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Relative effects of grazers and nutrients on seagrasses: a meta-analysis approach

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ABSTRACT: Recent large-scale seagrass declines have prompted experimental investigations of potential mechanisms. Although many studies have implicated eutrophication or reductions of epiphyte grazers in these declines, few experiments have simultaneously manipulated both factors to assess their relative effects. This study used meta-analyses of 35 published seagrass studies to compare the relative strength of 'top-down' grazer effects and 'bottom-up' nutrient effects on epiphyte biomass and seagrass above-ground growth rate, above-ground biomass, below-ground biomass, and shoot density. A surprising result was that seagrass growth and biomass were limited *in situ* by sediment nutrients; light limitation has been emphasized in the literature to date. Water column enrichments, which were correlated with increased epiphyte biomass, had strong negative effects on seagrass biomass. Grazers overall had a positive effect on shoot density, but negligible effects on seagrass biomass and growth rate. However, analyzing epiphyte grazers separately from other grazers revealed positive effects of grazing on seagrass response variables and corresponding negative impacts on epiphyte biomass. The positive effects of epiphyte grazers were comparable in magnitude to the negative impacts of water column nutrient enrichment, suggesting that the 2 factors should not be considered in isolation of each other. Until the determinants of epiphyte grazer populations are empirically examined, it will be difficult to address the contribution that overfishing and cascading trophic effects have had on seagrass decline. Because increases in water column nutrients are documented in many regions, efforts to reduce coastal eutrophication are an appropriate and necessary focus for the management and conservation of seagrass ecosystems.

KEY WORDS: Seagrasses · Meta-analysis · Epiphyte · Nutrients · Grazers · Management · Eutrophication · Top-down/bottom-up

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INTRODUCTION

Recent theoretical and empirical studies have clearly linked anthropogenic stressors to dramatic and widespread declines in the functioning of coastal marine ecosystems (Dayton et al. 1998, Lenihan & Peterson 1998, Fourqurean & Robblee 1999, Hughes et al. 2003, Stankelis et al. 2003). Among the most pervasive anthropogenic disturbances to coastal ecosystems are eutrophication (Howarth et al. 2000) and overfishing (Jackson et al. 2001). Anthropogenic changes have a particularly strong impact on ecosys-

tem function when they affect ecologically important species such as seagrasses (Orth & Moore 1983, Short & Wyllie-Echeverria 1996, Hall et al. 1999). The prevalence of fishing pressures and nutrient loading in coastal systems and the strong experimental tradition in seagrass community ecology make seagrass beds ideal systems in which to explore the basic ecological importance of 'top-down' (i.e. higher trophic level influences, including predation) and 'bottom-up' (i.e. resource supply to primary producers) processes (Williams & Heck 2001; see Fig. 1 for a depiction of the seagrass food web).

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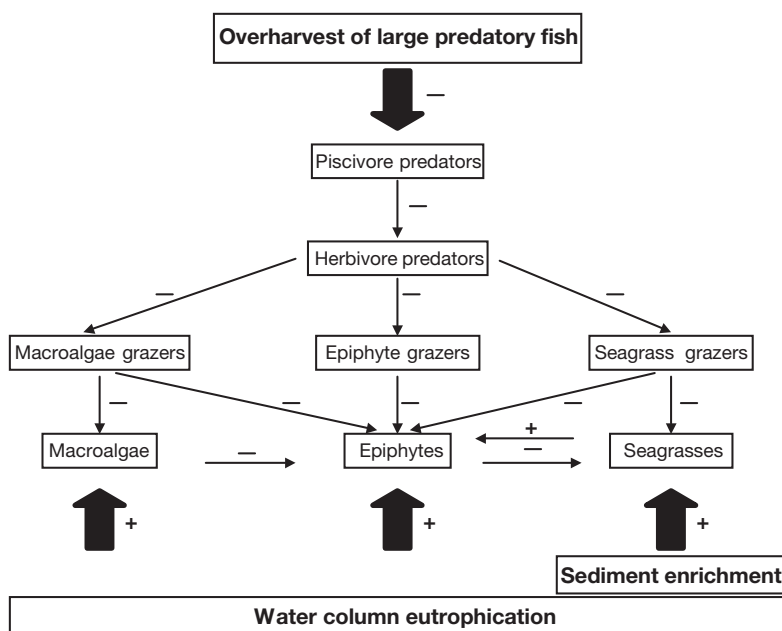


Fig. 1. Food web diagram depicting key seagrass species groups, their interactions, and key anthropogenic disturbances (overharvesting large predators, eutrophication). +/- signs by arrows indicate direction of effect. The negative effect of macroalgae on epiphytes is hypothesized

In recent years, seagrass ecosystems have experienced significant global declines in areal extent and habitat value (Orth & Moore 1983, Short & Wyllie-Echeverria 1996, Hall et al. 1999). Eutrophication is generally regarded as a major driver of widespread contemporary declines of seagrasses and other submerged aquatic vegetation because it stimulates overgrowth of epiphytic algae and macroalgae from the 'bottom-up' (Walker & McComb 1992, Duarte 1995, Valiela et al. 1997). By virtue of their physical position in the water column and their superior nutrient uptake kinetics, algal epiphytes can intercept light and water column nutrients and reduce the diffusion of carbon and oxygen across seagrass leaves (Sand-Jensen 1977, Sand-Jensen et al. 1985), leading to seagrass decline. Similarly to epiphytes, macroalgal blooms shade seagrasses, leading to declines (Hauxwell et al. 2003).

Trophic interactions are also gaining recognition as critical structuring forces in seagrass systems (Cebrián & Duarte 1998, Hauxwell et al. 1998, Heck et al. 2000, Williams & Heck 2001). Large herbivores including sea urchins, fishes, geese, manatees, dugongs and green turtles can significantly reduce seagrass biomass (Thayer et al. 1982, Valentine & Heck 1991). Small invertebrate grazers of epiphytes (i.e. amphipods, isopods, gastropods and herbivorous crabs) and their predators can also play important structuring roles that include mediating the effects of water column eutrophication on seagrasses (Howard

1982, Hootsmans & Vermaat 1985, Neckles et al. 1993, Williams & Ruckelshaus 1993). Clear documentation that large predatory fishes are over-harvested in coastal waters has led to the hypothesis that over-exploitation of top predators contributes to seagrass decline through the same proximate mechanism as eutrophication: overgrowth by seagrass epiphytes (Williams & Heck 2001). From the 'top-down', the loss of top predators releases smaller predators that feed on grazers, thus reducing herbivore populations and decreasing their control of epiphytes. Strong 'top down' effects are most evident in freshwater systems with relatively simple trophic structures (Brooks & Dodson 1965, Carpenter et al. 1987, Power 1990) but also occur in marine systems (Paine 1966, Estes & Palmisano 1974, Wootton 1992). However, relatively few studies have simultaneously addressed both 'bottom-up' and 'top-down' influences in benthic marine communities (Wootton et al. 1996, Menge 2000, Worm et al. 2000), including seagrass beds (McGlathery 1995, Heck et al. 2000).

This study assessed the relative effects of 'bottom-up' nutrient and 'top-down' consumer influences in regulating seagrass populations. Understanding the relative importance of nutrients and grazers may be necessary for reversing seagrass declines, given that the eutrophication and overfishing hypotheses predicate very different management responses. However, the relative importance of cascading effects from higher trophic levels in causing seagrass decline is difficult to assess because little experimental research has been done at more than 1 trophic level. Although the effects of epiphyte grazers have been studied fairly extensively (reviewed by Jernakoff et al. 1996), few studies have examined the factors, including predation, that control epiphyte grazer abundances (Main 1987, Edgar 1990, Schneider & Mann 1991, Edgar & Robertson 1992, Heck et al. 2000). In addition, few experimental manipulations of both nutrients and grazers have been conducted in seagrass beds (see Results). We conducted meta-analyses of experiments from 35 published seagrass studies in which nutrient concentrations and/or grazer abundances were manipulated to estimate the overall magnitude and relative importance of seagrass and epiphyte responses to nutrients and grazers. If grazers emerged as important drivers of seagrass responses, the inference would follow that higher-order trophic effects could be as well.

MATERIALS AND METHODS

Study identification and selection. We conducted 2 extensive searches of the published literature. The first search targeted experiments testing grazer or nutrient effects on seagrasses. The second search involved publications containing data on effects of grazers or nutrients on seagrass epiphytes. Our searches uncovered very few manipulative experiments examining how nutrients or grazers influence macroalgal blooms associated with seagrass decline, which remains an important gap to fill. For both searches, we identified potential references using the Biosis and Web of Science electronic databases, which included literature published between 1985 and 2003. We searched both databases for the following keywords and their variants: nutrient, grazer, seagrass, epiphyte, herbivory, *Zostera*, *Phyllospadix*, *Thalassia*, *Cymodocea*, *Halodule*, *Syringodium*, and *Posidonia*; although the survey uncovered studies on additional species. We used the references cited in all studies identified through the searches to uncover additional sources, for a total of 140 citations. From these, we selected all identified laboratory and field experiments that met the following criteria: (1) grazers and/or nutrients were experimentally manipulated, (2) a seagrass or epiphyte response variable was measured, and (3) treatment and control sample sizes, means, and variance estimates were provided. The computer program TechDig V2.0 (Jones 1998, available at <http://home.xnet.com/~ronjones/#TECHDIG>) was used when necessary to extract data from figures.

The references that met our criteria were used to construct 2 final databases, one for seagrass response variables and one for epiphyte biomass. The final seagrass database included 28 suitable studies, which encompassed 420 cases (i.e. a comparison of a specific experimental treatment level against a control). We analyzed the effects of nutrients and grazers on 4 seagrass response variables: above-ground growth rate (20 studies, 78 cases); above-ground biomass (16 studies, 67 cases); below-ground biomass (10 studies, 42 cases); shoot density (12 studies, 62 cases). We analyzed data from the final sampling date of each experiment, regardless of total experimental duration. The epiphyte database included 15 suitable studies and a total of 43 cases, of which 8 studies and 17 cases were shared with the final seagrass database.

Decisions to include or exclude particular studies can have a large impact on the results of a meta-analysis, particularly if the number of studies is small (Englund et al. 1999, Gates 2002, Lajeunesse & Forbes 2003). We used a single measure of each response variable for a given treatment to minimize non-independence among data points (Gurevitch et al. 1992, Englund et

al. 1999, Gurevitch & Hedges 1999). We created 2 additional data sets, one in which non-independent data were included, and one in which non-independent data and studies with low replication ($n = 2$) were excluded. In general, results were similar whether or not we restricted the data to a single measure of the response variable or eliminated studies with low replication; we present exceptions in the 'Results' section.

Meta-analysis. The program MetaWin 2.0 (Rosenberg et al. 2000) was used for all analyses. Effect sizes (i.e. differences between experimental and control means that are weighted by the standard deviation and sample size) and variances were calculated using the log-transformed response ratio ($\ln RR$) metric, which provides a robust comparison of effect sizes (Gurevitch & Hedges 2001). The results obtained from $\ln RR$ were consistent with those from another effect size metric, Hedges' d (data not presented; Gurevitch & Hedges 2001). To generate estimates of the degree and significance of variation within nutrient studies and grazer studies, we used a fixed-effects model, which assumes that all studies with similar characteristics have a single, true effect size in common (Gurevitch & Hedges 1999, 2001). If there was significant variation in effect sizes within nutrients or grazers, we divided them into categories and assessed differences between these more specific comparisons: seagrass grazers versus epiphyte grazers, laboratory versus field studies, temperate versus tropical/subtropical seagrass species, individual seagrass species, water column versus sediment enrichment, and nutrient type. Epiphyte and seagrass grazers were designated according to information provided in the relevant study; when such information was not provided, we assigned categories based on the natural history of the organism. We then used a random-effects model to estimate mean effect sizes, confidence intervals and the probability of differences between categories. We generated confidence intervals with the conservative bias-corrected bootstrapping process (Hedges & Olkin 1985, Gurevitch & Hedges 2001). If the mean effect sizes of lab and field studies differed ($p < 0.05$) for grazers or nutrients (e.g. field nutrients versus lab nutrients), subsequent analyses within that group (e.g. nutrients) were run exclusively with field data to limit potentially confounding variation.

Effect sizes and variances were calculated for the epiphyte data set using the methods described above. An additional analysis of epiphyte responses was conducted by dividing studies of epiphyte biomass into 2 categories: (1) studies in which only epiphyte responses were measured (4 studies, 9 cases) and (2) studies in which both epiphyte and seagrass responses were measured (11 studies, 34 cases). The second group included studies that were excluded from our primary seagrass data-

base for various reasons, including insufficient data reporting or the incompatibility of the measured seagrass response variable(s) with our analyses. We assessed the consistency of results between these categories by comparing the mean effect sizes of the 2 groups of grazer or nutrient manipulations. Similar responses would suggest that patterns from studies that only assess epiphyte responses could be used to infer impacts to seagrasses.

The duration of the experiments included in our seagrass analyses varied considerably (Table 1). To assess the effects of this variation on our results, we utilized data from experiments that measured seagrass above-ground growth rate at multiple times over the course of the experiment, which allowed us to standardize the data to a single common time interval (i.e. 90 d following the manipulation). We selected

Table 1. Classification information for references used as sources for meta-analysis data. AGB: above-ground biomass; AGR: above-ground growth rate; BGB: below-ground biomass; SD: shoot density; EB: epiphyte biomass; d: duration (d); n: no. cases/study; sed.: sediment enrichment; and water col.: water column enrichment. Genus abbreviations are *C*: *Cymodocea*; *E*: *enhalus*; *H*: *Halodule* (except *Heterozostera tasmanica*); *P*: *Posidonia*; *R*: *Ruppia*; *S*: *Syringodium*; *T*: *Thalassia*; and *Z*: *Zostera*

Region and species	Study description	Response(s) measured					Nutrient treatment(s) d					n	Location and source
		AGB	BGB	AGR	SD	EB	N	P	N,P	N,P,K			
Subtropical and Tropical													
<i>C. rotundata</i> , <i>C. serrulata</i> , <i>S. isoetifolium</i> , <i>T. hemprichii</i>	Field: sed.			x	x				x	120–150	44	Indonesia (Erftemeijer et al. 1994)	
<i>C. rotundata</i> , <i>E. acoroides</i> , <i>T. hemprichii</i>	Field: sed.	x		x	x				x	120	14	Philippines (Agawin et al. 1996)	
<i>E. acoroides</i>	Field: sed.	x		x				x		98	24	Philippines (Terrados et al. 1999)	
<i>H. uninervis</i> , <i>S. isoetifolium</i>	Field: sed.	x	x	x	x				x	80	25	Australia (Udy et al. 1999)	
<i>H. wrightii</i>	Lab: crustacean	x	x	x	x	x				90	7	USA (Howard & Short 1986)	
<i>H. wrightii</i> , <i>R. maritima</i>	Field: sed.		x						x	35	8	USA (Pulich 1985)	
<i>H. wrightii</i> , <i>T. testudinum</i>	Lab: water col.					x	x	x		28	6	USA (Lapointe et al. 1994)	
<i>S. filiforme</i>	Field: sed.			x			x	x	x	210	7	Bahamas (Short et al. 1990)	
<i>S. filiforme</i> , <i>T. testudinum</i>	Field: sed.				x				x	1110	2	Virgin Islands (Williams 1990)	
<i>T. testudinum</i>	Field: turtle			x	x					90	2	Virgin Islands (Williams 1988)	
<i>T. testudinum</i>	Field: urchin	x		x	x	x				120	8	USA (Valentine et al. 1997)	
<i>T. testudinum</i>	Field: urchin	x	x	x	x	x				90	18	USA (Valentine et al. 2000)	
<i>T. testudinum</i>	Field: water col., fish	x		x	x	x		x		176	11	USA (Heck et al. 2000)	
<i>T. testudinum</i>	Lab: water col.			x		x			x	30	2	USA, Mexico, Honduras (Tomasko & Lapointe 1991)	
<i>T. testudinum</i>	Field: sed.	x	x		x		x			180	7	USA (Lee & Dunton 2000)	
<i>T. testudinum</i>	Field: sed., urchin	x							x	70	6	Bermuda (McGlathery 1995)	
<i>T. testudinum</i>	Field: urchin	x								120	2	USA (Heck & Valentine 1995)	
<i>T. testudinum</i>	Field: urchin	x	x							42	8	USA (Macia 2000)	
<i>Z. japonica</i>	Field: mollusc					x				120	1	China (Fong et al. 2000)	
Temperate													
<i>C. nodosa</i>	Field: water col.			x			x	x	x	150	6	Spain (Perez et al. 1991)	
<i>H. tasmanica</i>	Field: sed.	x			x	x	x	x	x	150	17	Australia (Bulthuis et al. 1992)	
<i>P. sinuosa</i>	Field: crustacean					x				35	3	Australia (Jernakoff & Nielsen 1997)	
<i>Z. marina</i>	Field, Lab: water col., crustacean			x		x	x			20	10	USA (Williams & Ruckelshaus 1993)	
<i>Z. marina</i>	Lab: mollusc, crustacean					x				14	3	Netherlands (Hootsmans & Vermaat 1985)	
<i>Z. marina</i>	Lab: water col.	x	x			x	x	x		180	11	USA (Taylor et al. 1995)	
<i>Z. marina</i>	Lab: water col., mollusc, crustacean					x			x	30–60	8	USA (Neckles et al. 1993)	
<i>Z. marina</i>	Lab: mollusc					x				10–12	2	USA (Nelson 1997)	
<i>Z. marina</i>	Lab: water col.					x	x	x		114	3	USA (Lin et al. 1996)	
<i>Z. marina</i>	Field: sed.			x				x		243	6	USA (Kenworthy & Fonseca 1992)	
<i>Z. marina</i>	Field: sed.			x			x	x		49	6	USA (Murray et al. 1992)	
<i>Z. marina</i>	Field: sed.			x	x				x	210	8	Germany (Worm & Reusch 2000)	
<i>Z. marina</i>	Lab: crustacean	x	x							42	8	USA (Duffy et al. 2001)	
<i>Z. marina</i>	Lab: sed., mollusc	x	x	x			x	x	x	45	4	USA (Zimmerman et al. 1996)	
<i>Z. marina</i>	Lab: water col.			x				x		84	1	USA (Burkholder et al. 1994)	
<i>Z. marina</i>	Lab: water col.	x	x	x					x	30	15	USA (Moore & Wetzel 2000)	

studies on growth rate for this analysis because of the large range in experimental duration within this response variable (12 to 243 d, see Table 1). Although there was larger variation in experimental duration for studies measuring shoot density, there were not enough time series data to run separate analyses. We analyzed the effects of grazers (4 studies, 7 cases) and nutrients (5 studies, 12 cases), as well as field sediment (3 studies, 10 cases) and water (2 studies, 2 cases) enrichments on above-ground growth rate for all instances in which a treatment and control were compared 90 d following the manipulation. If these results were consistent with the overall analyses, then the results were considered robust to variation in the duration of the experiments.

RESULTS

Table 1 summarizes data from seagrass and epiphyte studies included in our analyses. Complete references are given in Appendix 1. Specific information for each of the cases is available on request.

In the results that follow, a significant effect is one for which the 95% bias confidence interval around the mean effect size does not include zero. Means indicate the effect size of a particular category (i.e. the difference between experimental and control groups). The p-values represent the probability that the difference(s) between the mean effect sizes of the categories being compared (e.g. laboratory nutrient studies versus field nutrient studies) are due to chance alone.

All nutrients versus all grazers

The overall effect of nutrient additions on above-ground biomass (mean = 0.20) and above-ground growth rate (mean = 0.32) was positive (Fig. 2). In contrast, the impact of nutrients on below-ground biomass and shoot density was negligible (Fig. 2). However, when we excluded 1 nutrient enrichment study (4 cases) with low replication, there was a significant positive effect of nutrient additions (mean = 0.14) on below-ground biomass, consistent with the effects on above-ground biomass and growth rates.

All grazers combined had effects on above-ground biomass, below-ground biomass and above-ground growth rate that were not different from zero, but grazers resulted in an increase in shoot density (mean = 0.22) (Fig. 2).

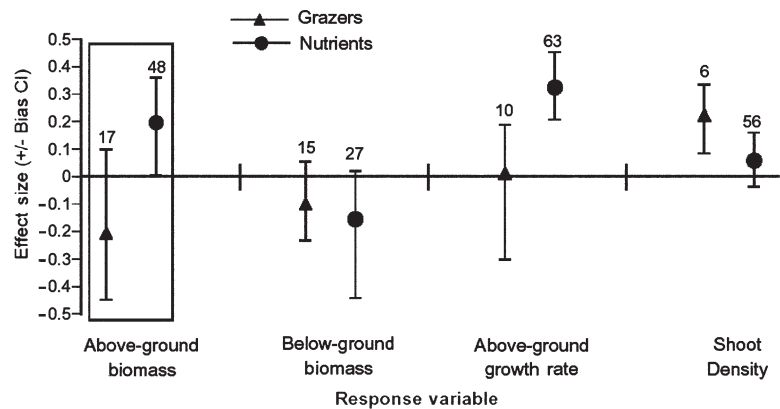


Fig. 2. Log-transformed response-ratio effect sizes (with bias confidence intervals) of grazer versus nutrient treatments for each of the 4 response variables. Effect sizes are significantly different from zero if confidence intervals do not overlap zero ($p < 0.05$). A box enclosing both values from 1 response variable indicates that those values were significantly different from each other ($p < 0.05$). Values at the upper edge of each bar indicate sample sizes for each effect size

Nutrients had a stronger overall effect than grazers on above-ground biomass ($p = 0.04$). However, the relative effects of grazers and nutrients on the remaining 3 response variables were not distinguishable. Further differentiation of the effects of nutrients and grazers required more refined comparisons using categories.

Categorical comparisons for nutrients and grazers

Water column versus sediment enrichment

Water column nutrient enrichment negatively affected above-ground biomass (mean = -0.61) and below-ground biomass (mean = -0.55), and these effects differed significantly ($p = 0.001$) from the positive impact of sediment nutrient additions on seagrass above- and below-ground biomass (means = 0.35 , 0.16) (Fig. 3). The 2 methods of enrichment did not differentially affect growth rate. Low sample sizes prevented the comparison of shoot density responses to different enrichment methods.

Laboratory versus field nutrient manipulations

Whether nutrients were added in the laboratory or in mesocosms versus in the field led to strikingly different effects on above-ground biomass, below-ground biomass and above-ground growth rate ($p < 0.05$) (Fig. 4). Laboratory nutrient additions caused no change in above-ground biomass or growth rate but a decline in

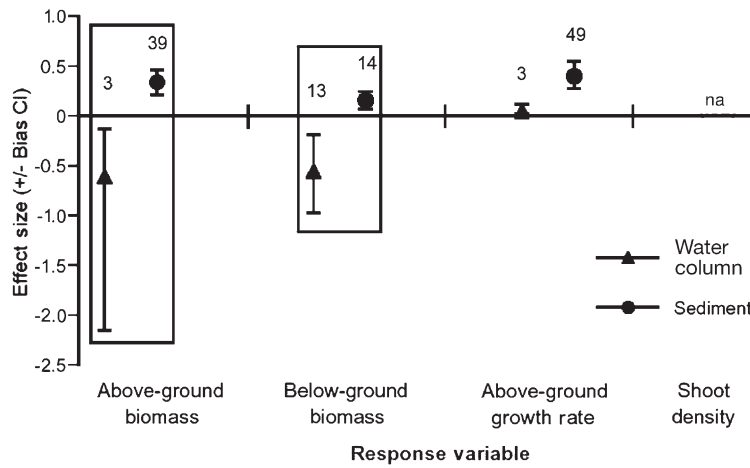


Fig. 3. Log-transformed response-ratio effect sizes (with bias confidence intervals) of enrichment type (water column versus sediment) for each of the 4 response variables. Effect sizes are different from zero if confidence intervals do not overlap zero ($p < 0.05$). A box enclosing both values from 1 response variable indicates that those values were significantly different from each other ($p < 0.05$). Values at the upper edge of each bar indicate sample sizes for each effect size. na indicates that not enough data were available for that analysis

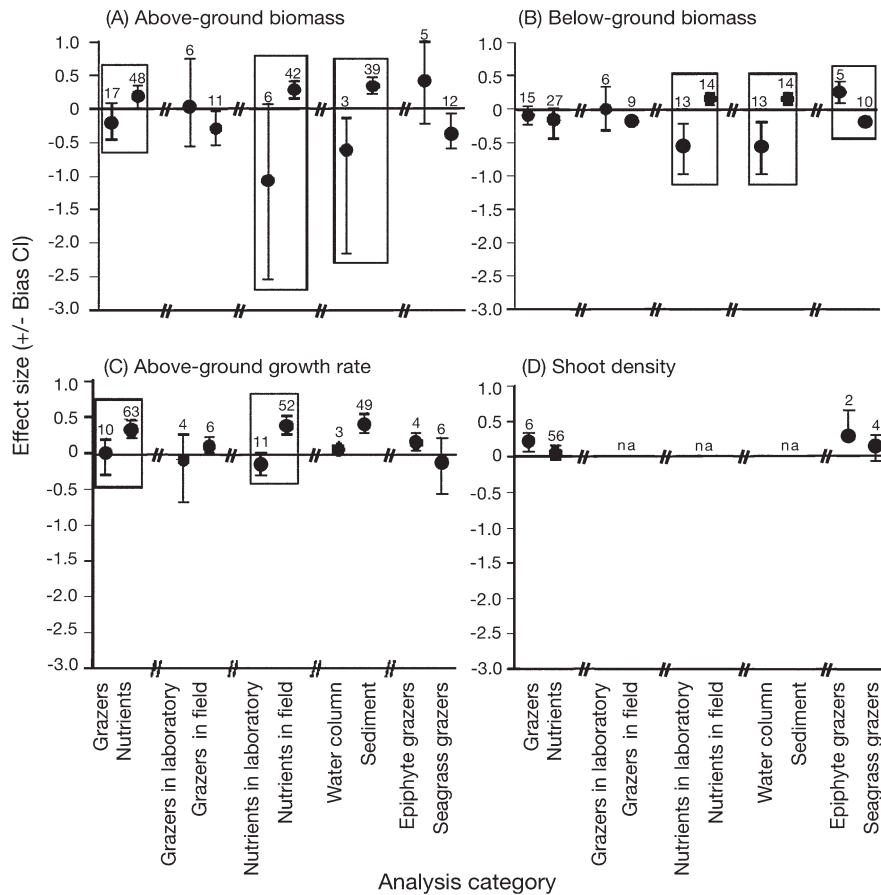


Fig. 4. Log-transformed response-ratio effect sizes (with bias confidence intervals) for each of the 4 seagrass response variables. Effect sizes are significantly different from zero if confidence intervals do not overlap zero ($p < 0.05$). A box enclosing 2 values indicates that those values were significantly different from each other ($p < 0.05$). Values at the upper edge of each bar indicate sample sizes for each effect size. na indicates that not enough data were available for that analysis

below-ground biomass (mean = -0.55), while nutrient enrichment in the field caused increases in these response variables (means = 0.29 , 0.38 , 0.16 , respectively). Shoot density responses to field and laboratory nutrient additions could not be compared due to insufficient laboratory manipulations. The water column was fertilized in most laboratory studies as opposed to the sediments in field manipulations (Table 1). When the difference in the site of enrichment is accounted for, the difference between responses to field and laboratory nutrient additions is consistent with results for water column versus sediment enrichment (see above). This pattern can be explained further by the results to follow on the response of epiphyte biomass to nutrient enrichments.

Epiphyte versus seagrass grazers

As expected, seagrass grazers had a negative effect on both above-ground biomass and below-ground biomass (mean = -0.36 and -0.19 , respectively) and tended to produce a negative effect on above-ground growth (Fig. 4). In direct contrast, the effects of epiphyte grazers on growth rate, below-ground biomass and shoot density were positive. Although epiphyte grazers had a positive

effect on above-ground biomass (mean = 0.43), the effect was highly variable among studies and thus, not different from zero. Despite the general differences between the negative effects of seagrass grazers and the positive impacts of epiphyte grazers, the 2 categories were only significantly different from each other for below-ground biomass ($p = 0.001$).

Laboratory versus field grazer manipulations

Negligible grazer effects on below-ground biomass in laboratory studies contrasted with the significantly negative impacts of grazers (mean = -0.18) on below-ground biomass in field experiments ($p = 0.05$) (Fig 4). However, laboratory and field grazer manipulations resulted in indistinguishable responses in above-ground biomass and growth rate ($p > 0.05$). Low sample sizes prevented the same comparison for shoot density.

Other factors

There were no differences between the effects of different nutrient combinations for any of the response variables ($p > 0.05$), although the combination of nitro-

Table 2. Summary of mean effect sizes (log-transformed response-ratio) by seagrass species, nutrient type and geographic location for nutrient categories, and by seagrass species and geographic location for grazer categories. A numerical value is presented when the effect size differs significantly from zero ($p < 0.05$) and from other effect sizes within that category ($p < 0.05$); + or -: effect size differs significantly from zero ($p < 0.05$), but not from other effects within that category ($p > 0.05$); 0: effect size does not differ significantly from zero ($p > 0.05$). na: not enough data were available for that analysis

	Above-ground biomass	Below-ground biomass	Above-ground growth rate	Shoot density
Nutrient				
Species comparison:				
<i>Halodule wrightii</i>	0.2513	0.1473	na	0.3700
<i>Zostera marina</i>	na	-0.5442	0.2235	0
<i>Enhalus acarooides</i>	0.3201	na	0.3432	na
<i>Thalassia hemprichii</i>	0.5978	na	0.2712	0
<i>Thalassia testudinum</i>	0	na	0	0.2574
<i>Halodule uninervis</i>	0.8094	0.1242	0	na
<i>Ruppia maritima</i>	0.3041	0.2105	na	na
Nutrient type:				
N	0	na	+	0
P	0	na	0	+
N and P	+	0	+	0
N, P and K	+	+	+	+
Geographic comparison:				
Tropical/subtropical	+	0	+	0
Temperate	+	0	+	+
Grazer				
Species comparison:				
<i>Zostera marina</i>	0	0	0	na
<i>Thalassia testudinum</i>	-	-	0	na
Geographic comparison:				
Tropical/subtropical	0	-	+	0
Temperate	0	0	0	+

gen, phosphorous, and potassium consistently resulted in a positive seagrass response (Table 2). With 2 exceptions, all seagrass species responded positively to nutrient additions, although to varying degrees (Table 2). The exceptions were that nutrients negatively impacted *Zostera marina* below-ground biomass (mean = -0.54) and *Thalassia testudinum* above-ground biomass (mean = -0.09). The effects of nutrients did not vary by geographic location ($p > 0.05$) (Table 2).

Grazer manipulations were primarily conducted with *Zostera marina* or *Thalassia testudinum*. Neither species responded to the presence of grazers overall ($p > 0.05$) (Table 2), a result that is not surprising given the opposing results between the categories of epiphyte versus seagrass grazers presented above. Low sample sizes prevented a comparison of epiphyte versus seagrass grazers for individual seagrass species. Grazer effects were consistent across tropical/subtropical and temperate locations for all response variables ($p > 0.05$) (Table 2).

Epiphyte results

Effect of nutrients on epiphyte biomass

Water column and sediment nutrient additions had strong contrasting effects on epiphyte biomass ($p = 0.04$) (Fig. 5). Epiphyte biomass increased in response

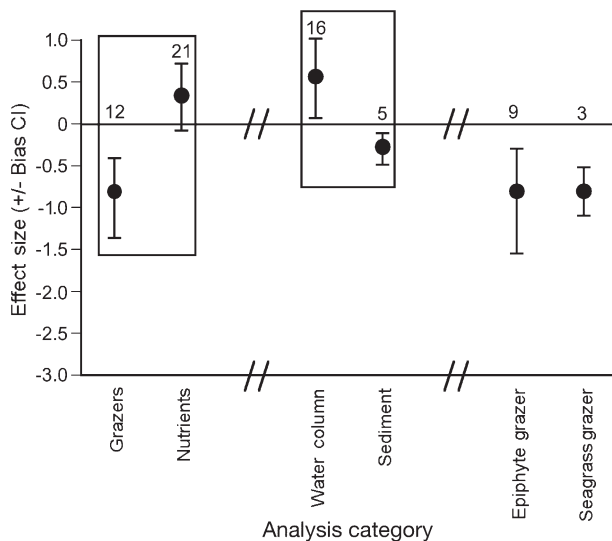


Fig 5. Log-transformed response-ratio effect sizes (with bias confidence intervals) of epiphyte biomass analyses. Effect sizes are significantly different from zero if confidence intervals do not overlap zero ($p < 0.05$). A box enclosing 2 values indicates that those values were significantly different from each other ($p < 0.05$). Values at the upper edge of each bar indicate sample sizes for each effect size

to water column enrichment (mean = 0.56) and decreased in response to sediment enrichment (mean = -0.27). The effect of nutrients on epiphyte biomass did not differ between studies measuring both epiphyte and seagrass responses and the single study (3 cases) that only evaluated the response of epiphytes ($p > 0.05$).

Effect of grazers on epiphyte biomass

Combined grazers had a strong negative effect on epiphyte biomass (mean = -0.81). Both seagrass grazer and epiphyte grazer categories individually suppressed epiphyte biomass. Curiously, the negative effect of grazers in studies assessing both epiphyte and seagrass response was different from the negligible impact of grazers found among studies measuring only epiphyte responses ($p = 0.02$). The small sample size of studies measuring only epiphyte responses to grazers ($n = 6$ cases) likely contributed to the large variation in effect sizes within this group, making the comparison less informative.

Duration of the experiment

When we controlled for variation in experimental duration (i.e. all data were taken 90 d following the manipulation), nutrient enrichments overall (mean = 0.42) and field sediment enrichments (mean = 0.50) increased seagrass above-ground growth rate, consistent with results from the overall data set that varied in experimental duration from 12 to 243 d (see above, Fig. 2). There was a trend towards increased growth rate after 90 d due to water column nutrient additions, but this effect was not different from zero (in contrast to the small but significant effect of water enrichment in the overall analyses). Grazers had negligible effects on above-ground growth rate after 90 d, also consistent with the overall data set.

DISCUSSION

The strength of a meta-analysis is that it can directly compare experiments that vary widely in execution. Although empirical studies have implicated both eutrophication and reduced epiphyte grazing pressure in seagrass declines, this study represents the first quantitative analysis of the relative effects of nutrients and grazers with respect to several factors including nutrient placement and identity, grazer type, experimental location and seagrass species. Our meta-analyses demonstrated that the negative effects of

water column nutrients are comparable in magnitude to the positive effects of epiphyte grazers on seagrasses. In addition, our results confirmed that these effects are likely mediated through changes in epiphytes, as water column nutrients increased and epiphyte grazers decreased epiphyte biomass. Finally, the stark differences between lab and field nutrient manipulations, particularly in the site of nutrient enrichment, revealed the importance of experimental design and the use of caution when extrapolating results from the laboratory to the field.

Although seagrasses responded positively to many nutrient manipulations (including when all nutrient experiments were analyzed together), water column nutrient additions clearly had a negative impact on seagrass biomass. These results were consistent with predictions that epiphytes and/or macroalgae can out-compete seagrasses in the presence of excess water column nutrients. The subsequent analysis of the effect of nutrient manipulations on epiphytes revealed that water column nutrient additions increased epiphyte biomass, in sharp contrast to sediment nutrient additions. Sediment nutrient additions increased seagrass growth rates, resulting in less time for epiphyte accumulation (Borum 1987). Thus, our results supported the hypothesis that eutrophication contributes to seagrass decline by promoting epiphytic overgrowth.

The deleterious effects of macroalgal blooms on seagrass beds are gaining attention (McGlathery 2001), yet there were too few studies of macroalgae that directly manipulated nutrients or grazers to be included in our meta-analysis. Although large mats of drifting seaweeds have been observed in seagrass beds for over 20 yr (Williams Cowper 1977), they seem to be more apparent recently and have been linked to eutrophication (McGlathery 1995, Valiela et al. 1997). These observations have shifted the focus from epiphyte overgrowth to macroalgae as the cause for seagrass decline under eutrophication (Hauxwell et al. 2001). To bloom, macroalgae require higher loading rates than epiphytic algae because they maintain higher individual biomass and have longer turnover times and lower nutrient uptake rates (McGlathery 1992, Havens et al. 2001). Once nutrient loading rates are high enough to support macroalgal blooms, they persist a long time (Havens et al. 2001), which could lead to shading of epiphytes, as well as seagrasses (Hauxwell et al. 2003). We hypothesize that progressive increases in nutrient loading to coastal areas have led to a serial loss of seagrasses, first through overgrowth by epiphytes and then macroalgae. As studies on seagrass-macroalgal interactions accumulate, it will become possible to test this hypothesis, directly and through meta-analysis. Our analyses highlight the importance of considering both nutrient and consumer

effects with respect to interactions between seagrass and macroalgae.

Positive seagrass responses to field and sediment nutrient enrichments indicated that nutrient limitation of seagrass growth and biomass is more common than anticipated by studies emphasizing light limitation (Dennison 1987, Zimmerman et al. 1987, Thom & Albright 1990, Czerny & Dunton 1995, Dunton 1996). Udy et al. (1999) suggested that increased nutrient loading from terrestrial sources has increased seagrass distribution and abundance on the Great Barrier Reef, rather than causing a decline. The relative importance of light versus nutrients in controlling seagrass decline merits a separate meta-analysis.

In addition to the strong 'bottom-up' effects of nutrient additions, we found support for the hypothesis that immediate 'top-down' forces can impact seagrasses. The lack of an impact of all grazers on seagrasses (Fig. 2) can be explained by the opposing effects of seagrass grazers and epiphyte grazers (Fig. 4). Our analyses support the contention of Valentine & Heck (1999) that direct consumption of seagrasses has an important effect on seagrass growth rates and above- and below-ground biomass. Although they point out that seagrass herbivores can have a positive effect on seagrasses due to their capacity to compensate for loss of grazed tissues through utilization of carbohydrate reserves in below-ground rhizomes, our results provided evidence for an overall negative effect that was independent of the duration of the herbivory, particularly over the short-term before reserves would be depleted.

Epiphyte grazers also exhibited 'top-down' control through consistent, positive impacts on seagrass response variables (Fig. 4) and a strong negative effect on epiphyte biomass (Fig. 5). Many grazer studies, including a number of experiments in our analyses, have lumped grazers into functional groups based on similarity in body size and general diet. However, species-specific differences in the diets of small invertebrate grazers can underlie significant variation in epiphyte biomass and community composition, and have important implications for seagrass communities (Zimmerman et al. 1979, Kitting 1984, Duffy & Hay 2000, Duffy & Harvilicz 2001, Duffy et al. 2001). In particular, some key invertebrate grazers (e.g. *Idotea resecata*) consume both epiphytes and seagrasses, and thus, may have positive or negative effects depending on the context (Williams & Ruckelshaus 1993). Furthermore, the species composition of algal epiphytes can shift under nutrient enrichment (Coleman & Burkholder 1994, 1995), which could impact grazer diets. The divergent effects of seagrass and epiphyte grazers in our analyses emphasize the importance of understanding the diet of the particular grazer species manipulated.

Despite our findings that epiphyte grazers benefit seagrasses by consuming epiphytes, our analyses cannot confirm the links between grazer abundances and higher trophic levels that form the basis of the overfishing hypothesis. A better understanding of factors controlling epiphyte grazer abundances is required. Until then, overgrowth of seagrasses by epiphytes following the loss of top predators can only be inferred. Theoretical and empirical research has demonstrated that complexities such as age-structured omnivory, intraguild predation and anti-consumer defenses can diminish the effects of strong 'top-down' forces or trophic cascades (Strong 1992, Polis & Strong 1996, Duffy 2002). Small fishes (e.g. pinfish, *Lagodon rhomboides*) in seagrass systems consume both epiphytes and invertebrates during different parts of their life cycle (Heck et al. 2000), complicating predictions of the consequences of decreased predation pressure from large fish. Within the diverse seagrass-epiphyte association, organisms vary in trophic position and vulnerability to predators (Marsh 1973, Stoner 1980, Main 1987), making 'runaway consumption' less likely (Strong 1992). Epiphytes and seagrasses interact negatively within the same trophic level, which further complicates expectations for trophic cascades in seagrass food webs. Thus, the many direct and indirect links encompassed by the 'top-down' hypothesis increase the likelihood that higher-order trophic effects on seagrasses will be dampened.

Meta-analysis is a valuable tool for generalizing the results of experimental studies, but its power to generate insight into ecological processes is limited by the design of published studies, the quality of data reporting and the inherently coarse resolution of this type of analysis (Goldberg et al. 1999). We were forced to exclude nearly half of the experimental studies uncovered because variances were not supplied or graphs were scaled such that error bars overlapped and could not be differentiated. Although the duration of the experiments used in our analyses varied considerably, the effects of grazers and nutrients on seagrass growth rate at 90 d compared to a wide range of times did not differ, indicating that our results likely provided a robust indication of seagrass short-term response. We could not compare effects that might be evident over a longer term because we uncovered only a single study lasting longer than 1 yr. Certainly, persistent grazing pressure on seagrasses can lead to the depletion of stored reserves and contribute to seagrass decline (Camp et al. 1973, Williams 1988, Zimmerman et al. 1996).

In contrast to the consistency of results across different experimental durations, a striking difference emerged in our analyses between the effects of laboratory and field nutrient manipulations on seagrasses. We believe this difference was because the water col-

umn was fertilized in the laboratory but the sediments in the field, favoring epiphytes versus seagrasses, respectively. We noted a tendency in the literature to generalize to nutrients overall, which is not necessarily appropriate considering the opposing effects of sediment versus water column enrichments. Few studies combined laboratory and field experiments (Williams & Ruckelshaus 1993), a synthetic approach that would help to identify other factors contributing to the variation between the 2 settings.

Finally, simultaneous manipulations of grazers and nutrients were few, yet would allow an evaluation of the interactions between these factors. The need to include both factors in any assessment of the causal mechanisms behind seagrass declines is emphasized by studies showing that grazers can compensate for the effects of increased nutrients (Orth & Van Montfrans 1984, Neckles et al. 1993, Williams & Ruckelshaus 1993). An important caveat is that nutrient enrichment can also lead to at least transient catastrophic grazing of turtlegrass (Williams 1987, McGlathery 1995), in response to either increased epiphyte availability or more nutritious seagrass. Accordingly, rather than the last word on the relative importance of grazers and nutrients to seagrass communities, we view our analysis as a necessary first step in summarizing the available data and highlighting areas in need of further investigation.

For now, the consensus that epiphyte grazers have strong positive effects on seagrass biomass and growth was supported by our meta-analysis. A critical next step is to understand responses of epiphyte grazer populations to changes in higher trophic levels. The degree to which top predators have been lost in seagrass ecosystems is unclear, so their 'top-down' effect on epiphyte grazers remains conjectural. However, increases in water column nutrient concentrations have been documented in many coastal areas. In our analyses, such enrichment, associated with significant reductions in above-ground biomass and below-ground biomass, had a strong overall effect on seagrasses. This result validates efforts to reduce nutrient loading to seagrass beds as an appropriate and necessary focus for management of these ecosystems.

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