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DISTRIBUTION PATTERNS AND ECOLOGICAL ROLE OF THE RED ALGA *FURCELLARIA LUMBRICALIS* (HUDSON) J.V. LAMOUROUX OFF THE EXPOSED BALTIC SEA COAST OF LITHUANIA

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RAUDONDUMBLIO ŠAKOTOJO BANGUOLIO (*FURCELLARIA LUMBRICALIS* (HUDSON) J. V. LAMOUROUX) PASISKIRSTYMO DĖSNINGUMAI IR EKOLOGINĖ REIKŠMĖ ATVIROJE LIETUVOS BALTIJOS JŪROS PRIEKRANTĖJE

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1. INTRODUCTION

Relevance of the problem

Scientific interest to the studies of benthic macrophytes (both higher plants and macroalgae) has essentially increased in recent decades. This interest is driven by perception of the important role of the macrophytes in marine coastal and freshwater ecosystems (France, 1996; McGlathery et al., 2007), their emergent commercial use (McLachlan, 1985) and their environmental sensitivity which provides consistent indicator value for environmental assessments (Niemi et al., 2004; Onaindia et al., 2005; Orfanidis, S., 2007 and references therein), and molecular taxonomical studies (Cheong-Xin et al., 2006).

In the Baltic Sea, the macrophytobenthos studies have long-term tradition dating back to late 19th century (Kangas et al., 1982; Kautsky et al., 1986; Kruk-Dowgiallo, 1991; Kiirikki, 1996; Martin, 2000; Boström, 2001; Pedersén & Snoeijs, 2001; Eriksson et al., 2002; Torn et al., 2006 and references therein). Pioneering studies on ecological role of benthic macrophytes have been performed at the Denmark (Boström & Bonsdorff, 1997 and references therein), Swedish (Voipio, 1981; Walentinus, 1991; Kautsky & Kautsky, 1993 and references therein), Germany (Messner & von Oertzen, 1991 and references therein), Poland (Plinski, 1982), Estonia (Martin, 2000 and references therein) and Finish (Haage, 1975) coast of the Baltic Sea. Therefore, regular macrophytobenthos monitoring has been established since 1990s in Denmark and Sweden (Boström et al., 2003; Bäck et al., 2002), since 1993 in Finland (Bäck et al., 2006), since 1995 in Estonia and Germany (Kersen & Martin, 2007), since 2000 in Poland, since 2004 in Latvia and Russia, since 2007 in Lithuania.

In the south-eastern (SE) part of the Baltic Sea, the macrophytobenthos studies were initiated in the late 1950s being exclusively focused on stock assessment of the commercially important species, the red alga *Furcellaria lumbricalis* (Hudson) J.V. Lamouroux (Kireeva, 1960a,b; Blinova & Tolstikova, 1972; Blinova, 2007). The environment here differs from other Baltic sub-regions by its frequency of storms, height of waves and wave-induced bottom friction velocity which are among the highest for the entire Sea (Jönsson et al., 2002; 2005). The coastline at the SE Baltic is mostly straight and free of sheltered areas, making its vast mobile sand bottoms unsuitable for macrophytobenthos growth. Only relatively small stony bottom areas located within the euphotic zone are suitable for development of attached macroalgae (Bučas et al., 2007). Due to hostile physical conditions and reduced salinity (6-8 PSU) the species richness of macrophytes is low, less than 40 species were recorded here (Labanauskas, 1998; Blinova, 2007).

The only habitat forming perennial macrophyte off the SE Baltic coastal zone is *F. lumbricalis* (Olenin et al., 1996; Bučas et al., 2007). The densely vegetated areas of this red alga are known as natural spawning substrates for the Baltic herring *Clupea harengus membras* L. (Maksimov et al., 1996) and as the secondary substrate for filamentous macroalgae and blue mussels *Mytilus edulis* L. (Blinova & Tolstikova, 1972). Also, *F. lumbricalis* may significantly contribute to the total primary production and carbon turnover in the coastal ecosystem (Kautsky & Kautsky, 1993). However, unlikely to other habitat forming perennial macrophytes, the ecological role of *F. lumbricalis* is yet poorly understood not only in the Baltic Sea but also in other regions of North Atlantic where this species occurs (Guiry & Guiry, 2009).

Surveys of *F. lumbricalis* made off the Lithuanian coast of the SE Baltic in late 1980s – early 1990s (Korolev et al., 1993; Olenin & Labanauskas, 1994; Maksimov et al., 1996) indicated the decline in distribution area and standing stock of this alga in comparison to the historical records (Blinova & Tolstikova, 1972). However, so far these long-term changes were not described quantitatively and analysed using formal statistical methods.

Along with the progress in field techniques, ecological modelling of spatial species distribution has been developing since the 1990s (Jørgensen, 2005). Statistical methods are being frequently used to predict the aquatic plant distribution in relation to relevant environmental variables (Miller et al., 2007). Several types of models were applied for the prediction of occurrence of *F. lumbricalis* (Müller-Karulis et al., 2007) and few other macroalgae species in the Baltic Sea (Sandman et al., 2008). However, environmental factors shaping the species distribution may vary in different areas (Kiirikki, 1996), and may significantly differ at different spatial scales (Al-Hamdani & Reker, 2007).

In this study, the central research object is the attached form of *F. lumbricalis* in the hostile environment off the exposed Baltic Sea coast of Lithuania. The main questions which were formulated in the beginning of this work were:

- How environmental factors shape distribution of *F. lumbricalis* within a local habitat (at microscale, 10 cm^2–100 m^2) and between habitats within a coastal zone (at mesoscale, 1000 m^2–10 km^2)?
- What are the historical changes in the species distribution and standing stock in the study area and within the entire Baltic Sea?
- How environmental status of the coastal waters may be assessed using the indicator value of this red alga?
- What is the role of *F. lumbricalis* as a habitat forming species and a primary producer in the specific conditions off the exposed coast?

Objectives and main tasks of the study

The aim of this study was to assess distribution and ecological significance of the red alga *Furcellaria lumbricalis* off the exposed Baltic Sea coast of Lithuania.

The following tasks were raised for this work:

1) to describe distribution patterns of *F. lumbricalis* at different spatial scales and to determine the physical and biological factors shaping the species distribution in the sublittoral zone off the Lithuanian coastal waters;
2) to model the resent area of *F. lumbricalis* distribution and estimate the species stock;
3) to evaluate the long-term changes in *F. lumbricalis* distribution in the study area and within the entire Baltic Sea;
4) to evaluate the role of *F. lumbricalis* in shaping structure and abundance of benthic macrofauna and epiphytes;
5) to create a trophic model for the ecosystem of coastal waters within sublittoral stony bottom in the Lithuanian Baltic in order to analyse the trophic role of *F. lumbricalis*.

Novelty of the study

This study provides one of the first comprehensive analyses of the sublittoral red alga *F. lumbricalis* distribution and constraining environmental factors at different spatial scales (micro- and mesoscale). Combination of remote underwater video and novel parameters (e.g. the minimum distance between the seabed and holdfast of alga on substrate) enabled to reveal the effects of hydrodynamic on the red alga as one of the main factors limiting the species distribution at the exposed coast. The species occupied area and cover were modelled on the coast of Lithuania using the modern statistical prediction methods in combination with deterministic interpolation technique. The long-term changes of the area occupied by the red alga and its stock were thoroughly analysed applying formal statistical within the local (Lithuania) and Baltic-wide scales. Trophic model was developed and the contribution of *F. lumbricalis* was evaluated at the level of coastal ecosystem. Additionally the species role to benthic macrofauna was also determined at the study area.

Scientific and applied significance of the results

The results of this study increased understanding of the distribution patterns of the red alga *F. lumbricalis* and significance of environmental factors shaping its distribution on the Baltic Sea coast of Lithuania. The proposed methodology of video data analysis may be applied for other small scale distribution studies of the benthic sessile species. Evaluated effects of wave exposure and sediment abrasion in shaping cover of *F. lumbricalis* might help to predict the shift of species distribution in case of climate changes, e.g. increase of storminess.

Assessment of the distribution area and stock of *F. lumbricalis* on the Lithuanian coast provides knowledge for the upcoming ecosystem-based coastal zone management. This data is important for planning of coastal activities, such as development of a deep-sea port, coastal protection or nourishment of recreational beaches. The estimated maximum depth of the red algae is suggested as a water quality parameter for monitoring of the transitional and coastal waters of the SE Baltic. Understanding of the ecological role of *F. lumbricalis*, its importance as a structural component of habitat forming function provided well-founded rationale for planning of marine protected areas under Natura 2000 network. In the conditions of the species poor SE Baltic Sea, the habitats formed by this species were considered as potential biogenic reefs, a type of habitats listed in the EU Habitat Directive Appendix 1 (Council Directive 92/43/EEC).

Defensive statements

1. At the microscale (10 cm^2-100 m^2) distribution of the red alga *F. lumbricalis* depends on the substrate size and stability, properties of sediment types around the substrate and direction of predominated stormy wave exposure.
2. At the mesoscale (1000 m^2–10 km^2) distribution of *F. lumbricalis* is primarily influenced by availability of substrate, bathymetry (as a proxy of irradiance attenuation), wave exposure (according to the bottom slope) and salinity/turbidity gradient related to the vicinity to the Curonian Lagoon outflow.
3. The total area of *F. lumbricalis* and standing stock values decreased according to the studies in 1950s and 1980-1990s, whereas in the recent study they were closer to the level determined in 1968-1969. The long-term data of maximum depth limit of *F. lumbricalis* has not changed significantly since the late 1960s.
4. The most valuable area of the dense cover and high standing stock of the red alga is situated near Palanga, due to predominance of relatively stable substrates within the euphotic zone, low wave exposure caused by the gentle bottom slope inclination and sufficient distance from the Curonian Lagoon outflow.
5. The red alga is an important engineering species on the exposed coast, which provides habitats and substrate for macrofauna and epiphytes.
6. Contribution of slow growing *F. lumbricalis* to primary production is relatively low in the coastal waters of Lithuania, in the sublittoral zone with stony bottom. Its energy mainly transported to detritus due to low pressure of herbivores.

Scientific approval

The results of this study were presented at four international, twelve Baltic Sea regional and four local conferences and seminars:

- Germany macrophytobnethos monitoring program (GMMP) workshop “Intercalibration of macrophytobenthos monitoring methods”, Helgoland, Germany, April 2005;
- Baltic Sea Region project workshop “Intercalibration of macrophytobenthos monitoring methods”, Saaremaa, Estonia, May 2005;
- International conference “The Baltic Sea a changing ecosystem”, Sopot, Poland, June 2005;
- GMMP workshop “Intercalibration of macrophytobenthos monitoring methods”, Hiddensee, Germany, June 2005;
- Estonian national monitoring workshop “Intercalibration of macrophytobenthos monitoring methods”, Saaremaa, Estonia, August and September 2005;
- Regional student conference “Biodiversity and Functioning of Aquatic Ecosystems in the Baltic Sea Region”, Anykščiai, Lithuania, October 2005;
- Marine Biodiversity and Ecosystem Functioning (MARBEF) RMP project 17 seminar “The role of ecosystem engineers in explaining biodiversity”, Yerseke, Netherlands, January 2006;
- LIFE project seminar “Mapping of benthic habitats and intercalibration”, Saaremaa, Estonia, April 2006;
- International Young Researchers’ Symposium “Environment and the World”, Šiauliai, Lithuania, April 2006;
- LIFE project seminar “Mapping of benthic habitats”, Saaremaa, Estonia, May 2006;

- 2nd International student conference “Biodiversity and Functioning of Aquatic Ecosystems in the Baltic Sea Region” Palanga, Lithuania, October 2006;
- MARBEF workshop “The role of native and/or invasive ecosystem engineers in explaining biodiversity“ Klaipėda, Lithuania, April 2007;
- Conference “Change in Aquatic Ecosystems: Natural and Human Influences”, Plymouth, UK, July 2007;
- International student conference “Development of scientific-technical support for reproduction of fish stocks in trans-boundary waters of Lithuania and Russia” Klaipėda, Lithuania, September 2007;
- 10th Regional student conference “Biodiversity and Functioning of Aquatic Ecosystems in the Baltic Sea Region” Molėtai, Lithuania, September 2007;
- Regional conference “Marine and coastal research”, Palanga, Lithuania, April 2008;
- 3rd International student conference “Biodiversity and Functioning of Aquatic Ecosystems in the Baltic Sea Region” Klaipėda, Lithuania, October 2008;
- 2nd Regional conference “Marine and coastal research”, Nida, Lithuania, April 2009;
- 8th International conference and workshop “Marine geological and biological habitat mapping (GeoHab)”, Trondheim, Norway, May 2009;
- 7th Baltic Sea Scientific Congress “Towards better understanding and improved technology for serving the society”, Tallinn, Estonia, August 2009.

The material of this dissertation was presented in 3 original publications, published in peer-reviewed scientific journals.

1. 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. Estuarine and Coastal and Shelf Science 75(3): 308-316.
2. Bučas, M., Daunys, D., Olenin, S., 2009. 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. Oceanologia 51(3): 1-19.
3. Tomczak, M.T., Müller-Karulis, B., Leili Järv, Kotta, J., Martin, G., Minde, A., Põllumäe, A., Razinkovas, A., Strake, S., Bučas, M., Blenckner, T., 2009. Analysis of trophic networks and carbon flows in South Eastern Baltic costal ecosystems. Progress in Oceanography (in Press).

Thesis structure

The dissertation includes seven chapters: introduction, literature review, materials and methods, results, discussion, conclusions and references. Four appendixes contain supplementary information and the raw data of transects are recorded to an attached CD. The material is presented in 124 pages, 29 figures and 20 tables. The dissertation refers to 171 literature sources. Dissertation is written in English with extended summary in Lithuanian language.

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2. LITERATURE REVIEW

2.1. Description of the study area

2.1.1. Hydrometeorological conditions and hydrodynamics

The southeastern Baltic Sea coast is exposed from any westerly direction, with a wind fetch exceeding > 200 km (Olenin et al., 2003). The strong cyclonic winds of SW and SE directions prevail forming on average 43 storms (> 15 m s^{-1}) per year (according to Klaipėda Hydrometeorological station). Permanent influence of winds, waves and water currents produces a hydrodynamically very active environment resulting in no oxygen deficiency. Wave exposure is a very important factor shaping benthic biotopes and bottom communities in the upper part of the underwater slope down to the depth of approx. 20 m (Olenin et al., 1996).Waves are wind-induced with a mean height of ca 2 m (Žaromskis, 1982; Ašmontas, 1994). The highest measured waves are as high as 6.7 m, while in conditions of extreme storms (wind > 30 m s^{-1}) the hight of modelled waves may attain 12 m. Near the bottom, speed of currents vary from 5 to 50 cm s^{-1} depending on direction and velocity of winds as well as bottom topography (Dubra, 1994). Generally, the near-bottom current is directed to the North along the shore transporting soft sediments such as mud and/or sand. During strong storms, the wind usually varies from the SW to NW directions, which alters the direction of sediment transport. This can include pebble transport (Žaromskis, 1994).

2.1.2. Bottom sediments and seabed geomorphology

The sublittoral part of the underwater slope (up to 20 m depth, acc. to Olenin et al., 1996) stretches within 3-7 km from the shore in the Lithuanian part of the southeastern Baltic. Along the Curonian Spit it is covered by sand being unsuitable for the red alga *F. lumbricalis*, whereas, at the mainland coast the seabed is dominated by glacial deposits (Fig. 1): morainic clay, large boulders, cobbles, pebbles, gravel and sand (Gulbinskas & Trimonis, 1999). Sediment distribution is determined by the sedimentation of the material transported from the Curonian Lagoon, as well as the coastal abrasive-erosive processes (Gudelis & Janukonis, 1977; Žaromskis, 1982).

2.1.3. Water physics and chemistry

Data of salinity, temperature, nutrients and Secchi depth in the study area during 2003-2007 were taken from the Center of Marine Research (CMR). Near-bottom salinity ranged from 6 to 7.5 PSU. However, part of the study area stretching 25-30 km to the North off Klaipeda is occasionally affected by salinities below 5 PSU due to the freshwater outflow from the Curonian Lagoon, therefore it was classified as transitional water body (Daunys et al., 2007).

Water temperature regime in the study area showed typical boreal pattern with the highest temperatures (15±3.3 °C) in July-August and the lowest (1.3±0.8 °C) in January-February.

Total nitrogen concentrations near-bottom ranged between 7.5 and 634.0 µg l^{-1} with a mean of 62.3±33.5 µg/l, while total phosphorus concentration was between 10 and 74 µg l^{-1} with a mean of 31.2±6.7 µg l^{-1}.

Secchi depth varied between 2 and 8.5 m with a mean of 4.5±1.7 m. These values correspond to the euphotic zone depth between 10 and 16 m with a mean of 13.5±7.4 m when calculated according to Urbanski & Szymelfenig (2003). Near bottom water transparency during SCUBA diving and video recording ranged from 1 to 7 m, although, it has usually been less than 3 m.

2.1.4. Benthic biotopes and communities

Benthic biological studies in Lithuanian coastal zone of the Baltic Sea date back to 1928, when a Danish hydrobiologist (H. Blegvad) was invited by the Lithuanian government to perform assessment of benthic macrofauna stock (Olenin & Daunys, 2004, and references therein). In the 2nd half of the last century several descriptive studies were performed by I. Gasiūnas, J. Lukšėnas, A. Bubinas and S. Olenin focused on distribution of benthic communities, trophic groups of macrofauna, and structure of benthic communities in relation to various human impacts such as an oil spill and dredge spoil dumping (Olenin & Daunys, 2004, and references therein). Since early 1990s several studies were initiated to identify and map benthic biotopes in the Lithuanian coastal zone (Olenin et al., 1996; Olenin, 1997) which resulted in the first benthic biotope classification for the Lithuanian coast (Olenin et al., 1996), later modified by Olenin & Daunys (2004). In total five main biotopes were classified according to the nature of substrate (soft or hard bottoms), depth range and light climate (within or below the euphotic zone). The biological features of these biotopes were identified by dominant conspicuous benthic species in the biotopes. The red alga *Furcellaria lumbricalis* being one of the most abundant macroalgae species was one of the main structural feature in classifying stony bottom biotopes within the euphotic zone: "Boulder reefs with the red alga *F. lumbricalis*" and "Stony and gravel bottoms with red alga *F. lumbricalis*".

Labanauskas (1998; 2000) was the first marine botanist who described macrophytobenthos diversity and communities at the Lithuania coast. He described 36 taxa of macrophytobenthos, which were classified into 5 communities: annual filamentous green algae (mainly *Cladophora glomerata*) within 0-3 m depth, perennial filamentous green algae (mainly *Cladophora rupestris*) within 2-7 m depth, filamentous brown algae dominated by *Sphacelaria* spp. within 1-15 m depth, rare community of brown alga *Fucus vesiculosus* within 2-3 m depth and red algae community dominated by *F. lumbricalis* within 4-12 m depth. According to his data the community of bladder wrack (*F. vesiculosus*) as well as of rare standings of eelgrass (*Zostera marina*) occurred in vicinity of Palanga, however, in this study SCUBA diving and underwater video methods were used and any sign of the species presence was not found (Olenin et al., 2003). It could be that theses macrophytes are being transported from other subregions of the Baltic Sea and cast ashore at the coast of Lithuania.

2.2. Biology and ecology of *Furcellaria lumbricalis*

2.2.1. Taxonomy

The red alga *Furcellaria lumbricalis* (Hudson) J.V. Lamouroux (Fig. 1) has controversial synonyms *Furcellaria fastigiata* and *Fucus fastigiata* (Guiry & Guiry, 2009). Taxonomically *F. lumbricalis* is placed in the phylum Rhodophyta, class Rhodophyceae, subclass Florideophycidae, order Gigartinales and family Furcellariaceae.

Figure 1. The red alga *F. lumbricalis* on stony bottom, 8 m depth at the Lithuanian coast of the Baltic Sea (photo: S. Olenin).

2.2.2. Morphology, anatomy and growth rate

Like other macroalage, *F. lumbricalis* is subject to phenotypic variation and several morphological ecotypes consequently have been reported (Bird et al., 1991). One of them is a free-living (loose-lying) form reffered to as f. *aegagropila* Reinke and the attached form typical of subtidal polyhaline habitats. The free-living form has a globose thallus of radiating fronds and is smaller in stature and frond diameter, with denser and less regular branching than the attached form. The later plants reach 30 cm in height, are erect from a branched holdfast, and are terete, repeatedly dichotomous, and cartilaginous (Guiry & Guiry, 2009). Their colour varies from dark red to greenish purple or greenish brown, according to physiological conditions (Bird et al., 1991).

The medulla is densely crowded with axial and rhizoidal filaments. Gametophytes are dioecious, the spermatangia borne in superficial subapical sori (Guiry & Guiry, 2009). Carpogonial branches are 3-5-celled, and usually borne several per supporting cell. Tetrasporangia are scattered in the cortex of isomorphic tetrasporophytes.

Bird et al. (1979) reported growth rates of *F. lumbricalis* in the laboratory as a doubling in weight in 25-50 days or a 3.3% increase in fresh weight per day. For comparison, the corresponding rates for *Chondrus crispus* are 10 days and 7.3%, and for *Fucus serratus* are 12.5 days and 6.2%. These figures suggest that *F. lumbricalis* grows slowly in comparison to other red and brown seaweeds. The reported growth rates from the field are even slower: Blinova (1975) recorded a doubling in fresh weight every 167 days.

2.2.3. Reproduction

The typical attached form of *Furcellaria lumbricalis* reproduces asexually through tetrasporangial plants and sexually through dioecious gametangial plants (Bird et al., 1991). Plants become fertile when they achieve their full size of 90-300 mm according to habitat, during the 4th to 6th year (Austin, 1960). The male and female plants are usually in equal proportions but are outnumbered by the tetrasporophytes. The free-living form of *F. lumbricalis* reproduces only vegetatively through fragmentation, regeneration and proliferation (Bird et al., 1991). Proliferation, where propagules develop on the parent plant and then detach, is probably the most important mechanism of reproduction.

The mode and timing of reproduction in *F. lumbricalis* was reviewed by Bird et al. (1991). On the male plants, spermatangial ramuli begin development in late October, developing superficially in the much swollen apical regions and are conspicuous until late April or early May. Discharge of the spermatia occurs from December to April with a peak in February and March. On the female plants, the carpogonial branches are initiated in late December, with carpogonia developing internally in the apical regions. Fertilization probably only occurs over a short period commencing in mid January. The zygote is retained on the female plant but the carposporophyte is not obvious until mid summer. Maturation of the carposporophytes does not occur until a year after fertilization, with a massive discharge of carpospores occurring over a 2-4 week period from late December. One million 35-50 µm diameter carpospores may be released from an average sized plant when a tract of cells disintegrates forming an ill defined pore to the exterior.

On diploid plants, tetrasporangia are initiated in early April and develop in markedly thickened apical regions. They mature in December and 1-2 million tetraspores are liberated per plant over 2 weeks following disintegration of the thallus surface. The fruiting pods of all plants fall when they are past maturity and new shoots arise from the resulting truncated tips.

2.2.4. World wide distribution of *Furcellaria lumbricalis*

The red alga *F. lumbricalis* is amphiboreal species, widely distributed in North Atlantic, both in North America and Europe (Fig. 2). According to the AlgaeBase (Guiry, 2006), in America it is found in Nova Scotia north and east, in Newfoundland and the Gulf of St

Lawrence and its outer coasts. Around Prince Edward Island, Canada, *F. lumbricalis* is sometimes found growing epiphytically on *Phyllophora* sp. (Sharp et al., 1993). In Europe *F. lumbricalis* occurs from northern Russia and Norway to the British Isles, Basque France, including the Faroe Islands and the Baltic Sea. Possibly the red alga occurs in Greenland and Iceland. In the Mediterranean Sea *F. lumbricalis* is known from Italy and Spain and it was also reported from the Indian Ocean from the coasts of Pakistan (Silva et al., 1996).

Figure 2. World wide distribution of *F. lumbricalis* (black colour) according to AlgaeBase (Guiry & Guiry, 2009).

2.2.5. Habitat and environmental tolerance

The red alga *F. lumbricalis* is a marine species, which is found on rocks, lower intertidal and shallow subtidal zones, in pools and runnels, in open situations, often on sandy and muddy shores, tolerating lowered salinities (Guiry & Guiry, 2009). In the tideless south-eastern part of the Baltic Sea the species occurres in sublittoral zone where salinity is higher than 4 PSU (Table 1).

Table 1 Habitat preferences of *F. lumbricalis* within its larger geographical area of northern Atlantic (Rayment, 2008) and in the south-eastern part of the Baltic Sea (Blinova & Tolstikova, 1972, Martin, 1999, Labanauskas, 2000; Bučas et al., 2007; L. Kruk-Dowgiałło, pers. comm..; author, pers. obs.)

Habitat characteristics	In NW European Seas	In the SE part of the Baltic Sea
Physiographic preferences:	strait/sound, sea loch, enclosed coast/ embayment	strait/sound, open coast, enclosed coast/ embayment
Biological zone preferences:	from upper eulittoral to upper circalittoral	upper sublittoral (= circalittoral)
Substratum / habitat preferences:	bedrock, large to very large boulders, small boulders, water column (pelagic), rockpools, cobbles, pebbles, algae	large to very large boulders, small boulders, water column (pelagic), cobbles, pebbles
Tidal strength preferences:	moderately strong (1-3 kn), weak (< 1 kn), very weak (negligible)	-
Wave exposure preferences:	from exposed to extremely sheltered	from exposed to moderately sheltered
Salinity preferences:	from < 18 to 40 PSU	From 4 to 8 PSU
Depth in metres:	in pools in eulittoral to 30 m	1–21 m
Migration pattern:	non-migratory/resident	Non-migratory/resident

According to Rayment (2008) attached form of *Furcellaria lumbricalis* is evidently sensitive to substratum loss, desiccation and increase in emergence regime (Appendix 1). Removal of the substratum would also remove the entire population of *F. lumbricalis* growing on it. A small proportion of the population may grow epiphytically on other algal species, e.g. *Phyllophora* sp., and these would also be removed by substratum loss. Like many sublittoral algae, *F. lumbricalis* is very intolerant of desiccation. An increase in emergence of 1 hour every tidal cycle for a year would place the portion of the population furthest up the shore in a zone where it would be vulnerable to desiccation.

The sensitivity of *F. lumbricalis* to increase of smothering (sediment loads), suspended sediment, water flow rate, wave exposure, abrasion and physical disturbance, synthetic compound contamination, hydrocarbon contamination, changes in nutrient levels, is considered of low confidence (Rayment, 2008). The red alga is tolerant to wide range of temperature and salinity. Under experiment conditions the species tolerated -5 to 27 °C and grew well from 0 to 25 °C, with optimal growth at 10-15 °C (Bird et al., 1979; Novaczek & Breeman, 1990). *F. lumbricalis* growth declined above 30 PSU to negligible levels at 50 PSU. On the other hand the red alga occurs in the lowest category on the salinity scale in British waters (Rayment, 2008) and therefore probably relatively tolerant of decreases in salinity. *F. lumbricalis* forms extensive populations in the main basin of the Baltic Sea where salinity is 6-8 PSU in the upper 60-70 m and its extension into the Gulfs of Bothnia and Finland is limited by the 3.5 PSU isohaline (Kostamo & Mäkinen, 2006).

In view of the species slow growth, time to maturity and limited dispersal, recoverability of *F. lumbricalis* is assessed as moderate (only partial recovery is likely within 5 years and full recovery is likely to take up to 10 years) after damage sustained by factors described above (Rayment, 2008).

2.2.6. Commercial use

Commercial utilization of *F. lumbricalis* is based on the gelling properties of its extracted structural polysaccharide, furcellaran (Bird et al., 1991). Denmark was the chief producer of furcellaran, mostly processing *F. lumbricalis* extracted from the Danish waters, whereas a mixture of the species and *Chondrus crispus* was harvested in the past from the Gulf of St Lawrence, Canada (Rayment, 2008). Small quantities of the species have been commercially exploited in Estonia since 1960s (Kersen & Martin, 2007). Utilization of furcellaran centres on the food industry, with other applications in pharmaceuticals, wherever water or milk based gels or stabilizers are required (see review by Bird et al., 1991).

2.2.7. Historical studies of *Furcellaria lumbricalis* distribution on the coast of Lithuania

Spatial distribution of *F. lumbricalis* on the Baltic Sea coast of Lithuania has been investigated since 1956 (Table 2). The first survey was performed by Kireeva (1960b), however, the species distribution map and coordinates of transects were not provided. More accurate survey aimed at assessment of distribution of the *F. lumbricalis* stock was carried in 1968-1969 (Blinova & Tolstikova, 1972). They created a distribution map of the alga and estimated the standing stock based on 192 transects performed by SCUBA divers up to 10 m depth. Although this study remains the main reference source for later comparisons, it is not free of some methodological limitations: 1) only few transects were performed in the southernmost part of the *F. lumbricalis* distribution area which makes uncertain the southernmost limit of the species occurrence; 2) a maximal depth limit of *F. lumbricalis* was not found within half of the transects; 3) an interpolation method used to build the distribution map was not described.

In 1970s-1990s several surveys have been performed by the Baltic Fishery Research Institute (BaltNIIRX, Riga) using both diving and underwater TV system (Korolev et al., 1983; 1993). Unfortunately, the methods used in these surveys are not described in necessary details. Neither the number nor location of study sites is indicated, nor is the map of the vegetated area provided. Therefore, these results can hardly be used for any historical comparisons.

Several small scale surveys aimed at delineation of spatial distribution of *F. lumbricalis* overgrowths as potential spawning ground for the Baltic herring *Clupea harengus membras* have been performed during 1993-1996 (Olenin & Labanauskas, 1994; Maksimov et al., 1996). They used both SCUBA diving and a drop-down underwater video camera (MARISCOPE). However, during these surveys only 22% of the total number of transects) were located within the main known vegetated area (Karklė-Šventoji; within the depth range 3-10 m), therefore the actual area of *F. lumbricalis* distribution could have been underestimated. V. Labanauskas (1998) carried out 68 SCUBA diving transects of mapping of macrophytobenthos communities during 1997-1998, however he did not provide coordinates of the transects.

Table 2. Inventory of ealier studies (1955-2000) of *F. lumbricalis* by different techniques at the Lithuanian coast.

Year	Number of transects by three methods:			Reference
	dredging	diving	video	
1955-1956	15	19		Kireeva, 1960b
1968-1969		193		Blinova & Tolstikova 1972
1973-1980		NA	NA*	Korolev et al., 1983
1981-1991		NA	NA	Korolev et al., 1993
1993			148	Olenin & Labanuskas, 1994; Maksimov et al., 1996 Olenin, unpublished;
1994		23		
1995		32		
1996	6		234	Olenin, unpublished; Labanauskas, 2000
1997		51		
1998	6	17		
2000		13	4	Olenin et al., 2001

NA – information not presented in the paper.

2.3. Macroalgae as indicators of ecological water quality

Generally attached macroalgae integrate the effects of long-term exposure to nutrients or other pollutants. Macroalgae communities are impacted by fish farming activity (Boyra et al., 2004), waste waters and sewage (Diez et al., 1999; Terlizzi et al., 2002) as well as trace metals (Jayasekera & Rossbach, 1996) and other chemical elements (Serfor-Armah et al., 2001). Therefore macroalgae are considered as one of the best water quality indicators in general. Despite existing knowledge on the impact of different pollutants on the structure of algal communities, a relatively small number of biotic indices based on macroalgae were proposed (Ballesteros et al., 2007 and references therein). One of them is the Rhodophyta/Phaeophyta mean ratio index that displays strong changes in relation to water quality. Ecological evaluation index, based on the concept of morphological and functional groups, was recently proposed by Orfanidis et al. (2003)

and successfully tested in Attica coast of Greece (Panayotidis et al., 2004). Another recent method of monitoring water quality, based on the cartography of littoral and upper-sublittoral rocky-shore communities (CARLIT), was applied in the North-West Mediterranean (Ballesteros et al., 2007).

Moreover, macroalgae is a biological key element for the assessment of the ecological status in coastal waters in the frame of European Water Framework Directive (WFD, 2000/60/EC). According to WFD, the resulting ecological status has to be expressed as a ratio between the values of the biological elements observed by given body of surface water and the values for these elements in a site with no, or very minor, disturbance from human activities (reference conditions). List of ecological quality elements related to macroalgae were proposed, discussed and summarized in Kuuppo et al., (2006).

Depth limit of macroalga. Several studies documented the shifts in the depth distribution of perennial macroalgae due to eutrophication (Kautsky et al., 1986; Eriksson et al., 1998; Torn et al., 2006). Depth limits of algal communities and few species of brown macroalgae correlated with water quality in terms of Secchi depth and total nitrogen. However, the relationships were area specific depending on water salinity, and the lack of substrate may limit depth penetration of macroalgae in some areas.

Abundance of macroalgae can be measured in terms of cover and biomass at specific water depths (Kuuppo et al., 2006). Abundance is typically quite variable in shallow areas where exposure to wind and waves plays a major regulating role, but from intermediate water depths towards deeper water abundance tends to decline in parallel to reductions in light availability with depth. Macroalgal cover responds to large-scale differences in water quality, therefore this indicator is not sufficiently sensitive to reflect smaller year-to-year changes. More studies of factors regulating algal cover are needed to apply this bioindicator.

Algal community structure and relative abundance of opportunistic macroalgae are considered sensitive water quality elements that reflect changes in nutrient load and decreases in water transparency (Kuuppo et al., 2006). There are indicators that the relative abundance of green opportunists alone may be “better” indicator than the entire group of opportunists. However the abundance of opportunistic macroalgae is extremely dynamic, therefore a dense net of sampling stations with frequent sampling is necessary in order to assess abundance.

2.4. Macroalgae as ecosystem engineers

Ecosystem engineers are organisms that directly or indirectly modulate the availability of resources to other species via biophysical processes (Jones et al., 1994). Such indirect species-interactions are ubiquitous and have the potential to drastically alter the environmental configuration. In doing so ecosystem engineers modify, maintain and/or create habitats by changing resource flows, influencing structure/composition of organisms, creating landscape mosaics, and thus affecting the spatial arrangement of current and future diversity of organisms. For instance – mussels are generally considered as ecosystem engineers due to ability to modulate environment by their structure, as substrate and shelter for other organisms to avoid predators and physical or physiological stress, and by physiology controlling the transport of particles and solutes to benthic ecosystem (Gutiérrez et al., 2003; Borthagaray & Carranza, 2007). Large kelps are also recognized as ecosystem engineers or habitat-forming species (edificators) since they host variety of benthic organisms (Sapper & Murray, 2003; Bates & DeWreede, 2007). Introduced macroalgae species are often ecosystem engineers (Wallentinus, 2007), and the number of introductions is increasing with concern of ecosystem health and economics (Schaffelke et al., 2006; Mineur et al., 2008).

Only two species of macrophytes have been described as ecosystem engineers or habitat-forming species in the Baltic Sea, such as eelgrass *Zostera marina* L. (Boström & Bonsdorff, 1997; Baden & Boström, 2001; Ferraro & Cole, 2007) and bladder wrack *Fucus* *vesiculosus* L. (Haage, 1975; Kautsky, 1989; Råberg & Kautsky, 2007). Generally their belts form benthic habitats with higher number of species than the plain bottom around. However, these species usually are not found at very exposed coast due to active hydrodynamical conditions (Pankov & Kukk, 1984; Trei, 1984; Kautsky, 1989; Kautsky & van der Maarel, 1990). Contrarily the red alga *F. lumbricalis* dominates at such type of coast and most likely is a keystone species in the sublittoral communities. According to earlier macrophytobenthic studies (Pankov & Kukk, 1984; Trei, 1984; Labanauskas, 2000) *F. lumbricalis* formed associations with *Coccotylus truncatus, Polysiphonia fucoides* and *Ceramium tenuicorne*. The red alga is also known as one of the natural spawning subrates of Baltic herring in the Baltic Sea (Aneer, 1989). The habitat-forming role of loose-lying *F. lumbricalis* was found by Orav-Kotta & Kotta (2004), where the alga provided secondary substrate for zoobenthic species and generated the higher biomass than the plain sandy bottom.

3. MATERIAL AND METHODS

3.1. Field methods

Underwater surveys were performed between 2003 and 2008 for different seabed mapping and monitoring purposes: biodiversity inventories (Olenin et al., 2003), habitat mapping and macrophytobenthos monitoring (Table 3). 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 *Furcellaria lumbricalis* (Olenin & Labanauskas 1994, Olenin et al. 1996, Bučas et al. 2007).

Table 3. Number of transects by three methods (diving, drop down and hand-held videos), and number of biomass samples of *F. lumbricalis* at the Lithuania coast from 2003 to 2008.

Year	Diving	Drop down video	Hand-held video	No. biomass samples
2003	37	121		9
2004	15			
2005	44			5
2006	79	239		9
2007	22	68	3	1
2008	10			10
Total:	207	428	3	34

Three methods have been used for estimation of *F. lumbricalis* biomass and/or cover: SCUBA diving, drop down and hand-held underwater video cameras (Table 3, Figure 3). Location of all study stations (transects) was determined by GPS with accuracy error less than 25 m. In total 207 diving and 183 video transects (from 10 to ca. 2000 m long) were performed, and 34 samples of the species biomass were collected. The author took part in all underwater sampling works.

3.1.1. Diving surveys

Mapping benthic features was performed by SCUBA divers along transects of 10-20 m length according to Davies et al. (2001) and Blinova et al. (2005) recommendations. Percentage cover of sessile epifauna (mussels, barnacles and hydrozoans), epiflora (macroalgae) and composition of the bottom sediments was usually estimated in sections of 1-4 m^2 along the diving transects. In cases, where relatively high transparency of water (visible area > 10 m) occurred the parameters were determined for the whole transect. Depth was estimated by diving depth gauge or computer. In total 207 transects were described within the depth range from 1 to 19 m.

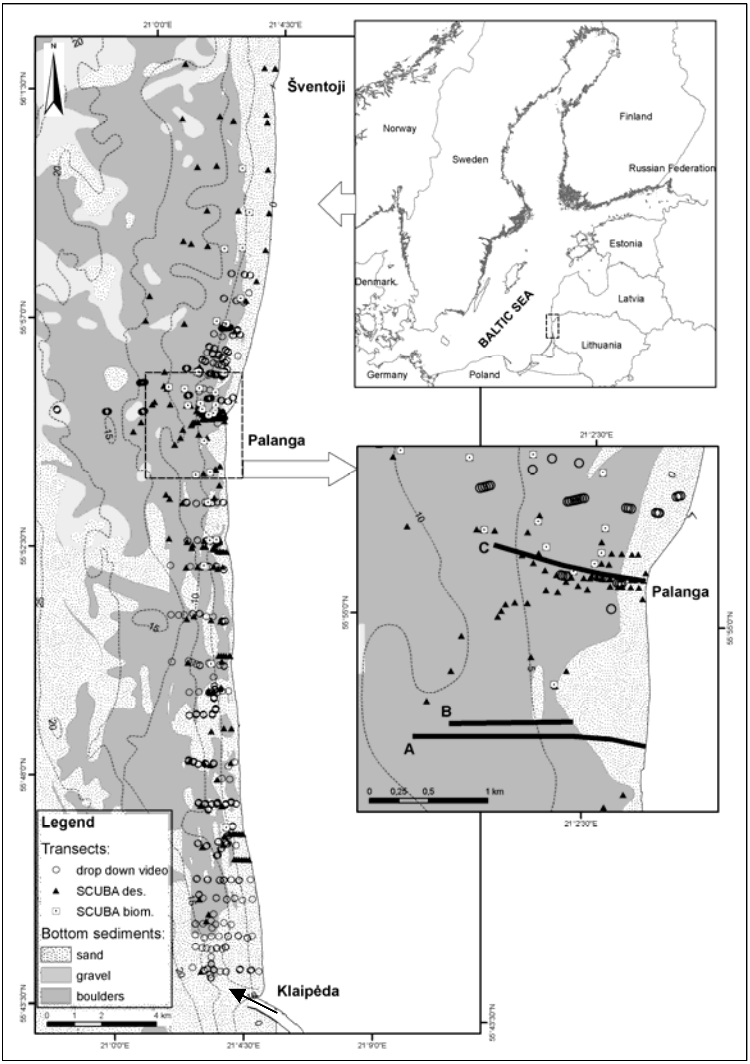

Figure 3. Location of the study sites at the Lithuanian coast, the Baltic Sea: drop down video transects (○) and hand-held long distance video transects (▬ A, B and C); descriptions made by SCUBA divers (▲ SCUBA des.); biomass samples taken by SCUBA divers (⊡ SCUBA biom.); outflow from the Curonian Lagoon (←).

Biomass samples of *F. lumbricalis* (2-8 replicates per transect) were collected by divers in 34 transects between 1 and 16 m depth. The samples were taken from the species maximum cover within transects due to high patchiness of *F. lumbricalis* cover and diving-time limitations (< 40 min per transect). The thalli of the red alga were scraped from the surface of substrate using a frame (Fig. 4) of 0.04 m^2 (Kautsky, 1993). Further treatment of samples is described in section 3.4.1.

Figure 4. The frame, mesh-bag and scraper were used to take biomass samples of *F. lumbricalis*.

3.1.2. Underwater video surveys

Seabed recording by a drop-down underwater video system was performed in 180 transects at depths between 1 and 22 m. Underwater video system consisted of two cameras (color SONY TRV-DCR 950 Mini DV and black-white C-Technics Subsea Video 302), mounted in a housing at ca 40° angle to the bottom. Two laser diodes projected two dots onto the bottom at a constant distance of 10 cm one from another, enabling determination of a spatial scale and object size in the video footage. A depth sensor was mounted in the housing and a signal from the sensor was embedded into the video stream. Continuous seabed recording was performed while drifting (velocity

0.5-1 knots) from a boat along transects of ca 10-120 m distance (instantaneous visual area was ca 1 m^2).

A hand-held video was used for the seabed recording along the three long-distance (1-2 km) transects in depths from 1 to 15 m. Collected data were used to determine changes in depth distribution of *F. lumbricalis* and substrates along the depth gradient more precisely than it was done with a drop-down video system. A diver was towed by a boat (at a speed of ca 1-1.5 knots) along the transect filming the seabed by underwater video camera (Sony Handycam DCR HC42E) at a distance ca 0.5-1 m from a sea bottom, covering visual area ca 1 m^2.

3.2. Video analysis

Two methods for underwater video processing and analysis were developed during this study. The first method was designed to evaluate the microscale (10 cm^2-100 m^2) patterns of *F. lumbricalis* distribution. The second method was aimed at estimation of the species distribution at mesoscale (1000 m^2–10 km^2).

The first method was based on drop-down video data in 2003. Video footage was captured in AVI format and segmented into still images (frames) in JPG format using VirtualDub software (www.virtualdub.org, verified November 2005). The images, containing the same information (overlapping frames) and poorly recognizable physical and biological features were not used. Selected 1241 frames were treated as random samples from the video transect, and analysed by eye. Differences of zoom in the images ranged from 400 to 2100 cm^2 of the visible seabed surface area. If a selected frame had closer zoom to a bottom or some unclear objects, neighbouring frames were repeatedly studied and data of the selected still image reanalysed and/or corrected.

Five physical and eight biological parameters were derived from each sample. Not all images were suitable for deriving all the parameters, therefore the number of frames for parameters was different (Table 4 and Fig. 5).

In this analysis bottom sediments were characterized using two parameters: types of substrate and surrounding bottom sediments (SBS) (Table 1). Both parameters were also classified by sediment mobility. The sediment classes from sand to cobbles were considered to be mobile substrates under storm conditions, while boulders were considered stable. Mobility of SBS was classified by the stability of the predominant sediment class. Where small and large boulders comprised > 70% of sediment on the seabed, the SBS was considered stable. In cases where the seabed consisted of > 70% of mobile sediments, the SBS was determined mobile. The intermediate SBS was represented by equal surface areas of mobile and stable SBS.

The cover of *F. lumbricalis* on substrates (CFS) was evaluated for each class of substrate (Fig. 5). Certain sediment classes did not occur in each depth interval, thus the CFS parameter could not be estimated within the whole depth gradient. Therefore the CFS was averaged for all substrate classes and a further parameter (TCF) was included in the analysis, to reflect the changes of the total algae cover along the depth gradient. Cover of epifauna and epiflora on *F. lumbricalis* were also determined where it was possible. Percentage cover of sessile macrofauna, macroalgae and types of substrate was visually measured in five ordinal classes since the error of this method is ca 20% (author, pers. observation) and relatively small amount of information is lost converting the absolute values into the classes.

Table 4. List of parameters derived from the video analysis.

Parameter name & abbreviation	Description	No. of Samples
Depth	measured from the depth sensor; m	1025
Type of substrate	sediments on which *F. lumbricalis* occurred; classified according to Wentworth scale (Wentworth, 1922)	1025
Type of surrounding bottom sediments (SBS)	sediments around the substrates; classified according to Wentworth scale	1025
Mobility of substrate*	mobile (sand, granules/gravel, pebbles, cobbles) stable (small and large boulders)	1025
Mobility of surrounding bottom sediments (MSBS)	mobile (> 70% sand, gravel, pebbles, cobbles)	1025
	stable (> 70% small and large boulders)	
	intermediate (~50% mobile and ~50% stable bottom types)	
Cover of *F. lumbricalis* on substrate (CFS)	percentage of algal cover measured in five ordinal classes on individual types of substrates:	939
	0 (absence of alga)	
	1 (single thalli, < 20% area of substrate)	
	2 (solitary groups of thalli, 20-50%)	
	3 (moderate overgrowth, 50-80%)	
	4 (entire overgrowth, > 80%)	
Total cover of *F. lumbricalis* (TCF)	evaluated as weighted average of algal cover on all types of substrates in an image; same units as in the CFS	1025
Minimum distance between the seabed and holdfast of the alga on substrate (MDSF)	measured perpendicularly from the seabed to a lowest attached holdfast of the alga on substrate; cm	1025
Cover of *F. lumbricalis* on substrate surfaces of different orientation (CFSDO)	The algal cover measured on the surfaces of substrates divided by the 4 cardinal and 4 intermediate points: N, NE, E, SE, S, SW, W, NW; same units as in the CFS	672
Cover of barnacles (*Balanus improvisus* L.) on *F. lumbricalis*	percentage cover of barnacles measured in five ordinal classes; same units as in the CFS	121
Cover of mussels (*Mytilus edulis* L.) on *F. lumbricalis*	percentage cover of mussels measured in five ordinal classes; same units as in the CFS	47
Cover of bryozoans (*Electra crustulenta* L.) on *F. lumbricalis*	percentage cover of bryozoans measured in five ordinal classes; same units as in the CFS	121
Cover of filamentous epiphytes	percentage cover of *Ceramium tenuicorne* and *Polysiphonia nigriscens* measured in five ordinal classes; same units as in the CFS	175

* according to Connor et al., (2004) and Osborne (2005), see text for details.

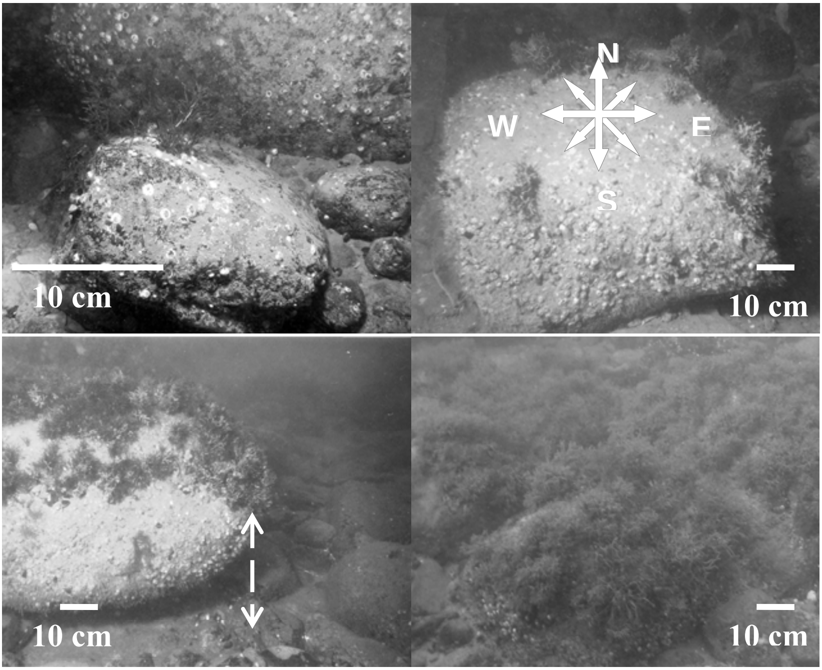

Figure 5. Examples of the estimation of biological parameters (see Table 1) from the still images. The CFS: class 1 on cobble (upper left image), class 2 on small boulder (upper right image), class 3 on large boulder (lower left image), class 4 on small boulders (lower right image). The MDSF measured as the minimum distance between the seabed and the lowest holdfast of the algae on substrate (lower left image): ca 35 cm. The CFSDO measured by the 4 cardinal and 4 intermediate points (upper right image), the cover is: 2, 3, 2 on the NE, E, SE surfaces respectively and 0 on other surfaces of substrate.

The second method (mesoscale analysis) was based on estimation of the percentage cover of sessile epifauna (mussels, barnacles and hydrozoans), epiflora (*F. lumbricalis* and filamentous green, brown and red macroalgae) and composition of the bottom sediments within the visual area of seabed for each 1 min of video footage. This time interval was chosen empirically as trade off between amount of visual information which an operator can memorise and variability of the seabed (sediment composition, conspicuous species and their cover).

3.3. Spatial analysis of *Furcellaria lumbricalis* distribution at the mesoscale

The data from divers' descriptions and video analysis was pooled since there were no significant difference in mean *F. lumbricalis* cover estimated by hand-held video and diving methods ($t= -0.5$, $p= 0.6$). Video transects in length longer than ca 20 m were divided into 10-30 m length transects in order to standardize the sample size among the different methods. Therefore, *F. lumbricalis* cover and substrate composition was averaged within these transects. In total, database consisted of 566 diving and video transects.

Continuous distribution of *F. lumbricalis* (occurrence and cover) was modelled by two methods: geostatistical interpolation and statistical approach (regression analysis). All predictions were made in the raster data with a grid size of 50 m. Spatial models of *F. lumbricalis* occurrence and cover were selected from the simulations by different methods according to the highest values of goodness of fit. The latter was estimated over cross-validation approach: subsets were made of the entire dataset, where each subset contained an equal number of randomly selected data points. Each subset was then dropped from the model, which was recalculated and predictions made for the omitted data points. Combination of the predictions from the different subsets was then plotted against the observed data. Spearman and simple correlation coefficients were used for binomial and normally distributed data respectively. The final *F. lumbricalis* distribution was obtained by overlaying the predicted red alga cover over the predicted area of the species occurrence in GIS.

Before analysis the data of *F. lumbricalis* cover was explored for the spatial autocorrelation and trends by ArcGIS toolbox-Exploratory Spatial Data Analysis (ESRI® ArcMap^{TM} 9.2). *F. lumbricalis* cover was spatially clustered (Morans I= 0.36, p< 0.01), however, the variance was very high from tens of meters to tens of kilometers (Appendix 2), therefore the spatial dependence considered relatively low and was not incorporated in the statistical models.

3.3.1. Geostatistical modeling

Natural Neighbor interpolation technique is one of the deterministic geostatistical methods, which is applicable in case of irregular spread of sampled locations throughout the study area (Sibson, 1981). This was the case in the present study because of patchiness in occurrence and cover of *F. lumbricalis* within transects. According to this approach the value at an unsampled location is computed as a weighed average of the nearest neighbor (point) values with weights dependent on areas/volumes rather than distances. The modelled species occurrence/cover was set to zero in areas covered by unsuitable substrates (sand and gravel) or below euphotic zone (< 15 m).

3.3.2. Statistical modeling

Generalized regression analysis and spatial prediction for R v2.0 (GRASP-R) was used for modelling the natural distribution of *F. lumbricalis* cover and occurrence. This is another method used for making spatial predictions from point measurements. Differently from the geostatistical approach GRASP is based on the relationships between the spatial species distribution and relevant environmental variables, or predictors (Miller et al., 2007). This method has more reasonable ecological explanation because it produces a complex function between a species distribution and environmental parameters (Austin, 2002).

Four physical environmental variables were used to predict cover and occurrence of *F. lumbricalis*: occurrence of suitable substrate (boulders and cobbles), bathymetry, a proxy of salinity/turbidity and a proxy of wave exposure (Appendix 3). The first two variables were primary factors that determine the suitable environment for the red alga: available substrate for the attachment and euphotic depth for photosynthesis, therefore, bathymetry was used as a proxy of decrease of irradiance. The input data was obtained from the geological and bathymetrical maps respectively (Gelumbauskaitė et al., 1999). The salinity/turbidity was taken into account as environmental variable, since less saline, more turbid and nutrient rich waters from the Curonian Lagoon flow in the southern part of the coast. The gradients of salinity/turbidity may influence the distribution limits of marine species *F. lumbricalis* and its euphotic depth. Therefore, the distance from the mouth of the Lagoon to a given grid in the study area was calculated. The wave exposure was introduced due to known effect of storms when the red alga was dislodged from the substrate and casted ashore in relatively high quantities (Blinova, 2007). The wave exposure was calculated as an average distance from a given grid along directions of predominant storms (SW, W and NW) to the depth of 20 m. At this depth the seabed is still influenced by waves (Olenin et al., 1994). Thus, the longer the distance to 20 m isobath - the more gentel slope of seabed and the wave exposure is relatively low; and vice versa.

Explanatory analyses were performed before starting the process of model selection in order to investigate possible data problems such as presence of outliers and correlation between predictors. Two variables, distance to the outflow of Curonian Lagoon and distance to 20 m isobath, strongly cross correlated ($r = 0.85$, $p < 0.0001$, $n = 566$), thus the former was excluded from further analysis. Remaining environmental factors were used as input for the prediction of *F. lumbricalis* distribution.

For the presence-absence data of *F. lumbricalis*, the Binomial model with logit link function was chosen, whereas for the species cover the Poisson model with log link function was applied. In both cases a stepwise procedure (both backward and forward) was used to select significant predictors. The predictions were made using two degrees of freedom for the spline smoothers according to plots of residuals vs. each explanatory variable and recommendations by Sandman et al. (2008).

The selected models were evaluated by two methods (Lehmann et al., 2002): 1) a plot of the observed response values against the values predicted by the model; 2) a cross-validation of the model. Correlation between the observed and predicted values was then calculated to assess goodness of fit of Poisson model, whereas the ROC test was used for Binomial model. Three analyses were used for presentation and interpretation of the regression models: plots of the regression model, plots of response curves that result from the model, and graphs of the overall contribution of the variables to the model.

The predictions were exported to ArcGIS via ASCII files. Predicted probability surface of *F. lumbricalis* occurrence was translated into a presence-absence classification map based on thresholds calculated by two criteria (Freeman & Moisen, 2008): predicted prevalence is equal to the observed prevalence and the highest mean kappa.

3.4. Evaluation of ecological role of *Furcellaria lumbricalis*

Ecological importance of *F. lumbricalis* in the coastal ecosystem was analyzed according to two aspects: the species diversity within the thalli of *F. lumbricalis* and its role in the trophic ecosystem network based on Ecopath model.

3.4.1. Assessment of *Furcellaria lumbricalis* function of impact on species diversity

The habitat-forming function of the red alga was investigated in terms of composition and abundance of bentho-pelagic organisms found close to and on thalii of *F. lumbricalis*. Similarly, the composition and abundance of organisms was also determined within and on the clumps of blue mussels (*M. edulis*), which generally form dense colonies on the same substrates as *F. lumbricalis*. Generally, the blue mussels considered as ecosystem engineers (Gutiérrez et al., 2003), therefore, the structure and abundance of species found within two hosts (*M. edulis* and *F. lumbricalis*) were compared.

Thalli of the red alga and clumps of the blue mussels were sampled by divers at 3-4, 6, 9 and 12 m depths. The whole thallus of *F. lumbricalis* was enclosed by a mesh-bag (opening Ø 0.04 m^2) and detached from the substrate, whereas the blue mussels were scraped from the 0.04 m^2 surface of substrate into the mesh-bag. Each sample was preserved (4% formaldehyde solution) on board. Once in the laboratory, the macrofauna and epiphyte algae species were sorted out, identified and counted using a binocular microscope, at 15x magnification. Macrofauna and macroalgae found within the hosts were determined at the species level where practicable (macroalgae, polychaetes, most of molluscs and crustaceans); other taxonomic groups were identified at higher levels (family, order or class), e.g. Oligochaeta, Chironomidae. Abundance of macrofauna taxa within the two hosts was determined and calculated per square meter. Wet weight of macroalgae was determined with accuracy of 0.001 g. In statistical analyses the groups identified to different taxonomic levels were treated as individual "species".

Multivariate analyses were conducted in order to compare the species composition (presence/absence data) and abundance of macrofauna and epiphyte taxa within *M. edulis* and *F. lumbricalis* using the PRIMER 5 software (Clarke & Warwick, 2001). Bray-Curtis similarities were calculated for occurrence and abundance data of associated macrofauna. These groups were graphically examined by hierarchical cluster analysis (Clarke & Warwick, 1994). One factor analysis-of-similarities (ANOSIM) was used to test the differences between groups of associated macrozoobenthic species from the host organisms. ANOSIM Global R-values > 0.50 indicated difference between the groups (Clarke & Gorley, 2001) and were reported as significant differences in this study. Taxa responsible for observed similarity for each group were identified by similarity percentages (SIMPER), where the cut-off percentage was set to 70. Additionally Canonical correspondence analysis was applied in order to link macrofauna species (according to their abundance) to environmental factors (Zuur et al., 2007), such as depth, biomass of mussels (*M. edulis*), *F. lumbricalis* and its filamentous red macroalgae epiphytes (*Ceramium tenuicorne, Polysiphonia fucoides* and *Cladophora rupestris*).

3.4.2. Ecopath modeling of the carbon flow in the coastal ecosystem

The contribution of *F. lumbricalis* in the trophic network was analyzed at the local coastal ecosystem level using ECOPATH with ECOSIM (Christensen et al., 2004; Christensen & Pauly, 1992). Originally proposed by Polovina (1984), the ECOPATH model has been combined with routines for network analysis based on the approach developed by Ulanowicz (1986). ECOPATH's basic equation represents a mass balance for each trophic group i in a system of n trophic groups,

$$B_i \frac{P_i}{B_i} EE_i - \sum_{j=1}^{n} B_j \frac{Q_j}{B_j} DC_{ji} - EX_i = 0$$

where Bi is the biomass of group i; Pi is its total production; DCji is the proportion of trophic group j in the diet of group i – is a diet matrix coefficient that describes the trophic relationship between groups; Qi is the total food consumption of group i; the production/biomass ratio Pi/Bi and the consumption/biomass ratio Qi/Bi are metabolic rates that express the productivity and consumption per unit of biomass, respectively. EEi is the Ecotrophic efficiency, which is the fraction of production of group i that is utilized – i.e. consumed, exported or harvested – within the system. EXi is the net export.

The trophic network model was created for Lithuanian coastal waters in the sublittoral zone with stony bottom, where the modelling area covered ca 70 km^2. Twelve functional model groups were selected in the model in order to represent the main specific species functional groups (Fig. 6). Phytoplankton was represented by a single functional group, while benthic primary producers were divided into annual (*Ectocarpus siliculosu, Pilayella litoralis, Cladophora spp., Ulva spp.*) and perennial (*Furcellaria lumbricalis*) macrophytes (Appendix 4). Pelagic zooplankton was divided into 2 groups: micro- and mesozooplankton as the first group and macrozooplankton as the second group. Benthos was represented by benthic deposit feeders and benthic filter feeders. Three functional groups of fish were included: planktivorous, benthivorous (including also omnivorous species), and piscivorous fish. Birds were included as a single functional group. The human impact was indicated by using single fishing fleet. Seals occurred only infrequently in the investigated coastal system and were, therefore, omitted. Data for model derived from area-specific research and literature and were collected during a Baltic Sea Regional Project workshop (Anon., 2004). The trophic network defined for the Lithuanian Baltic Sea coast is illustrated in Figure 7.

	Group name	Color	Consumer	Producer	Detritus	PP
1	Birds	■	☑	☐	☐	0
2	Piscivorous fishes	■	☑	☐	☐	0
3	Planktivorous fishes	■	☑	☐	☐	0
4	Benthivorous fishes	■	☑	☐	☐	0
5	Benthic deposit feeders	■	☑	☐	☐	0
6	Benthic suspension feeders	■	☑	☐	☐	0
7	Macrozooplankton	■	☑	☐	☐	0
8	Micro- and mesozooplankton	■	☑	☐	☐	0
9	Perennial macroalgae	■	☐	☑	☐	1
10	Annual macroalgae	■	☐	☑	☐	1
11	Phytoplankton	■	☐	☑	☐	1
12	Detritus	■	☐	☐	☑	2

Figure 6. Functional groups of trophic network model of the coastal waters within the euphotic zone and stony bottom area at the Lithuanian Baltic Sea coast.

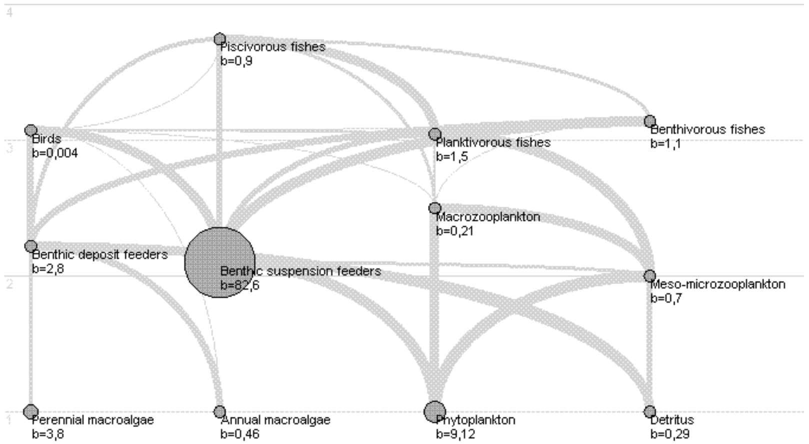

Figure 7. Structure of trophic network model of the coastal waters within the euphotic zone and stony bottom area at the Lithuanian Baltic Sea coast. The size of each round box is proportional to the biomass it represents (b); lines are scaled by flow amount.

The input parameters B (biomass), P/B (production to biomass ratio), Q/B (consumption to biomass ratio) (Table 5) and diet composition (Table 6) were estimated by using data derived from own investigations and literature (Appendix 4). The Ecotrophic Efficiency (EE) was estimated for all functional groups in the models.

The Mixed Trophic Impact (MTI) routine (Majkowski, 1982) in EwE was used to evaluate critical trophic interactions between functional groups in the ecosystems. Christensen & Pauly (1992) introduced MTI into ECOPATH to study the interaction of direct and indirect effects of functional groups.

Table 5. Basic ECOPATH input parameters for the network model of the coastal waters within the euphotic zone and stony bottom area at the Lithuanian Baltic Sea coast: biomass (B in g C m^{-2}), production to biomass ratio annual average (P/B), consumption to biomass ratio annual average (Q/B) and landings (g C m^{-1} year^{-2}).

	B	P/B	Q/B	Landings
Birds	0.002	0.5	5	
Piscivorous fish	0.32	0.98	2	0.07
Planktivorus fish	2.6	0.7	2	0.18
Benthivorous fish	0.01	0.7	4	0.0004
Benthic deposit feeders	1.6	1.62	8.12	
Benthic suspension feeders	5.5	0.88	4.41	
Macrozooplankton	0.029	3.1	15	
Micro- and mesozooplankton	0.8	40	160	
Perennial macrophytes	0.1	11.9	n.r	
Annual macrophytes	0.004	10	n.r	
Phytoplankton	0.82	190	n.r	
Detritus	4	n.r	n.r	

n.r-not relevant

Table 6. Diet composition for the network model of the coastal waters within the euphotic zone and stony bottom area at the Lithuanian Baltic Sea coast.

	Prey \ Predator	1	2	3	4	5	6	7	8
1	Birds	0	0	0	0	0	0	0	0
2	Piscivorous fish	0	0.07	0	0	0	0	0	0
3	Planktivorus fish	0.12	0.57	0	0.24	0	0	0	0
4	Benthivorous fish	0.02	0	0	0	0	0	0	0
5	Benthic deposit feeders	0.44	0.36	0.01	0.06	0	0	0	0
6	Benthic suspension feeders	0.42	0	0	0.53	0	0	0	0
7	Macrozooplankton	0	0	0	0.11	0	0	0	0
8	Micro- and mesozooplankton	0	0	0.99	0.06	0	0.01	0.68	0
9	Perennial Macrophytes	0	0	0	0	0	0	0	0
10	Annual Macrophytes	0	0	0	0	0	0	0	0
11	Phytoplankton	0	0	0	0	0.23	0.88	0.3	0.67
12	Detritus	0	0	0	0	0.77	0.11	0.02	0.33
13	Import	0	0	0	0	0	0	0	0

3.5. Data analysis and statistical procedures

Data was tested for normality and homogeneity of variances before analysis employing Kolmogorov-Smirnov and F' tests respectively. In cases where these conditions were not met, transformations were applied (Sokal & Rohlf, 1995). The Spearman rank correlation (r_S) was used for determination of relationship between categorical variables, whereas linear regression was used for prediction of continuous variables. A t-test was applied to test for differences between the means of two independent groups. Two-way analyses of variance (ANOVA) and Tukey's studentized range test (Quinn & Keough, 2002) were used to verify the following hypotheses:

- **the cover of *F. lumbricalis* should be greater on large and stable substrates (e.g. boulders) which help the algae to avoid scouring and detachment;**
- **the cover of the species should be greater on substrates surrounded by immobile sediments (e.g. boulders) when compared with those substrates adjacent with mobile sediments (e.g. sands, gravels);**
- **the distribution of the *F. lumbricalis* cover should be higher above the seabed on a more mobile sediment, on account of abrasion effect;**
- **the substrate mobility and effect of sediment abrasion upon the cover of alga should be greater at lower depths than at deeper sites;**
- **the cover of *F. lumbricalis* should be denser on sheltered surfaces of substrates (in case of this study site: E, NE and SE) compared to exposed ones (W, NW and SW).**

Diagnostic tools for distribution of dependent variable, studentized residuals, normal probability plots as well as correlation between mean and standard deviation (S.D.) were also used in ANOVA models (StatSoft Inc., 2006).

The parameter of frequency of stormy winds (speed of ≥ 10 m s^{-1}) in 4 cardinal and 4 intermediate points (data for the period 2000-2003 obtained from the Lithuanian Hydrometeorological Service) was used for analysis of effect of storms on *F. lumbricalis* cover on substrate.

Means and standard deviations were used in the study to represent the estimated parameters and their variability.

4. RESULTS

4.1. Spatial distribution of *Furcellaria lumbricalis*

4.1.1. The species distribution at the microscale

The substrates, the red alga *F. lumbricalis* grew on, were: pebbles, cobbles, small and large boulders. The surrounding bottom sediments (SBS) included also sands and gravel besides the substrates listed above. Where the cover of algae was dense the underlying substrate often could not be determined from video data. This mainly occurred in cases of algae overgrowth on pebbles therefore this substrate type was excluded from the analysis of the species cover.

The mean cover of *F. lumbricalis* (CFS) significantly differed between the substrate types (Fig. 8, Table 7). Cobbles were the least suitable substrate where the mean algal cover was low within all mobility types of surrounding bottom sediments (MSBS): 0.3±1.0, 1.0±1.0, 0.7±1.0 on the mobile, intermediate and stable sediments, respectively. The maximum cover of *F. lumbricalis* (average 2.7±1.0) determined on large boulders did not differ statistically significantly from the cover on small boulders (average 2.4±1.0). The CFS on the stable SBS was the highest, followed by the intermediate and mobile SBS.

Table 7. Results of two-way ANOVA mixed models (bold P values indicate significant factors).

Sources of variation	d.f.	MS	F	P
	CFS			
Substrate	2	6.768	6.810	**<0.001**
MSBS	2	17.994	18.106	**<0.001**
substrate x MSBS	4	2.78	2.80	**<0.05**
Residual	81	0.994		
	MDSF			
MSBS	4	0.267	4.066	**<0.01**
depth	1	0.02	0.33	>0.05
MSBS x depth	10	0.554	8.452	**<0.001**
Residual	176	0.066		

			TCFS	
MSBS	4	6.713	9.007	**<0.001**
depth	1	22.513	30.205	**<0.001**
MSBS x depth	10	3.650	4.897	**<0.001**
Residual	176	0.745		
			CFSDO	
Orientation of substrate surface	7	4.92	3.34	**<0.01**
Depth	5	12.276	8.332	**<0.001**
CFS x depth	35	1.80	1.22	>0.05
Residual	624	1.473		

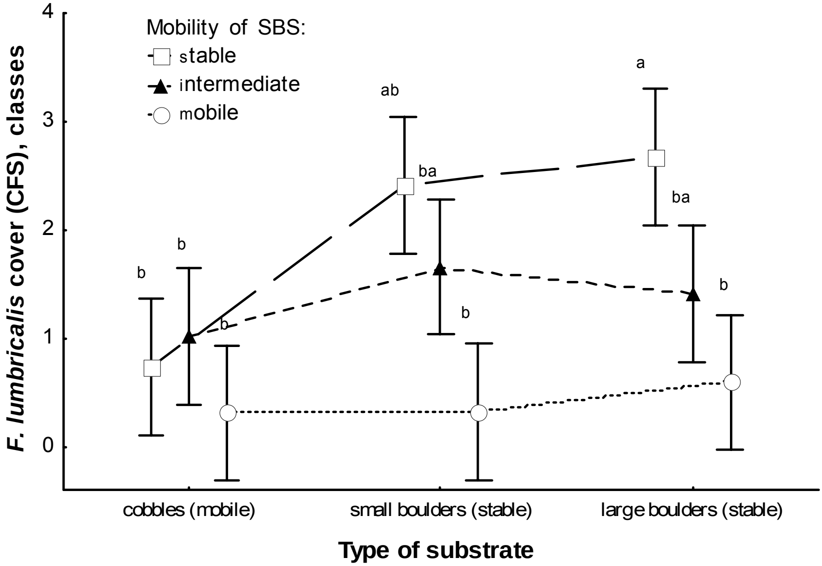

Figure 8. The mean cover of *F. lumbricalis* on different substrate types (CFS) within mobile, intermediate and stable surrounding bottom sediments (SBS). The letters above indicate homogeneous groups of Tukey's HSD test (N= 90, Mean ±0.95 Conf. intervals). Data transformed by S.D. of the groups.

In general the density of total *F. lumbricalis* cover (TCF) on the stable and intermediate SBS increased from 6 to 9 m, and decreased from 9 m (Fig. 9). On the mobile SBS, the cover values were low (average 0.3±0.8) and displayed no particular pattern along the whole depth gradient. The TCF was twice as dense on the stable SBS (average 2.3±1.2) where compared with the intermediate SBS in range of 6 to 9 m depth. On both types of SBS, however, the highest mean values of TFC were reached at 9 m depth (4.0±0.0 on stable and 1.7±1.3 on intermediate SBS) and were consistently low at greater depths.

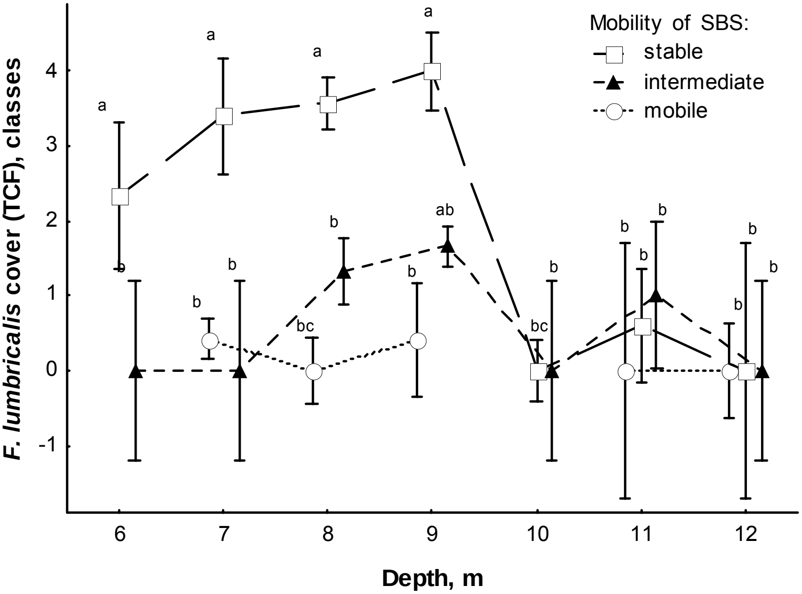

Figure 9. The TCF on different types of surrounding bottom sediments (SBS) along the depth gradient (N= 195, Mean ±0.95 Conf. intervals). The letters above indicate homogeneous groups according to Tukey's HSD test. Mobile SBS were not observed at 6 and 10 m depth.

F. lumbricalis on the substrates occurred in distance of 3 cm to 50 cm above the seabed, however different patterns of algae position were found on various types of SBS (Fig. 10). On stable SBS the minimum distance between the seabed and the holdfast of *F. lumbricalis* (MDSF) was similar at 6 to 9 m (average 5±1 cm) and was significantly greater below 10 m depth (30±0 cm). On the intermediate SBS, this was constant at 6 to 10 m (6±2 cm), and reached 25±7 cm at greater depths. On the mobile SBS, the algae occurred 14±11 cm at depths of 7 to 8 m, whereas below 10 m the MDSF was significantly lower (6±6 cm). In general, the differences in the MDSF between bottoms of different mobility were more pronounced at depth below 9 m, whereas those within the depth range 6-9 m the MDSF were relatively similar on all the SBS.

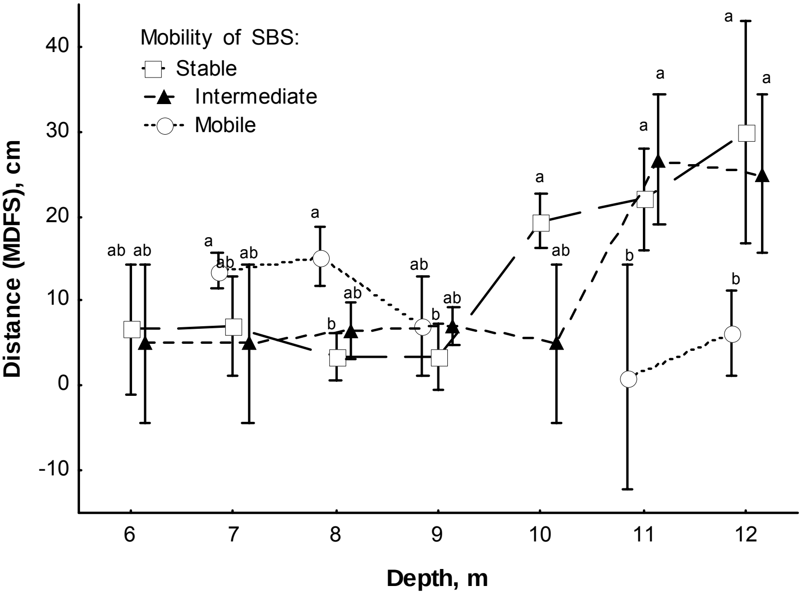

Figure 10. The MDSF on different types of surrounding bottom sediments (SBS) along the depth gradient (N= 195, Mean ±0.95 Conf. intervals). The letters above indicate homogeneous groups according to Tukey's HSD test. Mobile SBS were not observed at 6 and 10 m depth.

The mean cover of *F. lumbricalis* was significantly greater on sheltered surfaces (E and NE) of substrates than on the exposed surface (W) (Table 7, Fig. 11). The largest mean cover of the algae was the same on the NE and E surfaces (1.8±1.3), with least on western facing surfaces (1.1±1.2).

The frequency of stormy winds affected the exposed western surfaces of substrates (Fig. 11). Significant negative relationship (r_S= -0.97, $p< 0.05$) was determined between the mean cover of *F. lumbricalis* on substrate surfaces of different orientation (CFSDO) and frequency of stormy winds. The algal cover was lower on the exposed western surfaces of the substrate, facing predominant stormy wind directions, when compared to the sheltered eastern surfaces.

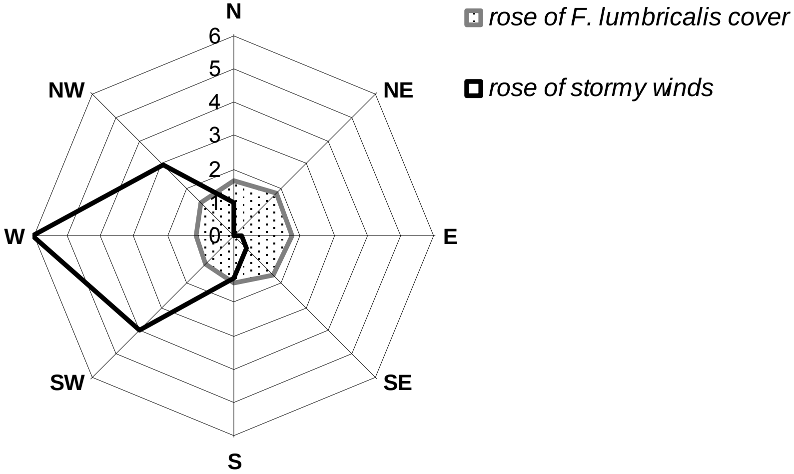

Figure 11. Mean annual frequencies of stormy winds and the mean cover of *F. lumbricalis* on substrate surfaces of corresponding orientation (CFSDO).

4.1.2. The species distribution at the mesoscale

4.1.2.1. Vertical distribution

The vertical distribution of *F. lumbricalis* was restricted to the depths between 1 and 15 m (Fig. 12). At 1 m depth, however, the species occurred only in two transects out of 18. The cover of the red alga in the study area ranged from less than 10% in case of single or few plants up to 89% in areas of species overgrowths. Mean *F. lumbricalis* cover along the entire depth gradient was 20±15%. Above this overall mean species cover was between 3 and 8 m depths. The mean algal cover was evidently lower at 1 and 13-15 m depths than between 2 and 12 m depths.

F. lumbricalis cover was not evenly distributed along the irregular bottom slope at three long-distance transects (Fig. 13). Algal cover tend to be lower at depressions (19±15%) than at elevations (26±19%), however, this difference was not significant ($t= -1.0$, $df= 12$, $p= 0.3$), presumably, due to low number of cases. The steepness of the bottom slope differed between the transects from 9° (slope B in Fig. 3) to 12-13° (slopes A and C in Fig. 13 respectively). Maximum cover of *F. lumbricalis* was twice higher on the gentle bottom slope (80%) than on the steep ones (40%). The mean algal cover was evidently higher ($t= -2.58$, $df= 38$, $p< 0.05$) at plain stony bottom (27±24%) than at mixed one (12±9%), covered by sand and stones in equal proportions.

The mean biomass of *F. lumbricalis* strongly correlated ($r_s= 0.76$, $p< 0.05$) with the mean species cover along the depth gradient (Fig. 12). The overall mean biomass of the red alga was 485.6±456.8 g m^{-2} between 1 and 15 m depths. The mean species biomass above the overall mean was between 2 and 7 m depths, where maximum biomass (ca 4000 g m^{-2}) occurred at 4 m depth. The mean algal biomass was evidently lower at 1 and 11-15 m depths than between 2 and 10 m depths. In contrast to high maximum cover distribution along the relatively wide depth range, high maximum biomass values occurred only at 4 m depth.

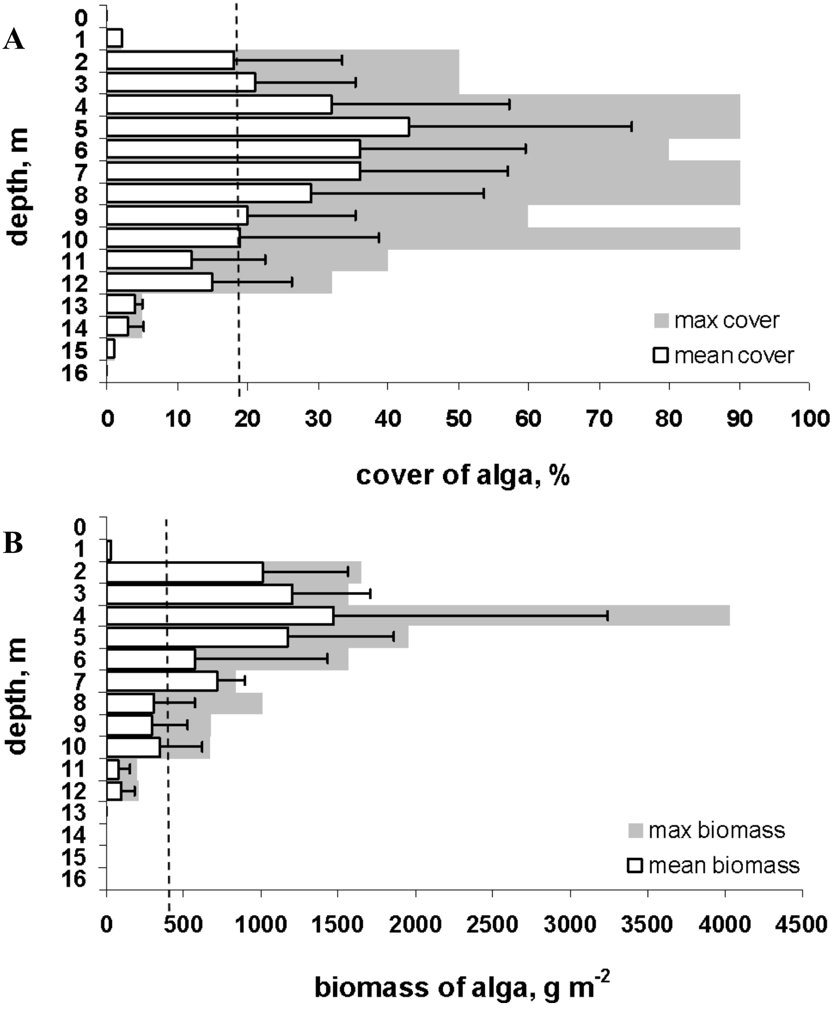

Figure 12. Distribution of maximum and mean values of *F. lumbricalis* cover (A) and biomass (B) at the Lithuania coast in 2003-2008. Dotted line – overall mean of cover and biomass of the species respectively.

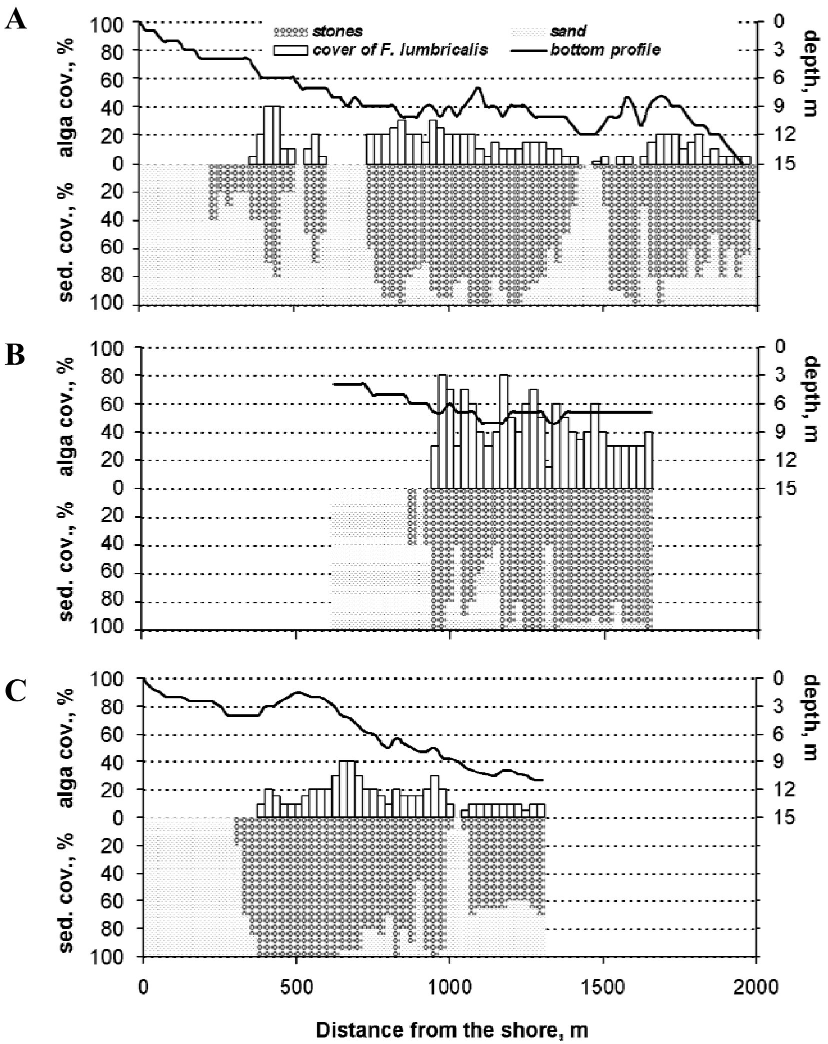

Figure 13. Schematic presentation of the bottom slope profile (bottom profile), *F. lumbricalis* cover (alga cov.) and composition of sediments (sed. cov.), expressed as ratio between sand (dots) and stones (circles), along the 3 long-distance transects (A, B and C). For explanation see text.

4.1.2.2. Horizontal distribution of *Furcellaria lumbricalis* and limiting physical factors

Horizontal distribution of the red alga was modelled by two statistical techniques (see methods). The predictive model of *F. lumbricalis* occurrence by GRASP and the model of species cover by NNI were selected due to their highest results of cross-validation (Table 8).

Table 8. Correlation coefficients obtained during cross-validation of two models using different methods.

Method	**Model of *F. lumbricalis***	
	occurrence	**cover**
Generalized regression analysis and spatial prediction (GRASP)	0.9	0.6
Natural Neighbor interpolation (NNI)	0.7	0.7

In the GRASP model four environmental variables were highly significant predictors alone ($p< 0.0001$) and altogether explained 49% of variation in *F. lumbricalis* occurrence. Comparison of change in residual deviance when dropping each predictor indicated that occurrence of suitable substrate made the greatest contribution to the final model of *F. lumbricalis* occurrence (Fig. 14). The next important environmental factors were distance to 20 m isobath and bathymetry.

Both the cross-validation and the simple validation of model of *F. lumbricalis* occurrence presented high ROC values with no difference between them, indicating good model stability (Fig. 15). The correlation between observed and predicted species richness was relatively high corresponding to more than half the variation in the species richness explained by the model. The level of correct matching between the observed and predicted values was lower for *F. lumbricalis* absence data than presence (Table 9). The model produced up to 22% of misclassifications in predicting the species occurrence for sampling sites where the red alga has not been observed, whereas only 3% of misclassifications were made in predicting true presence of *F. lumbricalis*.

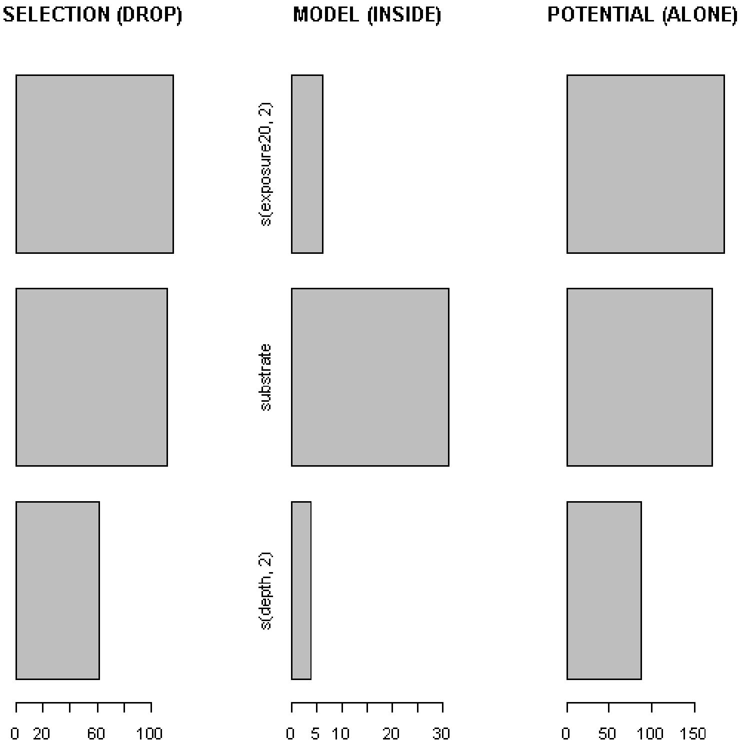

Figure 14. Contribution of predictors, occurrence of suitable substrate (substrate), distance to 20 m isobath (exposure20) and bathymetry (depth), in the explanation of the total variance of *F. lumbricalis* occurrence by dropping each predictor from the model, leaving all predictors inside the model and leaving each predictor alone in the model.

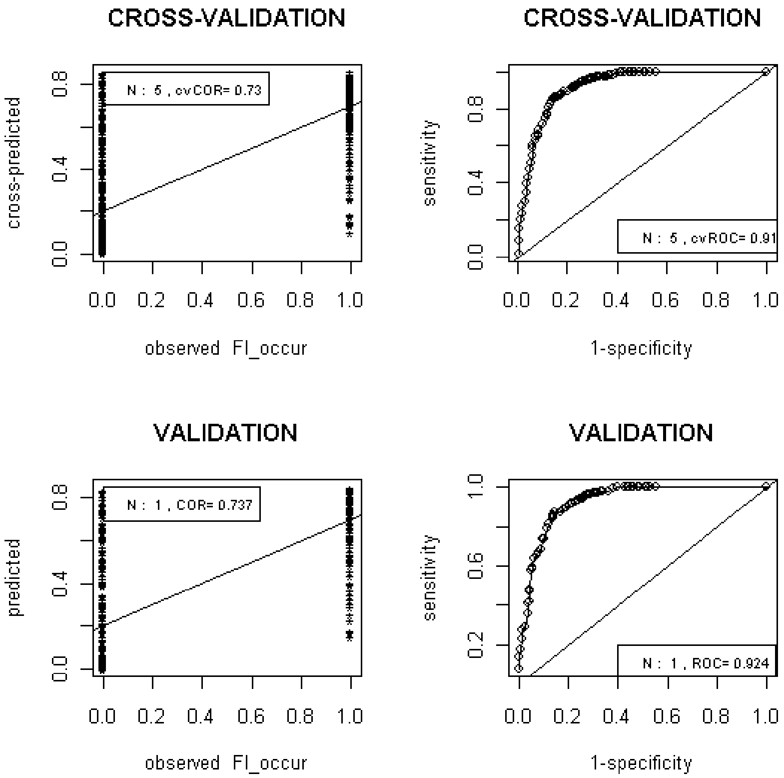

Figure 15. Validation and cross-validation for the model of *F. lumbricalis* occurrence.

Table 9. Contingency table of observed occurrence (presence and absence) of *F. lumbricalis* vs. predicted ones.

		Predicted		
		absence	presence	row total
Observed	absence	201 (36%)	123 (22%)	324 (59%)
	presence	16 (3%)	212 (38%)	228 (41%)
	column total	217 (39%)	335 (61%)	552 (100%)

Partial response curves were typical bell-shaped relationships indicating non-linear change in the *F. lumbricalis* occurrence along the environmental gradients (Fig. 16). The occurrence of the red alga was increasing to 9 m depth and after that it was decreasing and at 17 m depth was absent. The species occurrence was increasing to 8 km from the 20 m isobath, whereas after that it stayed relatively constant. The highest species occurrence (> 0.5) was between 5 to 10 m depths, 17 and 29 km distance from the outflow of Curonian Lagoon and within the distance of 6-10 km from the 20 m isobath and on suitable substrates.

The final model of distribution area of *F. lumbricalis* and its cover were calculated by adding the predicted results (raster maps) of *F. lumbricalis* occurrence by GRASP and the species cover by NNI (Fig. 17). Comparison of observed *F. lumbricalis* distribution with the predicted one generally showed tendency to overestimate the area occupied by the red alga.

The size of the modelled area occupied by *F. lumbricalis* was 47±11 km^2 (Fig. 17 and Table 2). It comprised more than 50% of the stony bottoms in the euphotic zone (≤ 15 m). Algal cover of less than 5% comprised more than half (26±1 km^2) of the total occupied area. Approximately 98% of the species distribution area (46±10 km^2) was taken by < 50% *F. lumbricalis* cover.

According to the species modelled distribution it was stretched for ca 26 km along the coast (Fig. 17). The northernmost limit of *F. lumbricalis* was at ca 56°1.55’N and the southernmost one at ca 55°46.30’N. In the southern part of the study area the species cover was relatively low (1-50%) and patchy with narrow belt between 5 and 10 m depth. In the central part the algal cover ranged from ca 1 to 90%, and *F. lumbricalis* belt stretched between 3 and 15 m isobaths. Although, the densest overgrowths of *F. lumbricalis* were located in depths of 4 to 10 m in the vicinity of Palanga, however, they were very patchy within tens of meters. In the northern part of the study area the algal belt remained wide (between 5 and 15 m depths), but the species cover was relatively low (1-30%).

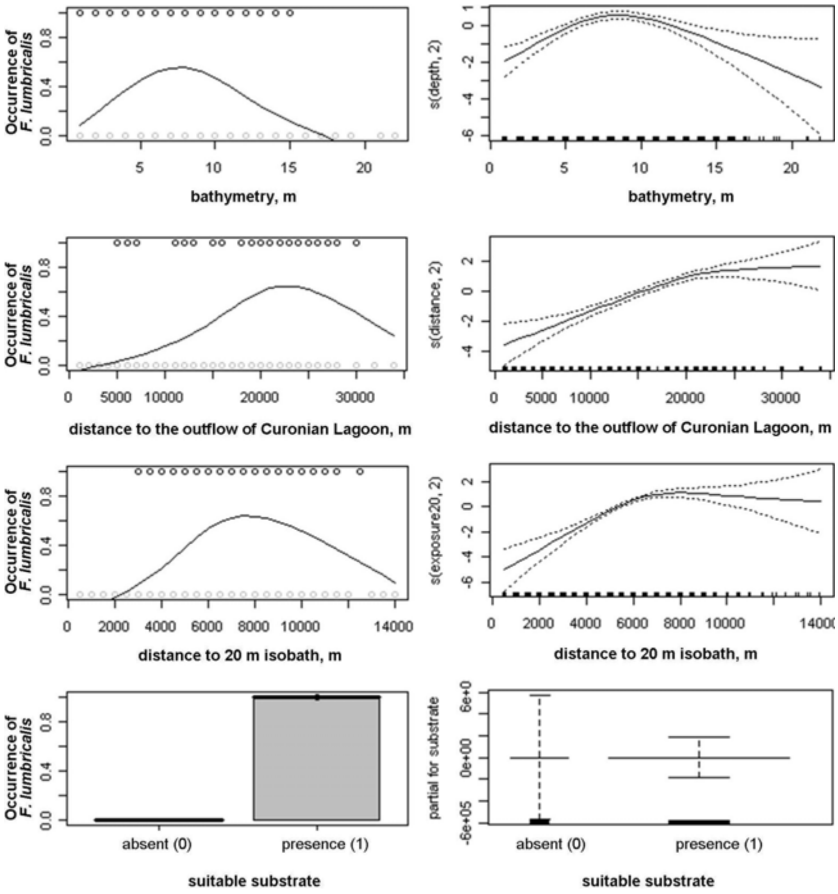

Figure 16. Plots of occurrence of *F. lumbricalis* vs. predictors (on the left) and partial response curves (on the right) of *F. lumbricalis* occurrence to the environmental gradients and factors: bathymetry, distance to the outflow of Curonian Lagoon, distance to 20 m isobath and occurrence of suitable substrate. The Y axes, expressed in logits, indicate the relative influence of each environmental variable on the prediction on the base of partial residuals. Dashed line indicate two time the point-wise standard errors for each curve of factor level.

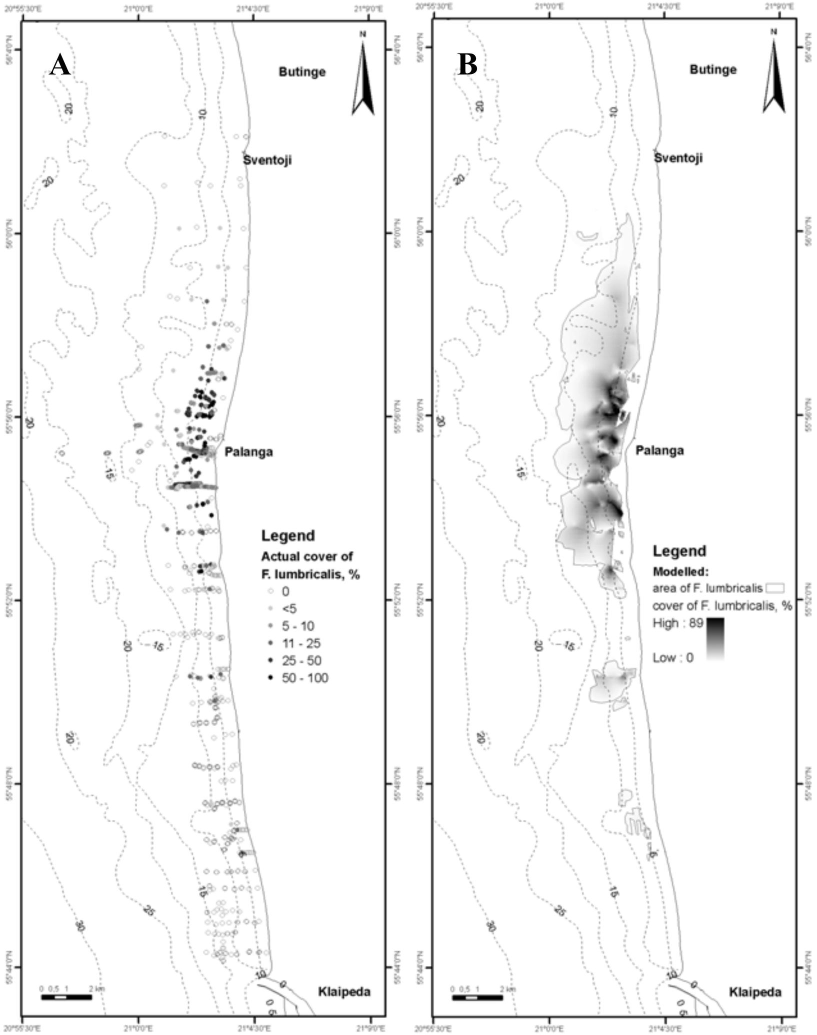

Figure 17. Actual (A) and modelled (B) distribution of *F. lumbricalis* occupied area in 2003-2008.

Table 10. Estimated areas of different *F. lumbricalis* covers at the Lithuania coast in 2003-2008.

Cover classes of the alga, %	Area,	
	km^2	%
< 5	26±1	55
5–9	7±3	14
10–24	9±3	20
25–49	4±2	8
50–100	1±1	2
total	47±11	100

4.1.3. Stock of *Furcellaria lumbricalis* at the Lithuanian coast

The species stock assessment was based on relatively strong and statistically significant correlation ($r= 0.95$, $p< 0.05$, $n= 89$) between *F. lumbricalis* mean biomass and cover (Fig. 18). This allowed estimating the species standing stock using modelled distribution and cover for the study area. *F. lumbricalis* mean cover of 50% corresponded 976±689 g m^{-2} mean biomass of the species, whereas, the dense overgrowths of the red alga (mean cover of 90%) weighted ca 2018±1361 g m^{-2}. Standing stock of *F. lumbricalis* in the modelled distribution was estimated to be 8449±3813 t (Table 11). The areas of algal cover of ≤ 50% and > 50% consisted of ca 7449±2097 t (85% from the total biomass) and 1304±1715 t (15%) respectively.

Vertical distribution of *F. lumbricalis* stock is presented in Figure 19. The algal stock gradually increased from 3 to 6 m depth, with a sharp peak at 7 m. Irregular decrease pattern of the species biomass below 7 m depth was not clear, whereas more than 50% of the total biomass was concentrated between 7 and 11 m depth.

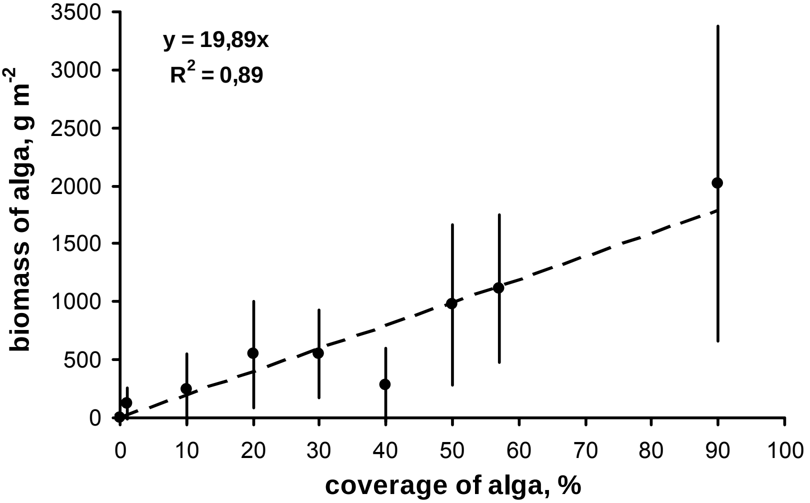

Figure 18. Relationship between mean *F. lumbricalis* biomass and cover. Dots and whiskers: mean±SD.

Table 11. Estimated and predicted mean biomasses of different *F. lumbricalis* covers at the Lithuania coast in 2003-2008.

Cover classes of *F. lumbricalis*, %	**Biomass,**	
	t	**%**
< 5	781±36	9
5–9	929±259	11
10–24	2734±721	32
25–49	2700±1082	32
50–100	1304±1715	15
total	8449±3813	100

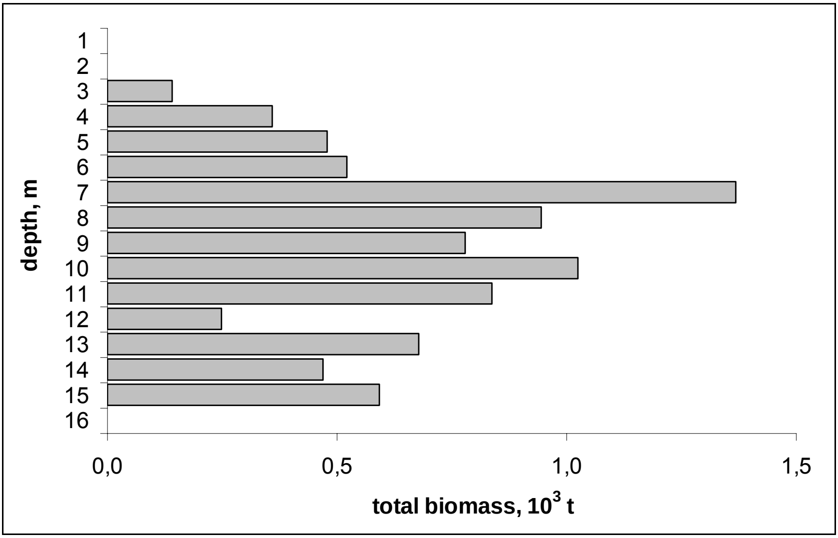

Figure 19. Total *F. lumbricalis* biomass vertical distribution in the modelled species area at the Lithuania coast in 2003-2008.

4.2. Ecological role of *Furcellaria lumbricalis*

4.2.1. Associated macrofauna and epiphyte species of *F. lumbricalis* and *Mytilus edulis*

Species richness. In total 24 and 18 species were determined in the samples taken from *F. lumbricalis* and *M. edulis*, respectively. (Table 12, 13). Of them, there were four macroalgae species. The mean number of species was similar between the two hosts: 9±3 and 7±2 species respectively for the red alga and blue mussels. At the depth range 3-4 m, the colonies of blue mussels were absent, while *F. lumbricalis* contained 11±2 species. Within the depth ranges 6, 9 and 12 m there was no statistically significant difference between the two hosts in terms of the mean number of species (Fig. 20).

The same host, *F. lumbricalis*, contained the highest mean number (12±3) species at 6 m depth comparing to 4±1 at 12 m depth interval

(F= 4.74, df= 2, p< 0.05, square root transform.) (Fig. 20). In opposite, where was no statistically significant difference in terms of mean species number in the colonies of blue mussels within different depth intervals.

All four macroalgae species were found on both hosts. The maximum mean number of macroalgae species (3±1) was found on *F. lumbricalis* at 3-4 m depth. In general, the mean number of macroalgae species decreased along the depth gradient.

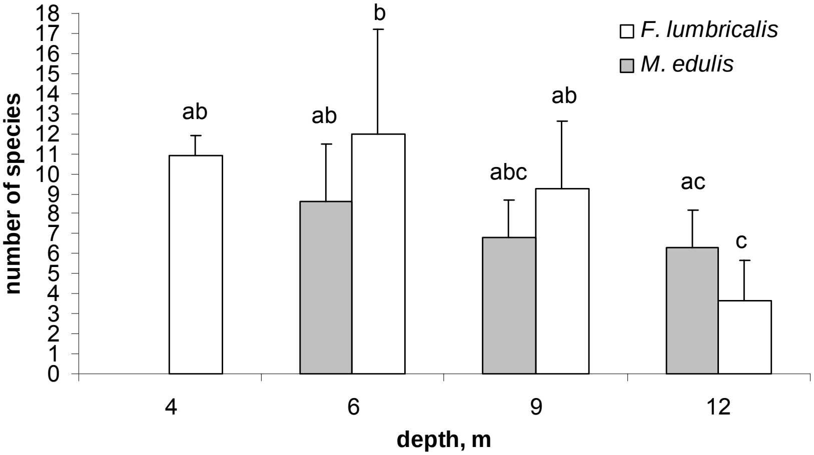

Figure 20. Mean number of macrofauna and macroalgae species within the two hosts, the red alga (*F. lumbricalis*) and blue mussels (*M. edulis*), at different depths.

Species composition. The blue mussels were the most occurrent (> 100 %) species both within the *F. lumbricalis* and, naturally, in *M. edulis* colonies. Therefore, in order to reveal possible differences between the two hosts, the occurrence of *M. edulis* was excluded from further analysis. Species composition of macrofauna was similar (Global R= 0.235, p< 0.01) on the two hosts within the entire depth range where colonies of *F. lumbricalis* and *M. edulis* co-occurred

(Table 12); this was also true for the separate depth intervals (6, 9 and 12 m). The most frequent species (mean occurrence > 80% on both hosts within the entire depth range) were: briozoan *Electra crustulenta,* gastropods *Theodoxus fluviatilis* and *Hydrobia* spp., and barnacle *Balanus improvisus.* On the other hand, there was obvious preference of the blue mussels by hydroid *Cardylophora caspia* (mean occurrence 100% versus 19% on the red alga); whereas the occurrence of crustaceans *Gammarus* spp., *Idotea baltica, Jaera albifrons* and flat worms *Planaria* spp. was higher on *F. lumbricalis* than on *M. edulis*: 63% versus 38%, 46% versus 7%, 46% versus 13% and 33% versus 6% respectively. Other macrofauna species were rather rare (mean occurrence < 50%). Six of these rare species were found in *F. lumbricalis* only, while one species (polychaete *Marenzelleria neglecta*) within the blue mussels.

As with the number of macrofauna species, their composition on *F. lumbricalis* differed significantly (Global R= 0.645, p< 0.01) between 12 m and other depth ranges (Table 12).

Table 12. Occurrence (%) of macrofauna species within *F. lumbricalis* (first row) and *M. edulis* (second row) at different depths. *M. edulis* colonies were absent (-) at 3-4 m depth.

Species of macrofauna	**Occurrence of macrofauna (%) at different depths:**			
	3-4 m	**6 m**	**9 m**	**12 m**
Cardylophora caspia	0	33	25	0
	-	100	100	100
Planaria spp.	44	50	50	0
	-	0	0	17
Nemertini undet.	0	17	25	0
	-	0	0	0
Hediste diversicolor	11	0	25	0
	-	0	0	0
Marenzelleria neglecta	0	0	0	0
	-	0	17	0
Fabricia sabella	0	50	75	0
	-	0	17	33
Oligochaeta undet.	22	17	25	0
	-	33	40	17
Piscicola geometra	0	0	25	0
	-	0	0	0
Balanus improvisus	78	67	100	83
	-	100	100	100
Idotea baltica	100	100	38	0
	-	20	0	0
Jaera albifrons	56	100	38	0
	-	40	0	0
Gammarus spp.	100	100	88	0
	-	80	17	17
Bathyporeia pilosa	44	83	63	0
	-	60	17	17
Corophium lacustre	56	67	13	0
	-	40	0	17
Corophium volutator	11	33	38	0
	-	0	0	0
Corophium multisitosum	0	17	0	0
	-	0	0	0
Chironomidae undet.	0	33	0	0
	-	0	0	0
Theodoxus fluviatilis	100	100	100	67
	-	80	100	100
Hydrobia spp.	44	17	100	100
	-	80	100	100
Mya arenaria	56	67	38	0
	-	40	33	17
Electra crustulenta	100	100	100	100
	-	100	100	100
Total:	13 -	16 11	17 10	3 11

The composition of macroalgae species was similar between both hosts (Global R= 0.437, p< 0.01). The occurrence of macroalgae species was relatively low (< 50%), where filamentous green macroalga *Cladophora rupestris* was found only once within the samples at different depths (Table 13). On the other hand, the most frequently found macroalga was *Ceramium tenuicorne*, which occurred more often on the red alga than on the blue mussels: 46% versus 7% respectively.

Table 13. Occurrence (%) of macralgae species within *F. lumbricalis* (first row) and *M. edulis* (second row) at different depths. The blue mussel colonies were absent (-) at 3-4 m depth.

Species of macrofauna	**Occurrence of macrofauna (%) at different depths:**			
	3-4 m	**6 m**	**9 m**	**12 m**
Coccotylus truncatus	0	0	38	0
	-	0	33	0
Ceramium tenuicorne	100	100	38	0
	-	20	0	0
Polysiphonia fucoides	100	50	0	0
	-	60	0	0
Cladophora rupestris	67	0	13	17
	-	17	20	0
Total:	3 -	2 3	3 2	1 0

Structure of macrofauna community. The blue mussels were most abundant (dominant) species both in the *F. lumbricalis* (50%) and, naturally, in *M. edulis* colonies (53%). Therefore, in order to reveal possible differences between the two hosts, the abundance of *M. edulis* was excluded from further analysis. Also, the briozoan *E. crustulenta* and hydroid *Cardylophora caspia* were not taken into account because the abundance of these colonial animals has not been estimated.

The structure of the macrofauna community associated with the red alga and the blue mussels was fairly different within the entire depth range: crustaceans (*Gammarus* spp.) were the most abundant in the first and barnacle (*Balanus improvisus*) in the later host (Fig. 21, Table 14). ANOSIM revealed statistically significant but marginal difference between both hosts (Global R= 0.5, p< 0.01), whereas this dissimilarity was more pronounced at 6 m than at 9 m depth: Global R= 0.795 and R= 0.562, p< 0.01 respectively. No differences were found at 12 m depth. At 6 m depth the crustaceans (*Gammarus* spp., *Jaera albifron* and *Idotea baltica*) were significantly more abundant within the red alga than the blue mussels. Flat worms *Planaria* undet. were only found on *F. lumbricalis*. At the same depth abundance of barnacle *B. improvisus* was greater on the blue mussels than within the red alga. At 9 m depth crustaceans *Gammarus* spp. and *Bathyporeia pilosa* were more abundant within the red alga than within the blue mussels. Flat worms *Planaria* undet. and crustacean *J. albifron* were only found within *F. lumbricalis*. At the same depth abundance of barnacle *B. improvisus* and gastropods *Hydrobia* spp. were more abundant on the blue mussels than on the red alga.

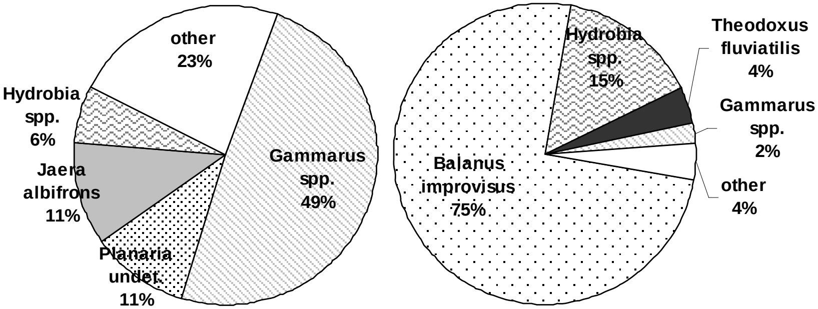

Figure 21. Structure of the macrofauna community associated with the red alga (left) and the blue mussels (right).

Table 14. Mean abundance of macrofauna species within *F. lumbricalis* (first row) and *M. edulis* (second row) at different depths. The blue mussel colonies were absent (-) at 3-4 m depth.

Species of macrofauna	**Abundance of macrofauna (ind~~v~~. m^{-2}) at different depths:**			
	3-4 m	**6 m**	**9 m**	**12 m**
Planaria spp.	72±139	375±555	331±678	0
	-	0	0	4±10
Nemertini undet.	0	8±20	9±19	0
	-	0	0	0
Hediste diversicolor	3±8	0	9±19	0
	-	0	0	0
Marenzelleria neglecta	0	0	0	0
	-	0	4±10	0
Fabricia sabella	0	96±160	75±135	0
	-	0	8±20	50±111
Oligochaeta undet.	11±25	4±10	6±12	0
	-	35±49	63±97	4±10
Piscicola geometra	0	0	6±12	0
	-	0	0	0
Balanus improvisus	33±28	83±86	175±190	83±65
	-	2515±1150	2413±1373	1496±919
Idotea baltica	142±169	83±85	9±13	0
	-	5±11	0	0
Jaera albifrons	342±520	271±315	213±458	0
	-	70±143	0	0
Gammarus spp.	2289±3375	888±998	447±552	0
	-	140±210	4±10	4±10
Bathyporeia pilosa	14±18	63±70	188±263	0
	-	40±45	4±10	13±31
Corophium lacustre	28±34	42±67	3±9	0
	-	20±27	0	4±10
Corophium volutator	3±8	25±42	31±55	0
	-	0	0	0
Corophium multisitosum	0	4±10	0	0
	-	0	0	0
Chironomidae undet.	0	0	13±21	0
	-	0	0	0
Theodoxus fluviatilis	75±52	92±61	125±90	54±58
	-	40±28,5	179±83	96±62
Hydrobia spp.	22±34	4±10	225±294	192±136
	-	55±48	838±436	425±257
Mya arenaria	33±40	46±46	47±74	0
	-	25±35	33±54	4±10
Total:	4756±5323 -	3833±3693 7190±3694	5013±5097 6979±3803	1067±7921 4092±2381

Role of *F. lumbricalis* in shaping of macrofauna community. Canonical correspondence analysis revealed the relationships between abundance of macrofauna species and four independent variables: biomass of two hosts (*F. lumbricalis* and *M. edulis*), filamentous macroalgae (*Ceramium tenuicorne*, *Polysiphonia fucoides* and *Cladophora rupestris*) and depth (Fig. 22). The results indicated that the first two axes explain 92% of the variation in four independent variables, which in turn were associated with 39% of the macrofauna abundance variation. All explanatory variables were statistically significant ($p< 0.05$), except for the biomass of filamentous macroalgae, which statistically significantly correlated ($r= 0.76$, $p< 0.0001$, $n= 46$) with biomass of *F. lumbricalis*. However, using each of the variables separately, the biomass of the filamentous macroalgae and *F. lumbricalis* were the most important, followed by depth and biomass of the blue mussels.

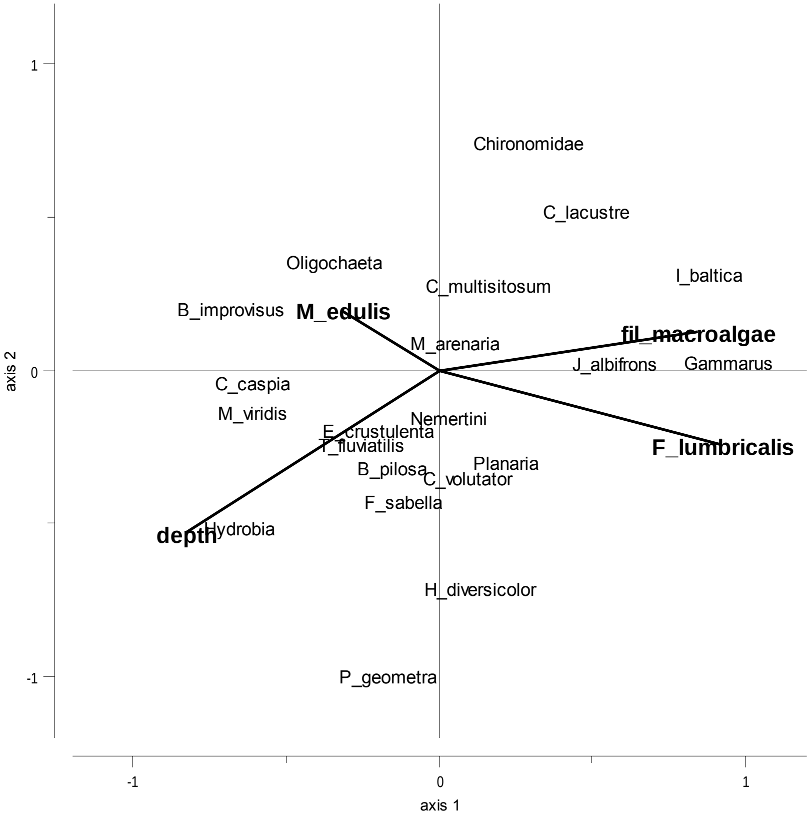

Figure 22. CCA biplot of abundance data of macrofauna species constrained to the gradients of depth, biomass of *M. edulis* (M_edulis), *F. lumbricalis* (F_lumbricalis) and filamentous macroalgae (fil_macroalgae) in the study area.

The biomass of filamentous macroalgae and *F. lumbricalis* negatively correlated with the depth: r= -0.49 and r= -0.34 respectively, p< 0.0001 and p< 0.05, n= 46. The crustaceans *Gammarus* spp., *Jaera albifrons* and *Idotea baltica* were abundant within dense cover of *F. lumbricalis* and filamentous macroalgae at small depths. On the other hand, *B. improvisus, Hydrobia* spp., *C. caspia, Marenzelleria neglecta* and *Oligochaeta* undet. were abundant on the mussels at greater depth (9 and 12 m). Relatively strong correlations (r= 0.67-0.91; p< 0.0001-0.01; n= 15) were found between the three macrofauna species (*Gammarus* spp., *J. albifrons* and *I. baltica*) and biomass of *F. lumbricalis* and filamentous macroalgae at 3-4 and 6 m depth (Fig. 23).

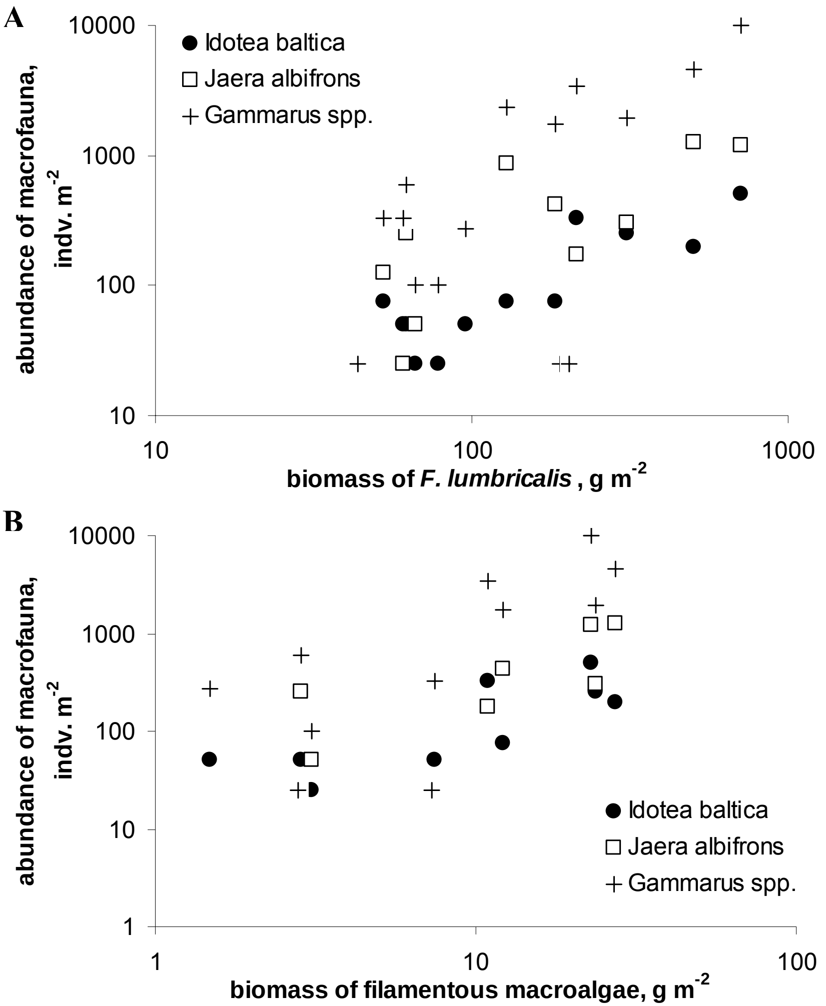

Figure 23. Relationships between the abundance of three macrofauna taxa (*Idotea baltica, Jaera albifrons* and *Gammarus* spp.) and biomass of *F. lumbricalis* (upper scatterplot) and filamentous macroalgae (lower scatterplot). The logarithmic scale used on the y and x axes.

Structure of epiphyte community. Both hosts marginally differed (Global R= 0.46, $p < 0.01$) in terms of macrophyte community. However, the more significant dissimilarity was found at 6 m depth (Global R= 0.63, $p < 0.01$), where biomass of *Ceramium tenuicorne* was higher on *F. lumbricalis* than on *M. edulis*. The biomass of epiphytes was very small on the blue mussels, less than 0.04 g m^2 (Table 15). The highest mean biomass on *F. lumbricalis* was found at 3-4 m depth, gradually decreasing along the depth gradient. Using underwater video materials it was found that the cover of mussels and filamentous red macroalgae (*C. tenuicorne* and *Polysiphonia fucoides*) significantly correlated with the cover of *F. lumbricalis:* respectively r= 0.57 and 0.53, $p < 0.0001$, n= 47 and 175.

Table 15. Mean biomass of macroalgae taxa within *F. lumbricalis* (first row) and *M. edulis* (second row) at different depths. The blue mussel colonies were absent (-) at 3-4 m depth.

Taxa of macroalgae	**Biomass of macroalgae (g m^{-2}) at different depths:**			
	3-4 m	**6 m**	**9 m**	**12 m**
Coccotylus truncatus	0	0	0.2±0.5	0
	-	0	0.04±0.1	0
Ceramium tenuicorne	7.0±6.0	4.7±8.3	0	0
	-	< 0.01	0	0
Polysiphonia fucoides	3.5±5.9	0.4±0.9	0	0
	-	< 0.01	0	0
Cladophora rupestris	0.3±0.6	0	< 0.01	< 0.01
	-	< 0.01	< 0.01	0
Total:	10.3±12.5 -	5.1±9.2 < 0.01	0.2±0.5 0.04±0.1	< 0.01 0

4.2.2. Role of *Furcellaria lumbricalis* in the carbon flow

Phytoplankton and macroalgae production was 13.4 g C m^{-2} $year^{-1}$ in the euphotic zone with stony bottom at the Lithuanian Baltic Sea coast (Fig. 24). Pelagic production made 6.9 g C m^{-2} from the total production, whereas production of annual and perennial benthic macroalgae was 0.5 and 3.8 g C m^{-2} respectively. *F. lumbricalis* comprised 3.4 g C m^{-2} from the total benthic production of macroalgae.

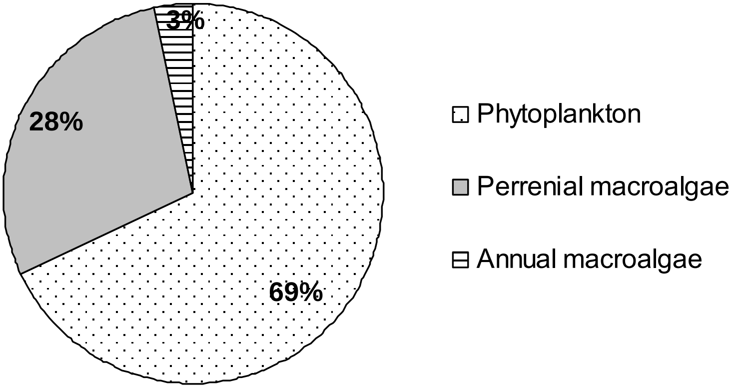

Figure 24. Relative primary production of different algae groups in the euphotic zone with stony bottom at the Lithuanian Baltic Sea coast.

The carbon flows to higher trophic levels could be roughly divided into pelagic and benthic fluxes. In the pelagic fluxes the carbon was channelled from phytoplankton to micro- and mesozooplankton, macrozooplankton and further to planktivorous fishes, which were preyed by piscivores fishes (Fig. 25). Benthic fluxes were based on detritus, which originates from decaying phytoplankton and phytobenthos. Detritus was mainly consumed by benthic suspension and deposit feeders, which were in turn consumed by benthivorous fish and birds.

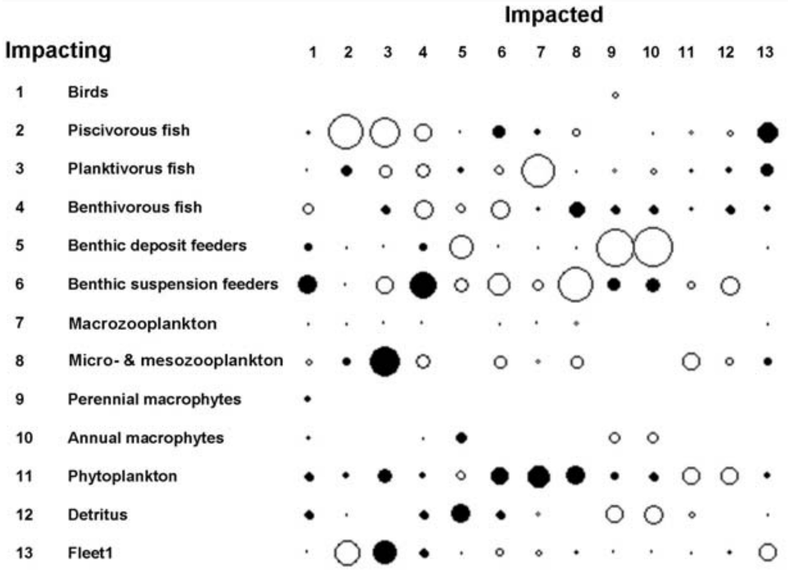

Figure 25. Mixed trophic impact of 12 functional groups and fleet in the euphotic zone with stony bottom off the Lithuanian Baltic Sea coast. An infinitesimal increase of any of the groups on the left is predicted to have positive (black circle) or negative trophic impacts (white circle) on the groups in the columns.

Calculated ecotrophic efficiency (EE) for each trophic group is given in Table 16. The highest ecotrophic efficiency (EE= 0.76) was estimated for the micro- and mesozooplankton, which indicated the significant consumption by macrozooplankton and planktivorous fish. The piscivores fishes were heavily exploited by fishing fleets (EE= 0.72), whereas the consumption of birds and *F. lumbricalis* (perennial macrophyte) were one of the lowest in the ecosystem (EE< 0.03).

Table 16. Estimated ecotrophic efficiency (EE) in the ECOPATH model for the study area.

Fuctional groups	EE
Birds	0.01
Piscivorous fish	0.72
Planktivorous fish	0.64
Benthivorous fish	0.63
Benthic deposit feeders	0.58
Benthic suspension feeders	0.10
Macrozooplankton	0.58
Micro- , mesozooplankton	0.76
Perennial macrophytes	0.02
Annual macrophytes	0.35
Phytoplankton	0.46
Detritus	0.23

5. DISCUTION

5.1. Physical and biological factors shaping distribution patters of *Furcellaria lumbricalis* at different spatial scales off the exposed Baltic Sea coast

Phytobenthos distribution in the Baltic Sea is mainly constrained by physical rather than by biological factors (Kautsky & van der Maarel, 1990; Isæus & Lindblad, 2003; Sandman et al., 2008). Environmental characteristics such as wave exposure, water salinity, transparency, sediment cover, nutrients, depth, type of substrate and scouring by ice are considered as key factors (Mäkinen et al., 1988; Wallentinus, 1991; Kiirikki, 1996; Eriksson & Bergström, 2005). However, their impact on distribution of macroalgae varied depending on spatial scale and species traits (Kautsky, 1995; Middelboe & Sand-Jensen, 2004; Torn et al., 2006; Larsen & Sand-Jensen, 2005).

In this study, the microscale (10 cm^2–100 m^2) analysis explains patterns of the *F. lumbricalis* distribution within a benthic habitat (Fig. 26). Frequency of stormy winds and mobility of substrate and surrounding bottom are the factors playing the major role at this spatial scale. Their effect changes with the depth. The results showed that surfaces of substrate oriented at directions of more frequent storms are less covered by the alga in comparison to surfaces exposed to storms of lower frequency. Since strong stormy winds occur basically from all directions, frequency of storms rather than a single storm event is important in shaping the species distribution on the substrate. Additionally, position of *F. lumbricalis* on substrate is also adjusted by type of the surrounding bottom. Mobile sediments around the substrate reduce the potential surface for growth of the species by scouring and/or preventing colonization. Therefore the higher cover of alga occurs on substrates situated on the seabed of lower mobility. The role of surrounding sediments seems to be also dependent on frequency of storms.

The results of study at the mesoscale (1000 m^2–10 km^2) describe patterns of the *F. lumbricalis* distribution within the coastal zone, i.e. between habitats, and reveal the importance of other physical factors, such as: availability of suitable substrates and bathymetry in general, water tubidity/salinity related to the outflow of Curonian Lagoon and wave exposure linked to the geomorphology of the seabed (Fig. 26). Vast areas of the SE Baltic coastal zone are not suitable for growth of *F. lumbricalis* being covered by sands and gravel, movable by waves and near-shore currents. The stony bottoms provide the appropriate stable substrate, though only within the sufficient light zone down to 15 m (Olenin & Labanauskas 1994; Labanauskas, 1998; Bučas et al., 2007; Müller-Karulis et al., 2007; Daunys et al., 2008; present study). However, *F. lumbricalis* was not distributed evenly even within these areas, occurring only in a half of the stony bottoms potentially suitable for its growth. The gradients of freshwater and turbid Curonian Lagoon waters and wave exposure could be the main factors restricting available area for the species distribution (Fig. 26). According to statistical relationships between the red alga occurrence and distance from the mouth of Curonian Lagoon as well as distance to 20 m isobath, the water transparency/salinity and wave climate were the most suitable in the coastal area off Palanga, where the densest overgrowths of *F. lumbricalis* were found in this study and in previous investigations (Blinova & Tolstikova, 1972).

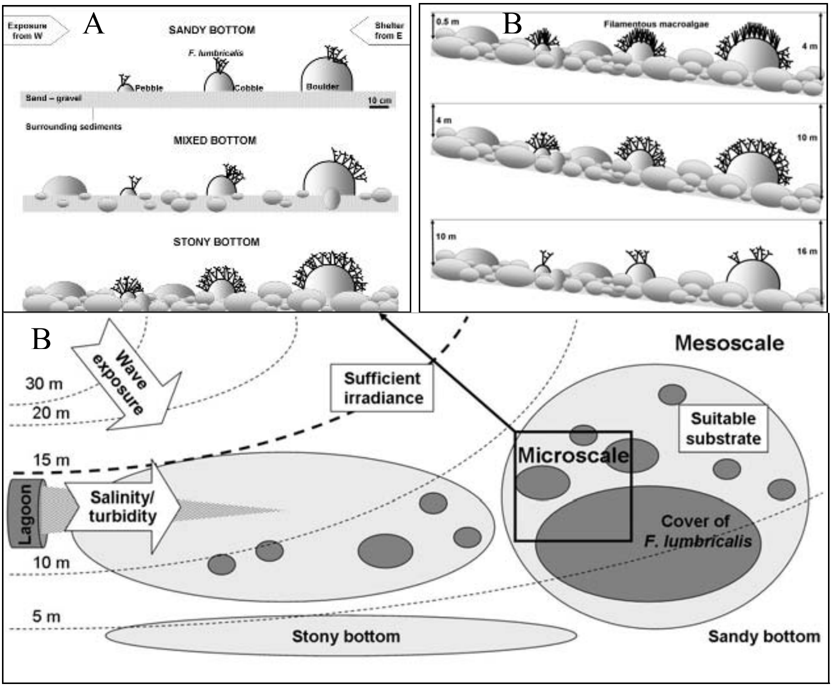

Figure 26. Schematic representation of the environmental factors shaping distribution of the red alga *F. lumbricalis* at micro- and mesoscales. A – microscale; B – mesocale, changes in along the vertical gradient; C – mesocale, changes the coastal zone. Explanation in text.

The most important factor limiting the attached form of *F. lumbricalis* distribution within the spatial micro- and mesoscales is presence of suitable type of substrate (Fig. 27), such as cobbles, small and large boulders in the conditions of exposed SE Baltic coast (Bučas et al., 2007; Blinova & Tolstikova, 1972). The importance of this factor extends to the higher spatial scale (Bird et al., 1991), however other physical factors (e.g. irradiance, salinity) may also become crucial for the distribution of the red alga.

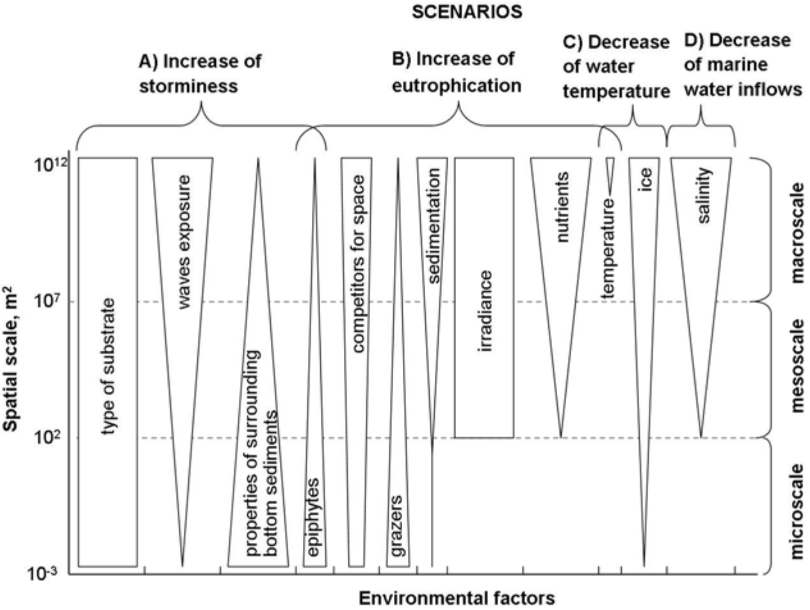

Figure 27. Environmental factors shaping distribution of the red alga *F. lumbricalis* at different spatial scales (micro-, meso- and macroscales) and according to four scenarios (A, B, C and D). Relative impact of factors correlates with width of column.

Generally, irradiance is considered as one of the most important factors constraining depth distribution of macroalgae at the mesoscale (Snoeijs, 1999). According to Kiirikki (1996), Andrulewicz et al. (2004), Eriksson & Bergstrom (2005), Bučas et al. (2007) *F. lumbricalis* is one of the deepest growing perennial macroalgae species in the Baltic Proper, including exposed SE Baltic coast. Maximum depth distribution of the species (15 m) in the Lithuanian coastal waters corresponds well to the lower limit of the euphotic depth calculated from the Secchi depth measurements during this study (see section 2.1.3). The sharp decrease of *F. lumbricalis* cover is observed below 10 m depth and the thalli of the species usually are growing on the upper parts of substrates, presumably due to reduced light climate (Bučas et al., 2007). In this study, evident influence of irradiance attenuation due to the northward outflow of less saline and turbid waters of the Curonian lagoon was found at the mesoscale (Fig. 16). The closer the stony bottoms were to the outlet of the Curonian Lagoon, the less was the maximum depth limit of the red alga and the smaller was the area occupied by the species. However, it remains unclear, whether the lower salinity or increased turbidity is the more important for *F. lumbricalis* distribution, since both factors highly correlate with a plume of the Lagoon outflow.

Distribution pattern of *F. lumbricalis* at the mesoscale, beyond the zone of the direct influence of the Curonian Lagoon, depends also on the direction and intensity of wave exposure. Due to peculiarities of the seabed relief the wave climate is the most suitable in the coastal area off Palanga, where the densest overgrowths of the species were found. The influence of the wave exposure on the distribution of *F. lumbricalis* was found at the coast of Finland (Kiirikki, 1996), Estonia (Martin, 2000) and Sweden (Sandman et al., 2008). However, in contrast to the western and northern Baltic coasts, where the wave exposure effect is constrained mainly by complex coastlines and islands, at the SE Baltic coast, which is free of sheltered areas, the seabed topography (e.g. steepness of the coastal slope) plays the fundamental role (Müller-Karulis et al., 2007) in shaping the wave exposure at the mesoscale (Fig. 16). On the other hand, the influence of wave effect was found also at the microscale, where the western direction stormy waves dislodged and abraded the red alga on the exposed sides of the substrates (Bučas et al., 2007).

The properties of surrounding bottom sediments were seldom addressed in the studies of macroalage distributions, however in this study it was found that they shape the distribution of *F. lumbricalis* mainly at the microscale (Fig. 27). The mobile surrounding sediments (sand and gravel) essentially reduce the surface suitable for its growth by scouring and/or smothering and preventing colonization (Bučas et al., 2007).

At the Baltic scale, the number of red macroalgae species is reduced followed the step wise decline of salinity from the waters of Kattegat to the Bothnia Bay (Wallentinus, 1991). Low salinity (ca <3 PSU) prevents distribution of the red alga *F. lumbricalis* in the Bothnian Sea and Gulf of Finland (Kostamo & Mäkinen, 2006). At the SE Baltic coastal zone, such critical salinity limit may be found only in the closest vicinity to the outlet of the Curonian Lagoon due to diluting effect of its waters (Daunys et al., 2007).

Other physicochemical factors such as temperature, sedimentation and nutrients are also important for the distribution of phytobenthos (Wallentinus, 1991; Kautsky, 1995; Snoeijs, 1999). However these factors seldom change at a small spatial scale (Fig. 16). *F. lumbricalis* is tolerant to wide range of temperature (0-30 °C) (Bird et al., 1991) and sedimentation (Eriksson & Johansson, 2005). On the other hand, it has one of the lowest nutrient uptake rates among species of macroalgae (Bird et al., 1991). However, concentration of nutrients did not show particular gradient across the study area, therefore, their influence on *F. lumbricalis* distribution was considered negligible.

Scouring by ice generally does not take place in this region of the Baltic Sea and is not important for *F. lumbricalis* distribution (Fig. 27). However, at the Finish coast the ice scraping may influence the lower limit of *Fucus vesiculosus* belt down to 6 m depth (Kiirikki, 1996). Therefore, the impact of ice on the red alga distribution might possibly be more evident in the northern Baltic Sea waters.

Generally, the number of biological interactions among benthic species in the brackish Baltic Proper considered to be smaller than in fully marine waters due to much lower species richness (Kautsky et al., 1986). Biological factors (e.g. competitors for space, epibionts, grazing etc.) were not directly assessed in this study, however they were addressed using literature data accomplished with underwater observations in situ. Potential competitors for space in the SE Baltic Sea included filamentous algae, mussels, bryozoans, hydrozoans and barnacles (Bučas et al., 2007). Generally, the filamentous macroalgae dominated both on mobile and stable substrates, where the *F. lumbricalis* took the lower vertical surfaces of substrate, especially within the upper, 1-4 m depth range (author, personal observation). According to Olenin et al. (2003) the colonies of mussels and barnacles on vertical surfaces of boulders and cobbles were denser than on the horizontal surfaces on the upper part of these substrates. These observed distribution patterns imply possible competition for space on the uppermost surfaces of substrate between *F. lumbricalis* and other sessile organisms: filamentous macroalgae, barnacles and mussels. Bryozoans and hydrozoans were infrequent and unlikely to have impact. Validation of this hypothesis in the future will require complex and comparatively longstanding underwater experiments.

In the northern part of the Baltic Sea epibionts such as filamentous macroalgae limited growth of *F. vesiculosus* by shading (Kangas et al., 1982). In the SE Baltic, however, the greatest abundance of epibionts was found on the densest overgrowths of *F. lumbricalis*, indicating negligible role of shading.

Experimental studies with macroinvertebrate grazer, the isopod *Idotea baltica*, showed that this species uses *F. lumbricalis* mostly for a shelter rather than as a food source (Kotta et al., 2000; Orav-Kotta & Kotta, 2004) The significant effect of *I. baltica* on *F. vesiculosus* was found at much higher abundance of isopod (1073±1517 ind. per 100 g wet weight of algae) (Kangas et al., 1982) than in our study area (5±5 ind. per 100 g wet weight of *F. lumbricalis*). These observations allow a conclusion of a relatively low grazing effect on the red alga in the SE Baltic (Fig. 27).

Physical and biological factors, constraining *F. lumbricalis* distribution, could be classified in few groups according to several scenarios of environmental change (Fig. 27). For example, the negative impact of mobility of substrate and surrounding bottom sediments, wave exposure and cover of epiphytes on the red alga may enhance in case of increase in storminess. On the other hand, eutrophication processes may lead to increase negative effect on *F. lumbricalis* by lowering irradiance, increasing cover of competitors of space (e.g. filamentous annual macroalgae), epiphytes, grazers and sedimentation. The destructive effect of ice on the species distribution may increase in case of general decrease of temperature over the whole Baltic Sea region. Salinity gradient is one of the main factors regulating distribution of marine and freshwater species in the brackish Baltic Sea by the inflows of marine waters through the narrow Danish straits (Walentinus, 1991; Snoeijs, 1999). Thus the salinity changes may also cause distribution of *F. lumbricalis*. According to prognosis of climate change, where the temperature of surface water is expected to increase in the near future (BACC author group, 2008). To this related the increase of extreme events (e.g. storminess) and eutrophication are the most likely scenarious at the exposed SE Baltic coast, resulting in degradation of the red alga habitat.

5.2. Historical changes in distribution of *Furcellaria lumbricalis* stock at the Lithuanian coast and in the entire Baltic Sea

The vegetation area of *F. lumbricalis* at the Lithuanian coast is isolated from other colonies of this alga in the Baltic Sea by large fields of mobile sand or deep waters. The nearest *F. lumbricalis* vegetation areas are situated within ca 25 km to the north at the Latvian coast (Müller-Karulis et al., 2007), while to the south they are within ca 100 km at the coast of Sambian Peninsula, Kaliningrad/Russia (Blinova, 2007). The historical data concerning changes in the stock and distribution of *F. lumbricalis* are known in the waters of Germany (Messner & Von Oertzen, 1991; HELCOM, 1993), Poland (Kruk-Dowgiallo, 1991), Latvia (Blinova & Tolstikova, 1972), Sweden (Eriksson et al., 1998) and Estonia (Martin, 2000), therefore, they could be used to compare with the recent results from the Lithuanian coast (see section 2.2.7).

The minimum depth of *F. lumbricalis* in 1956 was indicated as 5 m (Kireeva, 1960b) and 3 m in late 1960s (Blinova & Tolstikova, 1972) and in early 1990s (Olenin & Labanauskas, 1994), while in the present study it was found in more shallow location, 1 m (Table 17). One reason for that may be much greater number of sampling sites visited during the present study. On the other hand, in the 1950s the sampling was performed using a dredge, which is not suitable for collecting of the red alga at lower depths, because, according to our observations, here it growths on the lower sides of substrates (i.e. is unreachable for the dredge).

The greatest maximum depth (19 m) of *F. lumbricalis* was recorded in 1956 (Kireeva, 1960b). Bearing in mind their sampling method, it may be concluded that the red alga had to be abundant enough to be sampled by the dredge. According to our observations, at the greater depths (see section 4.1.2) only individual talli of *F. lumbricalis* may be found which grow on the uppermost side of the substrate. Therefore, this historical record may be considered as the reliable evidence and can be used to determine the reference conditions in pre-eutrophication phase (see section 5.3). In later years, the maximum depth decreased to 14-16 m but was rather constant from late 1960s till the recent years. This situation may be regarded as state of *F. lumbricalis* under contemporary eutrophication phase. Also, maximum biomass in 1950s was the highest, which indicate that at that time the stock of *F. lumbricalis*, most probably, was in the optimal conditions versus 1960s and 2000s.

The recent total *F. lumbricalis* area off the Lithuania coast was similar to the late 1960s (Blinova & Tolstikova, 1972); while the area reported in early-mid 1990s (Olenin & Labanauskas, 1994; Maksimov et al., 1996) was 2.3 times smaller (Table 17). Pronounced changes of maximum and total biomass and species cover were recorded in late 1970s and 1980s (Korolev et al., 1993). However, these results should be interpreted carefully due to serious methodological drawbacks of this paper (see section 2.2.7 for details).

Table 17. Long term changes in *F. lumbricalis* area, stock, minimum and maximum depth off the Baltic coast of Lithuania. "-" data not given in the refferences.

	1956	1968-1969	1976	1986	1993-1994	2003-2008
Minimum depth, m	5	3	-	-	3	1
Maximum depth, m	19	14	-	-	16	15
Maximum biomass, g m^{-2}	3260	2000	3000	400	-	2000
Total area, km^2	-	21*	-	-	9	21±9*
Total biomass, 10^3 t	-	7.0*	25.0	0.3	-	7.5±3.7*
Maximum cover, %	-	100	100	30	90	100
Reference	Kireeva, 1960b	Blinova & Tolstikova, 1972	Korolev et al., 1993		Olenin & Labanauskas, 1994; Labanauskas, 2000	This study

* Estimated using data on the species cover > 5%.

In each of these studies (Table 17) the cover and area of *F. lumbricalis* at the Lithuanian Baltic Sea coast were estimated by different methods. In order to make possible historical comparisons, the Natural Neighbor interpolation was used for the datasets with known locations of transects. The results of the interpolation are given in Table 18 and Figure 28.

Table 18. Estimates of *F. lumbricalis* interplotated area of different species cover at the Lithusnian Baltic Sea coast during 1968-1969 (Blinova & Tolstikova, 1972), 1993-1996 (Olenin & Labanauskas, 1994; Maksimov et al., 1996; S. Olenin, unbubl.) and 2003-2008 (this study).

Cover of *F. lumbricalis*	**1968-1969**		**1993-1996**		**2003-2008**	
	km^2	**%**	**km^2**	**%**	**km^2**	**%**
1-10%	26.5	63.0	20.5	75.8	22.7	73.0
11-50%	14.6	34.0	6.6	24.0	7.2	23.0
51-100%	1.3	3.0	0.1	0.2	1.2	4.0
Total:	42.3	100	27.1	100	31.2	100

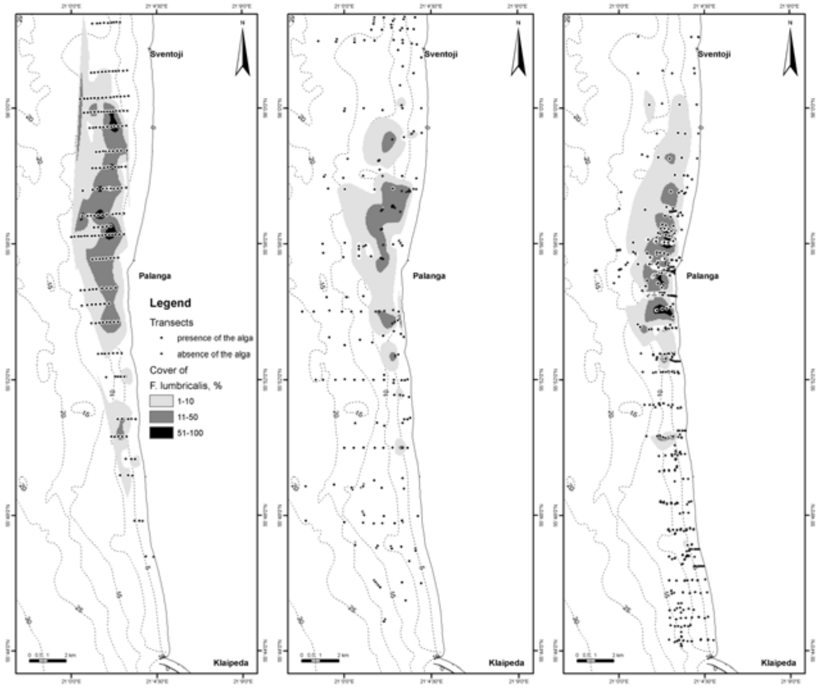

Figure 28. Dstribution of *F. lumbricalis* occurrence (estimated within transects), cover and area (calculated using Natural Neighbor interpolation) at the Lithuanian Baltic Sea coast during 1968-1969 (left) according to Blinova & Tolstikova (1972), 1993-1996 (middle) according to Olenin & Labanauskas (1994), Maksimov et al. (1996), S. Olenin, unbubl. and 2003-2008 (right) according to this study.

First of all, the difference was found in the total area estimation for 1968-1969: according to Blinova & Tolstikova (1972) it was 20.8 km^2 (unfortunately the authors did not explain how they performed the estimation of the area), while our interpolation area was estimated as twice as larger, 42 km^2. Similarly the area given for 1990s (Olenin & Labanauskas, 1994) was three times smaller than the interpolated area: 9 versus 27 km^2. In 1993-1994, the area of the red alga was calculated manually by interpolation of field observation data, where *F. lumbricalis* was found, to the suitable substrates according to the geological map (S. Olenin, pers. comm.). In our interpolation we used additional underwater video and SCUBA diving data obtained in episodic surveys in 1996 (S. Olenin, unbubl.). Nevertheless, the red alga area could be underestimated in 1993-1994 due to relatively small number of transects within the optimal depth of *F. lumbricalis* (see section 2.2.7).

In the recent study, where the number of sampling sites was several times greater than in any previous investigation, the total area was estimated as 31 km^2. A comparison of the estimated distribution areas in 1960s versus 2000s, shows that the red alga area reduced at the southern edge (close to the Curonian Lagoon outlet) and, although in less extent, at the northern edge. Also, area of *F. lumbricalis* in 2000s became more fragmented and the region of the dense alga cover (>11-50%, dark grey area at Fig. 28) has reduced in comparison to the 1960s. The difference is even more evident while comparing the late 1960s situation with 1990s (Table 18). Thus, the results obtained in 2000s indicate recovery signs of the species area and standing stock after historically the smallest documented *F. lumbricalis* area in late 1990s.

The reduction of *F. lumbricalis* stock in the Lithuanian coast during late 1980s–1990s was related to the catastrophic crude oil spill from the tanker „Globe Assimi” in 1981 (Korolev et al., 1993). Regrettably, the survey was performed ca 5 years after the accident, moreover, the authors did not provide any habitat map, coordinates of the transects or the number of samples taken. Therefore, this paper provides no documented evidence for such conclusion. Moreover, the reduction of the red alga vegetation area was not recorded in the Palanga area, where the most dense and large colonies have been found both historically and recently (Blinova & Tolstikova, 1972; Olenin & Labanauskas, 1994; this study). On the other hand, it was in the Palanga area where one of the largest patches of crude oil was cast ashore (Olenin, 1990; S. Olenin, pers. comm.). So far there are no experimental or documented field studies showing effect of the crude oil on *F. lumbricalis,* therefore the presumable effect of the "Globe Assimi" oil spill remains unclear.

In general, reduction of vegetation areas and decline of the maximum depth limit on the exposed coast may be interpreted as the influence of both, storms and eutrophication. It was noticed that when the Beaufort number exceeded 4-5, large amounts of *F. lumbricalis* were cast-ashore (Kireeva, 1960a; Orlov, 1965; Blinova, 1971). Moreover, after the 1969 hurricane the amount of cast-ashore red alga 3.5 times exceeded its estimated standing stock at the Lithuanian coast; this was explained by transport of the dislodged *F. lumbricalis* from the adjacent vegetated areas at the coast of Latvia (Blinova, 1971). The decline period of *F. lumbricalis* on the Baltic coast of Lithuania was consistent to the period of maximum increase of storminess recorded in the whole Baltic Sea during the late 1980s and early 1990s over the last five decades (Alexandersson et al., 2000; The BACC author group, 2008). According to Kirlys (1990) and Boldyrev et al. (1990) the strongest and the longest duration storm was reccorded along the south-eastern Baltic coast in 1983.

On the other hand, eutrophication was considered as the main factors causing changes in decline of attached and/or loose lying form *F. lumbricalis* from 1930-1960s till 1980-1990s in different sub-regions of the Baltic Sea (Table 19). Eutrophication processes negatively acted through decreased light penetration (according to the Secchi depth) and stronger competition with filamentous fast-growing macroalgae (Rönnberg, 2001) resulting the decline of *F. lumbricalis* maximum depth limits and area. Enhanced negative effect of eutrophication on the red alga was in relatively sheltered coastal areas (e.g. gulf, fjord, bay, etc.) rather exposed: e.g. *F. lumbricalis* almost disappeared in the Bay of Greifswald since late 1950s (Messner & Von Oertzen, 1991), whereas relatively lower decline of the species stock and depth distribution were found on the exposed coast of Lithuania during late 1950s and 1960s (Kireeva, 1960b; Blinova & Tolstikova, 1972).

Table 19. Long-term changes of attached and/or loose lying form *F. lumbricalis* in the sub-regions of the Baltic Sea: Skagerrak (Eriksson et al., 1998; Johansson et al., 1998), Kattegat (HELCOM, 1993), Southern Baltic Proper (Messner & Von Oertzen, 1991), Gulf of Gdansk (Plinski, 1982; Kruk-Dowgiallo, 1991), South-eastern Baltic Proper (Kireeva, 1960; Blinova & Tolstikova, 1972;. Korolev et al., 1993, Olenin & Labanauskas, 1994; Bučas et al., 2009), Gulf of Riga (Kukk & Martin, 1992; Kukk, 1993) and Gulf of Finland (Rönnberg & Bonsdorff, 2004) The species decline period is determined by the time interval between the reference conditions and the last record of *F. lumbricalis* decline. Presence and absence of change in particular parameter is indicated by (+) and (-) respectively; no data (?).

Sub-region of the Baltic Sea	Skagerrak	Kattegat	Southern Baltic Proper	Gulf of Gdansk	South-eastern Baltic Proper		Gulf of Riga	Gulf of Finland
Study area	Gulmar Fjord	Kiel Bay	Bay of Greifswald	Puck lagoon	Exposed coast of Latvia	Exposed coast of Lithuania	Pärnu Bay, Ragaciems, Salacgriva, Skulte, Tuja	East of Helsinki
Decline period of *F. lumbricalis* area or cover	1940s-1990s or 1960s-1990s	1960s-1980s	1930s-1980s	1960s-1980s	1980s-1990s	1950s-1990s	1960s-1990s or 1970s-1990s	1980s-1990s
Restoration period of *F. lumbricalis* area or cover	?	?	?	?	1990s-2000s	Since 2000s	?	?
Decline of the species maximum depth	+	+	+	?	-	+ and – since 1960s	?	?
Decline of secchi depth	+	?	+	?	?	+ and – since 1980s	?	+
Increase of abundance of filamentous annual macroalgae	+	?	-	+	?	?	+	+

Negative effect of eutrophication on key perennial macrophytes (*Fucus vesiculosus* and *Zostera marina*) was also recorded in the

Baltic Sea, especially in relatively sheltered coastal areas during the same period of decline of *F. lumbricalis* distribution (HELCOM, 1993; Rönnberg & Bonsdorff, 2004).

Contrarily, to the other sub-regions of the Baltic Sea the maximum depth limit of *F. lumbricalis* at the Lithuanian coast (14–16 m) did not differ significantly since late 1960s (Table 19), meaning that there was no critical decline in the euphotic zone. This was in accordance with the long-term data of Secchi depth in the coastal area of Lithuania (Figure 29). Moreover, signs of restoration of the red alga area and stock were determined off the exposed coast of Latvia and Lithuania since 1990s and 2000s respectively. According to H. Kausky (pers. comm.) the regeneration of the species abundance was also recorded in the coastal waters of the western Baltic Proper (Askö area) during the recent decades. These positive changes in *F. lumbricalis* area might be related to decrease of storminess (Alexandersson et al., 2000; The BACC Author Team, 2008) and marginal increase in the transperancy of coastal waters (Figure 27).

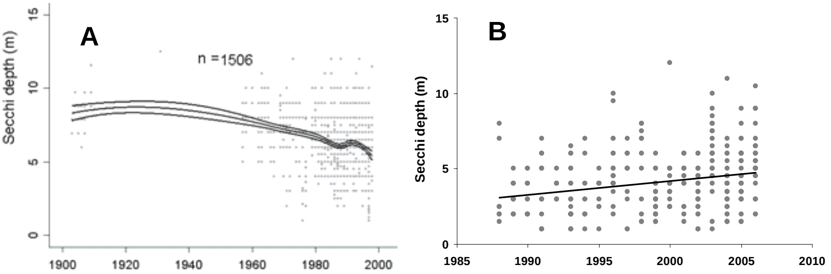

Figure 29. Long-term data of Secchi depth in the south-eastern Baltic Proper: A-offshore and coastal area of Lithuania and Poland during 1903-2004 (Laamanen et al., 2004), B-coastal area of Lithuania during 1988-2006 (unpublished data of Center of Marine Research).

The comparative analysis of historical and recent data showed that there was a gradual decline in the area of *F. lumbricalis* since 1950s, which reached its greatest extent in 1990s (probably, it happened already in 1980s), while in 2000s it converted to a restoration phase.

It is obvious that the long-term changes of *F. lumbricalis* at the exposed coast differed from the relatively sheltered waters in other Baltic sub-regions (especially during the last three decades). The increased storminess and eutrophication, most likely, are the main factors that have caused decrease of the species habitat at the Lithuanian coast. Eutrophication could add to impoverishment of state of the red alga due synergetic effect of reduced water transparency, which “forces” *F. lumbricalis* towards the smaller depths and the increased wave effect which destructively affects the algal overgrowths.

5.3. Use of depth distribution of *Furcellaria lumbricalis* as possible ecological quality indicator in the study area

At the Lithuanian coast of the Baltic Sea, *F. lumbricalis* is the only macrophytobenthos species for which the historical record dates back to the pre-eutrophication time (Kireeva, 1960a,b; Blinova & Tolstikova, 1972). In this study, the water quality assessment was based on comparison of historical data with patterns of recent vertical distribution of *F. lumbricalis* at the Lithuanian coast (Table 20). Two parameters were defined: 1) the maximum depth limit of the red alga and, 2) the maximum depth of the dense overgrowths (see section 4.1.3). The overgrowths were chosen because of their important habitat forming function (see section 5.4). Also, the peculiarities of the Lithuanian coastal zone were taken into account: the water quality criteria based on *F. lumbricalis* were assessed separately for the coastal and transitional (plume of Curonian Lagoon) waters. According to the WFD suggested procedure for establishment of the water quality classes we used historical data, modelling approach and expert judgement (Wallin et al., 2003).

In the coastal waters the reference conditions are defined according to the maximum depth records of *F. lumbricalis* in late 1950s, when the species individuals were found at 19 m depth (Kireeva, 1960b). Although they used dredging to determine the lower and upper depth limits of *F. lumbricalis*, the data is considered as reliable since several replicates were made at each station. The maximum depth of the species overgrowths was at 11 m depth.

Good status is defined by the maximum depth records of *F. lumbricalis* specimen between 15 and 19 m. The 15 m depth is chosen because, according to historical and recent study data, this was an approximate depth limit during the recent four decades (see section 5.2). In these conditions, the maximum depth of the overgrowths is found at 9-10 m.

Moderate status is defined by the maximum depth records of *F. lumbricalis* individuals within the 9-15 m range following the assumption that such decline would result in the subsequent reduction of the most valuable overgrowths at lower depths (4-8 m).

Poor status is defined by the maximum depth limit of the red alga specimen within the range of 3-9 m. It is highly unlikely that the overgrowths would survive in such conditions at lower depths (< 4 m). In fact, *F. lumbricalis* habitat would be still present, however it would degraded and would not perform the habitat forming function.

Bad status is defined by the maximum depth limit at less than 3 m. This situation is regarded as a very high risk of *F. lumbricalis* extinction at the Lithuanian coast. At smaller depths, the strong effect of braking waves and shortage of suitable substrates would prevent settlement of the red alga.

Classification of water quality according to maximum depth of *F. lumbricalis* in the transitional waters (Table 20) followed the same principle as those used in the coastal waters. Generally, the maximum depth limits of the species were set lower (ca 2 m) in the transitional than in the coastal waters, since the red alga was found shallower in the transitional waters, most likely, due to reduced water transparency (see section 5.1).

Table 20. Suggested description of water quality of transitional (plume of the Curonian lagoon in the Baltic Sea) and coastal water bodies according to the maximum depth limit of the red algae *F. lumbricalis* individuals and overgrowths.

Water quality status	**maximum depth limit of *F. lumbricalis*, m**				**Description**
	individuals		**Overgrowths**		
	transitional	**coastal**	**transitional**	**Coastal**	
Reference (very good)	≥17	≥19	≥9	≥11	The maximum depth limit according to historical data (pre-eutrophication) time
Good	≥13 & <17	≥15 & <19	≥7 & <9	≥9 & <11	Recent depth limit which did not change significantly since 1968
Moderate	≥7 & <13	≥9 & <15	≥4 & <7	≥4 & <9	decline in the most valuable overgrowths
Poor	≥1 & <7	≥3 & <9	<4	<4	Loss of the most valuable overgrowths
Bad	<1	<3	-	-	Loss of the red alga

5.4. *Furcellaria lumbricalis* as ecosystem engineering species

In the Baltic Sea, perennial brown alga bladder wrack *Fucus vesiculosus* is considered one of the most important habitat-forming macroalgae species (Haage, 1975; Kautsky, 1989; Råberg & Kautsky, 2007). Relatively large number (up to 30) of macrofauna and macroalgae species is found in the bladder wrack beds. Maximum cover of brown alga usually ends up at 4 m depth at sheltered coasts. Bladder wrack bed becomes rare deeper and at exposed coast and usually is replaced by red alga belt, where *F. lumbricalis* is the dominant species in general (Kautsky, 1995). In the coastal waters of Trosa archipelago, below the *F. vesiculosus* belt (at 3 and 9 m depth), the mean number of macrofauna taxa (19±1) within the red alga (according to Kautsky, 1974) is significantly higher than within the thalli of *F. vesiculosus* (11±1) at 3, 4 and 6 m depth (according to Haage, 1975). Similarly, on the exposed coast of Lithuania, where the bladder wrack is absent, the mean number of macrofauna taxa is 17±2 within the thalli of *F. lumbricalis*. This shows that the red alga may change the role of habitat-forming species such as bladder wrack at the exposed Baltic Sea coast.

At the exposed Lithuanian coast two perennial benthic species, the blue mussels *Mytilus edulis* and red alga *F. lumbricalis* dominate on the stony bottom (Olenin & Daunys, 2004). They both form three-dimensional structures on substrates, which might be important for the bentho-pelgic organisms living within the hosts in unfavorable environment of exposed coast. In general, both hosts contained a similar number of taxa and composition of benthic fauna and flora. However, differences were found within different depths. At shallow places *F. lumbricalis* provided substrate for epiphytes such as filamentous red macroalgae (*Ceramium tenuicorne*, *Polysiphonia fucoides*) and crustaceans (*Gammarus* spp., *Jaera albifrons and Idotea baltica*). These crustaceans could possibly feed on filamentous macroalgae, whereas thalli of *F. lumbricalis* mainly were used as substrate (Kotta et al., 2000). According to the water flow experiments through the algal thalli of similar structure as for *F. lumbricalis*, it was found that the thalli may reduce the flow velocity in half (Hurd & Stevens, 1997). This suggests that the thalli of *F. lumbricalis* may protect the associated species from the strong water movement, especially at the exposed coast. The cover of epiphytic macroalgae and abundance of crustaceans significantly decreased at greater depth, most likely due to reduced irradiance. Only 5 macrofauna species were found within *F. lumbricalis* at 12 m depth. In contrast, the role of the blue mussels as engineering species, increased with depth, since *M. edulis* generally formed dense clumps on hard substrates between 10 to 30 m depth (Jarvekiulg, 1979; Snoeijs, 1999; Olenin & Daunys, 2004). The barnacles (*Balanus improvisus*) and hydrozoans (*Cardylophora caspia*) were positively associated with the biomass of the blue mussels and depth.

Contribution of *F. lumbricalis* in the primary production of phytoplankton and macroalgae (PPPM) depended on the spatial scale. The species importance was insignificant (< 1%) at the scale of the Lithuanian Exclusive Economic zone of the Baltic Sea (ca 7000 km^2). However, at the scale of the Lithuanian coastal sublittoral stony bottom area (ca 180 km^2) this species contributed up to 28% of the PPPM. This corresponds well with estimated PPPM of macrophytobenthos (12-50%) along the western Baltic Sea Proper up to 25 m depth (Kautsky & Kautsky, 1993). At the Baltic Sea scale only ca 25% of total area is above 20 m depth (euphotic depth) suitable for the primary benthic production (Wallentinus, 1991).

The results of ECOPATH model showed insignificant direct impact of *F. lumbricalis* on trophic transfers in the ecosystem of coastal waters within sublittoral stony bottom area. Comparative trophic flow and network analysis in the five coastal Baltic Sea ecosystems (Tomczak et al., 2009) suggested that biomass of macrophytes was mainly transformed into detritus. Kotta et al. (2000) found that mesoherbivores (*Idothea baltica*) mostly grazed filamentous macroalgae than *F. lumbricalis,* indicating a low transport of carbon into higher trophic levels of ecosystem. *F. lumbricalis* had also significantly low grazing pressure based on the abundance of *I. baltica* on the red alga (Olenin et al., 2003; Bučas et al., 2007) compared to the bladder wrack *F. vesiculosus* (Kangas et al., 1982). The red alga was found in the diet of wintering birds, however it comprised very small amount, most likely the branches of the alga accidently were caught while feeding on the macrofauna within the overgrowths of *F. lumbricalis* (Žydelis, 2002).

The large amount of *F. lumbricalis* was usually cast ashore after storm events, whereas after some time it was washed out back into the Sea (Orlov, 1965; Author, pers. observation). This extra algal input to detritus in turn might be used by sublittoral deposit feeders.

5.5. Gaps and future perspectives

Most of the obtained recent results in the coastal area of Lithuania could be applicable in the whole south-eastern Baltic Sea coast, due to similar physical environmental conditions and benthic assemblages (Labanauskas, 1998). However, some care should be taken, when extraplating the effects of physical factors constraining *F. lumbricalis* distribution at the mesoscale. For example, the distance to the waters of Curonian Lagoon should not influence the occurrence and maximum depth limit of the red alga in the coast of Latvia or Kaliningrad, whereas the distance to other biger outflows of freshwater sources (Aistmares, Lielupe, etc.) could be significant factor for the secies distribution.

The precision of underwater mapping methods remains the main problem in the field work. The accuracy of the Global Positioning System (GPS) used in the SCUBA diving and underwater video surveys was ca 20 m, which is quite low, since the variation of *F. lumbricalis* cover may vary up to 100% at this scale. On the other hand the cover of the red alga is closely related to the occurrence of hard and relatively stable substrate, which is also patchy within meters, however the bottom sediment types can be precisely scanned using advanced remote systems such as side scan sonar (Davies et al., 2001). The obtained continues cover of sediments may increase accuracy of prediction of *F. lumbricalis* distribution using different spatial statistical analysis.

Despite numerous underwater surveys during the last few years in the Lithuanian coast there is still lack of data of species distribution in the northern most part. It is necessarily to extend monitoring in this coastal area since pollution from Oil Terminal “Būtingė” may have influence on the benthic communities including *F. lumbricalis*. Impact of petroleum products on the red alga should be tested in acute and chronical experimental approachs (Hoffman et al., 2002).

On the other hand the macrophytobenthos monitoring in the Lithuania coast just have started and it is planed to be performed every three year. At the start of monitoring it is important to get a picture of seasonal or at least annual variation of the red alga distribution as well as other macroalgae species. Therefore it would be necessary to study the changes of macroalgae communities at fixed sites at least the first three year.

Despite simple and relatively quick assessment of water quality by suggested maximum depth limit of the red algae *F. lumbricalis*, care should be taken into account while interpreting the results. First of all design of a field work, where diver and/or underwater video has to map sufficient depths in order to be certain that the real maximum depth of the red alga was not missed. Usually the bottom inclination is irregular and the first record of depression without *F. lumbricalis* does not mean the true limit of its distribution. Another problem may arise due to measurement errors associated with diving computers (error ±0.5 m; author, personal observation), distance of diving computer from the seabed during a measurement and height of water level (±0.4 m in the study area according to the data of CMR). Thus the accuracy of maximum depth of *F. lumbricalis* may vary up to ±1.5 m complicating decision to which class of water quality it belongs, especially in cases when it is on the limit between two classes. The best solution to that would be additional field measurements that are not so easy to perfom in conditions of the exposed coast. Another way could scientific judgement based on complex of other biological and physicochemical water parameters measured during the monitoring. If some evident patterns of changes were found within these water indicators-then the lower class should be attributed in case of maximum depth of *F. lumbricalis*.

Moreover, there is still lack of estimations of evident impact of storm events on the sublittoral communities and their regeneration rate after disturbance. The release and settlement of *F. lumbricalis* spores maybe the most crucial factor limiting its distribution patterns on the stony bottom. The impact of water movement on dislodgement of algal thalli, spore and associated macrofauna transport, might be tested in wave-generating tanks.

The importance of *F. lumbricalis* in forming natural spawning substrates for fishes is yet not clear in the study area due to unfavourable field conditions and stochastic spawn of fishes. Mapping of distribution of Baltic herring spawning grounds is ongoing on the coast of Lithuania.

The role of macrophytes in the trophic transfers of the coastal Baltic ecosystems is most likely underestimated in the models (Tomczak et al., 2009) and the reasons for that should be investigated more thoroughly in the future using advanced techniques such as stable isotope ($\delta^{13}C$ and $\delta^{15}N$) analysis (Fredriksen, 2003).

6. CONCLUSIONS

1. At the microscale (10 cm^2–100 m^2) the distribution patterns of *F. lumbricalis* are determined by the frequency of stormy winds and mobility of surrounding bottom sediments; the effect of these factors changes with the depth and type of substrate.
2. At the mesoscale (1000 m^2–10 km^2) the distribution patterns of the red alga are mainly determined by the occurrence of suitable substrate and bathymetry (as proxy of irradiance). These distribution patterns are modified by the effect of the wave exposure, which depends on the bottom slope inclination, and the influence of the Curonian Lagoon outflow.
3. The recent distribution area of the red alga *F. lumbricalis* at the Lithuanian Baltic Sea coast stretches for 26 km within the depth limits from 1 to 15 m. The modelled total area of *F. lumbricalis* covers 47±11 km^2 (ca 50% from the total area of the suitable habitat) with predicted total biomass of 8449±3813 t.
4. Based on available historical data, the contemporary estimated total vegetation area and stock of *F. lumbricalis* show recovery after the decline reported in 1980-1990s. Yet, the reference conditions recorded in 1950s are not reached. The maximum depth limit of *F. lumbricalis* did not differ significantly from 1960s till 2000s, meaning that there was no critical decline in the euphotic zone during this period.
5. The most valuable area of dense cover and high standing stock of *F. lumbricalis* were observed in the coastal area off Palanga, between 5 and 10 m depth, due to optimal conditions in terms of suitable type of substrates, water transparency and shelter provided by underwater bottom slope geomorphology.
6. *F. lumbricalis* showed an important engineering role providing substrate for epiphytes (*Ceramium tenuicorne*, *Polysiphonia fucoides* and *Mytilus edulis*) and the shelter for associated

crustaceans (*Gammarus* spp. *Jaera albifrons* and *Idotea baltica*) in the study area.

7. Production of *F. lumbricalis* made up to 25% of the total production by phytoplankton and macroalgae in the coastal waters within the stony bottom in the sublittoral zone. The species biomass mainly transformed into detritus, due to low number and abundance of herbivores.

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APPENDIX 1. Sensitivity assessment benchmarks for *F. lumbricalis* (Rayment, 2008).

Physical Factors	**Intolerance***	**Recoverability ****	**Sensitivity *****	**Evidence/ Confidence**
Substratum Loss	High	Moderate	Moderate	High
Smothering	Intermediate	Moderate	Moderate	Low
Increase in suspended sediment	Intermediate	Moderate	Moderate	Low
Decrease in suspended sediment	Tolerant	Not Relevant	Not sensitive	High
Desiccation	High	Moderate	Moderate	Moderate
Increase in emergence regime	Intermediate	Moderate	Moderate	Moderate
Decrease in emergence regime	Tolerant	Not Relevant	Not sensitive	High
Increase in water flow rate	Intermediate	Moderate	Moderate	Very low
Decrease in water flow rate	Tolerant	Not Relevant	Not sensitive	High
Increase in temperature	Low	Very high	Very Low	Moderate
Decrease in temperature	Tolerant	Not Relevant	Not sensitive	High
Increase in turbidity	Tolerant	Not Relevant	Not sensitive	Moderate
Decrease in turbidity	Tolerant	Not Relevant	Not sensitive	Low
Increase in wave exposure	Intermediate	Moderate	Moderate	Low
Decrease in wave exposure	Tolerant	Not Relevant	Not sensitive	High
Noise	Tolerant	Not Relevant	Not sensitive	High
Visual Presence	Tolerant	Not Relevant	Not sensitive	High
Abrasion & physical disturbance	Intermediate	Moderate	Moderate	Low
Displacement	Low	Very high	Very Low	Low
Chemical Factors	**Intolerance**	**Recoverability**	**Sensitivity**	**Evidence/ Confidence**
Synthetic compound contamination	High	Moderate	Moderate	Low
Heavy metal contamination	Insufficient information	Not Relevant	Insufficient information	Not Relevant
Hydrocarbon contamination	High	Moderate	Moderate	Low
Radionuclide contamination	Insufficient information	Not Relevant	Insufficient information	Not Relevant
Changes in nutrient levels	Intermediate	Moderate	Moderate	Low
Increase in salinity	Low	Very high	Very Low	High
Decrease in salinity	Tolerant	Not Relevant	Not sensitive	High

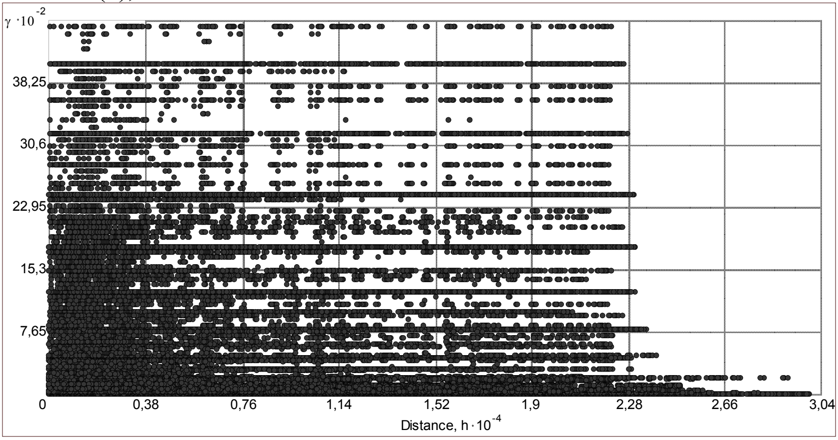
Changes in oxygenation	Insufficient information	Not Relevant	Insufficient information	Not Relevant
Biological Factors	**Intolerance**	**Recoverability**	**Sensitivity**	**Evidence/ Confidence**
Introduction of microbial pathogens/parasites	Insufficient information	Not Relevant	Insufficient information	Not Relevant
Introduction of non-native species	Insufficient information	Not Relevant	Insufficient information	Not Relevant
Extraction of this species	High	Moderate	Moderate	Low
Extraction of other species	Intermediate	Moderate	Moderate	Low

* the susceptibility of the species population to damage or death from an external factor;

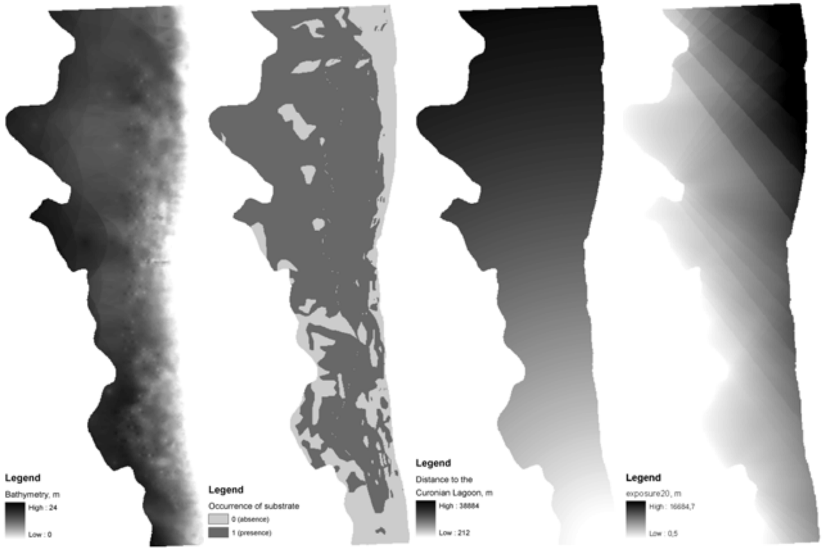
** the ability of the species to redress damage sustained as a result of an external factor;

*** sensitivity is defined according to scenarios (see Rayment. 2008) that give rise to rationale used to combine intolerance and recoverability.

APPENDIX 2. Semivariogram of *Furcellaria lumbricalis* cover, where on the y axis is difference of the species cover between two locations in a distance (h), m.



APPENDIX 3. Input data (raster maps with 50x50 m grid) of environmental factors for prediction of distribution of *Furcellaria lumbricalis* by GRASP (from left to right): bathymetry, occurrence of substrate, distance to the outflow of Curonian Lagoon and distance to 20 m isobath (wave exposure) respectively.



APPENDIX 4. The main species and data sources for Lithuania Baltic Sea coast Ecopath model.

Functional Group	Main species in the group	Biomass	P/B	Diet Matrix information
Birds	*Clangula hyemalis;* *Melanitta fusca;* *Melanitta nigra;* *Gavia arctica;* *Gavia stellata;* *Polysticta stelleri*	Švažas et al., 2001 Žydelis, 2001	Nelson 1979	Žydelis 2002 Vaitkus & Bubinas, 2001
Piscivorous fish	*Gadus morrhua callarias;* *Osmerus operlanus;* *Psetta maxima;* *Stizostedion lucioperca;* *Salmo trutta m.trutta*	Repečka et al., 1994; Bubinas & Vaitonis, 2003	Harvey et al., 2003	Bubinas & Vaitonis, 2003; Stankus 2003
Plankti-vorous fish	*Sprattus sprattus balticus;* *Clupea harengus membras*	Repečka et al., 1994	Harvey et al., 2003	Möllmann et al., 2004; http://www.fishbase.de
Benthi-vorous fish	*Platitchies flesus trachurus;* *Abramis brama;* *Vimba vimba vimba*	Repečka et al., 1994; Bubinas & Vaitonis, 2003	Harvey et al., 2003	Bubinas & Vaitonis, 2003; Fishery Research Laboratory
Benthic deposit feeders	*Marenzelleria neglecta;* *Pygospio elegans;* *Hediste diversicolor;* *Harmothoe sarsi;* *Oligochaeta spp.;* *Mesidothea entomon;* *Corophium spp.;* *Chironomidae undet.;* *Turbellaria undet.;* *Piscicola geometra;* *Crangon crangon;* *Gammarus sp.;* *Jaera albifrons;* *Idothea baltica;* *Theodoxus fluviatilis;* *Hydrobia sp.*	Olenin 1997; Bubinas & Repečka, 2003	Ostrovski, 1984; Wallentinus, 1991	Olenin 1997; Jarvekiulg 1979; Jansson, 1967
Benthic suspension feeders	*Fabricia sabella;* *Bathyporea pilosa;* *Balanus improvisus;*	Olenin, 1997; Bubinas & Repečka, 2003	Ostrovski, 1984; Wallentin	Olenin, 1997; Jarvekiulg, 1979;

	Mytilus edulis trossulus; *Macoma balthica; Cerastoderma glaucum. Mya arenaria*		us, 1991	Dolmer, 2000
Macrozoo-plankton	*Mysis mixta.* *Neomysis intiger*	Coastal Research & Planning Institute (CORPI)	Witek, 1995	Viherluoto, 2001
Mesozoo-plankton	*Acartia* sp. ; *Nauplius;* *Evadne nordmanni;* *Bosmina coregoni maritima;* *Cladocerans;* *Rotatoria*	Witek, 1995 (borrowed data)	Witek, 1995	Gasparini & Castel, 1997
Perennial Macrophytes	*Furcellaria lumbricalis;* *Cladophora rupestris;* *Polysiphonia fucoides*	Olenin et al., 2003; CORPI	Wallentinus, 1991	Kotta et al., 2000
Annual Macrophytes	*Ectocarpus siliculosus;* *Pilayella litoralis* *Cladophora* sp. *Ulva* sp.,	Olenin et al., 2003; CORPI	Wallentinus, 1991	Kotta et al., 2000
Phyto-plankton	Including Blue-green alga	Center of Marine Research	Witek, 1995	
Detritus	Including import of DOC and POC from Curonian Lagoon	Pauly, Soriano & Palomares 1993; CORPI		