Functional traits of marine macrophytes predict primary production

Holger Jänes[a*], Jonne Kotta[a], Merli Pärnoja[a], Tasman P. Crowe[b], Fabio Rindi[c] and Helen

Orav-Kotta[a]

[a] Estonian Marine Institute, University of Tartu, Mäealuse 14, 12618 Tallinn, Estonia

[b]Earth Institute and School of Biology and Environmental Science, University College

Dublin, Dublin, Ireland

[c]Dipartimento di Scienze della Vita e dell'Ambiente, Università Politecnica delle Marche, Via

Brecce Bianche, 60131 Ancona, Italy

Corresponding author: holger.janes@sea.ee

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Summary

1. The relationship between community structure and the functioning of ecosystems is the subject of ongoing debate. Biological or functional trait-based approaches that capture life strategy, morphology and behavioural characteristics have received far less attention than taxonomic diversity in this context, despite their more intuitive link to ecosystem functioning.

2. Macrophyte primary production underpins aquatic food webs, regulates benthic and pelagic ecosystems and is a key aspect of the global carbon cycle. This study spans a range of aquatic biomes across Europe and aims to examine potential for predicting primary production of macrophyte communities based on the functional traits of species and identify the traits that are the most informative indicators of macrophyte production.

3. Macrophyte primary production was assessed based on the oxygen production of the whole community, linked to biomasses of selected biological traits derived of its component species and analysed using the novel boosted regression trees (BRT) modelling technique.

4. Results showed that functional traits derived from macrophyte community data explained most of the variation in primary production of macrophyte communities without the need to incorporate environmental data on the habitats. Macrophyte primary production was influenced by a combination of tolerance, morphology and life habit traits; however tolerance traits contributed most of variability in macrophyte primary production when all traits were analysed jointly.

5. The study also showed the existence of trait clustering as the studied trait categories were not fully independent; strong interlinkages between and within trait categories emerged.

6. Our study suggests that functional trait analysis captures different aspects of ecosystem functioning and thereby enables assessing primary production of macrophyte communities over geographically distinct areas without extensive taxonomic and environmental data. This could result in a novel framework through which a simplification of the general procedure of production estimations and comparisons across environmental gradients can be achieved.

Key-words: algae, benthic communities, biological traits, community ecology, community production, ecosystem ecology, ecosystem functioning, functional characteristics

Introduction

A key debate in current ecology focuses on the relationship between community structure and the functioning of ecosystems (Hooper *et al.* 2005). This debate originates from the historically poor interaction between community and ecosystem ecology, despite general consensus that community level phenomena should translate directly into various ecosystem processes (Naeem *et al.* 2002). Following an accumulation of evidence from experimental ecology in the last two decades, strong but multifaceted relationships between various measures of community structure and functional properties of ecosystem have been established (Schmid *et al.* 2000; Cardinale *et al.* 2011; Hooper *et al.* 2012). Importantly, the studies also suggested that ecosystem functioning is closely linked to ecosystem services, which are becoming central to environmental policy, management and spatial planning (Perrings *et al.* 2011; Hauck *et al.* 2013; Sutton-Grier *et al.* 2014). It is currently believed that

certain types of community elements are needed to maintain the functioning and stability of ecosystems which are also linked to ecosystem services such as the provision of food, clean water and nutrient cycling. Therefore, cost-effective tools are required for assessing and indicating ecosystem functioning as well as the effects of human activities upon it (de Groot *et al.* 2010; Kristensen, Baattrup-Pedersen & Andersen 2012).

Traditionally, assessments of biodiversity-ecosystem functioning relationships have been based primarily on taxonomic classification, abundance and diversity estimates (Bruno *et al.* 2005; Tittensor *et al.* 2010; Isbell *et al.* 2011; Wardle *et al.* 2011), whereas trait-based applications that also refer to life strategy, morphology and behavioural characteristics have received far less attention, despite a more intuitive potential link to important aspects of ecosystem functioning (Chave *et al.* 2009; Cadotte, Carscadden & Mirotchnick 2011). Biological or functional trait analysis (FTA) has been proposed as a suitable method for relating community traits to ecological functioning. The aim of this approach is to provide an overview of ecosystem functioning based on the biological features of its components (Bremner 2008). For example, FTA can capture a mixture of life history, morphological and behavioural characteristics of species present in a community and use them to indicate ecosystem functioning. During the past decade, significant progress has been made in applying this approach to marine benthic assemblages (Bremner 2008; Marchini, Munari & Mistri 2008; Van Der Linden *et al.* 2012; Bolam & Eggleton 2014). Moreover, taxonomically distinct organisms may possess similar traits, which enable the FTA approach to be used for describing functional processes, which may be consistent between different taxonomic groups (Dolédec, Statzner & Bournard 1999). FTA can also be applied over extensive geographical areas where variation in taxonomic identities for functionally similar species make traditional species-based estimates challenging (Statzner, Hildrew & Resh 2001). Many

studies have examined linkages between community processes and prevalence of various functional traits in terrestrial ecosystems (Lavorel & Garnier 2002; de Bello *et al.* 2010; Finegan *et al.*, 2015). However, none of these studies actually combined community functioning and associated structure elements (traits) in the same experimental framework, but rather used compiled information from various databases (but see a good example by Conti & Diaz 2013). This hinders their ability to draw robust conclusions about relationships between functional traits and community or ecosystem functioning. Therefore, the extent to which the structure and dynamics of ecological communities can be predicted from the traits of their component species is still one of the most important questions in ecology (see e.g. Sutherland *et al.* 2013).

Primary production supports food webs, regulates terrestrial as well as aquatic ecosystems, and is a key aspect of the global carbon cycle (Thompson *et al.* 1996; Field 1998; Tynan 1998; Zavala Sansón & Provenzale 2009). In terrestrial ecosystems, primary production is mainly performed by vascular plants whereas in aquatic environments, algae carry out almost all photosynthesis and vascular plants contribute only a small fraction (Field 1998). Together with the expanding human population, near-coastal areas are impacted by multiple anthropogenic stressors and in such habitats benthic macrophytes contribute the majority of primary production. These ecosystems require actions to reduce and mitigate human impacts on community structure, ecosystem functioning and ecosystem services. Traditionally, the rate of benthic primary production has been predicted based on various abiotic and biotic factors such as light, temperature and nutrient availability, efficiency of nutrient uptake and assimilation, as well as by chemical and physical processes within an ecosystem (Best *et al.* 2001; Gattuso *et al.* 2006; Gruner *et al.* 2008). Alternatively, macrophyte primary production may be viewed as a product of the combined contribution of each species in a community

(Binzer, Sand-Jensen & Middelboe 2006; Pärnoja *et al.* 2014) such that variation of macrophyte species biomass in a benthic floral community causes variation in total primary production (Eriksson, Rubach & Hillebrand 2006). Depending on the functional traits of macrophyte species (e.g. morphological and physiological features, habitat choice etc.), the range and rate of primary production could be predicted and therefore the overall level of community production can be defined.

Macrophyte primary production and related ecosystem functioning have been often estimated based on the biomass or diversity assessments of its component species (Chase & Leibold 2002; Bruno *et al.* 2005; Tittensor *et al.* 2010; Gang *et al.* 2011). These studies require a complex mixture of input data for model estimations, which can be time consuming and often resource inefficient. Moreover, without any inherent structure-function linkage, this approach can potentially yield very context-specific and likely biased estimates of production. However, functional trait analysis does not require extensive taxonomic or systematic information about studied species, which will ultimately save a significant amount of time compared to traditional methods. Using well-established relationships between traits and community functioning enables a simple and transparent approach to studying ecosystem functioning. This differs from earlier approaches, where structural elements of species and communities were directly related to selected aspects of ecosystem functioning without actually validating such relationships. Furthermore, estimates of primary production of macrophyte communities based on relevant functional traits would enable assessment of production over geographically distinct areas, thereby leading to simplification of the general procedure of production estimations and comparisons across environmental gradients.

The main aim of this study was to explore whether trait-based approaches can help predict variation in the primary production of macrophyte communities. In particular, our aim was to assess whether functional traits display clusters (i.e the likelihood for traits to co-occur) and to reveal which functional traits are the most effective indicators of macrophyte primary production. When doing so, the photosynthetic production of macrophyte communities was assessed based on the oxygen production of the whole community and linked to selected functional traits derived from its component species and weighted by their biomass. This study covers a range of aquatic biomes across Europe, selected to represent different environmental conditions and communities, which together enable a comprehensive analysis of the relationship between functional traits and photosynthetic production of macrophyte communities. Its findings could potentially lead to the development of a widely applicable framework for estimating production of macrophyte communities despite geographical variation in taxonomic identities.

Material and methods

Study area

Data for this study were obtained over several consecutive years of fieldwork during which photosynthethic production of benthic macrophyte communities (primarily algal communities) in major marine environments in Europe was measured (Fig. 1). However, higher order plants such as *Zostera marina* and *Stuckenia pectinata* were common in some areas. Specifically, data were collected in the Baltic Sea, Mediterranean Sea, North Sea, Barents Sea, Celtic-Biscay Shelf and Iceland Shelf. All of the data were collected in shallow coastal seas incorporating areas with significant tidal ranges (in low to high intertidal and

shallow subtidal areas) as well as the virtually tideless Baltic and Mediterranean Seas (see Table S1, supporting information, for taxonomic composition of the studied macrophyte communities).

Study sites in each sea were selected based on their ability to represent it in the context of the overall marine ecosystem at the given area in terms of geomorphological characteristics and community composition. Throughout the area of study, the seafloor was mainly dominated by rock, boulders, pebbles and gravel. Sites comprising soft sediments such as sand and silt were included when their occurrence in the region was common. In soft bottom habitats only rooted macrophytes were included in the study. Sampling was undertaken from 2010–2014 in the season when the communities were most fully developed and light conditions were favourable, mostly from the early spring to the late summer.

Locations under significant anthropogenic impact (e.g. proximity to sewage pipes and aquaculture facilities) were avoided when selecting appropriate sites to reduce extraneous variation and potential confounding factors. Avoiding anthropogenic impact in the Baltic Sea was not possible, however, because almost all aquatic communities in the Baltic Sea are impacted to some degree by various anthropogenic pressures (HELCOM 2010).
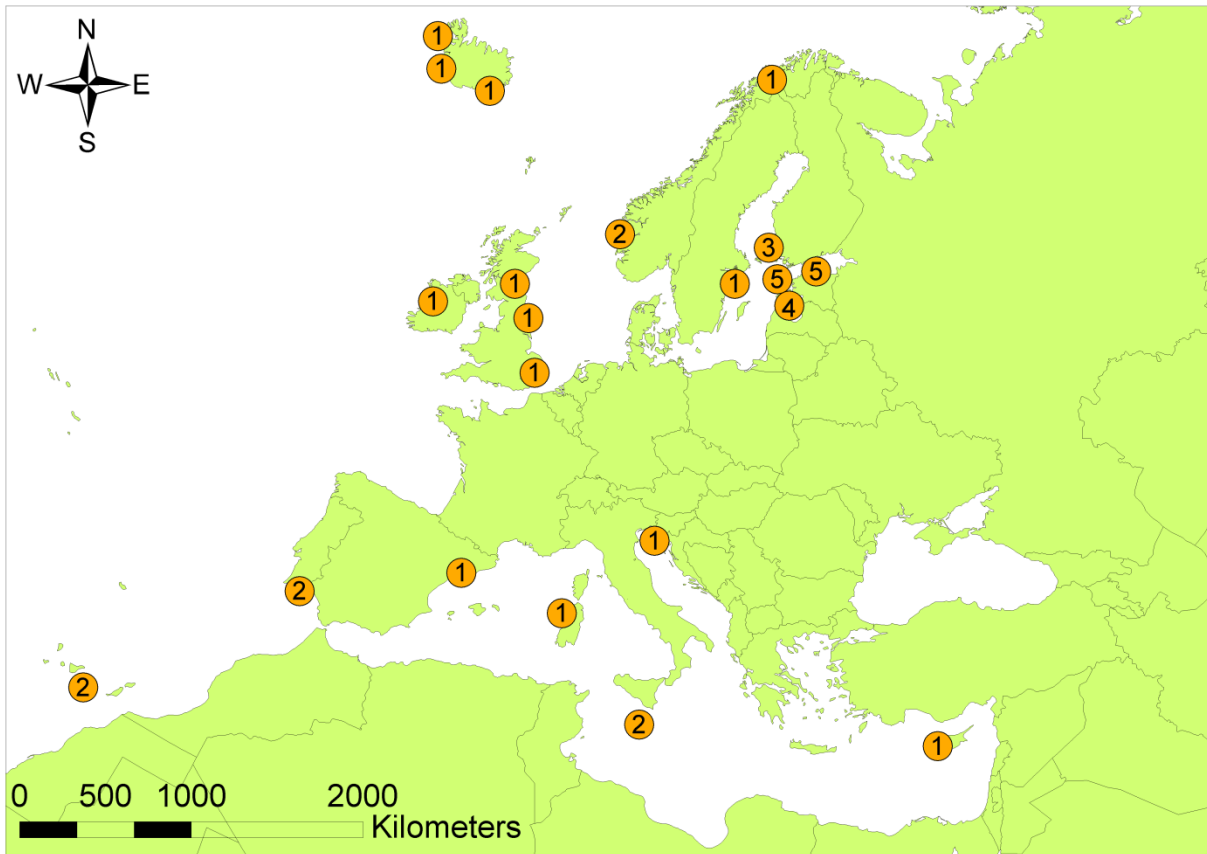
Figure 1. Study area with bullet values referring to the number of sampling sites in the particular location. In each site, measurements of photosynthetic production were made for three different types of community.

Sampling procedure

At each study site a standardized methodology was used. First the coverage of macrophyte communities was assessed at every selected study site along a tidal gradient (from the shoreline to the upper subtidal) by visual transects. Snorkelling equipment or scuba diving gear was used when needed. As a result, the three most commonly observed communities were selected for the assessment of production of macrophyte communities with the same average coverage as they were observed at the study site. Species coverages of most

commonly observed communities were spatially homogenous at their expected distribution ranges, thus, sampling bias was not a concern.

The net primary production of macrophyte communities was measured *in situ* at 1 m depth in natural seawater close to the site of algal collection. Macrophytes attached to stones were collected from intertidal or upper subtidal areas. On soft bottoms, macrophytes were gently removed from sediment including root material. Drift macrophytes were excluded from all study sites. Larger benthic invertebrates were removed from macrophytes prior to making measurements.

The net primary production of macrophyte communities was measured in a transparent chamber holding 15 l of water. The chamber consisted of a circular transparent Plexiglas base of 35.5 cm diameter and a transparent supporting Plexiglas frame attached to the base of the chamber in order to sustain a consistent volume of water throughout the incubation. During incubation, the frame was placed in a transparent plastic bag of a thickness of 60 μm filled with ambient seawater. An airtight seal between the chamber and the surrounding environment was achieved using a rubber seal. Stones with attached macrophytes were placed into the chambers at coverages similar to field conditions. The net primary production of each macrophyte community was monitored under full diel cycles from sunrise to sunset, during this period the water in the chamber was exchanged every 2 hours.

Oxygen concentration in the chamber was measured every second using a calibrated Optode type oxygen sensor (Aanderaa Instruments) connected to a data logger (data recorder by Alec Electronics). This instrument also provides data on water temperature. Changes in dissolved oxygen averaged over one minute intervals were used as a proxy for the community's net

photosynthetic production. During deployment, irradiance above the canopy was measured every minute using a calibrated spherical quantum sensor connected to a data logger (ultra-miniature logger for light intensity by Alec Electronics).

After daily O_2 flux measurements, bivariate scatterplots between light irradiance and net primary production were inspected for each macrophyte community in order to determine the saturation onset parameter. In further analyses only light levels above saturation were considered as this is a common procedure to compare community primary production between sites and over time (see e.g. Migné *et al.* 2004). Moreover, we did not want to introduce another source of variability that may potentially distort or obscure relationships between trait domination and primary production of macrophyte communities. In fact, light levels were not too influential as evidenced by a poor global relationship between light and photosynthetic production of macrophyte communities (spearman rank correlation n = 8756, r = 0.08, p > 0.05). Importantly, not a single community observed in this study experienced photoinhibition.

After deployment, all studied macrophyte communities were stored in a deep freezer at − 20 °C. The subsequent sorting, counting, and determination of species were performed in the laboratory using a stereomicroscope. The dry weight of each macrophyte community was obtained after drying the individuals at 60 °C for two weeks. Combining this information with the oxygen flux measurements described above enabled us to express net primary production in mg O_2 g dw macrophyte^{-1} minute^{-1}.

Trait assignment

The overall approach of functional traits in this study is based on the Biological traits information catalogue (BIOTIC) developed by Marine Life Information Network for Britain and Ireland (MarLIN 2006). Traits in this study were assigned to three broad trait groups: macrophyte life habit traits, morphology traits and tolerance traits (Table S2, supporting information). Traits capturing pigment type were not included in this study because initial analyses suggested that they described only a small proportion of variability in macrophyte community primary production (approximately 0.8 %). Life habit traits refer to longevity and environmental position of the macrophyte species (e.g. epiphytic or epizoic). Morphology traits indicate morphological growth form characteristics (e.g. cylindrical or articulate) as well as the relative size of individual species. Tolerance traits capture macrophyte tolerances to variations in salinity (e.g. marine species, brackish water species and freshwater species) and to wave stress (species having low, moderate and/or high tolerance to wave exposure). In the natural environment, biotic interactions have the potential to restrict or facilitate species and thereby modify patterns that would be observed if driven solely by environmental tolerances (Hawkins & Harkin 1985; Jonsson *et al*. 2006). However, in this study tolerance traits were based on expert assessment of species' physiological abilities to tolerate specific ranges of salinity and wave stress. In some instances this information was not well documented and therefore some caution is needed in interpretation of tolerance traits.

For each species, presence or absence of a trait category was scored as 1 or 0, respectively. The assignment to more than one trait category was also possible, e.g. a species could be both epilithic and epiphytic. In such cases, both categories were given a score of 1. Trait information for the 68 species-level taxa present in the dataset was collected from the

literature (Einav 2007; Tabraue *et al.* 2009; Braune & Guiry 2011; Bunker *et al.* 2010), existing traits databases such as BIOTIC, ALGAEBASE (http://www.algaebase.org/), and SEAWEED (http://www.seaweed.ie/), and by consulting experts. In certain cases, where no information for the species could be retrieved, traits were inferred from the genus level. Functional trait scores for each individual within the community were combined using a weighting procedure. To do this, the trait category scores for a species at a given community were multiplied by its share of the total biomass of species in the community. The category scores were then summed over all taxa present within each community, resulting in a trait matrix containing the overall expression of each trait category in each studied macrophyte community (e.g. the biomass share of macrophytes expressing epiphytic growth form). Interdependence of studied functional traits was analysed using the similarity profile permutation test (SIMPROF) which is a multivariate non-parametric approach to testing for structure in an *a priori* unstructured set of samples and thereby to look for meaningful (significant) divisions in the clustering process using permutations (Clarke, Somerfield & Corley 2008)

Linking traits and community net primary production

The associations between different biological trait categories and the net primary production of benthic macrophyte communities were explored using a novel predictive modelling technique called Boosted Regression Tree modelling (BRT), which combines machine learning and statistical modelling approaches (Elith, Leathwick & Hastie 2008). BRT models are capable of handling different types of predictor variables and their predictive performance is superior to most traditional modelling methods (see e.g. comparisons with GLM, GAM and multivariate adaptive regression splines (Elith *et al.* 2006; Leathwick *et al.* 2006). Over-

fitting is often seen as a problem in statistical modelling which in this case can be alleviated by using independent data sets. BRT iteratively develops a large ensemble of small regression trees constructed from random subsets of the data. Each successive tree predicts the residuals from the previous tree to gradually boost the predictive performance of the overall model (Elith, Leathwick & Hastie 2008).

In this study the BRT modelling consisted of a two-stage process. Firstly, BRT modelling was done separately for each broad trait group (macrophyte life habit traits, morphology traits and tolerance traits) in order to assess the relative contribution of different traits categories within each trait group. Secondly, all studied trait categories were analysed jointly to assess the relative contribution of different trait categories to net primary production of macrophyte communities.

When fitting a BRT the learning rate and the tree complexity must be specified. The learning rate determines the contribution of each successive tree to the final model, as it proceeds through the iterations. The tree complexity fixes whether only main effects (tree complexity = 1) or interactions are also included (tree complexity > 1). Ultimately, the learning rate and tree complexity combined determine the total number of trees in the final model. For both types of model, the model learning rate was kept at 0.01 and tree complexity at 5. Nevertheless, a selection of model parameters had only marginal impact on model performance with optimal models improving predictions less than 1 %. In order to avoid potential problems of overfitting, unimportant variables were dropped using a simplification tool. This tool is a cross-validation based program described by Elith, Leathwick & Hastie (2008) (details in Appendix S2). In order to eliminate non-informative variables, the tool progressively simplifies the model, then refits the model and sequentially repeats the process

until the stopping criterion set by the tool is reached. Such simplification is most useful for small data sets where redundant predictors may degrade performance by increasing variance. As a consequence, auto-correlated variables were omitted such that collinearity did not severely distort model estimation and subsequent prediction in our final models (Dormann *et al.* 2013). Model performance was evaluated using the cross validation statistics calculated during model fitting (Hastie, Tibshirani & Friedman 2009). A random 10 % of the data was assigned for testing model accuracy. The BRT modelling was done in R using the gbm package (Elith, Leathwick & Hastie 2008).

Results

1. Interdependence of biological traits

The studied trait categories were not fully independent as shown by cluster formation between and within traits (Fig. 2). Strong statistically significant associations were seen between perennial macrophytes and leathery growth form, annual macrophytes and filamentous growth form, marine species and low-moderate tolerance to exposure and corticated foliose growth form and psammophotic life habit (SIMPROF analysis, $p < 0.05$). Moreover, macrophytes that were able to tolerate high exposure to wave stress often had epiphytic growth form and finally brackish and fresh water species were grouped together.
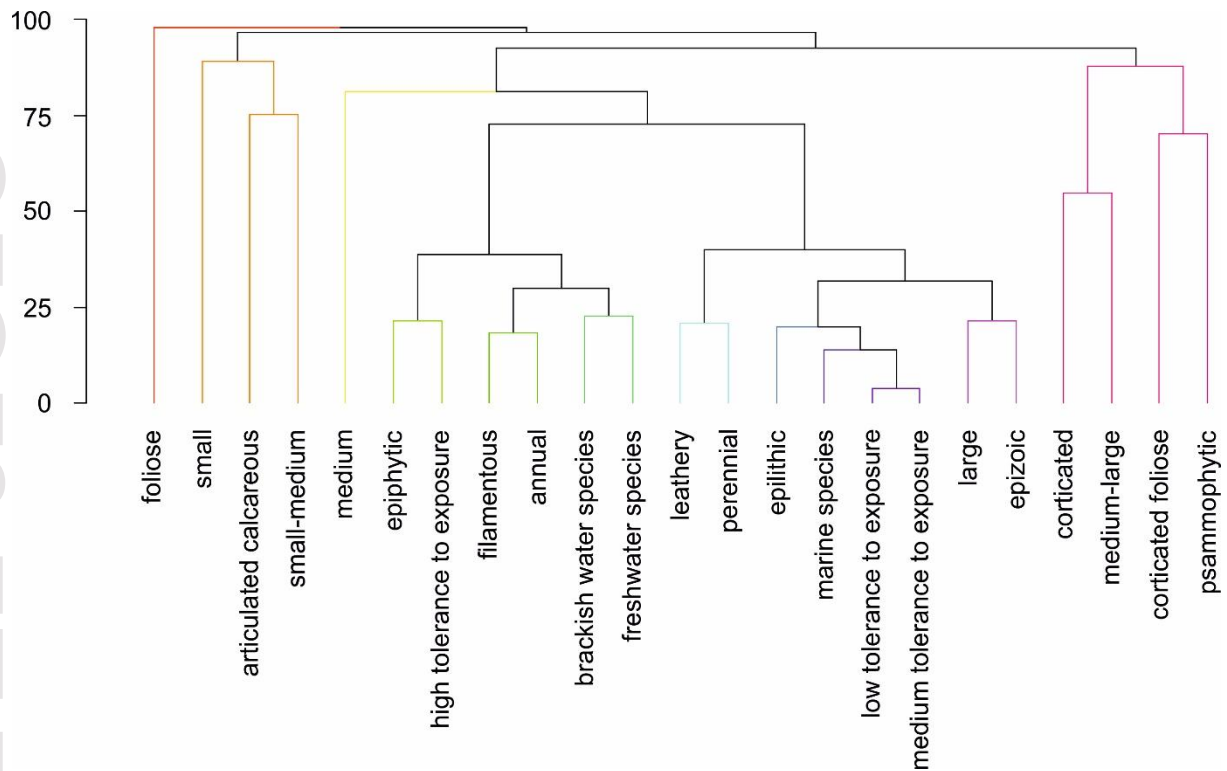
Figure 2. Interdependence among biological traits categories described by similarity profile analysis (SIMPROF).

2. Relationships between traits and net primary production

The dominance of functional trait categories within macrophyte communities described a significant proportion of variability in the production of benthic macrophyte communities in six different European marine ecosystems. When functional trait groups were analysed separately then there was no large difference in their predictive power with all these models explaining between 80 and 87 % of variation in net primary production. In general, there was no emerging trait category explaining most of the variance of net primary production. Instead, it was a function of multiple trait categories (Table 1).

When all trait categories were analysed jointly (Table 1, global analysis), the production of macrophyte communities was primarily a function of macrophyte tolerance-related traits, the

latter explaining approximately 42 % of the overall model variability. Morphology and life habit traits explained 30 and 28 % of variability respectively. Macrophyte species characterised by marine origin, filamentous growth form and large size were the most important variables that respectively explained 15.3 %, 14.1 % and 12.9 % of primary production. Similar to separate models of trait groups, no single dominating trait emerged in the global analysis that would explain a notably higher proportion of variability than any other studied trait.

3. Functional form relationships

All functional form relationships between trait categories and macrophyte community production were non-linear, mainly either positive or negative logistic growth (Fig. 3). Several trait categories that showed strong interlinkages in SIMPROF analysis also showed similar functional form relationships with macrophyte community production (e.g. exposure tolerance and epiphytic growth form or annual algae and filamentous growth form). The BRT models predicted that an elevated contribution of annual, filamentous, epiphytic, exposure tolerant and/or marine algae within algal communities resulted in increased production. Alternatively, when macrophyte communities were dominated by large freshwater species with epilithic life habit and low tolerance to exposure, their net primary production was low. Several functions levelled off at a moderate expression of trait categories after which the relative share of the trait in a community did not increase or decrease the production of macrophyte communities.
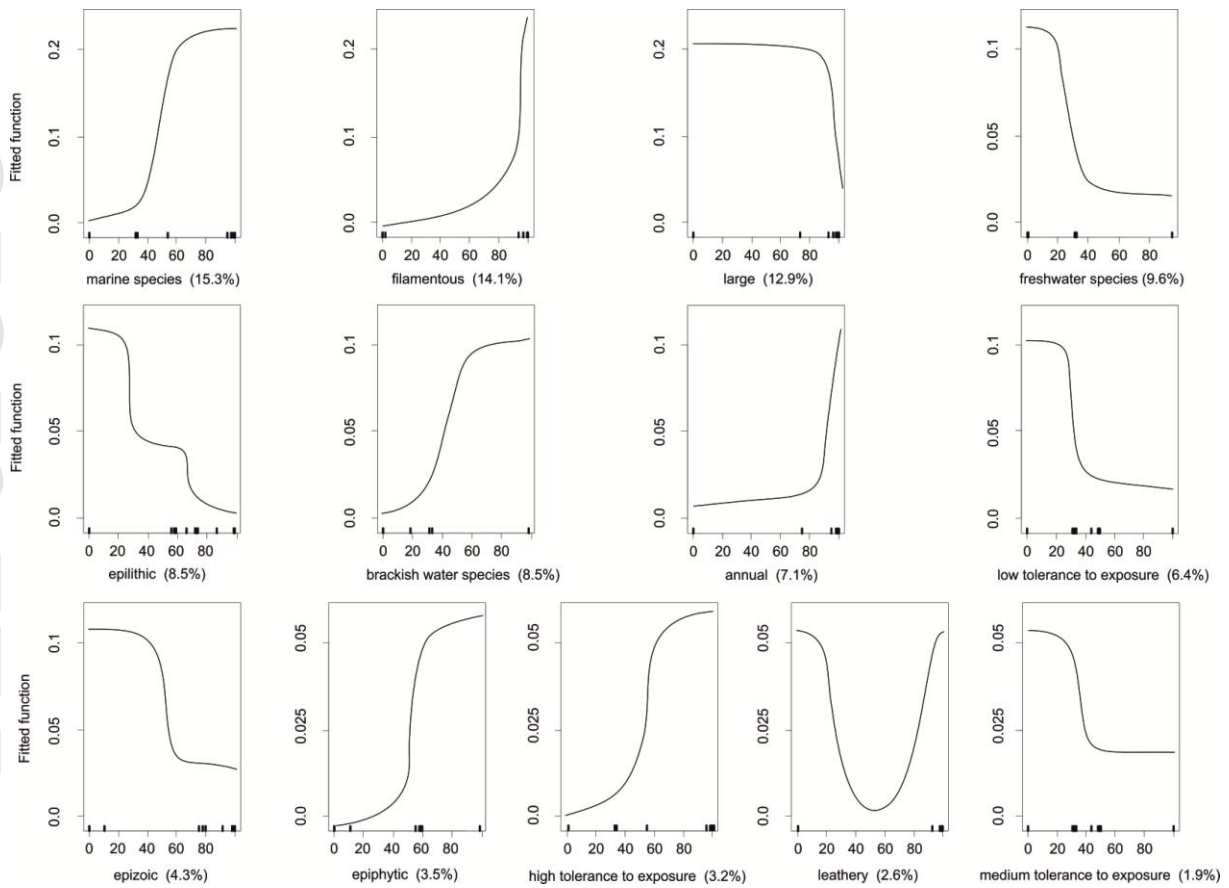
Figure 3. Standardized functional-form relationships of BRT analysis between the dominance of trait categories based on biomass within macrophyte communities and the photosynthetic production of macrophyte communities (fitted function) whilst all other variables are held at their means. The variables are ordered by their relative contribution in the BRT model (shown in brackets). Upward tickmarks on the x-axis show the frequency of distribution of data along this axis with each upward tickmark represents 10 % of the data found in that area.

Discussion

This study covers a range of aquatic biomes across Europe, selected to represent different environmental gradients and communities, which together enable a comprehensive analysis of the relationship between functional traits and macrophyte community production.

Functional traits analysed in this study were shown to be valuable indicators of macrophyte community production, through which the elements of community structure reflected ecosystem functioning, thereby demonstrating how various biotic processes can be assessed from structural data. In contrast to traditional assessments of ecosystem functioning that focus on diversity, abundance, identity or richness (Bruno *et al.* 2005; Tittensor *et al.* 2010; Isbell *et al.* 2011), trait-based characteristics provide a transparent and simple basis to link structural community information to ecosystem functioning without the need to incorporate environmental or taxonomic information (Frid *et al.* 2008; Törnroos & Bonsdorff 2012; Törnroos, Nordström & Bonsdorff 2013).

Functional traits are considered to reflect variation in the physical and biotic environment and trade-offs among different functions within an organism. The Grime's C-S-R Triangle Theory focusing on light competition, reviewed by Craine (2005) suggests that terrestrial ecosystems display very well structured microhabitats where canopy-forming tree species are required to possess certain traits that allow them to produce and maintain high leaf area above competitors in order to reach evolutionary success. However, this theory may not apply well in marine environments due to high inertia in fluid environments and the fundamentally different arrangement of communities. Specifically, canopy-forming species in terrestrial environments are normally large long-lived trees that induce light limitation to related understory vegetation which is often comprised of species characterised by short opportunistic life spans. In contrast, surface layers of seawater are often dominated by phytoplankton and various ephemeral species with the best exposure to light, whereas stable perennial communities can be shaded as they are normally attached to the seabed. Nevertheless, light limitation in marine systems is less severe because constant water motion even affects the canopy of the largest kelp forests to a scale that allows light to reach the

bottom of the seabed. Thus, although the C-S-R theory predicts that certain species thrive in a certain environment (e.g. competitors excel in low intensity stress and disturbance environment), notable deviations emerge in marine environments, e.g. species with competitive strategies can be easily found in very disturbed marine habitats such as shores exposed to wave action.

Relationships between community structure, processes and various functional traits have been established in terrestrial systems and provide a comprehensive overview about how plants functional traits can be linked to various ecosystem services ranging from forestry to nutrient cycling (Lavorel & Garnier 2002; McGill *et al.* 2006; de Bello *et al.* 2010; Garnier & Navas 2012; Pérez-Harguindeguy *et al.* 2013). However, none of these studies actually validated relationships between community structure (traits) and functioning. Therefore, important functional trait categories of macrophytes that were identified in this study illustrate how to link community composition to community specific processes (i.e. primary production) and services (e.g. the provision of raw materials for biodiesel, fertilizers, food supplements, cosmetic products and in wastewater management). Trait-based linkage has a strong potential to provide a faster route to achieve desired management or conservation goals through the identification of the traits that relate to important ecosystem processes.

Strong interlinkage among and between different trait categories reflects how studied traits are indicative of multiple ecological functions. This suggests that in nature, the patterns of trait occurrence are not independent, but instead multiple super-traits emerge that relate tolerance traits, morphology and life habit of macrophytes. It is important to note that when the roles of different trait groups are assessed independently then each trait may actually represent all of those that were co-varying in a cluster and misinterpretation can be avoided

by careful experimentation with a large set of relevant traits. The phenomenon that multiple traits are simultaneously involved in various ecosystem processes and form clusters has been also displayed in terrestrial ecosystems (de Bello *et al.* 2010). Establishment of super-traits enables detection of relatedness of various aspects of functionality in nature, thus, offering the capacity to develop and validate novel ecological theories based on the functional traits of component species.

Provided that clusters of trait categories do not form by chance, then it is possible to question whether clustering is due to the environment, evolution or the combination of both. Cluster formation of trait categories indicates that the occurrence of one trait category increases the likelihood of another trait to occur within the same community (e.g. annual longevity and filamentous growth form). Thereby, each ecosystem function is determined by a mixture of various individual trait categories. Better knowledge on how trait clusters are formed can enhance our understanding on the roles of species in an ecosystem (Bremner, Rogers & Frid 2006; Törnroos & Bonsdorff 2012; Törnroos, Nordström & Bonsdorff 2013). Global climate change, various anthropogenic pressures and increasing frequency of stochastic events (Scheffer *et al.* 2001; Crain, Kroeker & Halpern 2008; Vergés *et al.* 2014) make it important to determine the processes behind cluster formation and their relation to ecological function. This is because the loss of one trait category could likely transfer to malfunction of an entire trait cluster through their functional interlinkage.

When comparing the predictive power of functional traits in global analysis then tolerance traits explained 40 % of production whereas morphology and life habit traits each explained 30 % of production. Analysed tolerance traits indirectly incorporate information about environmental properties as each trait is likely to be found in a well-defined environmental

niche space (Bremner, Rogers & Frid 2006; Törnroos & Bonsdorff 2012). This reflects the practical value of trait-based information as macrophyte community production could be predicted based on community-specific species composition and dominance patterns without incorporating further environmental data. BRT models predicted that elevated contributions of filamentous marine macrophytes and high exposure tolerance resulted in higher production than large freshwater algae with low exposure tolerance. Higher production of macrophytes associated with higher exposure tolerance may be a result of more severe physical disturbance. Communities that are frequently subject to significant disturbance may favour r-selected life strategies (Jacobsen & Simonsen 1993; Jennings *et al*. 1999) whereas in low disturbance habitats energy could be devoted for developing strong and well developed macrophyte communities. Exposed marine habitats also have more consistent turbulence in the water column which provides better nutrient transfer (Graham *et al.* 1997; Pfaff *et al.* 2011) and tend to be characterized by higher salinities compared to sheltered areas that intensify metabolic processes of species with marine origin (Roff, Taylor & Laughren 2003).

In most cases functional relationships between studied traits and macrophyte production were not linear but often expressed exponential or logistic form. The shapes of these functions indicate that functional traits may have quantifiable thresholds in a community after which change in trait expression has negligible effect on macrophyte community production. The exponential or logistic response functions are commonly reported when relating limiting factors to biotic patterns (Luo *et al.* 2004; Binzer & Middelboe 2005; Queenborough *et al.* 2009). The production of macrophytes is often a function of light and under optimal light conditions (as used in the current study) species composition and structural configuration of the macrophyte community canopy largely define photosynthetic production values. At low trait dominance, its expression is expected to be negligible in terms of macrophyte

community production. With increasing trait expression the photosynthetic production of macrophyte communities is expected to increase fast when the trait under selection relates to high efficiency of light absorption. At a certain threshold level, however, the community photosynthetic production levels off as the lower photosynthetic tissue in the community has an unused photosynthetic potential (Binzer & Middelboe 2005). Thus, the highest photosynthetic yield is expected in communities expressing a mixture of traits that are interactively boosting the efficiency of light absorption at community level (Paalme *et al.* 2013).

Macrophyte communities and habitats are located in coastal photic zones where high rates of primary production are often known to support greater biomasses of higher trophic levels (Miller, Reed & Brzezinski 2011; Heymans *et al.* 2014; Kefi *et al.* 2015). This study convincingly demonstrates that trait-based primary production estimates linked to community biomass could be considered an applicable indicator of ecological sustainability through the ability to forecast ecosystem functioning. Such knowledge provides a solid basis for research to improve understanding of various aquatic ecosystems and can be applied to the implementation of environmental policies. For example, marine ecosystem-based management seeks to manage marine resources in accordance to ecosystem health while providing socio-economic services needed by people (Crowder & Norse 2008; Espinosa-Romero *et al.* 2011; Long, Charles & Stephenson 2015). A significant amount of monitoring data that includes morphological characteristics of macrophytes has been compiled in various databases worldwide. Thus, morphological traits identified in this study that can explain a significant amount of variability of primary production could be used to provide production estimates for various coastal areas worldwide, indicating vast practical potential for currently underused data. For example, when all morphology traits were analysed jointly, then the

highest proportion of model variability was described by morphology traits such as large (38.8 %), filamentous (38.4 %) and leathery growth form (10.5 %). Primary production of macrophyte communities could potentially be used as an integrated measure of ecosystem health and used to direct and prioritise management measures. However, most productive ecosystems are not necessarily the healthiest. Eutrophication and algal blooms are often considered to be major environmental issues (Valiela *et al.* 1998; Diaz & Rosenberg 2008; Rabalais *et al.* 2009). Therefore, it is important to identify functional traits that best describe temporal stability in primary production and thereby ensure sustainable provision of related ecosystem services.

To the best of our knowledge, this study represents a first attempt to use functional traits of macrophytes to reflect capacity for regional scale primary production and describe structure–function relationships. Here we demonstrated how functional traits can be interlinked and describe a significant proportion of a measure of ecosystem functioning. The findings of this study can be used to select the combinations of trait categories in further studies that aim to examine primary production linked to ecosystem services. This study could be also used as an initial starting point for further investigations into the linkages between traits and a wider range of ecosystem processes in the marine realm and determine whether such relationships are common for other groups of organisms. The main difficulty in undertaking FTA as performed in this study is a generic lack of process studies replicated at large spatial scales and the amount of time required in order to compile an extensive dataset about the species and their traits, both because of the lack of information for many species (Tyler *et al.* 2012) and because the available information has not yet been fully collated into databases (see Costello *et al.* 2015). If such databases become more widely available and fully populated, the assessment could be performed on a routine and cost-effective basis.

Data accessibility

DData deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.964pf, (Jänes et al., 2016)

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Tables

Table 1. BRT analyses on relative contribution of the dominance of different trait categories

within macrophyte communities to community net primary production. Firstly, separate

models for each trait groups were run followed by a global analysis including all trait groups

and categories. The Simplify tool was used to remove redundant variables from the models.

Non-redundant variables are marked in bold.

Trait group	Trait	Trait category	% variance explained
Life habit	Life habit	**Epilithic**	27.302
		Epiphytic	22.909
		Epizoic	14.088
		Psammophotic	0.011
	Longevity	**Annual**	25.701
		Perennial	9.948
Morphology	Size	**Large**	38.775
		Medium large	2.918
		Medium small	2.774
		Medium	1.132
		Small	0
	Growth form	**Filamentous**	38.39
		Leathery	10.496
		Corticated	3.059
		Foliose	1.683
		Corticated foliose	0.702
		Articulated calcareous	0.072
Tolerance	Salinity tolerance	**Marine species**	25.594
		Brackish water species	24.715
		Freshwater species	13.479
	Exposure tolerance	**High exposure tolerance**	14.227
		Low exposure tolerance	12.192

		Medium exposure tolerance	9.524
Global analysis			
Life habit	Life habit	Epilithic	8.477
		Epizoic	4.330
		Epiphytic	3.498
	Longevity	Annual	7.108
		Perennial	0.404
Morphology	Growth form	Filamentous	14.133
		Leathery macrophyte	2.643
		Corticated	0.306
		Corticated foliose	0.019
	Size	Large	12.919
		Medium large	0.756
		Medium small	0.485
		Medium	0.187
Tolerance	Salinity tolerance	Marine species	15.253
		Freshwater species	9.560
		Brackish water species	8.456
	Exposure tolerance	Low exposure tolerance	6.438
		High exposure tolerance	3.162
		Medium exposure tolerance	1.865

Table 2. List of trait categories within broad trait groups assigned to all studied macrophyte species (continued).

Species	Morphology		Tolerance					
			Salinity			Exposure		
	Growth form	Size	Marine	Brackish	Freshwater	Low	Moderate	High
Acrosiphonia arcta	filamentous	small-medium	Yes	No	No	Yes	Yes	Yes
Ascophyllum nodosum	leathery macrophyte	large	Yes	No	No	Yes	Yes	No
Battersia arctica	filamentous	small-medium	Yes	No	No	Yes	Yes	Yes
Boergeseniella fruticulosa	filamentous	medium	Yes	No	No	Yes	Yes	Yes
Caulerpa prolifera	corticated foliose	medium-large	Yes	No	No	Yes	Yes	No
Caulerpa racemosa	filamentous	medium-large	Yes	No	No	Yes	Yes	Yes
Ceramium tenuicorne	filamentous	small-medium	Yes	No	No	Yes	Yes	Yes
Ceramium virgatum	filamentous	medium-large	Yes	No	No	Yes	Yes	Yes
Chara aspera	filamentous	medium	No	No	Yes	Yes	Yes	No
Chondracanthus acicularis	corticated macrophyte	small-medium	Yes	No	No	Yes	Yes	Yes
Chondrus crispus	corticated macrophyte	medium-large	Yes	No	No	Yes	Yes	Yes
Chorda filum	corticated macrophyte	large	Yes	No	No	Yes	Yes	Yes
Chorda sp.	corticated macrophyte	large	Yes	No	No	Yes	No	No
Cladophora cf. laetevirens	filamentous	medium-large	Yes	No	No	Yes	Yes	Yes
Cladophora glomerata	filamentous	large	Yes	Yes	Yes	Yes	Yes	Yes
Cladophora sp.	filamentous	medium-large	Yes	No	Yes	Yes	Yes	Yes
Coccotylus truncatus	corticated foliose	medium	Yes	No	No	Yes	Yes	Yes
Codium vermilara	corticated macrophyte	medium-large	Yes	No	No	Yes	Yes	Yes
Corallina sp.	articulated calcareous	medium	Yes	No	No	Yes	Yes	Yes
Cymopolia barbata	corticated macrophyte	medium	Yes	No	No	Yes	No	No
Cystoseira abies-marina	leathery macrophyte	medium-large	Yes	No	No	Yes	Yes	Yes
Cystoseira amentacea var. stricta	leathery macrophyte	medium-large	Yes	No	No	No	No	Yes

Cystoseira cf. susanensis	leathery macrophyte	medium-large	Yes	No	No	Yes	Yes	No
Cystoseira compressa	leathery macrophyte	large	Yes	No	No	Yes	Yes	Yes
Cystoseira crinita	leathery macrophyte	large	Yes	No	No	Yes	Yes	Yes
Cystoseira foeniculacea	leathery macrophyte	medium-large	Yes	No	No	Yes	Yes	No
Cystoseira humilis	leathery macrophyte	medium	Yes	No	No	Yes	Yes	No
Cystoseira mauritanica	leathery macrophyte	medium-large	Yes	No	No	No	Yes	No
Cystoseira sp.	leathery macrophyte	large	Yes	No	No	Yes	Yes	Yes
Dasycladus vermicularis	corticated macrophyte	small-medium	Yes	No	No	Yes	Yes	Yes
Dictyota dichotoma	corticated foliose	medium-large	Yes	No	No	Yes	Yes	Yes
Dictyota fasciola	corticated foliose	medium	Yes	No	No	No	Yes	Yes
Ectocarpus siliculosus	filamentous	medium	Yes	No	No	Yes	Yes	No
Ellisolandia elongata	articulated calcareous	medium	Yes	No	No	Yes	Yes	Yes
Flabellia petiolata	corticated macrophyte	small-medium	Yes	No	No	Yes	Yes	Yes
Fucus distichus	leathery macrophyte	medium-large	Yes	No	No	No	No	Yes
Fucus radicans	leathery macrophyte	medium	No	Yes	No	Yes	Yes	No
Fucus serratus	leathery macrophyte	large	Yes	No	No	Yes	Yes	No
Fucus vesiculosus	leathery macrophyte	large	Yes	No	No	Yes	Yes	No
Furcellaria lumbricalis	corticated macrophyte	medium-large	Yes	No	No	Yes	Yes	Yes
Gelidium pusillum	corticated macrophyte	small-medium	Yes	No	No	Yes	Yes	Yes
Halimeda tuna	corticated macrophyte	medium	Yes	No	No	No	Yes	Yes
Halopithys incurva	corticated macrophyte	medium-large	Yes	No	No	No	Yes	Yes
Jania sp.	articulated calcareous	small-medium	Yes	No	No	Yes	Yes	Yes
Jania virgata	articulated calcareous	small-medium	Yes	No	No	Yes	Yes	Yes
Laurencia sp.	corticated macrophyte	medium-large	Yes	No	No	Yes	Yes	Yes
Liagora viscida	corticated macrophyte	small-medium	Yes	No	No	Yes	Yes	No
Myriophyllum spicatum	corticated macrophyte	large	No	Yes	Yes	Yes	Yes	No
Padina pavonica	corticated foliose	medium	Yes	No	No	Yes	Yes	Yes
Palisada maris-rubri	corticated macrophyte	medium	Yes	No	No	No	Yes	No

Palisada thuyoides	corticated macrophyte	small-medium	Yes	No	No	Yes	Yes	Yes
Palmaria palmata	corticated foliose	medium-large	Yes	No	No	Yes	Yes	No
Plocamium cartilagineum	corticated macrophyte	medium-large	Yes	No	No	No	Yes	Yes
Polysiphonia fucoides	filamentous	medium	Yes	No	No	Yes	Yes	Yes
Porphyra sp.	foliose	large	Yes	No	No	Yes	Yes	Yes
Pterosiphonia pennata	filamentous	small	Yes	No	No	Yes	Yes	No
Pylaiella littoralis	filamentous	medium	Yes	No	No	Yes	Yes	Yes
Rhodomela lycopodioides	corticated macrophyte	large	Yes	No	No	No	Yes	Yes
Rytiphlaea tinctoria	corticated macrophyte	medium	Yes	No	No	Yes	Yes	No
Saccharina latissima	leathery macrophyte	large	Yes	No	No	Yes	Yes	No
Sargassum vulgare	corticated foliose	large	Yes	No	No	Yes	Yes	Yes
Stuckenia pectinata	filamentous	large	No	Yes	Yes	Yes	Yes	No
Stypocaulon scoparium	filamentous	medium	Yes	No	No	Yes	Yes	Yes
Zostera marina	corticated foliose	medium-large	Yes	No	No	Yes	Yes	No
Ulva compressa	foliose	medium	Yes	Yes	No	Yes	Yes	Yes
Ulva intestinalis	foliose	large	Yes	No	No	Yes	Yes	No
Ulva linza	foliose	large	Yes	Yes	No	Yes	Yes	Yes
Ulva sp.	foliose	large	Yes	Yes	No	Yes	Yes	Yes