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Patterns of shading tolerance determined from experimental light reduction studies of seagrasses

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Abstract

A review and analysis of the experimental literature on seagrass shading evaluated the relationships among experimental light reduction, experimental duration, additional modifying factors and common meadow-scale seagrass response metrics to determine whether there were consistent statistical relationships. Modifying factors included study latitude, field site depth, season of experiment initiation, rhizome connectivity (severed, intact), experiment type (field, mesocosm), and seagrass life history strategy. Highly significant, best fit linear regression models were found for both biomass and shoot density reduction that included light reduction, duration and other modifying variables, although unexplained variation in the data were high. Duration of light limitation affected extent of response for both metrics, and unexplained variance was greatly reduced by analysis of data from durations >60d for shoot density and for >60d <120d for biomass. Life history strategy was also a significant factor in three of four regression models. While the slopes of the responses were relatively similar for biomass and shoot density, unexplained variation was generally greater for shoot density than biomass in models for data pooled across species. There were highly significant, best fit regression models found for both biomass and shoot density for both genus and species level analyses, with the extent and duration of light reduction the most important model factors. Season of experiment, rhizome status, latitude, and experiment type all were also included in multiple models. Biomass regression models again tended to have lesser unexplained variation than shoot density models. Life history was invariant within genus and species, and separate analyses for data divided among Colonizing, Opportunistic, and Persistent strategies found relatively similar, best fit regression models among strategies. However, the mean percent reduction of both biomass and shoot density was generally lower for the Persistent strategy than for the other two life histories, suggesting a greater buffering capacity against effects of light reduction for such species. Overall, biomass based models explained more of the variance in seagrass response to light reduction than shoot density, and may be the preferred response variable for meadow-scale impact assessments. The relationships observed may inform management decisions by helping define the scope of expected responses of seagrasses in general to the range of factors that may reduce light availability to seagrasses.

Keywords

Seagrass light reduction; shading; light limitation; seagrass biomass; seagrass shoot density

Introduction

The central role of light limitation on seagrasses is well defined both in the context of natural distribution and abundance and in the context of anthropogenic disturbances (e.g. nutrients, suspended sediments) that affect seagrass growth and survival (Biber et al., 2005; Lee et al., 2007; Ralph, 2007a, 2007b; Leoni et al., 2008). Duarte (1999) commented that a major limitation to seagrass conservation and management was the lack of predictive ability in terms of magnitude and time scale of seagrass responses to particular stressors. Conceptual models have been developed to represent the hierarchy of seagrass impacts from biochemical to population levels together with the relative temporal sequence in response to light limitation (Leoni et al., 2008; McMahon et al., 2013; Roca et al., 2016). Some generally predictive relationships have been developed, including the relationship of seagrass depth distribution to water clarity (Duarte, 1991; Krause-Jensen et al., 2003; Greve and Krause-Jensen, 2005), and minimum light requirements for seagrasses (Dennison, 1987; Kenworthy and Fonseca, 1996; Dennison et al., 1993; Thom et al., 2008). However, in the course of recent work to develop an epiphyte load indicator of nutrient impacts to seagrasses (Nelson 2017), the question arose as to whether there was a general predictive relationship available to translate a reduction in light available to seagrass, e.g. through epiphyte shading, into a predicted magnitude of impact to seagrass populations in terms of metrics such as biomass or shoot density. Search of the literature failed to find such a generalized relationship. The considerable experimental literature, both field and laboratory, provides a data source to assess development of empirical relationships. Therefore, literature review and analysis of composite experimental data were conducted.

Experimental studies of light reduction involve both a magnitude and a duration of light reduction for any given treatment, both of which will affect the extent of impact on population characteristics of seagrasses, and therefore the relative effects of both factors must be accounted for. Additional sources of variation including seagrass species, experimental type and approach, seasonal timing of experiments, and location may also affect the outcomes of light reduction experiments. The current analysis focused on population level response metrics (biomass, shoot density) both because these were among the most commonly measured metrics, and because these metrics most directly translate into unequivocal measures of population status that can be monitored to support regulatory standards for water quality. The literature analysis addressed the following questions. Do general statistical relationships across seagrass species exist for light reduction versus magnitude of impact on population parameters? Do such relationships differ for different population metrics, and are there differences among species and/or genera of seagrasses?

Methods

A review of the literature on experimental light reduction on seagrasses was conducted in order to evaluate whether predictive relationships could be discerned between magnitude of light reduction and seagrass population response metrics. Studies utilized were primarily peer reviewed literature, but included some theses, dissertations and technical reports (Supplemental Material). Searching for relevant studies relied on previous reviews of seagrass responses to light (particularly Leoni et al., 2008, McMahon et al., 2013; Roca et

al., 2016), and included bibliographic searches for relevant terms using Google Scholar, Web of Science, and search engines for scientific journal web sites.

The principle focus of the literature review was experimental studies that manipulated light availability to seagrass, typically through use of shade screens. The considerable literature associated with light reduction to seagrasses from epiphytes is reviewed by Nelson (2017) and is not considered here. Another potential source of data on light reduction was studies that focused on the impact of fixed or floating dock structures on seagrass (Molnar et al., 1989; Fresh et al., 1995, 2001, 2006; Burdick and Short, 1999; Shafer, 1999; Beal and Schmidt, 2000; Landry et al., 2008). Unfortunately, there were few cases in which all necessary parameters were measured. Given the potential for additional sources of physical disturbance to seagrass associated with dock structures (Gladstone and Courtenay, 2014), such studies were not included in the current analysis.

While a wide variety of metrics have been used to assess the response of seagrass from physiological to population levels (Biber et al., 2005, McMahon et al., 2013), the focus of the present effort was on population level responses measured with the most commonly recorded metrics in seagrass light reduction studies, biomass and shoot density. Because original units for both biomass and shoot density were highly variable among publications, all metric values were converted to percent reduction compared to control values measured at the same times. Positive changes for response metrics in light reduction treatments versus control were excluded from analysis. Percent light reduction was calculated relative to control values, and where given by authors, was also recorded as percent of incident irradiance (I_0).

Additional continuous and categorical variables were collected for each study. Duration of experimental treatment was recorded as days. Where exact sampling dates were provided, dates were converted to Julian calendar, and duration was calculated; otherwise duration was estimated based on multiplying number of months by 30 d. Latitude (absolute value) of field studies or field collections for mesocosm studies was recorded, and if not provided, was determined from study site maps and descriptions using Google Earth. Depths were recorded for field studies, but only for a few instances in mesocosm studies where deeper tanks were used. For field studies, status of rhizome connection was recorded as to whether rhizomes had been severed or not, while rhizome status for mesocosm studies was classified as severed, since in all cases experimental plants were dug up from relatively small areas and transported from the field. Season of experiment initiation was broadly classified as falling either during Spring-Summer or Fall-Winter, generally representing principal versus secondary or senescent growing seasons. Austral Spring-Summer was assumed to occur from September-February. Whether the experiment was a field or mesocosm study was recorded.

Kilminster et al. (2015) proposed the utility of a multi-attribute classification of seagrasses in understanding responses to environmental disturbances. Seagrass life history was one attribute, and Australian seagrass species were assigned to predominantly Colonizing, Opportunistic, or Persistent strategies. Non-Australian species in the present study were assigned the life history strategy of their genus as given by Kilminster et al. (2015).

Data were extracted from 42 publications (Table 1, Supplementary Material), representing 17 species of submerged aquatic vegetation (15 seagrass species plus *Ruppia maritima* and *Vallisneria americana*), which reported light reduction experiments either in mesocosms of various sizes or in the field. For convenience, the data set will be referred to as “seagrass” data since observations using *Ruppia* and *Vallisneria* represented about 5% of the total observations. In several cases, taxonomic classification had changed since original publication. *Heterozostera tasmanica* is now *Zostera nigricaulis* (Jacobs and Les, 2009), and *Zostera capricorni* is now *Zostera muelleri* subsp. *capricorni* (Jacobs et al., 2006). Data tables (e.g. Supplementary Material) use the current nomenclature while noting the taxonomy as originally published. All data for subspecies of *Zostera muelleri* were pooled and treated only at the species level. The data set was heavily weighted toward Australian species (82% of shoot density and 50% of biomass observations). This was particularly true of more recent data sources (e.g. Chartrand et al., 2012, 2016; Collier et al., 2009, 2011, 2012, 2016; Lavery et al., 2009; York et al., 2013).

Experiments that were conducted for durations too short to show impacts on biomass or shoot density (e.g. Bach et al., 1998) were excluded from analysis, as were results that showed positive responses (i.e. release from photoinhibition) to decreased light (e.g. Fokeera- Wahedally and Bhikajee, 2005). A total of 594 experimental observations of one or both metrics were available for analysis, including 216 measurements of biomass reductions and 448 measurements of shoot reductions. Number of observations per species ranged from 0–72 for biomass and 0–85 for shoot density (Table 1).

To acquire data from published graphs, data were digitized with Grab It!™ software (Datatrend Software). Images of graphs from PDF files of publications were copied with the Microsoft Snipping Tool app, saved to JPG format image files, and imported into Grab It!™, which operates within Microsoft Excel. Repeated measurements of the same data points with the software gave a measurement error of less than 0.1%. Comparison of the values extracted via software to values for the same data points that were given in the publication gave a measurement accuracy on the order of 2–3%. These sources of error were small relative to other potential sources of variation in the data.

Data quality from secondary data sources used in the paper was assessed by cross checking data from tables or figures with text statements for internal consistency, assessment of the clarity and completeness of methods descriptions, and recomputation of regression equations for comparison where appropriate. Most data analysis was conducted in SAS™ with a variety of regression approaches. Preliminary assessments of variable relationships were conducted with the SAS REG (regression) and GLM (general linear model) procedures. Depth for field studies showed no relationship to either response metric, presumably because metrics were expressed as percent reduction relative to controls that were located at the same depth, and the variable was excluded from further analyses. Examination of the distributions of the continuous variables indicated a reasonable fit to normal distributions. Therefore, best regression model selection was conducted with SAS GLMSELECT, which accommodates analysis of many continuous and categorical variables. Stepwise selection of variables was selected with the stopping criteria that none of the variables omitted from the model was significant at the entry significance level (0.15) and every variable included in the model was

significant at the stay significance level (0.15). AIC (Akaike's information criterion) was used as the best fit criterion. Regression analyses were conducted for the two seagrass response metrics with data pooled for all species combined, for pooled congeneric species and for individual species where $n > 14$. Sigmaplot 13™ software was used to generate regression figures. ANOVA was conducted with both SAS and Sigmaplot. All data collected and their sources are provided in a spreadsheet in Supplementary Materials.

Results and Discussion

General Relationships

There was a highly significant, linear relationship of percent biomass reduction versus percent light reduction (versus controls) when all available data were plotted (Fig. 1), although variability in the relationship was very high. The best fit, general linear model increased the proportion of variance explained from 0.19 to 0.49, and found biomass reduction to be a function of light reduction, duration of reduction, experiment type, seagrass life history, latitude and season (Table 2; variables in order of contribution to reduction of AIC). When data were binned into 30 day intervals (Fig. 1), there was a tendency for longer durations to have higher percent biomass reduction for equivalent percent light reduction levels.

To further examine the influence of experimental duration, simple linear regressions of percent biomass reduction and duration were computed for each 30d temporal data bin (Table 3). For duration < 30 d, the regression was non-significant, with r^2 values increasing for intervals 61–90d and 91–120d, before decreasing somewhat (Table 3). Therefore, a best fit, general linear model was computed with only data for duration $60 < d < 120$, generating a model with biomass reduction as a function of light reduction, duration of reduction, season, seagrass life history, and rhizome status, which now explained 73% of variance. While included in the model, rhizome status contributed very little to improved fit (Table 2). The limited impact of cutting rhizomes is consistent with the limited experimental data (Fitzpatrick and Kirkman, 1995), which showed no effect of severing rhizomes on seagrass responses to light reduction for *Posidonia australis*.

There was also a highly significant, linear relationship of percent shoot density reduction versus percent light reduction when all data were plotted, although the percent of variation explained by the regression was again low (Fig. 2). The best fit, general linear model increased the proportion of variance explained from 0.19 to 0.39, and found shoot density reduction to be a function of only light reduction, duration of reduction, and seagrass life history (Table 2). Shoot density appears to respond less readily than biomass to high levels but shorter durations of light reduction, as indicated by the pattern of response for data with < 90 days of light reduction in Figure 2. Simple linear regressions for percent shoot density reduction versus experimental light reduction for data binned by 30d intervals showed increased r^2 values for durations > 60 d (Table 3). The best fit, general linear models computed with data for duration > 60 d included the same variables as for all data (light reduction, duration of reduction, seagrass life history, Table 2), and the model r^2 (0.43) was considerably lower than that for biomass reduction.

For a subset ($n = 404$) of observations, light reduction was also expressed as a percent of I_0 . Exploratory simple linear regressions of biomass ($n=151$, $r^2 = 0.14$, $p<0.0001$) and shoot density reduction ($n=290$, $r^2 = 0.14$, $p<0.0001$) against I_0 failed to reduce the level of unexplained variation, and this variable was not further considered.

To further explore the influence of duration on the seagrass response metrics, percent biomass and percent shoot density reduction were regressed on duration of light reduction (Fig. 3). Both metrics had highly significant regression relationships (exponential rise to maximum) to duration of light reduction, but there tended to be less variation among observations at long durations of light reduction (300–400d) for biomass as compared to shoot density. For both response metrics, the maximum reduction response estimated from regression was 66–75% compared to controls, which was reached by approximately 100 days duration

In the present data set, percent shoot density reduction had a positive, significant relationship to percent biomass reduction for given light reduction levels (Figure 4). The regression slope of shoot density on biomass (0.71) was <1 , indicating percent biomass reduction is slightly larger than percent shoot density reduction for equivalent light reduction. While changes in leaf size in response to shading might explain such a result, leaf morphology responses have been shown to be highly variable among species, and increases (e.g. Short, 1991), decreases, and neutral responses have all been observed (Ralph et al., 2007a).

Recent work by Collier et al. (2016) has determined that there are differential species responses of shoot density reduction to light limitation, and has shown that temperature has a highly significant effect on the slope of the response relationship. Therefore, it might be expected that differences in responses among the 17 species in the present analysis would contribute additional variation given the differences in minimum light requirements among species (Dennison, 1991; Duarte, 1991). However, there was no evidence of any consistent species related pattern when the data were binned by taxon and plotted for either response metric. General linear regression model analyses with species coded as a categorical variable failed to include species as a significant model variable for either response metric, confirming the conclusion from the visual inspection of the data.

Collier et al. (2016) also demonstrated that loss of shoots occurred more rapidly at higher temperature in mesocosm experiments for all four seagrass species examined, suggesting that environmental temperature may be an important source of variation in the results compiled herein. However, latitude as a potential proxy for temperature was not included in the general linear regression models for shoot density reduction, and was a very minor contributor to the model for biomass reduction. A more precise measure of temperature would be difficult to include in analyses since it was not generally continuously monitored, and the temporal variation in temperature at field study sites may be large.

Given that studies have observed differences in seagrass response depending on the season in which light reduction was imposed (Fitzpatrick and Kirkman, 1995; Moore and Wetzel, 2000; Serrano et al., 2011), it was surprising to find that season provided only a small improvement in fit to the biomass reduction model and was not included in the shoot density

reduction model (Table 1). In the present analysis, season was restricted to two general categories, and it is conceivable that utilizing more precise information on the experimental period in field studies might be necessary to discern an impact in the composite data set.

Genus and Species Level Relationships

The best fit, general linear regression models for data combined at the level of seagrass genus for biomass and shoot density reduction relative to controls are shown in Table 4. There were significant models for three of four genera for biomass (r^2 range from 0.47 – 0.76), and for all four genera examined for shoot density (r^2 range from 0.44 – 0.78). As data sets became more constrained, some categorical variables had only one class and were not included in regression models. Life history was not included for any genus, and experimental type was not included for *Zostera* species biomass, and for *Posidonia* spp and *Thalassia* spp shoot density reduction.

All significant models included both light reduction and duration, usually as the first two factors included. In contrast to the composite data sets, status of rhizome was included in four models, including both biomass and shoot density reduction (Table 4). Both latitude and season were each included in three models, but only for shoot density. Experiment type was significant in two models, both for biomass and shoot density. In general, inclusion of significant terms for rhizome status, latitude, season and experiment type decreased unexplained variance by only small amounts. The exception was experiment type for *Halodule* spp, reflecting a highly significant difference ($t=-3.05$, $p=0.008$) in percent biomass reduction reported from mesocosm (76.2) versus field experiments (42.9). Since there was no significant difference for shoot density ($n=67$), this may simply be an artifact of small sample size ($n=17$).

Analysis of data for individual species with sample sizes $n>15$ yielded four best fit, general linear regression models for biomass reduction (r^2 range from 0.47 – 0.83), and six models for shoot density reduction (r^2 range from 0.41 – 0.70, Table 5). As for genus level analyses, some categorical variables had only one class and were not included in regression models. For biomass reduction, experimental type was not included for *R. maritima*, and rhizome status for *R. maritima* and *Z. muelleri*. For shoot density reduction, experimental type was not included for *C. serrulata*, and rhizome status for *C. serrulata*, *Z. muelleri*, and *Z. nigricaulis*. All models included significant terms for light reduction and duration, usually as the first terms included in the regression models. Season and latitude were again the two factors most often included as significant terms in the models, with season in two biomass and four density models and latitude included in two models each. Experiment type and rhizome status were significant factors in only one shoot density model each (Table 5), but were influenced by limitations of the data sets. The model for *Zostera muelleri* was unusual in that duration and light reduction contributed less to reducing the unknown variation than latitude and season terms, for reasons that are unclear.

Because life history was not included in either the genus or species level regression analyses, life history data were compiled for each strategy and each response variable and analyzed independently (Table 6). Duration and light reduction were significant in all models (r^2 range from 0.33 – 0.66). Latitude was significant in four models, and rhizome status was

significant in three. Experiment type and season were each significant in two models. All four factors decreased the unexplained variance by only small amounts. There was relatively little difference among the three life history strategies in the percentage of variance explained by the combination of light reduction and duration. The percentage of variance explained was generally higher for the regression models computed at genus or species taxonomic levels as compared to life history groups.

Relevant to life history considerations, Hemminga (1998) has suggested that under low light conditions, a higher proportion of belowground biomass may be deleterious to the plant because the larger respiratory demands of the roots and rhizomes can no longer be supported. Persistent species such as *Thalassia* spp and *Posidonia* spp tend to have a higher proportion of belowground to aboveground biomass (1.1 – 5.5, Duarte and Chiscano 1999) than for Colonizing species such as *Ruppia maritima* (0.5, Pulich, 1985; 0.6 Dunton, 1990) and Opportunistic species such as *Zostera marina* (0.5, Duarte and Chiscano, 1999). Classifying the species in Table 1 of Duarte and Chiscano (1999) according to Kilminster et al. (2015), the belowground/aboveground biomass ratio was significantly higher for Persistent species compared to the other two life history strategies (ANOVA, $F=6.6$, $p=0.007$). ANOVA comparisons of the mean values for both biomass and shoot density reduction found significant differences among life history strategies, results that were contrary to the proposal of Hemminga (1998). Mean percent biomass reduction for the Persistent strategy (47.5) was significantly less than that for the Colonizing (62.3) strategy, but not the Opportunistic (57.5) strategy (ANOVA, $F=3.09$, $p=0.048$). Mean percent shoot density reduction for the Persistent strategy (40.3) was significantly less than that for both the Opportunistic (49.6) and Colonizing (51.7) strategies (ANOVA, $F=3.56$, $p=0.029$). These results suggest that seagrasses with the Persistent life history strategy may be somewhat better buffered against reduced light than species with other life history strategies.

Conclusions

In their review of bioindicators of light stress in seagrasses, McMahon et al. (2013) found comparable levels of positive response of the “meadow scale” variables biomass and shoot density. Their analysis suggested that the response period of biomass was on the order of months while shoot density responded to light decreases on the order of weeks to months. In the present analysis, the clearest patterns of response of both biomass and shoot density were not observed until after at least 2 months of light reduction. The analyses conducted in the present review indicate that the rates of reduction for biomass and shoot density due to light reduction are relatively similar (Figs. 1, 2). The initial slopes of the curves fit to the relationship of biomass and shoot density versus duration of light reduction (Fig. 3) were very similar, suggesting comparable initial responses to duration. For example, the regression equations in Fig. 3 generate roughly similar estimates of decreases of 25.6% in biomass and 23.5% in shoot density at 21 days of light reduction. Cabaço et al. (2013) found that average shoot biomass increases with shoot density in all seagrass species analyzed, so a general similarity in a negative response might also be anticipated. Correlation of the response pattern between shoot density and biomass was confirmed (Fig. 4), but there was considerable variability. Overall, levels of unexplained variation tended to be lower for biomass reduction than for shoot density reduction for composite data (Figs. 1–3, Tables 2–

3), and particularly when multivariate models were fit to data binned for durations of light reduction >60 days (Table 3). These results suggest that biomass may be the preferred “meadow scale” response metric, although to date shoot density has been recorded almost two times more frequently (Table 1).

The importance of additional explanatory factors in reducing unexplained variance in the regression models tended to vary with the level at which data were analyzed. Life history and season were included in models for the entire data set. Season, rhizome status, and latitude were included more frequently for genus level regression models, which did not include life history because of uniform values within genus. Similarly, season and latitude were most commonly included in species level regression models, but other variables (experiment type, rhizome status) became artificially limited by the input data available. While the multivariate regression models at species level could explain >70% of variance in a number of cases, in others (Table 5) >50% of variance remained unexplained. Variation among studies within a single subject species represents an important uncontrolled source of variation in the present analyses, and may stem from multiple sources, including source population variation and variation in the precise experimental methods and conditions, that are difficult to quantify.

As Leoni et al. (2008) pointed out, few experimental studies include treatments with relatively small reductions in light, and thus the data sets tend to be skewed towards higher values of light reduction. In the present review, relatively few studies included treatments for light reduction that were less than 50% relative to controls (see Fig. 1). This is unfortunate in that establishment of protective criteria to limit damage to seagrass from anthropogenic disturbances would benefit from higher levels of certainty in terms of expected changes from smaller rather than larger light reductions. A notable recent exception is the work by Collier et al. (2016), which presents light reduction data for multiple species at levels of 30 and 40 percent light reduction relative to surface incident light. While durations were limited to 14 weeks, and may not have been sufficient to observe effects at these higher light levels in all cases, there was evidence of reduction in shoot density in some species, particularly in elevated temperature treatments.

The analysis of the results from experimental light reduction, summarized across multiple SAV species for meadow scale metrics of seagrass response, shows that in spite of considerable variability arising from multiple sources, there are useful patterns that may be discerned.

These patterns may assist in management decisions by helping define the scope of expected responses of seagrasses in general to the range of factors (epiphytes, phytoplankton, sediments, and dock structures) that may reduce light availability to seagrasses. In a very similar fashion, Collier et al. (2016) have recently proposed the use of species-specific regression relationships of morphological response (shoot density) to light reduction as an approach to develop protective water quality guidelines. The generalized relationships developed here may also have implications for seagrass monitoring programs, particularly associated with activities such as dredging operations, which may have a known, anticipated duration. Reference to the regression relationships allows estimation of the percent change

in seagrass metrics associated with potential level and duration of light reduction from a project. Power analyses may then be employed to design monitoring programs with statistical power to detect levels of impact to seagrasses that are anticipated (Heidelbaugh and Nelson, 1996). While the development of detailed, species and location specific, relationships of seagrass response metrics to magnitude and duration of light reduction would ultimately be most desirable, such studies can be costly and time consuming, and more generalized relationships may help to protect seagrass resources in the interim.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Figure 1.

Linear regression relationships of response metrics versus percent light reduction compared to controls for all data, with data binned by duration of the light reduction. Bins are 0–30 d, 31–60 d, 61–90 d, 91–120 d, > 120 d. A. Percent biomass reduction ($y = 0.74x + 1.8$, $r^2 = 0.19$, $p < 0.0001$, $n = 216$). B. Percent shoot density reduction ($y = 0.68x - 4.2$, $r^2 = 0.18$, $p < 0.0001$, $n = 448$).

Figure 2. Linear regression relationships of response metrics versus percent light reduction compared to controls for the 91–120 d data bin of duration of light reduction. A. Percent biomass reduction. B. Percent shoot density reduction.

Figure 3. Regression relationships (exponential rise to maximum) of response metrics versus the duration of shading experienced. A. Percent biomass reduction (n = 216). B. Percent shoot density reduction (n = 448).

Figure 4.
Regression relationship of percent shoot density reduction versus percent biomass reduction (n=70) for given light reduction levels.

Table 1.

Summary of submerged aquatic vegetation species and number of observations for percent biomass reduction and percent shoot reduction metrics. References for data sources are given in Supplemental Material.

Species	n (Biomass)	n (Shoots)	Data Source Numbers
<i>Amphibolis griffithii</i>	14	14	26, 29
<i>Cymodocea serrulata</i>	3	47	12, 13
<i>Halodule pinifolia</i>	6	5	28
<i>Halodule uninervis</i>	8	57	11, 12, 13, 38
<i>Halodule wrightii</i>	3	5	15, 31
<i>Halophila ovalis</i>	5	35	13, 28, 41
<i>Posidonia australis</i>	0	10	17
<i>Posidonia oceanica</i>	10	15	34, 35
<i>Posidonia sinuosa</i>	4	23	10, 18
<i>Ruppia maritima</i>	28	0	14
<i>Thalassia hemprichii</i>	4	22	12, 38
<i>Thalassia testudinum</i>	18	16	7, 15, 19, 21, 27, 32
<i>Vallisneria americana</i>	2	0	24
<i>Zostera marina</i>	72	46	2, 3, 6, 16, 20, 22, 23, 30, 36, 37, 39, 40
<i>Zostera muelleri</i>	36	85	1, 8, 9, 12, 13, 39, 42
<i>Zostera nigricaulis</i>	0	68	4, 5, 25
<i>Zostera noltii</i>	3	0	33
Total	216	448	

Table 2.

Best fit, general linear regression models for biomass or shoot density reduction relative to controls, computed for the entire data sets or for temporally binned data. Continuous variables included in model evaluation (with abbreviations) were percent light reduction relative to control (lt_reduc), experimental duration (days), and latitude. Categorical variables were season of experiment initiation (season), experimental type (exp_type), life history, and status of rhizome connection (rhizome).

Biomass (all)			Biomass (60 < d 120)		
Model term	Model r ²	AIC	Model term ¹	Model r ²	AIC
Intercept	0.00	1657.38	Intercept	0.00	701.17
lt_reduc	0.19	1613.93	lt_reduc	0.45	647.84
days	0.38	1558.13	days	0.67	603.34
exp_type	0.43	1543.83	season	0.69	598.1
life history	0.46	1535.78	life history	0.72	593.0
latitude	0.48	1530.83	rhizome	0.73	591.59
season	0.49	1526.40			
Density (all)			Density (>60d)		
Model term	Model r ²	AIC	Model term	Model r ²	AIC
Intercept	0.00	3546.67	Intercept	0.00	2183.67
lt_reduc	0.17	3462.60	lt_reduc	0.26	2100.94
days	0.37	3342.21	days	0.40	2046.53
life history	0.39	3336.85	life history	0.43	2036.44

¹Experimental type was excluded from model assessment as it was removed from a preliminary regression model.

Table 3.

Comparison of linear regression equations for biomass or shoot density reduction relative to controls versus light reduction for data binned into 30 day intervals of duration.

Duration	N	Regression Equation	t	P	r ²
Biomass					
0–30	41	$y = 0.24x + 14.6$	1.12	0.2687	0.0313
31–60	40	$y = 0.67x + 2.3$	3.11	0.0035	0.2031
61–90	37	$y = 1.05x - 29.7$	6.61	<.0001	0.5555
91–120	57	$y = 1.13x - 12.9$	8.73	<.0001	0.581
>120	41	$y = 0.9x + 6.2$	4.83	<.0001	0.3741
Shoot Density					
0–30	74	$y = 0.46x - 13.7$	3.65	0.0005	0.1561
31–60	94	$y = 0.71x - 13.0$	4.49	<.0001	0.1796
61–90	87	$y = 0.87x - 21.6$	6.01	<.0001	0.2982
91–120	80	$y = 0.90x - 15.4$	6.69	<.0001	0.3649
>120	113	$y = 0.85x + 4.5$	7.89	<.0001	0.3596

Table 4.

Genus level comparisons of best fit, general linear regression models for biomass or shoot density reduction relative to controls. Variable abbreviations as in Table 2.

<i>Halodule</i> spp - Biomass n=17			<i>Posidonia</i> spp - Biomass n=14			<i>Thalassia</i> spp - Biomass n=22			<i>Zostera</i> spp - Biomass n=111		
Model term	Model r^2	AIC	Model term	Model r^2	AIC	Model term	Model r^2	AIC	Model term	Model r^2	AIC
Intercept	0.00	513.10	No model			Intercept	0.00	175.17	Intercept	0.00	864.51
exp_type	0.32	488.92				lt_reduc	0.41	165.38	days	0.27	831.27
days	0.47	474.58				days	0.67	154.97	lt_reduc	0.47	797.42
lt_reduc	0.59	459.58				rhizome	0.76	149.91			
rhizome	0.62	456.93									
<i>Halodule</i> spp - Density n=67			<i>Posidonia</i> spp - Density n=48			<i>Thalassia</i> spp - Density n=38			<i>Zostera</i> spp - Density n=199		
Model term	Model r^2	AIC	Model term	Model r^2	AIC	Model term	Model r^2	AIC	Model term	Model r^2	AIC
Intercept	0.00	513.10	Intercept	0.00	374.68	Intercept	0.00	293.34	Intercept	0.00	1587.80
days	0.32	488.92	days	0.39	352.87	lt_reduc	0.29	282.34	lt_reduc	0.17	1553.27
lt_reduc	0.47	474.58	lt_reduc	0.53	341.94	days	0.60	262.10	days	0.41	1487.10
latitude	0.59	459.58	latitude	0.66	329.28	rhizome	0.74	247.65	latitude	0.42	1486.85
season	0.62	456.93	season	0.75	315.99	season	0.78	243.86	rhizome	0.43	1483.59
									exp_type	0.44	1483.42

Table 5.

Species level comparisons of best fit, general linear regression models for biomass or shoot density reduction relative to controls. Variable abbreviations as in Table 2.

<i>Ruppia maritima</i> - Biomass n = 28			<i>Thalassia testudinum</i> - Biomass n = 18			<i>Zostera marina</i> - Biomass n = 72			<i>Zoster muelleri</i> - Biomass n = 50		
Model term	Model r^2	AIC	Model term	Model r^2	AIC	Model term	Model r^2	AIC	Model term	Model r^2	AIC
Intercept	0.00	217.26	Intercept	0.00	146.05	Intercept	0.00	561.78	Intercept	0.00	281.96
days	0.52	198.51	lt_reduc	0.52	135.01	days	0.38	529.02	latitude	0.24	274.28
lt_reduc	0.71	186.22	days	0.81	120.00	lt_reduc	0.57	504.28	season	0.35	270.21
season	0.83	173.80				latitude	0.59	502.81	days	0.43	268.03
									lt_reduc	0.47	267.27
<i>Cymodocea serrulata</i> - Density n = 36			<i>Halodule uninervis</i> - Density n = 47			<i>Halophila ovalis</i> - Density n = 57			<i>Zostera marina</i> - Density n = 35		
Model term	Model r^2	AIC	Model term	Model r^2	AIC	Model term	Model r^2	AIC	Model term	Model r^2	AIC
Intercept	0.00	363.09	Intercept	0.00	434.94	Intercept	0.00	284.72	Intercept	0.00	362.88
days	0.28	349.61	days	0.28	418.06	lt_reduc	0.54	259.77	days	0.34	346.01
lt_reduc	0.51	334.00	lt_reduc	0.47	402.76	days	0.65	251.79	lt_reduc	0.41	342.49
season	0.54	332.43	season	0.55	395.71	exp_type	0.70	248.95	rhizome	0.49	338.12
			latitude	0.57	394.67				season	0.52	337.13
<i>Zostera muelleri</i> - Density n = 46			<i>Zostera nigricaulis</i> - Density n = 85								
Model term	Model r^2	AIC	Model term	Model r^2	AIC						
Intercept	0.00	691.57	Intercept	0.00	520.49						
lt_reduc	0.38	653.32	season	0.14	512.20						
days	0.57	624.02	lt_reduc	0.22	507.96						
			days	0.30	501.90						
			latitude	0.41	493.09						

Table 6.

Comparison among seagrass life history strategies of best fit, general linear regression models for biomass or shoot density reduction relative to controls. Variable abbreviations as in Table 2. *Halodule* spp includes *H. pinifolia*, *H. uninervis*, and *H. wrightii*; *Thalassia* spp includes *T. hemprichii* and *T. testudinum*; *Zostera* spp includes *Z. marina*, *Z. muelleri*, and *Z. noltii* for biomass, and *Z. marina*, *Z. muelleri*, and *Z. nigricaulis* for shoot density.

Colonizing -Biomass (<i>Halodulepinifolia</i> , <i>H. uninervis</i> , <i>Halophila ovalis</i> , <i>Ruppia maritima</i>) n = 50			Opportunistic - Biomass (<i>A. griffithii</i> , <i>C. serrulata</i> , <i>Zostera</i> spp) n = 128			Persistent - Biomass (<i>Thalassia</i> spp) n = 36		
Model term	Model r ²	AIC	Model term	Model r ²	AIC	Model term	Model r ²	AIC
Intercept	0.00	0.00	Intercept	0.00	996.07	Intercept	0.00	278.18
days	0.14	0.12	days	0.33	946.81	days	0.35	264.92
lt_reduc	0.32	0.29	lt_reduc	0.49	914.50	lt_reduc	0.55	253.71
exp_type	0.38	0.34	exp_type	0.51	912.02	rhizome	0.63	248.57
latitude	0.48	0.44				latitude	0.66	247.50
season	0.54	0.49						
Colonizing -Density (<i>Halodule</i> spp, <i>Halophila ovalis</i>) n = 102			Opportunistic - Density (<i>A. griffithii</i> , <i>C. serrulata</i> , <i>Zostera</i> spp) n = 260			Persistent - Density (<i>Posidonia</i> spp, <i>Thalassia</i> spp) n = 86		
Model term	Model r ²	AIC	Model term	Model r ²	AIC	Model term	Model r ²	AIC
Intercept	0.00	815.35	Intercept	0.00	2064.93	Intercept	0.00	665.27
lt_reduc	0.19	796.29	days	0.18	2016.78	days	0.21	647.48
days	0.30	783.09	lt_reduc	0.41	1931.19	lt_reduc	0.40	625.71
rhizome	0.32	782.68	rhizome	0.42	1930.33	season	0.49	613.74
latitude	0.33	782.32	latitude	0.43	1928.82			