

# The effect of underwater light availability dynamics on benthic macrophyte communities in a Baltic Sea archipelago coast

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**Abstract** Light availability and its variation have an impact on underwater vegetation. To study the impact at the macrophyte community level, we combined information from underwater vegetation inventories to in situ measured depth profiles of photosynthetically active radiation. The data were collected from the Baltic Sea archipelago of south-western Finland during the growing season in 2010. While macrophyte coverage was well explained by light variables in variance partitioning, the explained proportions were notably lower for both the species number and floristic similarity index. Light variables better explained the coverage of annual than perennial macrophytes, and from the algae groups, the green algae reached the highest explained proportion. As well as confirming that light availability has an important role in regulating the macrophyte growth density in the euphotic

zone, our results further indicate that intra-seasonal variability in light availability affects the macrophyte community structure.

**Keywords** Submerged aquatic vegetation · Community composition · Euphotic zone · Temporal variability · Coastal waters · Baltic Sea

## Introduction

Macrophyte communities support diverse ecological functions in aquatic environments (for review, see e.g. Carpenter & Lodge, 1986; Thomaz & Cunha, 2010; García-Llorente et al., 2011). For example, macrophytes support higher animal density and higher species diversity than nearby non-vegetated sediments by providing physical structures for other species (Boström & Bonsdorff, 1997; Lucena-Moya & Duggan, 2011). Additionally, they contribute to wave attenuation and sediment stabilisation (Terrados & Duarte, 2000; Gacia & Duarte, 2001), as well as to filtration of runoff (Schernewski & Schiever, 2002). The occurrence and state of the submerged macrophytes, in turn, are related to the availability of photosynthetically active solar radiation (PAR, 400–700 nm), which is efficiently attenuated as a function of depth due to absorption and scattering (Kirk, 2011). The attenuation efficiency is often illustrated by defining the euphotic depth at which

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1% of PAR entering the water remains and which reflects the lower limit of the zone where photosynthesis mostly occurs (e.g. Tett, 1990). The intensity of absorption and scattering depends on the concentration of optically active particles (OAPs) in water (Kirk, 2011). As the concentration of OAPs varies over time—for example, due to the dynamics of phytoplankton and changes in the particle supply provided by river runoff—the light attenuation potential of natural waters also shows great temporal variation (Dera & Woźniak, 2010). As different particles absorb and scatter radiation in different wavelengths, this spatio-temporal variation of the concentration of OAPs creates an underwater light environment which varies both qualitatively and quantitatively in space and time.

In the shallow coastal archipelago of south-western Finland, large seafloor areas have sufficient underwater light conditions to support photosynthesis (Tolvanen et al., 2013). Therefore, much of the primary production in the area is linked to seafloor macrophytes (Leppäkoski et al., 1999). In addition to challenging growing conditions, such as brackish water, annual ice cover and a short growing season, both the inter- and intra-seasonal changes in the underwater light field may be important stressors and thus also drivers for benthic ecosystem dynamics (Tolvanen et al., 2013). In addition, the northern Baltic Sea ecosystems are influenced by the marked deterioration in water transparency (up to a four metre decrease in mean Secchi depth) from the beginning of the twentieth century (Fleming-Lehtinen & Laamanen, 2012). These two processes, short-term light availability fluctuations and long-term water transparency deterioration, create an optically complex environment for macrophytes. Kautsky et al. (1986), among others, have shown that the depth penetration of bladderwrack (*Fucus vesiculosus*)—one of the key habitat-forming macroalgal species of the Baltic Sea—has declined in the Northern Baltic Sea during the twentieth century. Moreover, Snickars et al. (2014) pointed out that the bladderwrack communities in the SW-Finnish archipelago, which declined rapidly and even disappeared locally in the 1970s have not recovered since. In determining the lower depth limits of occurrences for macrophyte species, multiple simultaneous causes can be found, with a decrease in water transparency often being highlighted among the reasons (Rinne et al., 2011).

Most studies of underwater illumination dynamics and its impact on macrophytes have focused on a single species or taxon (Sand-Jensen et al., 2007), have been spatio-temporally limited or conducted in a controlled environment and therefore, lack natural fluctuations. This is partly due to the high cost in both time and effort of comprehensive underwater vegetation inventories, as well as the need to carry out such inventories in many different places. However, since environmental variations impact upon coastal systems at multiple spatial and temporal scales, a comprehensive understanding of the coastal systems' variability and functionality requires information from a range of scales (Boström et al., 2011). Furthermore, illumination conditions are often expressed as water transparency estimates measured by the Secchi disc method, the usability of which as a proxy for PAR availability is not necessarily straightforward in optically complex waters (Preisendorfer, 1986; Luhtala & Tolvanen, 2013). The Helsinki Commission's Underwater Biotope and Habitat Classification System, which is a compatible counterpart of the European Environment Agency's EUNIS Habitat classification system in the Baltic Sea (HELCOM HUB, see HELCOM, 2013), applies the photic—aphotic dichotomy at the first split-phase of the hierarchical classification. However, as the PAR availability is known to be highly variable in the Baltic Sea (Suominen et al., 2010a; Luhtala et al., 2013), this early-stage dichotomy, and the oversimplification of the light field it creates, may cause problems in habitat classification.

The aim of this study is to assess the role of underwater light availability for the macrophyte communities along the shallow coasts of the northern Baltic Sea. Our working hypothesis is that underwater light availability and its variation result in differences in benthic macrophyte communities. The communities are assessed by their cumulative macrophyte coverage, cover of specific taxonomic and functional groups, species richness and floristic similarity. To test this hypothesis, we utilised data from a macrophyte inventory (dive transects) and a dataset of in situ PAR measurements that were collected from the Baltic Sea coast of the SW-Finnish archipelago during the year 2010. In addition to light availability, selected aspects of the physical surroundings and environmental conditions were used as supporting material, while keeping the focus mainly on the impact of underwater light dynamics.

## Materials and methods

### Study area description

The Baltic Sea, as a relatively young marginal sea with negligible tidal activity, brackish water and seasonal ice cover, has a special combination of characteristics that distinguish it from the majority of the world's oceans and other sea areas (Leppäranta & Myrberg, 2009). In its optical properties, it resembles more coastal than pelagic ocean waters (Darecki & Stramski, 2004). The SW-Finnish archipelago (Archipelago Sea) is located in the northern part of the Baltic Sea and forms a specific part of this unique environment, with a complex mosaic of thousands of islands and a varying bathymetry (Granö et al., 1999). The average depth is about 20 m, with the deepest parts exceeding 100 m. The water flow is restricted by the bathymetric complexity and underwater thresholds, which is why turbid waters are efficiently retained within the area (Erkkilä & Kalliola, 2004). In this complex archipelago system, the growth conditions may exhibit remarkable geographical and seasonal variation.

The transition from the mainland towards the open sea is characteristic to the area in multiple ways (e.g. Suominen et al., 2010a), one evident example being the optical properties of sea water (Luhtala et al., 2013). On average, the euphotic depth increases from the turbid inner archipelago to clearer and less sheltered waters of the outer archipelago. The difference in euphotic depth can be four-fold between different parts of the archipelago. At a given location, up to a two-fold temporal euphotic depth variation occurs during the ice-free growing season (Luhtala et al., 2013). The region is at least partially ice-covered every winter (Kauppila & Bäck, 2001; Leppäranta & Myrberg, 2009).

Although salinity ranges from 5.0 to 6.5, there is no stable halocline (Suominen et al., 2010b). On the Baltic Sea scale, macrophyte species distribution is mainly determined by salinity, but within its sub-basins, other factors, such as water temperature, physical stress, bottom substrate and light availability, have a stronger impact on the structure of the macrophyte communities (e.g. Kautsky & van der Maarel, 1990; Kiirikki, 1996; Rinne et al., 2011). In general, the low salinity of the Baltic Sea results in low species richness because a limited number of species have adapted to the stressful living conditions at the

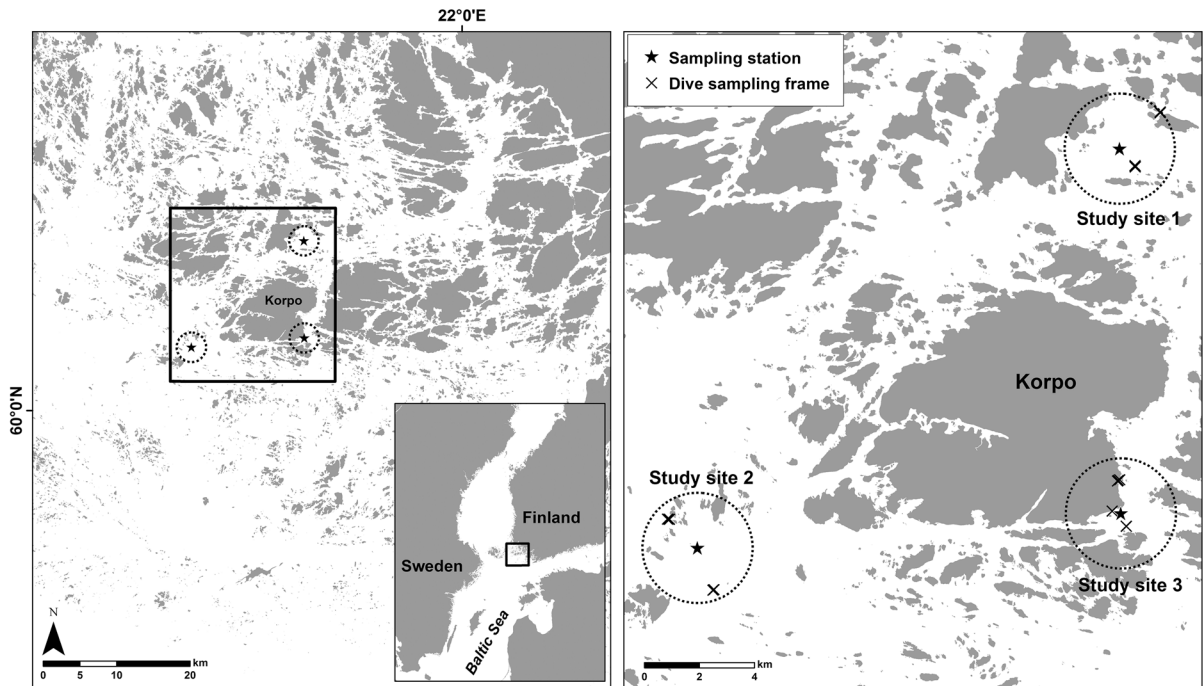
fringe of their salinity tolerance (Hällfors et al., 1981). The macrophyte communities in the area comprise a mixture of species with marine and fresh water origins.

Relatively high nutrient concentrations in the archipelago seawater (Hänninen et al., 2000; HELCOM, 2009) imply eutrophication in the area, where waters are regarded as nitrogen—rather than phosphorus limited (Hänninen et al., 2000; Tamminen & Andersen, 2007). The annual phytoplankton succession contributes to the spatio-temporal variation of the underwater illumination conditions. When sea ice melts in spring, the phytoplankton composition is dominated by diatoms and dinoflagellates. This is followed by a summer phytoplankton minimum, with a late-summer phytoplankton bloom dominated by nitrogen-fixing cyanobacteria (Hällfors et al., 1981).

### Field measurements and data sources

Data availability directed the choice of study sites: the locations of existing underwater PAR measurements and dive transects were compared, and based on their geographical distributions, three focus areas with adjacent PAR and vegetation inventories were selected. The buffer distance of 2 km was regarded as a suitable compromise between the representativeness of the water quality measurements and adequate sample size in macrophyte community data. The selected sites represented the best sample cases available, as most dive transects were located too far from the PAR sampling stations. The study area is located in the middle of the SW-Finnish archipelago, approximately 40–60 km from the mainland. The three study sites, numbered from 1 to 3, are located in the north, south-west and east of the island of Korpo (Fig. 1).

The in situ PAR measurements were extracted from a larger sampling dataset collected in 2010, when each sampling station was visited eight times at approximately three-week intervals, from late April to early October, to cover the temporal variability of the growing season. The entire dataset and the data handling procedure have been presented in detail by Luhtala et al. (2013). The instruments used for PAR measurements were LI-190 for incoming light above the sea surface and LI-193 for underwater light (LI-COR Biosciences, USA). They both measure radiation as  $\mu\text{mol s}^{-1} \text{m}^{-2}$  in the 400–700 nm wavelength area. At each sampling station, the underwater



**Fig. 1** Study area and the sampling sites. *Dashed circles* around the sampling stations (2 km buffer) delimit the extent of the study sites, within which all the vegetation information is collected (the dive sampling frames)

measurements began by measuring just below the sea surface and proceeding downwards at 1 m intervals. The procedure resulted in light profiles that represent the relative radiation shares of each measurement depth compared to the surface value (100%). The underwater PAR values were first normalised according to the readings of the terrestrial PAR sensor and then converted to relative values based on the reference level set by the surface measurement.

The relative amounts of light were interpolated for each dive frame according to their respective depth. With this procedure, each dive frame has an individual estimate of the illumination conditions, instead of utilising parameters that describe the attenuation conditions of the whole water column (such as  $K_d$  or euphotic depth). The PAR values measured at the sampling stations were considered to adequately represent their immediate surroundings and for each dive frame the reference values were used as such without any spatially adjusted corrections. Furthermore, the relative values were derived separately for all eight measurement weeks, and the median, minimum and total range of radiation were defined for each study frame. As the study focusses on light limitation rather than photoinhibition, maximum PAR values

were regarded as redundant. Simultaneously with underwater PAR, three water quality parameters, i.e. temperature, salinity and pH, were measured with a YSI 6600 V2 multi-parameter sonde (YSI Inc., USA). However, they showed only little geographical variation (median temperature 10.0–13.4°C; median salinity 6.0–6.3 PSU; median pH 8.1–8.4) and were therefore excluded from further analyses.

The dive data were gathered for the VELMU programme (The Finnish Inventory Programme for the Underwater Marine Environment, see <http://www.ymparisto.fi/en-US/VELMU>). To allow full comparability to the water quality data, we used only data sampled during the same growing season in 2010. However, in comparison to eight visits per water quality station, the vegetation inventory was conducted only once in August–September. In sampling, the SCUBA diver used a line sampling method, in which a dive transect was inventoried by following a rope sunk to the seafloor. Using a 1 m × 2 m sampling frame, information on macrophyte species and their relative cover (1–100%; single observations 0.1%) and cover of different bottom substrate types (1–100%) was recorded each time a distinctive change in the bottom type or macrophyte community

occurred, or when the diving depth decreased by 1 m (for detailed method description, see Rinne et al., 2011). During the vegetation inventory, the species were identified to the highest level possible in the field conditions. Typically, a dive transect consisted of 2–10 sampling frames, depending on the seafloor slope and heterogeneity of the environment.

In this study, the individual dive frames were considered as independent dive sampling units. The topmost dive frames were discarded from our data because the shallowest water is regulated by physical strain (due to ice scraping and waves) rather than light (e.g. Kiiirikki, 1996). Therefore, only frames below 1.5 m were considered. With the set boundary conditions, 30 dive sampling frames were included in the final dataset: nine frames at site 1 (average depth 3.9 m; range 1.7–9.4 m), nine at site 2 (8.0 m; 1.6–16.1 m) and twelve at site 3 (6.5 m; 2.8–8.5 m).

In addition, information on seafloor substrates and mussel cover (*Mytilus edulis*) was extracted from the VELMU dive data. In the analyses, mussel cover represented interspecific competition and its effect of macrophyte colonisation success. Bottom substrate types ranged from mud to rock, and they were divided into two groups: substrates smaller than 6 cm in diameter and substrates larger than that. The relative coverage of larger substrates was defined to indicate the availability of hard substances. In addition, the number of substrate types was calculated to show the possible heterogeneity within the study frames. The proportion of land around the dive frames was assessed to provide a proxy for anthropogenic influence from terrestrial sources. The proportions were computed using a buffer with radius of 3 km to include an area large enough to show an effect. The land area buffer (3 km) should not be confused to the buffer utilised in data selection (2 km). The fetch dataset represents the physical stress caused by wave activity to the macrophyte communities by estimating site-specific wave generation potential using average fetch lengths (Tolvanen & Suominen, 2005).

## Statistical analyses

### Data processing

The available datasets were processed into groups of response variables, bottom variables (BV), geographic distance (GD), variables describing the spatial

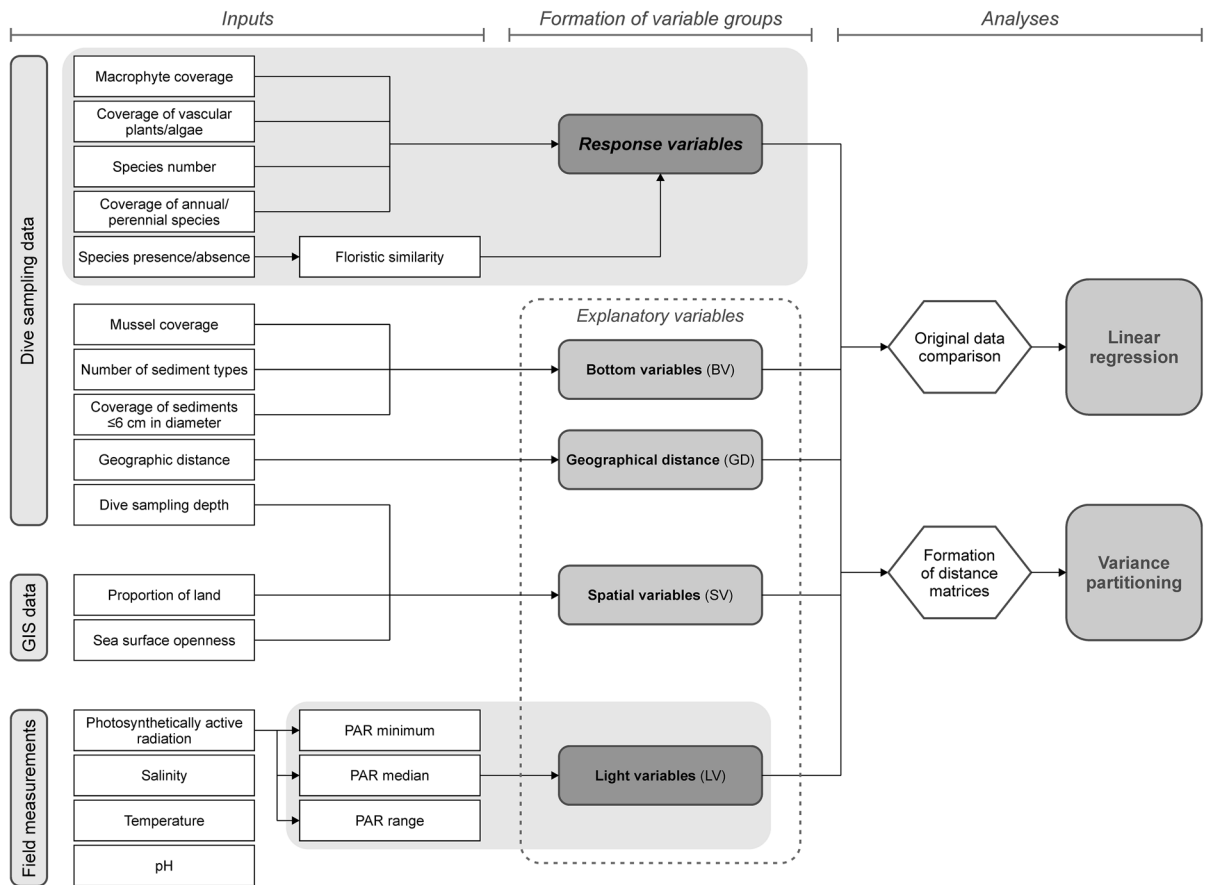
surroundings (SV) and light variables (LV) (Fig. 2). The response variables describe the macrophyte communities from eight perspectives: macrophyte total growth density (macrophyte coverage), macrophyte species diversity (species number), floristic similarity and the coverages of annual macrophytes, perennial macrophytes, green algae, brown algae and red algae. The coverage values are sums of all the respective species indicating cumulative cover and can therefore exceed 100% due to a multi-layered canopy structure, including the presence of epiphytic algae. The division of macrophytes into annual and perennial species was conducted according to Leinikki & Backer (2004) and Kotta & Möller (2014). The floristic similarity between the dive frames was calculated using the Jaccard similarity index (Jaccard, 1912) in R environment with the Vegan package (Oksanen et al., 2013).

The BV group was formed from variables describing the sea bottom of the respective dive frames. The variables are mussel coverage, number of bottom substrate types and the relative coverage of substrates larger than 6 cm in diameter, the latter indicating the availability of hard substrates. The GD group included only a measure of the geographic distance between the dive frames. For that, the Euclidean distance was regarded sufficient descriptor because of the small overall size of the study area. The values were log transformed prior to further analysis. The SV group consisted of dive sampling depth, proportion of land surrounding the dive sampling frames and fetch. The fetch values were log transformed prior to the analyses. The LV group included the PAR minimum, median and range at the depth of the dive frame. Finally, the degree of spatial autocorrelation in the selected response and explanatory variables was assessed by Moran's I test, which was performed with the ape package in R (Paradis et al., 2004).

### Analyses

To quantify the influence of explanatory variables on the response variables, the variance partitioning method suggested by Borcard et al. (1992) was utilised. The method has been successfully applied to studies of macrophyte community structure by, for example, Alahuhta et al. (2011, 2014) and is especially good when working in environments where complementary sets of hypotheses may be invoked to explain





**Fig. 2** Origins of the datasets, formation of variable groups and the main analyses performed. The main variables are highlighted with grey background shading

the ecological variability (Legendre & Legendre, 2012). This is highly beneficial regarding the stated variability of the study area. In order to execute the variance partitioning, the data were first transformed into Euclidean distance matrices, which increased the number of observations from 30 (the number of dive sampling frames) to 435 (the number of frame comparisons). The usage of distance matrices allowed the direct inclusion of floristic similarity as dependent and geographic distance as a control variable in the conducted analyses. The variation was partitioned with partial linear regression (pLR) in R environment with the Vegan package (Oksanen et al., 2013). A more detailed description of the process can be found in Legendre & Legendre (2012).

In the first phase of this study, the variation of macrophyte community structure was partitioned into four individual and twelve joint fractions: the pure

effect of (1) light variables (LV), (2) bottom variables (BV), (3) spatial variables (SV) and (4) the geographic distance (GD). The fractions from 5 to 15 were combinations of those above. The 16th fraction was the unexplained variation of the analysis. To gain unbiased estimation, the variation explained by each variable group was evaluated with adjusted  $R^2$  (Peres-Neto et al., 2006). The significance of pure fractions was obtained with the Monte Carlo permutation test (1000 permutations,  $\alpha$  0.05). In the approach, individual explanation fractions may result in negative readings (Legendre, 2008; Legendre & Legendre, 2012). In this study, all negative values were regarded as zero percentages in further comparisons.

The importance of the different aspects of the light variables (minimum, median, range) to the response variables was assessed by further variance partitioning and additionally by linear regressions. The aim was to

identify whether the macrophyte species distribution is most affected by the poorest light availability conditions, general accessibility to illumination or variability (or stability) of light conditions. The second variance partitioning was conducted identically to the first and resulted in three pure fractions (PAR minimum, PAR median and PAR range) and four joint combinations of PAR variables. Linear regressions were performed to include also analysis with absolute values of the original datasets. However, to maximise the sample size, the regressions were computed only for the response variables including the entire dataset, i.e. total macrophyte coverage and species number (floristic similarity is not included here as it is a distance-based variable). All regression results were examined at the 5% significance level.

## Results

### Spatial variation of light and biological variables

The spatial surroundings (SV) had rather similar conditions within the study sites, the individual frames being close to each other, but there were more notable differences between sites. The study site 3 was most sheltered, where the proportion of land reached 50% within the 3 km buffer zone surrounding each dive sampling frame. By comparison, in those frames within study site 2, situated in the south-west, further away from the large islands of the archipelago, the proportion of land was approximately 5%. The northernmost study site (site 1) was nearest to the mainland and here the proportion of land ranged from 10 to 20% for the individual frames.

Further, both bottom variables and macrophyte compositions (for species list, see Online Resource 1) varied markedly between study sites (Fig. 3). At site 2, the dive sampling frames were mainly on hard bottom (seafloor substrate >6 cm) and were relatively deep with almost half of the frames deeper than 10 m. No vascular plants were registered at all, with red algae most abundant at this site. Site 1 had less hard substrates, and although the coverage of red algae was lower compared to other sites, both green algae and vascular plants were more abundant. At site 3, most frames and particularly the deepest showed low coverages of both algae and vascular plants. In general, the share of species number between annual

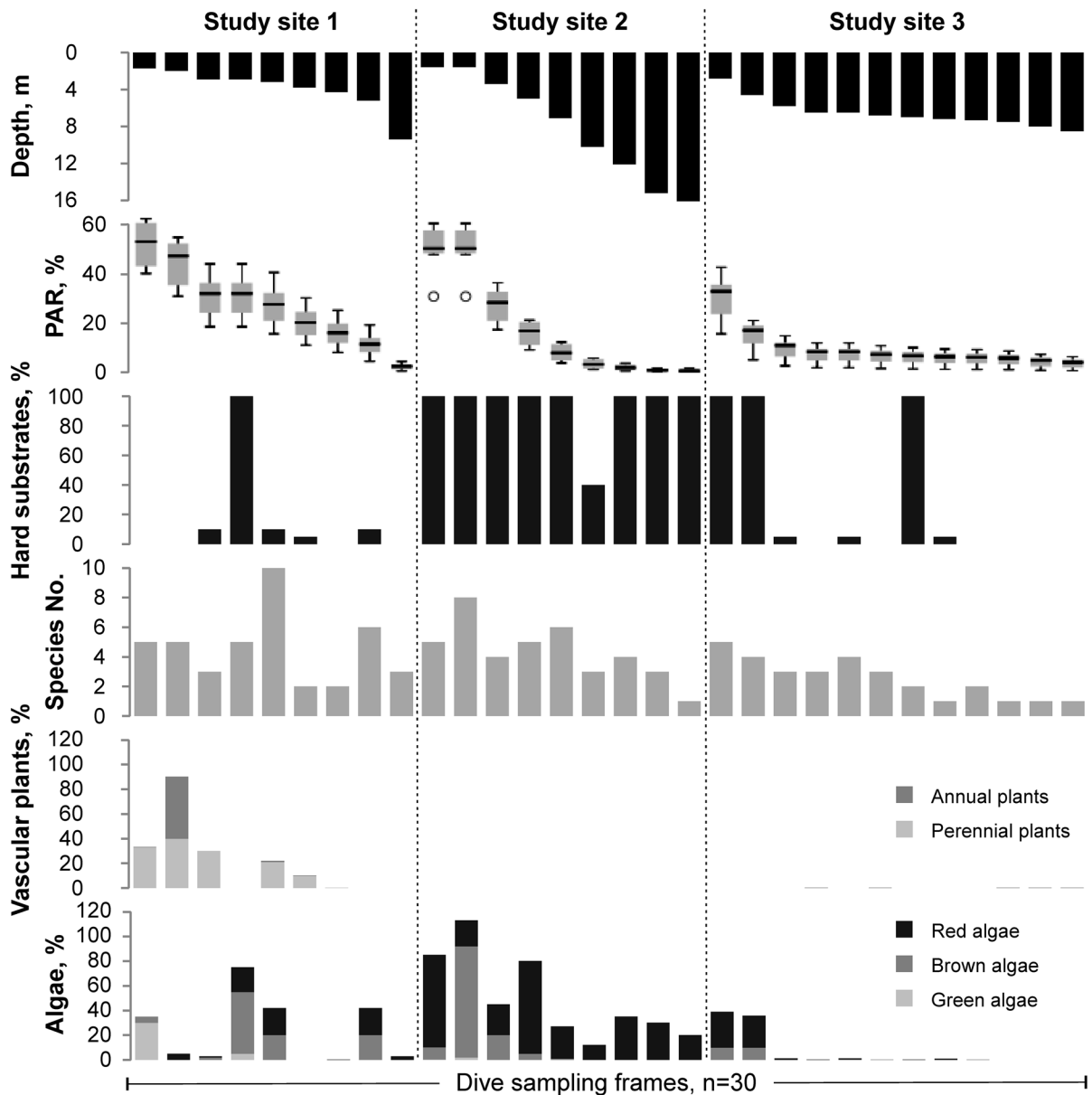
and perennial macrophytes was rather equal at all study sites, perennial species being somewhat more common at site 2 and annual species at site 3. The overall species number roughly decreased towards the deeper frames, except in site 1, where the number varied more irregularly among the frames. Mussels were present at all study sites but were most abundant at site 2. Most of the variables showed significant spatial autocorrelation. Only the coverages of green and brown algae from the response variables and mussel coverage, PAR minimum and PAR median from the explanatory variables showed no statistically significant spatial autocorrelation. The descriptive statistics of all the study variables are presented in Online Resource 2.

The deepest frames, where vascular plants were identified, were 8.5 m for annual and 4.3 m for perennial plants. These depths respond to median PAR levels of approximately 4 and 16%, respectively. Green algae were recorded down to 7 m depth (~7% PAR left), whereas brown algae were observed only 30 cm deeper (7.3 m; ~6%). Deeper frames were dominated by red algae, and the deepest observation was made at a depth of 16.1 m. However, in general, there were six dive frames where the PAR availability had dropped below 1% at least once during the eight occasions of PAR measurements. For two of these, the median PAR value also remained lower than 1%. The dominant species at these frames was the red algae *Hildenbrandia rubra*.

### The explanation potentials derived by variance partitioning

In the variance partitioning analysis, the overall explanation rates ranged from less than 20% to almost 70% (Table 1). In general, the explanatory variables explained greater fractions of total variation in pure form than in joint combinations of two or more variables. All the pure fraction results that had explanation power higher than 1% were statistically significant. For most cases, the light variables (LV) had the greatest effect on response variables. On average, the pure LV fraction explained 24% of the variation in the eight response variables. Bottom variables (BV) explained 2%, spatial variables (SV) 6% and geographic distance (GD) 1%.

However, there were deviances from this overall order when exploring the response variables separately.



**Fig. 3** Selected characteristics of dive sampling frames presented on top of each other so that each column of bars represents one sampling frame. The three study sites are separated by grey dashed lines. Each site includes data from several dive transects, the frames of which are re-organised according to their sampling depth. PAR availability (%) refers to the proportion of photosynthetically active radiation left at the

depth of each sampling frame. The boxplots illustrate the full range of PAR availability detected within the eight measurement occasions during a growing season. Hard substrates (%) refers to the areal coverage of sea bottom where substrates >6 cm are found. Coverages of macrophytes (algae and plants) are cumulative and may therefore exceed 100%

The light variables were most important for macrophyte coverage, species number, annual and perennial macrophyte coverage, green algae coverage and brown algae coverage. The explanation rate of light variables was

exceptionally high for macrophyte coverage (46%) and green algae coverage (55%). The effect of bottom variables was highest for red algae coverage (9%), whereas spatial variables explained most of the floristic



**Table 1** Explanation fractions of variable groups derived by variance partitioning

	Macrophyte coverage (%)	Species number	Annual macrophytes (%)	Perennial macrophytes (%)	Green algae (%)	Brown algae (%)	Red algae (%)	Floristic similarity (Jaccard)
Light variables (LV)	0.46	0.08	0.36	0.22	0.55	0.22	0.03	0.02
Bottom variables (BV)	0.03	0.01	0.00	0.02	0.00	0.01	0.09	0.02
Spatial variables (SV)	0.11	0.03	0.02	0.07	0.05	0.10	0.07	0.05
Geographic distance (GD)	0.04	0.01	0.00	0.00	0.00	0.00	0.00	0.02
LV + BV	0.00	0.02	(−0.01)	0.00	0.04	(−0.01)	0.00	0.00
LV + SV	0.01	0.00	0.00	0.02	0.00	0.00	0.07	(−0.01)
LV + GD	0.00	(−0.01)	0.00	(−0.04)	(−0.05)	(−0.09)	(−0.02)	0.01
BV + SV	0.00	(−0.01)	0.01	0.01	0.00	0.00	0.00	0.00
BV + GD	0.00	(−0.01)	0.01	0.00	0.00	0.00	0.00	0.01
SV + GD	0.00	(−0.01)	0.00	0.00	0.00	0.00	0.01	0.03
LV + BV + GD	0.00	0.00	0.01	0.02	0.01	0.00	0.00	0.00
LV + BV + SV	(−0.01)	(−0.01)	0.00	0.00	0.01	0.01	0.00	0.00
LV + SV + GD	0.01	0.01	0.00	0.03	0.00	0.00	0.06	0.01
BV + SV + GD	0.02	0.01	0.01	0.01	0.00	0.00	0.00	0.01
LV + BV + SV + GD	0.01	0.00	0.00	0.00	(−0.01)	0.00	0.00	0.00
Unexplained	0.31	0.83	0.58	0.60	0.34	0.66	0.67	0.82

The negative values should be regarded as zeros

similarity variance (5%). The proportions explained by pure geographic distances remained very low. The highest proportion was recorded for macrophyte coverage (4%). The explanation rates of the joint variables remained small. In most cases, their shares compared to pure effects of LV, BV and SV were negligible and negative readings were often recorded. The greatest exceptions were the joint effect of light variables and spatial variables for red algae coverage (LV + SV = 7%, LV + BV + GD = 6%) and the joint effect of light variables and bottom variables to green algae coverage (LV + BV = 4%).

The total fraction of explained variation from each response variable was further examined to assess the role of underwater PAR more closely. The proportion explained by light variables—pure or joint fractions—varied markedly, ranging from a combined share of <25 to >90%. With macrophytes in general, the influence of light variables is greater to the cumulative coverages (71%) than to the species number (64%), and furthermore, the effect is more notable for the species number compared to the floristic similarity (22%). Of these explained shares, the pure LV fractions were more important than the combined joint LV fractions for macrophyte coverage (66%

compared to 4%) and species number (50 and 14%), whereas the pure and joint fraction were almost equally influential for floristic similarity (11 and 12%).

For annual macrophytes, the pure fraction of LV covered as much as 84% of the total explained fraction. Although lower, the coverage of perennial macrophytes was also mostly explained by pure LV fraction (59%), whereas the proportion of the joint fraction of perennials was notably higher (24%) compared to annual macrophytes (2%). For the three algae groups, the importance of light variables was highest for the green and lowest for the red algae. Of the relatively high total proportion of explained variation in the green algae coverage, the effect of other variables beside LV remained very low. The pure fraction of LV explained more than 80%. After adding the proportion of joint LV variables (8%), the share of other fractions remained below 10%. For the brown algae coverage, the pure effect of LV covered only 65%, leaving the other variables' explanatory influence to more than 30%. Finally, for the red algae coverage, the effect of pure LV was 8%. However, the joint fractions with LV as one of the variables explained almost 40%. Therefore, about half of the

red algae coverage (53%) was explained by parameters other than underwater PAR.

#### The relationship between PAR variables and macrophyte communities

Even though the light variables (median, minimum and range of PAR availability) were all strongly and positively correlated with each other (Spearman correlation  $>0.95$ ,  $P$  value  $<0.001$ ), they explained changes in the biological response variables to a different degree. Differences can be seen in the explanation potentials derived by the variance partitioning that was further conducted for PAR variables separately (Table 2). The internal importance of light variables varied as the most important light variable did not always remain the same among the response groups.

Similarly, the overall explanatory capacity derived by the regression analyses varied notably between the total macrophyte coverage and the species number. For the macrophyte coverage, the coefficients of determination,  $R^2$ , was 0.67 for the PAR minimum (Fig. 4a) and 0.66 for the PAR median, although the same for PAR range was only 0.50. In the variance partitioning of macrophyte coverage, while the individual PAR variables gained very low explanation values, all the joint fractions that include both minimum and median were relatively high (Table 2). For species number, the internal differences among the PAR variables were lower in the regression analyses (0.31–0.38), the PAR range having the highest coefficient (Fig. 4b). In the variance partitioning of species number, the PAR range was the only variable having

some importance in the pure fractions, and it is included in the highest joint fractions. For floristic similarity, the total explanation share remained very low, the pure PAR minimum fraction having the greatest value. All the pure fractions for all macrophyte variables with explanation power were statistically significant. Regression analyses were not calculated for floristic similarity because of its distance-based nature.

Annual macrophytes reached higher overall explanation levels than perennial ones, indicating some differences in responses to PAR availability variables between the life strategies. Annual macrophytes had strong emphasis on joint fractions (particularly min + med and min + med + rng), whereas perennial macrophytes had some importance for all the pure variables, the overall effect still being higher within the joint fractions. Furthermore, the three algae types indicated differences in their relationship to PAR levels. For green algae, the PAR minimum clearly reached a greater explanation power than the PAR median (0.20 compared to 0.09), whereas the PAR range did not result in a statistically significant value. By contrast, for brown algae, none of the pure fractions gained importance and the highest joint fraction included all variables. Comparisons could not be made for red algae as the variance partitioning resulted in negligible readings.

## Discussion

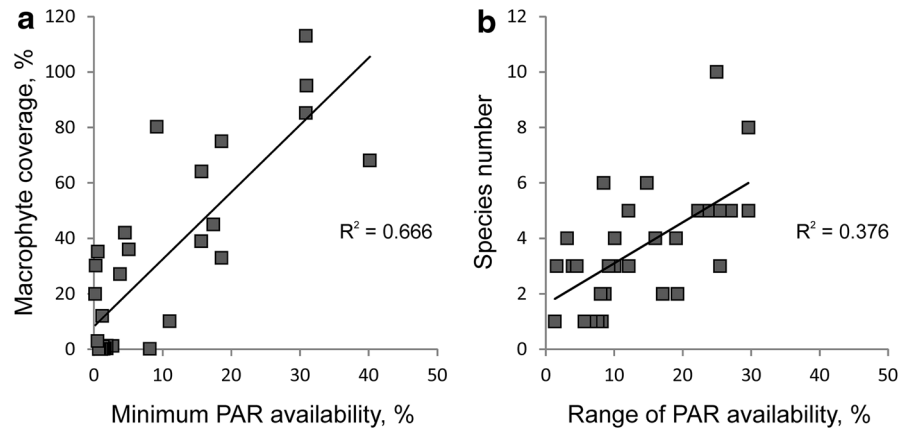
Our results showed that the availability of underwater light has a significant impact on the regulation of

**Table 2** Explanation fractions of PAR variables derived by variance partitioning

	Macrophyte coverage (%)	Species number	Annual macrophytes (%)	Perennial macrophytes (%)	Green algae (%)	Brown algae (%)	Red algae (%)	Floristic similarity (Jaccard)
PAR minimum	0.00	0.00	0.02	0.01	0.20	0.00	0.00	0.02
PAR median	0.01	0.00	0.00	0.03	0.09	0.00	0.00	0.01
PAR range	0.00	0.02	0.00	0.02	0.00	0.00	0.00	0.00
min + med	0.20	0.00	0.15	0.07	0.25	0.02	0.00	0.00
med + rng	0.00	0.01	0.00	(−0.02)	0.19	0.02	0.00	0.00
min + rng	0.01	0.00	0.00	(−0.01)	0.20	0.01	0.00	0.00
min + med + rng	0.24	0.06	0.21	0.10	(−0.39)	0.09	0.01	0.00

The negative values should be regarded as zeros. In the joint fraction, min, med and rng refer to PAR minimum, PAR median and PAR range, respectively

**Fig. 4** Macrophyte coverage in relation to minimum PAR availability (a), and species number in relation to PAR range (b)



macrophyte assemblages at deeper depths. Not only does light availability limit the depth penetration of macrophytes physiologically, but it also plays an important role in regulating the growth density of the euphotic zone. Our results support the earlier findings of studies from various shallow water environments. Duarte (1991) demonstrated that a link between decreased light availability and reduced seagrass biomass occurs in coastal waters around the world. In the Baltic Sea, Krause-Jensen et al. (2007a, b) have shown that limitations in underwater light availability alter the community density of marine macroalgae. Similarly, macrophyte biomass or cover has been connected to light conditions in other coastal environments, such as Mediterranean lagoons (e.g. Obador & Pretus, 2010; Antunes et al., 2012) or along the western coast of Florida (e.g. Livingston et al., 1998; Hoyer et al., 2004), as well as in freshwater ecosystems (e.g. Wallsten & Forsgen, 1989; Robin et al., 2014).

Although the focus of this study was on light availability, there are of course other factors affecting macrophyte growth. For example, salinity is one of the key forces driving the general distribution of macrophytes in the Baltic Sea (e.g. Hällfors et al., 1981; Rinne et al., 2011), as well as elsewhere in fluctuating salinity conditions (e.g. Antunes et al., 2012). Bottom variables (BV), such as bottom substrate type and substrate heterogeneity, are important characteristics explaining which macrophytes can colonise and thrive in an area (Sousa, 1979; Appelgren & Mattila, 2005; Malm & Isaacs, 2005). Both hard and soft bottom types were available in the area studied. As various substrata were present and variously colonised, the

substrate availability hardly limits the formation of macrophyte communities within the studied area. One plausible mechanism to explain the higher importance of the bottom variables to red algae coverage (9%) may originate from a depth-induced increase in sedimentation and the lower availability of hard substrata in deeper frames mainly colonised by red algae (Kiirikki, 1996; Eriksson et al., 1998).

Eriksson et al. (2006) suggested that lower light availability limits the diversity of macrophyte assemblages by increased resource competition. The removal of suitable growing areas by reduced light availability forces species to move upwards, which, in turn, may increase interspecific competition in more shallow regions (Schmieder, 1997). The diversity of macroalgae is often highest at those depths of intermediate disturbance and multiple disturbance factors (Kautsky & Kautsky, 1989; Krause-Jensen et al., 2007b). In the variance partitioning, the macrophyte species number and floristic similarity gained lower explanation rates than the overall macrophyte coverage. The northern Baltic Sea is a challenging environment for both marine and freshwater organisms and the number of species is naturally low (Hällfors et al., 1981). Therefore, it is plausible that the limited sampling and low variation in species number and floristic similarity were themselves the main causes of low explanation rates and the connection could have been clearer with higher species diversity.

Of the three algal groups, light availability had the highest explanation rate of the cover of green algae, whereas red algae cover was only weakly explained by PAR parameters. Red algae coverage was not limited only to the deepest areas, being high on the shallowest

parts also. As red algae were present at all the depths studied, no clear pattern related to light reduction and their abundance could be found. Talarico & Maranzana (2000) suggested that red algae are a diverse group and both light-intensity and light-quality adapters. Thus, they are able to outcompete other algal groups in areas with low light availability while being able to maintain a niche at lower depths.

Light availability better explained the variation in coverage of annual than perennial macrophytes. This result corresponds with the earlier findings of Rinne et al. (2011), who pointed out how limitations in water transparency favour annual macrophyte species in the Baltic Sea. In addition, Worm et al. (1999) showed that the cover of perennial *Fucus vesiculosus* was negatively correlated with that of annual algae. These findings indicate that with lower light availability, annual macrophyte species have an increased potential to outcompete perennial species and thus alter the structure of macrophyte assemblages.

Previous studies have shown that submerged macrophytes interact with the environment across multiple spatial scales and that macrophyte species have strong individualistic responses to environmental disturbances (Bulleri et al., 2012; Kendrick et al., 2008; Kotta et al., 2014). The notably low rates of joint fractions and higher rates of individual fractions in the variation partitioning analysis indicate low or non-existent variable collinearity and thus further support the claim of complex environment with multiple co-existing stressors. Despite the challenges in studying macrophytes at the community level, an increasing need to apply and evaluate landscape level analytical techniques in coastal ecosystems has been identified (Boström et al., 2011).

This study can be seen as a preliminary trial. Because it relied on existing data sources, the setting of the study, i.e. the study area locations and the sample number, was not ideal, even though the data itself were of high quality and accuracy (in situ measured PAR profiles and dive sampling data). As the number of observations was low and the data showed spatial autocorrelation, caution should be used when interpreting the results. Due to the eminent risk of type II error, the control of PAR availability to macrophyte community structure cannot be ruled out even when the analyses showed no significant statistical connection. Despite the limitations of the data and consequent weaknesses in the statistical analyses,

the tested study methods proved to be suitable and provided useful insights to the research subject.

Our results further indicate that in addition to the overall amount of illumination, the intra-seasonal variability in light availability may also have an impact on the community structure of marine macrophytes. Even though both the dataset and its spatial representativeness are relatively small, they nonetheless provide some indications of the importance of seasonal variability in underwater light availability to these communities. At the very least, species number showed a marked connection to the PAR range. Thus, it would be beneficial to study the light variability and its impact further, for instance, by applying a more spatio-temporally comprehensive PAR dataset or alternatively utilising a light sum as a possible explanatory variable. A reasonable estimate of seasonal fluctuations cannot be reached with information that represents only a narrow time frame, such as from field measurements focused on one short sampling period. The minimum values of the growing season will easily be missed if using only a limited dataset on illumination conditions and, more obviously, the understanding of the overall range of the variability will remain poor.

It is noteworthy that multi-dimensionally fluctuating phenomena fit poorly to dichotomies where the feature either exists or not. Therefore, the photic-aphotic dichotomy used in both the HELCOM HUB and EUNIS classification systems poorly describes the real world dynamics. In the rather limited dataset of this study, the commonly used delineation of 1% PAR availability did not fully represent the growth limit of underwater vegetation, as some macrophytes (mainly red algae) were also found below the depth which corresponded to a 1% illumination. On the contrary, the observed depth limits for macrophytes other than red algae generally corresponded better with the findings of Duarte (1991), who found that seagrasses extend to depths of 11% illumination.

The presented findings confirm our hypothesis: underwater light availability and its variation result as differences in benthic macrophyte community structure. As a possible implication, a further deterioration in underwater light conditions may reduce the quality of the habitats, alter the ecological interactions as well as endanger the ecological functionality of the littoral zone. Therefore, knowledge of the community level responses of macrophytes to changes in underwater

light conditions provides crucial information for both the management and preservation of the coastal zone, as well as for modelling the underwater habitats. Since fluctuations in underwater light availability can be important in defining macrophyte community structures, the PAR variability should also be included in modelling, in addition to more generalised information on water transparency.

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