

Light requirements of marine rooted macrophytes

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1. Rationale and aim

The lower depth limit of eelgrass (*Zostera marina*) is a key indicator for assessment of ecological quality according to the water framework directive in Denmark. Hence, reference levels for good ecological status and class boundaries defining status classes are based on eelgrass depth limits.

However, even though eelgrass is, by far, the most dominant soft bottom macrophyte in Danish coastal waters, constituting >50% of all observations of soft bottom macrophytes (Manscher & Krause-Jensen 2010), mixed communities of other soft bottom macrophytes also occur, particularly in relatively protected areas of low salinity. For these communities, no reference depth limits or class boundary depth limits have been defined. The definition of reference depth limits for eelgrass has been supported by a very large database on historic depth limits of eelgrass in Danish coastal waters (Krause-Jensen & Rasmussen 2009). However, for other softbottom macrophytes than eelgrass, information on historical depth limits is much more limited (Høgslund et al. 2018) and not of sufficient scale to serve the purpose of defining countrywide reference depth limits.

The light environment and physiological light requirements for photosynthesis and growth are key parameters defining the depth limits of seagrasses and other rooted/soft bottom macrophytes. Information on light requirements is, therefore, needed for an evaluation of whether different species have the capacity to obtain similar depth limits in a given light setting.

Here, we summarize the factors affecting the variability in light requirements and depth limits of rooted macrophytes and compile information on light requirements of various species of seagrasses and other soft bottom macrophytes. This work is conducted under the Ministry of Environment and Food as part of a larger task on developing a macrophyte index for assessing the ecological quality of coastal waters.

Our aim is to evaluate whether species of seagrasses and other rooted/soft bottom macrophytes in Danish coastal waters may have comparable light requirements and, therefore, similar depth limits when exposed to a given light environment. More specifically, we aim to answer the question of whether the reference condition and class boundaries for eelgrass depth limits can be used for mixed communities of other macrophytes. For Danish waters, a total 23 marine rooted macrophyte species have been recorded as part of the Danish marine monitoring programme. A summary in 2010 showed that among these, the *Zostera* species comprised more than half (56%), followed by *Ruppia* species (22%), *Zanichellia* species (13%) and *Potamogeton* species (9%) and Charophytes (Manscher & Krause-Jensen 2010). Based on this, we chose to focus on the following soft bottom macrophytes in Danish coastal ecosystems:

Zostera marina

Zostera noltei

Ruppia sp.

Potamogeton pectinatus

Zannichellia sp.

Charophytes

2. Introduction

2.1 Methods to define minimum light requirements of seagrasses

Measurements of % surface irradiance at the depth limit of seagrasses are often used to define minimum light requirements for seagrass growth and survival. A global study shows that variability in seagrass depth limits is, to a large extent, defined by variability in water column light attenuation and that seagrasses extend to water depths receiving, on average, 11% of surface irradiance (Duarte 1991).

Still, it is well known that % surface irradiance available at the depth limit varies markedly in the field. For example, seagrasses growing in turbid waters exhibit markedly higher % surface irradiance at their depth limits and, hence, require more light to sustain growth at their depth limit relative to seagrasses growing in clear waters (Duarte et al. 2007). This may be associated with more adverse conditions in shallow nutrient rich waters, higher temperature in the shallow waters or high biomass loss rates, e.g. to grazing and exposure in shallow waters (Duarte et al. 2007).

Minimum light requirements can also be determined based on **relationships between underwater irradiance (I) and photosynthesis (P)**, so-called P-I curves. Similar curves can be established based on growth and irradiance. P-I relationships typically show three phases: (1) a light-limited phase, where photosynthesis increases linearly with increasing irradiance, (2) a light-saturated phase, where photosynthesis is independent of irradiance, and (3) a photo-inhibited region, where photosynthesis decreases with further increases in irradiance. From these relationships, the light compensation irradiance/minimum light requirement (I_c) represents the light level, where net photosynthesis is zero, and the saturation irradiance/the light level needed to saturate photosynthesis (I_k) represents the light level at the intersection between the initial slope (α) of the P-I curve and the maximum photosynthesis rate (P_{max}). I_c and I_k can be used to determine light requirements in terms of the daily light compensation period (H_{comp}) and the daily light saturation period (H_{sat}).

P-I relationships for a given seagrass species may, however, vary markedly depending both on the method applied and the environmental conditions in play.

2.2 Methodological and environmental issues affecting light requirements

A major methodological issue affecting measured light requirements is the **plant unit** used for the measurements. It makes a huge difference in light requirements whether P-I curves are determined for photosynthetic tissue (i.e. a leaf/tissue fragment), whole plants or entire plant communities.

Most P-I relationships are based on laboratory measurements on leaf fragments without non-photosynthetic tissues. However, non-photosynthetic tissues typically account for >50% of the total seagrass biomass and, therefore, the respiratory demand of whole plants is much greater than that of leaf fragments. As a consequence, light compensation points (I_c) and light saturation

points (I_k) are markedly higher for whole plants than for leaf fragments (Lee et al. 2007; Staehr and Borum 2011). Compensation irradiance estimated using leaf segments is therefore of limited use in predicting whole plant carbon balance and depth limits (Lee et al. 2007).

It is evident that P-I relationships of whole plants are much more ecologically relevant than P-I relationships derived from plant fragments. However, as plants typically occur in communities, it is often even more ecologically relevant to assess P-I relationships for entire plant communities. A comparison of P-I relationships for plant tissues versus plant communities based on 190 experiments on freshwater and marine macrophytes showed about 6-fold higher light compensation point and 3-fold higher saturation light for communities than for plant tissues because of the multilayered structure and extensive self-shading in the communities, which increase respiration rates of communities relative to tissues (Binzer et al. 2006).

Whether P-I relationships are derived based on **laboratory or field measurements** also markedly affects light compensation levels, with laboratory experiments typically reporting lower light compensation points than field experiments, as other environmental conditions and loss factors are in play in the field (see below).

A given species growing under different **environmental conditions** may exhibit wide range in light requirements (Lee et al. 2007). For example, light compensation points vary **seasonally** with I_k and I_c , typically being lowest in winter, increasing in early spring and peaking during summer, with the seasonality largely controlled by water temperature (Lee et al. 2007). Increased temperature may stimulate respiration, thereby causing higher light compensation levels, which implies that more light is needed at higher temperatures to allow for a positive carbon balance. Still, seasonal acclimation helps the plants adjust to different temperature/light regimes, e.g. as shown for Danish eelgrass populations (Staehr & Borum 2011) and for species of *Chara* and *Ruppia* in German Boddens (Piepho 2017). Adaptive responses to given temperature settings have also been reported for Danish versus Greenland eelgrass populations (Beca et al. 2018).

Different **light environments** may also affect light compensation levels. Hence, plants collected near their maximum depth limits tend to have saturated photosynthesis at lower light levels compared to plants growing in shallower waters (Lee et al. 2007 and references therein). Beca et al. (2018) reported average I_c levels of $31.1 \mu \text{mol photons m}^{-2} \text{s}^{-1}$ for light limited versus $42.3 \mu \text{mol photons m}^{-2} \text{s}^{-1}$ for light-replete *Zostera marina* plants grown under a temperature range of 10-25°C. This changed to 61.4 and $68.9 \mu \text{mol photons m}^{-2} \text{s}^{-1}$, respectively, for plants grown at 28°C.

Moreover, as already mentioned, % surface irradiance at the depth limit is markedly higher for seagrasses growing in turbid than clear waters (Duarte et al. 2007), highlighting the fact that environmental variables and loss factors beyond light, including high water temperature, unsuitable sediments etc., may also affect the depth limit and, hence, apparent minimum light requirements (Koch 2001, Lee et al. 2007).

Plant height may also affect the light requirements determined in the field, as tall plants reach higher into the water column and, hence, receive more light than short plants rooted at similar water depth (e.g. Middelboe and Markager 1997).

Competition between species is yet another factor that may prevent growth at a depth where light levels would otherwise have supported growth (Pedersen & Snoeijs 2001).

3. Methods

3.1 Literature review

We conducted a literature survey to compile existing information on light requirements of marine soft bottom macrophytes with particular focus on common soft bottom plants occurring along Danish coastlines, i.e.

Zostera marina

Zostera noltei

Ruppia sp.

Potamogeton pectinatus

Zannichelia sp.

Charophytes.

Several studies have already, to some extent, reviewed light requirements, so we used such comparative studies as our main source of information. As both methodological and environmental issues have major effects on measured light requirements, as outlined above, we highlight these effects, but primarily compare light requirements based on data that have been obtained in a similar way.

We organize the results section by first summarizing key information from specific reviews on light requirements and then summarize this information in the final paragraph of the results.

3.2 Analysis of Danish monitoring data

We extracted depth limits for common coastal soft bottom plants from the national database ODA. Max depth limits and depth limits for the main population for other species than *Zostera marina* were determined as the deepest occurrence of the species and the deepest occurrence of the species with at least 10% cover, respectively. We constrained the analysis to 20 taxonomical distinctions at species or genus level and aggregated these to the following groups (similar to above, except that *Zostera noltei* was too rare to include):

Zostera marina

Ruppia sp.

Potamogeton sp.

Zannichelia sp.

Charophytes.

In rare cases with depth limits for more than one species belonging to one of the groups at the same transect and in that case, the deepest depth limit was used.

The analysis was further restricted to 15 coastal areas, where depth limits for other rooted vegetation than *Zostera marina* were recorded. These areas were characterized by low salinity and mainly located south of Funen and Zealand as well as the two lagoons on the west coast of Jutland (Ringkøbing Fjord and Nissum Fjord). From the database, we extracted for each transect both the maximum depth limit, i.e. the deepest shoot, and the main depth limit, i.e. deepest occurrence of 10% cover, for the species groups present. Depth limits for *Ruppia* sp., *Potamogeton* sp., *Zannichelia* sp., and *Charophytes* were then plotted against those of *Zostera marina* in order to visualize their relative level.

4. Results

4.1 Literature review

4.1.1 Plant community types in lakes

(Based on review by Middelboe & Markager 1997)

Several of the macrophytes occurring in brackish waters also grow in lakes, and studies of these macrophytes in lake ecosystems may, therefore, also help understand their performance in shallow brackish waters. Middelboe & Markager (1997) analyzed data for maximum colonization depth (Z_c) of five groups of submerged macrophytes (bryophytes, charophytes, caulescent (i.e. long) angiosperms, rosette-type angiosperms and *Isoetes* spp.) and associated information on Secchi disc transparency (Z_s) in lakes (45 Danish lakes, 108 non-Danish). Among the plant groups studied by Middelboe & Markager (1997), charophytes are also represented in coastal areas and the group 'caulescent angiosperms' is also a relevant grouping for the brackish *Ruppia* sp., *Potamogeton* sp., *Zannichelia* sp. and *Zostera* sp, so the results also have relevance for coastal areas and are therefore summarized here.

The relationships between Z_c and Z_s reflect the light availability at the depth limit for the different species and, hence, their light requirements. The relationship of Z_c to Z_s differed systematically among groups (Appendix 1) and could be explained by three distinct processes regulating Z_c .

- In lakes with low transparency, tall macrophytes (caulescent angiosperms and charophytes) grew deepest, as they compensate for light limitation by shoot growth towards the water surface and Z_c is therefore independent of transparency.
- In lakes with medium transparency, bryophytes grew deepest followed by charophytes, caulescent angiosperms and *Isoetes* spp. Z_c was constrained by light attenuation with a linear relationship between Z_c and Z_s .
- In the most transparent lakes, charophytes grew deepest* and the minimum light requirement at Z_c increased with increasing transparency for angiosperms, charophytes and *Isoetes* spp.

Middelboe & Markager (1997) further concluded that the minimum light requirements among the submerged macrophytes (including marine macroalgae) depend on their plant-specific carbon value (plant biomass per unit of light-absorbing surface area) for the species/group, indicating that the light requirements of submerged plants are tightly coupled to the plants' opportunity of harvesting light and, hence, to the growth form. In addition, the light requirements were found to increase on average by 0.04% surface irradiance per degree increase in latitude, corresponding to an average decrease in Z_c of 0.12 m per degree latitude.

A pioneering comparison of depth limits of aquatic macrophyte communities also identifies deeper depth limits of charophytes than rooted angiosperms (Chambers & Kalff 1985). A new review by Schubert et al. (2018a and references therein) further underlines that charophytes have evolved mechanisms to maximize efficient use of light, enabling them to exist with as little as 1.5%

of surface light and, hence, charophytes can be found in oligotrophic lakes as deep as 65 m (Kufel & Kufel 2002).

4.1.2 Seagrass data

(Based on review for global seagrasses by Gattuso et al. 2006 and comparison among northeastern Atlantic seagrasses by Schubert et al. 2018b)

The compilation of seagrass minimum light requirements (I_c) by Gattuso et al. (2006, Appendix 2, raw data available) does not specify whether data represent leaf fragments, whole plants or communities, but is likely dominated by laboratory studies of leaf fragments, which are the most commonly reported in the literature. The compilation includes two of the species (*Ruppia sp.*, and *Zostera marina*), which appear on our list of focus species, and the single observation of minimum light requirements of *Ruppia sp.* fell within the range of those of *Zostera marina* (45 obs). Recalculated to $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$, the values are:

- *Zostera marina*: Range: 13.9-145.8, mean: 69.4, median: 62.5 $\mu\text{mol phot m}^{-2} \text{ s}^{-1}$
- *Ruppia sp.*: 38.2 $\mu\text{mol phot m}^{-2} \text{ s}^{-1}$.

A recent study of light acclimation among North Atlantic seagrasses reported data on light compensation levels for two of our focus species *Zostera marina* and *Zostera noltei* (Schubert et al. 2018b). *Z. marina* had somewhat lower light compensation levels than *Z. noltei*, and for both species, the compensation level varied along the leaves, i.e. between younger and older leaf fragments. Hence, in *Z. marina* I_c varied from 11.1 ± 1 at the tip of the leaf to 26 ± 6 at the centre of the leaf, while for *Z. noltei* I_c varied from 29 ± 5 at the centre of the leaf to 37 ± 13 at the tip of the leaf. This study also underlined that *Z. marina* typically grows deeper than *Z. noltei*, and that *Z. noltei* is often confined to the intertidal.

4.1.3 Plant tissues versus whole plants

(Based on review by Lee et al. 2007)

Lee et al. (2007) compiled information on % surface irradiance at the depth limit for three of our focus species with 9 observations for *Zostera marina* and just one observation for each of *Zostera noltei* and *Ruppia maritima*, so the data set is too limited to offer any proper comparison among the three species (Lee et al 2007, Appendix 3).

Lee et al. (2007) also compared minimum light requirements for the same three species, including, for *Z. marina*, observations from 24 studies on above-ground tissue and one study of whole plants, for *Z. noltei*, 2 studies on above-ground tissue and one study of whole plants and, for *R. maritima*, one study of whole plants (Lee et al. 2007, Appendix 4). On average, the data show about 4 times higher I_c for whole plants compared to aboveground tissue (Lee et al. 2007, Appendix 5). For comparison across species, the limited data set shows that I_c of *R. maritima* (23 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ for above ground tissue) is within the range of that for *Z. marina* ($21.7 \pm 4.1 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$, for above-ground tissue; 85 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ for whole plant), while I_c of *Z. noltei* is higher ($44.3 \pm 11.8 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ for aboveground tissue; 175.5 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ for whole plants, Lee et al. 2007, Appendix 5). For *Z. marina* in Roskilde Fjord, Denmark, a seasonal study shows that I_c of leaves as well as of whole plants increases markedly with incubation temperature and is also higher in winter than in summer (Stæhr & Borm 2011).

Optimal temperatures for photosynthesis ($T_{\text{opt}}(\text{ph})$) and growth ($T_{\text{opt}}(\text{gr})$) are slightly lower for *Z. marina* ($T_{\text{opt}}(\text{ph})=23.3\pm 1.8$, $T_{\text{opt}}(\text{gr})=15.3\pm 1.6$) than for *R. maritima* ($T_{\text{opt}}(\text{ph})=25.5\pm 2.5$, $T_{\text{opt}}(\text{gr})$: no data) and other species (Lee et al. 2007, Appendix 6), which suggests that *Ruppia sp.* is better adapted to living at higher temperatures. This has also been confirmed in other studies (Moore et al. 2014).

4.1.4 Plant tissues versus plant communities

(Based on review by Binzer et al. 2006)

This comparison of P-I relationships for plant tissues versus plant communities based on 190 experiments on freshwater and marine macrophytes showed about 6-fold higher light compensation point and 3-fold higher saturation light for communities than for plant tissues because of the multilayered structure and extensive self-shading in the communities, which increase respiration rates of communities relative to tissues (Binzer et al. 2006, Appendix 7). The comparison includes two of the macrophytes that are on our list of focus species for coastal ecosystems: *Potamogeton pectinatus* (4 data sets) and *Zostera marina* (24 data sets).

4.1.5 Softbottom macrophytes in German Boddens

(Based on review by Domin et al. 2004 and citations therein and Selig et al. 2007.)

Domin et al. (2004) and Selig et al. (2007) defined reference levels and ecological status class boundaries based on light requirements for macrophytes to be used for assessment of ecological status of German Boddens according to the Water Framework Directive. Domin et al. (2004) calculated depth limit boundaries for macrophytes based on annual depth-dependent light intensities for reference lagoons in combination with minimum light requirements for growth of typical species. The computed depth limits for growth were found to be in accordance with historical records. Data on minimum light requirements were based on I_k rather than I_c -values, so that they represent the maximum depth where light allows maximum photosynthesis.

The study included information on the following macrophytes of our list of focus species/groups (Domin et al. 2004, Appendix 8):

Chara baltica

Chara canadensis

Potamogeton pectinatus

Zostera noltei.

E_k values were lower for *Chara* species than for *P. pectinatus* and *Z. noltei* and computed depth limits therefore deeper for *Chara* species than for *P. pectinatus* and *Z. noltei*, particularly so in the clearest boddens (Domin et al. 2004, Appendix 8).

Based on the identified light requirements, reference depth limits as well as class boundary depth limits were defined for four German boddens (Selig et al. 2007, Appendix 9). A similar approach has been applied to calculate reference depth limits for *Myriophyllum spicatum*, *Najas marina* and *Zostera noltei* (Eggert et al. 2009).

4.2 Depth limit comparison based on Danish monitoring data

The main and max depth limits typically ranged up to 8 and 9 m, respectively, for the 15 investigated areas with depth limits for other rooted vegetation than

Zostera marina (Figs. 1 and 2). There were considerably more max depth limits than main depth limits because the species group did not always reach 10% cover or higher. Importantly, *Zostera marina* typically grew deeper than the other species groups, as indicated by the majority of data points below the 1:1 (Figs. 1 and 2), but many transects also displayed depth limits for the other species groups that were similar to *Zostera marina*. This indicates that these other species can grow to approximately same depth as *Zostera marina*, but they do not always reach their depth potential due to competition. Similarly, it is also possible that *Zostera marina* does not always reach the full depth limit potential due to competition. This could be the case for Ringkøbing Fjord, where *Ruppia sp.* seems to grow deeper, and inner parts of Roskilde Fjord, where *Potamogeton sp.*, *Ruppia sp.*, and *Zannichellia sp.* occasionally grow deeper than *Zostera marina*. These tendencies are also seen in Bøgestrømmen, Fakse Bugt, Guldborgsund, Karrebæk Fjord and Præstø Fjord, although to a lesser degree. Another interesting pattern was that *Chara sp.* occasionally grew deeper than *Zostera marina* in Bøgestrømmen, Fakse Bugt, Guldborgsund, and Nivå Bugt, which are all clear water areas sheltered from the dominant westerly winds. This indicates that *Chara sp.* has the potential to grow at lower light intensity, probably because it can grow relatively tall and has a relatively low plant biomass per unit of light absorbing surface area (Middelboe & Markager 1997), e.g. due to high above-ground: belowground biomass ratio. This pattern was also observed for the main depth limit (Fig. 2A), although there were fewer observations.

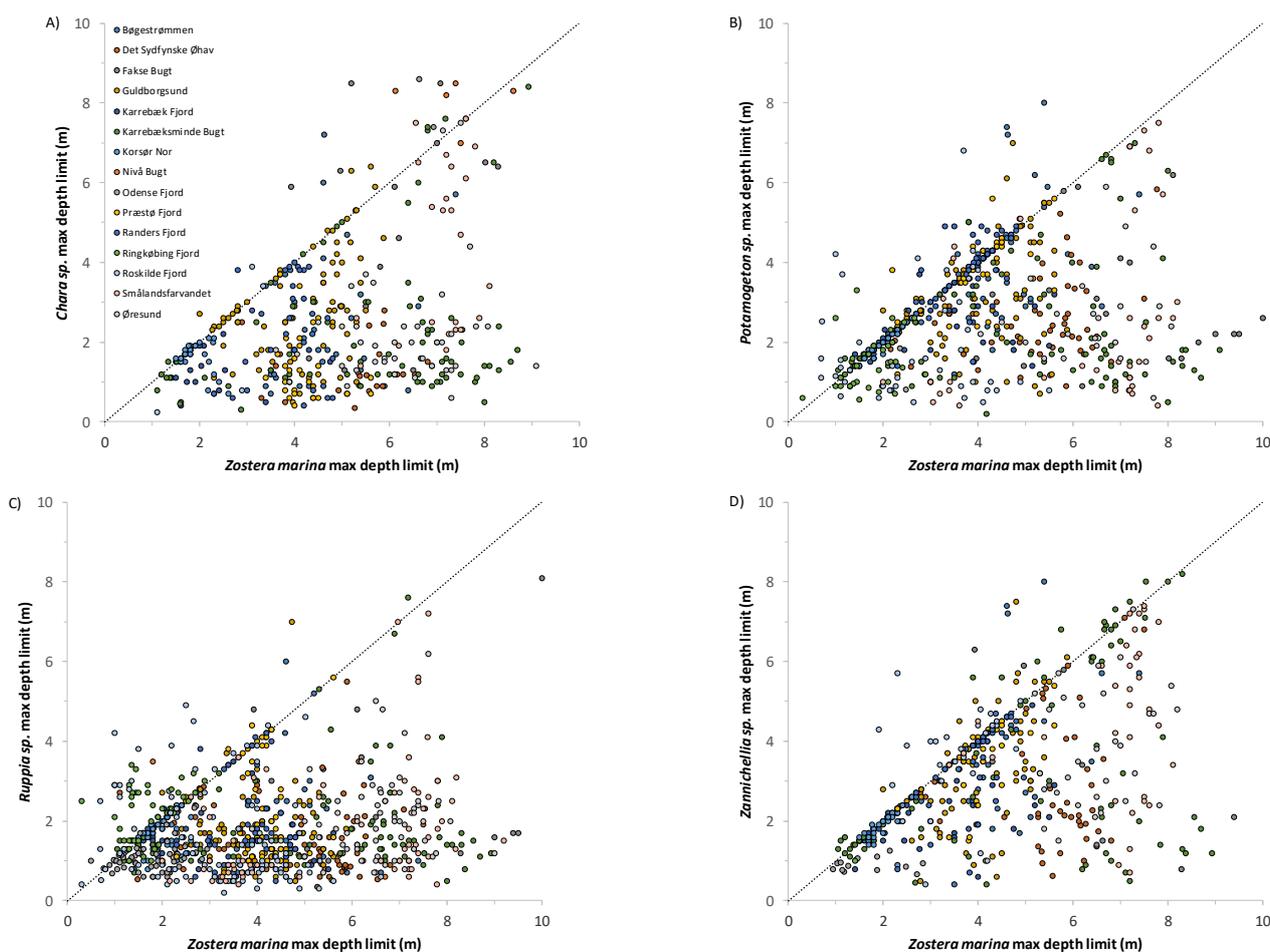


Figure 1. Max depth limits for *Chara sp.*, *Potamogeton sp.*, *Ruppia sp.*, and *Zannichellia sp.* versus *Zostera marina*. Observations represent depth limits of the different groups identified from the same transect. Depth limits from the 15 areas are shown with different colors.

The lack of consistent patterns in depth limit between the different species groups highlights that competition among rooted vegetation is important in these brackish areas. The analysis suggests that *Chara sp.*, *Potamogeton sp.*, *Ruppia sp.*, and *Zannichellia sp.* frequently do not reach their depth distribution potential, and that this may also affect *Zostera marina* in some areas. Consequently, indicators of depth distributions for rooted vegetation should include observations of more species in brackish areas, where competition among species is important. In summary, our comparison between depth limits of *Zostera marina* and other rooted macrophytes suggests that it would be reasonable to apply the same reference depth limits and ecological status class boundary depth limits for mixed communities of rooted macrophytes as for *Zostera marina*.

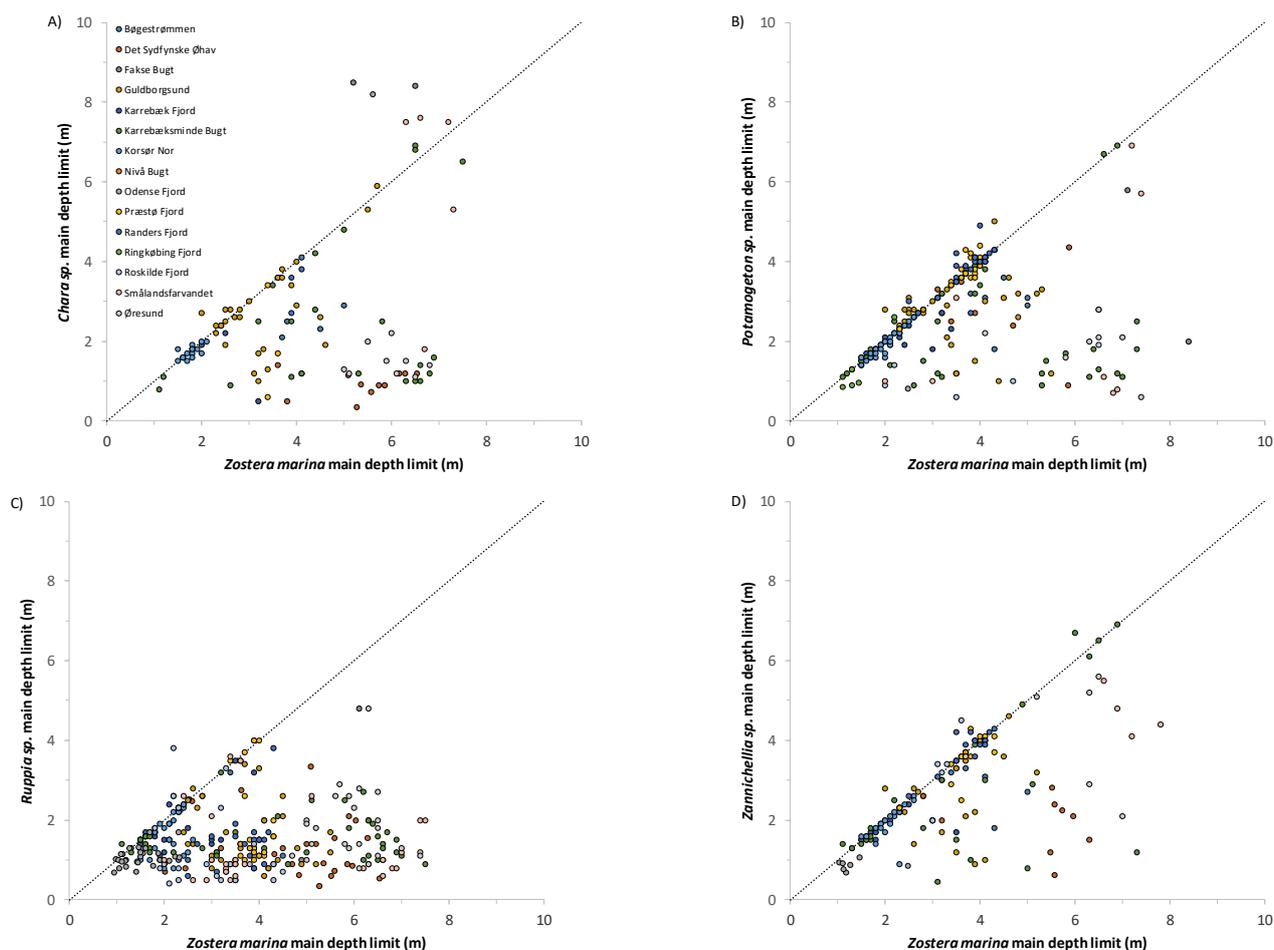


Figure 2. Main depth limits for *Chara sp.*, *Potamogeton sp.*, *Ruppia sp.*, and *Zannichellia sp.* versus *Zostera marina*. Observations represent depth limits of the different groups identified from the same transect. Depth limits from the 15 areas are shown with different colors.

5. Summary

Based on the reviewed information, it is clear that light requirements of marine macrophytes vary depending on methods and depending on a wide range of environmental conditions, implying that comparisons of light requirements among species should be based on data obtained in a similar way. Alternatively, a very large data set is needed.

Each of the individual reviews presented on the previous pages generally compared data collected in similar ways, but each review contained only few data on our focus species other than *Zostera marina*. In summary, the literature review showed:

- The few observations of light requirements for *Ruppia sp.* fell within the range reported for *Z. marina* (Gattuso et al. 2006, Lee et al. 2007).
- The few observations of light requirements of *Z. noltei* were higher than for *Z. marina* (Lee et al. 2007, Schubert et al. 2018b), but the low number of studies does not allow generalization.
- A comparison between *P. pectinatus*, *Z. noltei* and Chara species showed higher light requirements of *P. pectinatus* and *Z. noltei* than charophyte species, with *Chara sp.* having the deepest depth limits (Domin et al. 2004 and references therein).
- Also, the comparison of light requirements among freshwater macrophytes showed that in the clearest lakes, charophyte species have the potential to grow deeper than tall angiosperms (which include species like *Potamogeton sp.*), while in turbid lakes depth limits of tall plants, like charophytes and tall angiosperms, were independent of light attenuation, as their length allowed them to compensate for limited light at the seafloor.

In summary, the analysis of depth limits based on Danish monitoring data showed:

- Depth limits for *Zostera marina* were typically deeper than for the other soft bottom macrophytes. In many cases, these could also reach depth limits similar to *Z. marina* and, in some cases, deeper than *Z. marina*. This indicates that at least some other soft bottom macrophytes (angiosperms and charophytes) have the potential to grow to similar depths as *Z. marina*, but do not always reach the potential, due to competition or other ecological constraints.

Overall, this data survey suggests that it is reasonable to apply similar reference depth limits and class boundary depth limits for a *mixed* community of soft bottom angiosperms as for *Z. marina*, as there is no strong support for these being significantly different. Charophytes have the potential to grow deeper than angiosperms in clear water areas and may, therefore, represent deeper reference depth limits, although, as illustrated in this report, the variability between areas/measurement settings is so large and the datasets so limited that we cannot define separate reference depth limits for charophytes.

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APPENDICES

Appendix 1. From Middelboe & Markager (2007, their Table 3)

Table 3 Parameters and statistics for relationships between maximum colonization depth (Z_c) and Secchi disc transparency (Z_s). Parameters for the linear model were calculated by Kendall's robust line-fit method (Sokal & Rohlf, 1995). Parameters in the nonlinear model (eqn 5) were calculated by an iterative Gauss-Newton procedure. Units: Slope and a (dimensionless), intercept, K and Z_m (m). All relationships were significant at the 0.1% level

	Slope or a	Intercept or K	Z_m	n	Range for Z_c	Range for Z_s	Kendall's rank correlation coefficient (linear model) or Pearson's correlation coefficient (nonlinear model)
$Z_c = \text{intercept} + \text{slope} * Z_s$							
Bryophytes	0.73	0.56	–	24	0.5–10	0.95–10.8	0.72
Charophytes	1.19	0.17	–	64	0.25–16.5	0.23–11.5	0.67
Caulescent angiosperms	0.95	0.37	–	70	0.5–9	0.3–11.7	0.58
Rosette-type angiosperms	0.38	0.88	–	25	0.45–6.8	0.78–12	0.64
<i>Isoetes</i> spp.	0.59	0.58	–	26	0.8–6	0.78–11.5	0.45
Nonlinear curve fit eqn 5							
Bryophytes	0.81	0.28	(n.d)†	24	0.5–12	0.95–10.8	0.88
Charophytes	1.96	–0.51	9.9	64	0.25–16.5	0.23–11.5	0.75
Caulescent angiosperms	2.09	–0.32	6.6	70	0.5–9.0	0.3–11.7	0.74
Rosette-type angiosperms	0.69	0.034	7.06	25	0.45–6.8	0.78–12	0.79
<i>Isoetes</i> spp.	1.37	–0.66	6.09	26	0.8–6	0.78–11.5	0.82

†The data for this group did not approach a saturating value.

Appendix 2. From Gattuso et al. (2006, their Table 4)

Table 4. Minimum light requirements (mol photons $\text{m}^{-2} \text{d}^{-1}$) of seagrasses. The complete data set is available in Appendix C.

Species	Number of data	Range	Mean	Median
<i>Cymodocea nodosa</i>	2	0.1–0.1	0.1	0.1
<i>Halophila decipiens</i>	1	–	3.8	3.8
<i>Halophila engelmannii</i>	1	–	10.2	10.2
<i>Halophila stipulacea</i>	1	–	0.2	0.2
<i>Heterozostera tasmanica</i>	9	0.7–8.2	2.9	1.7
<i>Posidonia angustifolia</i>	2	2.4–10.1	6.2	6.2
<i>Posidonia coriacea</i>	1	–	3.2	3.2
<i>Posidonia oceanica</i>	2	0.1–2.8	1.4	1.4
<i>Posidonia ostenfeldii</i>	1	–	10.1	10.1
<i>Posidonia sinuosa</i>	1	–	10.1	10.1
<i>Ruppia</i> sp.	1	–	3.3	3.3
<i>Syringodium filiforme</i>	3	0.2–8.3	5.3	7.5
<i>Thalassia testudinum</i>	15	0.2–14.1	8.6	8.5
<i>Thalassodendron ciliatum</i>	3	1–4.4	2.2	1.3
<i>Zostera marina</i>	45	1.2–12.6	6.0	5.4
All	88	0.06–14.1	5.8	5.1

Appendix 3. From Lee et al. (2007, their Table 1)

Table 1
Minimum light requirements of various seagrass species distributed worldwide

Species	Location	Latitude	Minimum light requirement (%)	Source
Temperate				
<i>Amphibolis antarctica</i>	Waterloo Bay, Australia	27°S	24.7	Dennison et al. (1993)
<i>Heterozostera tasmanica</i>	Waterloo Bay, Australia	27°S	20.2	Dennison et al. (1993)
	Chile	30°S	17.4	Dennison et al. (1993)
	Spencer Gulf, Australia	32°–35°S	4.4	Dennison et al. (1993)
	Victoria, Australia	38°S	5	Dennison et al. (1993)
	Port Phillip Bay, Australia	38°06'S	5	Bulthuis (1983a)
	Mean		10.4	
<i>Posidonia oceanica</i>	Malta	35°N	9.2	Dennison et al. (1993)
	Fraile Island, Murcia, Spain	37°N	10–16	Ruiz and Romero (2001)
	Port Lligat, Spain	40°–42°N	11.5	Olesen et al. (2002)
	Medas Island, Spain	42°N	7.8	Dennison et al. (1993)
	Mean		10.9	
<i>Posidonia angustifolia</i>	Waterloo Bay, Australia	27°S	24.7	Dennison et al. (1993)
<i>Posidonia ostenfeldii</i>	Waterloo Bay, Australia	27°S	24.7	Dennison et al. (1993)
<i>Posidonia sinuosa</i>	Waterloo Bay, Australia	27°S	24.7	Dennison et al. (1993)
<i>Ruppia maritima</i>	Brazil	32°S	8.2	Dennison et al. (1993)
<i>Ruppia megacarpa</i>	Wilson Inlet, Australia	34°–35°S	24	Carruthers and Walker (1999)
<i>Zostera noltii</i>	Cadiz Bay, Spain	36°30'N	2	Peralta et al. (2002)
<i>Zostera marina</i>	Japan	35°N	18.2	Dennison et al. (1993)
	Denmark	54°–57°N	20.6	Dennison et al. (1993)
	Western Long Island Sound, USA	41°N	13	Koch and Beer (1996)
	Eastern Long Island Sound, USA	41°N	12	Koch and Beer (1996)
	Woods Hole, USA	41°N	18.6	Dennison et al. (1993)
	Netherlands	51°N	29.4	Dennison et al. (1993)
	Roskilde, Denmark	55°N	19.4	Dennison et al. (1993)
	Aarhus Bight, Denmark	56°N	11	Olesen and Sand-Jensen (1993)
	Kattegat, Denmark	57°N	20.1	Dennison et al. (1993)
	Mean		18	
Tropical/subtropical				
<i>Cymodocea nodosa</i>	Malta	35°N	7.3	Dennison et al. (1993)
	Ebro Delta, Spain	40°S	10.2	Dennison et al. (1993)
	Alfacs Bay, Spain	40°–42°N	4.4	Olesen et al. (2002)
	Mean		7.3	
<i>Halodule wrightii</i>	Laguna Madre, USA	27°21'N	18	Dunton (1994)
	Laguna Madre, USA	27°21'N	15–20	Burd and Dunton (2001)
	Indian River Lagoon, USA	27°30'N	24–37	Kenworthy and Fonseca (1996)
	Indian River Lagoon, USA	27°30'N	20	Steward et al. (2005)
	Corpus Christi Bay, USA	27°49'N	18	Dunton (1994)
	Corpus Christi Bay, USA	27°49'N	20	Czerny and Dunton (1995)
	San Antonio Bay, USA	28°15'N	18	Dunton (1994)
	Florida, USA	25°–30°N	17.2	Dennison et al. (1993)
	Mean		20.7	
	<i>Halophila decipiens</i>	Cuba	23°N	8.8
<i>Halophila decipiens</i>	St. Croix, USA	17°N	4.4	Dennison et al. (1993)
<i>Halophila engelmanni</i>	Cuba	23°N	23.7	Dennison et al. (1993)
<i>Syringodium filiforme</i>	Cuba	23°N	19.2	Dennison et al. (1993)
	Florida, USA	25°–30°N	18.3	Dennison et al. (1993)
	Florida, USA	25°–30°N	17.2	Dennison et al. (1993)
	Indian River Lagoon, USA	27°02'N	24–37	Kenworthy and Fonseca (1996)
	Mean		23.1	
<i>Thalassia testudinum</i>	Puerto Rico	18°N	24.4	Dennison et al. (1993)
	Cuba	23°N	23.5	Dennison et al. (1993)
	Florida Bay, USA	25°N	13	Fourqurean and Zieman (1991)
	Corpus Christi Bay, USA	27°49'N	20	Czerny and Dunton (1995)
	Corpus Christi Bay, USA	27°49'N	>14	Lee and Dunton (1997)
	Florida, USA	25°–30°N	15.3	Dennison et al. (1993)
	Mean		18.4	

Appendix 4. From Lee et al. (2007, their Table 2)

Table 2
Photosynthesis–irradiance parameters reported for various seagrass species including the light-saturated photosynthetic rate (P_{max}), compensation irradiance (I_c), saturation irradiance (I_k), photosynthetic quantum efficiency (α), and growing and/or measuring conditions

Species	Tissue	P_{max} ($\mu\text{mol O}_2 \text{ g}^{-1} \text{ dw h}^{-1}$)	I_c ($\mu\text{mol m}^{-2} \text{ s}^{-1}$)	I_k ($\mu\text{mol m}^{-2} \text{ s}^{-1}$)	α ($\mu\text{mol O}_2 \text{ g}^{-1} \text{ dw h}^{-1}$)	Condition	Source
Temperate							
<i>Amphibolis antarctica</i>	Whole plant	31.3–46.9	17–23	32–40	0.039–0.054 ^a	Temperature (13–23 °C)	Masini and Manning (1997)
<i>Amphibolis griffithii</i>	Whole plant	2.42±0.18 ^a	20±0.9	70±2.4	0.035±0.003 ^a	Gross P_{max}	Masini et al. (1995)
	Whole plant	31.3–109.4	15–17	25–56	0.039 ^a	Temperature (13–23 °C)	Masini and Manning (1997)
<i>Phyllospadix torreyi</i>	Above-ground	26.0 ^b	5 ^k	36 ^k		Intertidal	Drew (1979)
<i>Posidonia australis</i>	Whole plant	0.84±0.07 ^a	25±1.2	90±4.1	0.009±0.001 ^a	Gross P_{max}	Masini et al. (1995)
	Whole plant	25.0–62.5	17–20	35–50	0.015–0.024 ^a	Temperature (13–23 °C)	Masini and Manning (1997)
<i>Posidonia oceanica</i>	Above-ground	240.6	37	257	0.323	Yearly and tissue age means	Alcoverro et al. (1998)
	Above-ground	12.5–96.9				Variable pH, AZ inhibitor	Invers et al. (1999)
	Above-ground	28.1–125.0				Variable pH, control	Invers et al. (1999)
	Above-ground	218.4	21		1.431	Average water temp. (20 °C)	Enriquez et al. (1995)
	Above-ground	106.9	12.01±3.8	44.2±17.4	2.188±0.094	Control, May	Ruiz et al. (2001)
	Above-ground	213.8	4.3±1.9	44.5±10.8	4.688±0.031	Fish farm station (HA), May	Ruiz et al. (2001)
	Above-ground	211.3	5.38±1.56	38.6±8.56	5.313±0.625	Fish farm station (HB), May	Ruiz et al. (2001)
	Above-ground	188.1	3.88±2.17	66.4±11.8	2.813±0.031	Control, Aug.	Ruiz et al. (2001)
	Above-ground	328.1	2.57±2.18	74.3±11.3	4.375±0.063	Fish farm station (HA), Aug.	Ruiz et al. (2001)
	Above-ground	337.5	2.03±4.32	72.2±22.6	4.688±0.313	Fish farm station (HB), Aug.	Ruiz et al. (2001)
	Above-ground	110–175	3.1–5.4		3.9–5.0	0.7–15.6 m depth	Olesen et al. (2002)
	Above-ground	215.3	12.8±1.7	72.5±5.1	2.969±0.313	Control (1993, 60 d)	Ruiz and Romero (2001)
	Above-ground	141.9	1.97±1.83	12.3±3.2	14.063±10.0	16.7% of SI (1993, 60 d)	Ruiz and Romero (2001)
	Above-ground	92.2	0.68±0.42	2.45±0.7	37.500±23.125	10.4% of SI (1993, 60 d)	Ruiz and Romero (2001)
	Above-ground	80.0	7.2±1.6	19±4.7	4.063±0.625	Control (1995, 20 d)	Ruiz and Romero (2001)
	Above-ground	340.6	14.2±2.79	228.7±20.2	3.125±1.531	Control (1995, 50 d)	Ruiz and Romero (2001)
	Above-ground	390.6	15±1	191.8±14	2.031±0.094	Control (1995, 90 d)	Ruiz and Romero (2001)
	Above-ground	96.3	8.12±1.18	22.5±3.7	4.063±0.313	16.7% of SI (1995, 20 d)	Ruiz and Romero (2001)
	Above-ground	226.9	7.44±1.08	65.7±7.3	3.438±0.313	16.7% of SI (1995, 50 d)	Ruiz and Romero (2001)
	Above-ground	160.9	1.5±0.07	20.9±0.31	7.500±0.094	16.7% of SI (1995, 90 d)	Ruiz and Romero (2001)
	Above-ground	161.9	0.46±1.8	20.9±7.8	7.719	Inner harbor	Ruiz and Romero (2003)
	Above-ground	221.3	1.08±1.5	23.2±6.81	9.531	Intermediate harbor	Ruiz and Romero (2003)
	Above-ground	273.1	3.6±3.4	75.9±18.8	3.594	Outer harbor	Ruiz and Romero (2003)
	Above-ground	264.1	4.5±3	113.1±50.1	2.313	Reference station	Ruiz and Romero (2003)
	Above-ground	8.1 ^d	4 ^k	26 ^k		5 and 33 m depth	Drew (1979)
<i>Posidonia sinuosa</i>	Whole plant	0.89±0.12 ^a	24±1.6	55±3.2	0.016±0.002 ^a	Gross P_{max} 2 m depth at 18 °C	Masini et al. (1995)
	Whole plant	1.11±0.19 ^a	24±2.3	59±3.7	0.019±0.003 ^a	Gross P_{max} 4 m depth at 18 °C	Masini et al. (1995)
	Whole plant	65.0	22±1.9	62±9.1	0.015±0.002 ^a	Uniform light field, Gross P_{max}	Masini et al. (1995)
	Whole plant	77.8	31±3.7	91±8.3	0.012±0.001 ^a	Attenuated light field, Gross P_{max}	Masini et al. (1995)
	Whole plant	37.2–76.6	22–28	37–56	0.014–0.019 ^a	Temperature (13–23 °C)	Masini et al. (1995)
	Whole plant	18.8–37.5	20–25	38–55	0.015 ^a	Temperature (13–23 °C)	Masini and Manning (1997)
<i>Ruppia maritima</i>	Above-ground	426.3	23		1.922	Average water temp. (20 °C)	Enriquez et al. (1995)

(continued on next page)

Table 2 (continued)

Species	Tissue	P_{max} ($\mu\text{mol O}_2 \text{ g}^{-1} \text{ dw h}^{-1}$)	I_c ($\mu\text{mol m}^{-2} \text{ s}^{-1}$)	I_k ($\mu\text{mol m}^{-2} \text{ s}^{-1}$)	α ($\mu\text{mol O}_2 \text{ g}^{-1} \text{ dw h}^{-1}$)	Condition	Source
<i>Zostera carpriconi</i>	Above-ground	4.2 ^c	45	182		Leaf segments, artificial seawater	Flanigan and Critchley (1996)
	Above-ground	179.4		195±45		Intertidal, winter	Schwarz (2004)
	Above-ground	167.5		242±21		Subtidal, winter	Schwarz (2004)
<i>Zostera marina</i>	Above-ground	0.5–1.7 ^c		100–290	0.0035 ^c	Seasonal variations	Zimmerman et al. (1995)
	Above-ground	0.20±0.03 ^b		27±5	0.010 ^b	Control	Zimmerman et al. (1997)
	Above-ground	0.30–0.78 ^b		27–82	0.011 ^b	CO ₂ enrichment	Zimmerman et al. (1997)
	Above-ground	0.40 ^b	12	125	0.0021 ^b	Leaf No. 1, Base	Mazzella and Alberte (1986)
	Above-ground	0.24 ^b	7	40	0.0053 ^b	Leaf No. 1, Apex	Mazzella and Alberte (1986)
	Above-ground	0.36 ^b	25	115	0.0022 ^b	Leaf No. 2, Base	Mazzella and Alberte (1986)
	Above-ground	0.22 ^b	14	85	0.0024 ^b	Leaf No. 2, Middle	Mazzella and Alberte (1986)
	Above-ground	0.23 ^b	13	55	0.0041 ^b	Leaf No. 2, Apex	Mazzella and Alberte (1986)
	Above-ground	0.26 ^b	33	80	0.0024 ^b	Leaf No. 3, Base (+epi.)	Mazzella and Alberte (1986)
	Above-ground	0.23 ^b	21	80	0.0023 ^b	Leaf No. 3, Base (-epi.)	Mazzella and Alberte (1986)
	Above-ground	0.23 ^b	9.1	80	0.0023 ^b	Leaf No. 3, Middle (+epi.)	Mazzella and Alberte (1986)
	Above-ground	0.19 ^b	6.6	80	0.0020 ^b	Leaf No. 3, Middle (-epi.)	Mazzella and Alberte (1986)
	Above-ground	0.22 ^b				Leaf No. 3 Base (+epi.), early Aug.	Mazzella and Alberte (1986)
	Above-ground	0.23 ^b				Leaf No. 3 Middle (+epi.), early Aug.	Mazzella and Alberte (1986)
	Above-ground	0.59 ^b				Leaf No. 3 Apex (+epi.), early Aug.	Mazzella and Alberte (1986)
	Above-ground	0.17 ^b				Leaf No. 3 Base (+epi.), late Aug.	Mazzella and Alberte (1986)
	Above-ground	0.50 ^b				Leaf No. 3 Middle (+epi.), late Aug.	Mazzella and Alberte (1986)
	Above-ground	0.25 ^b				Leaf No. 3 Apex (+epi.), late Aug.	Mazzella and Alberte (1986)
	Above-ground	0.47 ^b	10	100		1.3 m depth	Dennison and Alberte (1982)
	Above-ground	0.32 ^b				5.5 m depth	Dennison and Alberte (1982)
	Above-ground	14.2 ^d	6 ^k	50 ^k		10 m depth	Drew (1979)
	Whole plant	156.3–193.8	85	450	0.156–0.250	NO ₃ enrichment	Touchette (1999)
	Above-ground	0.055±0.0026 ^b	0.9	7	9.1 ^b	Variable temp. 0 °C	Marsh et al. (1986)
	Above-ground	0.095±0.0060 ^b	1	16	6.2 ^b	Variable temp. 5 °C	Marsh et al. (1986)
	Above-ground	0.15±0.018 ^b	3	36	4.5 ^b	Variable temp. 10 °C	Marsh et al. (1986)
	Above-ground	0.33±0.057 ^b	8	90	4.0 ^b	Variable temp. 15 °C	Marsh et al. (1986)
	Above-ground	0.32±0.031 ^b	17	78	5.2 ^b	Variable temp. 20 °C	Marsh et al. (1986)
	Above-ground	0.44±0.051 ^b	13	102	5.0 ^b	Variable temp. 25 °C	Marsh et al. (1986)
	Above-ground	0.45±0.093 ^b	19	99	5.6 ^b	Variable temp. 30 °C	Marsh et al. (1986)
	Above-ground	0.30±0.044 ^b	36	120	3.5 ^b	Variable temp. 35 °C	Marsh et al. (1986)
	Above-ground	3–6.5 ⁱ	30–35	250	0.008 ⁱ	Young leaf segments	Jiménez et al. (1987)
	Above-ground	8.44±0.04 ^b	12.0±2.5	210±20.2	0.0038±0.0002 ^b	Low sulfide	Goodman et al. (1995)
	Above-ground	0.54±0.03 ^b	42.5±9.0	220±19.8	0.0028±0.0003 ^b	Medium sulfide	Goodman et al. (1995)
	Above-ground	0.33±0.02 ^b	60.0±10.1	198±22.5	0.0020±0.0003 ^b	High sulfide	Goodman et al. (1995)
	Above-ground	214.1	40		0.156	Average water temp. (20 °C)	Enriquez et al. (1995)
	Above-ground				0.78±0.06	Initial	Holmer and Bondgaard (2001)
	Above-ground	130–190			0.84±0.09	Control (full-oxygenated water)	Holmer and Bondgaard (2001)
	Above-ground	55–130			0.25±0.03	Low oxygen	Holmer and Bondgaard (2001)

	Above-ground	25–90			0.56±0.01	Low sulfide	Holmer and Bondgaard (2001)
	Above-ground	20–80				High sulfide	Holmer and Bondgaard (2001)
	Above-ground	0.7–2.4 ^c		50–200	0.09–0.029 ^e	Lagoon, seasonal	Cabello-Pasini et al. (2002)
	Above-ground	0.5–1.8 ^c		10–350	0.05–0.062 ^e	Open coast, seasonal	Cabello-Pasini et al. (2002)
<i>Zostera noltii</i>	Whole plant	71–236 ^f	98–300	222–390	0.23–0.63 ^f	Seasonal variations	Vermaat and Verhagen (1996)
	Above-ground	3–6.5 ^d	30–35	350	0.008 ^d	Young leaf segments	Jiménez et al. (1987)
	Above-ground	378.8	56		1.425	Average water temp. (20 °C)	Enriquez et al. (1995)
	Above-ground			175	0.042±0.003 ^e	Seasonal	Silva and Santos (2004)
Tropical/subtropical							
<i>Cymodocea nodosa</i>	Above-ground	93.8				Water flow >0.64 m s ⁻¹	Koch (1994)
	Above-ground	27.2–75.0	0.07–50.6	25.9–165.9	0.281–1.219	10 °C	Terrados and Ros (1995)
	Above-ground	60.6–237.2	18.1–32.1	77.8–231.2	0.625–1.219	20 °C	Terrados and Ros (1995)
	Above-ground	59.1–438.1	26.0–116.4	135.1–400.9	0.156–0.159	30 °C	Terrados and Ros (1995)
	Above-ground	62.5–228.1				Variable pH, AZ inhibitor	Invers et al. (1999)
	Above-ground	150.0–290.6				Variable pH, control	Invers et al. (1999)
	Above-ground	262.2	61		1.444	Average water temp. (20 °C)	Enriquez et al. (1995)
	Above-ground	165–250	5.7–10.7			0.4–3.8 m depth	Olesen et al. (2002)
	Above-ground	21.8 ^d	4 ^k	38 ^k		0.3 and 33 m depth	Drew (1979)
<i>Cymodocea rotundata</i>	Above-ground	169.7–261.3	12.5–37.1		0.625–3.125	Seasonal	Agawin et al. (2001)
<i>Cymodocea serrulata</i>	Whole plant	0.476±0.135 ^g				0.5 m depth	Hena et al. (2001)
	Whole plant	0.292±0.030 ^g				2.0 m depth	Hena et al. (2001)
<i>Enhalus acoroides</i>	Above-ground	40.9–196.3	2.5–26.0		0.313–6.250	Seasonal	Agawin et al. (2001)
<i>Halodule uninervis</i>	Above-ground	0.12 ^b	20–40	50		Variable depth	Beer and Waisel (1982)
<i>Halodule wrightii</i>	Whole plant	456–651	48–66	245–429	1.5–2.3	<i>In situ</i> , Blackjack peninsula	Dunton (1996)
	Whole plant	203–652	48–164	147–652	0.6–2.2	<i>In situ</i> , East Flats	Dunton (1996)
	Whole plant	140–1104	37–177	189–453	0.5–2.4	<i>In situ</i> , seasonal	Dunton and Tomasko (1994)
	Whole plant	441±80	111±21	349±27	1.3±0.2	Field (28–30 °C)	Dunton and Tomasko (1994)
	Above-ground	421±21	22±2	101±4	4.2±0.3	Lab (29 °C)	Dunton and Tomasko (1994)
<i>Halophila engelmannii</i>	Above-ground		10–60	432–504		Seasonality, salinity	Dawes et al. (1987)
<i>Halophila johnsonii</i>	Above-ground	10–510	2–14	14–41	5–13	Salinity (0–60 PSU)	Torquemada et al. (2005)
	Above-ground	125–480	2–10.5	25–52	6.2–11.8	Temp. (15–25 °C)+Salinity (30, 50 PSU)	Torquemada et al. (2005)
	Above-ground	310–720	2–7.2	28–65	9–18	pH (5–8.2)+Salinity (30, 50 PSU)	Torquemada et al. (2005)
<i>Halophila stipulacea</i>	Above-ground	40 ^h	20–40	100		Variable depth	Beer and Waisel (1982)
	Whole plant	9.0 ^d	2 ^k	20 ^k		0.5 m depth	Drew (1979)

(continued on next page)

Table 2 (continued)

Species	Tissue	P_{max} ($\mu\text{mol O}_2 \text{ g}^{-1} \text{ dw h}^{-1}$)	I_c ($\mu\text{mol m}^{-2} \text{ s}^{-1}$)	I_k ($\mu\text{mol m}^{-2} \text{ s}^{-1}$)	α ($\mu\text{mol O}_2 \text{ g}^{-1} \text{ dw h}^{-1}$)	Condition	Source
<i>Syringodium filiforme</i>	Whole plant	200–220	125–140	370	0.6–0.7	<i>In situ</i> , Gross P_{max}	Major and Dunton (2000)
	Whole plant	180–305	10–25	144	1.3–2.0	Lab, Gross P_{max}	Major and Dunton (2000)
<i>Thalassia hemprichii</i>	Above-ground	141.3–330.3	8.3–31.9		0.02–0.17	Seasonal	Agawin et al. (2001)
<i>Thalassia testudinum</i>	Above-ground	352.6			2.605	Basal leaf segment	Enriquez et al. (2002)
	Above-ground	349.0			2.622	Apical leaf segment	Enriquez et al. (2002)
	Whole plant	77.6±25.2		49.3±10.0	1.62±0.30	Age (0.25 months), Gross P_{max}	Kaldy and Dunton (1999)
	Whole plant	58.1±4.7	73.0±7.6	94.6±19.6	0.67±0.08	Age (2 months), Gross P_{max}	Kaldy and Dunton (1999)
	Whole plant	222.9±9.4	30.0±4.3	119.1±16.3	2.05±0.25	Age (6 months), Gross P_{max}	Kaldy and Dunton (1999)
	Whole plant	224.1±13.7	36.0±9.7	137.9±10.6	1.65±0.07	Age (9 months), Gross P_{max}	Kaldy and Dunton (1999)
	Whole plant	215.3±16.5	56.0±9.0	218.6±48.6	1.14±0.19	Age (15 months), Gross P_{max}	Kaldy and Dunton (1999)
	Whole plant	480.0		438	1.097	P/I Model 2	Fourqurean and Zieman (1991)
	Whole plant	348.8		407	0.819	P/I Model 3	Fourqurean and Zieman (1991)
	Whole plant	346.9		357	0.971	P/I Model 5	Fourqurean and Zieman (1991)
	Whole plant	320.6		426	0.789	P/I Model 6	Fourqurean and Zieman (1991)
	Above-ground	100.0				Water flow >0.25 m s ⁻¹	Koch (1994)
	Above-ground	270	44	110	2.45	Corpus Christi Bay	Herzka and Dunton (1997)
	Above-ground	208	36	87	2.44	Lower Laguna Madre	Herzka and Dunton (1997)
	Whole plant	195	107	281	0.7	<i>In situ</i> , Lower Laguna Madre	Herzka and Dunton (1997)
	Above-ground	141.9	39		1.969	Egmont Key, shallow	Dawes and Tomasko (1988)
	Above-ground	197.2	45		2.156	Egmont Key, deep	Dawes and Tomasko (1988)
	Above-ground	190.0	32		3.219	Anclote Key, shallow	Dawes and Tomasko (1988)
	Above-ground	81.3	24		3.031	Anclote Key, deep	Dawes and Tomasko (1988)
<i>Thalassodendron ciliatum</i>	Above-ground	30–50 ⁱ		1.5–5 ^k		0.5–33 m depth	Parnik et al. (1992)

a. $\mu\text{g O}_2 \mu\text{g chl}^{-1} \text{ h}^{-1}$; b. $\mu\text{mol O}_2 \text{ mg chl}^{-1} \text{ min}^{-1}$; c. $\mu\text{mol O}_2 \text{ g}^{-1} \text{ fw min}^{-1}$; d. $\mu\text{g C cm}^{-2} \text{ h}^{-1}$; e. $\mu\text{mol O}_2 \text{ m}^{-2} \text{ s}^{-1}$; f. $\mu\text{g O}_2 \text{ g}^{-1} \text{ AFD min}^{-1}$; g. $\text{mg O}_2 \text{ g}^{-1} \text{ fw h}^{-1}$; h. $\mu\text{g C mg}^{-1} \text{ dw h}^{-1}$; i. $\text{mg C g}^{-1} \text{ dw h}^{-1}$; j. $\mu\text{mol CO}_2 \text{ kg}^{-1} \text{ dw s}^{-1}$; k. W m^{-2} .

Appendix 5. From Lee et al. (2007, their Table 3)

Table 3
Average values of $P-I$ parameters for temperate and tropical/subtropical seagrass species

Species	Tissue	P_{max} ($\mu\text{mol O}_2 \text{ g}^{-1} \text{ dw h}^{-1}$)	I_c ($\mu\text{mol m}^{-2} \text{ s}^{-1}$)	I_k ($\mu\text{mol m}^{-2} \text{ s}^{-1}$)
Temperate				
<i>Amphibolis antarctica</i>	Whole plant	37.5	19	36
<i>Amphibolis griffithii</i>	Whole plant	58.4	18±2	49±21
<i>Posidonia australis</i>	Whole plant	34.7	21.5±3.5	66±24
<i>Posidonia oceanica</i>	Leaf segment	199.3±18.9	7.8±1.8	73.3±16.1
<i>Posidonia sinuosa</i>	Whole plant	58.5±9.8	24.8±1.3	60.6±6.5
<i>Ruppia maritima</i>	Leaf segment	426.3	23	
<i>Zostera carpriconi</i>	Leaf segment	173.5±6.0	45	206±18.2
<i>Zostera marina</i>	Leaf segment	119.9±31.1	21.7±4.1	116.0±17.2
	Whole plant	175	85	450
<i>Zostera noltii</i>	Leaf segment	378.8	44.3±11.8	262.5±87.5
	Whole plant		175.5	341.5
Tropical/subtropical				
<i>Cymodocea nodosa</i>	Leaf segment	174.1±28.5	35.1±11.2	149.2±45.3
<i>Cymodocea rotundata</i>	Leaf segment	223.4	24.1	
<i>Enhalus acoroides</i>	Leaf segment	127.5	14.1	
<i>Halodule uninervis</i>	Leaf segment		30	50
<i>Halodule wrightii</i>	Leaf segment	421	22	101
	Whole plant	424±51.3	89.5±11.3	337.5±5.8
<i>Halophila engelmannii</i>	Leaf segment		30	468
<i>Halophila johnsonii</i>	Leaf segment	307.8±55.3	5.7±0.5	35.8±3.5
<i>Halophila stipulacea</i>	Leaf segment		30	100
<i>Syringodium filiforme</i>	Whole plant	215.0±5.0	75.5±57.5	257.0±113.0
<i>Thalassia hemprichii</i>	Leaf segment	237.2	19.9	
<i>Thalassia testudinum</i>	Leaf segment	210.0±32.7	36.7±3.2	98.5±11.5
	Whole plant	248.9±40.7	60.4±13.9	252.9±47.0

Appendix 6. From Lee et al. (2007, their Table 7)

Table 7
Average values of optimal temperatures for growth and photosynthesis of temperate and tropical/subtropical seagrass species

Species	Optimal temp. (°C)	
	Growth	Photosynthesis
Temperate		
<i>Amphibolis antarctica</i>	26	23
<i>Amphibolis griffithii</i>		23
<i>Heterozostera tasmanica</i>		30
<i>Phyllospadix torreyi</i>	13	23
<i>Posidonia australis</i>	19	23
<i>Posidonia oceanica</i>	15.5±2.5	32
<i>Posidonia sinuosa</i>		20.5
<i>Ruppia maritima</i>		25.5±2.5
<i>Zostera asiatica</i>	12.6	
<i>Zostera capensis</i>	17.5	
<i>Zostera japonica</i>	18.5±3.5	
<i>Zostera marina</i>	15.3±1.6	23.3±1.8

Appendix 7. From Binzer et al. (2006, their Table 2)

Table 2. Photosynthetic parameters of aquatic macrophyte phytoelements (Phyt) and communities (Comm). (Data for phytoelements are from Dring and Brown 1982, Madsen and Sand-Jensen 1994, Frost-Christensen and Sand-Jensen 1992, Kirk 1994, Olesen et al. 2002, Binzer and Sand-Jensen 2002a, Necchi 2005, and Plus et al. 2005)

	Average		Median		5–95th percentiles		<i>n</i>		Unit
	Phyt	Comm	Phyt	Comm	Phyt	Comm	Phyt	Comm	
GP _{max}	8.80	14.2	8.90	14.4	2.92–13.6	3.15–25.2	31	190	O ₂ , μmol m ⁻² s ⁻¹
α	0.048	0.036	0.042	0.035	0.014–0.096	0.007–0.076	61	190	O ₂ , mol mol ⁻¹ photon
E _c	21.7	119	16.3	106	5.0–52	40–226	75	190	Photon, μmol m ⁻² s ⁻¹
E _k	151	455	128	407	57–308	203–795	151	190	Photon, μmol m ⁻² s ⁻¹
Saturation	337	Not sat.	250	Not sat.	82.0–700	Not sat.	35	190	Photon, μmol m ⁻² s ⁻¹
R:GP _{max}	0.098	0.279	0.048	0.273	0.023–0.267	0.106–0.503	134	190	

Appendix 8. From Domin et al. (2004, their Table 4)

Table 4. Calculated depth limits according to E_k ($\mu\text{mol m}^{-2} \text{s}^{-1}$) and computed pristine k_0 of Bodden. Maximum depth of distribution [m below surface] and light period with intensities $\geq E_k$ at upper distribution limit, listed in brackets (week of the year). If no period is listed, light at -0.3 m is always $\geq E_k$.

Bodden	<i>Chara baltica</i>	<i>Chara canescens</i>	<i>Potamogeton pectinatus</i>	<i>Ulva lactuca</i>	<i>Ulva curvata</i>
Salzhaff	9.48	9.11 (3–48)	7.90 (5–47)	16.89	5.41 (7–43)
Saal	0.65 (11–38)	0.63 (11–38)	0.54 (12–35)	1.16 (5–48)	0.37 (19–30)
Bodstedt	0.79 (10–40)	0.75 (9–39)	0.65 (5–37)	1.39 (4–50)	0.45 (16–32)
Barth	1.05 (9–42)	1.01 (3–42)	1.07 (9–41)	1.88 (2–51)	0.60 (13–33)
Grabow	1.38 (8–43)	1.33 (8–43)	1.15 (9–41)	2.46 (1–51)	0.79 (12–35)
Greifswald	3.61 (5–47)	3.47 (5–46)	3.01 (6–45)	6.44	2.06 (9–40)
E_k	235	250	305	70	7.90
Author	Laboratory, Yousef, 1999	Laboratory, Yousef, 1999	Menendez & Sanchez, 1998	Fortes & Lüning, 1980	Rosenberg & Ramus, 1982
Bodden	<i>Fucus serratus</i>	<i>Fucus vesiculosus</i>	<i>Ceramium rubrum</i>	<i>Zostera noltii</i>	<i>Ceramium glanduliferum</i>
Salzhaff	14.71	9.11 (3–48)	18.37	7.90 (5–47)	4.46 (8–41)
Saal	1.01 (6–45)	0.63 (11–38)	1.26 (4–51)	0.54 (12–35)	–
Bodstedt	1.21 (5–46)	0.75 (9–39)	1.51 (2–51)	0.65 (5–37)	0.37 (20–39)
Barth	1.63 (5–48)	1.01 (3–42)	2.04 (1–51)	1.07 (9–41)	0.49 (15–32)
Grabow	2.14 (4–51)	1.33 (8–43)	2.67	1.15 (9–41)	0.65 (13–33)
Greifswald	5.61	3.47 (5–46)	7.00	3.01 (6–45)	1.70 (9–38)
E_k	100	250	55	305	551
Author	Bird et al., 1979	Niemeck & Mathieson, 1978	Leukart & Lüning, 1994	Vermaat & Verhagen, 1996	Stirk et al. 1995

Notes from sources cited in Table:

Domin (2004): "Yousef (1999) studied photosynthesis, growth and distribution of *Chara baltica* and *Chara canescens* in the Bodden. The measurement of light intensity at the lower distribution limit of those species, together with laboratory growth experiments, showed, that in situ light intensities matched quite well laboratory based determination of E_k for growth. In situ light intensities at the lower distribution limit during vegetation period (May–September) was $47.6 \pm 22\%$ of SI ($\sim 15 \text{ mol m}^{-2} \text{ d}^{-1}$) for *C. canescens*, and $41.3 \pm 21\%$ of SI ($\sim 13 \text{ mol m}^{-2} \text{ d}^{-1}$) for *C. baltica*. In the laboratory, growth efficiency was found to be maximal at light intensities of $17.6 \text{ mol m}^{-2} \text{ d}^{-1}$ for *C. canescens* and between 17.6 – $22.6 \text{ mol m}^{-2} \text{ d}^{-1}$ for *C. baltica*. However, the E_k values for photosynthesis determined during the laboratory experiments were lower than E_k values for growth by approximately 50% for both species (Yousef, 1999)."

Menendez & Sanchez (1998): I_k increased from spring (about $200 \mu\text{mol m}^{-2} \text{ s}^{-1}$) to winter (between 260 and $440 \mu\text{mol m}^{-2} \text{ s}^{-1}$) ($p < 0.05$) in *P. pectinatus*. In *C. hispida* no significant differences were found. I_k was higher for *P. pectinatus* from SC ($250 \pm 440 \mu\text{mol m}^{-2} \text{ s}^{-1}$) than for *P. pectinatus* from TP ($150 \pm 360 \mu\text{mol m}^{-2} \text{ s}^{-1}$) in incubations made in December ($p < 0.05$), although these differences were not significant if I_c values were compared. Only seasonal significant differences on I_c values for *P. pectinatus* were observed (Table 2), with the highest values in summer ($84 \pm 151 \mu\text{mol m}^{-2} \text{ s}^{-1}$) and the lowest in autumn and winter ($26 \pm 64 \mu\text{mol m}^{-2} \text{ s}^{-1}$) (Fig. 2).

Vermaat & Verhagen (1996): From iteratively fitted photosynthesis–light curves we conclude that this intertidal *Z. noltii* population is high-light adapted compared with permanently submerged seagrasses and freshwater angiosperms: estimates for the light compensation point (LCP) and half-saturation constant (K_m) were comparatively high (July LCP and K_m : $98 \mu\text{mol m}^{-2} \text{ s}^{-1}$ and $236 \mu\text{mol m}^{-2} \text{ s}^{-1}$, respectively), maximum photosynthetic rate was high ($P_{r\sim}$: $236 \text{ p.g O}_2 \text{ g}^{-1} \text{ AFDW min}^{-1}$) and the initial slope of the curve was low (a : $0.63 \text{ l-g O}_2 \text{ g}^{-1} \text{ AFDW min}^{-1} \text{ l}^{-1} \text{ E m}^{-2} \text{ s}^{-1}$). Estimated daily oxygen balances confirmed that positive net photosynthesis was largely limited to low tide daylight in this turbid estuary (mean high tide light attenuation coefficient: 2.1 m^{-1}).

Appendix 9. From Selig et al. (2007, Their Table 5)

Table 5
Definition of the depth limit of vegetation [m] for the five ecological states

	High Pristine condition	Good 5% reduction	Moderate 25% reduction	Poor 50% reduction	Bad 75% reduction
<i>SH</i>					
40% SI	1.2	1.1	0.8	0.5	0.2
10% SI	2.9	2.4	1.4	0.7	0.3
1% SI	5.8	3.5	1.7	0.9	0.4
<i>GB</i>					
40% SI	2.6	2.4	1.7	1.0	0.5
10% SI	6.4	5.4	3.1	1.7	0.7
1% SI	12.9	7.9	3.8	1.9	0.8
<i>DZBK</i>					
Inner 1% SI	2.4	1.3	0.6	0.3	0.1
Middle 1% SI	2.8	1.7	0.8	0.4	0.2
Outer 1% SI	4.8	2.9	1.4	0.7	0.3
<i>RBB</i>					
Inner 1% SI	5.7	3.5	1.7	0.8	0.4
Outer 1% SI	12.1	7.4	3.6	1.8	0.7

Light demand of SI levels for the study areas were calculated based on the pristine light conditions according to Domin et al. (2004).