HERBIVORE VS. NUTRIENT CONTROL OF MARINE PRIMARY PRODUCERS: CONTEXT-DEPENDENT EFFECTS

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Abstract. Pervasive overharvesting of consumers and anthropogenic nutrient loading are changing the strengths of top-down and bottom-up forces in ecosystems worldwide. Thus, identifying the relative and synergistic roles of these forces and how they differ across habitats, ecosystems, or primary-producer types is increasingly important for understanding how communities are structured. We used factorial meta-analysis of 54 field experiments that orthogonally manipulated herbivore pressure and nutrient loading to quantify consumer and nutrient effects on primary producers in benthic marine habitats. Across all experiments and producer types, herbivory and nutrient enrichment both significantly affected primary-producer abundance. They also interacted to create greater nutrient enrichment effects in the absence of herbivores, suggesting that loss of herbivores produces more dramatic effects of nutrient loading. Herbivores consistently had stronger effects than did nutrient enrichment for both tropical macroalgae and seagrasses. The strong effects of herbivory but limited effects of nutrient enrichment on tropical macroalgae suggest that suppression of herbivore populations has played a larger role than eutrophication in driving the phase shift from coral- to macroalgal-dominated reefs in many areas, especially the Caribbean. For temperate macroalgae and benthic microalgae, the effects of top-down and bottom-up forces varied as a function of the inherent productivity of the ecosystem. For these algal groups, nutrient enrichment appeared to have stronger effects in high- vs. low-productivity systems, while herbivores exerted a stronger top-down effect in low-productivity systems. Effects of herbivores vs. nutrients also varied among algal functional groups (crustose algae, upright macroalgae, and filamentous algae), within a functional group between temperate and tropical systems, and according to the metric used to measure producer abundance. These analyses suggest that human alteration of food webs and nutrient availability have significant effects on primary producers but that the effects vary among latitudes and primary producers, and with the inherent productivity of ecosystems.

Key words: benthic; bottom-up; context dependency; coral reef; eutrophication; herbivory; marine; meta-analysis; nutrient enrichment; primary producers; top-down.

INTRODUCTION

A key question regarding the forces that structure communities is the relative influence of consumers (top-down) vs. resources (bottom-up) in controlling community composition, structure, and function (Hairston et al. 1960, Oksanen et al. 1981, Leibold et al. 1997). Understanding the relative effects of these forces is becoming increasingly important as humans alter ecosystems by removing consumers (Duffy 2003) and increasing nutrients (Smith et al. 1999) over large spatial scales. For example, the recent switch from coral-dominated to algal-dominated reefs in many tropical regions, especially the Caribbean, could be due to loss of herbivores, increased eutrophication, or an interaction between decreased herbivory and increased nutrient

loading that reduces the ability of reefs to rebound in the face of disturbance (McCook 1999, Hughes et al. 2003, Bellwood et al. 2004). Such large-scale changes in community structure following alterations of top-down and bottom-up forces are becoming more common in marine ecosystems (Valiela et al. 1997, Smith et al. 1999, Steneck et al. 2004), making it critical to understand how changes to these forces cascade through the community.

Many marine ecosystems are typified by primary producers such as kelps and seagrasses that are the foundation species that facilitate whole ecosystems (Bertness et al. 2001). Other primary producers, such as coral reef macroalgae that can overgrow and kill corals (McCook et al. 2001), are pivotal interactors that strongly impact foundation species (corals), fundamentally changing the physical and ecological structure of the entire ecosystem. Thus, knowing how consumers and resource availability affect primary producers is critical for understanding how marine ecosystems function. Benthic marine communities are commonly regulated by consumers (Duffy and Hay 2001, Steneck and Sala

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2005). However, nutrient availability and larval recruitment are influential bottom-up forces that also affect benthic communities (Menge et al. 1997, Nielsen and Navarrete 2004). These multiple forces are not mutually exclusive and may rarely act in isolation (Leibold et al. 1997), making it important to identify when and where they interact (or fail to interact) as drivers of community organization. Given the context-dependent nature of most ecological interactions (Polis et al. 1996, Hay et al. 2004), it is unlikely that any single experiment can address this general question. A quantitative synthesis of the data from individual studies investigating the interactions of herbivores and nutrient loading on the abundance of primary producers is needed to critically evaluate the relative roles of herbivores vs. nutrients in controlling the abundance of primary producers and mediating phase shifts.

Recent meta-analyses have shown complex interactions between herbivores and nutrients in controlling the species diversity of primary producers (Worm et al. 2002) and in affecting periphyton abundance (Hillebrand 2002), suggesting that these interactions might be important for controlling primary-producer abundance across a range of ecosystems, environmental conditions, and types of producers. Therefore, we used factorial meta-analysis (Gurevitch et al. 2000) to synthesize the results of 54 field experiments that orthogonally manipulated nutrient availability and herbivore pressure in benthic marine ecosystems representing a wide diversity of habitats and primary-producer types. We assessed the relative roles of herbivores, nutrients, and their interaction on primary-producer abundance for: (1) marine primary producers pooled across all habitats and producer types, (2) different types of producers (i.e., macroalgae vs. seagrasses vs. microalgae), (3) producers in different habitats (i.e., low- vs. high-productivity environments or temperate vs. tropical systems), and (4) producers in different functional groups (i.e., crustose vs. upright macroalgae). Instead of debating the role of bottom-up vs. top-down forces, we focus instead on the types of primary producers responding to these forces and the conditions under which their relative roles change, i.e., the context-dependent nature of the answer to this debate.

METHODS

We found studies by searching the Institute for Scientific Information (ISI) Web of Science database (1945–2005; search terms included herbiv* and marine, herbiv* and nutrient, nutrient and marine, etc.) for field experiments manipulating both herbivory and nutrients. We also searched the reference lists of papers identified by this search. Studies had to satisfy three criteria to be included in our analyses: (1) experimentally manipulate nutrient availability and herbivore presence orthogonally in a field setting, (2) measure the abundance of primary producers in response to these treatments, and (3) report abundance means, error measurements, and sample sizes for experimental treatments. All studies that satisfied criteria 1 and 2 also satisfied criterion 3.

We found 23 published studies with a total of 50 experiments and also included three unpublished studies for a total of 26 studies with 54 experiments (Appendix A). Twenty-one experiments were on benthic microalgae, 15 on tropical macroalgae, 14 on temperate macroalgae, three on seagrasses, and one on the marsh grass Spartina alterniflora. Benthic microalgae consisted primarily of diatoms and cyanobacteria (Appendix A). Common species in the tropical macroalgal communities were Dictyota spp., Lobophora variegata, Dasycladus vermicularis, Amphiroa spp., and cyanobacteria. Filamentous/turf algae and crustose algae were rarely identified in tropical studies. In temperate macroalgal communities, common algae were Fucus spp., Ascophyllum nodosum, Pilayella littoralis, Enteromorpha intestinalis, Callithamnion tetragonum, and Cladophora spp. Seagrasses were Thalassia testudinum and Halodule wrightii. Fishes were the dominant herbivores in tropical macroalgal communities while fishes and urchins were common in seagrass beds. Gastropods and crustaceans were the dominant herbivores in temperate macroalgal, benthic microalgal, and Spartina communities (Appendix A). Urchins were common in only one of the experiments in temperate macroalgal communities.

Herbivore removal was accomplished via barriers (i.e., cages or anti-fouling paint) preventing access to experimental plots. Nutrient enrichment was generally accomplished via reservoirs containing nitrogen and phosphorus that continually released nutrients to the water column except for two studies that enriched sediment pore water. When a single study enriched at multiple nutrient concentrations or with both a nitrogen and phosphorus and a nitrogen-only treatment, we used data from the nitrogen and phosphorus treatment at the highest concentration tested; this maximized our probability of detecting a nutrient enrichment effect. Most studies monitored nutrient levels to ensure significant nutrient enrichment of the water column or sediment pore water. Primary-producer abundance was measured as biomass (20 experiments), absorbance of chlorophyll a (a proxy for microalgal biomass; nine experiments), biovolume (nine experiments), primary-producer density (eight experiments), or percent cover (eight experiments). If data were reported as a time series, we used data from the final sampling period. We did not analyze effects on species diversity or richness because such metrics were rarely reported.

We performed meta-analyses on the total, pooled data set and then separately on tropical macroalgae, temperate macroalgae, benthic microalgae, and seagrasses. Because effects of herbivory and nutrient availability may differ depending on the inherent productivity of the ecosystem (Hillebrand 2002, Worm et al. 2002), we divided the studies on temperate macroalgae and benthic microalgae into those conducted in either low- or high-productivity habitats (Appendix A). To classify the

Nutrient treatments

	+	−
Herbivore treatments +	1 +N, +H	2 −N, +H
Herbivore treatments −	3 +N, −H	4 −N, −H

Meta-analysis calculations:

Mean effects
Nutrient enrichment: (1 + 3) − (2 + 4)
Herbivore removal: (3 + 4) − (1 + 2)
Interaction: (3 − 4) − (1 − 2)

Individual effects
Enrichment with herbivores [E (with H)]: (1 − 2)
Enrichment without herbivores [E (without H)]: (3 − 4)
Herbivore removal without enrichment [no H (without E)]: (4 − 2)
Herbivore removal with enrichment [no H (with E)]: (3 − 1)

FIG. 1. A depiction of the four treatments present in all orthogonal manipulations of herbivore (H) pressure and nutrient (N) availability. Mean effects refer to the average effect of herbivore removal or nutrient addition. Individual effects refer to the effects of nutrient enrichment in the absence and presence of herbivores and the effects of herbivore removal in the absence and presence of nutrient enrichment. The effect size calculations are represented by the addition or subtraction of the number labels for each treatment in the figure. These equations represent the numerator in the effect size calculation equations as in Gurevitch et al. (2000).

experiments into low- or high-productivity categories, we used designations by the studies' authors or other publications related to the study areas as in Worm et al. (2002). Different studies used different measures (i.e., dissolved vs. total nutrients) to assess the productivity of the habitat, making absolute thresholds for classification difficult to define. We did not divide tropical macroalgal or seagrass studies according to productivity because all studies were performed in areas of similar productivity. To see whether the way investigators assessed changes in abundance of primary producers affected our analyses, we also performed analyses on the different abundance metrics (i.e., biomass, density, percent cover) for each type of primary producer (except for seagrasses due to low sample size).

Because different algae may respond differently to experimental treatments (Pedersen and Borum 1996), we used functional group designations based loosely on Steneck and Dethier (1994) to lump algae from tropical and temperate macroalgal studies into three categories: (1) crustose algae, (2) filamentous/turf algae, and (3) upright macroalgae. Steneck and Dethier (1994) listed seven morphological categories; we collapsed their categories into only three groups due to the range of seaweeds commonly included in the studies we assessed. This coarser designation of algal types also produced larger samples sizes (and greater statistical power) for each algal type. Our crustose algae category equaled their group of the same name (e.g., Neogonolithon and Peyssonnelia). Our filamentous/turf algae included their

functional group filamentous algae (e.g., Ectocarpus and Piayella). Our upright macroalgal grouping included their functional groups: (1) foliose algae (e.g., Ulva and Porphyra), (2) corticated foliose algae (e.g., Padina and Lobophora), (3) corticated macrophytes (e.g., Sargassum and Gigartina), (4) leathery macrophytes (e.g., Fucus and Ecklonia), and (5) articulated calcareous algae (e.g., Halimeda and Amphiroa). Not all studies reported data for the abundance of specific functional groups so our sample sizes were not consistent for all analyses across functional groups.

We used factorial meta-analysis (Gurevitch et al. 2000) that calculates the mean effect of the major factors as well as how the two main factors interact to determine the response variable (conceptually similar to a two-factor ANOVA). This allowed us to compare the mean effects of herbivore removal, nutrient addition, and their interaction. In addition, we calculated the individual effects of herbivore removal under ambient and enriched nutrient status and of nutrient enrichment in the presence and absence of herbivores. (See Fig. 1 for an outline of experimental treatments and their use in computing effect sizes.) These calculations are based on Hedges' d (Gurevitch and Hedges 1993), which measures the difference between treatment and control means divided by a pooled standard deviation from the treatment and control and multiplied by a correction factor to account for differences in sample size among studies. For the analyses of algal functional groups from temperate vs. tropical habitats, we used the response ratio metric ($L = \ln[x_t/x_c]$ where x_t is the treatment mean and x_c is the control mean; Hedges et al. 1999) because it does not require error measurements for its calculation (as does Hedges' d), and many studies did not report error measurements for functional group response variables. However, using the response ratio precluded using factorial meta-analysis, allowing us to calculate only the individual effects for the analyses of functional groups.

Means, error measurements, and sample sizes used to calculate effect sizes were obtained from tables or extracted from graphs using Grab It! XP (Datatrend Software, Raleigh, North Carolina, USA). Error measurements reported as standard errors were converted to standard deviation for use in effect size calculations. Calculations of effect sizes were performed as outlined in Gurevitch et al. (2000) for factorial analysis with Hedges' d, and Hedges et al. (1999) for the response ratio using workbooks in Microsoft Excel. We performed unweighted, mixed-effect model meta-analyses with MetaWin 2.0 (Rosenberg et al. 2000). Confidence intervals (95%) were calculated using a bias-corrected bootstrapping technique with 9999 sampling iterations (Adams et al. 1997). Effect sizes were considered significant if 95% confidence intervals did not cross zero. Effect sizes within analyses (e.g., herbivore removal effect vs. nutrient enrichment effect) were

considered different from one another if their 95% confidence intervals did not overlap.

To facilitate comparison of treatment effect sizes, we constructed our calculations so that the effects of both nutrient enrichment and herbivore removal were positive. Thus, we tested (1) the effect of removing herbivores from the system, not the effect of adding herbivores to the system, and (2) the effect of nutrient enrichment. A positive effect size for herbivore removal or nutrient enrichment means that these manipulations enhance the abundance of primary producers. A positive effect size for the interaction term means that nutrient enrichment has a larger effect in the absence of herbivores than in their presence. For factorial analyses, mean effect sizes are designated d^{++}, whereas individual effect sizes are designated d^+. Response ratio effect sizes in the analyses of algal functional groups are designated L.

To determine whether effect sizes were correlated with experimental duration or experimental plot size, we used linear least-squares regression to compare effect sizes with the log-transformed duration (in days) or the log-transformed experimental plot size (in square meters) of each experiment. Regressions were performed only for mean effects and were performed for all studies pooled and for each primary-producer type except for seagrasses due to low sample size ($n = 3$).

RESULTS

Factorial meta-analysis across all experiments showed that both nutrient enrichment ($d^{++} = 0.98$) and herbivore removal ($d^{++} = 1.55$) strongly affected abundance of primary producers (Fig. 2A). There was also a significant interaction ($d^{++} = 0.42$), indicating that nutrient enrichment had a greater effect in the absence of herbivores. Further, herbivore removal in the presence of enrichment ($d^+ = 1.84$) had a much greater effect than enrichment when herbivores were not removed ($d^+ = 0.51$; Fig. 2B).

For tropical macroalgae (Fig. 2C), nutrient enrichment ($d^{++} = 0.90$), herbivore removal ($d^{++} = 2.84$), and their interaction ($d^{++} = 0.60$) were all positive. Nutrient enrichment enhanced tropical macroalgae in the absence of herbivores ($d^+ = 1.37$) but not in their presence ($d^+ = 0.28$) (Fig. 2D). In contrast, herbivore removal had a strong, positive effect both with ($d^+ = 3.23$) and without ($d^+ = 2.15$) enrichment; the effects of herbivore removal were greater under either nutrient regime than were the effects of nutrients in the presence of herbivores (Fig. 2D).

Seagrass communities (Fig. 2E) showed no effect of nutrient enrichment ($d^{++} = 0.09$), a positive effect of herbivore removal ($d^{++} = 0.97$), and no interaction ($d^{++} = 0.08$). Nutrient enrichment did not affect seagrasses either with or without herbivores, but herbivore removal was positive in both the absence and presence of nutrients (Fig. 2F). These analyses suggest that herbivores have strong effects while nutrients have limited
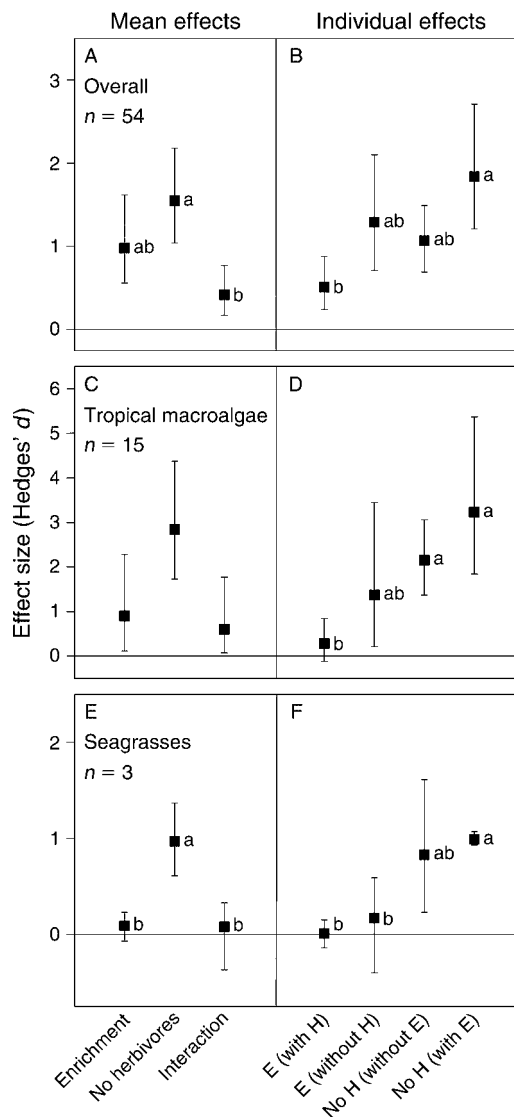

FIG. 2. Results of meta-analyses on mean and individual effects (left panels and right panels, respectively) for (A, B) all primary producers, (C, D) tropical macroalgae, and (E, F) seagrasses. Effect sizes are Hedges' d and 95% CI. Effects are statistically significant ($P < 0.05$) if confidence intervals do not overlap $d = 0$. A positive d indicates an increase, and a negative d indicates a decrease in primary-producer abundance. Different lowercase letters designate differences among categories within an analysis based on 95% CI, i.e., data points with different letters do not have overlapping confidence intervals. Graphs with no letters had no significant differences among data points. Note different scales on y-axes.

effects on seagrass abundance, but the low sample size ($n = 3$) constrains these conclusions.

Temperate macroalgae (Fig. 3A) were positively affected by both nutrient enrichment ($d^{++} = 1.06$) and herbivore removal ($d^{++} = 1.27$). The effect size for the interaction term was positive ($d^{++} = 0.40$, CI $= -0.03/0.93$) but not significant (the confidence intervals overlapped zero). The nutrient enrichment effect was
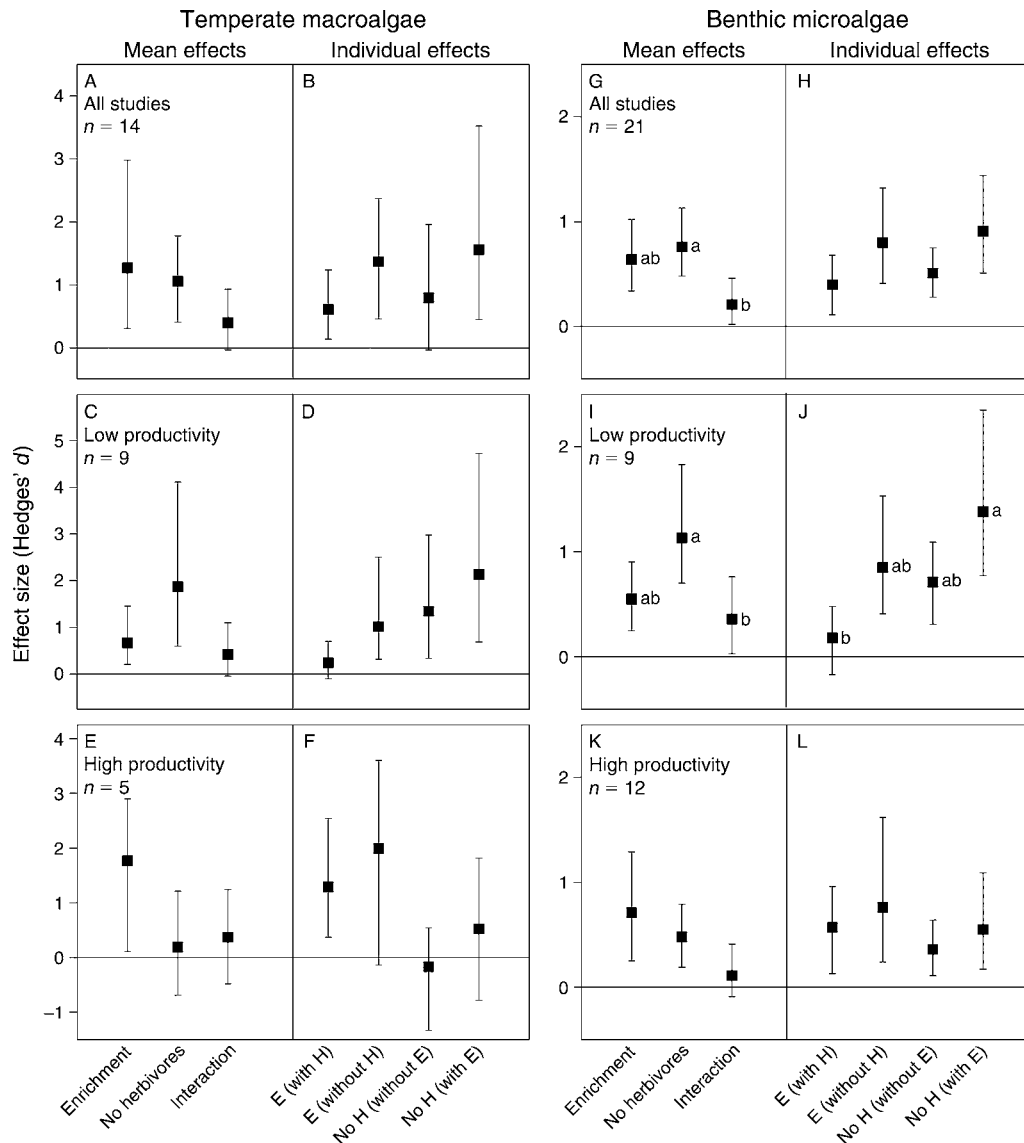
FIG. 3. Results of meta-analyses on mean and individual effects for temperate macroalgae for (A, B) all studies, (C, D) studies in low-productivity areas, and (E, F) studies in high-productivity areas and for benthic microalgae for (G, H) all studies, (I, J) studies in low-productivity areas, and (K, L) studies in high-productivity areas. Symbols and analyses are as in Fig. 2. Note different scales on y-axes.

significant both in the presence ($d^+ = 0.61$) and absence ($d^+ = 1.37$) of herbivores (Fig. 3B). Herbivore removal had a significant positive effect in the presence of added nutrients ($d^+ = 1.56$), but without added nutrients the effect size was smaller ($d^+ = 0.80$) and slightly overlapped zero, making the effect statistically nonsignificant.

The background nutrient status of the ecosystem affected the relative roles of herbivory and enrichment on temperate macroalgae. In low-productivity environments, both nutrient enrichment ($d^{++} = 0.67$) and herbivore removal ($d^{++} = 1.87$) had positive effects (Fig. 3C), while the interaction effect was marginally nonsignificant ($d^{++} = 0.42$, CI $= -0.03/1.10$). However,

analyses of individual effects showed that enrichment significantly enhanced algal abundance only in the absence of herbivores ($d^+ = 1.02$; Fig. 3D). Herbivore removal effects were strong in the absence ($d^+ = 1.35$) and presence ($d^+ = 2.31$) of enrichment. In high-productivity areas, there was a positive nutrient enrichment effect ($d^{++} = 1.77$) but no herbivore removal effect ($d^{++} = 0.19$) or interaction ($d^{++} = 0.37$; Fig. 3E). The enrichment effect appeared strong in both the presence ($d^+ = 1.29$) and absence ($d^+ = 1.99$) of herbivores but was statistically significant only with herbivores present despite the effect size being larger without herbivores (Fig. 3F).
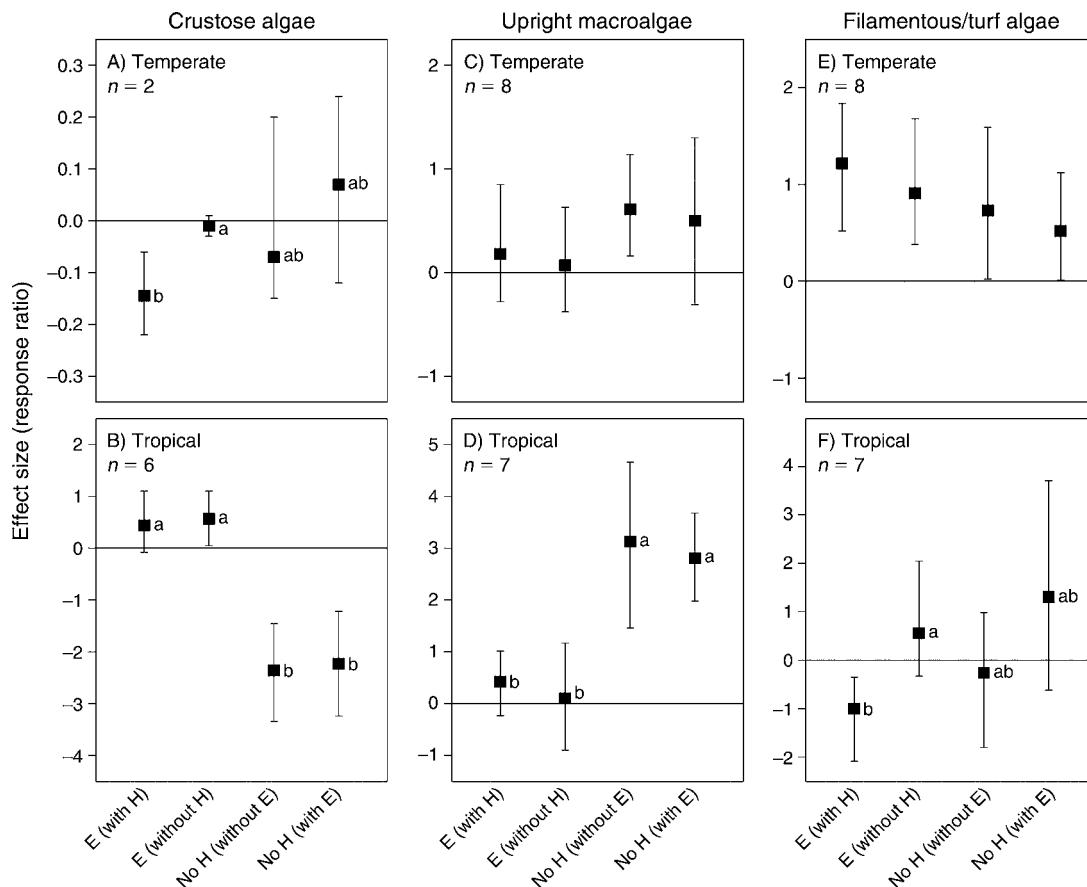
FIG. 4. Results of meta-analyses on individual effects for (A, B) crustose algae, (C, D) upright macroalgae, and (E, F) filamentous/turf algae in temperate and tropical ecosystems. Effect sizes are response ratio and 95% CI. Symbols and analyses are as in Fig. 2. Note different scales on y-axes.

For benthic microalgae, the mean effects of nutrient enrichment ($d^{++}=0.64$), herbivore removal ($d^{++}=0.76$), and the interaction ($d^{++} = 0.21$) were all positive (Fig. 3G). Additionally, all individual effects were significantly positive and did not differ from one another (Fig. 3H). In low-productivity areas, the effects of nutrient enrichment ($d^{++} = 0.55$), herbivore removal ($d^{++} = 1.13$), and their interaction ($d^{++} = 0.36$) were significant (Fig. 3I). However, nutrient enrichment was significant only in the absence of herbivores ($d^{+}=0.85$), while herbivore removal was significant both with ($d^{+} = 1.38$) and without ($d^{+}=0.71$) nutrient additions (Fig. 3J). In high-productivity areas, enrichment ($d^{++}=0.71$) and herbivore removal ($d^{++}=0.48$) were significant but the interaction was not ($d^{++} = 0.11$; Fig. 3K). Individual effects for microalgae in high-productivity areas were all significantly positive and did not differ from one another (Fig. 3L).

When we divided temperate and tropical macroalgae into functional groups, effects of herbivore removal and nutrient enrichment depended on latitude and algal type. For crustose algae in temperate systems (Fig. 4A), enrichment in the presence of herbivores significantly

decreased abundance, and no other contrasts were significant. However, this contrast should be viewed with caution due to low sample size ($n = 2$). Crustose algae in tropical systems (Fig. 4B) were modestly enhanced by nutrient enrichment in the absence of herbivores ($L = 0.57$). However, herbivore removal strongly decreased the apparent abundance of crustose algae in the absence ($L = -2.36$) and presence ($L = -2.23$) of enrichment. For upright macroalgae, nutrient enrichment had no effect in either temperate or tropical habitats (Fig. 4C, D), but herbivore removal increased macroalgal abundance in both temperate ($L = 0.60$ in the absence of nutrient enrichment; Fig. 4C) and tropical communities ($L = 3.13$ and $L= 2.81$ in the absence and presence of nutrient enrichment; Fig. 4D). Filamentous/turf algae in temperate systems were enhanced both by nutrient enrichment ($L = 1.12$ and $L = 0.91$ with and without herbivores) and by herbivore removal ($L = 0.52$ and $L = 0.73$ with and without nutrient enrichment; Fig. 4E). In tropical systems, filamentous/turf algae decreased under nutrient enrichment in the presence of herbivores ($L = -1.02$), with no other effects being significant (Fig. 4F).
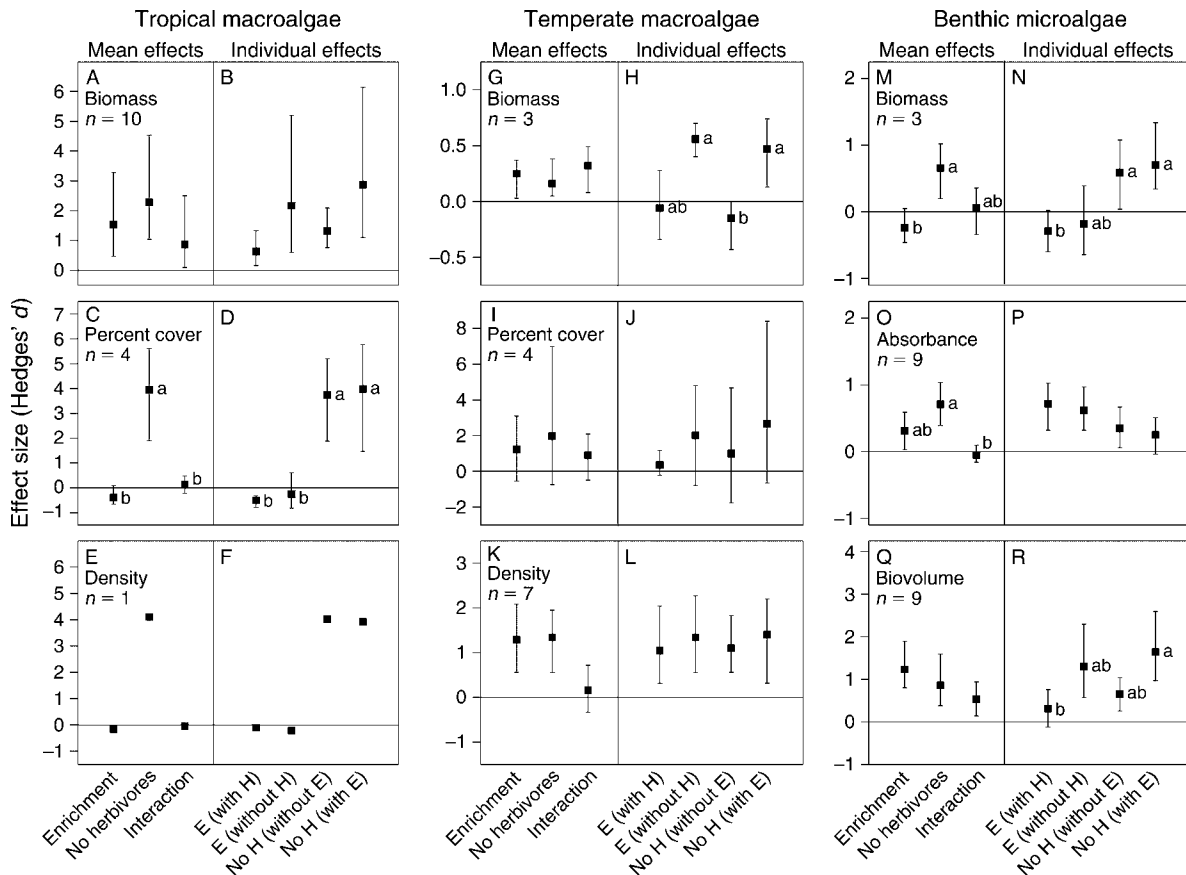
FIG. 5. Results of meta-analyses on mean and individual effects (left panels and right panels, respectively) comparing types of abundance measurements for (A–F) tropical macroalgae, (G–L) temperate macroalgae, and (M–R) benthic microalgae. Symbols and analyses are as in Fig. 2. Note different scales on y-axes.

Just as effects differed as an effect of latitude, local nutrient regimes, and algal type, they also differed depending on how producer responses were assessed (as biomass, percent cover, density, etc.). When biomass was used in studies on tropical macroalgae ($n = 10$), the mean effects for enrichment, herbivore, and interaction effects were positive as were all the individual effects (Fig. 5A, B). However, using percent cover ($n = 4$) showed a positive mean effect of herbivore removal but no mean enrichment or interaction effects (Fig. 5C). Individual effects for percent cover showed positive herbivore removal effects, no enrichment effect in the absence of herbivores, and a negative effect of enrichment in the presence of herbivores (Fig. 5D). Measuring density of tropical macroalgae showed the same pattern as percent cover, but only one study measured density so an analysis was not run for this metric (Fig. 5E, F). For temperate macroalgae, measuring biomass ($n = 3$) showed positive mean effects for enrichment, herbivory, and their interaction (Fig. 5G). Individual effects for biomass showed no effect for enrichment with herbivores, positive effects for enrichment without herbivores and herbivore removal with enrichment, and a negative effect for herbivore removal without enrichment (Fig.

5H). Analyses of percent cover for temperate macroalgae ($n = 4$) showed no significant effects (Fig. 5I, J). Measuring density of temperate macroalgae ($n = 7$) gave positive enrichment and herbivory effects but no significant interaction, while the individual effects were all significantly positive (Fig. 5K, L). For benthic microalgae, biomass ($n = 3$) showed a positive mean herbivore effect but no enrichment or interaction effect while individual herbivore removal effects were positive but enrichment effects were not significant (Fig. 5M, N). Measuring absorbance of chlorophyll a ($n = 9$) showed positive mean enrichment and herbivore effects but no interaction (Fig. 5O). Individual effects when measuring absorbance were positive except for herbivore removal in the presence of nutrient enrichment (Fig. 5P). When biovolume was measured for benthic microalgae ($n = 9$), the mean effects for enrichment, herbivore removal, and their interaction were positive (Fig. 5Q). Individual effects for biovolume showed positive effects of herbivore removal in the absence and presence of enrichment but a positive enrichment effect only in the absence of herbivores (Fig. 5R).

Regressions comparing effect sizes and experiment duration showed relationships for only two of the 12

comparisons (i.e., the herbivore removal and interaction effects for benthic microalgae; Appendix B). Experiments lasted on average 119.2 ± 17.8 d (mean ± SE) with a range of 12–540 d. Regressions comparing effect sizes and experimental plot size showed no significant relationships for any of the comparisons (Appendix C). Mean experimental plot size was 0.14 ± 0.03 m^2 with a range of 0.023–1 m^2.

DISCUSSION

When averaged across all experiments in our study, herbivore pressure and nutrient availability both significantly affected the abundance of primary producers (Fig. 2A, B). The positive interaction terms for the overall analysis (Fig. 2A), for tropical macroalgae (Fig. 2C), and for benthic microalgae (Fig. 4A) demonstrate that effects of nutrient enrichment are magnified in the absence of herbivores and that herbivory and nutrification can act synergistically to alter communities (Scheffer et al. 2001, Worm et al. 2002). Further, context-dependent patterns of top-down and bottom-up regulation were evident when comparing temperate vs. tropical macroalgae (Figs. 2, 3), low- vs. high-productivity systems (Fig. 3), and different functional groups of algae (Fig. 4). Outcomes could also differ based on the metrics used to assess abundance of primary producers (Fig. 5).

On coral reefs, both loss of herbivores (Hughes 1994, Hughes et al. 1999) and increased eutrophication (Lapointe 1997, 1999) have been emphasized as the primary mechanism driving the transition of many reefs from coral- to macroalgal-dominated ecosystems. Our analyses suggest that reduced herbivory is the primary factor increasing macroalgal abundance but that nutrient enrichment can interact with reduced herbivory to magnify these effects (Figs. 2C, D, 4F). This interaction has been emphasized in recent conceptual models of the decline of coral reef health (McCook 1999, Bellwood et al. 2004) as well as experimental manipulations addressing this problem (e.g., Miller et al. 1999, Smith et al. 2001). The compounding effects of reduced herbivore pressure and increased nutrient loading likely make reefs less resilient to disturbance (Hughes et al. 2003) because herbivores are necessary to keep open space free of algae and facilitate coral recruitment following coral bleaching, hurricanes, and disease epidemics (Aronson et al. 2005) and because increased nutrient loading in the absence of herbivores increases coral mortality by stimulating macroalgal growth (Jompa and McCook 2002). Additionally, excess nutrients can increase the severity of coral diseases (Bruno et al. 2003), decrease coral growth rates (Koop et al. 2001), and increase bioerosion of reef substrate (Carreiro-Silva et al. 2005), enhancing the transition from coral- to algal-dominated reefs.

Removal of herbivores on reefs dramatically depressed the appearance of crustose algae (Fig. 4B) but increased the abundance of upright macroalgae (Fig. 4D). Many corals preferentially recruit to crustose coralline algae (Heyward and Negri 1999), but their recruitment and survival are suppressed by upright macroalgae (Lewis 1986, McCook et al. 2001, Jompa and McCook 2002), making herbivores crucial to reef health because they indirectly facilitate coral recruitment and survival by promoting crustose corallines and suppressing upright macroalgae. However, the true, vs. apparent, effects of herbivores on crustose coralline algae (Fig. 4A, B) are difficult to determine with certainty because crustose corallines may be overgrown but not killed by macroalgae (Steneck and Dethier 1994). Because the studies in our analyses measured percent cover of crustose algae instead of biomass, crustose algae may have been present but obscured by a fleshy algal canopy, decreasing their relative abundance but perhaps not their absolute abundance. However, this change, even if it is only in apparency, is still ecologically significant for corals because their larvae prefer to settle on unobscured crustose corallines, and even larger corals are damaged by direct contact with larger macroalgae (McCook et al. 2001, Jompa and McCook 2002). Thus, overgrowth of living corallines may both preclude coral recruitment and suppress the growth and survivorship of previously established corals.

The results from experiments on tropical macroalgae appear to depend in part on the metric used to measure macroalgal abundance (Fig. 5A–F). Studies measuring percent cover ($n = 4$) showed strong herbivore effects but minimal enrichment effects, while studies measuring biomass ($n = 10$) showed strong herbivore and enrichment effects. However, it is difficult to assess how biomass and percent cover differ when measuring the same community as only one study (McClanahan et al. 2003) reported both biomass and percent cover measurements for the whole community. Thus, any inherent differences in the metrics used to assess the relative effects of herbivores and nutrients are confounded by differences between the study sites, the species unique to each site, and other procedural differences among studies. For example, all of the studies on tropical macroalgae that used percent cover as the metric were conducted in the Florida Keys, USA. Thus, the strong herbivore effects shown when measuring percent cover may be a bias of the metric or may be due to particularly intense herbivory in the Florida Keys as compared to other study sites. Differences in the relative roles of herbivores and nutrients when comparing different abundance metrics were evident for both temperate macroalgae (Fig. 5G–L) and benthic microalgae (Fig. 5M–R). Thus, future studies of top-down and bottom-up interactions would benefit from measuring community responses in a variety of metrics as no single metric may be the most meaningful in terms of primary producer abundance. For example, an increase in percent cover as opposed to biomass of tropical macroalgae may be more damaging to coral reef health

because an increase in percent cover may mean that algae are more likely to contact and overgrow corals or prevent juvenile corals from recruiting to the benthos. However, measuring biomass instead of percent cover may give a better approximation of how herbivory and nutrients affect the absolute production of primary producers.

The scale of experimentation also may constrain the conclusions for these analyses. Although we showed little effect of scale on the experimental effect sizes (Appendix C), the maximum plot size for these experiments was 1 m^2, which is far smaller than the kilometer-wide scale that may represent anthropogenic effects on ecosystems. This smaller scale may diminish the effects of nutrients but magnify the effects of herbivores on primary producers, especially in systems such as tropical reefs, where herbivores (fishes) are very mobile and large compared to the primary producers. For example, nutrient enrichment in the presence of herbivores did not show an effect for tropical macroalgae (Fig. 2D) and even showed a negative effect when only filamentous/turf algae (Fig. 4F) or percent cover of the whole community was considered (Fig. 5C). Highly mobile fishes could generate these patterns by concentrating their feeding efforts on small patches of algae that are nutritionally enriched. However, experimental nutrient enrichment on coral patch reefs averaging >250 m^2 (over two orders of magnitude larger than experiments in our analyses) also showed no effect of enrichment on algal abundance in the presence of herbivores (Koop et al. 2001). Further, exclusion of herbivores on reefs of 50–230 m^2 with no nutrient addition (Sammarco 1982, Hay and Taylor 1985, Lewis 1986) shows dramatic increases in macroalgal abundance similar to our analyses (Figs. 2C, 4B). Although these "large-scale" experiments are still smaller than the scale of eutrophication or overfishing of herbivores, their results suggest that the processes regulating the abundance of tropical macroalgae on the scale of ~1 m^2 are similar to those that operate on the scale of hundreds of square meters.

For temperate macroalgae and benthic microalgae the relative importance of herbivores and nutrients differed between areas of low vs. high productivity. In low-productivity areas, both temperate macroalgae and benthic microalgae were significantly affected by herbivore removal and nutrient enrichment (Fig. 3C, I), but nutrient enrichment was significant only when herbivores were absent (Fig. 3D, J). For temperate macroalgae in high-productivity areas, the effects of nutrient enrichment were significant, whereas the effects of herbivore removal were not (Fig. 3E, F). However, all of the studies for temperate macroalgae in high-productivity systems were conducted in the Baltic Sea, meaning that this effect could be a region-specific pattern rather than a general phenomenon. For benthic microalgae in high-productivity areas, both nutrient enrichment and herbivore removal were significant (Fig.

3K, L). However, herbivores exert greater control on benthic microalgal abundance in low-productivity areas because nutrient enrichment in the presence of herbivores had no effect on abundance in low-productivity (Fig. 3J) areas but a significant effect in high-productivity areas (Fig. 3L). Thus, herbivores appear to exert stronger top-down control in low-productivity systems while nutrient enrichment can affect producer abundance in both low- and high-productivity temperate systems.

Two other meta-analyses of aquatic systems have addressed how system productivity affects the interaction of top-down and bottom-up forces. Hillebrand (2002) showed that for freshwater and marine benthic microalgae the effect of herbivores appears to decline as system productivity increases and also that the interaction between herbivores and nutrients is significant at low and high productivity but nonsignificant in moderately productive areas. Worm et al. (2002) showed even more dramatic effects of background productivity on the role of herbivores vs. nutrient availability in controlling species diversity in aquatic communities. Nutrient enrichment in low-productivity systems increased diversity but herbivores decreased diversity, whereas nutrients in high-productivity systems decreased diversity and herbivores increased diversity. The comparison of our analyses with those of Worm et al. (2002) suggests that the effects of herbivores and nutrients are more complex than merely changing overall abundance of primary producers. For example, herbivores may facilitate the replacement of palatable macroalgae with unpalatable macroalgae with little effect on actual primary-producer abundance (Lubchenco and Gaines 1981, Lotze et al. 2001). Thus, our meta-analysis could underestimate changes in community structure because we measure only producer abundance. Further, comparison of these three meta-analyses (Hillebrand 2002, Worm et al. 2002, this study) suggests that consumers may have lesser effects on the abundance of primary producers in high-productivity areas but larger effects on diversity, whereas nutrient enrichment affects both abundance and diversity. In low-productivity areas, consumers may depress both the abundance and diversity of producers while nutrient enrichment increases diversity but not abundance.

For temperate macroalgae, these patterns for low- and high-productivity studies may stem, in part, from the types of algae present. Larger perennial macroalgae (e.g., *Fucus*) tend to dominate natural intertidal areas, while ephemeral, filamentous algae (e.g., *Enteromorpha*) become more abundant with eutrophication (Worm et al. 2000, Worm and Lotze 2006). Physiological studies show that larger macroalgae often absorb nutrients more slowly than filamentous algae (Pedersen and Borum 1996), suggesting that larger macroalgae respond less quickly to nutrient pulses than filamentous algae. Our analyses agree with these physiological studies and show that upright macroalgae in temperate systems

show no response to nutrient enrichment and are only moderately affected by herbivores (Fig. 4C), while filamentous/turf algae are affected by both herbivores and nutrient availability (Fig. 4E). Filamentous/turf algae are often preferred foods for herbivores and may preempt larger macroalgae when they are not removed by grazers (Lubchenco 1978, Sousa 1979). If herbivores graze filamentous/turf algae to low levels, they may then be forced to feed on less preferred larger macroalgae, which may be why we show a modest effect of herbivores on temperate upright macroalgae.

Thus, producer abundance in low-productivity areas may be more strongly affected by herbivores because they keep filamentous algae to low levels, thereby increasing grazing on less preferred perennial macroalgae and because upright macroalgae may be minimally influenced by short-term changes in nutrient availability (Pfister and Van Alstyne 2003). Primary-producer abundance in high-productivity areas may show strong responses to nutrient enrichment because filamentous algae rapidly respond to nutrient pulses and more easily compensate for losses to herbivores with rapid growth. Grazer manipulations in both the laboratory (Lotze and Worm 2002) and the field (Worm and Lotze 2006) support this pattern, showing a declining effect of herbivores on filamentous algae as nutrient enrichment increases. In addition, field surveys across several replicate eutrophic and control rocky-shore communities show that larger macroalgae decrease while filamentous/turfs (e.g., *Enteromorpha*) increase as rocky shores become eutrophic (Worm and Lotze 2006). In these systems, producer abundance appears to be controlled by consumers when productivity is low and by nutrients when productivity is high.

A limitation of the analyses for temperate macroalgae is that all of the studies come from rocky intertidal or shallow subtidal systems where herbivores may be large (e.g., urchins or gastropods) relative to primary producers (filamentous/turf algae and small to medium-sized macroalgae). Our data set did not include experiments from large kelp communities (i.e., *Macrocystis* spp.) in which the producers are much larger than their consumers. These large, perennial macroalgae can respond strongly to pulsed inputs of nutrients (Dean and Jacobsen 1986) and suffer extensive die-offs when faced with nutrient-poor water for extended periods (Dayton et al. 1992), indicating that nutrient availability strongly affects their abundance. The fact that our analyses do not show a nutrient enrichment effect for smaller macroalgae (e.g., *Fucus*) (Fig. 4C) suggests that the experiments in our analyses potentially were not of sufficient duration to pick up a nutrient enrichment signal for these macroalgae. In addition, herbivores have weak (Sala and Graham 2002) to strong (Estes et al. 1998) effects on kelps, emphasizing the need for more in-depth experimental work on how the relative roles of herbivores and nutrient availability affect kelp communities and how the relative size or metabolism of

consumers and producers may alter the relationships between top-down and bottom-up forces.

Nutrient enrichment in the presence of herbivores significantly suppressed temperate crustose algae (Fig. 4A), tropical filamentous/turf algae (Fig. 4F), and overall tropical macroalgae as measured using percent cover (Fig. 5D). The studies we analyzed did not address the mechanisms producing these effects, and our analyses cannot rigorously assess the mechanisms involved. However, herbivores are commonly nitrogen-limited (Mattson 1980), suggesting that dominant herbivores in these systems could be selectively attacking algae with enriched levels of nitrogen. Fishes on tropical reefs will selectively attack filamentous algae growing on plots with elevated nutrients (D. E. Burkepile and M. E. Hay, *unpublished data*) and individual macroalgae that have been subjected to nutrient enrichment (Boyer et al. 2004). This aspect of nutrition and fish behavior could explain why filamentous/turf algae in temperate areas with few herbivorous fishes are enhanced by nutrients, while those in tropical areas with abundant fishes are significantly suppressed by nutrient additions only when herbivores are present (Fig. 4F). Similarly, nutrients may enhance the nutritional value of crustose algae to temperate grazers, resulting in their decline with enrichment when herbivores are present (Fig. 4A). Thus, integrating the study of herbivore nutrition with research on the relative roles of top-down and bottom-up forces could provide a more mechanistic understanding of how these forces interact.

Alterations to food webs and nutrient availability are pervasive across marine ecosystems. These changes produce context-dependent effects that vary across latitudes, primary producers, and the inherent productivity of ecosystems. Understanding the mechanisms driving these patterns may require greater focus on (1) how aspects of herbivore nutritional needs and algal physiology affect the strength of top-down and bottom-up forces, (2) how these forces vary across spatial and temporal scales (most experimental studies use small-scale manipulations to address what are fundamentally large-scale questions), and (3) integrating small-scale field experimentation with modeling of consumer movement and of eutrophication at large scales.

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APPENDIX A

A table and reference list of studies used in the analyses (*Ecological Archives* E087-189-A1).

APPENDIX B

Results of regression analyses testing for relationships between mean effect size and experimental duration (*Ecological Archives* E087-189-A2).

APPENDIX C

Results of regression analyses testing for relationships between mean effect size and experimental plot size (*Ecological Archives* E087-189-A3).