Recent distribution and stock assessment of the red alga *Furcellaria lumbricalis* on an exposed Baltic Sea coast: combined use of field survey and modelling methods*

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KEYWORDS Phytobenthos Sublittoral Depth limits Occupied area

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Abstract

Recent results of field studies on the exposed coast of Lithuania were used to model the area occupied by the red alga *Furcellaria lumbricalis* using the Natural Neighbor interpolation technique, while linear regression was applied to estimate the species' standing stock. The area covered by *F. lumbricalis* extended for 26 km along the

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coast between depths of 1 and 15 m. The maximum species cover in the study area ranged between 4 and 10 m depth, which is one of the widest in the Baltic Sea. The modelled area of *F. lumbricalis* covered $35 \pm 11 \text{ km}^2$ with a total biomass of 7554 ± 3813 t.

1. Introduction

The red alga *Furcellaria lumbricalis* (Hudson) J.V. Lamouroux is distributed mainly in the northern Atlantic Ocean, and also penetrates into the Baltic Sea (Guiry & Guiry 2009). It was harvested locally in Canada, Denmark and it is still used in Estonia for the food and/or pharmaceutical industries (Bird et al. 1991). Along the exposed coast of the south-eastern Baltic Sea F. lumbricalis is the only dominant perennial macrophyte (Labanauskas 2000, Bučas et al. 2007). The alga is attached to boulders, cobbles and pebbles; sand and gravel are unsuitable for its growth (Bučas et al. 2007). Densely vegetated areas of the red alga are valuable marine biodiversity spots surrounded by vast sandy bottoms (Olenin & Daunys 2004), they serve also as natural spawning grounds for the Baltic herring (Clupea harenqus membras L.) (Olenin & Labanauskas 1994). The overgrowths of F. lumbricalis are an important structural component of the reefs mentioned in Annex 1 of the EU Habitat Directive (Council Directive 92/43/EEC). Nevertheless, this red alga is on the list of threatened and/or declining species at several sites in the Baltic Sea (HELCOM 2007). The maximum depth distribution of F. lumbricalis was regarded as a water quality indicator during the implementation of the EU water Framework Directive (Bäck et al. 2006, Daunys et al. 2007).

Several studies concerning the spatial distribution and standing stock assessment of F. lumbricalis in the south-eastern Baltic Sea have been performed since 1955: by Kireeva (1960), Blinova & Tolstikova (1972), Korolev et al. (1983, 1993), Olenin & Labanauskas (1994), Maksimov et al. (1996) and Labanauskas (2000). Although reduced areas of the red alga were recorded in some coastal waters in 1993–94 (Olenin & Labanauskas 1994) and since 1968–69 (Blinova & Tolstikova 1972), the status of F. lumbricalis has never yet been analysed in detail. Moreover, the widespread impact of oil spills, sediment dredging and dumping, beach nourishment and port extensions into the natural coastal zone has been and will continue to be an important conservation and management issue.

General field survey methods (SCUBA diving and underwater video) have limited applicability on exposed coasts owing to the low transparency of the water and active hydrodynamic conditions (Bučas et al. 2007). The aim of this study was therefore to apply a modelling approach to the quantitative

estimation of F. lumbricalis cover and biomass at different depths and on different types of bottom sediments. The present study was based on the largest dataset collected hitherto in the area, during a period of intensive study from 2003 to 2008. The methods applied enabled the continuous distribution and stock of ecologically and economically important red alga species to be assessed, thereby providing a better basis for the future integrated coastal management of the study area.

2. Material and methods

2.1. Study area

The south-eastern Baltic Sea coast is exposed, with a wind fetch exceeding > 200 km in any westerly direction (Olenin et al. 2003). Waves are wind-induced with a mean height of ca 2 m (Žaromskis 1982, Ašmontas 1994). The largest measured waves have been as high as 6.7 m, whereas in extreme storm conditions (wind > 30 m s⁻¹) the height of modelled waves can attain 12 m. Near the bottom, current speeds vary from 5 to 50 cm s⁻¹, depending on the direction and velocity of winds, and the bottom topography (Dubra 1994).

The sublittoral part of the underwater slope (down to 20 m depth, according to Olenin et al. 1996) stretches for 3–7 km from the shore in the Lithuanian part of the south-eastern Baltic. Along the Curonian Spit it is covered by sand, which is unsuitable for the red alga, *Furcellaria lumbricalis*, whereas off the mainland coast the seabed is dominated by glacial deposits (Figure 1): moraine clay, large boulders, cobbles, pebbles, gravel and sand (Gulbinskas & Trimonis 1999). Sediment distribution is determined by the deposition of material transported from the Curonian Lagoon, as well as by coastal abrasive-erosive processes (Gudelis & Janukonis 1977, Žaromskis 1982). Generally, soft bottom sediments are transported northwards along the shore.

According to unpublished monitoring data of the Centre of Marine Research (CMR), the near-bottom salinity ranged from 6 to 7.5 PSU in the study area during 2003–07. However, as the salinity in part of the study area stretching 25–30 km to the north of Klaipeda occasionally falls to <5 PSU as a result of freshwater outflow from the Curonian Lagoon, these waters were classified as transitional (Daunys et al. 2007).

The water temperature regime in the study area exhibited the typical boreal pattern, with the highest temperatures $(15 \pm 3.3^{\circ}C)$ in July–August and the lowest ones $(1.3 \pm 0.8^{\circ}C)$ in January–February (calculations based on unpublished monitoring data, CMR).



Figure 1. Location of the study sites off the Lithuanian coast (Baltic Sea): drop down video transects (\circ) and hand-held long distance video transects – A, B and C (-); descriptions by SCUBA divers – SCUBA des. (\blacktriangle); biomass samples taken by SCUBA divers – SCUBA biom. (\Box)

Total near-bottom nitrogen concentrations ranged between 7.5 and 634.0 μ g dm⁻³ (mean = 62.3 ± 33.5 μ g dm⁻³), and total phosphorus concentrations varied between 10 and 74 μ g dm⁻³ (mean = 31.2 ± 6.7 μ g dm⁻³) (unpublished monitoring data, CMR).

The Secchi depth varied between 2 and 8.5 m with a mean of 4.5 ± 1.7 m. These values correspond to the depth of the euphotic zone between 10 and 16 m when calculated according to Urbanski & Szymelfenig (2003).

2.2. Field and laboratory methods

Underwater surveys were performed between 2003 and 2008 (Table 1) for different seabed mapping and monitoring purposes: biodiversity inventories (Olenin et al. 2003), habitat mapping and macrophytobenthos monitoring. Investigations were carried out in the coastal waters along the mainland coast of Lithuania (Figure 1), which, due to the presence of hard substrates in the euphotic zone is generally suitable for the attached form of the red alga F. lumbricalis (Olenin & Labanauskas 1994, Olenin et al. 1996, Bučas et al. 2007). Three methods were used to estimate the F. lumbricalis biomass and/or cover: SCUBA diving, drop down and hand-held underwater video cameras.

Table 1. Number of 10–30 m length transects using three methods (diving, drop down and hand-held videos), and number of biomass samples of *Furcellaria lumbricalis* off the Lithuanian coast from 2003 to 2008

Year	SCUBA diving	Drop down video	Hand-held video	Number of biomass samples
2003	37	121		9
2004	15			
2005	44			5
2006	79	239		9
2007	22	68	198	1
2008	10			10
Total	207	428	198	34

A total of 207 transects of the seabed were investigated by divers at depths between 1 and 19 m. Using recommended benchic monitoring methods (Davies et al. 2001), the percentage cover of F. *lumbricalis* and bottom substrates was estimated in 1–4 m² sections along 10–20 m diving transects. Depths were measured by diving depth gauge or computer.

Biomass samples of *F. lumbricalis* (2–8 replicates per transect) were taken by divers in 34 transects at depths between 1 and 16 m. The samples were taken from the maximum cover of the red alga within the transects using a modified Kautsky-type frame (0.04 m²). *F. lumbricalis* thalli in each sample were cleared of epiphytes, drained and weighed. The wet biomass of the species was calculated per 1 m² at each depth interval.

Seabed recording using a drop-down underwater video system was performed on 428 transects at depths between 1 and 22 m. The underwater video system consisted of two cameras (colour SONY TRV-DCR 950 Mini DV and b/w C-Technics Subsea Video 302), mounted in a housing at an angle of ca 40° to the bottom. Two laser diodes projected two dots 10 cm apart onto the bottom, enabling the spatial scale and object size in the video footage to be determined. The depth sensor was mounted in the housing, and the signal from the sensor was embedded in the video stream. Continuous seabed recording was performed from a boat drifting (velocity 0.5-1 knots) along transects ca 10–120 m in length (the instantaneous visual area was approximately 1 m²). The percentage cover of *F. lumbricalis* and bottom substrates were estimated in the visual area of seabed for each minute of video footage.

A hand-held video camera was used for the seabed recording along the three long-distance (1000–2000 m) transects at depths from 1 to 15 m. The data collected were used to determine changes in depth distribution of F. lumbricalis and substrates along the depth gradient more precisely than it was possible with the drop-down video system. Towed by a boat (velocity 1–1.5 knots) along the transect, a diver filmed the seabed with an underwater video camera (Sony Handycam DCR HC42E) at a distance of ca 0.5–1 m from the seabed, covering a visual area of approximately 1 m². The percentage cover of F. lumbricalis and bottom substrates were estimated in the visual area of seabed for each minute of video footage.

The location of all the study transects was determined by GPS with an accuracy error < 25 m. Video transects longer than ca 20 m were divided into 10–30 m sections in order to standardise the sample size among the different methods. *F. lumbricalis* cover and substrate composition were therefore averaged within these transects. In total, the database consisted of 842 diving and video transects, and 34 samples of the species biomass. The mean *F. lumbricalis* cover estimated by hand-held video and diving methods did not differ significantly (t = -0.5, p = 0.6). The water transparency during SCUBA diving and video recording ranged from 1 to 7 m, although it was usually < 2-3 m.

2.3. Modelling Furcellaria lumbricalis distribution

The spatial distribution of F. lumbricalis was explored and modelled using spatial statistics tools (ESRI® ArcMapTM 9.2). The Natural Neighbor interpolation technique was applied owing to the uneven coverage of stations throughout the study area (Sibson 1981). The modelled species cover was set to zero in areas covered by unsuitable substrates (sand and gravel) or below the euphotic zone (<15 m) using data of bottom substrates and bathymetry (Gelumbauskaitė et al. 1999).

2.4. Standing stock assessment

The linear regression between the cover and wet biomass of F. lumbricalis was calculated in order to predict the biomass for different values of the species cover in the modelled area. Thereafter, these biomasses were summed in order to estimate the standing stock of the red alga in the total area occupied by F. lumbricalis.

2.5. Statistical procedures

The t-test was applied to test for differences between the means of two independent groups (e.g. the cover of F. lumbricalis on depressions and on elevations of the bottom slope). Before analysis, the data was tested for normality and homogeneity of variance employing the Kolmogorov-Smirnov and F tests respectively. In cases where these conditions were not met, transformations were applied (Sokal & Rohlf 1995): F. lumbricalis cover was square-root-transformed. Spearman's rank correlation was used to quantify the relationship between F. lumbricalis cover and biomass at each depth interval. Means and standard deviations were used in the study to represent the estimated parameters and their variability.

3. Results

3.1. Vertical distribution of Furcellaria lumbricalis

The vertical distribution of *Furcellaria lumbricalis* was restricted to depths between 1 and 15 m (Figure 2). At 1 m depth, however, the species occurred in only two transects out of 18. The mean cover of the red alga in the study area ranged from < 1% in the case of single or a few plants up to 90% in densely vegetated areas. The mean *F. lumbricalis* cover along the entire depth gradient was $20 \pm 15\%$. The mean species cover above this value lay between 3 and 8 m. The mean algal cover was evidently lower at depths of 1 and 13–15 m than between 2 and 12 m.

F. lumbricalis cover was not evenly distributed along the irregular bottom slope on the three long-distance transects (Figure 3). Algal cover tended to be lower on depressions $(19 \pm 15\%)$ than on elevations $(26 \pm 19\%)$, but this difference was not statistically significant (t = -1.0; p = 0.3, df = 12), presumably due to the small number of cases. The steepness of the bottom slope differed between the transects from 9° (slope b in Figure 3) to 12° -13° (slopes a and c in Figure 3 respectively). The maximum cover



Figure 2. Distribution of maximum and mean values of *Furcellaria lumbricalis* cover (upper) and biomass (lower) off the Lithuanian coast in 2003–08; dashed lines: overall mean cover and biomass of the species

of *F. lumbricalis* was twice as high on gentle bottom slopes (80%) than on steep ones (40%). The mean algal cover was statistically significantly higher (t = -2.58; p < 0.05, df = 38) on a plain stony bottom (27 ± 24%) than on a mixed one (12 ± 9%) covered by sand and stones in equal proportions.

The mean biomass of *F. lumbricalis* was strongly correlated ($r_s = 0.76$; p < 0.05) with the mean species cover along the depth gradient (Figure 2). The overall mean biomass of the red alga was 485.6 ± 456.8 g m⁻² between depths of 1 and 15 m. The species' mean biomass above the overall mean was between 2 and 7 m, where the maximum biomass (ca 4000 g m⁻²) occurred at 4 m. The mean algal biomass was significantly lower at depths of 1 and 11–15 m than between 2 and 10 m. In contrast to the high maximum cover



Figure 3. Schematic presentation of the bottom slope profile (bottom profile), cover of *Furcellaria lumbricalis* (alga cov.) and bottom sediments (sed. cov.), expressed as the ratio of sand to stones along the three long-distance transects (a, b and c)

distribution along the relatively wide depth range, high maximum biomass values occurred only at 4 m.

3.2. Horizontal distribution of Furcellaria lumbricalis

The distribution of *F. lumbricalis* stretched approximately for 26 km along the coast (Figure 4). The northernmost limit of the red alga was at $56^{\circ}0.1'$ N, the southernmost one at $55^{\circ}46.5'$ N. In the southern part of the study area the species cover was relatively low (1–50%) and patchy, with



Figure 4. Modelled distribution of the area occupied by *Furcellaria lumbricalis* in 2003–08

a narrow belt between 5 and 10 m depth. In the central part the algal cover ranged from 1 to 90%, and the F. *lumbricalis* belt extended between the 3 and 15 m isobaths. The areas with the densest cover of F. *lumbricalis* were

Algal cover classes	Area		Biomass	
[%]	$[\mathrm{km}^2]$	[%]	[t]	[%]
< 5	16 ± 1	46	$552~\pm~36$	7
5 - 10	6 ± 3	17	$826~\pm~259$	11
10 - 25	8 ± 3	23	$2375~\pm~721$	31
25 - 50	4 ± 2	11	2525 ± 1082	33
50 - 90	1 ± 1	3	1276 ± 1715	17
Total	35 ± 11	100	$\textbf{7554} \pm \textbf{3813}$	100

Table 2. Estimated mean areas and predicted biomasses (mean \pm SD) of different *Furcellaria lumbricalis* cover off the Lithuanian coast in 2003–08

located at depths from 4 to 10 m in the vicinity of Palanga. However, the overgrowths were very patchy within tens of meters. In the northern part of the study area the algal belt was wide (between 5 and 15 m depth), but the species cover was relatively low (1-30%).

The modelled area occupied by *F. lumbricalis* was $35 \pm 11 \text{ km}^2$ in size (Figure 4 and Table 2). It comprised less than 50% of the stony bottoms in the euphotic zone (≤ 15 m). Nearly half (ca 16 km²) of the total area had an algal cover of < 5%. Approximately 97% of the species' distribution area (ca 34 km²) was covered with < 50% *F. lumbricalis*.

3.3. Standing stock assessment

A relatively strong and significant correlation (r = 0.95; p < 0.05) was found between the *F. lumbricalis* biomass and cover (Figure 5). A mean *F. lumbricalis* cover of 50% corresponded to a mean biomass of 976 ± 689 g m⁻², whereas the dense cover of the red alga (90%) weighed 2018 ± 1361 g m⁻². The standing stock of *F. lumbricalis* in the modelled distribution was estimated to be 7554 ± 3813 t (Table 2). The areas of algal cover of $\leq 50\%$ and > 50% consisted of 6278 ± 2097 t (83% of the total biomass) and 1276 ± 1715 t (17%) respectively.



Figure 5. Relationship between the mean *Furcellaria lumbricalis* biomass and cover; dots and whiskers – mean \pm SD

4. Discussion

The phytobenthos distribution in the Baltic Sea is constrained by physical rather than biological factors (Kautsky & van der Maarel 1990). Environmental characteristics such as wave exposure, water salinity, transparency, sediment cover, nutrients, depth, type of substrate and scouring by ice have been considered key factors (Wallentinus 1991, Kiirikki 1996, Eriksson & Bergstrom 2005). However, their impact on macroalgal distribution varies depending on spatial scale and species traits (Kautsky 1995, Kiirikki 1996, Middelboe & Sand-Jensen 2004, Eriksson & Bergstrom 2005, Larsen & Sand-Jensen 2005, Torn et al. 2006). At the Baltic scale, for example, a low salinity (ca < 3 PSU) prevents expansion of the red alga *Furcellaria lumbricalis* into the Bothnian Sea and Gulf of Finland (Kostamo & Mäkinen 2006). At a local scale, the species' depth distribution depends on the underwater light penetration (Eriksson & Bergstrom 2005).

The colonisation area of F. lumbricalis in Lithuanian coastal waters is separated from the species' range in the eastern Baltic by sandy bottoms in the south and north. Besides a restricted F. lumbricalis distribution (ca 35 km²), the recent study demonstrates both low algal cover and relatively shallow depths, favourable to the species' growth. Only 3% of the red alga distribution area is characterised by a species cover of $\geq 50\%$, and approximately half of the total area (ca 19 km²) is occupied by a F. lumbricalis cover of $\geq 5\%$. The latter estimate is close to the reported size of the main F. lumbricalis colonisation area (21 km²) on the Lithuanian coast in the late 1960s (Blinova & Tolstikova 1972). In contrast to Korolev et al. (1993), this finding demonstrates that the species' longterm distribution in the eastern Baltic is relatively stable.

The attached form of F. lumbricalis in the south-eastern Baltic Sea is generally limited by the euphotic depth and the occurrence of hard substrates (Labanauskas 1998, Bučas et al. 2007). According to Kiirikki (1996), Andrulewicz et al. (2004), Eriksson & Bergstrom (2005) and Bučas et al. (2007), F. lumbricalis is one of the deepest-growing perennial macroalgae species in the exposed waters of the south-eastern Baltic. The maximum distribution depth (15 m) of *F. lumbricalis* in Lithuanian coastal waters corresponds well to the lower limit of the euphotic depth calculated from Secchi depth measurements during this study. However, the species occupied only half of the stony bottoms at depths < 15 m that are potentially suitable for the red alga attachment and growth. Several factors are presumably responsible for this. Both the species' maximum depth limit and the euphotic depth in the study area decrease southwards. This pattern is well matched with the northward flow of turbid Curonian lagoon waters, which enter the coastal waters in the very south of the study area. It remains unclear whether lower salinity or increased turbidity is the more important for F. lumbricalis distribution, since both factors are highly correlated with the plume of the lagoon outflow. On the other hand, wave exposure has been shown to be an important factor, effectively modifying the species distribution at sites where the light conditions and

bottom substrates are generally suitable for the attachment and growth of individuals (Müller-Karulis et al. 2007, Daunys et al. 2008). In contrast to the coastal waters of the western Baltic, wave exposure effects in the eastern part are constrained by seabed topography rather than complex coastlines and islands.

The *F. lumbricalis* distribution off the Lithuanian coast is restricted to 15 m depth, whereas in different subareas of the Baltic Sea the maximum depth of this red alga varies from 6 to 22 m (Figure 6). The deepest limit of *F. lumbricalis* is found on the stony reefs of the Słupsk Bank in the southern Baltic Proper (Andrulewicz 2004, L. Kruk-Dowgiałło, personal communications). Our results regarding the species' maximum depth are consistent with those obtained from other areas in the Baltic Proper, which are generally higher than the records from more saline areas.



Figure 6. Maximum and minimum depth limits of *Furcellaria lumbricalis* (whiskers) and the depth range of the maximum species cover (boxes) along the Baltic salinity gradient (black dots): Skagerrak (Eriksson et al. 1998, Karlsson 2001), Kattegat (CHARM WP3 unpublished environmental report, Karlsson 2002), Belt Sea (CHARM), Arkona Sea (CHARM), southern Baltic Proper – SBP (L. Kruk-Dowgiałło, personal communications and paper in preparation), western Baltic Proper – WBP (Frederiksson & Tobiasson 2003, Petersson 2007), eastern Baltic Proper – EBP (this study, Müller-Karulis et al. 2007), northern Baltic Proper – NBP (CHARM), Gulf of Riga (CHARM)

The highest *F. lumbricalis* cover (80-90%) in the study area is recorded at depths from 4 to 10 m, which is among the widest optimum depth ranges reported for the species in the Baltic Sea (Figure 6). A similar optimum depth range is found in the western Baltic Proper (Frederiksson & Tobiasson 2003), although the species cover is <50%, most likely due to the predominance of filamentous red algae species (Kautsky 1995). *F. lumbricalis* displayes narrower depth ranges in other Baltic subareas owing to the lack of suitable hard substrates and/or a reduced light climate for the species (Mäkinen et al. 1988, Eriksson et al. 1998, Martin 1999). In almost fully marine waters (20–30 PSU) the distribution of the red alga (maximum cover at 2–6 m) could be constrained by competition among the high number (>300) of macroalgae species (Kautsky 1995). However, this diversity of macroalgae species decreases to ca 70 taxa in the Baltic Proper (Wallentinus 1991, Snoeijs 1999), so the competition should be potentially much less.

In comparison to the cover of F. lumbricalis, the algal biomass distribution along the depth gradient displays a different pattern: the highest values in the study area are reached at depths between 2 and 6 m. This depth range corresponds well to the relatively higher number of tetrasporophytes (authors' own observations) in comparison to gametophytes. Thalli of tetrasporophytes are generally thicker and taller than thalli of gametophytes, especially male plants (Austin 1960). The thalli of tetrasporophytes result in larger biomass samples than those of gametophytes taken from a similar F. lumbricalis cover. Therefore, a significant decrease in the tetrasporophyte to gametophyte ratio with depth may have resulted in a much higher rate of biomass decrease than the reduction in the species cover.

In different Baltic subareas the mean biomass of *F. lumbricalis* ranges from 90 to 691 g m⁻² (Table 3). The mean biomass of the species is highest

Subarea	Depth [m]	Biomass of the alga $[g m^{-2}]$	Reference
Kattegat	4-8	$90 \pm 120^{\rm a}$	CHARM WP3 unpublished environmental report
Southern Baltic Proper (BP)	5-10	$370 \pm 415^{\mathrm{a}}$	L. Kruk-Dowgiałło, personal communications
Western BP	5	$110\pm100^{\rm a}$	Wallin 2005
Eastern BP	5 - 8	691 ± 656	This study
Northern BP	5 - 8	$120 \pm 65^{\mathrm{a}}$	CHARM
Gulf of Riga	5 - 8	$130\pm85^{\rm a}$	CHARM

Table 3. Mean biomass of *Furcellaria lumbricalis* (mean \pm SD) in the subareas of the Baltic Sea

^a conversion used from dry weight (dw) to wet weight (ww) -dw = 20% ww (Bird et al. 1991).

in the eastern Baltic Proper at 5–8 m depth and is significantly different from the mean biomass values reported from other Baltic subareas. On the other hand, our mean biomass estimate is clearly overestimated due to the quantitative sampling from the maximum cover of the red alga.

Limited data are available on the recent distribution and standing stocks of *F. lumbricalis* at the scale of the Baltic Sea, except for the last 2–4 decades (Bird et al. 1991). This species replaces bladder wrack (*Fucus vesiculosus* L.) in exposed parts of the Baltic Proper (Kautsky 1995, Kiirikki 1996, Snoeijs 1999), playing an important role in shaping the benthic environment and structuring benthic biotopes (Olenin & Daunys 2004). It should be borne in mind that descriptive phytobenthic research has traditionally focused more on eelgrass (*Zostera marina* L.) and bladder wrack. However, modelling techniques based on relationships between macroalgae species and the most important environmental factors are becoming common for the prediction of their distributions (e.g. Müller-Karulis et al. 2007, Sandman et al. 2008). The use of basic macroalgae distribution datasets should therefore accelerate larger-scale species predictions in the near future.

5. Conclusions

- The recent (2003–08) distribution of the red alga *Furcellaria lum-bricalis* off the exposed SE Baltic Sea coast (Lithuanian mainland) extends for 26 km and between depths from 1 to 15 m.
- The depth range of maximum F. *lumbricalis* cover in the study area was between 4 and 10 m. This is one of the widest anywhere in the Baltic Sea, most likely due to occurrence of a suitable substrate, the relatively deep euphotic zone, and the absence of grazers and numerous competitors in the sublittoral zone.
- The overall mean biomass of alga in the study area was 486 \pm 457 g m^{-2}.
- The modelled mean total area of F. *lumbricalis* was $35 \pm 11 \text{ km}^2$ (ca 50% of the total area of suitable habitat) with a predicted mean total biomass of 7554 ± 3813 t.

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