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Distribution of macroalgal communities in the central Baltic Sea

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Two brown seaweeds, *Fucus serratus* and *F. vesiculosus*, are forming stands along the shores of the central Baltic Sea. We studied the regional variations in the abundance of *F. vesiculosus*, *F. serratus* and filamentous algae in the central Baltic Sea. Further, the hypothesis that regional differences in geomorphology and the north–south salinity gradient affect the dominance of the different species was tested. Extended manta tow diving and observations from a skiff with transparent shutters in the hull were used to map the distribution of macroalgae on different substrate types. Estimations of *F. serratus* recruitment and turf biomass were also performed. The results show significant differences in *Fucus* spp. vegetation among regions and substrate types. Both *Fucus* species were most abundant in the southern regions as compared with the northern regions. *Fucus serratus* was significantly more abundant on limestone bedrock than on boulders. The results are discussed in relation to salinity tolerance, eutrophication, life history, and interspecific competition.

Key words: ecology, *Fucus serratus*, *Fucus vesiculosus*, life history, macroalgae, *Polysiphonia*, recruitment, substrate

Introduction

The brown seaweeds *Fucus serratus* and *F. vesiculosus* form stands along the shores of the central Baltic Sea (Malm 1999) and this algal association is assumed as the most productive and diverse community on rocky shores in the littoral zone (Kautsky 1991). During the last 50 years the distribution of these valuable stands declined both geographically and vertically in many areas of the Baltic Sea. The ultimate reason for this deterioration is considered to be the basin-wide eutrophication that began in the middle of the last century (Cedervall & Elmgren 1990). Since the 1940s, human activities have raised the concentrations of inorganic nitrogen three times and phosphorus five times in the surface water of the Baltic Sea (Larsson *et al*. 1985, Rosenberg *et al*. 1990).

The eutrophication favours several filamentous brown, green and red algal species (Kiirikki & Blomster 1996) that compete with the larger perennial algae (Wallentinus 1978, 1984). Dense cover of filamentous algae prevents settling and attachment of perennial fucoids (Hruby & Norton 1979, Berger *et al*. 2003) and increases the early post-settlement mortality (Vadas *et al*. 1992). In addition, benthic filamentous algae have the ability to entrap large amounts of sediment, which may further decrease the settling ability and post-settlement survival (Airoldi 1998, Isaeus *et al*. 2004).

In the Baltic Sea, both *Fucus* species have substantially higher tolerance to low salinity as compared with that of 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 4 psu (Serrão *et al*. 1996), while the germination of *F. serratus* zygotes is very low in water with less than approximately 7 psu (Malm *et al*. 2001). The northern 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 (Bergström & Bergström 1999). 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 both species (Raven & Samuelsson 1988, Malm *et al*. 2001).

The geology of the sea floor in a coastal area provides variable surfaces for establishment and growth of benthic organisms, which may be of importance for the structure of the macroalgal community. Both small and large-scale texture of rocky surfaces have been pointed out as important factors in macroalgal species composition and biomass production (McGuinness & Underwood 1986, Wells *et al*. 1989). Optimum bedrock relief has been linked to different sizes of algal propagules (Fletcher & Callow 1992). Green algae, which have comparatively small propagules, have higher survival at a smoother relief than 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 sandstone than on crystalline bedrock, i.e. amphibolites and granite. 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 macrolgal 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 & Kautsky 2003). *Fucus vesiculosus* grows constantly submerged at 1–2.5 m depth and *F. serratus* grows deeper from 2.5 m down to 10–12 m depth. Sweeping of the leathery *F. serratus* thallus eradicate *F. vesiculosus* juveniles at exposed sites (Malm & Kautsky 2003), but in the shallowest zone, 0–2 m depth, disturbance factors such as desiccation, freezing, wave tearing, ice scraping, or fluctuating salinity may alter the competitive outcome and favour *F. vesiculosus* over *F. serratus* (Malm & Kautsky 2003). This higher tolerance to physical stress of *F. vesiculosus* as compared with that of *F. serratus* may also be explained by the ability of *F. vesiculosus* to regenerate from holdfast traces, a capacity that *F. serratus* lacks (Malm & Kautsky 2003). Contrariwise, Engkvist *et al*. (2004) suggest that grazing by the abundant isopod *Idotea baltica* may favour *F. serratus* over *F. vesiculosus* since *I. baltica* seems to prefer *F. vesiculosus* to *F. serratus* as food and shelter. In areas along the Swedish south coast, *F. serratus* stands persisted several years after *F. vesiculosus* stands were eradicated by grazers (Engkvist *et al*. 2004).

The aim with the present study was to investigate regional variations in the abundance of *F. vesiculosus*, *F. serratus* and filamentous algae in the central Baltic Sea and to test the hypothesis that regional differences in geomorphology and positions along the north–south salinity gradient affect the dominance of the different species.

Material and methods

Study area

During the years 2000 to 2003, extensive field investigations of macroalgal cover, community composition, and *F. serratus* population structure were performed along the eastern shores of the large islands Gotland and Öland, in the brackish and non-tidal central Baltic Sea (Fig. 1). The salinity of the surface water of the central Baltic Sea is stable over years but declines slowly northwards from on average 7.3 psu at southern Öland to on average 7.1 psu outside northern Gotland. The temperature of the surface water of the Baltic Sea ranges from 0–3 °C during winter to 12–17 °C in summer (Juhlin 1992). The seafloor substrate in the region consists of smooth limestone partly covered by glacial moraine of crystalline origin, ranging in grain size from sand to boulders. The seafloor at both islands gently slopes eastward and 10 m depth is reached at about one kilometre off the shore (Lidmar-Bergström 1994).

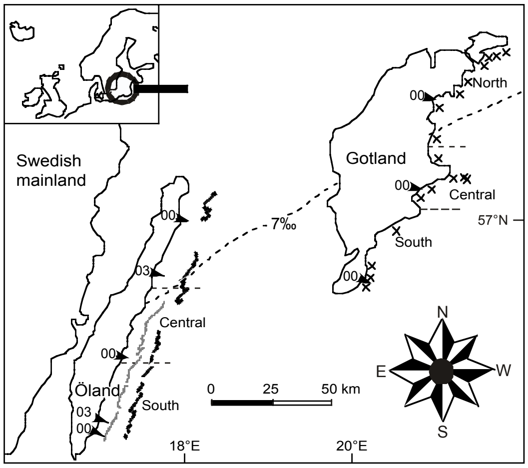

Fig. 1. Map of the investigated coastlines in the central Baltic Sea. The 00➤ symbol indicates the sites where quantitative sampling of the turf algae biodiversity were made in July 2000. The 03➤ symbol indicates the sites where the investigation of *F. serratus* population structure was made in July 2003. The thick grey line at Öland indicates the extension of the shallow (2.5 m) transects performed in April 2001, and the thick black line at Öland indicates the extension of the deep (7 m) transects performed in July 2000. The thin, hatched line indicates a 20 years average value for the 7‰ halocline (Juhlin 1992).

Methods

Regional investigations of macroalgal cover

Öland: 7-m-depth contour

During three weeks in July 2000, 102.8 km seafloor transects were investigated along the coast of eastern Öland at an average depth of 7 ± 1 m. The investigation was made with manta tow technique. The manta tow diver was dragged by a 30-m-long rope behind a boat with a speed of two to three knots. The diver was equipped with a full-face mask (IS-96319-01 AGA) and a cable-connected communication device (DB-10920 JHT 95 Divers telephone) 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 2 and 5 m depending on the transparency of the water. A new observation was reported each time the depth, substrate, or vegetation composition changed. The diver measured the depth with a diving computer (Mosquito Suunto Ltd.). The skipper noted the observations 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 the 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 0.04–0.25 m diameter, and sand < 0.04 m diameter (Wentworth 1922). With 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 1%, 5%, 10%, 25%, 50%, 75% and 100% cover. A cover of 25% or more was considered a stand (Jansson & Kautsky 1977). Bare substrate was rare but was also reported when it occurred.

The shore area of Öland consists of three regions. The southern region has an open coast and the bottom is dominated by bare limestone, the central part has similarly an open coast but moraine deposits dominate the bottom. Finally, the northern region has a relatively broken coast with moraine deposits.

Sand, moraine, and mixed bottoms making up 28.8 km were excluded from the analysis.

The remaining transects were divided into 50-m-long sections, a distance that gave a large number of independent replicates. These sections were used as the basic statistical units in the analysis. All sections covering two or several sea floor types or having larger internal depth differences than one meter were further excluded from the material, and if two sections were adjoining each other, one of them was randomly excluded. As a result, the minimum distance between two sections in the statistical analysis was 50 m. In the analysis, 785 sections, making up 43.55 km were used. The fraction, given as percentage 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 *F. serratus* and algal turf cover were tested against the independent factors substrate (boulder and bedrock) and region (north, central, and south) with the two-way analysis of variance (ANOVA). The association between *F. serratus* cover and turf-algal cover was analysed with the Pearson correlation analysis.

Öland: 2.5-m-depth contour

During two weeks in the beginning of April 2001, 74.1 km seafloor transects were surveyed along the coast of Öland at an average depth of 2.5 ± 1 m. The investigation was made with the glass-bottom boat technique. A small skiff, equipped with two 0.5 m^{-2} large windows in the hull, was constructed. In the boat, the observer was lying in his full length on the deck, covered by a dark tarpaulin to reduce reflexes. The sea floor type and vegetation structure were observed as in the manta tow investigation at 7 m depth (*see* above). Depth was recorded with an ordinary echo sounder. The speed of the boat was approximately two to three knots.

The arithmetic and statistical handling of the data was similar to that used for the manta tow investigation. In addition to two-way ANOVA, the Tukey HSD test was used. Sand, moraine, and mixed bottoms making up 26.8 km were excluded from the analysis. Used in the analysis were 510 sections making up 25.5 km.

Gotland

In July 2001, 18 transects transverse to the coast (1–10 m depth) were investigated from north to south at the eastern shore of Gotland (Fig. 1) with manta tow technique as described above. Geographical differences at Gotland were evaluated by dividing the coastline into three equally large parts with similar geomorphology. Arithmetic and statistical handling of the data was similar to that used for the investigations at Öland.

Biomass and diversity of the algal turf

Sampling of the algal turf for biomass and species composition was done during July 2000 at 5 m depth at three sites off the shore of Öland and at three sites off the shore of Gotland (Fig. 1). At each site all biomass in five 0.04-m^{-2} large frames was collected. The material was brought to the laboratory, sorted into species, and dried to constant weight at 60 °C. SCUBA diving technique was used for the field sampling.

Population structure of *Fucus serratus*

The density and size distribution of *F. serratus* fronds at 7 m 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 (1 m in diameter) was compared with two populations in the southern region. In the south, one population was growing on large boulders (1 m in diameter) and one was growing on clean swept limestone bedrock. The length in centimetres 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. 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 pairwise χ^2 analysis (expected *vs.* observed frequency). The data were grouped into size classes with 3-cm class width from 1- to 65-cm plant length.

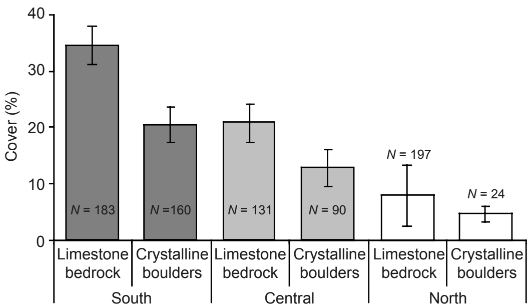

Fig. 2. Cover (average ± S.E.) of *Fucus serratus* on the major types of substrate, i.e., limestone bedrock and crystalline boulders, at 7 m depth in three different regions at eastern Öland, central Baltic Sea, July 2000.

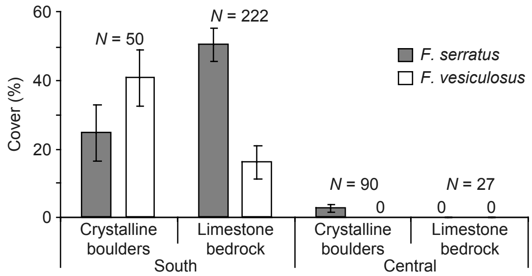

Fig. 3. Cover (average ± S.E.) of *Fucus vesiculosus* and *F. serratus* on the major types of substrate, i.e., limestone bedrock and crystalline boulders, at 2.5 m depth in two different regions at eastern Öland, central Baltic Sea, April 2001.

Additional statistics

All data given in percent were arc sin square root transformed to approximate normal distribution before analysis. The homogeneity of the variances was tested with Levin's test and further transformed if necessary. For all statistical analysis, Statistica (99 edition) was used.

Results

Regional investigations of macroalgal cover

Öland: 7-m-depth contour

The algal turf cover was similar in three regions (87.4% ± 2.3%, mean ± S.E.). The turf cover was negatively correlated with *F. serratus* cover in the southern (Correlation analysis: $r = -0.53$, $p < 0.001$) and central regions (Correlation analysis: $r = -0.55$, $p < 0.001$) but not in the northern region.

Fucus serratus specimens were found along 61 km of the investigated transect but stands (< 25% cover) were only found along 18 km. The cover of *F. serratus* stands declined northwards (Two-way ANOVA: $F_{2,862} = 13.62$, $p < 0.001$) (Fig. 2). The abundance of *F. serratus* was in all three regions larger on limestone bedrock than on crystalline rock boulders (Two-way ANOVA: $F_{2,862} = 3.26$, $p = 0.04$) (Fig. 2). An occasional *F. vesiculosus* specimen occurred along 26 km of the investigated transects but the cover nowhere exceeded 25%.

Öland: 2.5-m-depth contour

The total turf algal cover was lower in the southern region (40.0% ± 3.2%, mean ± S.E.) as compared with that in the central region (85.6% ± 1.8%, mean ± S.E.) (Two-way ANOVA: $F_{2,862} = 116.46$, $p < 0.001$). No significant difference in turf cover between boulders and limestone bedrock was found. *Fucus* spp. specimens were found along 38 km of the investigated transects but stands (< 25% cover) were only found along 10 km. On limestone bedrock, *F. serratus* was more abundant than *F. vesiculosus* (Tukey HSD test: $p < 0.001$) while on crystalline boulders no significant difference between the two species was found (Fig. 3). The total *Fucus* spp. cover was similar on shallow (2.5 m) and deep (7.5 m) sea floors in the southern region but lower on shallow than deep sea floors in the central region (Tukey HSD test: $p < 0.001$) (Figs. 2 and 3).

Gotland

Algal turf with at least 25% cover dominated 80.6% ± 1.7% (mean ± S.E.) of the bottoms. 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

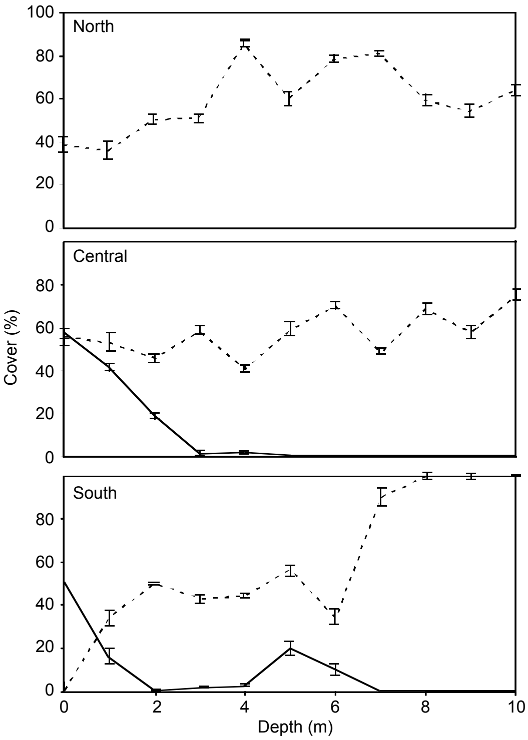

Fig. 4. Cover (average ± S.E.) of algal turf (at least a cover of 25%) (dashed line) and *Fucus vesiculosus* stands (continuous line) from the mean water level down to 10 m depth in three different regions at eastern Gotland, July 2001.

on Gotland was *F. vesiculosus* (Fig. 4). Out of twenty investigated transects, *F. serratus* stands were found only in one, situated close to the southern cape of the island. Generally, *Fucus* spp. stands occurred much more sparsely at Gotland as compared with Öland. In the northern region only scattered specimens of *F. vesiculosus* were found but no stands (i.e. more than 25% coverage) were observed in any transect. In the central region, *F. vesiculosus* stands occurred from the surface down to 2 m, and in the southern region, stands were observed from the surface down to 6 m (Fig. 4). No significant difference in *F. vesiculosus* cover between limestone bedrock and boulders was found.

Biomass and diversity of the algal turf

Eleven alga species were found along the eastern shores of Öland, one green, four brown and six red (Table 1). At 5 m depth, the red alga *Polysiphonia fucoides* was the dominating species at all sites (Table 1). 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 (Table 1). At 5 m depth,

Table 1. Biomass (g dw m^{-2}) of algal species in the turf of eastern Gotland and Öland, 5 m depth, July 2000. N = 5 for each site.

	Öland			Gotland		
Species	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 ± 2.0	0.22 ± 0.12

P. fucoides was the dominating species in the central and southern regions but in the northern region, the perennial red alga *Furcellaria lumbricalis* was the most common species (Table 1).

Population structure of *Fucus serratus*

The density and size distribution of fronds in three different *F. serratus* populations, growing at 7 m depth off the shore of eastern Öland, is presented in Fig. 5. One population in the northern region growing on a boulder field was compared with two populations in the southern region, one population was growing on a boulder field, and one population was growing on limestone bedrock. The relative size distribution of fronds (%) was significantly different between the northern boulder population and both the boulder population ($\chi^2 = 25.6$, d.f. = 15, $p = 0.04$) and the bedrock population ($\chi^2 = 38.6$, d.f. = 15, $p < 0.001$) in the south, with relatively more small individuals in the southern populations as compared with the northern population (Fig. 5). No significant difference was found between the two populations in the south.

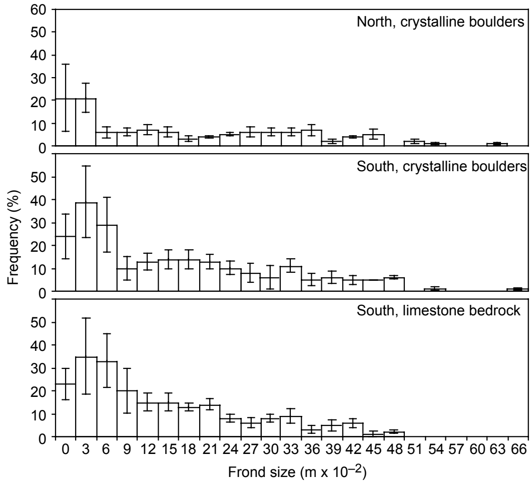

Fig. 5. Frequency (average ± S.E.) of each size group in three different *Fucus serratus* populations at 7 m depth, eastern Öland, central Baltic Sea, July 2003. *N* = 5 for each site.

Discussion

In this survey, considerable regional differences in *Fucus* spp. vegetation were 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 & 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 i.e., covering more than 25% of the bottoms. To possibly explain some of the patterns presented in this paper, it is believed important not only to understand the present conditions of the sea, but also to be aware of the kind of changes that took place during several decades. This is particularly important when discussing *Fucus* since both species are perennial and the average lifespan of an individual may be expected to be much longer in the Baltic Sea as compared with that in the North Sea and the Atlantic Ocean (Malm & Kautsky 2004).

Lack of previous studies on the distribution of *Fucus* vegetation makes it impossible to entirely confirm that a general decline has occurred along the shores of Öland and Gotland. However, there is a substantial amount of evidence from informants in the local community that a large decline of the *Fucus* stands has occurred. The several meters high cast walls of *Fucus* that were built up along the shores of Öland and Gotland during the autumn gales and reported among others by Linnè (1745) are today replaced by masses of red filamentous algae that may have detrimental effects on the coastal life (Eklund *et al.* 2004, Malm *et al.* 2004).

Irrespective of if and how the decline of the *Fucus* stands on Öland and Gotland occurred, there is today a lot of potential space for *Fucus* growth in the area occupied by red filamentous algae, mainly *Polysiphonia fucoides*. An important issue for future investigations is if the sparse populations of *Fucus* spp. found are expanding or retracting. Isæus *et al.* (2004) were able to demonstrate that the recruitment of *F. serratus* on the limestone plateau at southern Öland was controlled by a combination of thick mats of filamentous red algae, i.e., *P. fucoides*, and high loads of silty sediment. In this investigation a widespread distribution of *P. fucoides* mats was demonstrated and it is very likely that this eutrophication-driven growth is a major obstacle for the recovery of *Fucus* spp. in the area. Viable populations of the potential *Fucus* grazer, *Idotea baltica* have been observed, both in the *F. serratus* stands and in the red filamentous mat (Svensson *et al*. 2003), but grazed stands of *F. serratus* or *F. vesiculosus* were not observed during the survey presented here or elsewhere.

The salinity in the central Baltic Sea slowly rises and falls with time around an average of 7‰ (Winsor *et al*. 2001). Since *F. serratus* needs at least 7‰ for successful reproduction (Malm *et al*. 2001), the recruitment of the species has probably been restricted during extended periods through the last century. The present pattern with *F. serratus* stands found mainly along the southern parts of the islands, may partly be explained with declining salinity northwards. In this study, the *F. serratus* stands found in the northern part of Öland had significantly fewer juvenile individuals as compared with the southern population. This may be an indication of lower recruitment in the northern area as compared with that in the southern area as earlier demonstrated by Malm *et al*. (2001). If the increase in salinity during the last fifty years (Winsor *et al*. 2001) was more rapid than the colonisation rate of *F. serratus*, the rarity of *F. serratus* today, in the northern part of the investigated area, may be a matter of time, dispersal and recruitment ability.

The stability of the substrate affects the abundance and biomass of marine macroalgae (Sousa 1979), as well as the competitive outcome of sublittoral macroalgae (Littler & Littler 1984, Kloser *et al*. 1994). The present study seems to be in accordance with these earlier results. At the same depth, *Fucus serratus* was more abundant on bedrock than on boulders (Fig. 2). In shallow waters where the effects of waves are evident, *F. vesiculosus* was more common on boulders than on bedrock while the opposite was true for *F. serratus* (Fig. 3). This distribution pattern may reflect the morphologies and life histories of the three species, and the interactions among them. *Polysiphonia fucoides* with its annual growth is a rapid fast-growing colonizer (Wachenfeldt 1984) less dependent on a persistent substrate than the more slowly-growing perennial fucoides. *Fucus vesiculosus* has the capacity to regenerate from holdfast remnants (Malm & Kautsky 2004). The species may survive moderate wave-induced disturbance of the boulder substrate while the exclusively sexually reproducing *F. serratus* (Malm & Kautsky 2003) is probably more dependent on a stable substrate than 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 to be a better competitor than *F. vesiculosus* (Malm & Kautsky 2003).

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 discussed. However, all our assumptions are based on correlations and not on experimental evidence and must therefore be interpreted with caution. To confirm our conclusions, field experiments including transplantation and artificial seeding of macroalgae at different depths and in different regions must be executed.

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