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Implications of Macrophyte Distribution Patterns in the Curonian Lagoon for Monitoring of Submerged Vegetation in Transitional Water Bodies

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For the implementation of the Water Framework Directive and the Marine Strategy Framework Directive, numerous indicators based on macrophytes have been developed in coastal and shelf zones. However, transitional water bodies (e.g., estuaries, lagoons) have multiple overlaying strong environmental gradients that limit the assessment of the relationships between macrophyte ecological patterns and anthropogenic pressures. The aim of this study was to assess the abundance and distribution of macrophytes in the Curonian Lagoon and to analyze the spatial patterns of macrophyte species considering their morphofunctional properties (i.e., community surface index, which is the sum of the ratios between the specific surface of thallus structure elements and biomass of each macrophyte species in a sampling site) in relation to environmental factors, such as Secchi depth, salinity, wave exposure and area of wetlands. In the estuarine part of the Curonian Lagoon, the sampling of macrophytes was carried out in 2014–2015. Data on hydro-physical parameters were obtained from the water monitoring and hydrological model, while the CORINE data were used for the delineation of wetlands. The species diversity in the studied part of the Curonian Lagoon consisted 12 species (7 of them belong to phylum *Chlorophyta* and 5 to *Magnoliophyta*). From dominant algae, *Chara contraria* and *Chara aspera* mainly occurred along the northeastern part of the study area, whereas *Cladophora glomerata* mainly grew as epiphyte along the eastern shore of the lagoon. From dominant angiosperms, *Potamogeton perfoliatus* and *Stuckenia pectinata* occurred in the whole study area, while *Myriophyllum spicatum* rarely formed dense stands and usually was within the stands of charophytes or pondweeds. The salinity was the most important environmental factor, where the relative coverage of *Zannichellia palustris*, *Potamogeton rutilus* and all algae species, except *Nitellopsis obtusa*, correlated with salinity. The Secchi depth was of less importance and correlated with the relative coverage of *N. obtusa*, while a negative correlation was determined for *S. pectinata*. The mean community surface index depended on the depth gradient where it was significantly higher at ≤ 1.0 m depth than at 1.1–2.0 m depth. The community surface index significantly negatively correlated (the Spearman $r_S = -0.65$) with the area of wetlands, which surrounded the eastern shore of the study area. Therefore, the tested morphofunctional index has a potential to define the ecological status considering macrophyte communities in the transitional water bodies.

Keywords: submerged vegetation, specific surface of thallus structure elements, environmental factors.

Introduction

Macrophytes play an important structuring role of biodiversity in shallow water bodies by providing habitats and food for many aquatic organisms (Dugdale et al., 2006; Schmieder et al., 2006). Macrophytes also provide regulative ecosystem services as they can maintain a clear water and nutrient retention (da Silva et al., 2009; Friedland et al., 2019). Therefore, macrophytes are considered as one of the main biological elements in water quality monitoring of the Water Framework Directive (European Commission, 2000) and the Marine Strategy Framework Directive (European Commission, 2008). Submerged vegetation communities in the shallow, wind-exposed coastal environments of the Baltic Sea are characterized by small charophytes together with angiosperms (Torn et al., 2004; Steinhardt and Selig 2007; Blindow et al., 2016).

One of the main difficulties in using macrophytes as bioindicators, quality elements (sensum Water Framework Directive) or state variables in monitoring programs is a high temporal and spatial variability of communities between and within habitats (Orfanidis et al., 2007; Christia et al., 2018). In order to assess changes in macrophyte communities in transitional waters, indicators based on aquatic vegetation have already been proposed, but there are a number of concerns for their use (Mouillot et al., 2006). These concerns include macrophyte taxonomic classification issues, a lack of intercalibration for multi-site comparisons and difficulties in separating responses of indicators to natural factors and anthropogenic pressures in a highly stressful environment, the so-called estuarine quality paradox (Elliott and Quintino, 2007). Moreover, macrophyte-based indicators are usually tested and used in one or a few countries, whereas their applicability in other waterbodies has not been verified.

In ecosystems with a low diversity of macrophytes, the indicative value of morphological-functional traits is currently emphasized (Casanova et al., 2011; Beauchard et al., 2017). Morphofunctional parameters of macrophytes such as a specific surface area of species (population or community) can be easily determined and compared among waterbodies (Minicheva, 2013). The advantage of this approach is that there is no need of precise identification of macrophyte species and their classification to certain sensitive/functional groups, which is somewhat subjective (Orfanidis et al., 2011). According to Minicheva (2013), morphofunctional properties of submerged aquatic vegetation can quantitatively reflect the changes in the floristic structure under a shift of an ecological status in a waterbody. A specific surface area reflects an intensity of the primary production process (i.e., potential ecological activity) of macrophyte population, which depends on the morphological structure and the size of species. Moreover, the values of the specific surface area of macrophyte populations can be summarized by the community surface index, which considers species biomass or coverage and reflects the intensity of an autotrophic process by aquatic vegetation in an ecosystem. High values of this index indicate the dominance of species with a relatively high specific surface such as filamentous algae and an intensive production by these macrophytes usually under enhanced eutrophication conditions.

The aim of this study was to assess the spatial patterns of submerged macrophyte species in the estuarine part of the Curonian Lagoon and, considering their morphofunctional properties, to test the relationships between the community surface index and environmental factors such as Secchi depth, salinity and wave exposure. We also tested the relationship between the community surface index and the area of wetlands along the lagoon. We hypothesized that large areas of wetlands, functioning as a natural nutrient sink, might reduce nutrient loads, especially in the shallow littoral zone resulting in lower index values than along the shores without or with narrow areas of wetlands.

Methods

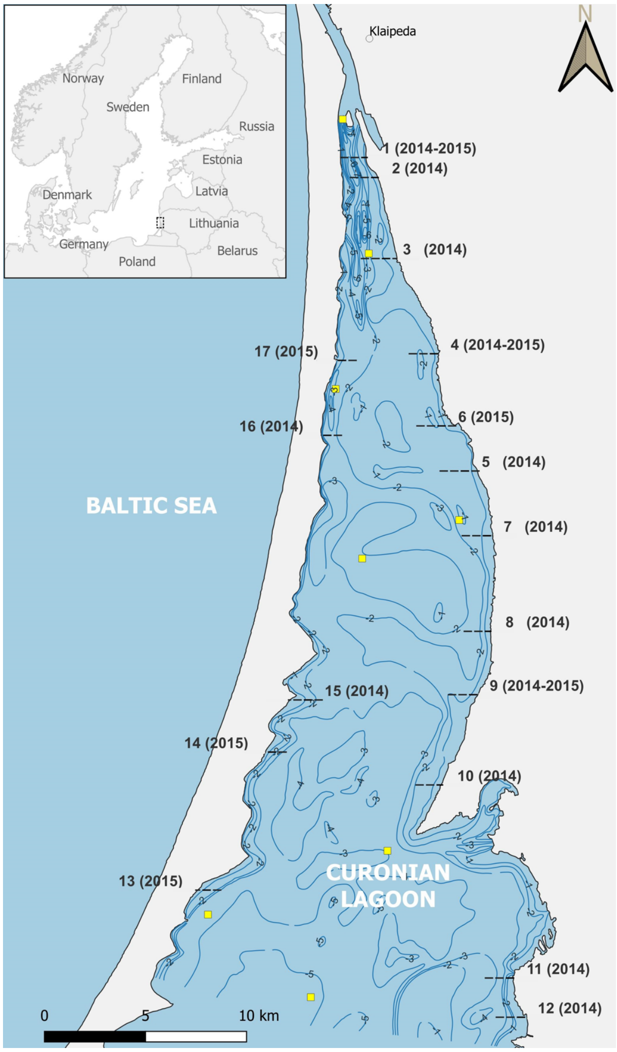
Study area

The Curonian Lagoon is located in the eastern part of the Baltic Sea. Its total surface area is 1584 km^2, making it the largest lagoon in Europe. The Curonian Lagoon is mainly a freshwater body connected to the southeastern part of the Baltic Sea by the narrow Klaipėda Strait (Zemlys et al., 2013). The northern part of the lagoon (from the Klaipėda Strait to the Nemunas River Delta) is typically defined as a transitional estuarine system with a mix of brackish, lagoon and riverine waters. Episodic inflows of brackish water cause irregular rapid (duration of hours or days) salinity fluctuations in the range of 0.1–7.0 g/kg in the northern part of the lagoon. The eastern phytolittoral of the lagoon is relatively wide (up to 2 km) with a gentle slope up to 2.5 m depth, whereas it is relatively short (< 0.5 km) and steep along the western shore due to the channel and a fairway (Sinkevičienė et al., 2017; Bučas et al., 2019). The southern part of the lagoon is more lacustrine and characterized by a relatively closed water circulation (Ferrarin et al., 2008), where the most intensive cyanobacteria blooms occur (Vaičiūtė et al., 2021). This part is considerably larger than the estuarine part, making the Curonian Lagoon one of the most severely eutrophicated coastal lagoons in the Baltic Sea (Zilius et al., 2018).

Sampling

Based on bathymetric and bottom sediment data (Trimonis et al., 2003) and previous studies on charophytes in the Curonian Lagoon (Žaromskis, 2002; Sinkevičienė, 2004), the estuarine part of the lagoon was more intensively surveyed along the eastern shore than the western shore due to the wider phytolittoral zone (Sinkevičienė et al., 2017). In total, 17 transects were sampled in 2014 and 2015 (*Fig. 1*), where 12 transects were mainly sampled along the eastern shore during July and August, whereas 5 transects were sampled along the western shore and mainly in September (according to the national water monitoring data during 1997–2007, there were no macrophyte species sensitive to seasonality such as *Tolypella nidifica*). Thirteen transects were sampled in 2014 and 7 transects were sampled in 2015 in order to test if the species composition significantly differed between the studied years. The transect samples were taken every ca. 0.25 m depth extending from the shoreline down to the maximum colonization depth of macrophytes in order to assess their occurrence and relative coverage along a depth gradient. Samples of submerged plants were collected from a boat using a double-headed rake. In

Fig. 1. *The study area and the distribution of sampling transects (indicated by dotted lines, numbers and years in parenthesis) in 2014–2015 in the estuarine part of the Curonian Lagoon. Isobaths are indicated by blue lines and depth values (m). Yellow squares indicate the sites of national monitoring performed by the Environmental Protection Agency*



each transect site, the rake was pulled 2–5 times in order to cover at least 1 m^2 area of the dredged bottom. The relative coverage of each macrophyte species on a rake was assessed using the Braun-Blanquet scale (Kent and Coker, 1992). Specimens of macrophytes were identified using the keys by Hollerbach and Krasavina (1983), Krause (1997), Blindow and Koistinen (2003), Lekavičius (1989) and Snoeijs and Johansson (2003).

Distribution of macrophyte species

The relative occurrence of macrophyte species was determined between the transects. The ordinal coverage of macrophytes was converted to numerical (relative coverage) according to the midpoints of Braun-Blanquet scale cover (Wikum and Shanholtzer, 1978) using the "simba" package (Jurasinski and Retzer, 2012) in R (R Core Team, 2021). For each species, the mean and maximum relative coverage was estimated. The spatial distribution of macrophyte species and their relative coverages were visualized by plotting them in stacked bars on the map of the study area using QGIS 3.22.6 (QGIS Development Team, 2022). The depth distribution of macrophyte species was analyzed by means of the generalized additive models (GAM) due to observed nonlinear patterns in the data. In GAM, the penalized cyclic cubic smoothing term was selected for the explanatory (independent) variables with 10 degrees of freedom, and the additional penalty against overly complex smooths (gamma = 1.4) was added due to overfitting (Wood, 2017). GAM was performed with the "mgcv" package in R.

Morphofunctional analysis

Two morphofunctional indicators of macrophytes were used in this study: the ratio of a specific photosynthetic surface (S) to weight (W) of a population (p) and the specific surface of a community (thereafter – a specific surface of a population - S/W$_p$ and community surface index – SI$_{cm}$, respectively). S/W$_p$ reflects the ecological activity (i.e., primary production process) of an individual species, depending on its morphological structure and size, and SI$_{cm}$ reflects the intensity of a primary production process of a community, depending on the S/W$_p$ value of species included in a community and their biomass (Minicheva, 1998). Both indicators have been used to assess the ecological status of marine ecosystems with the requirements of the Water Framework Directive and the Marine Strategy Framework Directive (Minicheva, 2013).

S/W$_p$ for each submerged macrophyte species was determined by measuring morphological parameters (diameter or thickness and height) of 30 randomly sampled specimens in 2020 along the eastern shore (1st–9th transects) within 0.5–1.0 m depth. The eastern shore was sampled due to the relatively wide phytolittoral zone, high species diversity and difference in morphology of the thallus of some species (M. Bucas, pers. obs.). It is possible to divide all morphological variety of the macrophyte thallus structure or its elements simple types based on the correspondence to the geometric shapes such as cylindrical or lamellar. An allometric method (Minicheva et al., 2003) was applied to calculate the mean specific surface for each type of thallus structure elements:

$$\textit{for cylindrical type } S/\mathrm{W}_{\bar{\mathrm{x}}} = \frac{\left(\sum_{i=1}^{n} 3334 \times d_i^{-0.916}\right)}{n} \quad (1)$$

$$\textit{for lamellar type } S/\mathrm{W}_{\bar{\mathrm{x}}} = \frac{\left(\sum_{i=1}^{n} 2000 \times h_i^{-0.988}\right)}{n} \quad (2)$$

Where: $S/\mathrm{W}_{\bar{\mathrm{x}}}$ – the mean specific surface thallus structure elements (m^2/kg); d_i – the diameter of the thallus ith structure element (μm); h_i – thicknesses of the transverse cut of the thallus ith structure element (μm).

For example, for the macrophytes having a cylindrical form (e.g., *Cladophora glomerata*), the mean diameter of branches (2–5) from the thallus was measured, and for the macrophytes having a laminated structure (e.g., *Ulva intestinalis*), the mean thickness of the thallus was measured. For the large (few millimeters in diameter) macrophytes with cylindrical and laminated structures (e.g., *Potamogeton perfoliatus*), the mean diameter of stems (2–5) and the mean thicknesses of leaves (2–5) were measured. These morphological parameters were measured with a caliper, while a stereomicroscope was used for the macrophytes with a thin thallus (some tens to several hundreds of μm). For each site of macrophyte sampling in 2014 and 2015, the estimated $S/\mathrm{W}_{\bar{\mathrm{x}}}$ of all thallus elements of each macrophyte species were summed in order to estimate S/W$_p$. Then SI$_{cm}$ was calculated as the sum of S/W$_p$ of all species in a sampling site multiplied respectively by the species biomass in a sampling site:

$$\mathrm{SI_{cm}} = \sum_{i=1}^{n} \mathrm{S/W}_{\mathrm{p}i} \times \mathrm{B}_{\mathrm{p}i} \tag{3}$$

Where: – SI_{cm} the community surface index in a sampling site; S/W_{pi} – the mean specific surface of thallus structure elements of i^{th} macrophyte species in a sampling site (m^2/kg); B_{pi} – the population wet biomass of i^{th} macrophyte species in a sampling site (kg/m^2); n – the total number of macrophyte species in a sampling site.

B_{pi} was calculated from the linear regression model between the mean relative coverage and biomass of macrophyte species within a sampling site ($B_{pi} = coverage_i \times 0.001$; $r^2 = 0.64$) derived from the macrophyte monitoring data in the study area in 2021 (unpublished data).

Environmental data

Based on previous studies of charophyte distribution (Bučas et al., 2019), Secchi depth, salinity and wave exposure were selected as the main environmental factors in the Curonian Lagoon, which could have an effect on other submerged macrophytes and SI_{cm}. For SI_{cm}, the wetland area was selected as a proxy for a nutrient gradient, where the load of nutrients should depend on the width of wetlands along the lagoon.

Monthly data (in 2014 and 2015) of Secchi depth were obtained from 8 monitoring stations in the study area (*Fig. 1*), and were collected by the Environmental Protection Agency. For each site of macrophyte sampling, the mean Secchi depth was interpolated for the vegetation period (May–September) using the inverse distance weighted interpolation with the "gstat" package (Gräler et al., 2016) in R. The mean near bottom salinity for the same period was derived in the sampling sites from the hydrodynamic model (with a grid size of ca 30 by 50 m) developed for the Curonian Lagoon (Zemlys et al., 2013). Wave exposure at each sampling location was assessed by the adjusted relative exposure index AREI (Malhotra and Fonseca, 2007), which is based on a wind fetch, bathymetry, wind direction and velocity. The wind data was obtained from the coastal hydrometeorological station for the studied period and AREI was calculated in R. The wetland data was obtained from the CORINE land cover 2012 (code – inland marshes). The area of wetlands for each sampling transect was calculated along a 1 km distance of the shoreline near a transect using a 1 km buffer zone from the shoreline using QGIS 3.22.

Statistical analysis

A univariate PERMANOVA (n = 999) through the 'adonis' function in the package "vegan" (Oksanen et al., 2015) was used to assess the difference of species composition (i.e., their mean relative coverages within the same depth range) in the same or very close transect between the two years (2014 and 2015).

The depth distribution of SI_{cm} was assessed by the comparison of mean SI_{cm} among four depth groups (< 0.5, 0.5–1.0, > 1.0–1.5 and > 1.5 m). The Games Howell post hoc test in the "rstatix" package (Kassambara, 2021) in R was used for the comparisons of means due to the heterogeneity of variance and the unequal sample size between the groups (Lee and Lee, 2018).

Redundancy analysis (RDA) was performed to test how the main natural gradients in the lagoon (water salinity, Secchi depth and AREI) correlated with the relative coverage of macrophyte species. The relative coverage of macrophyte species and environmental factors were averaged within the transects in order to assess the large scale (i.e., the lagoon) patterns. The marginal significance of explanatory variables (i.e. environmental factors) was assessed and the correlation biplot (scaling = 2) was chosen to represent the linear relationships between the response and explanatory variables (Zuur et al., 2007). The smooth surfaces of the most important explanatory variables were overplayed onto RDA biplot using the thin plate splines with cross-validatory selection of smoothness (i.e., using the GAM approach). RDA was performed with the "vegan" package (Oksanen et al., 2015) in R.

Correlations were determined between SI_{cm} and environmental factors: macrophyte relative coverage, area of wetlands (as a proxy for a reduced amount of nutrients from land), salinity, AREI and Secchi depth. Before the analysis, the data were visually checked by quantile-quantile plots for the normality assumption, and in a positive case, the Pearson product-moment correlation (r) was calculated; otherwise, the Spearman rank correlation (r_S) was used.

As it was mentioned that depth is generally considered as a proxy for light availability and wave exposure (AREI), and in order to check if other factors (e.g., the area of wetlands) correlated with SI_{cm}, we reduced the depth effect on the correlation analysis by splitting the data into different depth groups. These groups were determined from the comparison of SI_{cm} means among four depth groups; therefore, the correlation analysis with environmental factors was performed separately on each delineated group.

Results and Discussion

Distribution of macrophyte species and relationships to environmental factors

The species diversity in the studied part of the Curonian Lagoon was relatively low; 12 species (7 of them belong to phylum *Chlorophyta* and 5 to *Magnoliophyta*) were identified in the study area (*Table 1*). The eastern part of the lagoon with a relatively wide (up to 2.0 km) phytolittoral was richer in the species number compared with the western shore (the maximum width of phytolittoral was only 0.3 km), where only 5 species were recorded (*Fig. 2*). Depth gradient is generally considered as a proxy for light availability and wave exposure, which affect the zonation of macrophyte species, their growth forms, coverage and biomass along this gradient (Chambers and Kalff, 1985; Torn et al., 2014).

Table 1. *List of submerged macrophyte species, their relative frequency (among all transects), mean and maximum relative coverage in the studied transects in the Curonian Lagoon*

Species name	Relative frequency, %	Mean relative coverage, %	Maximum relative coverage, %
Potamogeton perfoliatus	82	29	61
Chara contraria	76	32	86
Stuckenia pectinata	71	28	61
Cladophora glomerata	65	31	86
Chara aspera	47	33	86
Myriophyllum spicatum	47	18	34
Nitellopsis obtusa	35	31	61
Chara baltica	29	22	34
Zannichellia palustris	24	17	34
Potamogeton rutilus	18	25	34
Tolypella nidifica	12	23	34
Ulva intestinalis	12	23	34

In the Curonian Lagoon, the maximum phytolittoral depth ranged from 1.0 to 2.0 m (*Fig. 3*). The macrophyte composition did not significantly differ between 2014 and 2015 (PERMANOVA test, F = 0.67, *P* = 0.80).

Among charophytes, *Chara contraria* and *Chara aspera* were the most frequent (≥ 45% of all transects). *C. contraria* formed dense stands (the maximum relative coverage was 86%), especially in the northeastern part of the study area (3rd–7th transects) from 1.0 to 2.0 m depth (*Fig. 2*). *C. aspera* also formed dense stands, mainly to 1.0 m depth. *Nitellopsis obtusa* was mainly found within the stands of *C. contraria* and *C. aspera* in the central part of the study area (4th–9th transects) along the eastern shore. Other algal species were relatively rare (< 30%), where *Chara baltica* occurred in the northeastern part of the study area (1st–6th transects), while *Tolypella nidifica* and *Ulva intestinalis* were restricted to the first two transects. The densest relative coverage of *C. baltica* and *U. intestinalis* were found at ≤ 1.0 m depth, while the maximum relative coverage of *T. nidifica* was between 1.0 and 1.3 m depth. It should be noted that several transects (especially along the western shore) were sampled in September, which could result in the underestimation of macrophyte species which are sensitive to seasonality such as *T. nidifica. Cladophora glomerata* was the most frequent (65%) among the green algae species, which mainly occurred to < 1.0 m depth and was growing as epiphyte.

Among pondweeds, *Stuckenia pectinata* and *Potamogeton perfoliatus* were the most frequent (> 70% of all transects) and widespread angiosperm species, which extended to 2.0 and 1.8 m depth, respectively. Monospecific stands of *P. perfoliatus* were found in different sizes of patches, whereas *S. pectinata* usually formed mixed stands with charophytes. *Myriophyllum spicatum* was relatively frequent (47%) but rarely formed dense stands and usually was within the stands of charophytes or pondweeds. *Zannichellia palustris* and *Potamogeton rutilus* were less frequent (< 25%) species and were mainly restricted to the northeastern part of the study area (1st–7th transects), where they formed the densest stands (the relative coverage up to 34%) between 0.8 and 2.0 m depth.

Salinity was the only statistically significant environmental factor (F = 9.21, *P* < 0.01), while Secchi depth was of less importance (F = 2.15, *P* = 0.02), and wave exposure (AREI) was not a significantly important

Fig. 2. *Distribution of submerged macrophyte species relative coverage (indicated by the height of a bar) in the study sites in the estuarine part of the Curonian Lagoon: (a) common species (the occurrence of > 45% of all transects), (b) less frequent species (< 45%), the depth distribution of relative coverage of algae species (c) and angiosperm species (d). Isobaths in the map are indicated by blue lines and depth values (m)*

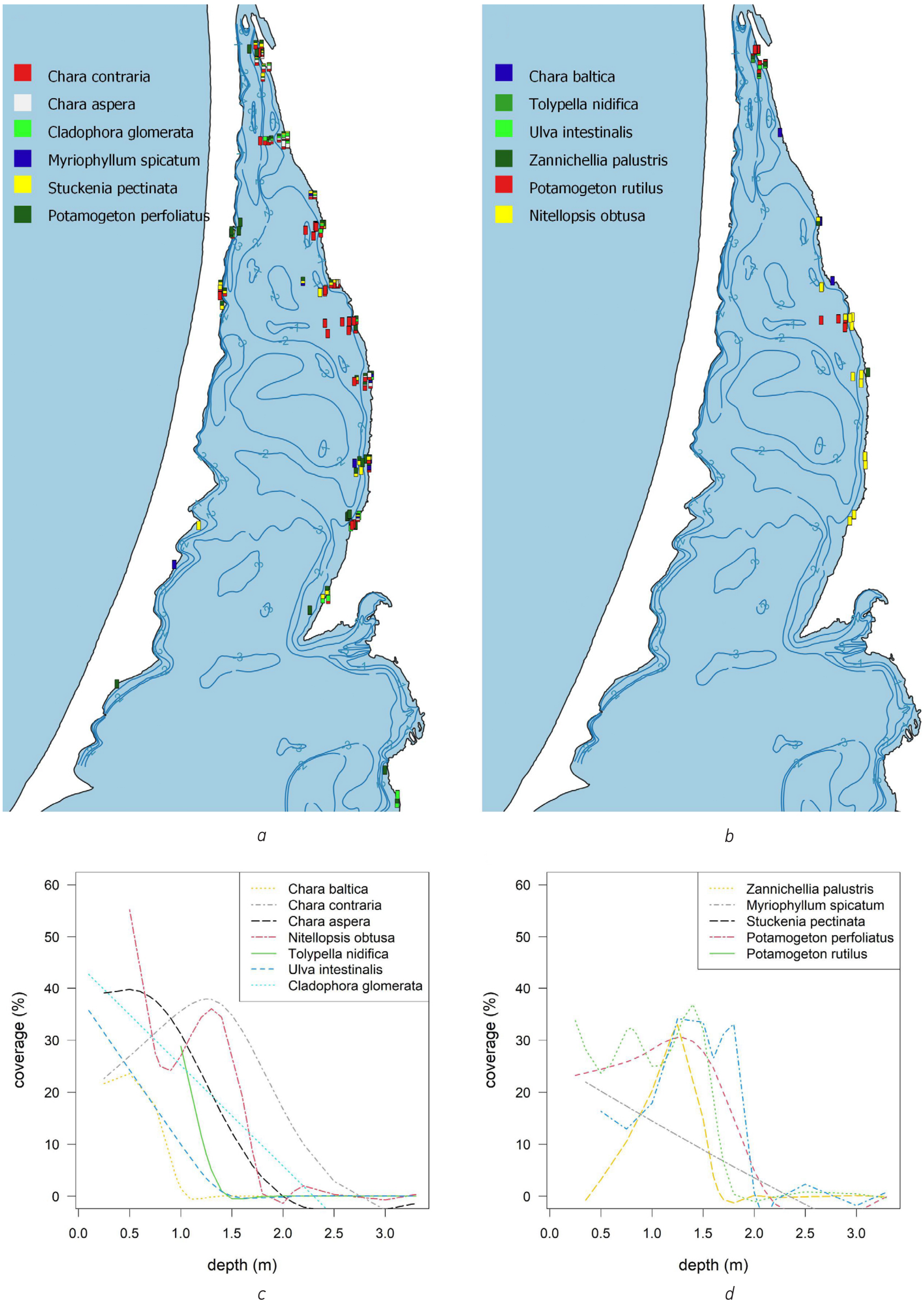
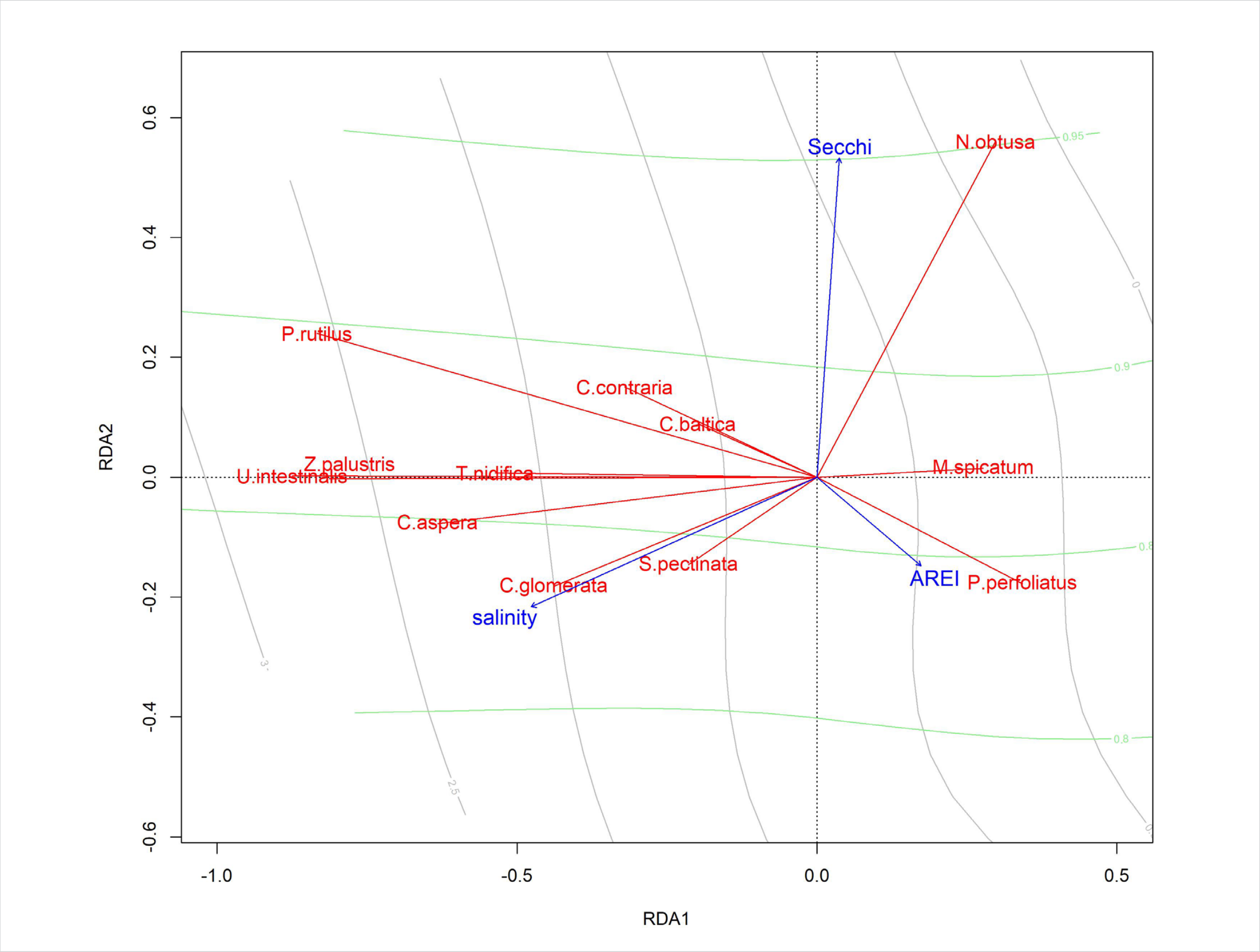


Fig. 3. *Correlation biplot (scaling type 2) from the redundancy analysis (RDA) between the relative coverage of submerged macrophytes species (red lines) and environmental factors (blue vectors). The gradients of salinity (grey lines and values) and Secchi depth (green lines and values) are superimposed on the RDA biplot*



factor (F = 1.51, *P* = 0.13). All environmental factors (with the first two axes) explained 12% of the variation in the species relative coverage data. The relative coverage of algae species (especially *T. nidifica* and *U. intestinalis*) correlated with salinity, except *N. obtusa* (*Fig. 3*). From angiosperms, the relative coverage of *Z. palustris* and partly *P. rutilus* correlated with salinity, while there was a negative high correlation with the relative coverage of *M. spicatum*. The fact that salinity is a limiting factor for the macrophyte species of different salinity tolerances was already determined in the coastal waters (Schubert and Blindow, 2003; Karus and Feldmann, 2012; Herkül et al., 2018; Bučas et al., 2019). Freshwater algae (*N. obtusa*) were mainly found in the areas with a mean near bottom salinity below 0.4 g/kg, whereas salinity-tolerant species (*C. baltica, T. nidifica* and *U. intestinalis*) were restricted to the areas with the mean near bottom salinity above 0.4 g/kg. *Cladophora glomerata* is widely distributed throughout freshwater and estuarine ecosystems of the world (Guiry and Guiry, 2020), and the species relative coverage correlated with the salinity in the Curonian Lagoon. The correlation between the salinity and the coverage of pondweeds (*Z. palustris* and *P. rutilus*) could be explained by the species tolerance to brackish waters in coastal lagoons (e.g., Van Vierssen, 1982; Mäemets, 2016).

The relative coverage of *N. obtusa* correlated with Secchi depth, while a negative correlation was determined for *S. pectinata*. The latter pattern could be explained that *S. pectinata* is more tolerant to reduced light in eutrophic waters than charophytes (e.g. Van den Berg et al., 1998; Larkin et al., 2018).

Although AREI was the least important factor in RDA, the relative coverage of most algae species (except *N. obtusa*), *Z. palustris* and *P. rutilus* negatively correlated with AREI, while the relative coverage of *P. perfoliatus* increased along with AREI. This was in line with the results from the coastal waters around Estonia (Herkül et al., 2018), where the biomass of charophyte species and *Z. palustris* corresponded with sheltered areas, whereas the biomass of *P. perfoliatus* corresponded with wave exposed areas.

Morphofunctional indicators of macrophytes

The measured specific photosynthetic surface of macrophyte thalli showed that the species in the Curonian Lagoon could be divided into two groups of a potential ecological activity (*Table 2*). The first group includes species sensitive to eutrophication (vascular plants and charophytes) with a mean specific surface of the population (S/W_p) of ca. 14 m^2/kg. The second group includes eutrophication tolerant species (short-live cycle, green algae) with a mean S/W_p of ca.76 m^2/kg.

Table 2. *Morphological growth form of submerged macrophyte species and the mean specific surface of their population (S/W_p) in the littoral of the Curonian Lagoon according to in situ measurements*

Systematic group	Species	Morphological growth form	S/W_p (m^2/kg)
Angiosperms	*Potamogeton perfoliatus*	Stem – cylindrical, leaves – lamellar	8.3
	Potamogeton rutilus	Stem – cylindrical, leaves – lamellar	13.8
	Stuckenia pectinata	Stem – cylindrical, leaves – lamellar	13.0
	Myriophyllum spicatum	Cylindrical	25.0
	Zannichellia palustris	Stem – cylindrical, leaves – lamellar	11.0
Charophyta	*Chara contraria*	Cylindrical	16.1
	Chara aspera	Cylindrical	17.5
	Tolypella nidifica	Cylindrical	11.0
	Nitellopsis obtusa	Cylindrical	12.7
	Chara baltica	Cylindrical	15.0
Chlorophyta	*Cladophora glomerata*	Cylindrical	116.9
	Ulva intestinalis	Lamellar	36.1

Fig. 4. *Variation of submerged macrophyte community surface index (SI_{cm}) within four depth groups. Red dots indicate means (horizontal lines – medians; boxes – 25th and 75th quantiles; whiskers extending from the boxes – minimum and maximum; and open dots – outliers)*

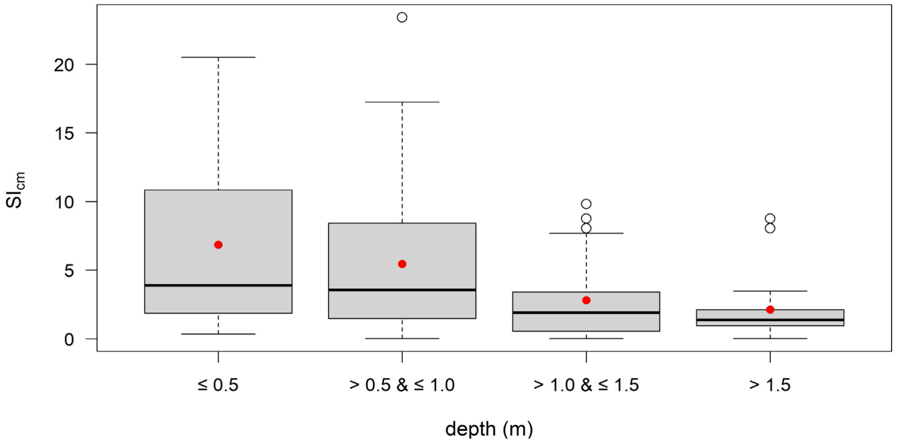
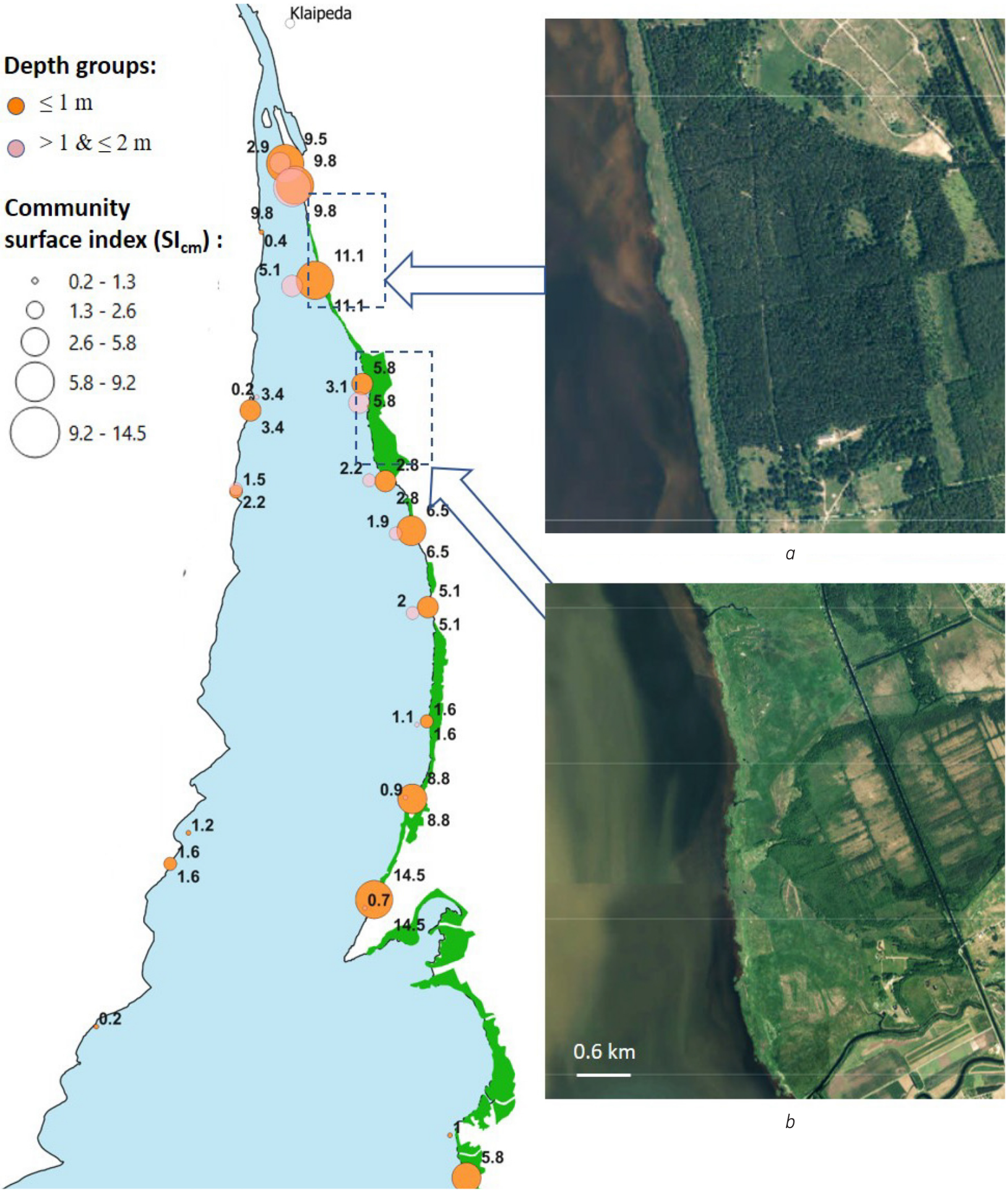


Fig. 5. *The distribution of submerged macrophyte community surface index (SI_{cm}) in the estuarine part of the Curonian Lagoon. The mean values of SI_{cm} are derived for two depth groups: ≤ 1.0 m and 1.1–2.0 m. The area of wetlands is indicated by green color within 1 km buffer along the shore (derived from the CORINE land cover 2012 product). Orthophotos of shoreline with narrow (a) and wide (b) areas of wetlands from 2012–2013 (obtained from the Lithuanian spatial information portal: https://www.geoportal.lt/map/)*



a

b

The mean community surface index (SI_{cm}) values decreased with the depth in the study area (*Fig. 4*), where the mean SI_{cm} was significantly higher at ≤ 1.0 m depth than at > 1.0 m depth (Games–Howell post hoc test, $P < 0.05$). Macrophyte species have a different light tolerance determining their maximum and optimal distribution depth (Chambers and Kalff, 1985; Torn et al., 2014). Unique community composition along the depth gradient in this way results in different intensity of autotrophic process.

In the studied transects, the mean values of SI_{cm} ranged from 0.2 to 14.5 depending on the part of the shore and depth (*Fig. 5*). This shows the wide range of intensity of potential primary production by macrophyte communities and a high potential for change of these groups under disturbances in local environmental conditions (e.g., illumination regime, nutrients availability). The maximum SI_{cm} values were recorded in the upper littoral part (≤ 1.0 m depth). The mean high SI_{cm} values (> 8.0) were observed along the eastern shore in the northern part (1st, 2nd and 3rd transects) and the southern part (9th and 10th transects) of the study area. The increase of SI_{cm} values in the northern part may indicate enhanced eutrophication process by anthropogenic pressure, which probably originates from the urban territory of Klaipėda. The increase of SI_{cm} values in the 10th transect may reflect an enhanced autotrophic process under the impact of natural factors – the outflow of the Nemunas River, which transports high loads of nutrients in water (Vybernaite-Lubiene et al., 2018). These areas corresponded to the distribution of opportunistic filamentous green algae species *Cladophora glomerata*, which formed dense mats on other submerged macrophytes. The mean values of SI_{cm} < 7.0 in 4th–7th transects corresponded to the largest stands of *Chara contraria*, which is considered between tolerant and sensitive to eutrophic conditions in freshwaters (Kolada et al., 2014). Relatively low mean SI_{cm} values (< 3.5) were recorded mainly along the western shore. These areas corresponded to the stands of *P. perfoliatus* and *S. pectinata* with a relatively low relative coverage.

The mean SI_{cm} values in > l.0 m depth varied less (from 0.2 to 9.8). The maximum SI_{cm} value was observed in the 2nd transect at 1.2 m depth, due to the high relative coverage by *S. pectinata* and brackish water species (*Z. palustris and P. rutilus*).

Relations of SI_{cm} with environmental parameters

The correlations between the environmental factors and SI_{cm} differed within ≤ 1.0 m and 1.1–2.0 m depth groups (*Table 3*). A negative significant correlation was found between the wetland area and SI_{cm} ($r = -0.65$, $P < 0.05$) at ≤ 1.0 m depth, while the relationship was not significant at > 1 m depth. The wetland areas were determined only along the eastern shore of the study area, where their size and distribution varied (*Fig. 5*). The wetland areas were absent or were relatively narrow in the northern part of the study area (1st–3rd transects), in the central part (5th and 7th transects) and in the southern part (10th transect). The wetland areas were wide in the central part (4th and 24th transects) and in the southern part (13th and 14th transects). We speculate that large areas of wetlands functioning as a natural nutrient sink may reduce their loads in the shallow littoral zone resulting in lower indicator values than along the shores without or with narrow wetlands.

Table 3. *Correlation between the environmental variables and SI_{cm} in two depth groups. Statistical significance ($P < 0.05$) indicated in bold; r – Pearson product-moment correlation; r_S – Spearman rank correlation*

Depth, m	Wetland area	Adjusted relative exposure index (AREI)	Salinity	Secchi depth
≤ 1.0	r = –0.65 (N = 10)	r_S = –0.12 (N = 16)	r_S = 0.13 (N = 16)	not relevant
1.1–2.0	r = 0.50 (N = 8)	r_S = –0.16 (N = 13)	r = 0.63 (N = 13)	r = –0.01 (N = 13)

A significant positive correlation between salinity and SI_{cm} was restricted to the depth range of > 1.0 m (*Table 3*). Although salinity affects brackish macrophyte species distribution in the estuaries (Blindow, 2000; Schubert and Blindow, 2003; Crain et al., 2004), the determined relationship on SI_{cm} could be explained by the distribution of opportunistic species with high growth rates, specific surface and nutrient uptake (e.g., *C. glomerata*) in the wide range of salinity within the study area (Bucas et al., 2019).

Correlations between the AREI, Secchi depth and SI_{cm} were low and not significant, most likely due to splitting the dataset into the two depth groups, while the depth gradient is a proxy for light climate and wave exposure (Stragauskaite *et al.* 2021).

Relatively low diversity of macrophytes in the Curonian Lagoon and other transitional water bodies (Selig et al., 2007; Rosqvist et al., 2010; Kovtun et al., 2011; Pawlikowski and Kornijów, 2018) is limiting the use of macrophyte based indicators (Hansen and Snickars 2014; Rinne et al., 2018) for comparison of an ecological status between different water bodies. Other macrophyte metrics as indicators of eutrophication have been suggested such as plant volume inhabited (PVI) and percent area covered; however, their variability was relatively high (Søndergaard et al., 2010). High PVI values indicate the dense macrophyte stands which provide potential availability of food and shelter to higher trophic levels (e.g., PVI correlates with high densities of plant-associated macroinvertebrates) and primary production. In contrast to PVI, SI_{cm} has an advantage as it gives a metric for a specific surface and, therefore, potential photosynthesis rates of the macrophyte communities. Opposite to PVI, SI_{cm} values increase with increasing eutrophication as long as when filamentous algae/macrophytes become dominant. Nevertheless, this morphofunctional indicator needs a spatial (i.e., in other transitional water bodies) and temporal (i.e., covering longer time-series) testing, and determining empirical relationships between a wider range of environmental parameters (e.g., irradiance, turbidity, dissolved organic matter, nutrient and chlorophyll-a concentrations, bird and fish abundance). Moreover, the experimental studies on the sensitivity of this indicator are also very recommended.

Conclusions

Twelve species were identified in the studied area of the Curonian Lagoon, where three species of algae (*Cladophora glomerata, Chara contraria* and *Chara aspera*) and angiosperms (*Potamogeton perfoliatus, Stuckenia pectinata* and *Myriophyllum spicatum*) dominated. Salinity-tolerant species (*Zannichellia palustris, Potamogeton rutilus,* all algae species except *Nitellopsis obtusa*) were restricted by salinity in the northern part of the study area. The relative coverage of *N. obtusa* increased with the water transparency (Secchi depth), whereas *S. pectinata* was tolerant to turbid waters. Filamentous algae and charophyte species preferred sheltered areas along the eastern shore of the lagoon. Based on the obtained correlations in this study, the community surface index (SI_{cm}) values decreased in the coastal areas with large wetlands and increased in the coastal areas without or with small wetlands. Therefore, the morphofunctional index has a potential to define an ecological status considering macrophyte communities in the transitional water bodies; however, more *in situ* (i.e., longer time-series covering different hydrometeorological conditions) and experimental testing is needed to quantify the sensitivity of SI_{cm} under eutrophication gradients such as water transparency and nutrient concentration.

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