore. Annual algae may form drifting mats beneath which there may be oxygen deficiency (Bonsdorff 1992). A stormy autumn may therefore be beneficial for *F. serratus* recruitment, although it may also rip off many adult *Fucus* specimens. (Berger et al. 2001) discussed the two reproductive strategies for *F. vesiculosus*, that also has two reproduction periods in the Baltic Sea. They suggested that recruitment from summer reproducing *F. vesiculosus* is negatively affected by large amounts of filamentous alga, and that from autumn reproducing plants by sedimentation. The sedimentation caught in sediment traps was high in autumn compared to summer in this study, which was explained by resuspension. However the amount of sediment on the seafloor or in the filamentous turf was not measured. In comparison, waves should have a larger direct effect on the *F. vesiculosus* stands than on *F. serratus* since *F. vesiculosus* grows at shallower sites.

Predictive GIS models

The GIS model (Paper I) was constructed from the abiotic factors that were considered most appropriate for describing the *F. vesiculosus* distribution due to the statistical analysis, and for technical reasons. Multicollinearity is not a problem for predictive models as long as the relevant predictors are included (Graham 2003) since it is the predictive power that is in focus, rather than the question of causality. Factors of unknown relevance may also be included if they improve the models performance, although that makes the model less general.

In the development of a method for estimating wave exposure (Paper II) the mean of

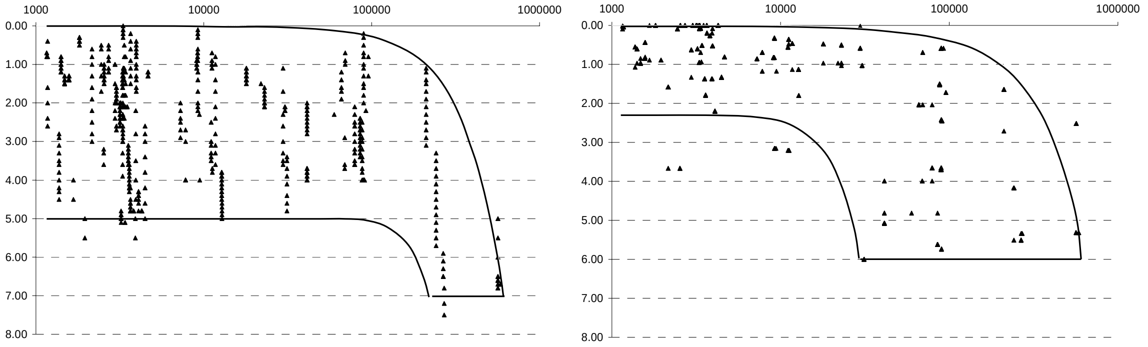

Figure 3. Depth distribution of *F. vesiculosus* over the wave exposure gradient (x-axis) enclosed by the limitations used in the GIS model. Depth values from the diving inventory (left) and from elevation grid (right). Wave exposure in m^2s^{-1}.

16 fetch directions magnified by the mean wind of the corresponding directions was the measure that best correlated to the biological index ($r=0.854$, $n=43$). The two indices correlated well in the validation area too ($r=0.839$, $p<0.001$, $n=34$), and also in the two areas together ($r=0.851$, $p<0.001$, $n=77$). The wave exposure model (Paper II) has been used in three studies on benthic vegetation in shallow inlets in Stockholm archipelago (Sundblad 2003, Eriksson et al. submitted manuscript, Sandström et al. submitted manuscript), as well as in Paper III. To improve the F. vesiculosus model of Paper I, the model was run again using the new fetch-model of Paper II. With the new fetch model a new pattern appeared where the lower vertical distribution seemed to be affected by wave action up to a threshold, where a maximum depth distribution seemed to be reached. The pattern was clearer when the model was run with grid values compared to measured depth data (Fig. 3). The formulae used to describe the occurrence of *F. vesiculosus* in this new setting were:

Measured depth values

Upper limit $\text{Depth} = (\text{Wave Exposure} / 280\,000)^{2.2}$

Lower limit $\text{Depth} = 4.8 + (\text{Wave Exposure} / 19\,000$

At Wave exposure > 225 000; Depth = 7

Depth values from grid
Upper limit Depth = (Wave Exposure / 200 000)$^{1.5}$
Lower limit Depth = 2.3 + (Wave Exposure / 19 000)$^{2.8}$
At Wave exposure > 30 000; Depth = 6

The formulae used to describe the occurrence of *F. vesiculosus* belt (25-100% cover) in this new setting were:

Measured depth values
Upper limit Depth = (Wave Exposure / 280 000)$^{2.2}$
Lower limit Depth = 5 + (Wave Exposure / 19 000)^{5}

At Wave exposure > 225 000; Depth = 7
Depth values from grid
Upper limit Depth = (Wave Exposure / 200 000)$^{1.5}$
Lower limit Depth = 1.6 + (Wave Exposure / 170 000)$^{2.8}$
At Wave exposure > 30 000; Depth = 6

The model performance slightly improved compared to Paper I. The performance is measured in three ways (type 1-3 in table 2) that should not be interpreted individually since they depend on each other. Type 1 describes how much of the selected area that really had *F. vesiculosus* or *F. vesiculosus* belt. Type 2 describes how much of the area known to have *F. vesiculosus* or *F. vesiculosus* belt that were selected. Type 3 is considered the most important value in this study and describes how much of the inventoried area that were correctly classified as having *F. vesiculosus* (or *F. vesiculosus* belt) or not. With the new model 83% (82%) of the area was correctly classified as *F. vesiculosus* habitat when measured depth values were used, and 76% (71%) when grid data were used (Tab. 1) (results from Paper I within brackets).

The most apparent difference of the outcome of the two wave exposure estimates were that adjacent cells always had similar values in the old model due to the interpolation technique used. In the new wave exposure grid differences between two sides of a land point were sometimes large since the point may act as a wave breaker. These differences were more pronounced at a small scale.

Table 1.

Model performance measured as the ability to predict the occurrence of *F. vesiculosus* or *F. vesiculosus* belt (25 – 100 % cover). Values from Paper I within brackets. (all values as %) n=1238

	F. vesiculosus occurrence		*F. vesiculosus* belt occurrence	
	Measured values	Grid values	Measured values	Grid values
Type 1 *	79 (75)	68 (66)	22 (22)	26 (22)
Type 2 **	88 (94)	96 (83)	73 (94)	83 (83)
Type 3 ***	83 (82)	76 (71)	59 (52)	64 (52)

* How much of the selected area did really have *F. vesiculosus* or *F. vesiculosus* belt

** How much of the area known to have *F. vesiculosus* were selected or *F. vesiculosus* belt

*** How much of all inventoried area were correctly classified as having *F. vesiculosus* (or *F. vesiculosus* belt) or not

At exposed sites the lower vertical *F. vesiculosus* distribution was better explained by another factor than wave action, at least when grid values were used was this pattern apparent. This factor is most certainly availability of light. At sites where the hard substrates are swept clean by waves, light is suggested to be the limiting factor in the Baltic (Kiirikki 1996). The maximum depth value should then be a consequence of the Secchi-depth at highly exposed sites. Such exposed sites were found in the outer archipelago where the Secchi-depth was about 9 m during the field period in June 1998 (Paper I). There was also a highly exposed site closer to the mainland, where the Secchi-depth was 6 m, but unfortunately this site was too steep to be inhabited by any *F. vesiculosus*. A possible connection between maximum depth distribution and Secchi-depth at highly exposed sites could therefore not be examined. A larger set of inventory data from exposed sites is needed to find the relationship between *F. vesiculosus* depth distribution, wave exposure and Secchi-depth, and to test this hypothesis properly.

The incorporation of a constant maximum depth as a factor of the model increased the performance of the model, especially when grid values were used (table 2). The used limit was 7 m for measured depth values, which corresponded to 78% of the Secchi-depth 9 m at the most exposed sites (6 m and 67% of the Secchi depth for grid data). If this assumption is correct the vertical distribution should vary geographically as a consequence of variation in water transparency at highly exposed sites, and due to wave exposure at somewhat more sheltered sites. However, the water transparency varies over the year, mainly due to variation of plankton densities, so when considering differences between areas a more stable measure should be used, the mean over the vegetation period for example. A large scale study on the subject may result in a model describing the geographical variation of *F. vesiculosus* vertical distribution as a result of wave exposure and water transparency, and perhaps its variation as a consequence of long-term trends of eutrophication.

Conclusions

The eutrophication of the Baltic Sea has widely changed the conditions for the macroalgal communities (Cederwall & Elmgren 1990). The increased sedimentation may be of great importance in inhibiting the recruitment of both *F. vesiculosus* and *F. serratus* by blocking hard substrates and choking fucoid recruits. The filamentous algae, which are favoured by eutrophic conditions, may directly inhibit fucoid zygotes from attaching to hard substrata, and indirect by accumulating sediment. Thus, the existence of an adult *F. serratus* population may allow continued recruitment in occupied patches but colonisation of new areas seems very difficult at the present conditions. Even though (Arrontes 2002) concludes that *F. serratus* has high competitive, and short-scale dispersal ability, wave action may be the key factor in clearing hard substrates from silt and other sediments, and thereby facilitate for fucoid recruitment.

The salinity has also changed considerably during the last century, which should affect the distribution of species living close to their salinity limit in the Baltic Sea. *F. serratus* may have decreased its recruitment ability due to the salinity decrease since 1980. However, this change coincide with the period when the turf-forming algae that *F. serratus* compete with probably have increased their abundance off the Öland coast indicated from that they constitute a larger part of the cast walls on the east coast of Öland.

This study demonstrates that it is possible to use physical factors, such as slope, geomorphology and wave exposure, to model the potential distribution of fucoids. However, within the physically determined distribution limits much variation of macroalgal abundance occurs, probably as a consequence of interspecific competition or other factors that are hard to include in predictive models. The interactions between species, or functional groups, may in turn be affected by environmental factors such as siltation or wave action, and thus possible to model. When a factor that affects many interacting organisms is used it should be hard to pick out the effects on the individual species, although the factor may be very useful in the model anyway. In open coastal areas the physical gradients are not as steep as in a complex environment like an archipelago. At the large shallow limestone plateaus out of the east coasts of Öland and Gotland, salinity, wave exposure and slope vary only at a large scale making small-scale macroalgal variation largely dependent on substrate patches and biological interactions. In the archipelago the potential habitats are smaller, although the biota varies within these smaller areas as well. The difference between the coastal types is thus largely a matter of physical heterogeneity and the difference in predictability a matter of scale.

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A predictive GIS model using factors structuring *Fucus vesiculosus* distribution in a Baltic Sea archipelago

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Abstract

The bladderwrack *Fucus vesiculosus* L. is the only large belt-forming brown alga in the brackish northern Baltic Sea proper, and thereby considered a key-species on shallow bottoms. It is found submerged at 0 – 8 m depth in the Stockholm archipelago where the study was performed. The aim of this study was to find and quantify abiotic factors structuring *F. vesiculosus* distribution, and to use these factors in a Geographic Information System (GIS) model to estimate its vertical and horizontal distribution and display this on a map. In a diving inventory, bottom shape, substratum type and species abundance data were collected at 30 transects. Fetch and wind data were used in the GIS to calculate a wave exposure estimate. Slope and wave exposure were shown to be important factors for describing *F. vesiculosus* distribution and they were also possible to convert to grids, so they were used in the GIS model. The model was 82% correct in predicting *F. vesiculosus* distribution when field data from the diving inventory were used. When grids were used as input data the model performance decreased to 71 %, most likely due to insufficient resolution and low quality depth data. The insufficiency of light, measured as the Secchi depth, was expected to delimit the vertical distribution in the area, but that was better modelled from wave exposure values. The reason for this was probably that waves clear substrata from silt that otherwise may inhibit *F. vesiculosus* establishment. A map was made from the model result showing the estimated distribution of *F. vesiculosus*, which included 8.8 % of the seafloor pixels of the study area.

Introduction

The bladderwrack *Fucus vesiculosus* L. is the only large belt forming brown algae in the northern Baltic Sea (Wallentinus, 1979)where it has also the largest biomass of the macroalgae (Kautsky, 1988). *Fucus vesiculosus* has a major role in structuring the benthic macroalgal community and many species depend on this species for their shelter, as nursery area, for grazing, or as substratum making it a key species for the coastal ecosystem of the Baltic Sea. Skult (1977)identified 44 fauna taxa in the *F. vesiculosus* belts outside Helsinki, Finland, northern Baltic Sea proper, which makes it one of the most diverse communities in the species-poor Baltic Sea. *Fucus vesiculosus* is mainly growing on rocky substrata although it also occurs attached to stones or secondary hard substrata on soft bottoms, or lying loose on the bottom at sheltered sites(Waern, 1952; Wallentinus, 1979).

The physical environment sets the ultimate limits for all species, but within this range much variation occurs. Light and water movement have been recognized as the most important abiotic factors influencing macroalgal distribution and density (Sheperd & Womersley, 1981). To those factors, Kautsky and van der Maarel (1990) added substratum type when studying *F. vesiculosus* in the Baltic Sea. These factors are all interrelated and it may therefore be hard to distinguish effects of one factor from the other. From a modelers perspective that could be an advantage, since some factors may be considered redundant. The availability of light at the bottom, which is limited by water turbidity and depth, is considered a major factor in limiting depth distribution of submersed plants (Chambers & Kalff, 1985; Kautsky *et al.*, 1986; Schwarz *et al.*, 2002)although biological interactions (Norton, 1985) and sediment (Kiirikki, 1996) also have been suggested. The water transparency is limited mainly in two ways, by inorganic detrital particles suspended in the water and by plankton. Wave action may both increase and decrease the turbidity. Eutrophication combined with low water exchange (low wave action) can lead to low transparency, mainly due to high plankton concentrations (Gerard & Mann, 1979), while resuspension at high wave action also can lead to low transparency (Sheperd & Womersley, 1981). Another effect of waves is the structuring of the bottom substratum by resuspending and transporting away particles to deeper or more sheltered areas. This phenomenon is connected to the shore slope as well since less energy is required to move stones and particles down a steep slope than over a flat bottom.

The upper limit of fucoids is generally set by desiccation, which also has been suggested for the Baltic Sea (Kautsky *et al.*, 1986). This limit is not due to tidal changes since the Baltic lacks significant tide, but to large water level surface fluctuations due to variations in air pressure. Wave exposure and ice scouring have also been suggested to set the upper limit for *F. vesiculosus* in the Baltic (Kiirikki, 1996; Kiirikki & Ruuskanen, 1996). Wave exposure affects seaweed, in particular larger species such as *F. vesiculosus*, with drag force (Carrington, 1990) and ice scouring is most severe at exposed sites where the ice flakes are pushed towards the shore, which could explain why *F. vesiculosus* is not found at the surface at the most exposed sites. However, since the effects of ice scouring decrease with depth the species may be present deeper down also at exposed sites (Kiirikki, 1996; Kiirikki & Ruuskanen, 1996).

In the brackish Baltic Sea salinity is the main limiting factor for *F. vesiculosus* at a large scale since the species regularly will be found only at salinities above of 2-4 ‰ (Waern, 1952; Pekkari, 1973)In the part of the Baltic Proper where the study area is located the salinity generally exceeds this limit. Thus, this factor was not expected to have any impact on the occurrence of *F. vesiculosus* and was not included in the investigation.

Many attempts have been made to measure wave exposure by constructing exposure scales from nautical chart characteristics (Baardseth, 1970; Håkanson, 1981; Keddy, 1984; Thomas, 1986). In this study Geographic information systems (GIS) and spatial modelling was used to set up a wave exposure model and to produce a map of the estimated distribution of *F. vesiculosus* in the study area.

The aims of this study were; 1) To determine the factors most useful for modelling the distribution of *F. vesiculosus* in an archipelago area, 2) To predict the *F. vesiculosus* distribution in the Ornö parish located in the southern part of Stockholm archipelago using these factors in a Geographic Information System (GIS).

To be used in the GIS model the factors had to fulfil two criteria; they had to significantly affect the distribution of *F. vesiculosus,* and they had to be displayed as grids for the GIS model.

Materials and methods

Diving inventory

The study area is located in southern Stockholm archipelago, Sweden, in the northern Baltic Sea proper (Fig. 1). The salinity in the area is 4 – 7.5 ‰ (Juhlin, 1992; Lindblad *et al.*, 1999) with lower salinity towards the mainland (west). Since the salinity is above 4 ‰ it is not expected to affect the distribution of *F. vesiculosus* (Pekkari, 1973). However, in semi-enclosed bays the salinity may be lower than 4 ‰. Such bays have been excluded from the inventory since their vegetation may differ completely from the phytobenthic community in the rest of the archipelago (Dahlgren, 1997; Munsterhjelm, 1997). Sites for the 30 diving transects were selected, not randomly, but with the intention to cover the whole range of wave exposure, and also the gradient from the inner part of the Ornö archipelago to the most remote islands (Fig. 1). At each site, the position and direction of the transect, and the

Secchi-depth was measured. When the Secchi-depth was larger than the maximum depth of the transect, the Secchi-depth was measured as close to the transect as possible. The inventory was carried out 8 – 27 June 1998 using the SCUBA diving method of the Swedish monitoring program (Kautsky, 1995). A weighted rope, marked at every meter, was placed at the sea floor, from the surface and down perpendicular to the shoreline. At the depth where no more macroalgae were present and the biota looked homogenous, the transect was ended. At this depth, sandy or soft sediments dominated by mussels were common. At shallow places where the lower macroalgal distribution limit was not reached the transect was terminated when the biota looked similar as far as could be sighted. Irrespective of the above mentioned conditions, the transect was terminated at a depth of 20 meters.

The diving inventory started at the end of the transect, usually at its greatest depth. At the end point and every time the dominating substratum, shape or biota changed a note was made about the marker on the line, the depth, the amount of silt and the dominating substratum (soft, sand, gravel or rock) and the presence of boulders, from there and further on. The amount of silt was subjectively classified into four classes by sweeping the hand over the substratum; 1) no silt resuspended , 2) only little resuspended silt, 3) rather high resuspension, and 4) high and persistent resuspension (Kautsky, 1995). *Fucus vesiculosus,* was estimated as classes of cover degree (1, 5, 10, 25, 50, 75 or 100%). *Fucus vesiculosus* is found attached to the substratum or loose lying on the bottom. Sometimes the plant was attached to a small stone or even a mussel shell, which made them appear as loose lying although they actually were attached. Since it was not possible to separate these two categories during the diving inventory, all healthy looking *F. vesiculosus* plants were included in the inventory.

The data was transferred to an Excel spreadsheet. In order to get data equally representing the whole transect, the position (Swedish grid RT90) and the depth was calculated by trigonometry to points at every meter along the line. This process resulted in 1272 data points that will simply be referred to as “points” from hereon. The information of dominating substratum, amount of silt and cover degree (%) of species was then transferred to the points from the places of change. The slope (in degrees) for a certain point was calculated as the slope between the previous and the next point of the transect.

Construction of the GIS

All the 1272 points of the inventory had a position, which made it possible to import the data into the GIS as a vector point theme. Values from grids were reversibly transferred to the attribute tables of the points and included in the statistical analysis (as described for the wave exposure estimate below). The factors of interest had to be transformed into grids of 10 x 10 m cell size, which was used in this study. That step was crucial because the GIS model performance is dependent upon it, and this procedure is thoroughly described below. The GIS software ArcView 3.2 with the extensions Spatial Analyst 2.0 and 3D Analyst 1.0 were used and freeware extensions and scripts for ArcView were downloaded from Internet.

Digital Elevation Model (DEM)

In this study depth values were used in several ways. To describe the bathymetry a digital elevation model (DEM) was made from a digital version of the Swedish 1:50 000 nautical charts. A triangular irregular network (TIN) was built from the depth curves and depth point values, and was then converted to a grid of 10 x 10 m cells. It would also have been possible to interpolate an elevation grid from all the points building up the depth curves, but the uneven distribution of these depth values would cause too much error in the resulting grid, so the TIN solution was preferred.

The slope grid was derived from the bottom topography grid by the ArcView 3.2 function “derive slope”. The grid size and the difference in elevation between adjacent grid cells was used for the calculation.

Wave exposure

In a previous study (Lindblad *et al.*, 1999) GIS was used to calculate wave exposure in Stockholm southern archipelago. The Ornö parish is located within this larger area and the wave exposure estimation was used in the present study as well. Wind data from a nearby meteorological station (Landsort) 1991 – 1995 were used for the calculations.

The number of wind observations, and the wind velocity at every observation was collected from 16 wind directions (N, NNE, NE, ENE, E etc.). For every wind direction a value for strength was calculated using the formula

$$\text{Wind strength (one direction)} = ((\sum(x^2))/n)^{1/2}$$

where **x** (m^{-s}) is the strength at one observation and **n** is the number of observations. This formula gives the strongest winds, which are supposed to have the largest impact, a heavier weight. Then 16 grids, one for every wind direction, were created. In every pixel, the fetch, i.e. the distance to nearest land opposite the wind direction, was calculated. The fetch layer for every direction was multiplied by the wind strength value for the corresponding direction, and all the 16 maps were summarized. This map algebra resulted in a map of the wind-induced wave exposure for every sea pixel in the archipelago (Lindblad *et al.*, 1999). There were two problems with this wave exposure grid that had to be solved to make it work in the present model: 1) The study was made in a lower resolution (200x200 m pixels) compared to the present study (10x10 m pixels). The low resolution did not follow the complex coastline of the archipelago, which resulted in sublittoral areas that were not included in the wave exposure grid. This problem can not be avoided in a grid, although it decreases with higher resolution. 2) Refraction or diffraction effects were not included in the wave exposure model. The modelled waves where therefore not dispersed in a natural way, and caused “rays of shelter” on the lee side of skerries and “rays of exposure” from sounds in each of the 16 directions. Both these problems were solved at the same time by adding a new vector point layer to the GIS. 500 vector points were inserted by hand evenly over the study area, but “rays” and the areas of missing data by the coastline were avoided. The values of the wave exposure grid were transferred to the attribute tables of the vector points, and a spline interpolation was made between the points using the grid size of 10 m, which resulted in a new map of wave exposure (Fig. 1). Wave exposure index values were transferred to the corresponding transects in the inventory data for statistical analysis.

Statistical analysis of structuring factors

For the identification of the most useful structuring factors for modelling the *F. vesiculosus* distribution, values measured in the field during the inventory were used, except for wave exposure where only grid values from the fetch calculations were available. Analyses were performed in Statistica 5.5, SAS 8.02 and Excel 2000.

The effect of substratum and silt on the *F. vesiculosus* distribution was analysed in SAS with a logistic Generalized Linear Model (function GENMOD) and likelihood type 3 test. Intra local dependency was tested by using the factor site as a repeated subject. The occurrences (0/1, not coverage percent) of *F. vesiculosus* on all points (1272 – missing data = 868 = n) from the diving inventory data set were used. Effects of slope and wave exposure were controlled for by including them in the analysis.

A Spearman rank test was used (in Statistica) to analyse the maximum slope that was found for each class of *F. vesiculosus* coverage (5, 10, 25, 50, 75 or 100 %)(n = 6). The six values came from six different transects which eliminated the potential problem of high impact from a single transect.

The effect of wave exposure and Secchi depth on the lower limit of the *F. vesiculosus* distribution, and on the lower limit of the *F. vesiculosus* belt (25 – 100 % cover) was analysed in Statistica with a multiple regression, and the correlation between wave exposure and Secchi depth was examined with the same test. One value per transect that had *F. vesiculosus* (n = 23) or *F. vesiculosus* belt (n = 19) were used. Since the two factors wave exposure and Secchi depth correlated in both the *F. vesiculosus* and the *F. vesiculosus* belt tests, redundancy analysis were made in Statistica, and the resulting tolerance values from that tests were used to calculate Variance Inflation Factors (VIF) in accordance to (Neter *et al.*, 1996). The effect of wave exposure on the upper limit of the *F. vesiculosus* distribution was examined in a regression analysis.

Results

F. vesiculosus occurrence

The mean depth of the 30 transects was 4.5 ±3.5m (SD) and the mean of the maximum depths was 7.8 ±4.9 m (SD). *Fucus vesiculosus* was found along 24 transects and at 48.6 % of the 1272 points of the diving transects and *F. vesiculosus* belt (25 – 100 % cover) was found at 19 transects and at 14.1 % of the points. The result of all tested potentially structuring factors is summarized in Table 1.

Dominating substratum

Rock (36.3 %) and sand (36.2 %) were the most common substrata in the diving transects followed by soft sediments (23.8 %) and gravel (3.7 %). *F. vesiculosus* occurred on 42 – 56 % of the data points of all substrata, and there were no significant differences between the occurrences of *F. vesiculosus* as an effect of the different substrata (Table 1). As a consequence, and due to the small differences between the occurrences of *F. vesiculosus* on the different substrata, the factor was considered not being a useful factor to include in the GIS model.

Silt

The occurrence of *F. vesiculosus* correlated negatively to the estimated amount of silt covering the substratum (Table 1), and the amount of silt correlated negatively with the wave exposure (GLZ Chi-sqr = 54.23, p < 0.001). Since silt is connected to wave exposure the factor was not separately used in the GIS model, However, it was considered an essential part of the effects of wave exposure on the *F. vesiculosus* distribution.

Maximum slope

There was a negative relationship between the maximum slope and the percent cover of each *F. vesiculosus* class (Fig. 2). Note that the trend line is made from the maximum slope value found for each of the six *F. vesiculosus* cover classes used in the diving inventory (n = 6). On flat bottoms, all coverage classes of *F. vesiculosus* were found, while *F. vesiculosus* cover was never high on steeper sites, and the species was absent at slopes steeper than 38°.

Wave exposure and Secchi depth

The level of wave exposure rather than the water transparency correlated to the lower limit of *F. vesiculosus* vertical distribution according to the multiple regression analysis (Table 1). The Secchi depth and the wave exposure were correlated (Beta = 0.64, p = 0.01), but not to an extent that multicolliniearity should be expected to affect the interpretation of the result (VIF = 1.695) (Neter *et al.*, 1996). When both factors were tested individually in simple regressions only wave exposure was significant. The result was similar for the *F. vesiculosus* belt (Wave Exp.: Beta = 0.76, p = 0.003, Secchi depth: Beta = 0.02, p = 0.92, VIF = 1.67), but when tested separately both factors significantly correlated to the lower limit of *F. vesiculosus* belt (Wave Exp.: Beta = 0.74, p = 0.0003, Secchi depth: Beta = 0.46, p = 0.049). Thus the wave exposure was chosen to be used to set the lower vertical distribution limit in the GIS model, both for *F. vesiculosus* and the *F. vesiculosus* belt.

There was no significant linear relationship between the upper limit of the *F. vesiculosus* distribution and the wave exposure (Table 1).

Construction of the *F. vesiculosus* GIS model

Silt, wave exposure and slope were the factors that were significantly correlated with the *F. vesiculosus* distribution. The factors had to be displayed in a grid form to be usable for the GIS model. For the factor wave exposure this condition was fulfilled from the start, since it was created in this form, and for the slope factor it was done from the digital elevation model (DEM) by the ArcView built-in function “derive slope”. Silt was considered best modelled by the wave exposure that already was within the model, and was thereby excluded from the GIS model. For the two remaining factors wave exposure and slope formulas for delimiting the *F. vesiculosus* distribution estimate were derived. The new formulas originated from the statistical formulas, but they were modified to achieve as high predictive ability as possible when combined with the other factors. The formulae were produced in an Excel spreadsheet, for all factors together, to best fit the inventory. The formulae were used to include and exclude points from the diving transects that were known to have *F. vesiculosus* or not, and were evaluated in three ways:

Type 1. How many of the selected points did really have *F. vesiculosus* (%),

Type 2. How many of the points known to have *F. vesiculosus* were selected (%),

Type 3. How many of all 1272 points were correctly labelled having *F. vesiculosus* or not (%)

By choosing a wider range of for example wave exposure, a higher percentage of the known *F. vesiculosus* would be selected (type 2) but many pixels without *F. vesiculosus* would also be selected which lead to a lower level of *F. vesiculosus* within selected points (type 1). So there was a trade-off between a high type 1 and a high type 2 value. The effort in this study was to get as correct result as possible (type 3), although other priorities were also plausible.
In order to analyse the errors connected with the use of grid data compared to measured data, two formulas were made for each issue, and the model performance was calculated for both measured and grid data. The wave exposure was only available as grid data and was used for both purposes.
The slope factor was used for delimiting the maximum *F. vesiculosus* cover in the model.

Measured data — Maximum Fucus cover = 120 – 4.3 * Slope
Grid data — Maximum Fucus cover = 120 – 8.0 * Slope

In both cases values larger than 100 were set to 100.

An effort was made to model the upper limit of the *F. vesiculosus* distribution as an effect of water level fluctuations. That was done by using a general minimum depth limit (0.1, 0.2, 0.3, 0.4 and 0.5 m were tested), but the performance of the model was not improved so the factor was abandoned. No statistical tests were made.

The factor wave exposure was then used not only to describe the maximum depth distribution, but also for the upper limit (Fig. 3 and 4). The formula that best described the upper limit of the *F. vesiculosus* gave an effect in the exposure interval 7000 – 10000, almost as a threshold effect, which explained why it did not come out in the linear regression. The two formulas used to describe the upper and lower limit of *F. vesiculosus* were:

Measured depth values

Upper limit	$\text{Depth} = (\text{Wave Exposure} / 7000)^{4.5}$
Lower limit	$\text{Depth} = 4.8 + \text{Wave Exposure} * 1.9 * 10^{-4}$

Depth values from grid

Upper limit	$\text{Depth} = (\text{Wave Exposure} / 7000)^{4.5}$
Lower limit	$\text{Depth} = 2.25 + (\text{Wave Exposure} / 3000)^{1.4}$

(Depth in meters, wave exposure index value)

An effort was made to derive formulas for delimiting the *F. vesiculosus* belt (25 – 100 % cover). However, no manipulation of the formulas above improved the result any further so the same formulas were used for the *F. vesiculosus* belt as well.

The model performance was measured as its ability to select points with *F. vesiculosus* from points without the fucoid in the inventory. The calculations were made both for formulae based on measured and grid values, and for *F. vesiculosus* occurrence and *F. vesiculosus* belt occurrence respectively (Table 2).

Estimate of *F. vesiculosus* distribution

Values from the grids representing each factor were used to produce new grids on 1. bottoms shallower than the lower limit, 2. bottoms deeper than the upper limit, and 3. maximum *F. vesiculosus* cover as an effect of slope. These grids were then used in an overlay analysis resulting in a grid showing the estimated *F. vesiculosus* distribution and maximum cover within this distribution according to the limitations used. Some areas at the nautical chart had incomplete depth data and were therefore excluded from the model. *Fucus vesiculosus* was estimated to occur on 8.8 % of the remaining sea surface pixels (Fig. 5). Based on the model performance 66 % of the selected pixels were expected to have *F. vesiculosus*, and 83 % of the *F. vesiculosus* distribution in the area was expected to occur at the selected pixels. The selected pixels were expected be 71 % correctly labelled as *F. vesiculosus* pixels or not.

A *F. vesiculosus* belt with a cover of at least 25 % was expected to occur at 22 % of the pixels marked as 25 – 100 % maximum cover. The selected pixels were expected to be 52 % correctly labelled and include 83 % of the real *F. vesiculosus* belt in the area. However, all these values could be expected to be somewhat lower in reality since they represented a more heterogeneous environment than the exact locations of the diving transects.

Discussion

Fucus vesiculosus was expected to be more abundant on hard substratum but no differences were found between any classes of dominating substratum. This result is probably influenced by the fact that stones and other hard substrata occurred in all substratum classes, although the quantity was not recorded, only the dominating substratum. Neither was it noted if the *F. vesiculosus* fronds were attached to some kind of substratum or detached. However, we have repeatedly observed that *F. vesiculosus* grows well also on sheltered sites with soft sediments and that the stands look healthy with large plants even, though they are often more readily overgrown by epiphytes.

Silt is constantly sedimented on all bottoms. On bottoms exposed to wave action or currents the silt is frequently resuspended, but at calm conditions it is accumulated and is a major agent for formation of soft bottoms. Silt or sediment has been shown to decrease the recruitment of *F. vesiculosus* in the Baltic Sea (Berger *et al.*, 2003; Eriksson & Johansson, 2003), and in the present study, silt was found to negatively correlate with *F. vesiculosus* occurrence. The mechanism behind this is probably that sediment blocks the hard substratum, lowering the attachment success of *F. vesiculosus* eggs or zygotes, and the decreases survival by burying *F. vesiculosus* recruits, which has been shown in laboratory experiments (Berger *et al.*, 2003).

Wave exposure turned out to be a key factor in explaining the distribution pattern of *F. vesiculosus* in the area. The maximum depth distribution of *F. vesiculosus* at each diving transect was correlated with wave exposure, a relationship used in the GIS model. The waves are probably not affecting the lower macroalgal distribution limit directly, but through their ability to resuspend and remove silt. The amount of silt is generally considered to correlate with the level of wave exposure (pers.com. H.Kautsky), which was confirmed by this study. The result is in accordance with Kautsky (1988) and Kiirikki (1996) who suggested that wave exposure clear the substratum from sediment that otherwise will delimit the depth distribution of *F. vesiculosus*. In other studies Secchi depth has been shown to set the maximum depth of submersed plants (Chambers & Kalff, 1985), and available light has generally been considered one of the main factors limiting depth distribution of *F. vesiculosus* in the Baltic (Waern, 1952; Kautsky *et al.*, 1986; Kautsky & van der Maarel, 1990). Available light is probably the limiting factor for exposed sites, where silt is consequently flushed away from the bottom substrata, in the study area as well. However, many dive sites in this study were located in sheltered areas, where silt can at least periodically accumulate, making water transparency insignificant in delimiting the depth distribution of *F. vesiculosus*.

The effects of slope on the distribution of macroalgae have been noted by some authors (Sheperd & Womersley, 1981; Hiscock, 1985). It has been suggested to be an effect of shading, or to affect the settlement and establishment (Hiscock, 1985). The effect of the slope factor on the occurrence of *F. vesiculosus* might partly be an effect of substratum competition. Blue mussel *Mytilus edulis* are often covering steep hard surfaces and they may outcompete *F. vesiculosus* by being better adapted to this habitat than *F. vesiculosus*.

The water level fluctuation in the Baltic Sea is considered an important factor for limiting the upper distribution of *F. vesiculosus* (Kautsky *et al.*, 1986; Kiirikki, 1996). This factor was not tested statistically in this study, but the performance of the model was not improved by using a general minimum depth limit, so the factor was abandoned. The distance between markers on the line was 1 m, which may not have been a sufficient resolution for measuring patterns of the first decimetres of depth. Instead the upper limit of the *F. vesiculosus* distribution was set by wave exposure in the model even though this was not a significant relationship (Table 1). *Fucus vesiculosus* was not found close to the water surface at the most exposed sites (Fig. 3), a threshold pattern that was used in the model.

It was not possible to find a better variable to explain the upper or lower limit of the *F. vesiculosus* belt than the ones used for the occurrence of *F. vesiculosus*. Apparently, there are other factors than the above mentioned that affects the density, i.e. the percentage cover, of *F. vesiculosus.* The slope seemed to limit the maximum cover of *F. vesiculosus* (Fig. 2), and contributed thereby to the models performance, but at flat bottom all densities of *F. vesiculosus* 0 – 100 % occurred.

In this study the ambition was to be as correct as possible in predicting the distribution of *F. vesiculosus* but there is a choice embedded in the evaluation method. If the matter of interest is to find areas that most certainly have *F. vesiculosus* the limits for each factor can be tightened up a bit. On the other hand, this action will also increase the amount of *F. vesiculosus* left out of the selection and thereby lower the share of known *F. vesiculosus* selected. The model was 82 % successful in selecting the correct points in having *F. vesiculosus* or not when measured values were used, and 71 % successful when grid values were used (Table 2). The two most likely reasons for this discrepancy are: (1) the resolution of the grid (10 m pixels) was lower than the resolution of the inventory data (meter by meter), (2) the input grids were not correctly describing the real world.

The resolution of the grid is a result of computing limitations and the accuracy of the nautical charts. The grids of this study have about 4 million pixels each, and an increased resolution to 1 m, the same as the dive inventory, would increase the grids to 400 million pixels, which would demand advanced computers to handle. With the 10 m resolution, up to 15 points from the dive transects will correspond to one pixel. That will make values transferred from the grid to the attribute tables of the vector points will come stepwise, which lower the models performance. The accuracy of the nautical chart depends on the time of production and differs between coastal areas, and between items on the chart (pers. com. Lars Jakobsson, Swedish Maritime Administration). Generally the accuracy is much higher in channels compared to surrounding areas, and very low in areas shallower than 3 m. The coastline of the used chart has an accuracy of about 25 m, and is generally better than the depth curves. To use a resolution of 10 m is to push the limit a little, but a lower resolution would make the model useless. It would increase the model performance to use an even higher resolution, such as 1 m pixels, but is not justified by the accuracy of the nautical chart.

Several problems are connected with the digital elevation model (DEM) that both the depth limits and slope estimate are dependent upon. Nautical charts are made for navigation, not for describing the bottom topography. In shallow waters, the surface is divided into zones defined as 3 m deep or shallower. Usually there is a 3 - 6 m zone outside the 0 – 3 m zone. Small or thin zones would make the chart too unclear to be viewed at the 1:25 000 or 1:50 000 scale they are produces for, and are therefore excluded (Bergman, 2000). Therefore the depth curves are often merged, leaving a single line representing both zones but displayed as the shallowest, to ensure safe navigation (Bergman, 2000).

In a TIN model only one elevation value can be used at every position. At positions where the depth curves are drawn on top of each other one curve has to be chosen for the model. In this study the shallowest depth curve has been used consequently, which affects both elevation values close to the coastline and the slope. However, giving higher priority to deeper curves than to shallower would make a less correct model, including islands shown as shallows.

The wave exposure turned out to be of great importance in predicting *F. vesiculosus* distribution. The calculated wave exposure values of this study were derived from a wave exposure grid from a previous study (Lindblad *et al.*, 1999), even though they were somewhat modified. This grid method has not been tested, but it uses fetch and wind data in a similar way as other studies (Håkanson, 1981, Keddy, 1984 #62) The discrepancy between the model performance for measured values compared to grid values is not affected by the accuracy of the wave exposure grid since both calculations are based on the same grid. The discrepancy is more likely an effect of incorrectness of the DEM, which was based on the nautical charts, since both depth and slope values were derived from it.

Conclusions

Among the factors investigated wave exposure and slope were shown to be important and the two most useful factors determining the distribution of the submersed *F. vesiculosus* community in the investigated archipelago area. How general this model and the factors are for the distribution of *F. vesiculosus* in a larger geographic area needs to be tested further. The GIS method is promising, but the potential predictable ability of the model can be increased considerably by using better depth data than the nautical charts. The model should be validated in a new area before it is used for coastal management or similar purposes.

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Table 1

Table 1
All the potentially structuring factors for the *F. vesiculosus* distribution that were tested.

Factor	Response variable	n	Regr.coef.	Statistica	p	Method
Dominating substrate	Occurrence of *Fucus*	868		Chi-sqr = 1.45	0.695	GLZ (Logistic)
Silt	Occurrence of *Fucus*	868		Chi-sqr = 9.50	0.023	GLZ (Logistic)
Slope	Maximum *Fucus* cover	6	R = -0.83	t = -2.96	0.04	Spearman
Wave exposure	Upper limit of *Fucus*	24	Beta = 0.31	t = 1.51	0.15	Regr
Wave exposure	Lower limit of *Fucus*	23	Beta = 0.65	t = 2.79	0.01	Mult.regr
Secchi depth	Lower limit of *Fucus*	23	Beta = 0.09	t = -0.39	0.70	Mult.regr
Wave exposure	Upper limit of *Fucus* belt	19	Beta = 0.02	t = 0.07	0.95	Regr
Wave exposure	Lower limit of *Fucus* belt	19	Beta = 0.76	t = 3.52	0.003	Mult.regr
Secchi depth	Lower limit of *Fucus* belt	19	Beta = 0.02	t = -0.11	0.92	Mult.regr

Table 2

Model performance measured as the ability to predict the occurrence of *F. vesiculosus* or *F. vesiculosus* belt (25 – 100 % cover)

	F. vesiculosus occurrence		*F. vesiculosus* belt occurrence	
	Measured values	Grid values	Measured values	Grid values
Type 1 *	75 %	66 %	22 %	22 %
Type 2 **	94 %	83 %	94 %	83 %
Type 3 ***	82 %	71 %	52 %	52 %

* How many of the selected points did really have *F. vesiculosus* or *F. vesiculosus* belt

** How many of the points known to have *F. vesiculosus* were selected or *F. vesiculosus* belt

*** How many of all 1272 points were correctly labelled having *F. vesiculosus* (or *F. vesiculosus* belt) or not

Figure legends

Fig. 1. The study area was located in Stockholm archipelago. Sites for diving transects (●) were located to cover the full range of calculated wave exposure levels.

Fig. 2. The maximum slope that each *F. vesiculosus* cover class (5, 10, 25, 50, 75 and 100%) was found on. No *F. vesiculosus* was found at sites steeper than 38°.

Fig. 3. The vertical distribution of *F. vesiculosus* over the wave exposure gradient. Depth values were measured during the dive inventory and wave exposure values (Log_{10}) were derived from a GIS calculation.

Fig. 4. The vertical distribution of *F. vesiculosus* over the wave exposure gradient. Depth values were derived from the DEM grid and wave exposure values (Log_{10}) were derived from a GIS calculation.

Fig. 5. The predicted *F. vesiculosus* distribution in Ornö archipelago, S. Stockholm. The distribution cover 8.8 % of the sea area. The striped areas have incomplete depth data and were excluded from the estimate.

/Isæus, M. & Lindblad, C.

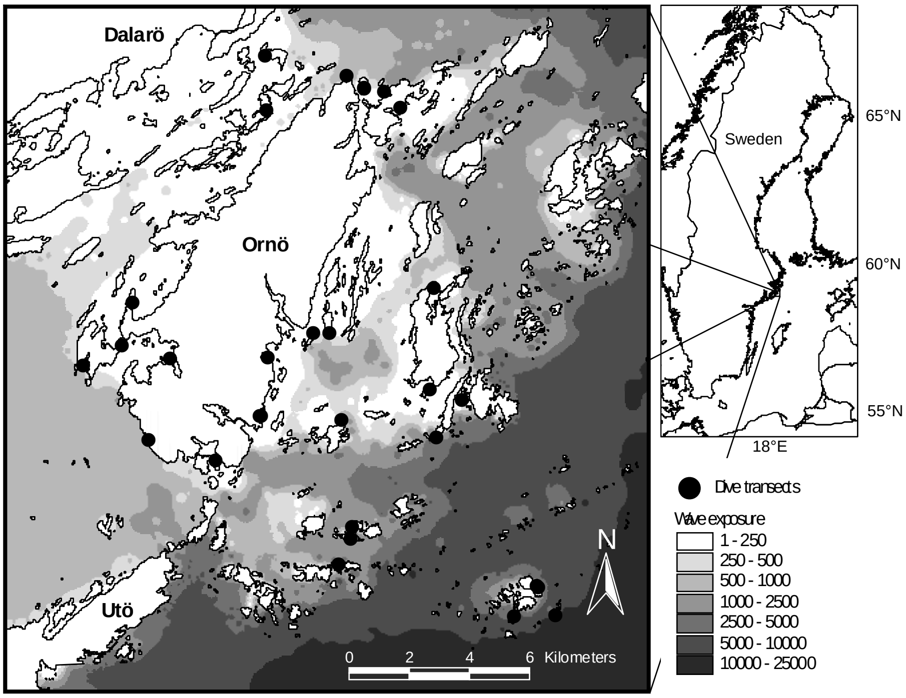


Figure 1
Isæus, M and Lindblad, C

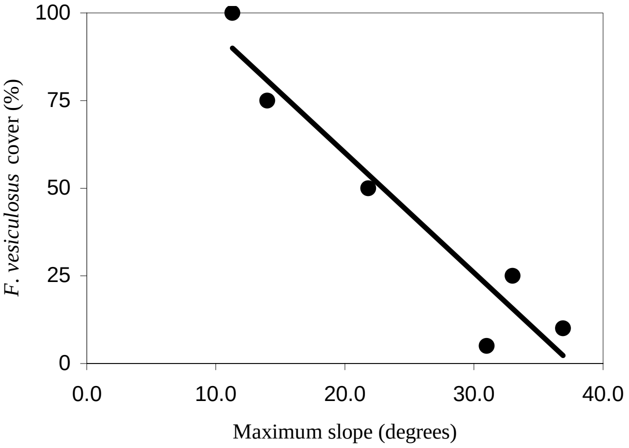
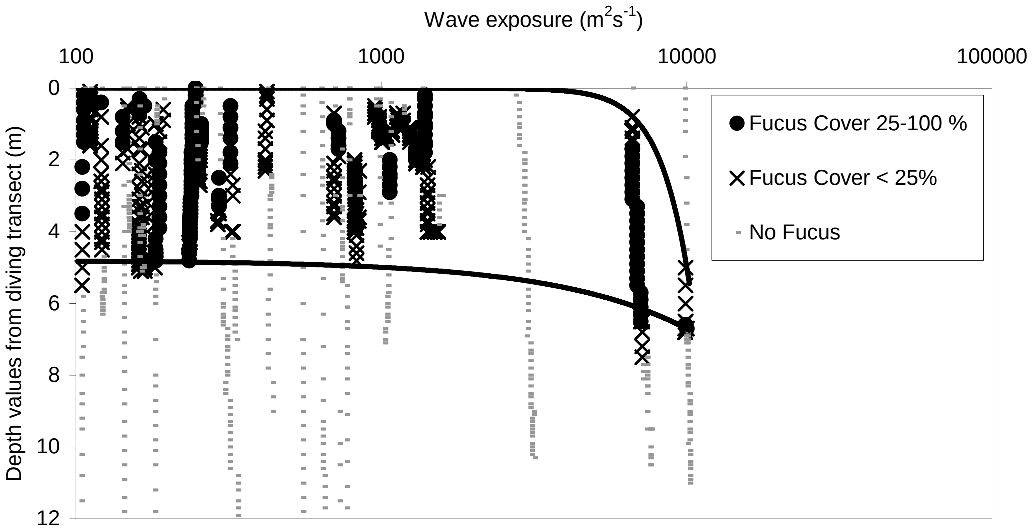


Figure 2
Isæus, M and Lindblad, C



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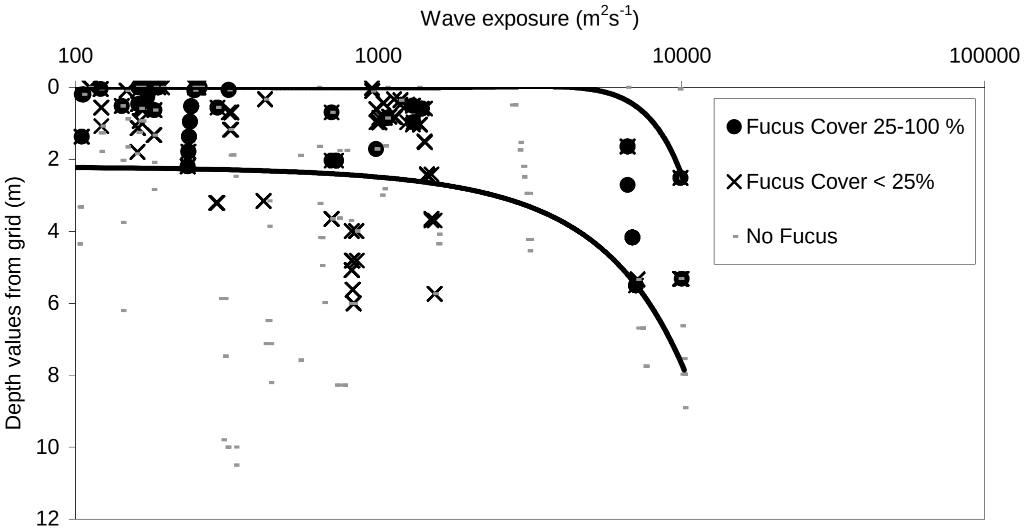

Figure 4

Isæus, M and Lindblad, C

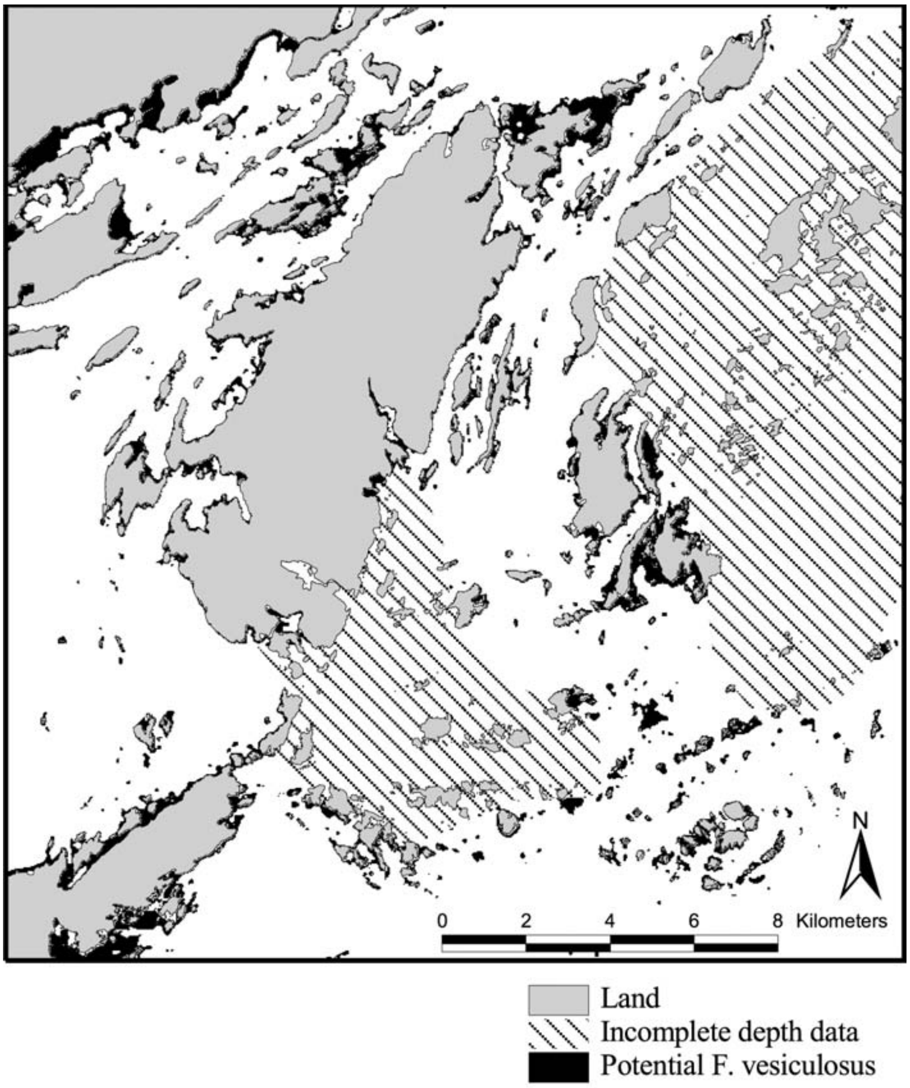

Figure 5
Isæus, M. and Lindblad, C.

A GIS-based wave exposure model calibrated and validated from vertical distribution of littoral lichens

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Abstract

Waves are one of the major factors structuring the biota at the sea shore. Methods to calculate ecologically relevant values of wave exposure are therefore of interest both for basic research and coastal management purposes. Wave exposure has generally been estimated by using either biologically derived indices, or cartographic methods. However, to ensure ecological relevance as well as generality these methods have to be combined. In the present study a cartographic GIS-method was developed, and calibrated by a biological index derived from zonation of epilittoral lichens. For the cartographic measure fetch was calculated for 16 directions using a grid solution. To mimic the wave pattern caused by diffraction and refraction, a spreading effect was added to the fetch model and calibrated from aerial photographs of waves deflected around islands. The adjusted fetch measure was then multiplied by wind data using ten different methods in order to find the cartographic index best correlated to the biological wave exposure index of the calibration sites. The resulting cartographic index correlated well with the biological index (r=0.854, p<0.001, n=43). The GIS-method was then validated in another area giving a similarly good fit (r=0.839, p<0.001, n=34). The resulting GIS-method, a grid solution, was developed to fulfil a need to quantitatively describe the patterns of wave exposure in a complex archipelago land/seascape for GIS usage, although it should also be suitable for lakes or open coastal systems.

Keywords

Geographic information system, GIS, PCA, zonation, Baltic Sea, archipelago, coastal management

Introduction

Wave action is one of the major factors structuring the biota at the sea shore (Southward 1958, Lewis 1964, Hiscock 1985, Norton 1985). The distribution and morphology of many benthic organisms are influenced by waves. Several attempts have therefore been made to quantify wave action. In this paper I concentrate on the long-term wave regime at a site, hereafter called the wave exposure, which is reflected in the biota but is difficult to measure since wave action varies over time due to weather conditions, tide and the chaotic nature of waves (Denny 1988). There are two main methods used to estimate wave exposure; biological exposure indices and cartographic methods.

Biological exposure indices are derived from the zonation of sessile sea shore organisms, usually above or in the tidal zone, such as algae, lichens and barnacles, but morphological characters may also be included (Ballantine 1961, Lewis 1964, Dalby et al. 1978, Kruskopf & Lein 1998). Unfortunately there are only brief quantitative descriptions of the zonation of shore species in the Baltic Sea (Du Rietz 1925a, b), although this zonation is described along wave exposure gradients elsewhere (Kylin 1918, Lewis 1964, Johannesson 1989). The biological exposure index approach has the advantage that it is ecologically relevant in the sense that it describes the pattern of the species on the shore, but other factors than waves that also affect the biota may disturb the pattern. The pattern of sessile organisms are a result of the long-term condition since tide, wave action and water surface fluctuations change over time, but the organism pattern is more or less stable. A disadvantage is that the species pool and environmental parameters vary geographically which makes the constructed index less general (Ballantine 1961). Another disadvantage is the circular argument biological indices are based on: a shore is exposed because it has a certain community and it has a certain community because it is exposed (Ballantine 1961). However, a study that measured both the wave action and the pattern of the biota confirmed the effects of waves on biota (Jones & Demetropoulos 1968).

Waves may be generated by seismic activity, streams or boats, but most waves are induced by winds. Cartographic methods therefore often use the fetch, the distance of open water at which the wind can act upon the sea, for estimating wave exposure. Fetch-based wave exposure indices were originally developed for lakes. They are usually calculated for several fetch directions, often combined with wind data and integrated into a single value (Håkanson 1981, Keddy 1984, Ekebom et al. 2003). In coastal areas the fetch may be extremely long and a maximum value for the fetch may be used. Alternative methods measures the sites' openness to the sea as the total width of a sector free from obstructing islands or shallows (Southward & Orton 1954, Baardseth 1970, Thomas 1986). The cartographic methods have the advantage that they are general and should work equally well independent of the biota. However, they are generally based on assumptions making their validity and ecological relevance unclear.

Geographic information systems (GIS) can be used to improve spatial modelling in several ways. The processing capacity and the exactness of execution makes computer-aided methods fast and repeatable, and new methods have become easy to handle, such as overlay analysis. However, the output quality is limited by the quality of the input map data, in this case nautical charts, and methods must be chosen to fit the maps. There are several examples of GIS solutions to map wave exposure (Lehmann 1998, Bekkby et al. 2002, Ekebom et al. 2003). They are all classical cartographic methods in the way that they are based on fetch or openness and wind data, although the advantages inherent to GIS techniques have been used.

Linear wave theory has been used for modelling of wave exposure, although assumptions have to be made about average wave characteristics (e.g. wave period and wave height, or the wind that causes them) (Ekebom et al. 2003), which make their advantage over simpler models less obvious.

The aim of this study was to develop a method to map wave exposure in an ecologically relevant way, and thereby produce a useful tool for research and coastal management purposes. The method chosen was to first construct a fetch/wind model by using GIS, and then calibrate it to a biological wave exposure index. The GIS method was then validated in a new area by comparing the outcome with a biological wave exposure index again. Correlations between cartographic estimates and biological indices have been used successfully before in the northern part of Norway (Kvist & Lein 1999), although other methods and species were used.

Materials and methods

Fetch calculations

The wave exposure estimate was computed in a geographic information system (GIS), and new software, WaveImpact 1.0, was developed for this purpose. Grids with only two classes, *Land* and *Sea*, were used for the calculations. WaveImpact uses ASCII grids (text files) of the format that can be exported and imported into the GIS software ArcView 3.2. The wave exposure values were based on fetch, i.e. the distance of open water at which the wind can act upon the sea and waves can develop. The fetch was calculated for every sea grid cell of the map, in 16 directions, which resulted in 16 maps. Basically this was done by starting at the map edge and increasing the grid cell values by the value of one cell size (in meters) for each sea grid cell in the propagation direction until land was reached, and then starting over again from zero if there were more sea cells on the other side of the land cells (Fig 1a). An advantage of using a grid solution is that the cell values of adjacent cells can be used as input data, which was used for mimicking the patterns of refraction and diffraction in this study. This is illustrated by an example for southerly wind (Fig 1b-c). Instead of adding the cell size to the cell value behind (the southern side in this example), the cells behind-to-the-right and behind-to-the-left were used (Formula 1, Fig 1b). When the adjacent grid cell on the left side of the current grid cell was *Land* then only cell values from behind and from behind-to-the-right were used and vice versa (Fig. 1c). This resulted in a pattern where the fetch values were evened out to the sides, and around island and skerries in a similar way that refraction and diffraction make waves deflect around islands. Aerial photographs of wave crests deflected around islands were used to coarsely calibrate the magnitude of the spreading effect (Fig. 2), which was made by changing the partial contribution from the cells on the sides. The formula used for calculating a southerly wind/wave direction (corresponding to figure 1), when no land pixels obstructed, was:

Formula 1.

$$\mathrm{OutputMatris}(i, J) = \mathrm{OutputMatris}(i + 1, J - 1) * (0.5 - \mathrm{Ref}) + \mathrm{OutputMatris}(i + 1, J + 1) * (0.5 - \mathrm{Ref}) + \mathrm{OutputMatris}(i + 1, J - 2) * \mathrm{Ref} + \mathrm{OutputMatris}(i + 1, J + 2) * \mathrm{Ref} + \mathrm{Cellsize}$$

where *OutputMatris(i, J)* is the current cell position in the grid, i is increased downwards (southwards) in the grid relative to the current position, J is increased to the right (eastwards) in the same way, *Ref* is the calibration value of the refraction/diffraction effect (set to 0.35), and *Cellsize* is the cellsize in meters.

When there was a land pixel on the left (western) side the following formula was used:

Formula 2.

OutputMatris(i, J) = OutputMatris(i + 1, J) * (0.5 - Ref) + OutputMatris(i + 1, J + 1) * (0.5 + Ref) + Cellsize

Corresponding formulas were used for land obstacles to the right (east), and for all 16 directions. As a consequence of the square grid cells the directions 0, 26.6, 45, 63.4, 90, 116.6, 135, 153.4, 180, 206.6, 225, 243.4, 271, 296.6, 315, 333.4° were used instead of 0, 22.5, 45, 67.5, 90, 112.5, 135, 157.5, 180, 202.5, 225, 247.5, 270, 292.5, 315, 337.5°. To ensure that the spreading effect was equally calculated for all directions, in spite of square grid cells, the model was run in an artificial system consisting of a circular island in a circular sea. The formulas were adjusted by using different *Ref*-values for different directions until the resulting pattern for the sum of all 16 directions was approximately radial symmetrical.

A high grid resolution (small grid cell size) is desired in an archipelago environment since the coastline is so complex. However, high computational power is needed to make these multiple calculations over large areas. To overcome this problem the calculations were first made in a large, coarse grid of 500 m cell size covering the entire Baltic Sea. Then a 100 m grid covering the Stockholm archipelago was used and grid values from the 500 m grids were imported as fetch start values at the edge of the 100 m grid. At last a 10 m grid covering the study area was used, and start fetch values were imported from the 100 m grid.

Fetch and wind calculations

Several ways to calculate a wave exposure index out of fetch and wind data have been suggested (Håkanson 1981, Keddy 1984, Thomas 1986). In this study ten different calculations were used in order to find the most appropriate method. Wind data from Landsort was used, a nearby metrological station. The wind was recorded 4 times per day during 1991-95 by the Swedish Metrological and Hydrological Institute. Four different wind measures were used for each wind direction; the mean of all wind speed recordings (W_{mean}), the square root of the mean of all wind speed recordings powered by 2 (i.e. $W^2_{mean} = \sqrt{\frac{\sum_{i=1}^{n} W_i^2}{n}}$), the maximum recorded wind speed (W_{max}), and the maximum recorded wind speed powered by 2 (W^2_{max}).

For each of the four wind measures the 16 fetch grids were multiplied by the wind value of the corresponding direction (denoted as $_d$) resulting in 16 wind/wave grids per wind measure. From each set of 16 grids two wave exposure grids were derived by overlay analysis; the mean of all fetch/wind directions (*Mean* in Tab. 1), and the largest value from any direction (*Largest* in Tab. 1). The *Mean* and *Largest* were also calculated for fetch grids without using wind data (Tab. 1). The result of these calculations was ten alternative wave exposure grids that were compared to the biological exposure index. The values from the grids were exported to the attribute tables of the points (sites) of the biological inventory by using the script GetGridValue (Elmquist 1998), and then correlation analyses were made between the biological index and the cartographic exposure estimates of the corresponding sites.

Biological index

For calibration of the GIS-model a biological index was constructed from zonation patterns of sea shore organisms. Seven lichen species and one cyanophyte that had been identified in a pilot study as potentially responding to wave exposure were used (Tab. 2). Data were collected during an inventory 23/6-4/7 and 29/9-9/10 2003 in the southern Stockholm archipelago, Sweden. Forty-six sites surrounding the island Askö were investigated for the calibration of the GIS-model, and 38 sites around Lacka for the validation. (Fig. 3). Sites as uniform as possible were chosen; a rock with an inclination <30°, and absence of boulders that might change the splashing of waves. At each site the slope of the rock (in degrees) and the aspect (16 directions) were measured. The level of wave exposure was subjectively estimated in four classes (very exposed, exposed, sheltered, very sheltered) for the subsequent identification of principal components (see below). The distance from the water edge to both the lower and upper boundaries of each species vertical distribution was measured (in cm), unless the upper boundary was further than 50 m from the shore or the rock was covered by other vegetation. These measures were adjusted for the fluctuations of water-level that is mainly an effect of atmospheric pressure in the Baltic Sea that lacks tides. The formula used for this was

Formula 3.

$$D_s = D - \frac{W}{\sin\alpha} \qquad D_s < 0 \text{ were set to } 0$$

where D_s is the adjusted distance between the water surface and the species boundary, D is the measured distance, W is the deviation from mean water level, and α is the angle of the slope of the shore in degrees. The distances D_s for all species boundaries were analysed in a principle component analysis (PCA). The first axis (PC1) was considered to describe wave exposure and PC1 values of each site were used as biological wave exposure index values (see results).

Validation of wave GIS-model

The GIS-model was validated by comparing it to a biological wave exposure index of a new area around Lacka (Fig. 3). The biological index was constructed in the same way, and with the same species measures, as for the calibration area.

Statistical analysis

Principle component analyses (PCA) were used for gradient analysis of the vertical distribution of shore species in the calibration area, the validation area, and the two areas together. Relations between the PC1 values from the biological inventories (calibration, validation, and both data sets together) and the calculated wave exposure values were analyzed with Pearson Product-Moment Correlations.

Software

The basic GIS software used in this study was ArcView 3.2 with the extension Spatial Analyst 2.0. Free scripts and extensions for ArcView were downloaded from the internet (www.esri.com/arcscripts) i.e. GetGridValue.ave (Elmquist 1998). For calculating fetch- and wind-indices new software, WaveImpact 1.0, was developed. The software can be downloaded after contact with the author, and will be free for research purposes. The software packages Canoco 4.5 and Statistica 5.5 (‘99 edition) were used for the analyses.

Results

In the calibration area most variation of the vertical distribution of shore species was explained by PC1 (PC1=0.54, PC2=0.19, PC3=0.11, PC4=0.05, n=46). The first principle component (PC1) was identified as wave exposure by comparing the extreme PC1 values to the conditions at the inventory sites. The 3 sites that had the highest PC1 values had all been subjectively described as very exposed during the inventory, and the 3 sites with the lowest PC1 values had all been considered very sheltered (Tab. 3). The axes PC2-4 were not apparently connected to any measured or estimated environmental parameter. Five lichen measures that were strongly connected to PC1 were selected for the biological wave exposure index (Fig. 4). These measures all had scores on PC1 of 0.8 or higher, which was distinctively higher than any other measure (Tab. 1, Fig. 4). A new PCA was made on the remaining five species measures and the eigenvalue for PC1 was now 0.883 which was considered sufficient. These five measures were available at 43 sites (n = 43). The value of PC1 for each location was considered a biological index of wave exposure and used for calibrating the cartographic method.

All fetch/wind measures were highly significantly correlated to the biological exposure index (Tab. 2). Of the two summarizing methods *Mean* was generally better than *Largest,* but incorporating wind data did not improve the fit much. However, the wind should be of some importance in the inner part of the archipelago where the effect of the sea is less pronounced, so the *Mean* of $Fetch_d$ magnified by *mean wind* was chosen as the preferred cartographic wave exposure estimate (Fig. 5). The simulations were also run with limitations of maximum fetch value of 100 km and 200 km. Neither improved the result.

The lichen measures of the validation area, which was constructed with the same lichens as in the calibration area, had the eigenvalue 0.815 for PC1 (n=34). The wave exposure values from the GIS-model correlated well with the biological index ($r=0.839$, $p < 0.001$) (Fig 6). The test was also performed for both areas together giving a similar result (eigenvalue for PC1 was 0.852, n=77, $r=0.851$, $p < 0.001$).

Discussion

The vertical distribution of shore species corresponded well to the subjective wave exposure estimate (Tab. 3). This pattern is well known (Lewis 1964, Johannesson 1989), and has been confirmed by wave measurements (Jones & Demetropoulos 1968). Higher up on the shore effects from the sea should decrease and other effects are evident. *Xanthoria parietina* for example is favoured by the presence of bird feces, which was observed during the field work. However, its lower boundary was strongly connected to PC1 and it was thus used in the biological wave exposure index. The aspect of the shore affects the occurrence of *Calothrix* and *Verrucaria* (Johannesson 1989). However, both these taxa were excluded from the biological wave exposure index as well. An index based on more than three species (five measures) should be more robust, but it would also include more unexplained noise, so the solution with five measures that responded well to PC1 was preferred.

The GIS-modelled wave exposure values correlated well with the biological wave exposure index. Measures based on mean wind correlated better than those based on maximum wind speed, which may be interpreted as that the biological index expresses the long-term wave regime. Shore lichens should not be subject to high drag force by waves due to their low profile, and should therefore avoid dislodgement during rare storm events. Thus the zonation pattern of the shore lichens is most likely a result of the long-term conditions.

The modelled wave exposure estimates should be relevant to many submerged organisms as well, although the effects of waves decrease with depth. Plastic morphological responses of sessile organisms should be sufficiently modelled by a model estimating long-term wave conditions. However, there are many examples of results from infrequent events. For example, storms may dislodge macroalgae (Seymour et al. 1988), or indirectly affect the benthic community by altering the substratum, e.g. by turning boulders (Sousa 1979). For effects from such extreme events other settings of the model may be used. Prolonged periods of unusually calm conditions or extreme water elevation should also change the patterns from those of the average wave regime.

In a coastal area the openness to the sea, with its overwhelming fetch, may be a measure that sufficiently describes the relative wave exposure pattern (Baardseth 1970). In lakes, where effects from the sea are absent, the wind regime is considered important and generally used in wave exposure estimates combined with fetch (Håkanson 1981, Keddy 1984, Lehmann 1998). In archipelagos these approaches should be combined since there are enclosures that should be treated more like lakes in this perspective and remote islands more similar to open coast habitat. The goal of the present study was to find a general method, to be used in lakes as well as archipelagos or open coastal environments, which made it important to include wind data even though it did not improve the outcome much. There is a limit at which a longer fetch does not cause larger waves, which should be used as a maximum fetch value in the model to make it general for coastal areas. However, a maximum fetch value of 100 or 200 km did not improve the result so this calibration should probably be made in a more exposed area than within the Baltic Sea.

GIS has for some time been an important tool for planning activities in municipalities and elsewhere, and has recently become a tool also for coastal ecology research. For prediction of shallow benthic habitat grids are often used in overlay analysis where each map layer represents a different structuring factor (Bushing 1994, Bekkby et al. 2002, Isæus & Lindblad manuscript). The wave exposure grid layer described in this study may be used as such a layer. However, the described GIS-method should not be used as guidance for building projects since it only describes average conditions, and rare events may cause strong wave impact at unexpected sites.

Acknowledgments

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Table 1. The species measures from the inventory, i.e. their upper or lower boundary, abbreviations used in Figure 2, included or excluded in the biological wave exposure index, and their PC1 values from the principle component analysis (PCA). Five of the 13 measures were used for the biological wave exposure index (bold).

Taxa	Boundary	Abbreviation	Used for index	PC1 score
Calothrix scopularum (Weber et Mohr) C.Agardh	lower	CALO_L	excluded	-
C. scopularum	upper	CALO_U	excluded	0.47
Verrucaria sp. Schrad.	lower	VERR_L	excluded	0.44
Verrucaria sp.	upper	VERR_U	excluded	0.42
Caloplaca marina (Wedd.) Zahlbr. In Du Rietz	lower	C_MAR_L	**included**	**0.85**
C. marina	upper	C_MAR_U	**included**	**0.91**
Caloplaca scopularis (Nyl.) Lettau	lower	C_SCOP_L	**included**	**0.93**
C. scopularis	upper	C_SCOP_u	**included**	**0.96**
Xanthoria parietina (L.) Th. Fr.	lower	XANT_L	**included**	**0.82**
X. parietina	upper	XANT_U	excluded	0.20
Aspicilia sp. A. Massal.	lower	ASPI_L	excluded	0.35
Neofuscelia pulla (Ach.) Essl	lower	NEO_L	excluded	0.43
Physcia caesia (Hoffm.) Fürnr.	lower	PHYS_L	excluded	0.47

Table 2. The correlation results between different calculations of wave exposure and the biological exposure index. The calculations are summarized as the *Mean*, or the *Largest* values of each of 16 fetch/wind directions$_{(d)}$ of adjusted fetch and wind data. *mean* is the mean, and *max* is the maximum wind recorded (*W*). (n = 43)

Mean of	Fetch_d	$r = 0.852$	$p < 0.001$
Largest of	Fetch_d	$r = 0.793$	$p < 0.001$
Mean of	$(\text{Fetch}_d * (W_{mean})_d)$	$r = 0.854$	$p < 0.001$
Mean of	$(\text{Fetch}_d * (W^2_{mean})_d)$	$r = 0.853$	$p < 0.001$
Largest of	$(\text{Fetch}_d * (W_{mean})_d)$	$r = 0.803$	$p < 0.001$
Largest of	$(\text{Fetch}_d * (W^2_{mean})_d)$	$r = 0.802$	$p < 0.001$
Mean of	$(\text{Fetch}_d * (W_{max})_d)$	$r = 0.850$	$p < 0.001$
Mean of	$(\text{Fetch}_d * (W_{max}^2)_d)$	$r = 0.842$	$p < 0.001$
Largest of	$(\text{Fetch}_d * (W_{max})_d)$	$r = 0.805$	$p < 0.001$
Largest of	$(\text{Fetch}_d * (W_{max}^2)_d)$	$r = 0.808$	$p < 0.001$

Table 3. The three highest and three lowest PC1 values compared to the degree of wave exposure (subjectively estimated as four classes; very exposed, exposed, sheltered, very sheltered), and the aspect (16 directions), of the sites respectively.

Highest PC1 value	Subj, exp.	Aspect	Lowest PC1 value	Subj, exp.	Aspect
3.96	very exposed	SE	-1.27	very sheltered	NW
2.00	very exposed	SSW	-1.21	very sheltered	SW
1.90	very exposed	WSW	-1.17	very sheltered	SW

Figure legends

Figure 1. The principles of the fetch calculation shown for a southerly wind/wave direction. a) The fetch values increase with one cell size (10 m) for each step in the wind/wave direction (block arrow). b) To mimic refraction and diffraction effects values from behind-to-the-sides are used instead of from just behind according to Formula 1. c) When the adjacent pixels on the side were land pixels the values from just behind and from behind on the opposite side were used.

Figure 2. Wave crests redrawn from aerial photographs (dark lines) used for coarse calibration of refraction/diffraction patterns of the fetch model. Waves from the south.

Figure 3. The study area located in the southern Stockholm archipelago, Sweden.
• = calibration sites (n=43), o = validation sites (n=34)

Figure 4. Biplot from the PCA analysis. The 5 encircled lichen measures were selected for the biological wave exposure index.

Figure 5. The resulting wave exposure grid in the Askö – Lacka area, southern Stockholm archipelago, Sweden (10 m cell size). Legend shows modelled wave exposure values (m^2s^{-1}).

Figure 6. The correlation between biological wave exposure index (PC1 scores) and modelled wave exposure values of the validation site.

Figure 1.

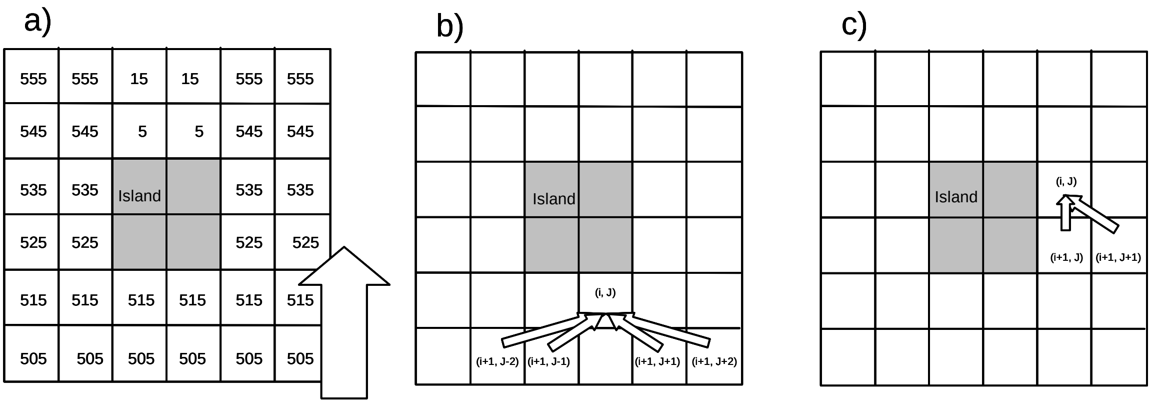

a)
555 555 15 15 555 555
545 545 5 5 545 545
535 535 Island 535 535
525 525 525 525
515 515 515 515 515 515
505 505 505 505 505 505
b)
Island
(i, J)
(i+1, J-2)
(i+1, J-1)
(i+1, J+1)
(i+1, J+2)
c)
Island
(i, J)
(i+1, J)
(i+1, J+1)

Figure 2.

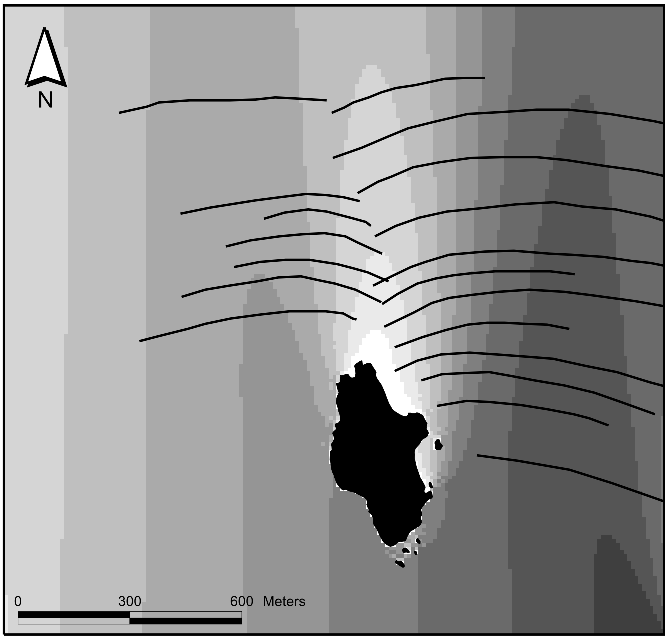


Figure 3.

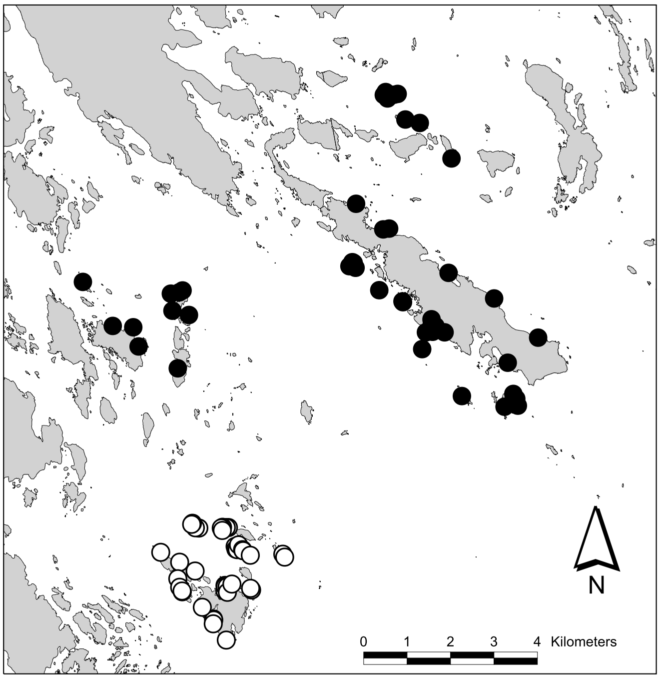
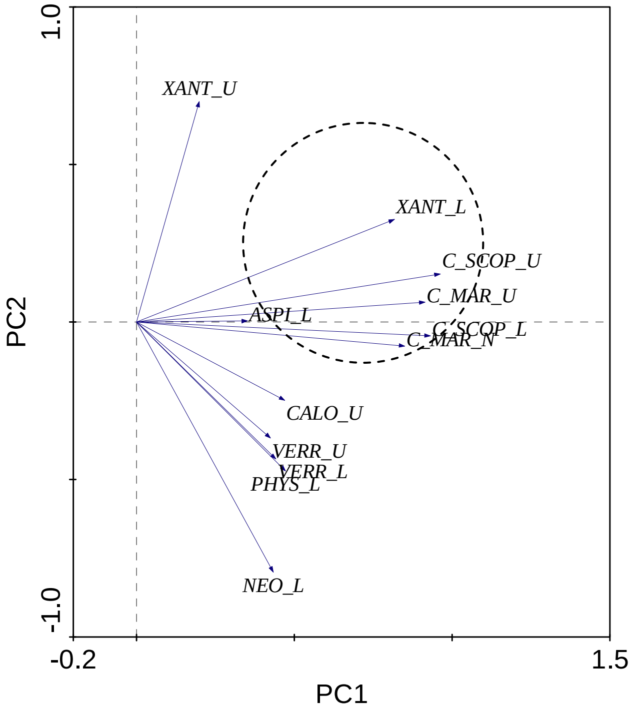
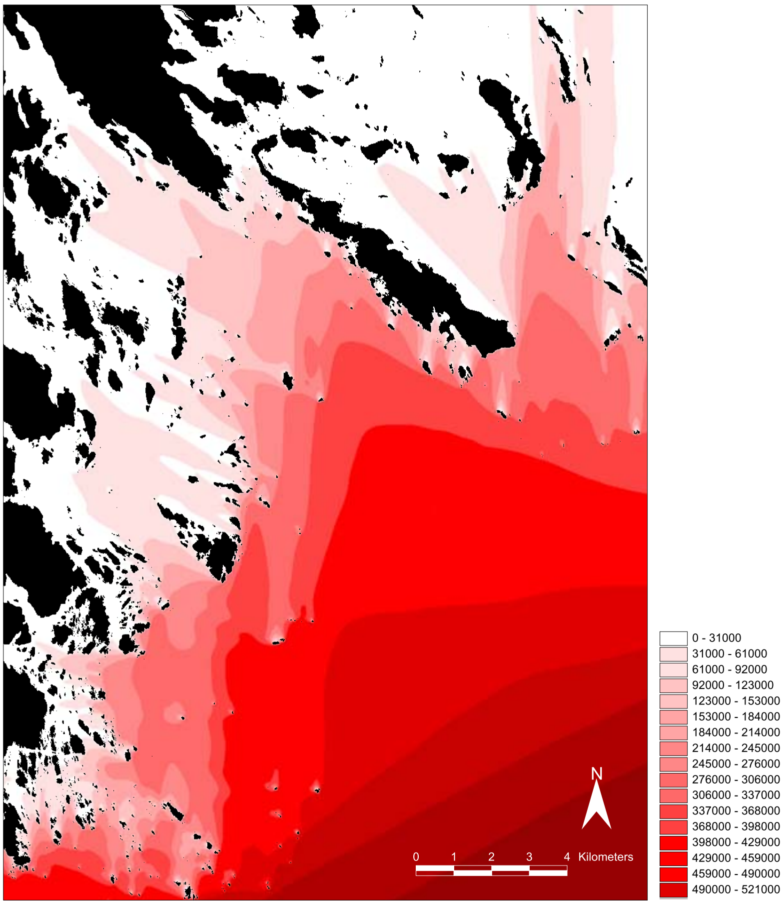


Figure 4.



1.0
-1.0
PC2
-0.2
1.5
PC1
XANT_U
XANT_L
C_SCOP_U
C_MAR_U
ASPI_L
C_SCOP_L
C_MAR_N
CALO_U
VERR_U
VERR_L
PHYS_L
NEO_L

Figure 5.


N
0
1
2
3
4
Kilometers
0 - 31000
31000 - 61000
61000 - 92000
92000 - 123000
123000 - 153000
153000 - 184000
184000 - 214000
214000 - 245000
245000 - 276000
276000 - 306000
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337000 - 368000
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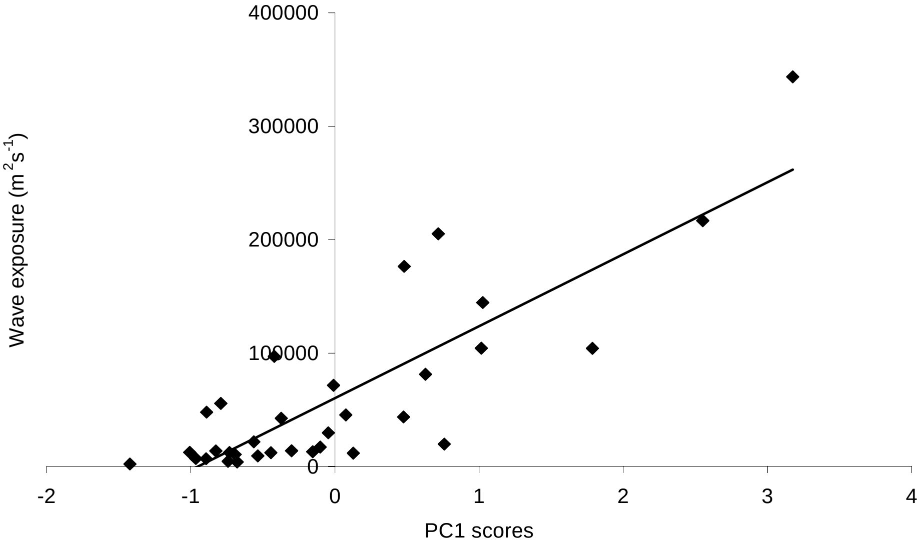
459000 - 490000
490000 - 521000

Figure 6.


400000
300000
200000
100000
0
Wave exposure (m2s-1)
-2
-1
0
1
2
3
4
PC1 scores

Morphological variation of *Fucus vesiculosus* caused by wave action, or by factors correlated to waves?

Abstract

The morphology of *Fucus vesiculosus* is considered to be different at sites of different degrees of wave exposure. However, the causal relationship between wave exposure and *F. vesiculosus* morphology is not clear. This is because other possible predictor variables, such as nutrients and temperature, may covary with wave exposure in archipelago areas. In this study the aim was to: (1) find potential correlations between wave exposure and water property parameters in Stockholm archipelago, (2) study morphological variation of *F. vesiculosus* at sites over a wave exposure gradient in the Stockholm southern archipelago, and (3) separate effects of waves on *F. vesiculosus* morphology from those caused by other potential factors. The field study on *F. vesiculosus* morphology was designed to control for possible differences in water chemistry parameters while examining effects of waves. There were significant correlations between wave exposure and temperature, salinity, total-P, NH_4, total-N and chlorophyll *a*. *Fucus vesiculosus* were generally taller with wider thalli, longer distances between dichotomies and fewer vesicles at sheltered compared to more exposed sites. However, when differences of water properties between sites were controlled for, only effects on thallus width were significant. The casual relationship between wave exposure and *F. vesiculosus* morphology is discussed, as well as the problem of multicollinearity of environmental parameters in archipelago areas.

Keywords

Wave exposure, multicollinearity, morphology, macroalgae, the Baltic Sea

Introduction

Sessile organisms, like macroalgae and sea anemones, depend on fluid passing over their tissues for gas exchange, nutrient or food uptake, removal of waste substances and dispersal of their gametes or young (Denny & Shibata 1989, Hurd 2000). But they also risk being damaged or dislodged by waves, or by ice, sediment or other objects that are carried by waves (Denny 1985, Seymour et al. 1988, Kiirikki 1996, Vadas et al. 1999). These positive and negative effects of wave action have led to great variation in morphology of organisms found at sites of different exposure. For example, macroalgal fronds are often broader, undulated, and thinner in sheltered areas compared to more elongated and thicker blades in exposed areas (Koehl & Alberte 1988, Gaylord et al. 1994, Friedland & Denny 1995, Blanchette et al. 2002).

Size-related characters (e.g. length, thallus width, and distance between dichotomies) are also affected by growth. Several parameters have been suggested to affect macroalgal growth e.g. salinity (Kamer & Fong 2001), temperature (Steen & Scrosati 2003), nutrients (Lehvo et al. 2001), light environment (Makarov 1999), water movement (Sjøtun et al. 1998). If environmental parameters are correlated with the degree of wave exposure, then it may be difficult to separate the effects of waves on growth or morphology from the effects of other factors. Growth rate of macroalgae has been shown to be higher in a sheltered site (Knight & Parke 1951), at intermediate wave exposure (Cousens 1982), and at high wave exposure (Sjøtun et al. 1998). The growth of Baltic *Fucus vesiculosus* L. has been shown to vary considerably, both between and within sites (Bonsdorff & Nelson 1996).

Baltic *F. vesiculosus* is known to differ morphologically between sites of different wave exposure (Waern 1952, Wallentinus 1979, Bäck 1993, Kalvas & Kautsky 1993). Bäck (1993) examined nine morphological characters using principal component analysis (PCA) and stepwise discriminant analysis to find inter-population variation of *F. vesiculosus* morphology between sites of different wave exposure. She found that plant length, thallus width, midrib and plant width, and distance between dichotomies were most important. Another often described pattern is that *F. vesiculosus* lacks vesicles at the most exposed sites (Waern 1952, Wallentinus 1979). Similarly, in a study by Kalvas and Kautsky (1993) Baltic *F. vesiculosus* individuals were significantly taller, heavier and had broader thalli at the most sheltered site compared to the most exposed.

The freshwater outflow from Lake Mälaren decreases the salinity as well as increases the concentration of nutrients in the water of the inner Stockholm archipelago in the northern Baltic Sea proper. The inner part of the archipelago is also more sheltered from the open sea compared to the outer parts, and covariation between wave exposure, salinity and nutrients could therefore be expected. Water transparency, measured as the Secchi-depth, has been shown to correlate with wave exposure (Isæus & Lindblad manuscript), phosphorous and nitrogen in the Stockholm archipelago (Elmgren & Larsson 2001), indicating that variation among environmental variables (multicollinearity) is an important feature of this area. Precautions can be made in the study design to avoid effects of multicollinearity, which was done in the present study.

The aims of the present study were (1) to examine if there are correlations between wave exposure and water property parameters in Stockholm archipelago, (2) to study morphological variation of *F. vesiculosus* at sites over a gradient of wave exposure in the Stockholm southern archipelago, and then (3) to try to separate effects of wave exposure on *F. vesiculosus* morphology from effects caused by water property parameters by using a study design in which water property parameters were controlled for.

Materials and methods

Wave exposure was calculated in a geographic information system (GIS) (Isæus manuscript). The wave exposure was calculated by using the fetch, i.e. the distance of open water in each of 16 directions, multiplied by the mean wind of the corresponding direction. Wind data from Landsort, a metrological station in the Stockholm southern archipelago, were used. Refraction and diffraction effects were also coarsely adjusted for in the model, and the result was a grid showing the pattern of wave exposure variation in the area. For the comparison with water property parameters a grid of 100 m cell size covering the whole Stockholm archipelago was used. For the analysis on *F. vesiculosus* morphology a finer grid of 10 m cell size was used. From these grids a values of the wave exposure (m^2s^{-1}) were extracted for each sampling site.

The samples for the water property analysis were provided by the SUCOZOMA project and were collected during a large survey that covered all large water basins of the Stockholm archipelago. The surface water samples were collected to give an overview of the spatial pattern of water property parameters. All 173 samples were collected within only 7 days, 16-22 August 2001, in order to avoid variation over time.

The algal material was collected 12–17 July 2002 in the Askö area in the Stockholm southern archipelago, Sweden (Fig. 1). The area is located in the NW Baltic Sea proper where the salinity of the surface water is 6.0-6.2 psu. During this sunny period the surface water temperature increased from about 15.5 to 20° C. Nine islands that were considered having free circulation of water around them, but had one side more exposed to the sea than the other, were chosen for the inventory. In four directions, i.e. N, E, W and S around the islands Secchi depth (m), and salinity (psu) and temperature (°C) at 1 m depth, were measured to ensure that the water was homogenous around each island. *Fucus vesiculosus* was surveyed at an interval of 10-50 m along the shoreline around each island at 0.75 and 1.5 m depths. At each sample site the absence or presence of *F. vesiculosus* was noted. If present, the three tallest specimens were collected since they were expected to be most affected by waves. The plants were brought to the laboratory for later measurements of morphological characters. Plants shorter than 15 cm were not collected to avoid a mixture of adult and juvenile specimens.

On each *F. vesiculosus* plant, six morphological characters were measured; 1) *plant length* as the distance between the holdfast and the tip of the longest frond, 2) *thallus width*, measured at a point midway between the youngest and the next youngest dichotomy of the longest frond, 3) *stipe width*, measured at a point midway between the holdfast and the oldest dichotomy, 4) *midrib width*, measured at the same point as the thallus width, 5) *distance* between dichotomies, measured as the mean of three distances between the acute angle of the dichotomy from the second oldest dichotomy upward, and 6) number of *vesicles*. Characters 1-5 were found to be the most important for distinguishing between specimens from sites of different wave exposure levels by Bäck (1993). Analyses were performed on the mean values of the three specimens collected at each sampling site.

Statistical analysis

The correlations between water property parameters and wave exposure were analysed by Pearson product-moment correlations. The wave exposure values were log-transformed. The effects of wave exposure on the six morphological characters were analysed using MANCOVA. One island (number 4) was excluded since *F. vesiculosus* was found only at one sampling site. Initially the variation of *F. vesiculosus* morphology over a wave exposure gradient was analysed using an unblocked design and *wave exposure* as a continuous predictor. In the next step, the design was blocked by using *island* as a factor in order to control for variation of water property between islands, and with only variation of wave exposure within islands. The response variables were tested for homogeneity of variances with Cochran C. test, and no transformations were needed. The relationship between Secchi-depth, temperature and salinity, and the wave exposure at four sides of the inventory islands was analysed by a Pearson product-moment correlation.

Software

The basic GIS software used to handle spatial information in this study was ArcView 3.2 with the extension Spatial Analyst 2.0. An additional script for ArcView, GetGridValue.ave (Elmquist 1998), was downloaded from www.esri.com. Wave exposure calculations were performed using the software WaveImpact 1.0, which has been developed by the author and is described in detail in (Isæus manuscript). The software package Statistica 6.0 was used for the statistical analyses.

Results

Several of the water property parameters correlated with wave exposure in Stockholm archipelago (Tab. 1). As expected, salinity was positively correlated with wave exposure. Temperature, total-P, total-N, NH_4 and chlorophyll *a* all correlated negatively to wave exposure. No significant effects were found between NO_2+NO_3 or PO_4 and wave exposure.

Table 1. Correlations between wave exposure and surface water property parameters in Stockholm archipelago, Baltic Sea. Bold r-values are significant at p<0.05. n=134

	Temp	Salinity	PO4	Tot-P	NO23	NH4	Tot-N	Chl *a*
Wave exposure	**-0.56**	**0.48**	0.13	**-0.35**	-0.13	**-0.29**	**-0.44**	**-0.27**

In the study area the water quality was rather homogenous around the single island with a maximum range (min-max) for salinity of 0.1 psu, for Secchi depth 0.5 m, and for temperature 0.9 °C (Fig. 2). The salinity was stable around 6.1-6.2 psu in the study area. The

Secchi-depth measured at the nine islands correlated positively, and temperature negatively, with wave exposure (R=0.73, $p<0.05$ and R=-0.71, $p<0.05$ respectively, n=36)(Fig. 3 and 4). There was no correlation between salinity and wave exposure (R=-0.08, $p>0.05$, n=36).

Length, *thallus width*, *distance* and number of *vesicles* were negatively correlated to wave exposure when island was not used as a blocking factor. The analysis thus examined among as well as within island variation, and did not control for differences in water property between islands (Unblocked MANCOVA in Tab. 2). In contrast, only *thallus width* was significantly negatively affected by wave exposure when island was used as a blocking factor, thus differences in water properties were controlled for (blocked MANCOVA in Tab. 2).

Table 2. The effects of wave exposure on six morphological characters of *F. vesiculosus* analysed by MANCOVA. Differences of water properties between islands were controlled for in the blocked MANCOVA.

	MANCOVA unblocked design	MANCOVA blocked design
Length	**$F_{(1)}$=26.75, p=0.00**	$F_{(1)}$=0.23, p=0.63
Thallus width	**$F_{(1)}$=26.67, p=0.00**	**$F_{(1)}$=5.10, p=0.03**
Stipe width	$F_{(1)}$= 0.17, p=0.68	$F_{(1)}$=0.16, p=0.90
Midrib width	$F_{(1)}$= 1.73, p=0.19	$F_{(1)}$=2.00, p=0.16
Distance	**$F_{(1)}$=18.14, p=0.00**	$F_{(1)}$=0.16, p=0.90
Vesicles	**$F_{(1)}$=20.30, p=0.00**	$F_{(1)}$=0.06, p=0.80

Discussion

Several water property parameters correlated with wave exposure in the Stockholm archipelago (Tab. 1). The general notion that water property parameters and wave exposure tend to correlate in the Stockholm archipelago was confirmed. This is essential to consider when variation along the wave exposure gradient is interpreted. However, neither NO_2+NO_3

or PO_4 that are considered important for limiting vegetation growth (Gerard & Mann 1979) were correlated to wave exposure.

The waters surrounding each island in the study area were rather homogenous, but the variation between the islands was much greater which may reflect spatial as well as temporal variation (Fig. 2). For example the water temperature increased considerably during the inventory period (islands in chronological inventory order in Fig. 2), although this trend may be reinforced by the fact that the last islands visited (8 and 9) were situated in a relatively sheltered and shallow area where the water temperature should increase faster than in an open area (Fig. 1). Temperature was negatively, and Secchi-depth positively correlated with wave exposure in the study area, but the salinity was stable and not correlated to wave exposure (Fig. 3 and 4). The salinity range is greater in the whole Stockholm archipelago compared to the study area which may explain the two different results. Even though nutrient concentrations were not measured during the inventory it is reasonable to believe that nutrient levels are higher at sheltered sites in the study area since water total-P and total-N concentrations correlate well with Secchi-depth in the nearby Himmerfjärden Bay (Elmgren & Larsson 2001), which also would correspond to the pattern of the whole Stockholm archipelago.

In accordance with earlier studies (Bäck 1993, Kalvas & Kautsky 1998), *F. vesiculosus* were shorter, had narrower thalli, and shorter distances between dichotomies and fewer bladders at more exposed sites (Tab. 2). These results may be caused by wave exposure or by factors correlated with wave exposure. The main reason for the spatial design of the inventory was to detect effects of wave exposure on *F. vesiculosus* morphology and to avoid effects due to variation in water properties. When controlling for differences of water properties between islands only thallus width was significantly correlated to wave exposure (Tab. 2). The variation of thallus width is then considered an effect of wave exposure, but it can not be ruled out that waves also affect length, number of vesicles and distance between dichotomies. This is because the blocked design also controls for differences in wave exposure levels between islands. This is illustrated by a diagram (Fig. 5) where the mean wave exposure is plotted against the mean thallus length recorded at the studied islands. The negative trend of means shown in the diagram is neglected as a result of the study design. The large horizontal standard deviation is indicative of the desired large range of wave exposure caused by the selection of islands with one side more exposed to the sea than the other. However, the large variation of plant length indicated by the vertical whiskers was not significantly correlated to the variation of wave exposure within islands. The growth of *F. vesiculosus* in the Baltic varies considerably, both within and between sites (Bonsdorff & Nelson 1996), and the variation in length may be a result of that. The lengths of the longest *F. vesiculosus* specimen measured at a site may represent the maximum size a thallus can have before it is ripped off by the waves, although the length may also be a result of growth.

It has been argued that benthic macroalgae are not growth limited by nutrients in the Askö area due to excessive excretion from mussels *Mytilus edulis* L. (Kautsky & Wallentinus 1980). Gerard & Mann (1979) measured water movement, NO_3+NO_2 content of the water and morphological characters of *Laminaria longicruris* de la Pylaie in a study in Nova Scotia, Canada. They found significantly narrower and thicker blades at the exposed site compared to the sheltered site, even though the NO_3+NO_2 content of the water was about equal at both sites. In a transplantation experiment they showed that *L. longicruris* plants moved from an exposed to a sheltered site produced broader and thinner blades than before the transplantation indicating phenotypic plasticity. Plants moved from the sheltered to the exposed site were torn apart, leaving only stipes and holdfasts. Although dissolved nitrogen is only one out of several environmental variables that possibly would affect macroalgal morphology, it was considered important as it was the growth limiting nutrient in the area, which makes the effects more likely a result of wave exposure. The larger area of *L. longicruris* blades in sheltered areas provided 3x more photosynthetic area/unit wet weight, which explained the higher growth rate even though concentrations of ambient NO_3+NO_2 were equal at the sites (Gerard & Mann 1979). In another transplant experiment (Blanchette 1997), *Fucus gardneri* individuals moved from an exposed to a protected area did not grow longer compared with reference individuals during the experiment period, and individuals reciprocally transplanted did not show a change in length either. However, the mean area of individuals increased when moved from the exposed to the protected area, and decreased by being tattered when moved the other way around. In accordance with these results the wider thalli found at sheltered sites in the present study may be a result of the less stress-full wave environment. The growth may be higher in sheltered areas, which was indicated by greater distance between dichotomies and longer plants. This result is in accordance with growth measurements of *F. vesiculosus* in Great Britain (Knight & Parke 1951).

The design used in this study to control for differences between islands was justified by the correlations between wave exposure and water property parameters. Even without those correlations attempts should be made to avoid multicollinearity in order to facilitate interpretation of the results. However, to be able to analyse the effects of different parameters directly these parameters should be measured at the sampling sites, which not was done in this study. Multicollinearity may not be possible to avoid in such studies but there are methods to deal with the problem (Graham 2003).

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Figure legends

Figure 1.
The location of the study area in the Baltic Sea (left map). Nine islands (encircled and numbered on the right map) with one side more exposed to the sea than the other, and surrounded by freely circulating water, were investigated.

Figure 2.
The range (min-max) of Secchi-depth, salinity and temperature measured at four sides (N, E, S, W) around each island. Island numbers in inventory order.

Figure 3.
Correlation between Secchi-depth and wave exposure at the surveyed islands.

Figure 4.
Correlation between temperature and wave exposure at the surveyed islands.

Figure 5.
Means of thalli length (±SD) per island (y-axis) plotted against means of wave exposure (±SD) at the corresponding sampling sites (x-axis).

Figure 1.

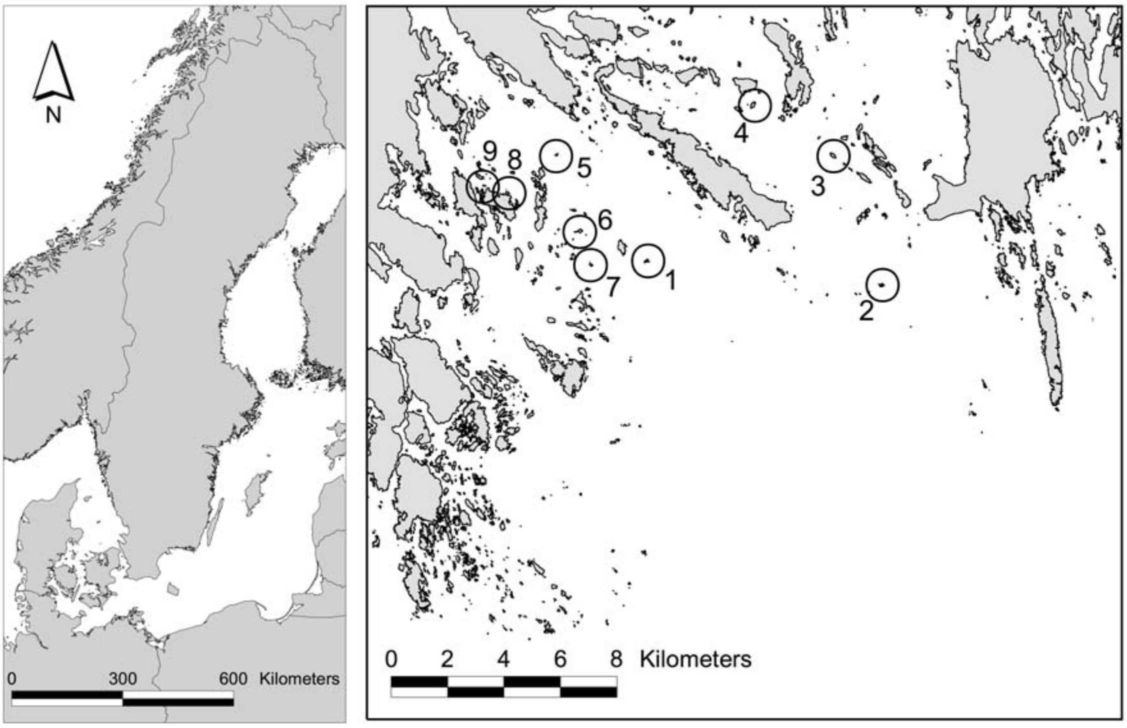
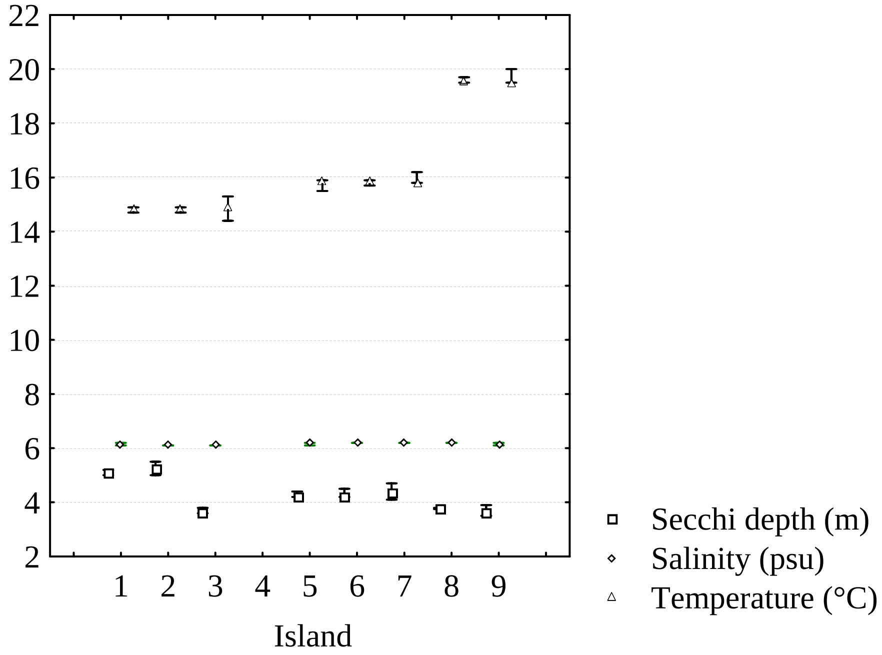


Figure 2.


22
20
18
16
14
12
10
8
6
4
2
1
2
3
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6
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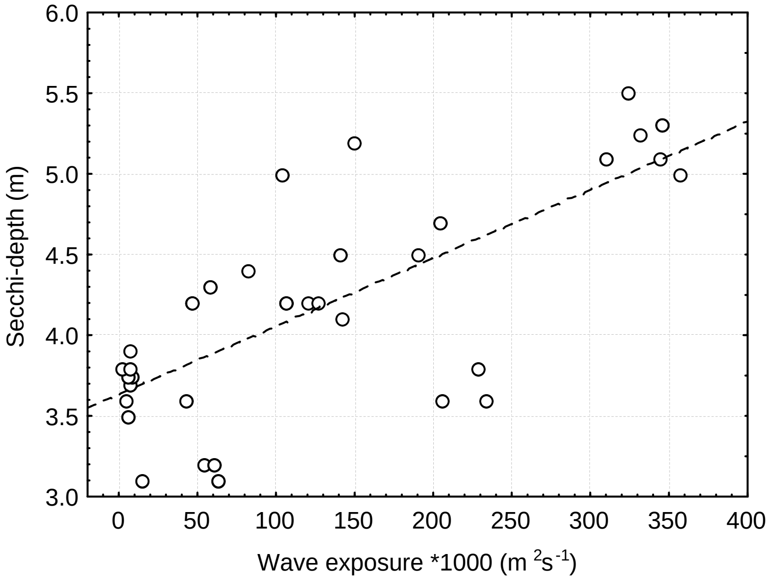
9
Island
Secchi depth (m)
Salinity (psu)
Temperature (°C)

Figure 3.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5.5
5.0
4.5
4.0
3.5
3.0
Secchi-depth (m)
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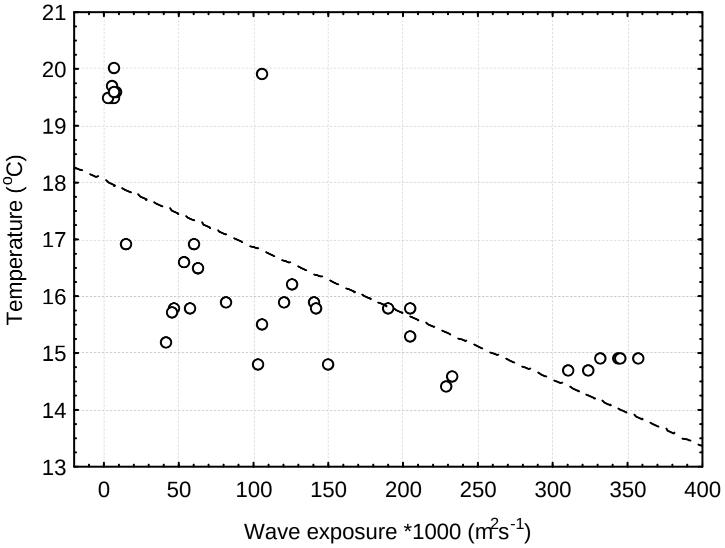
50
100
150
200
250
300
350
400
Wave exposure *1000 (m ^{2}s^{-1})

Figure 4.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17
16
15
14
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Temperature (^oC)
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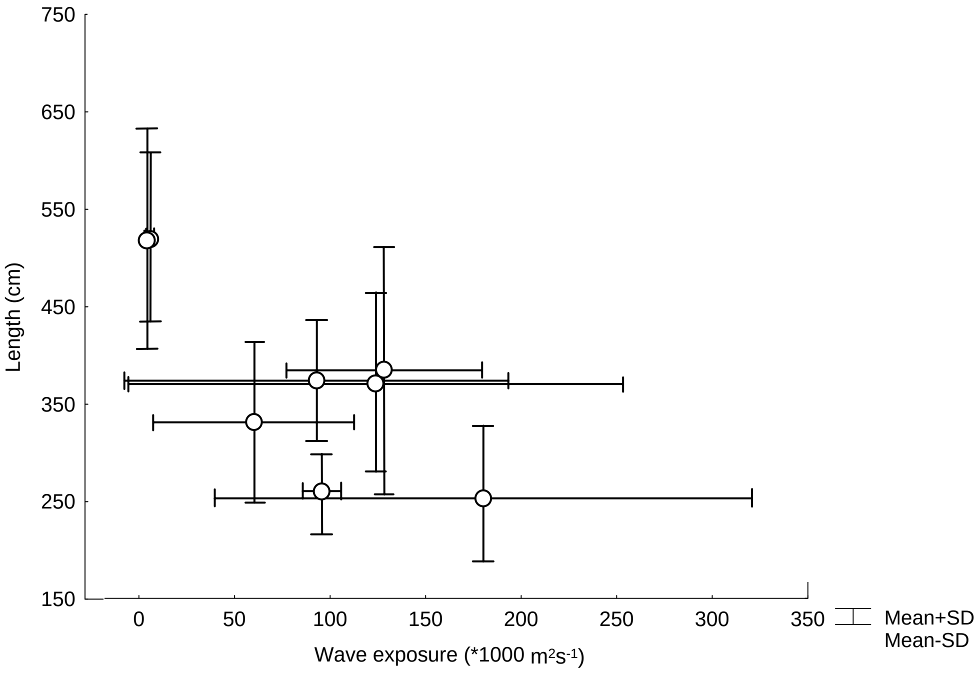
250
300
350
400
Wave exposure *1000 (m^2s^{-1})

Figure 5.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650
550
450
350
250
150
Length (cm)
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50
100
150
200
250
300
350
Wave exposure (*1000 m²s⁻¹)
Mean+SD
Mean-SD

Effects of salinity and geomorphology on the structure of macroalgal communities in the central Baltic Sea.

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Abstract

Two brown seaweeds *Fucus serratus* and *Fucus vesiculosus* are forming stands along the shores of the central Baltic Sea. The hypothesis of the present study was that temporal and regional variations in salinity together with regional differences of geomorphology affect the dominance of the two species. Biotic factors such as competition from filamentous algae may also be important. Extended manta tow diving and observations from a skiff with transparent shutters in the hull was used to map the distribution of macroalgae on different substrate types. Estimations of *Fucus* recruitment and turf biomass were also performed. The results show significant differences in *Fucus* vegetation between regions and substrate types. Both *Fucus* species were most abundant in the southern compared with the northern regions. *Fucus serratus* were significantly more abundant on bedrock than on boulders. The distribution pattern is assumed to be set mainly by regional differences in geomorphology. The results are discussed in relation to salinity tolerance, eutrophication, life history, and interspecific competition.

Keywords: bedrock, boulder, competition, *Fucus vesiculosus, Fucus serratus*, limestone, life history, *Polysiphonia*, recruitment, substrate.

1. Introduction

The two most important factors regulating macroalgal diversity in the brackish and non-tidal Baltic Sea are salinity and geomorphology (Middelboe et al. 1997) and the most productive and diverse community on rocky shores in the littoral zone is assumed to be the *Fucus* spp. belts (Kautsky 1991). In the central part of the Baltic Sea, these *Fucus* belt is made up of two species, *Fucus serratus* L. and *Fucus vesiculosus* L. (Malm 1999). Other fucoid or kelp species are only found in the southernmost part of the basin (Schueller and Peters 1994, Schaffelke et al. 1996).

In the Baltic Sea, both *Fucus* species have substantially higher tolerance to low salinity compared with Atlantic populations (Serrão et al. 1999, Malm et al. 2001). The geographical distribution of both species is nevertheless assumed to be set by infertility caused by the decreasing salinity towards the north (Serrão et al. 1999). *Fucus vesiculosus* in the Baltic Sea is able to successfully reproduce in water down to four psu (Serrão et al. 1999) while the germination of *F.serratus* zygotes is very low in water with less than approximately seven psu (Malm et al. 2001). The limit for *F.serratus* distribution is found in the central Baltic proper (Malm et al. 2001) while *F.vesiculosus* extends to the northern Quark in the Bothnian Bay 700 km further to the north (Pekkari 1973). At least for *F.vesiculosus,* the physiological limit for photosynthesis is 2.5 psu lower than the limit for fertilisation, (Bäck et al. 1992) and dense stands can be found close to the distribution limit of each species (Raven and Samuelsson 1988, Malm et al. 2001).

The geology of the sea floor in a coastal area provides variable surfaces for establishment and growth of bentic organisms, which may be of importance for the structure of the macroalgal community. Both small and large-scale texture of rocky surfaces has been pointed out as important factors in macroalgal species composition and biomass production (McGuinness and Underwood 1986, Wells et al. 1989). Optimum bedrock relief have been linked to different sizes of algal propagules (Fletcher and Callow 1992). Green algae, which have comparatively small propagules, have higher survival at a smoother relief than do the larger propagules of brown or red algae. At moderately exposed sites in the Strait of Kalmar, central Baltic Sea, Malm et al. (2003) observed significantly higher population densities of *F.vesiculosus* on Cambrian sandstone than on crystalline bedrock, i.e. amphibolites and granite rock. At wave-exposed stone-reefs, size and form of the boulders (i.e. flatness) are positively correlated with biomass of perennial macroalgae (Sousa 1979). Areas in the Baltic Sea dominated by rocky shores have a higher macro algal diversity than areas dominated by glacial moraine deposits (Middelboe et al. 1997).

In the central Baltic Sea, where the salinity normally is sufficient for full fertilisation of both *Fucus* species, a sharp zonation of the two species is found at exposed shores (Malm and Kautsky 2003). *Fucus vesiculosus* grow constantly submerged from 1 - - 2.5 meters depth and *F.serratus* grow deeper from 2.5 meters down to 10 - -12 meters depth. Sweeping of the leathery *F.serratus* thallus eradicate *F.vesiculosus* juveniles at exposed sites (Malm and Kautsky 2003), but in the shallowest zone, 0 - - 2 meters depth, disturbance factors as desiccation, freezing, wave tearing, ice scraping, or fluctuating salinity may alter the competitive outcome and favour *F.vesiculosus* over *F.serratus* (Malm and Kautsky 2003). This higher tolerance to physical stress of *F.vesiculosus* compared with *F.serratus* may also be explained by the ability of *F.vesiculosus* to regenerate from holdfast traces, a capacity that *F.serratus* lacks (Malm and Kautsky 2003). Contrariwise, Engkvist et al.(in press) suggest that grazing by the abundant isopod *Idotea baltica* Pallas may favour *F.serratus* over *F.vesiculosus* since *I. baltica* seems to prefer *F.vesiculosus* as food and shelter to *F.serratus.* In areas along the Swedish south coast, *F.serratus* stands persisted several years after *F.vesiculosus* stands were eradicated by grazers (Engkvist et al. in press).

Although *F.serratus* and *F.vesiculosus* are the only large perennial algal species in the Baltic Sea, several filamentous brown, green and red algal species also occur, (Wallentinus 1978). They compete with the larger perennial algae and are more efficient in their nutrient uptake since their surface/volume ratio is larger (Wallentinus 1984). Dense cover of filamentous algae prevents settling and attachment of perennial fucoids (Hruby and Norton 1979) and increases the early post-settlement mortality (Vadas et al. 1992). In addition, bentic filamentous algae have the ability to entrap large amounts of sediment, which may further decrease the settling ability and post settlement survival (Airoldi 1998). Since the 1940s, human activities have raised the concentrations of inorganic nitrogen three times and phosphorous five times in the surface water of the Baltic Sea (Larsson et al. 1985, Rosenberg et al. 1990). Consequently, the production of filamentous macroalgal species has increased (Kiirikki and Blomster 1996) with detrimental effects on the populations of *F.vesiculosus* (Berger et al. 2003) and *F.serratus* (Isaeus et al. in prep).

The aim of the study presented was to estimate the abundance of *F.vesiculosus*, *F.serratus* and filamentous algae in the central Baltic Sea, an area that so far have been poorly investigated. In the study, we also tested the hypothesis that salinity (i.e., north-south gradient) and geomorphology are the most important factors determinants for the vegetation structure on a regional scale. Extensive field investigations of macroalgal cover and *F.serratus* population structure were performed at the eastern sides of the large islands Gotland and Öland, central Baltic Proper during the years, 2000-2003.

2 Material and methods

2.1 Study areas

Field studies of macroalgal cover were performed outside the eastern shore of the island Öland in July 2000 and April 2001 and outside the eastern shore of the island Gotland in July 2001, in the brackish and non-tidal central Baltic Sea (Fig. 1). The seafloor substrate in both regions consists of smooth limestone bedrock partly covered by glacial moraine deposits of crystalline origin, ranging in grain size from sand to boulders. The sedimentary limestone bedrock is of Ordovician origin at Öland and Silurian at Gotland. The seafloor at both islands gently slopes eastward and ten meters depth is reached about one kilometre off the shore (Lidmar-Bergström 1994). For the statistical analysis, the shore area of Öland was divided into three regions based upon geomorphology of the coast and seafloor, i.e., open coast with dominance of limestone bedrock in the south, open coast with dominance of moraine deposits in the central part and a relatively broken coast with sandy moraine deposits in the north. The coastline of Gotland was more arbitrary divided into three equally large parts with similar geomorphology.

The salinity in the surface water of the central Baltic Sea is stable over years but declines slowly northwards from in average, 7.3 psu at southern Öland to in average 7.1 psu outside northern Gotland. The temperature of the surface water of the Baltic Sea range from 0 - - 3 ∞ C during winter to 12 - -17 ∞ C in summer (Juhlin 1992).

2.2 Methods

During three weeks in July 2000, approximately 110 km seafloor transects were investigated from south to north at eastern Öland, at an average depth of 7 +/- 1 m. In April 2001, 70 km seafloor transects were examined from south to the middle of eastern Öland, at 2.5 +/- 1 meters depth. In July 2001, twenty transects transverse to the coast (1 - - 10 m depth) were investigated from north to south at the eastern shore of Gotland (Fig. 1).

Manta tow diving was used for mapping the distribution of seaweed species along the transversal transects at Gotland and the alongshore transects at seven meters depth at Öland. The manta tow diver was dragged in 30 m long rope behind a boat with a speed of two to three knots. The diver was equipped with a facemask and a cable-connected communication devise that made it possible to continuously report observations to the skipper of the towboat. The transect width i.e., how far it was possible to observe at each side ranged between two to five meter depending of the transparency of the water. A new observation was reported each time the depth, substrate, or vegetation composition changed. The depth was measured by the diver with a diving computer (Mosquito Suunto Ltd). The observations were noted by the skipper together with the actual position obtained from a GPS (Garmin GPS 12 XL). The position of the diver was later calculated from the length of rope and the depth at the observation point. The degree of sand, gravel, boulders, and flat rock were estimated on a four-graded scale. To distinguish between different types of moraine fractions the Udden-Wentworth grain-size scale was used i.e. boulder > 0.25 m in diameter, gravel 0.25 - - 0.04 m diameter, and sand < 0.04 m diameter (Wentworth 1922). By this survey method, it was possible to accurately distinguish between the two *Fucus* species but not between the algal species in the filamentous turf. The degree of cover of dominating species i.e. *F.vesiculosus, F.serratus,* and turf were estimated as one, five, 10, 25, 50, 75, and 100 % cover. Twenty-five percent cover or more was considered a stand (Jansson and Kautsky 1977). Bare substrate was rare but was also reported when it occurred.

A small skiff, equipped with two 0.5 m - - 2 large windows in the hull, was used for alongshore observations at two and a half meters depth at Öland. The observer was lying in his full length on the deck of the boat, covered by a dark tarpaulin to reduce reflexes. Sea floor type and vegetation structure were observed as in the manta tray investigation. Depth was recorded by an ordinary eco sounder. The speed of the boat was approximately two to three knots.

Sampling of the algal turf for biomass and species composition was done during July 2000 at five meters depth at three sites off the shore of Öland and at four sites off the shore Gotland (Fig. 1). At each site all biomass in five 0.04 m - - 2 large frames were collected. The material was brought to the laboratory, sorted into species, and dried to constant weight at 60 ∞ C. Customary SCUBA diving technique was used for the field sampling.

The density and size distribution of *F.serratus* fronds at seven meters depth in three different areas, off the shore of eastern Öland were estimated in July 2003. One population in the northern region growing on large boulders (approx. one m in diameter) was compared with two populations in the southern region. In the south, one population was growing on large boulders and one was growing on clean swept limestone bedrock. The length in centimetre of all individuals at each area was measured in five, 0.25 m - - 2 large areas with approximately 10 m interspaces. SCUBA was used to accomplish this part of the study.

2.3 Statistics

All transects were divided into fifty meter long sections. These sections were the basic statistical units in the analysis. All transects covering two or several sea floor types or having larger internal depth differences than one meter were excluded from the material. If two transects were adjoining each other, one of them were randomly excluded. As a result, the minimum distance between two transects in the statistical analysis was 50 meter. The fraction (%) of each section covered by one or more types of algal vegetation dense enough to form a stand (25 % cover or more) was calculated. The dependent factors *Fucus* and algal turf cover were tested against the independent factors substrate (boulder and bedrock) and region (north, central, and south) with two-way analysis of variance (ANOVA). The association between *Fucus* cover and turf-algal cover was analysed with correlation analysis. The differences in population size structure between *F.serratus* populations growing on boulders and bedrock and between populations growing in northern and southern Öland were analysed with pair wise Chi square analysis (expected vs. observed frequency). The data were grouped in to size classes with 3 cm class width from 1 to 50 cm plant length. All data given in percent were arcsinqrot transformed to approximate normal distribution before analysis. The homogeneity of the variances was tested with Levin's test and further transformed if necessary. Standard error has throughout the text been used to estimate the average error in the estimation of the population mean. For all statistical analysis, Statistica (99 edition) was used.

3 Result

3.1 Öland

Along the eastern shores of Öland, algal turf was the dominating vegetation at all sites and at all investigated depths. Eleven algae species were found, one green, four brown and six red (Tab. 1). At five meters depth, the red alga *Polysiphonia fucoides* was the dominating species at all sites (Tab. 1).

At seven meters depth, the cover of the algal turf was similar between three regions (87.4 +/- 2.3 % [S.E]) while on two and a half meters depth the total turf algal cover was lower in the southern region (40.0 +/- 3.2 %[S.E]) compared with the central region (85.6 +/- 1.8 %[S.E]) (Two-way ANOVA, $F = 116.46_{(2,862)}$, $p < 0.001$). No significant difference in turf cover between boulders and bedrock was found. The turf cover was negatively correlated with *F.serratus* cover in the southern (Correlation analysis r= -0.53, $p < 0.001$) and central region (Correlation analysis, r= -0.55 $p < 0.001$) but not in the northern region.

The cover of mono-specific *F.serratus* stands on seven meters depths declined northwards (Two-way ANOVA, $F=13.62_{(2,862)}$, $p < 0.001$) but the abundance was in all three regions larger on limestone bedrock than on crystalline rock boulders (Two-way ANOVA, $F= 3.26_{(2,862)}$, $p=0.04$) (Fig. 2). The total *Fucus* cover was similar at shallow and deep sea floors in the southern region but lower at shallow than deep sea floors in the central region (Tukey HSD test, $p < 0.001$) (Fig. 2 and 3). In the southern region, the total cover of *F.vesiculosus* and *F.serratus* was not significantly different at two and a half meters depth. However, on limestone bedrock *F.serratus* was more abundant than *F.vesiculosus* (Tukey HSD test, $p < 0.001$) while on boulders no significant difference between the two species was found (Fig. 3). Occasional *F. vesiculosus* speciemen occurred at 7 m in most of the transects, in all regions but in no transect the cover exceed 25 %, e.g., no F.vesiculosus stands were found.

The density and size distribution of fronds in three different *F.serratus* populations, growing at seven meters depth off the shore of eastern Öland, is presented in (Fig. 4). One population in the northern region growing on a boulder field was compared with two populations in the southern region, one population were growing on a boulder field, and one population were growing on limestone bedrock. The relative size distribution of fronds (%) was significantly different between the northern boulder population and both the boulder population ($\chi2=25.6$, df=15, $p=0.04$) and the bedrock population ($\chi2=38.6$, df=15, $p< 0.001$) in the south, with relatively more small individuals in the southern populations compared with the northern population (Fig. 4). No significant difference was found between the two populations in the south.

3.2 Gotland

Similar to Öland, algal turf was the dominating vegetation in all regions and at all investigated depths (0-10 m) at Gotland. Twelve algal species were found, one green, four brown and seven red algal species (Tab. 1). At five meters depth, the red alga *Polysiphonia fucoides* was the dominating species in the central and southern region but in the northern region, the perennial red algae *Furcellaria lumbricalis* was the most common species (Tab. 1).

Algal turf with at least 25 % cover dominated 80.6 +/- 1.7 % [S.E] of the bottoms at Gotland. No differences in turf cover between boulder dominated or limestone bedrock dominated seafloors were found in any region and the total cover did not significantly change with increasing depth (Fig. 5).

The dominating perennial brown alga on Gotland was *F.vesiculosus* (Fig. 5). Out of twenty investigated transects, *F.serratus* stands were only found in one, situated close to the southern cape of the island. Generally, *Fucus* stands occurred much sparser at Gotland compared to Öland. In the northern region only scattered specimens of *F.vesiculosus* were found but no stands (i.e. more than 25 % coverage) was observed in any transect. In the central region, *F.vesiculosus* stands occurred from the surface down to two meters and in the southern region; stands were observed from the surface down to six meters depth (Fig. 5). No significant difference in *F.vesiculosus* cover between limestone bedrock and boulders was found.

4. Discussion

The stability of the substrate affects the abundance and biomass of marine macroalgae (Sousa 1979), as well as the competitive outcome of sublittoral macro algae, which was described for Antarctica (Kloser et al. 1994) and for the subtropical Caribbean (Littler and Littler 1984). The present study seems to be in accordance with these earlier results. *Fucus serratus* was more abundant on bedrock compared to boulders, when compared at the same depth (Fig. 2). On shallow depths where the effects of waves are evident, *F.vesiculosus* was more common on boulders than on bedrock while the opposite was valid for *F.serratus* (Fig. 3). This distribution pattern probably reflects the morphology and life history of the three species, and the interactions between them. *Polysiphonia fucoides* with its annual growth is a rapid fast-growing colonizer (Wachenfeldt 1984) less dependent of a persistent substrate than the more slowly growing perennial fucoides. *Fucus vesiculosus* has the capacity to regenerate from holdfast remnants (Malm et al. 1999) and thus may survive moderate wave induced disturbance of the boulder substrate while the exclusively sexual reproducing *F.serratus* (Malm and Kautsky 2003) is probably more dependent of a stable substrate than the other species for its survival up to adult age, which in the Baltic sea may take five to six years from settlement (Malm et al. 1999). On stable substrates at exposed sites, *F.serratus* seems on the other hand be a better competitor than *F.vesiculosus*, which is further, discussed below.

Considerable regional differences in *Fucus* vegetation were also found along the eastern shores of the large islands Öland and Gotland in the central Baltic Sea. The two *Fucus* species and particularly *F.vesiculosus* were much less abundant than could be expected from earlier estimations (Kautsky and Kautsky 1995). Only in the southern part of Öland and at some few shallow sites at central and southern Gotland, populations were found dense enough to be defined as stands (> 25% cover). The lack of earlier studies on the distribution of *Fucus* vegetation in these areas makes it impossible to confirm if a general decline has occurred during the last forty years as in many other areas (Kangas et al. 1982, Kautsky et al. 1986, Kautsky 1991, Vogt and Schramm 1991, Eriksson et al. 1998, Engkvist et al. 2000). However there is a substantial amount of evidence from many older informants in the local community that a large decline of the *Fucus* stands does have occurred during the last forty years. Fifty from each other independent informants claims that half a century ago several meter high cast walls of *Fucus* were regularly built up along the shores during the autumn gales. Today these cast walls mainly consists of filamentous red algae (Malm et al. unpubl). We therefore assume that the present *Fucus* populations at Öland and Gotland only are remnants of the earlier distribution.

It is more problematic to establish if this former macroalgal vegetation mainly consisted of *F.serratus* or *F.vesiculosus* stands. The botanical knowledge of our informants usually is not sufficient to distinguish between the two species. From Carl von Linnè (1745) we know that the cast walls at eastern Öland 250 years ago were built up of *F.vesiculosus*. During the last hundred years, the salinity in the central Baltic Sea has slowly fluctuated with more than one per mill around an average of approximately seven (Rhode 2003). Since *F.serratus* needs at least seven per mil for successful reproduction (Malm et al. 2001) the recruitment of the species probably have been restricted by low salinity during extended periods through the last century. The present pattern with *F.serratus* stands found only along the southern parts of the islands may be explained with a declining salinity northwards making successful reproduction less predictable. The differences in salinity are yet small and the salinity in the northern part of the investigated area is still sufficient for successful fertilisation of both *Fucus* species (Malm et al. 2001). The relative size distribution of individuals in the *F.serratus* stands found in the northern region of Öland was significantly different compared the stands found in the southern region with more juvenile individuals in the southern regions compared with the northern. This may be an indication of lower recruitment success in the north compared with the south. If the salinity in the central Baltic proper has increased more rapid during the last hundred years, than the colonisation rate of *F.serratus*, the absence of *F.serratus* stands in the northern parts of the investigated area may be a matter of time, dispersal and recruitment ability. The southbound current at the western side of the Baltic proper and the morphology of *F.serratus* with a thick leathery thallus without bladders probably makes long distance drifting of detached fertile *F.serratus* fronds more problematic than transportation of floating *F.vesiculosus* thallus parts.

Not only substrate, salinity, and time lag but also interspecific competition from other algal species may contribute to create the observed distribution pattern. The eastern shores of Öland and Gotland are unique for the Baltic Sea with extended shallow hard bottoms. Only a fraction of these areas are covered by *Fucus* stands and very little of the bottom is left bare. Most of the stable substrate i.e. boulders and bedrock are covered by a dense mat of turf algae. Sweeping and shading of the adult *Fucus* thalli normally cleans the rocky surface beneath a *Fucus* canopies from competing macroalgae (Kiirikki 1996). In an investigation by Berger et al. (2001) no shallow, adult *F.vesiculosus* stands in the central Baltic Sea were found completely devoid of recruitment even if a large variation occurred among the thirty investigated sites. However, in the absence of adult *Fucus* fronds, thick mats of filamentous algae prevent settling of *Fucus* zygotes (Berger et al. 2003, Isæus et al. in prep). Increased growth of filamentous algae may thus prevent reestablishment of *Fucus* in regions and areas devoid of adult populations, which may be one of the main reasons for the large-scale decline of *Fucus* in the Baltic Sea since it makes a possible patch-dynamic skewed. However, the sweeping effect of the thallus declines with decreasing wave action at increasing depth but still at eight meters outside eastern Öland the sea floor below dense *F.serratus* canopies was clean from filamentous algae and extended *F.serratus* recruitment was recorded also at the edge of the sweeping radius of the outermost adult *F.serratus* individuals (Isaeus et al., in prep). Thus it is possible that the thick leathery thallus of *F.serratus* compared with the more delicate morphology of *F.vesiculosus* gives *F.serratus* an advantage in the competition both with *F.vesiculosus* as earlier reported by Vadas et al. (1992) and with the eutrophication induced filamentous algae (Velimirov and Griffiths 1979), which should make the *F.serratus* patches rather persistant.

With field monitoring methods, a relatively large section of the Baltic Sea coast has been investigated and possible links between macroalgal distributions and abiotic factors, mainly salinity and geomorphology, as well as possible competitive interactions between macroalgal species has been found. However, all our conclusions are based on correlations and not on experimental evidence and must therefore be interpreted with caution. To confirm our conclusions, field experiment including transplantation and artificial seeding of macroalgae on different depths and in different region must be executed.

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Tab. 1. Biomass (g dw m- -2) of algal species in the turf of eastern Gotland and Öland, 5 m depth, July, 2002. N=5 for each site.

		Öland			Gotland	
Species / Region	South	Central	North	South	Central	North
Chlorophyta						
Cladophora rupestris	0.02+/-0.02	-	-	0.13+/-0.13	0.08+/-0.08	0.04+/-0.02
Phaeophyta						
Dictyosiphon foeniculaceus	0.93+/-0.93	5.00+/-0.58	11.0+/-0.6	-	4.13+/-2.22	-
Ectocarpus fasciculatus	0.42+/-0.30	6.00+/-0.58	12.0+/-0.6	-	-	-
Pilayella littoralis	1.82+/-1.45	0.45+/-0.39	-	5.37+/-3.69	2.90+/-2.81	0.02+/-0.01
Sphacelaria arctica	-	-	-	-	6.23+/-3.81	-
Sphacelaria plumigera	-	-	0.13+/-0.13	-	-	-
Stictyosiphon tortilis	-	-	-	-	0.59+/-0.59	-
Rhodophyta						
Ceramium tenuicorne	0.06+/-0.06	0.01+/-0.01	-	2.13+/-0.66	3.45+/-2.75	12.7+/-6.3
Coccotylus truncata	-	-	-	-	-	0.37+/-0.22
Furcellaria lumbricalis	0.06+/-0.06	0.60+/-0.60	-	0.69+/-0.53	39.8+/-22.1	249.1+/106.7
Hildenbrandia prototypus	0.01+/-0.01	0.01+/-0.01	0.01+/-0.01	0.01+/-0.03	0.01+/-0.02	0.01+/-0.01
Phyllophora pseudoceranoides	-	0.01+/-0.01	-	-	-	1.01+/-0.55
Polysiphonia fucoides	73.7+/-21.0	74.2+/-13.5	103.7+/-27.1	92.7+/-5.5	65.4+/-5.2	30.4+/-12.7
Rhodomela confervoides	5.41+/-4.92	7.49+/-5.79	3.76+/-3.56	-	2.24+/-2.00	0.22+/-0.12

Figure legend

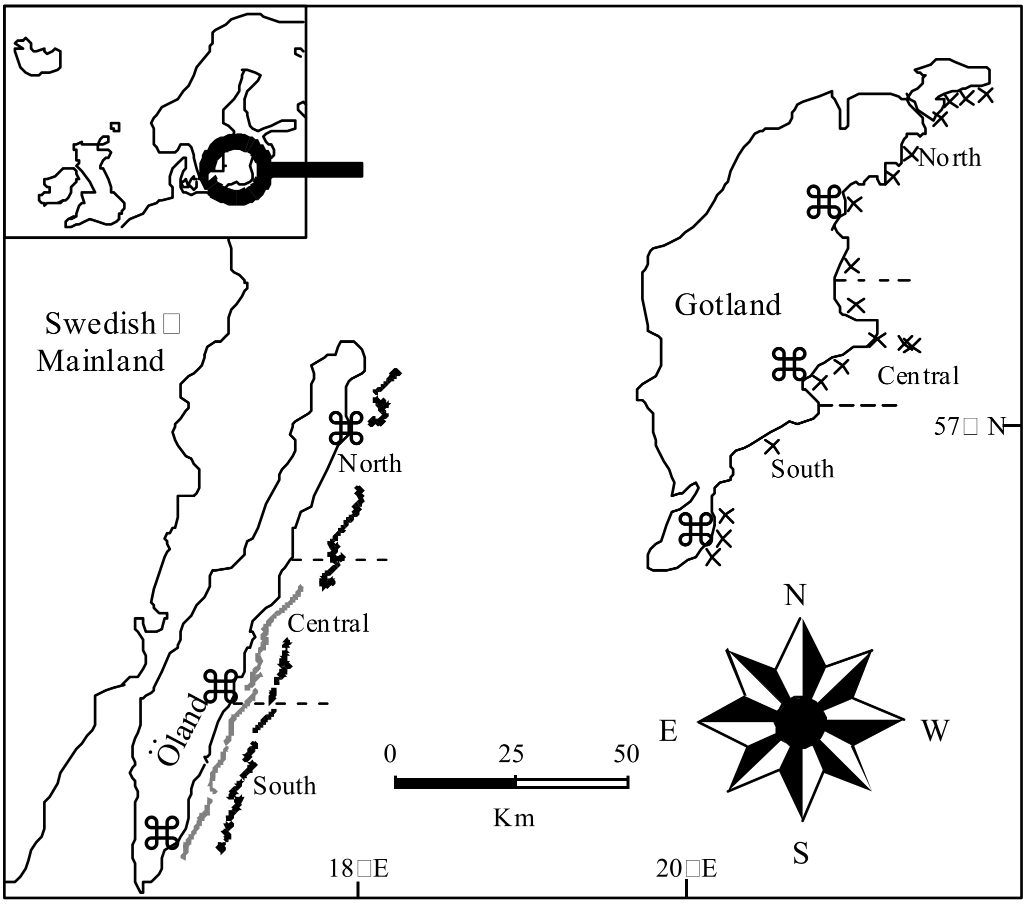
Fig. 1. Map of the investigated coastlines in the central Baltic Sea. The symbol ⌘ indicates the sites for quantitative sampling of the turf algae biodiversity in July 2002, × is a symbol for the transversal manta tray transects at Gotland in July 2001. The grey line at Öland indicates the extension of the shallow (two and a half meter) transects performed in April 2001, and the thick black line at Öland indicates the extension of the deep (seven meter) transects performed in July 2000.

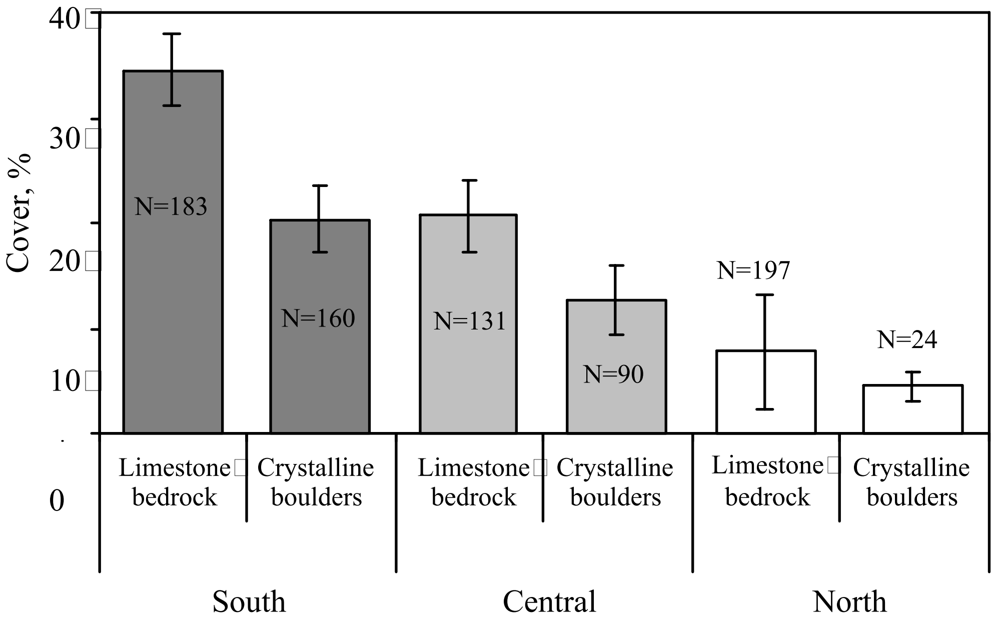
Fig. 2. Average +/- S.E. *F.serratus* cover (%) on the major types of substrate, i.e., limestone bedrock and crystalline boulders, at seven meters depth in three different regions at eastern Öland, Central Baltic Sea, July 2000.

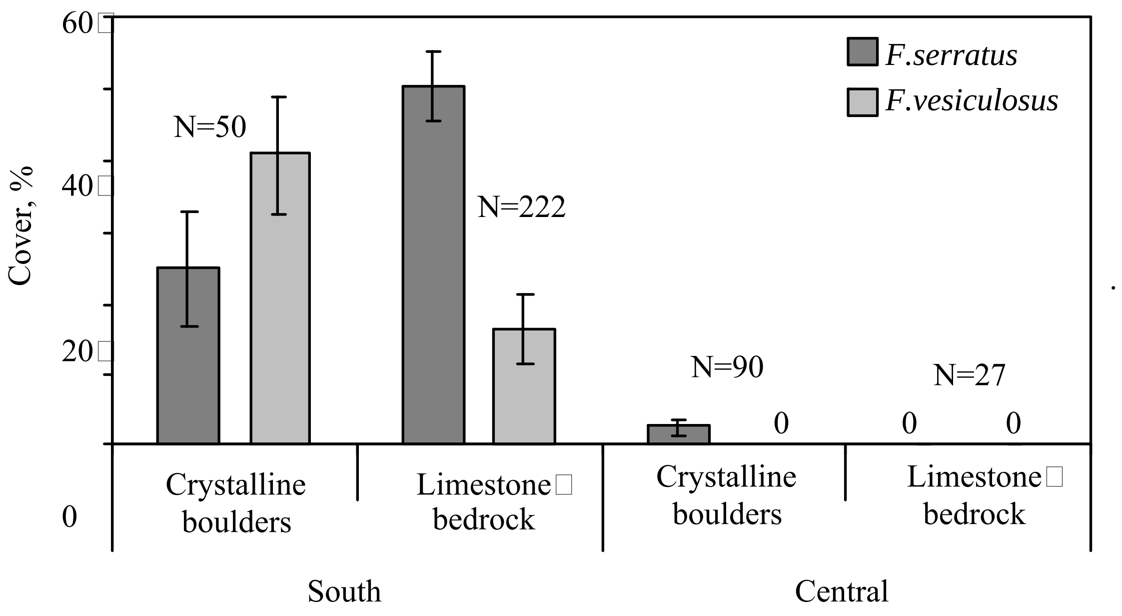
Fig. 3. Average +/- S.E of *F.vesiculosus* and *F.serratus* cover (%) on the major types of substrate i.e. limestone bedrock and crystalline boulders, at two and a half meters depth in two different regions at eastern Öland, Central Baltic Sea, April, 2001.

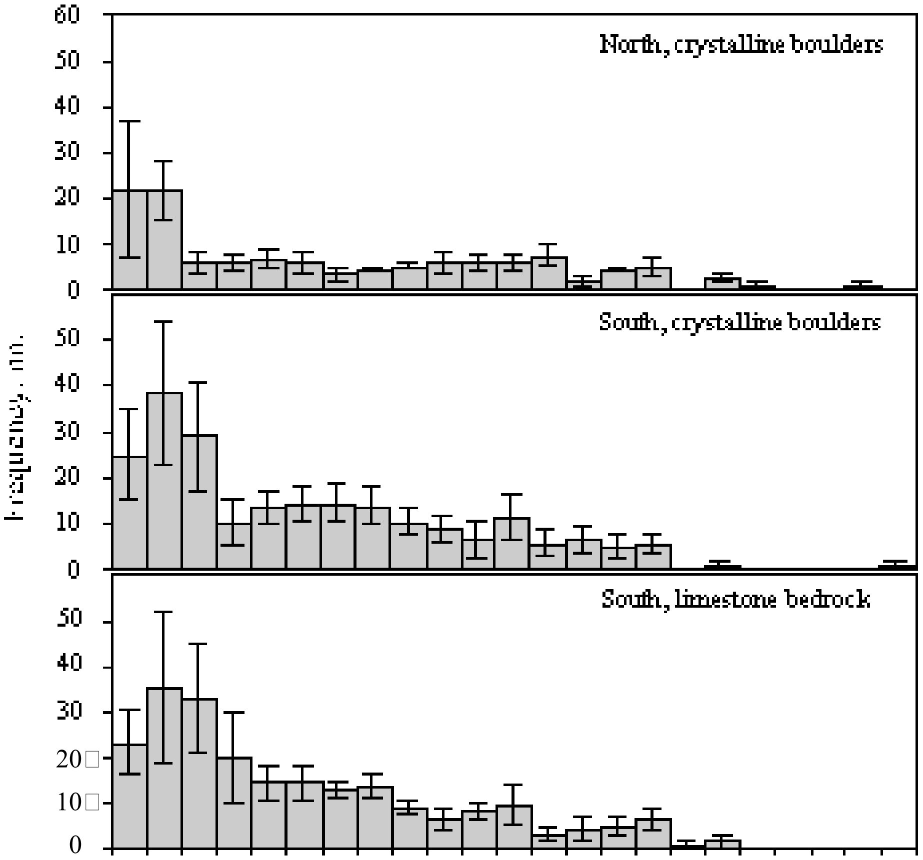
Fig. 4. Frequency of size and average +/- S.E for each size group in three different *F.serratus* populations at seven meters depth, eastern Öland, Central Baltic Sea, July, 2003. N=5 for each site.

Fig. 5. Average abundance of algal turf (at least a cover of 25%) (hatched) and *F.vesiculosus* stands (full line) from the mean water level down to ten meters depth in three different regions at eastern Gotland, July 2001. (+/- S.E)


Swedish
Mainland
Gotland
North
Central
South
57° N
North
Central
South
Öland
0
25
50
Km
N
E
W
S
18°E
20°E


Cover, %
40
30
20
10
0
N=183
N=160
N=131
N=90
N=197
N=24
Limestone bedrock
Crystalline boulders
Limestone bedrock
Crystalline boulders
Limestone bedrock
Crystalline boulders
South
Central
North


60
40
20
0
Cover, %
F.serratus
F.vesiculosus
N=50
N=222
N=90
N=27
0
0
0
Crystalline boulders
Limestone bedrock
Crystalline boulders
Limestone bedrock
South
Central


North, crystalline boulders
South, crystalline boulders
South, limestone bedrock
Frequency, m.
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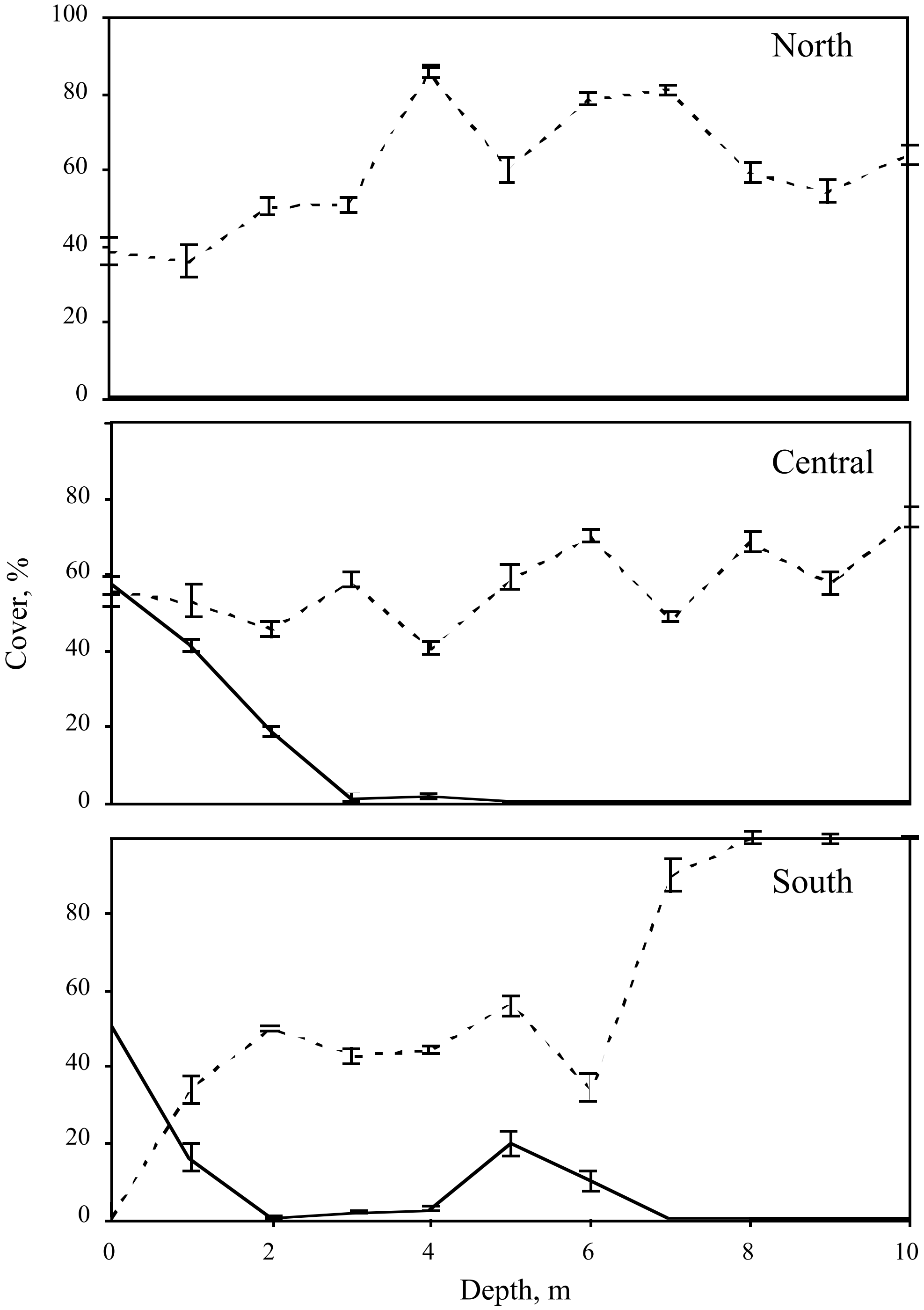
50
40
30
20
10
0


North
Central
South
Cover, %
Depth, m
0
20
40
60
80
100
0
2
4
6
8
10

Effects of filamentous algae and sediment on recruitment and survival of *Fucus serratus* L. (Phaeophyceae) juveniles in the eutrophic Baltic Sea

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Abstract

Eutrophication of the Baltic Sea has increased both the growth of annual filamentous algae and the rate of sedimentation. Together these factors may have a detrimental effect on the survival of perennial macroalgae populations. The aim of this research was to study how these factors affect the colonisation success of *Fucus serratus* at the local level. We investigated the settlement and survival of *F. serratus* germlings through a combination of field studies and laboratory experiments. The study area lay off the east coast of Öland, along the central Baltic Sea, where consistently-submerged, extended fucoid stands occur at depths of 2–10 m, together with turf-forming filamentous algae, mainly *Polysiphonia fucoides.* Very few *F. serratus* juveniles were observed outside the sweeping radius of adult *F. serratus* individuals at a 7-m depth, while abundant recruits were found inside *F. serratus* stands. Amounts of filamentous algae and sediment were significantly larger outside the *F. serratus* stands than inside, and the amount of fine sediment (< 0.25 mm) was positively correlated with the amount of filamentous algae, suggesting that fine sediment accumulates in the turf. Experimental studies showed that both filamentous algae and sediment negatively affect the settlement ability of *F. serratus* eggs and zygotes and the subsequent survival of the germlings, sediment having the strongest effect. Thus, prior existence of an adult *F. serratus* population may allow for continuing recruitment of juveniles, while colonisation of new areas unaffected by the sweeping effect of larger individuals seems very difficult under current conditions.

Keywords Eutrophication, macroalgae, patchy distribution, *Polysiphonia fucoides*, sediment accumulation

Introduction

Two closely related fucoid species, *Fucus vesiculosus* and *Fucus serratus* (Hull *et al.*, 2001), have been able to colonise the brackish southern Baltic Sea. The lack of tides, unpredictable prolonged changes in water levels, and ice scouring all impede growth in the shallowest parts of the littoral zone, and all fucoid populations in the Baltic Sea grow constantly submerged (Waern, 1952). *Fucus vesiculosus*, which generally grows at shallower depths and extends further into the Baltic Sea than *F. serratus*, is much more frequently studied. This study therefore makes comparisons with *F. vesiculosus*, even though its main focus is on the effects of eutrophication on *F. serratus* recruitment.

The Baltic Sea is currently a eutrophic inland sea. It is estimated that human activities increased the nitrogen load of the Baltic Sea by three times and the phosphorous load by five times during the twentieth century. Moreover, winter seawater concentrations of nitrogen and phosphorous have risen by 2.2 and 3.7 times, respectively, since 1950 (Larsson *et al.*, 1985; Rosenberg *et al.*, 1990). A possible consequence of the raised nutrient levels and increased production of phytoplankton is decreased depth distribution of submerged macroalgae due to decreased light penetration (Sand-Jensen & Borum, 1991; Cloern, 2001; Elmgren & Larsson, 2001). Light penetration, measured as the Secchi depth, decreased in the Baltic Sea during much of the twentieth century (Sandén & Håkansson, 1996). This has been suggested as the main reason for the upward movement of *F. vesiculosus* distribution between 1943/1944 and 1984 (Kautsky *et al.*, 1986; Kautsky *et al.*, 1992; Malm *et al.*, 2001), a trend that seems to have stopped during the 1990s, according to recent monitoring and research (Eriksson *et al.*, 1998; Kautsky, 2001). Older records of *F. serratus* distribution in the Baltic Sea are poor, but *F. serratus* was found growing at depths of up to 15 m in 1936/1939 – compared to a maximum depth of 12 m in the same region in recent years (Levring, 1940, Malm *et al.*, 2001, Malm & Isæus unpublished data) – indicating the same pattern.

Thin, thread-like algae rather than thick macroalgae (such as fucoids) are favoured by high nutrient conditions, and may therefore replace them under such conditions (Duarte, 1995), as has happened in the Baltic Sea (Schramm, 1996; Worm & Chapman, 1998). Similar changes in macroalgal species composition and depth distribution have also been reported from other eutrophic areas, such as the Kattegatt Strait (Wennberg, 1987; Rosenberg *et al.*, 1990), and the Northern Adriatic (Munda, 1993). Existing algal turf may prevent the settlement of spores or zygotes of other algae species on a hard substrate (Dayton *et al.*, 1984), or decrease early post-settlement survival (Vadas *et al.*, 1992; Hull *et al.*, 2001; Berger *et al.*, 2003), and several studies have shown how removal of turf can increase recruitment (Dayton *et al.*, 1984; Witman, 1987). Kangas *et al.* (1982) suggested that epilithic filamentous algae, microalgae, and detritus severely obstruct the attachment of *F. vesiculosus* zygotes in the Baltic Sea, and Berger *at al.* (2003) showed that epilithic filamentous algae had a negative effect on the survival of *F. vesiculosus* recruits, also in the Baltic Sea.

Another consequence of the eutrophication of the Baltic Sea is increased sedimentation (Elmgren, 1989). Sediment has been shown to inhibit the attachment and survival of macroalgal spores in the Baltic Sea (Berger *et al.*, 2003) and other areas (Devinny & Volse, 1978; Norton, 1978). Field studies have recently shown that sedimentation affects the colonisation and development of macroalgal communities in the Baltic Sea, and that *F. vesiculosus* is less tolerant of sediment than the ephemeral algae, *Cladophora glomerata* and *Enteromorpha* spp. (Eriksson, 2002; Johansson, 2002). A macroalgal turf can entrap large amounts of sediment (Kendrick, 1991), and the combined effect of turf and sediment may further decrease the settlement ability and post-settlement survival of fucoid recruits.

Our aim was to study what determines the distribution of submerged *F. serratus* at the local level off an open coast along the central Baltic Sea. We specifically wanted to answer the following questions: 1) Is the density of small (< 10 cm) *F. serratus* plants growing below an adult *F. serratus* canopy different from those growing in a filamentous algal turf? 2) Is the amount of filamentous algae and sediment different below the *F. serratus* canopy compared to within the filamentous algal turf? 3) Does the filamentous algal turf accumulate sediment? 4) Are sediment and filamentous algal turf preventing the settlement and survival of *F. serratus* zygotes and germlings?

Materials and methods

Study area

Both the field studies and the sediment collection for the laboratory experiment took place on the eastern side of Öland Island (N 56º 25.26’ E 16º 35.61’), central Baltic Sea (Fig. 1). The seafloor substrate east of Öland is flat limestone bedrock with occasional large stones and boulders. The shore gently tilts eastwards, and a depth of 7 m is reached about one kilometre off shore. In depths between 5 and 10 m the benthic vegetation consists of 1–10 m^2 patches of *Fucus serratus* L. and a turf of mainly filamentous algae with very little bare substrate. The turf is dominated by *Polysiphonia fucoides* (Huds.) Grev. (c. 65 %), *Sphacelaria arctica* Harv. (c. 10 %), and non-filamentous species *Furcellaria lumbricalis* (Huds.) J.V. Lamour (10 %), *Rhodomela confervoides* (Huds.) P.C. Silva (c. 4 %), and *Coccotylus truncatus* (Pall.) M.J. Wynne et J.M. Heine /*Phyllophora pseudoceranoides* (S.G. Gmel.) Newroth et A.R.A. Taylor (c. 10 %) (Malm, unpublished data). Although *C. truncata*, *P. pseudoceranoides*, and *R. confervoides* are not morphologically filamentous, they are all small and threadlike in the Baltic, and the turf will be referred to as filamentous in this study. The local water temperature usually ranges from 1 to 3 °C in winter and between 12 and 17 °C in summer, the salinity being stable at around 7.3 psu (Juhlin, 1992).

Number of juveniles in the field

The number of *F. serratus* juveniles growing below the adult canopy and in the filamentous algal turf at a depth of 7 m was investigated in August 2000 at Segerstad (Fig. 1), using SCUBA diving. A 2.0-m long "ladder" was placed over the patch edge, extending 1.0 m into the *F. serratus* patch and 1.0 m into the filamentous turf (Fig 2). The ladder was 60 cm wide and had 20 compartments of 6.0 dm^2 each. The number of *F. serratus* individuals, defined as fronds attached by a single holdfast, occurring in each compartment were counted and their lengths measured. To find small individuals, all fronds longer than 10 cm were removed. Fronds shorter than 1.0 cm were excluded, since they could not be counted with sufficient accuracy in the filamentous turf. Individuals of 10 cm length or shorter were considered juveniles since individuals are normally not reproductive at that size (Malm *et al.*, 2001). Seven patches of *F. serratus* were investigated.

Amounts of sediment and filamentous algae

Sediment was collected from 15 to 17 October 2001 at Segerstad (Fig. 1) using a venturi airlift of our own construction. All sediment and algae within the 20 × 20 cm frames placed at 7-m depths were collected. Ten samples from the filamentous turf and 10 from the *F. serratus* stands were randomly taken. The algae that were left after the "vacuum cleaning" were collected in net bags. The sampled water/sediment was collected in 20-L buckets and brought to the shore where the samples were filtered through a 1-mm sieve to sort out gravel, coarser sand, and torn-off algae. All algae were sorted as either filamentous algae or *Fucus*, and dried for three days at 60 °C to a constant dry weight. The remaining water/sediment suspension was repeatedly allowed to settle for 24 h and decanted down to a volume of 170 mL, then frozen until further processing. The final sediment slurry was dried for three days at 60 °C to a constant dry weight. The organic content of the sediment was measured by combustion of the dried sediment at 600 °C for 6 h (Carter, 1993).

The coarser sediment fraction that had been filtered from the water samples was also dried and large organisms, such as mussels and amphipods, were removed. All sediment samples were then silted to determine the following particle fractions: < 0.075, 0.075–0.125, 0.125–0.25, 0.25–0.5, 0.5–1, 1–2, 2–4, 4–5.5, 5.6–8, 8–11, 11–16, > 16 mm (Anonomous, 1966). Organic sediment was measured in g dm^{-2} since it was considered a more accurate measure for inhibition of propagule settlement and survival than the ratio (%) of organic sediment mass per total sediment mass that is more commonly used.

Fucus serratus settlement and survival experiments

A tank experiment was set up to test the ability of *F. serratus* zygotes to settle and attach in petri dishes filled with approximately 1-cm-thick layers of filamentous algae or sediment (empty dishes being the control); zygote survival *under* similar layers of algae or sediment was also tested. Sediment and attached filamentous red algae were collected from a depth of 8 m at Gräsgård (Fig 1) in October 2001, using the same venturi airlift method described above. The algae were separated out, and the water/sediment mixture was placed in two 60-L containers and left for one week so the particles could settle before the mixture was decanted. Receptacles from *Fucus serratus* were collected from a depth of 1 m at Sturkö in Blekinge (Fig. 1), since autumn-reproducing *F. serratus* are rare on the Öland east coast (Malm *et al.*, 2001).

Twenty-five petri dishes of 9.0-cm diameter were put in a 1 × 1 × 1-m container placed outdoors. The bottoms of the petri dishes were roughened with a piece of sandpaper to enhance the potential for settlement. The container was filled with sea water with of 6.5 psu salinity, artificially increased to 8.0 psu by adding commercial sea salt to ensure that salinity would not inhibit reproduction (Malm *et al.*, 2001). The water temperature decreased from 8 °C to 5 °C during the five weeks the experiment lasted. A net with a 1-cm mesh size was attached to a wooden frame and installed 10 cm beneath the water surface (90 cm above the petri dishes). To obtain maximal fertilisation and an even distribution of eggs on the petri dishes below, a layer of receptacles – 1/3 male and 2/3 female – was spread out on the net. The nets with receptacles were removed after two weeks.

In both experiments, approximately 1-cm-thick layers of either sediment (26 g dw dm^{-2}) or filamentous algae (1.6 g dw dm^{-2}) were used as the treatments. These amounts were chosen so as to mimic the natural conditions at the sampling site. In the settlement experiment, a layer of either sediment or filamentous algae was put in the petri dish before the receptacles were added, and empty dishes were used as controls (n = 5 for both treatments and for the control). After two weeks, settlement success was gauged by removing both the sediment and filamentous algae, and counting the attached zygotes in 10 stereomicroscope visual fields, 5 mm in diameter, for each petri dish.

The survival experiment was set up at the same time as the settlement experiment. In both treatments n = 5 and the same 5 control dishes were used in both experiments. *Fucus serratus* zygotes were allowed to settle in empty petri dishes as in the control dishes. The number of zygotes was counted after two weeks, and either sediment or filamentous algae were spread over the *F. serratus* recruits. After another three weeks, the sediment and algae were removed and survival was gauged by counting the remaining recruits and calculating the survival ratio.

Statistical analyses

Statistical analyses were performed using Statistica 5.5, 1999 release. In the field study, differences in the amounts of sediment and filamentous algae and the number of *F. serratus* recruits between the filamentous algae turf and the *F. serratus* stands were examined by a one-way analysis of variance – ANOVA. We used a Pearson Product-Moment correlation to assess the relationship between filamentous algae and amount of fine sediment (< 0.25 mm). In the experiment, a Kruskal-Wallis ANOVA was used to analyse the effects of the presence of sediment or filamentous algae on settlement and survival. The differences between treatments (control, algae, sediment) were tested pair-wise using a Bonferroni correction for repeated measures ($\alpha = 0.017$).

Results

Number of *F. serratus* juveniles in the field

The number of *F. serratus* juveniles in the filamentous turf was very low. In only one of the seven sites juveniles were found outside the sweeping radius of *F. serratus* plants at the edges of patches (Fig 3). On average, 0.99 ± 0.20 (mean ± SE) juveniles per dm^2 were found in the *F. serratus* patches, compared to 0.02 ± 0.02 (mean ± SE) juveniles per dm^2 outside the patches, which was a significant difference ($F_{(1,12)} = 6.38$, $p < 0,05$).

Sediment and filamentous algae amounts

The amount of filamentous algae, mainly consisting of *P. fucoides*, was significantly larger outside (0.6 ± 0.1 g dw dm^{-2}, mean ± SE) the *F. serratus* canopy than beneath the canopy (0.04 ± 0.02 g dw dm^{-2}, mean ± SE).

There was significantly more fine sediment (< 0.25 mm) in the filamentous algal turf than in the *F. serratus* stands (2.42 ± 0.26 g dw dm^{-2} and 0.20 ± 0.03 g dm^{-2}, mean ± SE, respectively) ($F_{(1,18)} = 21.4$, $p < 0.001$). The amount of sediment of organic origin was also significantly higher in the filamentous algal turf (0.32 ± 0.04 g dm^{-2}, mean ± SE) than in the *F. serratus* patches (0.08 ± 0.02 g dm^{-2}, mean ± SE) ($F_{(1,18)} = 44.0$, $p < 0.001$). There was a significant correlation between the biomass of filamentous algae and the amount of fine sediment ($r = 0.58$, $p < 0.05$).

F. serratus settlement and survival experiment

Both sediment and filamentous algae negatively affected the settlement ability of *F. serratus* zygotes ($\chi^2 = 10.0$, $p < 0.017$, $n = 5$ for both tests) (Fig. 4a). However, the sediment had a significantly larger effect than the algae on settlement success ($\chi^2 =$

10.0, $p < 0.017$, $n = 5$). The effects of sediment and filamentous algae on the survival of *F. serratus* germlings resembled the effect on settlement (Fig. 4b). Both treatments resulted in a significantly lower survival of recruits compared to the control ($\chi^2 = 10.0$, $p < 0.017$, $n = 5$ for both treatments vs. control), and the survival of *F. serratus* zygotes subject to the sediment treatment was significantly lower than the survival of those subject to filamentous algae ($\chi^2 = 10.0$, $p < 0.017$, $n = 5$).

Discussion

This study strongly suggests that the ability for *F. serratus* to recruit outside its existing patches into the filamentous algal turf is limited. Almost no recruits were found in the turf in the study area (Fig. 3), and in the laboratory experiment the filamentous algae had a significant effect in inhibiting the settlement and increasing the mortality of recruits. Very few filamentous algae were found within the *F. serratus* stands, possibly because of the scouring of surrounding substrate by *F. serratus* thalli (Kiirikki, 1996), or because of canopy shading (Robertson, 1987). There is plenty of available bedrock surface for attachment of *F. serratus* zygotes beneath the canopy, and they appear less negatively affected by the presence of adult plants than are filamentous turf species.

The filamentous algae had a negative effect on both the settlement and survival of recruits. It would have been preferable to use attached filamentous algae in the experiment, the better to mimic the filamentous turf, but zygotes or 3–5-week-old juveniles cannot be properly counted within a turf, so loose algae were used instead. Loose algae may more effectively block the substrate and cover juveniles than does turf, so these results should be interpreted with caution. However, attached filamentous algae were shown to have a negative effect on the survival of *F. vesiculosus* over a three-month period (Berger *et al.*, 2003), a finding which would tend to support our results. Drifting mats mainly consisting of loose filamentous algae have become increasingly common in the Baltic Sea as an effect of eutrophication (Bonsdorff, 1992). Their negative effects on the zoobenthos community and on the settling of mussel spat have been studied (Bonsdorff, 1992; Norkko & Bonsdorff, 1996), but to our knowledge their effects on macroalgae have so far been overlooked. Our experimental results suggest that algal mats could negatively affect macroalgal recruitment, though this matter should be more directly addressed in further research.

Sediment inhibited recruitment and reduced survival even more than did the filamentous algal treatment. The amount of sediment (1-cm-thick layer, 26.1 g dw dm^{-2}) used in the experiment was based on the natural conditions the year the laboratory experiment took place (2000). This amount lay within the natural range (3.9–34.8 g dw dm^{-2}) found the year after when the extended sediment sampling was carried out, but was, however, twice the mean value (12.7 g dm^{-2}). Both years the sediment samples were collected in October, but the amount of sediment apparently fluctuates considerably from year to year. Sediment has been shown to reduce the settlement and attachment success of *F. vesiculosus* in both the laboratory (Berger *et al.*, 2003) and the field (Eriksson & Johansson, 2003). A Canadian lab experiment found that a 3-mm layer of fine sediment (< 0.063 mm) had a strongly negative effect on the survival and growth of *F. serratus* embryos (Chapman & Fletcher, 2002). Light deprivation was excluded as a casual factor in this experiment by comparing survival in all treatments in both dark and light conditions. Instead, the authors suggest that the slow rate of diffusion resulting from the compact sediment layer caused waste products to accumulate around *Fucus* embryos resulting in high death rates (Chapman & Fletcher, 2002). Neither a 1-mm-thick fine sediment layer nor a 1−3-mm, coarse (0.25–0.35 mm) sediment layer caused such high death rates.

In the Baltic proper the sedimentation rate varies over the year, with high settlement rates of primary organic matter in spring, low sedimentation rates during the summer, and a considerable increase in resuspension in October−November (Heiskanen & Tallberg, 1999). Such resuspension is important and often represents over 50% of the sediment caught in sediment traps (Blomqvist & Larsson, 1994); fine sediment is the most motile due to its lower settlement velocity (Tarbuck & Lutgens, 1996). Fine sediment (< 0.25 mm) was found in significantly larger amounts in the filamentous turf than in the *F. serratus* stands. This may be because the algal turf itself increases the accumulation rate by inhibiting resuspension. This explanation is supported by the finding that the amount of fine sediment was correlated with the biomass of the filamentous algae, and the phenomenon that submerged vegetation accumulates sediment has been observed by several authors (Neuman *et al.*, 1970; Scoffin, 1970; Kendrick, 1991). A study from the Galapagos (Kendrick, 1991) found that the amount of sediment trapped within filamentous turf varied considerably over time (180−1850 g dw m^{-2}), but no such studies have been carried out in the Baltic Sea.

The combined effect of the presence of filamentous turf and fine sediment accumulation on *F. serratus* settlement and survival of recruits could be severe. Both the organic matter and fine sediment that accumulate in filamentous turf have been shown to have a strong negative effect on the survival of *F. serratus* juveniles (Chapman & Fletcher, 2002). *F. serratus* may only have a chance to establish itself in the dominant algal turf in gaps formed by physical disturbance or grazing, as suggested by Sousa (1979). Such events might be storms (Lubchenco & Menge, 1978), drifting algal mats that cause oxygen depletion (pers. obs.), or grazing (Sousa, 1979). In the Baltic Sea, autumn storms may be the key events that clear gaps in sediment-loaded algal turfs into which *F. serratus* could potentially disperse. We conclude that the effects of greater amounts of filamentous algae and sediment taken together may be reinforced by eutrophication to the disadvantage of *F. serratus*.

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Legends

Figure. 1. The study area is located in the Baltic proper on the SE coast of Sweden. ■ =major cities ● = study sites.

Figure 2. A 2 m ladder with 20 compartments was put over the *F. serratus* patch edge, 1 m into the fucoids and 1 m into the filamentous turf. For all compartments the *F. serratus* fronds >10 cm was measured and removed, and all the remaining juveniles measured and counted.

Fig. 3. The density of *F. serratus* juveniles (< 10 cm) found at both sides of the *F. serratus* filamentous algae patch edge (mean ± SE).

Fig. 4a. Number of zygotes per dm^2 that managed to settle and attach to the petri dish bottom in spite of a 1-cm layer of sediment or filamentous algae.

Fig. 4b. Average proportions of settled *F. serratus* germlings that survived sediment or filamentous algae treatment.

Figure 1
Scale 1:1

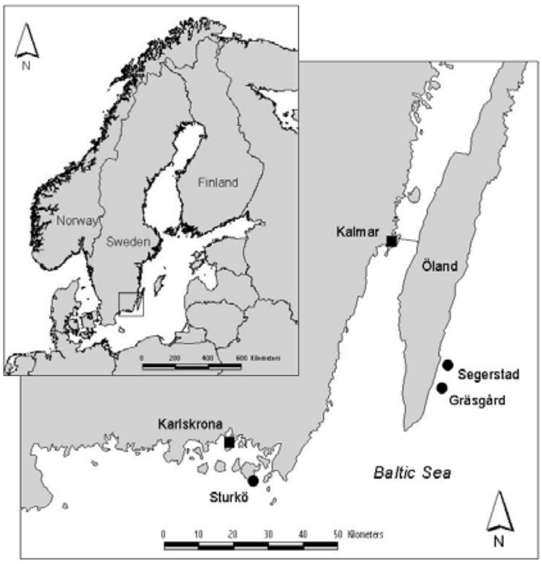


Figure 2.
Scale 1:1

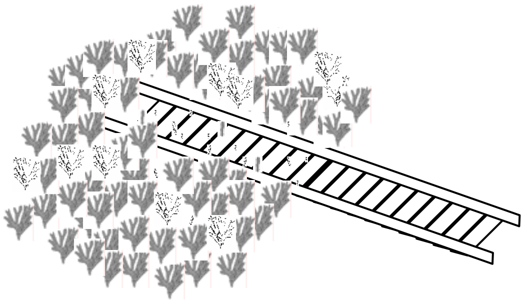


Figure 3.

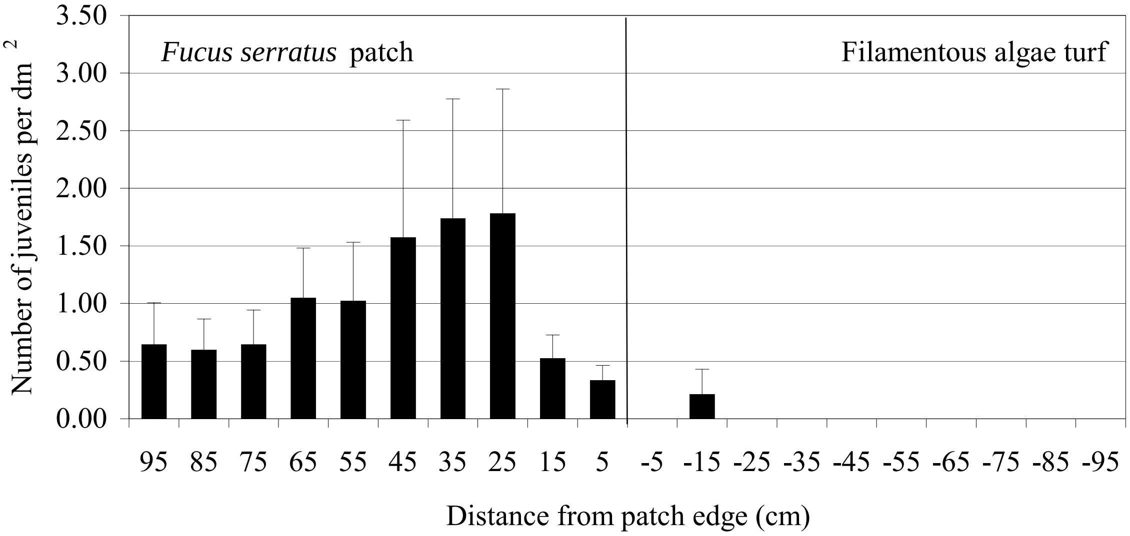
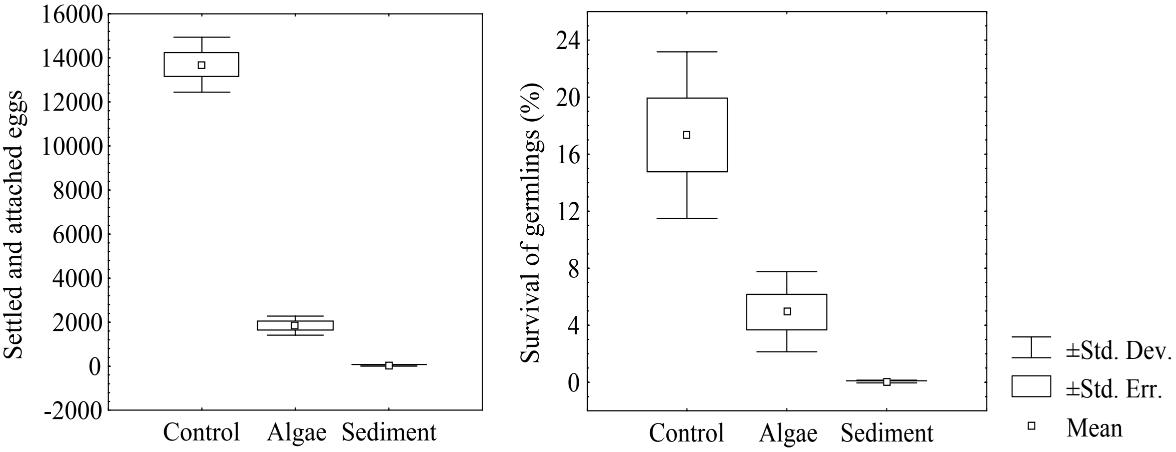

3.50
3.00
2.50
2.00
1.50
1.00
0.50
0.00
Number of juveniles per dm 2
Fucus serratus patch
Filamentous algae turf
95 85 75 65 55 45 35 25 15 5 -5 -15 -25 -35 -45 -55 -65 -75 -85 -95
Distance from patch edge (cm)

Figure 4.


16000
14000
12000
10000
8000
6000
4000
2000
0
-2000
Settled and attached eggs
Control
Algae
Sediment
24
20
16
12
8
4
0
Survival of germlings (%)
Control
Algae
Sediment
±Std. Dev.
±Std. Err.
Mean