Effect of abiotic environment on the distribution of the attached and drifting red algae *Furcellaria lumbricalis* in the Estonian coastal sea

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Abstract. Biomass distribution patterns of attached and drifting forms of *Furcellaria lumbricalis* in the whole Estonian coastal sea including the Gulf of Riga, the West Estonian Archipelago Sea, the Gulf of Finland, and the Baltic Proper are described. The study showed that the combination of multiple environmental variables explained the distribution of attached and drifting forms of *F. lumbricalis* and different environmental variables were important for different forms of the red alga. The attached *F. lumbricalis* inhabited deep hard-bottom areas that were exposed to waves. The drifting *F. lumbricalis* was confined to deep but more sheltered habitats characterized by the presence of a weak topographic depression, soft bottoms, and a high sediment load.

Key words: Baltic Sea, Rhodophyta, loose-lying seaweeds, biomass, spatial pattern, bottom topography, wave exposure, depth, substrate.

INTRODUCTION

Furcellaria lumbricalis (Hudson) J. V. Lamouroux is an abundant member of the marine flora in colder waters of the North Atlantic and Arctic oceans. The species is one of the few rhodophytes that prevails in the brackish Baltic Sea (Novaczek & Breeman, 1990; Bird et al., 1991; Nielsen et al., 1995). *Furcellaria lumbricalis* is the only economically important red algal species in the Baltic Sea and has been exploited in the study area since the 1960s (Trei, 1978; Martin et al., 2006a). Besides its economic value, the loose-lying macroalgae enhance the diversity of macroinvertebrates by offering a secondary substrate for several true hard-bottom species (Kotta et al., 2000; Kotta & Orav, 2001; Orav-Kotta & Kotta, 2004; Lauringson & Kotta, 2006).

There exist attached and drifting forms of *F. lumbricalis*. Bird et al. (1991) give an adequate review on the morphological differences between these distinct forms. *Furcellaria lumbricalis* can be confused with *Polyides rotundus* (Hudson) Gaillon, but *F. lumbricalis* lacks discoid holdfast and has wider branching angles compared to *P. rotundus* (Wærn, 1952; Dixon & Irvine, 1977; Guiry & Guiry, 2009). The attached form of *F. lumbricalis* can be found practically throughout the

photic range on hard substrates at salinities down to 4 (Snoeijs, 1999; Martin, 2000; Kotta & Orav, 2001; Kostamo, 2008). The attached *F. lumbricalis* has sexual and sporangial reproduction (Austin, 1960a, 1960b). In particular, sexual reproduction occurs occasionally and clonality is a common phenomenon in the northern Baltic Sea (Kostamo, 2008). Besides the attached form the West Estonian Archipelago Sea hosts a drifting red macroalgal community dominated by *F. lumbricalis* (= forma *aegagropila*) and the drifting form of *Coccotylus truncatus* (Pall.) M. J. Wynne & J. M. Heine. The community is truly unique in European seas and is likely maintained by the prevailing circular currents and the grid of islets that surround the area (Martin, 2000). Unlike the common attached *F. lumbricalis*, the drifting (also known as loose-lying, unattached, free-living, free-floating) form of the species appears only in sterility and reproduces only vegetatively, mainly by fragmentation (Austin, 1960c; Norton & Mathieson, 1983; Bird et al., 1991).

It is plausible that different environmental factors determine the patterns of attached and drifting forms of *F. lumbricalis*. In general, the large-scale distribution of *F. lumbricalis* is determined mainly by temperature. Within the optimum temperature range the species inhabits lower intertidal and subtidal hard bottoms and tolerates reduced salinities (Lüning, 1990; Guiry & Guiry, 2009). Within the Baltic Sea salinity is likely the most important factor setting the regional distribution limits of algal species (Kautsky & Kautsky, 2000) and within the optimum salinity range substrate type is considered to be the most important factor regulating local macroalgal community structure, including *F. lumbricalis* (Eriksson & Bergström, 2005). Earlier studies on the Baltic Sea red algal communities have shown that the type of substrate, wave exposure, and depth mainly explain the observed distribution patterns of the attached *F. lumbricalis* (Reitalu et al., 2002; Martin & Torn, 2004; Bučas et al., 2007). However, the importance of different environmental factors that govern the distribution of macroalgal communities may vary among water basins (Martin, 2000).

Nowadays, the drifting *F. lumbricalis* can be found only in semi-exposed habitats in the Baltic Sea (Martin et al., 2006b) but it may also occur in the lochs of Scottish and Irish seas (Levring et al., 1969: 421). The drifting *F. lumbricalis* was previously found in Polish waters but the community disappeared due to elevated eutrophication in the 1980s (Kruk-Dowgiałło & Szaniawska, 2008). Intensive harvesting decimated the stocks of the drifting *Furcellaria* stocks in the central Kattegat in the 1950s–1970s (Lund & Christensen, 1969; Pedersen & Snoeijs, 2001). Our knowledge about abiotic factors affecting the spatial distribution of the drifting *F. lumbricalis* is scanty but it is likely that the observed patterns are due to impoverished light conditions (Martin et al., 2006b). Besides, as most of the unattached algae, the drifting *F. lumbricalis* can grow in calm-water localities, where water motion is moderate avoiding seaweeds to wash ashore (Kain & Norton, 1990).

The aim of this study is to describe the biomass distribution patterns of attached and drifting forms of *F. lumbricalis* in the whole Estonian coastal sea including the Gulf of Riga, the West Estonian Archipelago Sea, the Gulf of

Finland, and the Baltic Proper. We also seek which environmental variables best predict the observed biotic patterns as such analyses enable us to reveal the causality of interactions between abiotic environmental variables and macrophyte species.

Earlier studies on *F. lumbricalis* have covered small areas, i.e. had a small range of environmental variability (Pliński & Florczyk, 1984; Mäkinen et al., 1988; Bergström & Bergström, 1999; Martin & Torn, 2004; Eriksson & Bergström, 2005; Bučas et al., 2007). Besides, many of these studies used algal cover as a proxy of density estimate. In field, however, the cover of *F. lumbricalis* is often 100% and in such habitats the direct estimate of biomass (in g dw m^{-2}) would be a much more useful indicator of algal spatial patterns. There is only one investigation (Reitalu et al., 2002) that covers the large-scale distribution of macroalgal communities along the Estonian coasts, but this study had a small number of samples, did not involve semi-enclosed marine habitats, and mostly emphasized classification of seaweed associations. On the larger spatial scales we are also aware but of three large-scale mapping studies of macrophyte communities in the Baltic Sea area (Kautsky & Kautsky, 1989; Middelboe et al., 1997; Snoeijs, 1999). However, the results of these studies were based on communities inhabiting the coastal sea of Scandinavia and did not cover the broad range of the mixed sediment types and wave exposure conditions that can be observed in the Estonian coastal range. To date we are not aware of any comparative studies where the distribution of different forms of *F. lumbricalis* is analysed in a systematic and comprehensive framework.

MATERIAL AND METHODS

Site description

This study was carried out in the eastern Baltic Proper, the Gulf of Riga, the West Estonian Archipelago Sea, and the Gulf of Finland. The Baltic Proper is the largest subdivision of the Baltic Sea with nearly 211 000 km^2 surface area. The average sea surface temperature in winter is around 2°C and annual surface layer salinity is 6–7 (Schramm, 1996). During August, the mean sea surface temperature is 15–16°C in the northern part of the Baltic Proper (Falandysz et al., 2000). Due to the absence of freshwater inflows the eastern Baltic Proper has the highest salinity in the Estonian coastal range. The dominating substrates are lime-stone rock, stones, sand, and a mixture of the above (Reitalu et al., 2002). The coasts of the eastern Baltic Proper are very exposed, hydrodynamically active, and in general characterized by a steep coastline (Suursaar et al., 2008). The phytobenthic communities in the eastern Baltic Proper are very diverse and penetrate deeper compared to the other studied water basins (Trei, 1987; Kautsky & Kautsky, 2000).

The Gulf of Riga is a wide, shallow, semi-enclosed brackish-water ecosystem of the Baltic Sea. A huge drainage area (134 000 km^2) supplies the gulf with fresh water, which mostly enters the southern part of the basin. The average salinity

varies from 0.5–2.0 in surface layers in its southern and northeastern areas to 7 in the straits. In most parts, however, the salinity is 5.0–6.5 and there is no permanent halocline. Due to the shallowness of the gulf, the dynamics of both its surface and deep water temperatures is directly coupled with air temperatures. In a 'typical' year the water is cold and no clear thermocline occurs until May. Later the surface water temperature rises to about 17–20 °C, and a thermocline builds up. The thermocline reaches a depth of 25 m in August and disintegrates in September–October due to intensive wind mixing. In the course of autumn storms the surface water cools down and the deep water temperature rises to 5–10 °C. The oxygen regime is relatively good due to strong vertical mixing. The gulf is on average twice as eutrophicated as the Baltic Proper, and the outflow of nutrients through the straits is higher than their inflow. In general, the bottom relief of the area is quite flat, with gentle slopes towards deeps. The northern part of the gulf is characterized by a wide coastal zone with diverse bottom topography and extensive reaches of boulders. The southern part of the Gulf of Riga is more exposed; steep and soft substrate prevails (Kotta et al., 2008a and references therein).

The West Estonian Archipelago Sea is the smallest studied basin with a surface area of 2243 km^2 (Suursaar et al., 2002). Salinity in this shallow area varies between 6 and 7. Temperature conditions resemble those of the Gulf of Riga. The region is periodically influenced by the nutrient-rich water of the Gulf of Riga. The state of the Gulf of Riga plays a significant role in the development of benthic communities in the West Estonian Archipelago Sea. The bottom relief of the area is flat, with gentle slopes towards deeps. The whole water basin is semi-exposed. Sand and sandy clay substrates prevail in the study area. Due to shallowness and clayey sediments already moderate winds result in strong resuspension of bottom sediments and poor underwater light conditions.

The surface area of the Gulf of Finland totals 30 000 km^2. As compared to other basins in the Baltic Sea, the Gulf of Finland has a relatively large catchment area and the greatest freshwater inflow. Therefore the gulf has a strong horizontal salinity gradient. The surface salinity varies from 0 in its eastern end to 7 in the western areas (Pitkänen et al., 2008). Near the bottom, the salinity increases from 5 in the eastern parts to approximately 10 in the western parts. The strength of the halocline varies both spatially and temporally. The average seawater temperature varies from 0 to 15 °C. The gulf is among the most eutrophicated basins in the Baltic Sea area (Pitkänen et al., 2007). Bottom sediments mainly consist of sand fractions and boulders at shallower areas and silt and clay sediments rich in organic matter in deeper areas (Pitkänen et al., 2008).

Sampling and sample analyses

The phytobenthos sampling and sample analysis followed the guidelines developed for the HELCOM COMBINE programme (HELCOM, 1999). The frame samples (400 cm^2 surface area) were collected randomly by a diver. A total of 386 stations were sampled and three replicate frame samples were taken in each station once

a year in summers 2007 and 2008 (Fig. 1). Altogether 1158 phytobenthic samples were collected. During sampling the geographic coordinates, depth, and the coverage of different sediment types and phytobenthos were recorded. Average salinity values were obtained from the database of the Estonian Marine Institute.

Samples were preserved in a deep freezer at −20 °C. In the laboratory, plants were counted and identified under stereo dissecting microscope. Dry weights of all taxa were obtained after keeping the material 2 weeks at 60 °C. Prior to biomass measuring, all macroscopic epibionts were removed from *F. lumbricalis* thalli.

A simplified Wave Model method was used to calculate the wave exposure for mean wind conditions represented by the ten-year period between 1 January 1997 and 31 December 2006 (Isæus, 2004). A nested-grids technique was used to ensure long distance effects on the local wave exposure regime and the resulting grids had a resolution of 25 m. The means and variability of the wave exposure were calculated at 25, 500, 1000, and 5000 m resolutions using the Spatial Analyst tool of ArcInfo software (ESRI, 2001).

The Spatial Analyst tool of ArcInfo software was also used to calculate the means and variability of the inclination of coastal slopes at 25, 500, 1000, and 5000 m resolutions based on depth charts (available at the Estonian Marine Institute). Coastal slope refers to the amount of inclination of sea bottom. Zero indicates flat bottoms and larger numbers indicate higher degrees of grade (i.e. depressions or hills). Resolution indicates the scale in which topographic features occur.
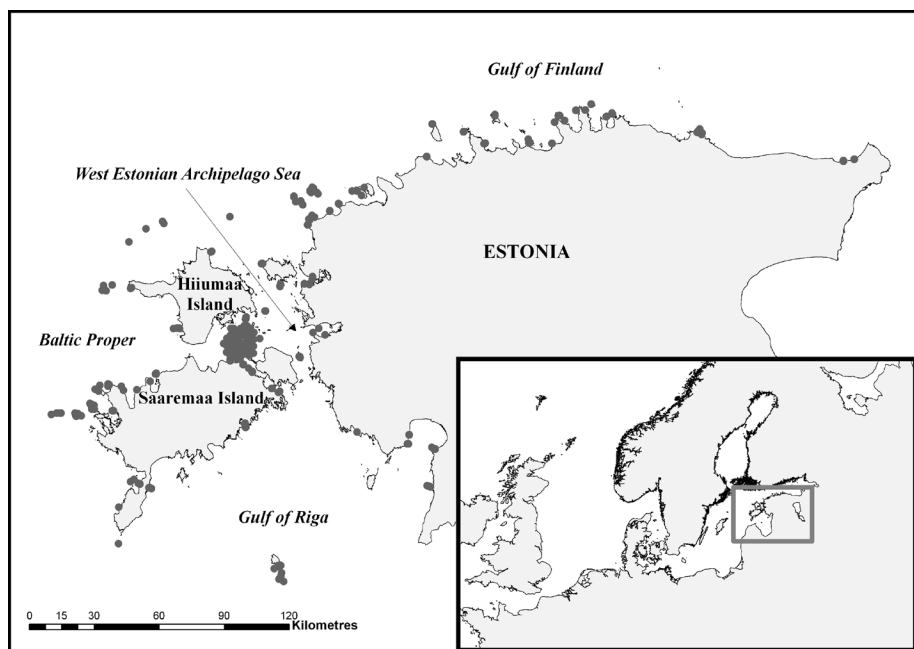
Fig. 1. Distribution of macrophyte sampling stations in the Estonian coastal sea.

Statistical analyses

Multivariate data analyses were performed by the statistical program 'PRIMER' version 6.1.5 (Clarke & Gorley, 2006). Similarities between all pairs of samples were calculated using a zero-adjusted Bray–Curtis coefficient. The coefficient is known to outperform most other similarity measures and enables samples containing no organisms at all to be included (Clarke et al., 2006). BEST analysis (BIOENV procedure) was used to relate the patterns of environmental variables measured at a sampling unit. The analysis shows which environmental variables best predict the observed biotic patterns. A global BEST match permutation test was run to examine the statistical significance of the observed relationships between environmental variables and biotic patterns.

RESULTS

In this study altogether 360 samples of 1158 (i.e. 31%) consisting either of attached or drifting forms of *F. lumbricalis* were investigated. The attached form occurred in 23% of the samples and the drifting form in 8% of the samples taken within the Estonian coastal range in 2007–2008. Table 1 lists all studied abiotic environmental variables and shows the distribution of the attached and drifting *F. lumbricalis* along these environmental gradients (means and variability). Compared to the drifting form, the attached *F. lumbricalis* tolerated a broader range of environmental variability and reached down to the lowest benthic macrovegetation limits ever monitored in the Estonian coastal sea (i.e. 18 m in the offshore waters of NW Hiiumaa Island, according to the database of the Estonian Marine Institute). The drifting *F. lumbricalis* occurred on average deeper than the attached *F. lumbricalis* but its depth range was smaller, estimated at 1–8.5 m. On the other hand, the biomass of the drifting form varied in a wider range than the attached *F. lumbricalis*.

The biomasses of both drifting and attached forms of *F. lumbricalis* reached up to 500 g dw m^{-2}. The attached *F. lumbricalis* was found all around the Estonian coastal waters except for the eastern Gulf of Finland, where the species was limited by the 4.8 psu isoline (compare Fig. 1 and Fig. 2), the central West Estonian Archipelago Sea, and the offshore waters of NW Hiiumaa Island. The biomasses were relatively large in the open Baltic Proper, especially adjacent to Saaremaa Island. The biomasses were relatively moderate and variable in the Gulf of Finland and the Gulf of Riga (Fig. 2). The drifting form of *F. lumbricalis* was found only in the West Estonian Archipelago Sea, except of one site at the northern coast of the Gulf of Riga (Fig. 3).
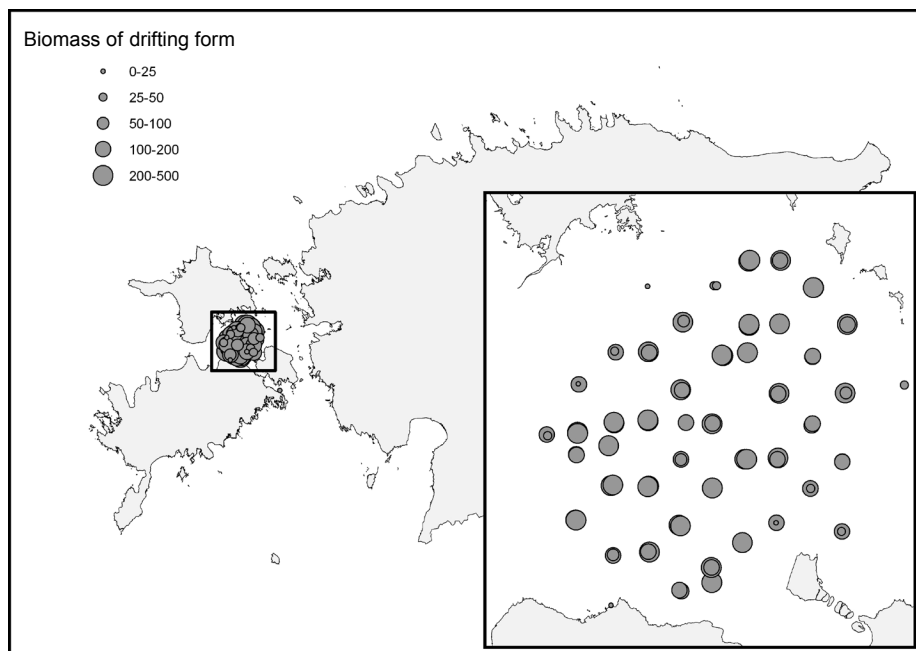
The BEST permutation test showed that the biomass distribution of the attached *F. lumbricalis* was best predicted by the combination of wave exposure, depth, and the percentage of gravel and pebble fractions at local scale (Rho 0.178; $p < 0.001$). Within the studied range increasing depth and wave exposure resulted in higher biomasses of the attached *F. lumbricalis*. On the other hand, the increasing

Table 1. Main environmental characteristics associated to attached and drifting forms of *F. lumbricalis* in the Estonian coastal sea. Only the samples in which *F. lumbricalis* was present were used

Variable	Attached *F. lumbricalis* (n = 272)		Drifting *F. lumbricalis* (n = 88)	
	Range (min to max)	Mean ± SE	Range (min to max)	Mean ± SE
Biomass, g dw m^{-2}	0.015...490.88	37.64 ± 0.03	0.33...568.58	210.02 ± 13.23
Depth distribution, m	0.1...17	5.45 ± 0.24	1...8.5	7.05 ± 0.13
Wave exposure, m^2 s^{-1}	13 106...968 172	256 328 ± 15 598	36 450...145 517	85 397 ± 3 369
Coastal slope 25 m scale, °	0.00...8.46	0.48 ± 0.07	0.00...1.29	0.11 ± 0.03
Coastal slope 500 m scale, °	0.00...2.65	0.19 ± 0.02	0.00...0.19	0.02 ± 0.003
Coastal slope 1000 m scale, °	0.00...1.40	0.19 ± 0.02	0.002...0.12	0.03 ± 0.004
Coastal slope 5000 m scale, °	0.00...0.38	0.08 ± 0.01	0.01...0.04	0.02 ± 0.001
Salinity	4.78...6.55	5.76 ± 0.03	5.54...5.83	5.76 ± 0.004
Sediment type, % of bottom coverage				
Clay	0...50	0.55 ± 0.26	0...75	18.47 ± 1.68
Silt	0...100	3.02 ± 0.88	0...30	0.74 ± 0.39
Sand	0...100	27.27 ± 2.06	25...100	79.83 ± 1.64
Gravel + pebbles	0...98	6.35 ± 1.00	Absent	Absent
Shingle	0...80	30.78 ± 2.01	0...10	0.57 ± 0.23
Boulder	0...100	14.31 ± 1.40	0...20	0.4 ± 0.26
Rock	0...100	12.41 ± 1.81	Absent	Absent
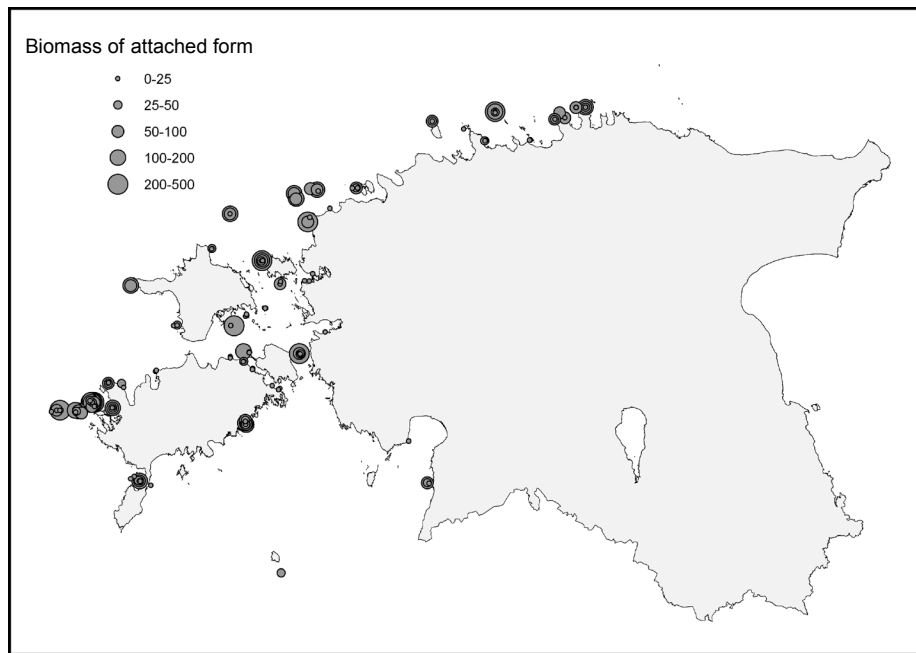
Fig. 2. Biomass distribution of the attached *F. lumbricalis* in the Estonian coastal sea. The size of bubbles indicates the biomass of the red alga (g dw m^{-2}).

Fig. 3. Biomass distribution of the drifting *F. lumbricalis* in the Estonian coastal sea. The size of bubbles indicates the biomass of the red alga (g dw m^{-2}).

percentage of gravel and pebble fractions in the sediment reduced the biomass of the attached *F. lumbricalis*. Surprisingly, salinity had no significant effect on the distribution and biomass of the attached *F. lumbricalis* along the Estonian coastal sea.

The biomass distribution of the drifting *F. lumbricalis* was best explained by the combination of wave exposure and bottom slope at 500 m scale. However, this interaction was significant only if there was no hard substrate available (Rho 0.378; $p < 0.001$). On soft bottoms the biomass of the drifting *F. lumbricalis* decreased with increasing slope and variability of wave exposure at the respective scale. On hard bottoms within the studied range of exposure and slope the community consisted of the attached *F. lumbricalis*.

DISCUSSION

The study showed that (1) the combination of multiple environmental variables explained the distribution of attached and drifting forms of *F. lumbricalis* and (2) different environmental variables were important for different forms of the red alga. Increased affinity of *F. lumbricalis* to deeper areas refers to the ability of the species to tolerate poorer light conditions compared to other macroalgae inhabiting the Estonian coastal sea (Paalme & Kukk, 2003).

Lowered preference of the attached *F. lumbricalis* to the bottoms dominated by gravel and pebbles is related to sediment instability as in such sediments *F. lumbricalis* can be dislodged during storms (Thomsen & Wernberg, 2005; Bučas et al., 2007). Increased affinity of the attached *F. lumbricalis* to elevated wave exposure suggests that the species prefers habitats where the competitive interactions among the macroalgae are the weakest (Kiirikki, 1996; Eriksson & Bergström, 2005) as highly exposed areas are characterized by low biomasses of perennial macrovegetation (Pratt & Johnson, 2002; Reitalu et al., 2002). However, too high wave exposure levels render habitat inhospitable for the attached *F. lumbricalis* (Bučas et al., 2007) but such values do not occur in the northeastern Baltic Sea. As such, the results agree with previous observations in the northern areas of the Gulf of Finland where a positive correlation between wave exposure and the biomass of *F. lumbricalis* was reported (Westerbom et al., 2008).

Surprisingly, salinity had no significant effect on the distribution and biomass of the attached *F. lumbricalis* along the Estonian coastal sea. Similarly, Kornfeldt (1979) reported no effect of salinity on the biomass of this algal species. The lack of a clear-cut effect suggests that the growth of the red alga is not affected by shifts in salinity at the lower limit of its salinity tolerance.

Strong links between wave exposure, bottom slope at 500 m scale, and the distribution of the drifting *F. lumbricalis* suggest that the mesoscale seabed topography and hydrodynamic regime largely determine the distribution pattern of this red algal form. Weak depressions of 500 m spatial scale and uniform wave regime seem very important for drifting algal mats to remain in the study area.

However, this interaction was significant only if there was no hard substrate available. On hard bottoms within the studied range of exposure and slope the community consisted of the attached *F. lumbricalis*.

This implies that interspecific interactions between the attached and drifting forms of *F. lumbricalis* are behind the observed distribution pattern of the drifting *F. lumbricalis*. Both the attached and drifting *F. lumbricalis* tolerate poor light conditions. However, the growth rates of different forms vary depending on the depth (light conditions) considered. On shallower areas the growth rate of the attached *F. lumbricalis* is higher than that of the drifting form and therefore the attached *F. lumbricalis* may outcompete the drifting form in such habitats (Martin et al., 2006b). In deeper areas (i.e. at poorer light conditions), however, the drifting form has an advantage over the attached form in terms of the growth rate. Similarly, the habitats that have a large share of clay and sand fractions are characterized by high sediment resuspension, sedimentation rates, low light levels, and thus are very inhospitable for the most of macroalgae (Kain & Norton, 1990; Eriksson & Johansson, 2005) but not so for the drifting *F. lumbricalis* (Martin et al., 2006b).

Moreover, the drifting *F. lumbricalis* hosts another red algal species *Coccotylus truncatus* (Kersen & Martin, 2007). A recent experimental study demonstrated that the growth of the red algae in such an inhospitable environment is highly density dependent (Kotta et al., 2008b) and thus the biomass pattern of the drifting *F. lumbricalis* is likely determined by the share of *C. truncatus* in the community. Total biomass values of the drifting *F. lumbricalis* and *C. truncatus* are set by regional weather conditions that (mainly through wind patterns) determine the underwater light regime and also influence seawater temperatures that are known to affect the growth of *F. lumbricalis* (Bird et al., 1979; Rueness & Tananger, 1984). It is likely, however, that large-scale abiotic variables primarily determine the broad patterns of the studied red algal species and within these broad patterns the competitive interactions among macroalgae modify algal distributions.

To conclude, our study showed that the attached *F. lumbricalis* prefers deep and exposed sea areas with bottoms not containing mobile sediment fractions. In other words, the attached *F. lumbricalis* is confined to the areas where the growth of other macroalgal species is suppressed either due to poor light conditions or elevated wave exposure (instability of sediments) and thereby the competitive interactions among the macroalgae are the weakest. The drifting *F. lumbricalis* is confined to deep habitats that are characterized by a weak topographic depression, soft bottoms, high sediment load, and poor light conditions. Such habitats are unsuitable for the other macroalgae (except for the drifting form of *C. truncatus*) and the attached *F. lumbricalis*. Because of its loose-lying nature, the spatial patterns of the drifting *F. lumbricalis* are mainly determined by the basin-scale hydrodynamical (light) regime and partly by the competitive interactions among other species within the drifting macroalgal community. In order to reveal the exact mechanisms and interactions, however, experimental studies with manipulated wave exposure, light conditions, sediment loading, and algal biomasses are needed.

ACKNOWLEDGEMENTS

REFERENCES

Austin, A. P. 1960a. Life history and reproduction of *Furcellaria fastigiata* (L.) Lam. 1. The haploid plants and the development of the carposporophyte. *Ann. Bot. N.S.*, **24**, 257–276.

Austin, A. P. 1960b. Life history and reproduction of *Furcellaria fastigiata* (L.). Lam. 2. The tetrasporophyte and reduction division in the tetrasporangium. *Ann. Bot. N.S.*, **24**, 296–312.

Austin, A. P. 1960c. Observations on *Furcellaria fastigiata* (L.) Lam. forma *aegagropila* Reinke in Danish waters together with a note on other unattached algal forms. *Hydrobiologia*, **14**, 255–277.

Bergström, L. & Bergström, U. 1999. Species diversity and distribution of aquatic macrophytes in the Northern Quark, Baltic Sea. *Nord. J. Bot.*, **19**, 375–383.

Bird, C. J., Chen, L. C.-M. & McLachlan, J. 1979. Effects of temperature, light and salinity on growth in culture of *Chondrus crispus*, *Furcellaria lumbricalis*, *Gracilaria tikhaviae* (Gigartinales, Rhodophyta), and *Fucus serratus* (Fucales, Phaeophyta). *Bot. Mar.*, **22**, 521–527.

Bird, C. J., Saunders, G. W. & McLahlan, J. 1991. Biology of *Furcellaria lumbricalis* (Hudson) Lamouroux (Rhodophyta: Gigartinales), a commercial carrageenophyte. *J. Appl. Phycol.*, **3**, 61–82.

Bučas, M., Daunys, D. & Olenin, S. 2007. Overgrowth patterns of the red algae *Furcellaria lumbricalis* at an exposed Baltic Sea coast: the results of a remote underwater video data analysis. *Estuar. Coast. Shelf Sci.*, **75**, 308–316.

Clarke, K. R. & Gorley, R. N. 2006. *PRIMER v6: User Manual/Tutorial*. PRIMER-E, Plymouth.

Clarke, K. R., Somerfield, P. J. & Chapman, M. G. 2006. On resemblance measures for ecological studies, including taxonomic dissimilarities and a zero-adjusted Bray-Curtis coefficient for denuded assemblages. *J. Exp. Mar. Biol. Ecol.*, **330**, 55–80.

Dixon, P. S. & Irvine, L. M. 1977. *Seaweeds of the British Isles. Volume 1. Rhodophyta. Part 1. Introduction, Nemaliales, Gigartinales*. British Museum (Natural History), London.

Eriksson, B. K. & Bergström, L. 2005. Local distribution patterns of macroalgae in relation to environmental variables in the northern Baltic Proper. *Estuar. Coast. Shelf Sci.*, **62**, 109–117.

Eriksson, B. K. & Johansson, G. 2005. Effects of sedimentation on macroalgae: species-specific responses are related to reproductive traits. *Oecologia*, **143**, 438–448.

ESRI, 2001. *ArcGIS Spatial Analyst: Advanced GIS Spatial Analysis Using Raster and Vector Data*. New York.

Falandysz, J., Trzosinska, A., Szefer, P., Warzocha, J. & Dragnik, B. 2000. The Baltic Sea, especially southern and eastern regions. In *Seas at the Millennium: An Environmental Evaluation* (Sheppard, C., ed.). *Mar. Pollut. Bull.*, **41**, 99–120.

Guiry, M. D. & Guiry, G. M. 2009. *AlgaeBase*. World-wide electronic publication, National University of Ireland, Galway. http://www.algaebase.org (accessed 2 February 2009).

HELCOM. 1999. *Guidelines for Monitoring of Phytobenthic Plant and Animal Communities in the Baltic Sea. Annex for HELCOM COMBINE Programme*. Compiled by S. Bäck.

Isæus, M. 2004. *Factors Structuring* Fucus *Communities at Open and Complex Coastlines in the Baltic Sea*. PhD Thesis, Department of Botany, Stockholm University, Sweden.

Kain, J. M. & Norton, T. A. 1990. Marine ecology. In *Biology of the Red Algae* (Cole, K. M. & Sheath, R. G., eds), pp. 377–408. Cambridge University Press.

Kautsky, L. & Kautsky, H. 1989. Algal species diversity and dominance along gradients of stress and disturbance in marine communities. *Vegetatio*, **83**, 259–267.

Kautsky, L. & Kautsky, N. 2000. The Baltic Sea, including Bothnian Sea and Bothnian Bay. In *Seas at the Millennium: An Environmental Evaluation* (Sheppard, C., ed.). *Mar. Pollut. Bull.*, **41**, 1–14.

Kersen, P. & Martin, G. 2007. Annual biomass loss of the loose-lying red algal community via macroalgal beach casts in the Väinameri area, NE Baltic Sea. *Proc. Estonian Acad. Sci. Biol. Ecol.*, **56**, 278–289.

Kiirikki, M. 1996. Mechanisms affecting macroalgal zonation in the northern Baltic Sea. *Eur. J. Phycol.*, **31**, 225–232.

Kornfeldt, R.-A. 1979. Biomass of macroalgae along the coast of Halland, SW Sweden. *Sven. Bor. Tidskr.*, **73**, 131–138.

Kostamo, K. 2008. The life cycle and genetic structure of the red alga *Furcellaria lumbricalis* on a salinity gradient. *W. & A. de Nottbeck Foundation Sci. Rep.*, **33**, 1–34.

Kotta, J. & Orav, H. 2001. Role of benthic macroalgae in regulating macrozoobenthic assemblages in the Väinameri (north-eastern Baltic Sea). *Ann. Zool. Fenn.*, **38**, 163–171.

Kotta, J., Paalme, T., Martin, G. & Mäkinen, A. 2000. Major changes in macroalgae community composition affect the food and habitat preference of *Idotea baltica. Int. Rev. Hydrobiol.*, **85**, 693–701.

Kotta, J., Lauringson, V., Martin, G., Simm, M., Kotta, I., Herkül, K. & Ojaveer, H. 2008a. Gulf of Riga and Pärnu Bay. In *Ecology of Baltic Coastal Waters* (Schiewer, U., ed.), pp. 217–243. Springer, Berlin.

Kotta, J., Paalme, T., Kersen, P., Martin, G., Herkül, K. & Möller, T. 2008b. Density dependent growth of the red algae *Furcellaria lumbricalis* and *Coccotylus truncatus* in the West-Estonian Archipelago Sea, northern Baltic Sea. *Oceanologia*, **50**, 577–585.

Kruk-Dowgiałło, L. & Szaniawska, A. 2008. Gulf of Gdańsk and Buck Bay. In *Ecology of Baltic Coastal Waters* (Schiewer, U., ed.), pp. 139–165. Springer, Berlin.

Lauringson, V. & Kotta, J. 2006. Influence of the thin drift algal mats on the distribution of macrozoobenthos in Kõiguste Bay, NE Baltic Sea. *Hydrobiologia*, **554**, 97–105.

Levring, T., Hoppe, H. A. & Schmid, O. J. 1969. *Marine Algae: A Survey of Research and Utilization*. Cram, De Gruyter & Co, Hamburg.

Lund, S. & Christensen, J. 1969. On the collection of *Furcellaria* in Denmark during the years 1961–1967. *Proc. Int. Seaweed Symp.*, **6**, 699–701.

Lüning, K. 1990. *Seaweeds: Their Environment, Biogeography, and Ecophysiology*. Wiley & Sons, New York.

Mäkinen, A., Kääriä, J. & Rajasilta, M. 1988. Factors controlling the occurrence of *Furcellaria lumbricalis* (Huds.) Lamour. and *Phyllophora truncata* (Pallas) Zinova in the upper littoral of the Archipelago of SW Finland. *Kiel. Meeresforsh. (Sonderh.)*, **6**, 140–146.

Martin, G. 2000. Phytobenthic communities of the Gulf of Riga and the inner sea of the West-Estonian Archipelago. *Diss. Biol. Univ. Tartu*, **64**.

Martin, G. & Torn, K. 2004. Classification and description of phytobenthic communities in the waters of the West-Estonian Archipelago Sea. *Hydrobiologia*, **514**, 151–162.

Martin, G., Paalme, T. & Torn, K. 2006a. Seasonality pattern of biomass accumulation in a drifting *Furcellaria lumbricalis* community in the waters of the West Estonian Archipelago, Baltic Sea. *J. Appl. Phycol.*, **18**, 557–563.

Martin, G., Paalme, T. & Torn, K. 2006b. Growth and production rates of loose-lying and attached forms of the red algae *Furcellaria lumbricalis* and *Coccotylus truncatus* in Kassari Bay, the West Estonian Archipelago Sea. *Hydrobiologia*, **554**, 107–115.

Middelboe, A. L., Sand-Jensen, K. & Brodersen, K. 1997. Patterns of macroalgal distribution in the Kattegat-Baltic region. *Phycologia*, **36**, 208–219.

Nielsen, R., Kristiansen, A., Mathiesen, L. & Mathiesen, H. (eds). 1995. Distributional index of the benthic macroalgae of the Baltic Sea area. *Acta Bot. Fenn.*, **155**.

Norton, T. A. & Mathieson, A. C. 1983. The biology of unattached seaweeds. *Prog. Phycol. Res.*, **2**, 333–386.

Novaczek, I. & Breeman, A. M. 1990. Thermal ecotypes of amphi-Atlantic algae. II. Cold-temperate species (*Furcellaria lumbricalis* and *Polyides rotundus*). *Helgol. Meeresunters.*, **44**, 475–485.

Orav-Kotta, H. & Kotta, J. 2004. Food and habitat choice of the isopod *Idotea baltica* in the northeastern Baltic Sea. *Hydrobiologia*, **514**, 79–85.

Paalme, T. & Kukk, H. 2003. Comparison of net primary production rates of *Pilayella littoralis* (L.) Kjellm. and other dominating macroalgal species in Kõiguste Bay, northeastern Baltic Sea. *Proc. Estonian Acad. Sci. Biol. Ecol.*, **52**, 125–133.

Pedersen, M. & Snoeijs, P. 2001. Patterns of macroalgal diversity, community composition and long-term changes along the Swedish west coast. *Hydrobiologia*, **459**, 83–102.

Pitkänen, H., Kiirikki, M., Savchuk, O., Räike, A., Korpinen, P. & Wulff, F. 2007. Searching efficient protection strategies for the eutrophicated Gulf of Finland: the combined use of 1D and 3D modeling in assessing long-term state scenarios with high spatial resolution. *Ambio*, **36**, 272–279.

Pitkänen, H., Lehtoranta, J. & Peltonen, H. 2008. The Gulf of Finland. In *Ecology of Baltic Coastal Waters* (Schiewer, U., ed.), pp. 285–308. Springer, Berlin.

Pliński, M. & Florczyk, I. 1984. Changes in the phytobenthos resulting from the eutrophication of the Puck Bay. *Limnologica*, **15**, 325–327.

Pratt, M. S. & Johnson, A. S. 2002. Strength, drag, and dislodgement of two competing intertidal algae from two wave exposures and four seasons. *J. Exp. Mar. Biol. Ecol.*, **272**, 71–101.

Reitalu, T., Paal, J. & Martin, G. 2002. Phytobenthic microcoenoses along Estonian exposed seashores. *Proc. Estonian Acad. Sci. Biol. Ecol.*, **51**, 257–276.

Rueness, J. & Tananger, T. 1984. Growth in culture of four red algae from Norway with potential for mariculture. *Hydrobiologia*, **116/117**, 303–307.

Schramm, W. 1996. The Baltic Sea and its transition zones. In *Marine Benthic Vegetation: Recent Changes and the Effect of Eutrophication* (Schramm, W. & Nienhuis, P. H., eds), pp. 131–163. Springer, Berlin.

Snoeijs, P. 1999. Marine and brackish waters. In *Swedish Plant Geography* (Rydin, H., Snoeijs, P. & Diekmann, M., eds). *Acta Phytogeogr. Suec.*, **84**, 187–212.

Suursaar, Ü., Kullas, T. & Otsmann, M. 2002. A model study of the sea level variations in the Gulf of Riga and the Väinameri Sea. *Cont. Shelf Res.*, **22**, 2001–2019.

Suursaar, Ü., Jaagus, J., Kont, A., Rivis, R. & Tõnisson, H. 2008. Field observations on hydro-dynamic and coastal geomorphic processes of Harilaid Peninsula (Baltic Sea) in winter and spring 2006–2007. *Estuar. Coast. Shelf Sci.*, **80**, 31–41.

Trei, T. 1978. The physiognomy and structure of the sublittoral macrophyte communities in Kassary Bay (an area between the Isles of Hiiumaaa and Saaremaa). *Kiel. Meeresforsch.*, **4**, 117–121.

Trei, T. 1987. Phytobenthos in the waters of the Vilsandi State Nature Reserve. *Proc. Acad. Sci. Estonian SSR. Biol.*, **36**, 227–235.

Thomsen, M. S. & Wernberg, T. 2005. Minireview: What affects the forces required to break or dislodge macroalgae? *Eur. J. Phycol.*, **40**, 139–148.

Wærn, M. 1952. Rocky shore algae in the Öregrund Archipelago. *Acta Phytogeogr. Suec.*, **30**.

Westerbom, M., Mustonen, O. & Kilpi, M. 2008. Distribution of marginal population of *Mytilus edulis*: responses to biotic and abiotic processes at different spatial scales. *Mar. Biol.*, **153**, 1153–1164.

Punavetikas agariku (*Furcellaria lumbricalis*) kinnitunud ja triiviva vormi levikumustrit kujundavad abiootilised tegurid Eesti rannikumeres

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Agarik on üks väheseid põhjaparasvöötme makroskoopilisi punavetikaid, kes on suutnud tungida ka madala soolsusega Läänemerre, ja seeläbi on tal lisaks majanduslikule tähtsusele ka funktsionaalselt oluline osa mereökosüsteemis. Läänemeres on teada kaks agariku morfoloogilist ökotüüpi – tavalisem, kinnitunud vorm, ja lahtine, põhja kohal lebav vorm. Käesoleva artikli eesmärgiks on kirjeldada kahe agarikuvormi levikumustreid Eesti rannikumeres ja välja selgitada abiootilised tegurid, mis neid mustreid kõige paremini kirjeldaksid. Uuringust selgus, et agariku kinnitunud vorm eelistab kasvada sügaval ja lainetusele avatud mereelupaikades. Agariku lahtine vorm on levinud samuti sügaval, kuid seal, kus merepõhi on lauge ja domineerivad pehmed setted. Sellistes elupaikades on valgustingimused põhjasetete resuspensiooni tõttu kehvapoolsed. Mõlema vormi biomassi väärtused ulatusid Eesti merealal ligi 500 g m^{-2} kuivkaalus. Põhjale kinnitunud agarik on levinud kõigil suurematel merealadel Eesti territoriaalmere ulatuses, kuid lahtine agarikuvorm kasvab ainult Väinameres.