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Species-specific acclimatization capacity of key traits explains global vertical distribution of seagrass species

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Abstract

Aim: The global vertical depth distribution of seagrass species remains poorly understood. Locally, the abundance and distribution of seagrasses is determined by light penetration, but at global levels each seagrass species has very distinct maximum distributional depth ranges, indicating that plant-associated traits must also influence their specific depth ranges. Seagrass-specific attributes, such as plant size or architecture, growth or reproductive strategy and their physiological and/or morphological acclimatization potential, have been suggested to be responsible for this variety of vertical distributions. We investigate here whether these species-specific traits drive differences in the global maximum vertical distribution of seagrasses.

Location: Global.

Time period: Publications between 1982 and 2020.

Major taxa studied: Seagrasses (order Alismatales).

Methods: We tested whether the species-specific maximum vertical distribution of seagrasses can be predicted by (1) their rhizome diameter (a proxy for plant size); (2) their functional resilience (growth/reproductive strategy); or (3) their acclimatization capacity. For the last aspect, we used a systematic review followed by meta-analytical approaches to select key seagrass traits that could potentially acclimatize to extreme light ranges across different seagrasses.

Results: We found that vertical distribution is best explained by the species-specific acclimatization capacity of various seagrass traits, including saturation irradiance (physiological trait), leaves per shoot (morphological trait) and above-ground biomass (structural trait). In contrast, our results indicate no predictive power of seagrass size or growth/reproductive strategy on the vertical distribution of seagrasses.

Main conclusions: Across the globe, the ability of seagrass species to thrive at a wide range of depths is strongly linked to the species-specific acclimatization capacity of key traits at different organizational levels.

KEYWORDS

acclimatization, depth, light, seagrasses, species traits, vertical distribution

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1 | INTRODUCTION

Like every other photosynthetic marine species, the abundance and distribution of seagrasses along the vertical gradient are strongly determined by light (Duarte, 1991a; Duarte et al., 2007). Light attenuates sharply with depth in the ocean, placing increasing demands on the photosynthetic machinery of the plant, and beyond a point, few species can cope (Dennison et al., 1993). Underwater irradiance is determined by the light attenuation coefficient (k), which, in turn, is mediated by a range of abiotic and biotic factors (e.g., eutrophication leading to phytoplankton blooms, natural or anthropogenic turbidity and sedimentation, latitude, topography; Lee et al., 2007). The parameter k has, on its own, been proposed as a powerful predictor of seagrass depth limits (Duarte, 1991a; Duarte et al., 2007). However, in similar environmental conditions, distinct seagrass species have very different abilities to colonize depth ranges (Lee et al., 2007). For example, in the Mediterranean Sea, *Posidonia oceanica* can colonize waters between 0 and 45 m in very clear conditions, whereas *Zostera noltii*, in the same conditions, has a highly restricted distributional range (between 0 and 10 m) (Short et al., 2011). Variations in seagrass strategies might drive differences in species-specific vertical distributions (i.e., the maximum depth ranges that each seagrass can colonize) (Short et al., 2011), raising the question of what traits and at which organizational level (from physiological to meadow scale) allow some species to occupy vast depth ranges, whereas others remain always limited to shallow waters across their global distribution.

Seagrasses are not a species-rich group but differ considerably in their vertical colonization abilities. Although most seagrass species are able to colonize the very shallowest waters (with some exceptions; Short et al., 2011), the vertical distribution in most seagrasses seems to be determined largely by their depth limit. At a global level, species such as *Posidonia sinuosa* can be found from shallow waters to a maximum of 15 m. In stark contrast, species such as *Halophila stipulacea* can have very large vertical colonization ranges and have been recorded from 0 to 70 m (Short et al., 2011). Thus, different seagrass species have characteristic maximum vertical distributional ranges independent of their environmental conditions. Several species-specific traits of seagrasses, such as plant size/architecture and growth/reproductive strategy (Duarte, 1991a), or physiological and morphological adaptations (Dennison et al., 1993) have been proposed to account for this variance in species-specific seagrass depth limits. It is possible that large species colonize a wider range of depths given their capacity to store carbohydrates in rhizomes and their larger photosynthetic tissue, which are crucial to compensate for plant carbon gains at light-poor depths for extended periods (Alcoverro et al., 1999). In contrast, larger sizes can also be a burden for respiration in the same light-limiting conditions (Alcoverro et al., 2001). Differences in photophysiology might also allow some species to photosynthesize more efficiently in reduced light conditions (Bité et al., 2007; Silva et al., 2013). Vertical distribution can also vary between seagrass functional resilience linked to their life history, including growth or reproductive strategies in response to disturbances (Kilminster et al., 2015). Species with a high capacity

for spatial recolonization and competition (fast-growing or pioneer species) (Fourqurean et al., 1995) might be advantaged by quickly colonizing deeper locations. However, seagrasses of very different sizes, rhizome diameters and growth strategies have been recorded with similar depth ranges. For instance, *P. oceanica* (large and “persistent” *sensu* Kilminster et al., 2015) and *H. stipulacea* (small and “colonizing” *sensu* Kilminster et al., 2015) both have extremely wide vertical ranges, from 0 to 45 and 70 m, respectively. The ability to colonize wide vertical ranges and adjust to changing light conditions is therefore dependent not merely on species-specific traits, but on the acclimatization potential of those traits (Schubert et al., 2018).

Studies describing specific acclimatization abilities of different seagrasses to light limitation are common, focusing on different levels of organization (i.e., physiological, morphological, structural or growth). These studies typically use field shading experiments or naturally occurring depth gradients (Collier et al., 2009; Enríquez et al., 2019; Marín-Guirao et al., 2022; Ruiz & Romero, 2001). The few studies that include more than one species observe that some species are characterized by more plastic phenotypes and traits that allow them to cope better with low-light environments than others (Bité et al., 2007; Olesen et al., 2002; Silva et al., 2013). In a similar vein, recent studies with several Mediterranean macroalgae show that their depth distributional range is closely related to species-specific photo-acclimatization capacities and light-harvesting strategies (Sant & Ballesteros, 2021). However, most studies of light acclimatization in seagrasses focus on a single species and often do not study plant responses across organizational levels (Schubert et al., 2018). A more holistic approach is required to understand how the ability of species to acclimatize by modulating particular seagrass traits can mediate differences in their vertical distribution.

In this study, we assessed whether the global maximum vertical distribution of seagrass species (obtained from Short et al., 2011) could be predicted by a series of species-specific plant attributes/traits (including size or growth/reproductive strategies) or the inherent acclimatization potential of traits (physiological, morphological, structural or growth traits). The average species-specific traits associated with size (Duarte, 1991b; Marbà & Duarte, 1998; Roca et al., 2016) and growth/reproductive strategies (Kilminster et al., 2015) were obtained from the literature, and the acclimatization capacity of the physiological, morphological, structural or growth traits was obtained with a systematic review and a meta-analytical approach.

2 | MATERIALS AND METHODS

2.1 | Relationship between the maximum vertical distribution of seagrass species and their size and growth/reproductive strategy

We tested the relationship between the maximum recorded vertical distribution (i.e., maximum depth range of colonization ever recorded) of seagrasses around the world (data from Short et al., 2011) and two potential predictors: (1) rhizome diameter (data from

Duarte, 1991b; Marbà & Duarte, 1998 and Roca et al., 2016); and (2) growth/reproductive strategy (data from Kilminster et al., 2015), with two separate linear models. For the first model, we used data from 37 species and 11 different seagrass genera, and for the second we used data of 62 species grouped into five different categorical predictors (colonizing, colonizing–opportunistic, opportunistic, opportunistic–persistent and persistent; *sensu* Kilminster et al., 2015). Model assumptions were checked visually and statistically using the functions of the “DHARMA” R package (Hartig, 2022). Assumptions were met adequately after logarithmic and square root transformation of the response variable “vertical distribution” for the first and second models, respectively (Zuur et al., 2009).

2.2 | Relationship between maximum vertical distribution and seagrass trait acclimatization potential

We tested the relationship between the globally maximum recorded vertical distribution of different seagrass species (data from Short et al., 2011) and selected key seagrass traits that could potentially acclimatize to extreme low-light conditions. To identify traits with potential acclimatization capacity, we first conducted a systematic review followed by a meta-analytical approach. Our review examined studies that included seagrass traits data in field shading experiments (with extreme low values vs. control) and depth-based studies comparing shallow versus depth limit (or close to) values. To be included in our study, the publication had to provide information on seagrass trait responses to light reduction at different organizational levels: (1) physiological [saturation irradiance (grouping data from I_k and E_k), maximum photosynthetic rate (grouping data from P_{max} and ETR_{max}) or photosynthetic efficiency (α); (2) morphological (leaf length, leaf width or leaves per shoot); (3) structural (shoot density or above-ground biomass); or (4) growth (shoot growth). We selected works published between 1982 and 2020. The search was conducted in Web of Science (WOS), with the following string for title, abstract and keywords: (seagrass* OR eelgrass* OR turtlegrass*) AND (“shad*” OR “depth” OR “bathymetric distribution*” OR “light*”) AND (“photosynthe*” OR “photo-physio*” OR “photo-acclima*” OR “acclima*” OR “morpho*”); and in Scopus with the following search string: TITLE-ABS-KEY((seagrass* OR eelgrass* OR turtlegrass*) AND (“shad*” OR “depth” OR “bathymetric distribution*” OR “light*”) AND (“photosynthe*” OR “photo-physio*” OR “photo-acclima*” OR “acclima*” OR “morpho*”)) AND (LIMIT-TO (SUBJAREA, “AGRI”) OR LIMIT-TO (SUBJAREA, “ENVI”) OR LIMIT-TO (SUBJAREA, “EART”)). These two searches yielded 617 and 695 scientific papers, in WOS and Scopus, respectively. Our final list did not include 11 relevant publications that we included manually in the list of selected studies, in addition to one publication conducted with collaborators, for which we had data prior to publication. For more details on the systematic review and meta-analyses (literature review, inclusion criteria, data extraction, calculation of the effect size and data analyses), see the Supporting Information (Appendix S1). After scrutinizing all these publications, we ended up with a total of 78 scientific studies (see Figure 1; Supporting Information Table S1 in Appendix S1). The final list summarizing the

number of publications, studies and species, grouped by trait, that we finally selected, is shown in Table 1. The Supporting Information (Figure S1 in Appendix S1) shows the species for which data meeting the criteria were available and the traits that were evaluated for each of them. We therefore obtained data on species-specific acclimatization potential to light reduction that were pooled by trait (effect sizes of each physiological, morphological, structural or growth trait) to be used as predictors of seagrass vertical distribution in the linear models.

Once effect sizes were obtained for each chosen trait, we fitted linear mixed-effects models (LMMs) with a logarithmic transformation of the response variable, maximum recorded vertical distribution (“vertical distribution”). In the model, we also included “article” as a random factor and incorporated the weights obtained from the separate meta-analytical models to provide robustness to linear models. We tested the effect of the random factor based on the Akaike information criterion (AIC) and likelihood ratio tests (Zuur et al., 2009). Thus, we used LMMs or linear models (LMs) when the random effect did not provide useful information to the model. Whenever possible (sample size permitting), linear models also included the effect of the type of study (experimental shading or depth-based study) and their interaction (“effect size” and “type of study”). Model assumptions were checked visually and statistically using functions from the R package “DHARMA” (Hartig, 2022). When residuals did not meet the assumption of homogeneity of variances (i.e., leaves per shoot), we estimated the model coefficients and quasi-t Wald test, using the “HC4m” proposed by Cribari-Neto and da Silva (2011), as the corrected estimates of the covariance matrix for inconstant variances (heteroscedasticity).

3 | RESULTS

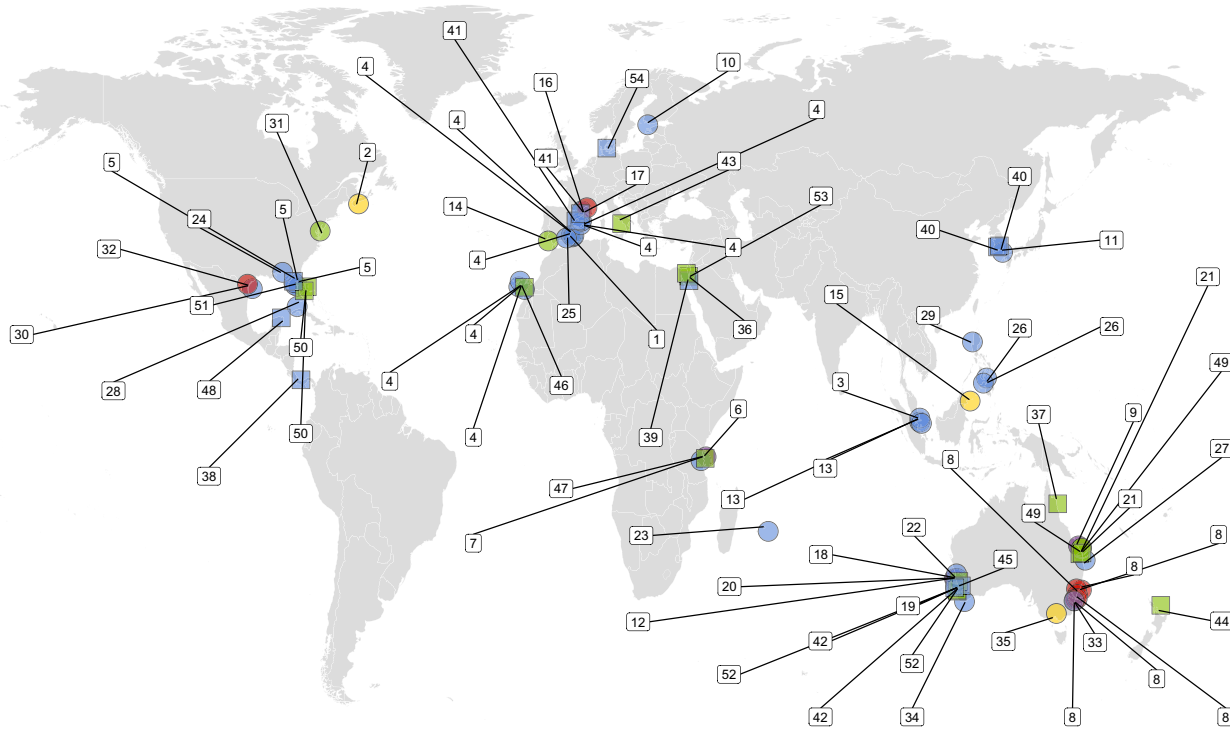
3.1 | Relationship between the maximum vertical distribution of seagrass species and their size and growth/reproductive strategy

We found no evidence of a relationship between the vertical distribution of seagrass species and rhizome diameter (our proxy for seagrass size, $p = .823$; Figure 2a; Supporting Information Table S2 in Appendix S1). In addition, there was no evidence of systematic differences in the vertical distribution of seagrasses according to their growth/reproductive strategies (using the classification of Kilminster et al., 2015; $p = .178$; Figure 2b; Supporting Information Table S3 in Appendix S1).

3.2 | Relationship between maximum vertical distribution and seagrass trait acclimatization potential

3.2.1 | Selecting seagrass traits with acclimatization potential: Separate meta-analyses

According to the results of our meta-analyses, there was evidence of an overall effect for seven of the nine traits studied in response to reduced incoming light: saturation irradiance (I_k), maximum photosynthesis



Type of Study ○ Shading ■ Depth Seagrass Traits ● Physiological ● Morphological ● Structural ● Growth ● Mix

FIGURE 1 Results of the literature review. Shape shows the type of study (manipulative shading and depth-based studies) and colour the type of trait (physiological, morphological, structural and growth) studied in each publication (54 publications and 78 studies). The numbers related to each point represent the ID number corresponding to each publication in the Supporting Information (Table S1 in Appendix S1).

Type of trait	Trait	Publications	Studies	Species
Physiological	Saturation irradiance (I_k and E_k)	17	35	13
	Maximum photosynthesis (P_{max} and ETR_{max})	25	45	14
	Photosynthetic efficiency (α)	22	40	14
Morphological	Leaf length	19	26	13
	Leaf width	16	24	9
	Leaves per shoot	11	16	7
Structural	Shoot density	25	49	15
	Above-ground biomass	19	27	12
Growth	Shoot growth	20	42	13

TABLE 1 Search results ordered by type of trait, with number of articles, studies and species for shading and depth-based investigations meeting our criteria.

(P_{max}), photosynthetic efficiency (α), leaves per shoot (LXS), shoot density (Sh.Dens), above-ground biomass (Ab.b) and shoot growth (Sh.G) (Figure 3; see Supporting Information Table S4 in Appendix S1). In contrast, leaf length (L.Length) and leaf width (L.Width) did not show an overall effect in response to contrasting light environments. We found very strong evidence for saturation irradiance ($p < .0001$) and strong evidence for maximum photosynthesis ($p = .0012$) decreasing as a result of light reduction, and data revealed strong evidence for an influence of light reduction in increasing photosynthetic efficiency ($p = .0015$). In the case of morphological traits, there was moderate evidence for a decrease in the number of leaves per shoot ($p = .0165$) with light reduction, but there was no evidence for an influence of light

reduction on leaf length ($p = .2490$) or width ($p = .8739$). There was also very strong evidence for structural traits, such as shoot density ($p < .0001$) and above-ground biomass ($p < .0001$), decreasing in lower light treatments. Finally, we found very strong evidence for shoot growth declining with light reduction ($p = .0002$).

3.2.2 | Influence of the selected traits on seagrass maximum vertical distribution

The acclimatization potential of the seagrass traits saturation irradiance, number of leaves per shoot and above-ground biomass

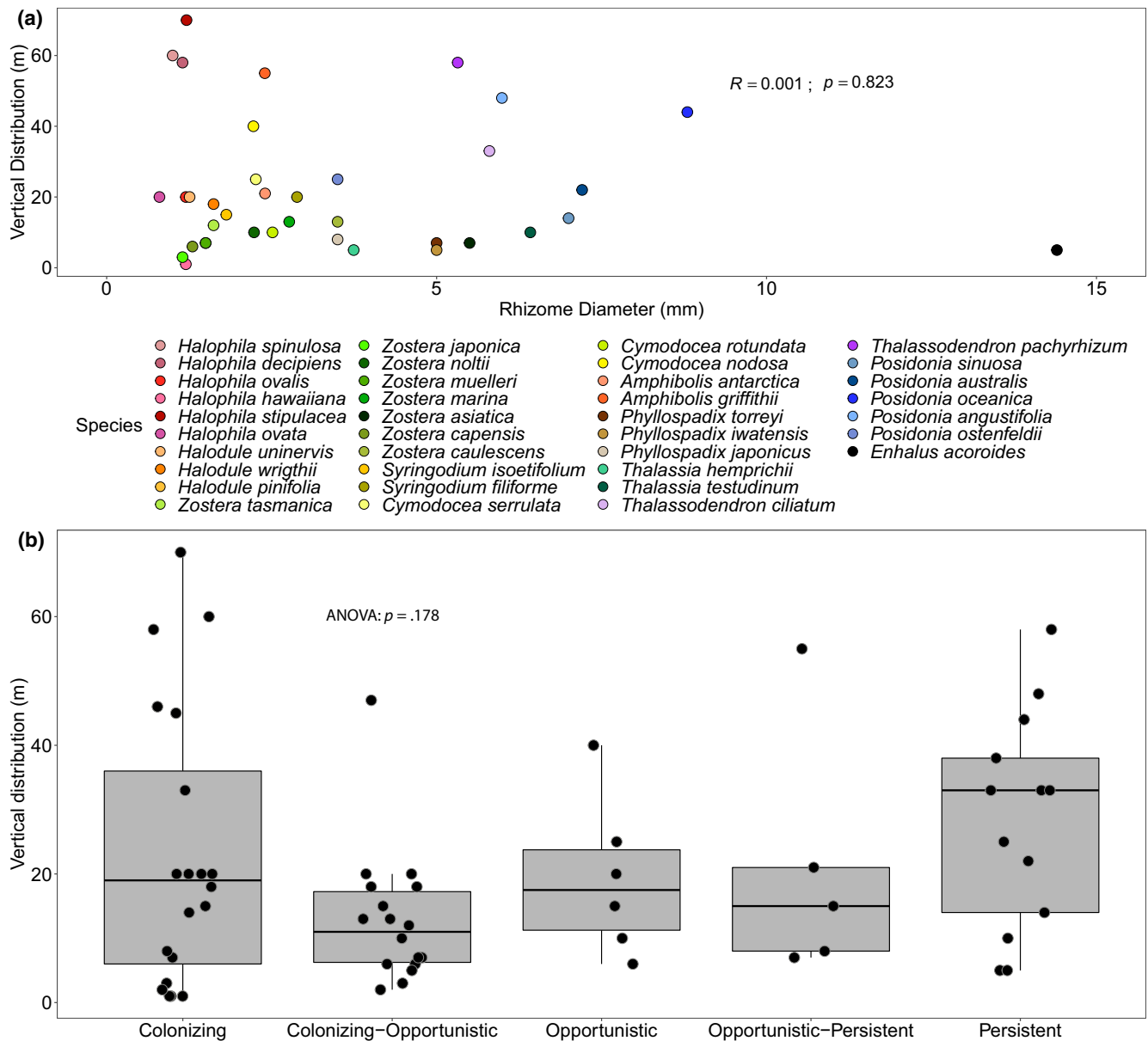


FIGURE 2 (a) Relationship between rhizome diameter and the maximum vertical distribution (i.e., maximum depth range of colonization) of 37 seagrass species. (b) Relationship between the maximum vertical distribution of 62 seagrass species and their classification according to seagrass growth/reproductive strategies. Points in panel (b) have been jittered horizontally to avoid overlapping.

(Figures 4 and 5) clearly explained the maximum vertical distribution of the analysed seagrass species. We found strong evidence for acclimatization potential (i.e., weighted effect sizes) of saturation irradiance (physiological trait) explaining the vertical distribution of seagrasses ($p = .004$; Supporting Information Table S5 in Appendix S1), in addition to very strong evidence for the acclimatization potential of leaves per shoot (morphological trait; $p < .001$; Supporting Information Table S6 in Appendix S1) and moderate evidence for above-ground biomass (structural trait; $p = .0288$; Supporting Information Table S6 in Appendix S1). In contrast, there was no evidence for the acclimatization potential of any other traits providing an adequate explanation of the vertical distribution of seagrasses (see Supporting Information Table S5 in Appendix S1)

4 | DISCUSSION

The reducing transparency of coastal seas is one of the surest imprints of human pressures on nearshore waters. Photosynthetic dependence places firm limits on how much reduction in water quality marine plants can take (Dennison et al., 1993; Duarte, 1991a), and the upward march of once-extensive seagrass meadows over the last few decades is a clear sign of accelerating environmental stress (Waycott et al., 2009). What is additionally worrying about the light requirements of seagrass meadows is that these systems are often strongly nonlinear in their behaviour (Marín-Guirao et al., 2022), implying that restoration of water clarity might not guarantee meadow recovery (Katwijk et al., 2016). Understanding what allows some species to

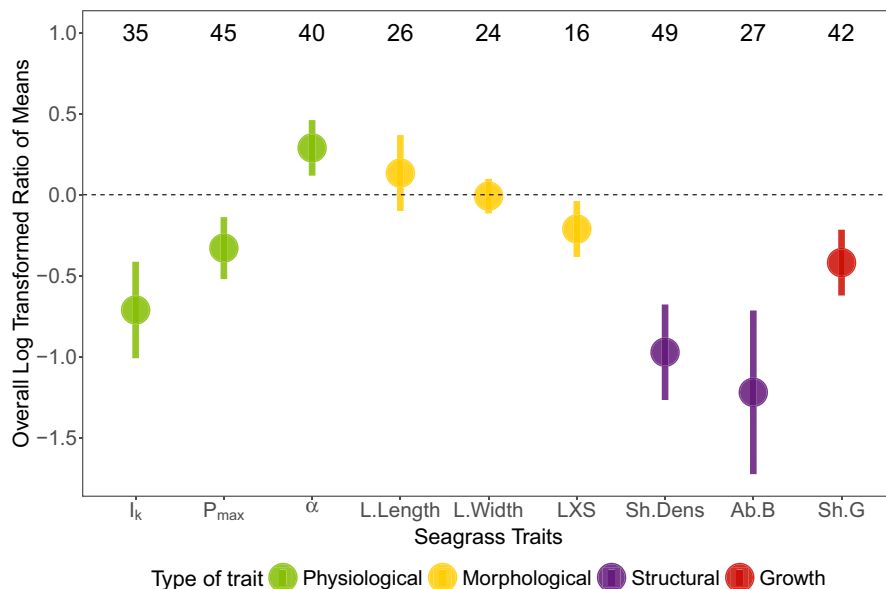


FIGURE 3 Overall effect sizes against light reduction calculated for each seagrass trait. Colours define the type of trait: physiological (green), morphological (yellow), structural (purple) and growth (red). Numbers above each trait represent the number of scientific studies for each seagrass trait analysed (for further explanation of these numbers, see Table 1). Seagrass traits shown from left to right, I_k , saturation irradiance; P_{max} , maximum photosynthesis; α , photosynthetic efficiency; L.Length, leaf length; L.Width, leaf width; LXS, leaves per shoot; Sh.Dens, shoot density; Ab.B, above-ground biomass; Sh.G, shoot growth.

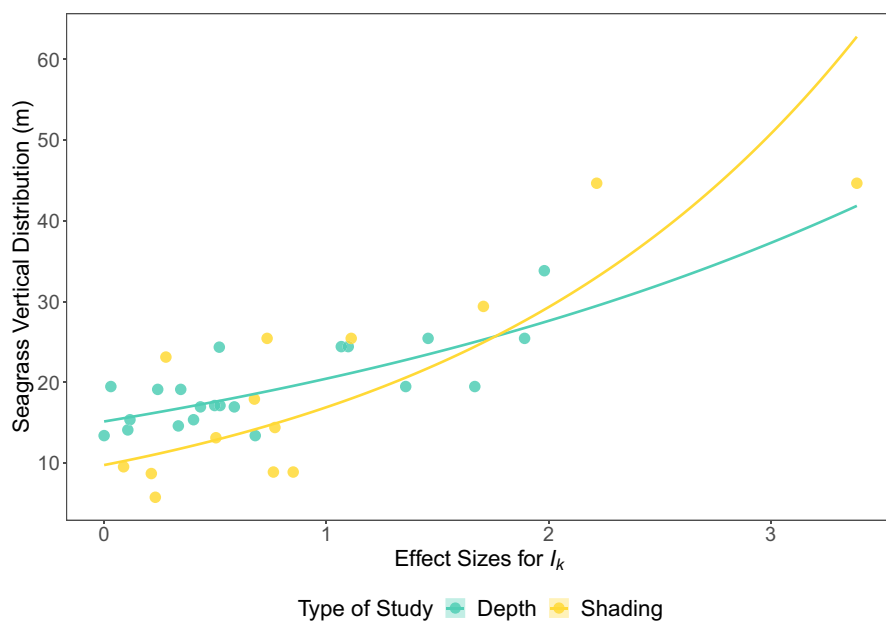


FIGURE 4 Relationships between seagrass maximum vertical distribution (in metres) and predictor variables, effect sizes (acclimatization potential for saturation irradiance, I_k) and type of study (depth-based and field shading). Data points represent distribution of standardized partial residuals of the fitted linear mixed model, where continuous lines represent the model fit through the data.

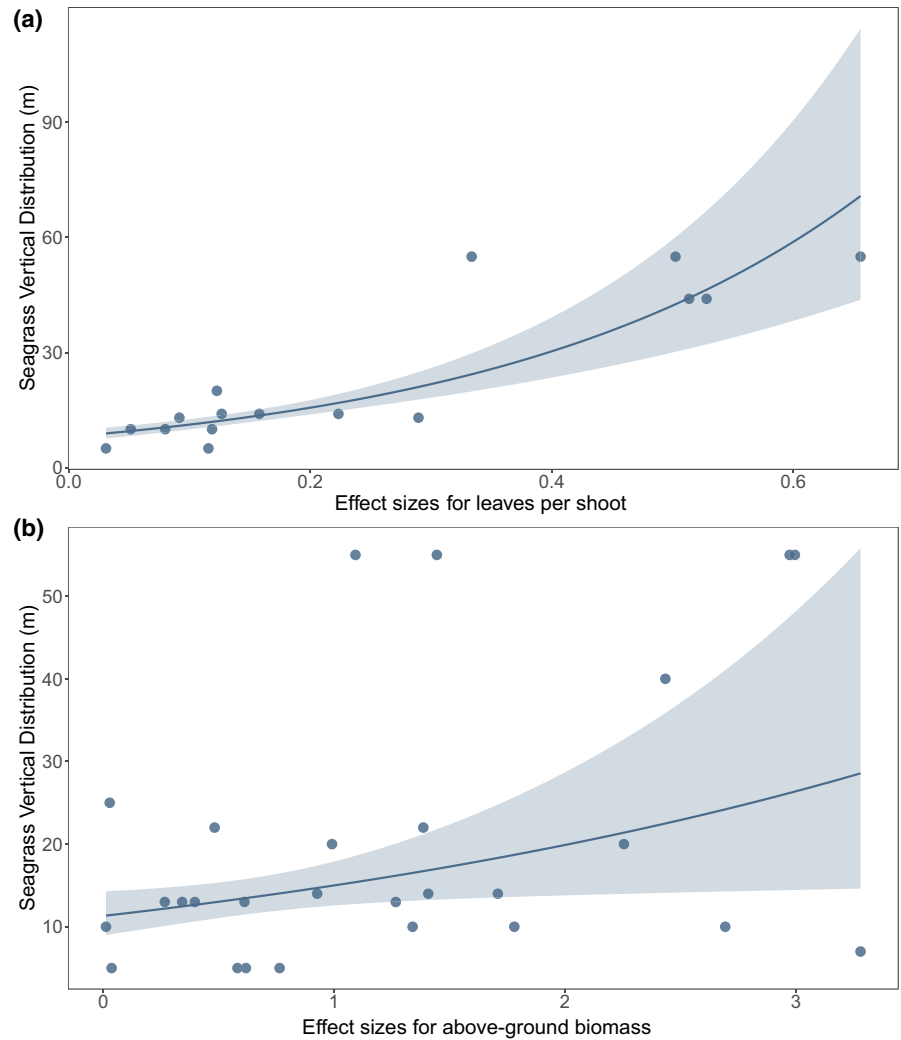
occupy wide depth distributions whereas others remain limited to much shallower ranges is therefore crucial to determine the differential susceptibility of seagrass assemblages to reduced water quality. Our survey of a large proportion of seagrass species world-wide indicates that their vertical distribution scales with acclimatization potential in key physiological, morphological and structural traits associated with low light. This ability transcends species size or functional groups, with trait acclimatization capacity found across species with large differences in rhizome width (our proxy for species size) or plant strategies. In addition, we found that these traits were not limited to a single organizational level but were a mix of physiological, morphological and structural traits. Of the traits we explored, the vertical distribution of seagrass species was best explained by the degree of species-specific capacity to reduce saturation irradiance

(physiological trait), along with the capacity to reduce leaves per shoot and above-ground biomass (morphological and structural traits, respectively) as light conditions worsened.

4.1 | Seagrass maximum vertical distribution and species size

Despite the strong negative relationship between the light attenuation coefficient (k) and the depth limit of seagrass meadows (Duarte et al., 2007), light availability alone cannot accurately predict species-specific vertical distributions of seagrasses (Koch, 2001). Earlier studies have already highlighted the striking interspecific differences in seagrass depth ranges, which were attributed to seagrass

FIGURE 5 Relationships between seagrass maximum vertical distribution (in metres) and predictor variables, effect sizes: acclimatization potential for (a) leaves per shoot and (b) above-ground biomass. Data points represent distribution of standardized partial residuals of the fitted linear model, where continuous lines represent model fit through the data and the shades show 95% confidence intervals.



growth strategies or architecture (Duarte, 1991a). For instance, it has been proposed that larger rhizomes are linked to better carbon allocation abilities, which could help to boost the carbon balance of plants against declines in benthic light and promote seagrass growth through increased carbohydrate reserves (Alcoverro et al., 1999). Our results, however, conclusively rule out plant size or architecture, which is strongly related to rhizome diameter (Duarte, 1991b), as the primary predictor of seagrasses colonizing deeper depths. In fact, large rhizomes might place a heavy respiratory burden on plant physiology at depth or during periods of severe light reduction (Alcoverro et al., 2001; Duarte, 1991a; Fourqurean & Zieman, 1991; Hemminga, 1998). This respiratory demand might well offset the reserve advantages of larger rhizomes. Having large rhizomes to allocate resources has clear advantages and might provide seagrasses with considerable resilience to seasonal light trends or in the face of disturbances such as herbivory, sedimentation or occasional light reduction (Roca et al., 2014; Ruiz & Romero, 2003; Vergés et al., 2008). However, the maintenance costs of this architecture make it untenable in low-light conditions (Hemminga, 1998), and some species might have to trade off resistance to short-term light deprivation against a larger vertical distribution.

4.2 | Seagrass maximum vertical distribution and growth/reproductive strategy

Our results show no evidence that growth/reproductive strategies reflect differences in the vertical distribution of seagrass species. Colonizing, opportunistic, persistent and their intermediate life-history strategies are a useful way to classify seagrasses of the world in relationship to their functional resilience. As conceived by Kilminster et al. (2015), they combine a range of species-specific attributes, including shoot turnover, sexual maturity and investment in dormant seeds, to characterize how species are likely to respond to disturbances. Colonizing plants are characterized by faster growth rates, shorter time to sexual maturity and a higher investment in dormant seeds. Persistent species, in contrast, adopt a contrasting strategy, taking longer to reach maturity, growing more slowly and investing more in vegetative growth. Opportunistic species adopt a mixed strategy (Kilminster et al., 2015). It has been suggested that some of these traits, such as a reduced leaf/shoot turnover in persistent species, might be a long-term tolerance mechanism against reduced light conditions. For a relatively minor loss of acquired resources, plants could maintain large amounts of biomass, to cope with light reduction better

(Olesen et al., 2002). However, what emerges from our analysis is that resilience strategies do not clearly map to vertical distribution.

4.3 | Seagrass maximum vertical distribution and trait acclimatization potential

The ability to deal with reducing light conditions represents a slightly different set of physiological challenges from other environmental or biotic stressors and requires a unique set of plant strategies. Thus, what separates species with the largest vertical distributions, such as *P. oceanica*, *Cymodocea nodosa*, *H. stipulacea* or *Amphibolis griffithii*, is not so much their morphologies (they have diverse above- and below-ground structures) or their resilience strategies (which differ considerably among them), but the remarkable acclimatization potential in their physiological and morphological responses with changing light (Mackey et al., 2007; Ruiz & Romero, 2001; Silva et al., 2013; Tuya et al., 2019). In contrast, species with lower acclimatization capacity in their photosynthetic traits have never been observed at great depths. These photosynthetically limited species include *P. sinuosa* (Collier et al., 2008), *Syringodium filiforme* (Major & Dunton, 2000) and *Thalassia testudinum* (Enríquez et al., 2019). Interestingly, the photo-acclimatization responses identified in this analysis range from physiological acclimatization through to the ability to modify morphologies and above-ground structure. Studies of individual species identify this acclimatization potential as being essential in dealing with light reduction (Bité et al., 2007; Campbell et al., 2007; Collier et al., 2009; Ruiz & Romero, 2001; Silva et al., 2013); our approach allows us to generalize this across species, linking it clearly to depth distributions.

Perhaps unsurprisingly, higher physiological acclimatization capacity in the photosynthetic machinery of the plant is crucial to their ability to occupy a wide range of light regimes. As light conditions reduce with depth, only species with the ability to acclimatize by counterbalancing their carbon gains can persist (Ruiz & Romero, 2001; Ruiz & Romero, 2003). This response is typically the primary mechanism by which plants deal with light reduction (Collier et al., 2012; McMahon et al., 2013; Ralph et al., 2007). Of the three physiological parameters we examined, the reduction in the saturation irradiance (I_k) allows plants, albeit at the cost of also reducing their maximum photosynthesis, to obtain higher photosynthetic efficiencies in low-light conditions (Marín-Guirao et al., 2022). Past studies have highlighted that a photo-acclimatization response in this trait might explain more efficient use of light, in addition to differences in vertical distribution for a limited set of species (Bité et al., 2007; Campbell et al., 2007). For instance, a recent paper by Park et al. (2021) indicates that interspecific variation in physiological traits, among other traits, helps to explain differences in the vertical distribution of three *Zostera* spp. (*Zostera japonica*, *Zostera marina* and *Zostera caespitosa*). Likewise, Silva et al. (2013) showed that *C. nodosa*, with larger vertical distributions, is better photosynthetically adapted to low-light conditions than the less plastic *Z. marina*. Our study shows that the acclimatization potential of physiological traits, specifically

the ability to modulate I_k , works across species and powerfully predicts the vertical distributions that might hold across the seagrass assemblage.

Acclimatization potential as a determinant of vertical distribution was also found at higher levels of plant organization. Across the assemblage, seagrasses showed considerable intraspecific variability in morphological, structural and growth traits, with a few notable exceptions. Crucially, the ability of the plant to reduce leaves per shoot and above-ground biomass explained species-specific vertical distributions. Many large seagrass species that form dense meadows (*P. oceanica*, *C. nodosa* and *A. griffithii* among them) adopt a leaf-reduction mechanism (defoliation) to minimize self-shading, an ideal strategy when colonizing deeper, darker locations (Mackey et al., 2007; Ruiz & Romero, 2001). For these species, defoliation might serve to mobilize carbohydrates (Silva et al., 2013). In addition, carbohydrate losses could be minimal if the leaf loss is restricted to older leaves, which make a minor contribution to carbon production (Alcoverro et al., 1999). This is also an ideal method for reducing the costs of above-ground respiration in impoverished light environments (Collier et al., 2009; Fourqurean & Zieman, 1991; Mackey et al., 2007). However, species showing limited ability to modify their leaves per shoot or above-ground biomass, compared with other species (for instance, *T. testudinum*, *Thalassia hemprichii* or *P. sinuosa*), are confined to shallower waters (Collier et al., 2009). Of the traits we measured, leaf dimensions (length and width) demonstrated a poor ability to change with light limitation across all species. This reduces the ability of seagrass species to expand their photosynthetic areas or (by growing taller) access shallower, more light-rich waters. For instance, leaf length and width have been found to decrease with light reduction in species such as *P. sinuosa* (Collier et al., 2009). In general, leaf morphology might be an unreliable predictor of seagrass responses to low-light environments (Tuya et al., 2019). Instead, at the deeper ends of their vertical distributions, seagrass species adopt strategies to minimize energy expenditure with structural modifications.

Across the assemblage, shoot density and shoot growth reduced, in general, with light reduction for most species in our dataset. Although the pattern of decline with reducing light was similar within species and within studies (see Supporting Information Appendix S1), the acclimatization potential of these traits did not adequately explain the specific vertical distributions of seagrasses. Declines in shoot density are strongly linked to the ability to store carbohydrate reserves, particularly in larger species possessing larger rhizomes (Alcoverro et al., 2001). Nevertheless, for structural traits, the relatively short timing and duration of shading studies might have influenced our results (Collier et al., 2009). In fact, for experimental studies, long-term responses are expected to see the effect of light not only in the survival, but also in the full development of true meadows at their edges.

A potential limitation of our study is that we did not control for other abiotic factors that vary with depth that could also play a role in determining vertical depth distributions (Beer & Waisel, 1982; Carr et al., 2010). We limited our investigation to depth-based

studies and shading manipulative experiments, where the only modified condition was light reduction. Our purpose was to obtain metrics related to plant identity that could explain depth distribution, but we cannot disentangle whether other factors, such as turbulence or sediment grain size, or overall differences between temperate and tropical waters additionally influenced these patterns. Our results are based on only a subset of species, because we do not yet have a comprehensive understanding of the responses of many seagrass species to reduced light. Shading experiments or comparative depth-based studies do not exist for all seagrass species, but represent c. 30% of the entire seagrass pool. As previous studies have already highlighted, our ability to generalize is necessarily circumscribed by gaps in research effort (McMahon et al., 2013). Moreover, this lack of species representation combines with an unequal distribution of our data across the entire range of depths suitable for seagrasses, which could have shaped the results found in this study.

5 | CONCLUSIONS

What seems clear is that seagrass species use different strategies, at different levels of organization, to colonize deeper locations. Physiological acclimatization is geared towards maximizing their light-harvesting strategy in the deep, whereas higher-level strategies are directed at minimizing costs and reducing plant architecture. These strategies work in tandem. The seagrass species with the greatest vertical distribution were able to acclimatize physiological, morphological and structural traits (I_k , leaves per shoot and above-ground biomass) simultaneously. A combined acclimatization ability at physiological and higher levels is what makes these species particularly successful across the entire depth gradient.

Although the decline in areal extent of seagrass meadows is easy to see as coasts succumb to a host of local and global stressors, the vertical contraction of meadows is often less visible. Yet it is one of the surest signs of an ecosystem in decline and serves as a warning of worsening ecological conditions. Identification of the mechanisms by which different seagrass species thrive within their natural depth ranges is crucial to establish species-specific baselines against which to measure this retreat and calibrate recovery programmes. Seagrass species have different vulnerabilities to declining light conditions, with some being particularly sensitive to even small changes in light regimes. What our work shows is that the ability to deal with reduced light is not linked to a few specialized traits, but with the acclimatization potential to modify trait parameters at physiological, morphological and structural levels. There are, however, limits to trait acclimatization, and many meadows are increasingly depth restricted as stressors increase. Reversing this retreat will require concerted and coordinated efforts to improve water quality but are essential to conserve the diversity and function of seagrass meadows across their depth range.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data and R code that support the findings of our study are available in the Supporting Information of this article at: https://zenodo.org/record/7659364#.Y_Q7sXZBy3A

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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