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REVIEW AND SYNTHESIS

Global patterns in the impact of marine herbivores on benthic primary producers

Alistair G. B. Poore,¹ Alexandra H. Campbell,^{1,2} Ross A. Coleman,³ Graham J. Edgar,⁴ Veijo Jormalainen,⁵ Pamela L. Reynolds,⁶ Erik E. Sotka,⁷ John J. Stachowicz,⁸ Richard B. Taylor,⁹ Mathew A. Vanderklift¹⁰ and J. Emmett Duffy⁶

Abstract

Despite the importance of consumers in structuring communities, and the widespread assumption that consumption is strongest at low latitudes, empirical tests for global scale patterns in the magnitude of consumer impacts are limited. In marine systems, the long tradition of experimentally excluding herbivores in their natural environments allows consumer impacts to be quantified on global scales using consistent methodology. We present a quantitative synthesis of 613 marine herbivore exclusion experiments to test the influence of consumer traits, producer traits and the environment on the strength of herbivore impacts on benthic producers. Across the globe, marine herbivores profoundly reduced producer abundance (by 68% on average), with strongest effects in rocky intertidal habitats and the weakest effects on habitats dominated by vascular plants. Unexpectedly, we found little or no influence of latitude or mean annual water temperature. Instead, herbivore impacts differed most consistently among producer taxonomic and morphological groups. Our results show that grazing impacts on plant abundance are better predicted by producer traits than by large-scale variation in habitat or mean temperature, and that there is a previously unrecognised degree of phylogenetic conservatism in producer susceptibility to consumption.

Keywords

Coral reef, crustacean, grazing, herbivory, latitudinal gradient, macroalgae, marine, meta-analysis, mollusc, plant-animal interaction, primary production, rocky reef, sea urchin, seagrass.

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INTRODUCTION

Consumers have a profound influence on community structure and ecosystem processes, and understanding variation in the strength of consumer impacts, relative to resource availability, has been a primary goal of community ecology (Hairton *et al.* 1960; Gruner *et al.* 2008). Predator control of prey populations and herbivore control of primary producers are spatially and temporally variable, and this variation underpins models explaining global gradients in biodiversity (Moles *et al.* 2011). Specifically, over evolutionary time, stronger biotic interactions at low latitudes are thought to contribute to high tropical biodiversity due to increased speciation rates (Dobzhansky 1950; Vermeij 1978; Mittelbach *et al.* 2007), and by promoting reduced niche breadth that allows greater species coexistence (Janzen 1970). Despite the long history of these theories, however, the relationship between latitude and the intensity of biotic interactions remains largely unresolved due to limited empirical support (Moles *et al.* 2011). Few studies have used consistent methodology

on the large scales needed to test this hypothesis (Pennings & Silliman 2005; Freestone *et al.* 2011), and a recent review called for comparative studies spanning global latitudinal gradients in the magnitude of biotic interactions using consistent methodology (Schemske *et al.* 2009).

Herbivory is a key process in all ecosystems as it results in the transfer of primary production to higher trophic levels and affects the physical structure and productivity of vegetated habitats. Critical to understanding the role of consumer control in ecosystems is quantifying the strength of herbivore impacts on primary producers and relating these impacts to mechanisms and traits that can explain variation in interaction strengths. These include rates of primary and secondary production (which vary on global scales), producer nutritional quality, producer resistance and tolerance to grazing, herbivore feeding behaviour and the stoichiometric match between producer and herbivore tissues (Cebrian *et al.* 2009). From the grazer perspective, differences in abundance, feeding efficiency, size, taxonomy, mobility, metabolism and predator regulation of herbi-

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vore populations can all contribute to variation in the rate at which primary production is removed by herbivores (Borer *et al.* 2005).

A key impediment to evaluating how environmental and biological variation among systems mediate general patterns in the strength of top-down control is inconsistency in methodology among studies (Borer *et al.* 2005). Laboratory and enclosure experiments can overestimate consumer impacts by confining prey with consumers, altering foraging behaviour and removing natural predators (Skelly 2002; Hillebrand 2009). The relatively poor understanding of top-down control in terrestrial systems is, in part, due to the difficulties in experimentally manipulating some vertebrate consumers in the field and the long time scale of terrestrial vegetation responses (Duffy 2002; Gruner *et al.* 2008; Allen & Crawley 2011).

In benthic marine habitats, there is a long tradition of experiments that manipulate consumers in field conditions where the response times of primary producers more closely align with the duration of the experiments. Macroalgae and seagrasses are foundation species that facilitate whole communities (providing habitat and food), and their dominance often depends on grazing (Steneck *et al.* 2002; Valentine & Duffy 2006). Knowing how benthic primary producers are controlled is crucial for understanding how marine ecosystems function and how anthropogenic impacts may ripple through marine ecosystems via indirect effects. In turn, the producer-herbivore relationship likely varies as a function of herbivore taxon and habitat. However, while many manipulative experiments have demonstrated important roles of marine herbivores, fewer have contrasted different groups of grazers (e.g. Carpenter 1986), compared habitats, or were conducted on the scales needed to test theories of large-scale gradients in the strength of herbivory (see Pennings & Silliman 2005 for an exception).

Although latitudinal gradients in the intensity of interactions have been proposed, at any given place the outcomes of interactions depend not only on abiotic environmental factors but also on the traits of the consumers and their prey. Morphologically based functional groups of algae have been proposed in models that seek to predict these outcomes (Littler & Littler 1980; Steneck & Watling 1982; Steneck & Dethier 1994). These models use the traits of thaluss morphology, size and toughness to predict responses to herbivory, with larger, tougher algae and crustose forms tending to be more resistant to herbivores (Steneck & Watling 1982). These models have been tested experimentally, but no synthesis of global patterns in the relationship between functional groups and herbivory has yet been produced.

Here, we present a global quantitative synthesis of herbivore impacts on marine benthic producers by analysing the results of 613 exclusion experiments conducted since 1969. We test the commonly held prediction that grazing impacts are highest at low latitudes, and test whether variation in grazer impacts on producer abundance is best explained by consumer traits, producer traits or environmental influences. The exclusion of consumers *in situ* is one of the most powerful techniques to identify their ecological roles (Paine 1980; Wootton & Emmerson 2005). By considering only exclusion experiments, we have the advantage of using data from a large number of experiments with consistent methodology – exclusion of herbivores in their natural environments, at ambient and naturally variable densities – across most of the global range of marine and estuarine systems, latitudes and producer and consumer taxa. In contrast, previous reviews of marine herbivory have been qualitative (e.g. Lubchenco & Gaines 1981), or have considered subsets of available

producers (e.g. periphyton, Hillebrand 2009) or interactions (e.g. grazer interactions with nutrient supply, Gruner *et al.* 2008).

We found no evidence that herbivore impacts on producer abundance are stronger in tropical seas, and demonstrate that producer traits (i.e. algal identity) explain substantially more variation in herbivore impacts than consumer traits or large-scale variation in habitat, temperature or nutrient availability.

MATERIAL AND METHODS

Data collection

We compiled literature on marine grazer exclusion experiments by searching the ISI Web of Science database (1900–2009) using the following systematic search criteria: (graz* or herbiv*) and (exclud* or exclus* or fenc* or cage* or remov*) and (macrophyte* or alga* or seagrass* or eelgrass* or seaweed*). The results from this search were supplemented by studies included in published reviews on marine herbivory (Lubchenco & Gaines 1981; John *et al.* 1992; Connell & Vanderklift 2007), seagrass ecology (Jernakoff *et al.* 1996; Valentine & Duffy 2006), mesograzers (Brawley 1992) and previous meta-analyses of top-down vs. bottom-up control in marine ecosystems (Hughes *et al.* 2004; Burkepile & Hay 2006; Gruner *et al.* 2008; Hillebrand 2009).

Experiments included in the review were those that featured the exclusion of any marine herbivore at natural densities *in situ* using physical barriers (i.e. cages or fences), removal by hand or methods of chemical deterrence (i.e. biocides or borders of copper-based paints). Inclusion experiments were not considered as these designs do not allow the natural spatial and/or temporal variation in herbivore abundances observed under natural conditions, and are known to overestimate the impact of grazer effects on primary producers (Bigger & Marvier 1998; Hillebrand 2009). Where additional experimental manipulations were made (e.g. shading or nutrient additions), we considered only the treatment that manipulated herbivores under ambient conditions and the relevant control. We included only experiments that were replicated, included spatially interspersed exclusion and control plots, and were not confounded by other known variables.

Experiments were included in the review if they presented data on the quantity (biomass, cover, density or length) of benthic primary producers (macroalgae, cyanobacteria, seagrasses or saltmarshes) in both ungrazed (exclusion) and grazed (control) plots. We included only studies that presented the means, sample sizes and measures of variance (all converted to standard deviations) for each of the treatments at the end of the experiment. When procedural controls were present (e.g. half cages to test effects of cages in the presence of grazers), data were also collected from this third treatment. Data were extracted from digital versions of the publications (pdf format) using the measuring tool in Adobe Acrobat 9 or DataThief.

Our search yielded 193 publications that met our criteria (Appendix S1 in Supporting Information). If the publication included herbivore exclusions conducted in different regions, at different sites, times or depths, these were treated as separate experiments in the meta-analysis provided each possessed an independent set of unmanipulated controls. When multiple exclusion treatments shared a control, they were considered as separate measures within the same experiment. From each experiment, data from all primary producers measured were recorded.

When measures of primary producers were presented from multiple times during the exclusion experiment, we collected data from the time in which there was the greatest absolute difference between exclusion and control treatments (i.e. the time of maximum grazer impact) and at the end of the experiment. For these experiments with time series data, the effect sizes measured at the end of the experiment were a very good predictor of the highest effect sizes observed during the experiment (linear mixed model with maximum effect size as response variable, final effect size as predictor and experiment as a random factor, $P < 0.001$). The slope of this relationship (0.96) did not differ significantly from a slope of 1 (95% confidence interval: 0.91–1.0), and thus all subsequent analyses used data from the final measurement time only. The final data set yielded 3608 measures of primary producers from 22 104 replicate plots in 613 exclusion experiments.

Quantifying grazer impacts

To quantify the effect of removing grazers from marine habitats *in situ*, we used the log response ratio, $LRR = \ln(X_e/X_c)$ where X_e is the mean of the producer variable from the exclusion (ungrazed) treatment and X_c is the mean of the producer variable from the control (grazed) treatment (Coleman *et al.* 2006). The log response ratio measures the proportional change due to the experimental manipulation such that LRR is greater than zero when herbivore presence reduces primary producer abundance, is less than zero when herbivore presence increases primary producer abundance, and equal to zero when herbivore presence has no effect (i.e. the grazed and ungrazed treatments are equivalent). If the mean values of either treatment were zero (e.g. no algae present in grazed plots), we substituted zero with the minimum value that was likely to be detected with the sampling method used (e.g. a count of 1 when numbers of individuals per plot was measured, 1% cover when percentage cover was measured).

Response and predictor variables

Primary producer variables were categorised by the types of measures taken (count, cover, biomass and size), and by whether the measures were taken from single species, groups of taxa, or from all primary producers present in each plot (totals). Primary producers were categorised by the functional groups defined by Steneck & Dethier (1994), and whether they were macrophytes, periphyton or epiphytes. When species were identified, variables were classified by phylum and order using currently accepted published taxonomy for algae and marine vascular plants (www.algaebase.org).

For each experiment, we recorded depth or height on the shore (in metres), the latitude and longitude (to nearest degree) and biogeographical region (the 12 realms defined by Spalding *et al.* 2007). The global distribution of experiments is shown in Fig. 1a. There was no interaction between hemisphere and absolute latitude for the magnitude of the effect size (linear mixed model, $F_{1,419} = 0.15$, $P = 0.70$), hence, all analyses were conducted with absolute latitude only. For each experimental site (one degree latitude by one degree longitude), we obtained sea surface temperature data from the Global Ocean Surface Temperature data set (HadISST_1.1_SST) available from the British Atmospheric Data Centre (<http://badc.nerc.ac.uk/data/hadisst/>, Rayner *et al.* 2003). We calculated the mean, maximum and minimum of the 12 monthly temperatures for

the year in which the experiment finished. Estimates of sea surface nutrient concentrations were taken from the World Ocean Atlas 2009 available from the National Oceanographic Data Center (http://www.nodc.noaa.gov/OC5/WOD/pr_wod.html, Garcia *et al.* 2010). We extracted annual nitrate and phosphate estimates ($\mu\text{mol. L}^{-1}$) for surface waters from each experimental site (one degree latitude by one degree longitude).

Each experiment was categorised into broad habitat types (intertidal rocky reefs, subtidal rocky reefs, coral reefs, seagrass beds, salt-marshes, intertidal soft sediments and subtidal soft sediments). The groups of marine herbivores excluded in each experiment were categorised by major taxonomic groups (gastropods, urchins, fish, crustaceans, mammals, birds, reptiles and polychaetes) and by size (macrograzer vs. mesograzer). Mesograzers were defined as small (less than 2.5 cm) mobile herbivores, such as amphipods, isopods and gastropods (Brawley 1992).

We recorded the duration of each experiment (days), the season in which the experiment ended, the size of experimental plots (m^2) and categorised the experimental methodology using the method of exclusion (cages, physical removals or chemical deterrence) and the substratum conditions at the start of the experiment (existing cover of primary producers or bare substrate following experimental clearing).

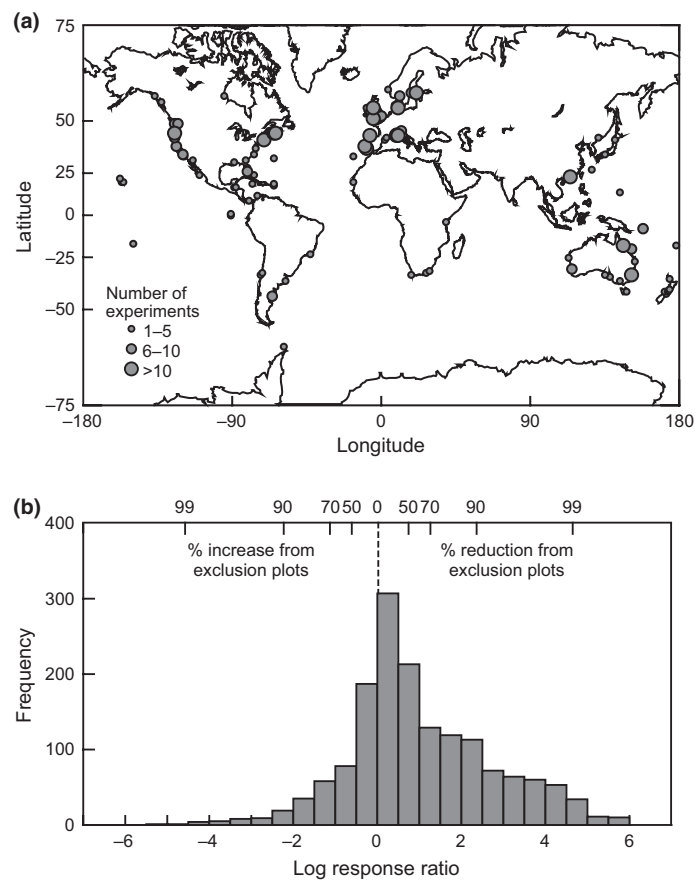


Figure 1 The global distribution of the 613 experiments that excluded marine grazers *in situ* (a) and the frequency histogram of the effect sizes (b). The effect size was quantified by the log response ratio, $\ln(X_e/X_c)$, where X_e is the mean of the exclusion (ungrazed) treatment and X_c is the mean of the control (grazed) treatment. The X-axis above displays the percentage change in producer variables between control and exclusion plots.

Statistical analyses

The degree to which variation in the effect size, LRR, was explained by categorical and continuous predictor variables was tested using linear mixed models in the PROC MIXED procedure in SAS 9.2, with predictors as fixed factors and experiment as a random factor to account for the non-independence of multiple measures of primary production taken from each experiment. The significance of fixed effects was tested using Type III *F* tests effects and Kenward-Roger adjusted degrees of freedom. REML estimates of fixed effects and their 95% confidence intervals were derived from the linear mixed models and used in all figures. Estimates of R^2 for the fixed effects were derived from the methods of Edwards *et al.* (2008). The assumptions of normality and homogeneity of variances were tested by examining frequency histograms of residuals, and scatterplots of residuals vs. means respectively.

Given the geographical clustering of experiments, we also considered the possibility that observations are linked by spatial proximity at spatial scales larger than the experiment. We analysed effect size vs. absolute latitude, mean sea surface temperature and nitrate and phosphate availability with location (each of the 111 unique 1° of latitude × 1° degree of longitude blocks) as a random factor, and experiment as a random factor nested within location.

We assessed which predictor variables most strongly associated with herbivore effects using 'best' model selection following univariate multiple regression (Anderson *et al.* 2008). This approach assesses all possible combinations of predictor variables and selects the best models based on commonly used criteria (AIC, BIC, Adjusted R^2). High multi-collinearity among continuous predictor variables, and missing combinations of levels of categorical factors prevented the use of all predictor variables, and we conducted two sets of analyses based on a subset of important predictors. First, we did a global scale analysis of the continuous, abiotic variables that were present for all experiments (absolute latitude, mean sea surface temperature, phosphate concentration, nitrate concentration, experimental duration and plot size). Second, for intertidal and subtidal rocky reefs, we analysed mean sea surface temperature (as the proxy for latitude and other temperature variables), phosphate concentration, grazer type, producer order, starting conditions, plot size and duration). Tests were run in the DISTLM procedure in Primer V6 (further detailed in Appendix 2).

The funnel plot of effect sizes vs. sample size did not indicate any publication biases as would be expected if non-significant results with low replication were unlikely to be published (Møller & Jennions 2001). Like several recent meta-analyses (Gruner *et al.* 2008; Mooney *et al.* 2010), we took the conservative approach of not weighting effect sizes by their variance as we considered most variation among the experiments to result from biological differences over a wide range of systems rather than the variation in sampling error expected with increasing numbers of replicate plots conducted in otherwise equal conditions.

RESULTS

Large scale patterns in grazer impacts

Removing natural densities of marine grazers *in situ* resulted, on average, in a 3.1-fold increase in the abundance of primary producers (biomass, cover or density) in contrast with control plots acces-

sible to herbivores (mean log response ratio, LRR = 1.14, 95% confidence interval: 0.82–1.45). This is equivalent to grazers reducing producer abundance by 68%. There was wide variation in effect sizes with 20% of observations featuring reductions of more than 90% (Fig. 1b).

Grazer impact increased slightly with distance from the equator (latitude) although this relationship explained very little of the variance in effect sizes (Fig. 2a, $F_{1,474} = 26.77$, $P < 0.001$, $R^2 = 0.02$). Given the uneven distribution of habitats among latitudes, we estimated contrasts with latitude separately for each of the four major habitats in the data set (intertidal rocky reefs, subtidal rocky reefs, coral reefs and seagrass beds). Grazer impact increased significantly with latitude for intertidal rocky reefs (where the average interaction strength increased from 0 to over 89% reduction from the equator to 60° from the equator), coral reefs and seagrass beds, but not in subtidal rocky reefs (Figure S1, Table S2).

Given that latitude itself is unlikely to causally influence grazing, we tested whether grazer impacts vary with mean sea surface temperatures and nutrient availability, each of which varied consistently with latitude. Across all habitats, grazer impacts decreased under warmer mean sea surface temperatures, but the relationship explained little of the variance in effect sizes (Fig. 2b, $F_{1,600} = 30.29$, $P < 0.001$, $R^2 = 0.05$). A similar decline in impact with temperature was observed using the temperature data from the coldest or warmest month in the year of the experiment (Table S2). Effect sizes decreased with mean sea surface temperature in intertidal rocky reefs and seagrass beds, but not in coral reefs or subtidal rocky reefs (Table S2). Mean sea surface temperatures also interacted with the season in which the experiments ended (Figure S2). Effect sizes declined with increasing temperatures when the experiments finished in the winter and spring, there was no relationship with temperature for experiments that finished in summer or autumn (Figure S2, Table S2). Nitrate and phosphate availability in surface waters were both positively correlated with effect sizes (Fig. 2c, nitrate, $F_{1,611} = 9.57$, $P = 0.002$; phosphate, $F_{1,611} = 14.78$, $P < 0.001$, Table S2). Nutrient availability increased with distance from the equator (nitrate, $F_{1,605} = 479$, $P < 0.001$, $R^2 = 0.44$; phosphate, $F_{1,605} = 938$, $P < 0.001$, $R^2 = 0.61$) and declined with mean sea surface temperature (nitrate, $F_{1,605} = 667.5$, $P < 0.001$, $R^2 = 0.52$; phosphate, $F_{1,605} = 1526$, $P < 0.001$, $R^2 = 0.72$).

Multiple regression modelling using a subset of abiotic, continuous variables across global scales (latitude, mean sea surface temperature, nitrate and phosphate concentration, experimental duration and plot size) demonstrated that each of these variables explained only a low proportion of the variance (all < 4%), and failed to identify any models simpler than that using the full set of variables (Table S3).

The weak pattern of stronger grazer impacts at high latitudes might be explained by higher levels of producer abundance in temperate regions with greater nutrient availability, and consequently a greater scope for change between control and exclusion plots. Consistent with this hypothesis, percentage cover in the exclusion plots increased with distance from the equator ($F_{1,235} = 18.7$, $P < 0.001$) (although the relationship was highly variable, $R^2 = 0.07$), whereas percentage cover in the grazed plots declined with distance from the equator ($F_{1,152} = 15.42$, $P < 0.001$).

The effect of removing herbivores on producer abundance differed strongly among habitats (Fig. 2d, $F_{6,707} = 9.70$, $P < 0.001$),

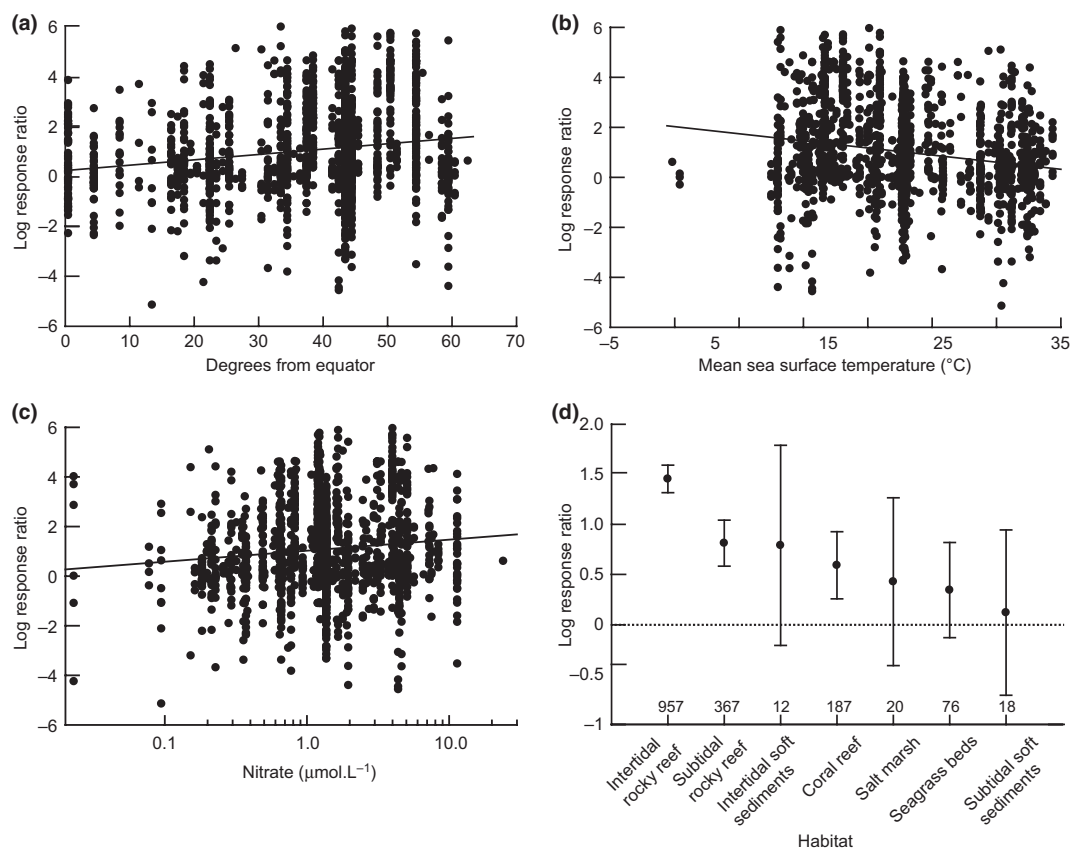


Figure 2 Variation in the effects of excluding grazers with (a) absolute latitude, (b) mean annual sea surface temperature, (c) nitrate availability at the surface and (d) habitat type. Means and 95% confidence intervals in (d) are derived from linear mixed models of log response ratio against predictor variables. The dotted line at zero in (d) is the effect size expected if there is no effect of removing herbivores. Sample sizes for the means are shown above the x-axis.

and was greatest in intertidal rocky reefs (Fig. 2d). On average, exclusion of herbivores had no effect on the abundance of primary producers in seagrass beds, salt marshes or the soft sediment habitats (95% confidence intervals overlapping zero, Fig. 2d), habitats that were less well represented in this analysis.

The large scale patterns were largely unaffected by the spatial clustering of experiments within locations. The observed variation in effect size with the predictor variables of latitude, temperature and phosphate availability all remained unchanged by consideration of location (each 1° of latitude by 1° of longitude block) and experiment (nested within location) as random factors in the linear mixed models (absolute latitude: slope = 0.02, $F_{1,10} = 6.74$, $P = 0.01$; mean sea surface temperature: slope = -0.04, $F_{1,119} = 8.0$, $P = 0.006$; phosphate: slope = 0.54, $F_{1,121} = 4.58$, $P = 0.03$). The relationship between effect size and nitrate availability became non-significant (slope = 0.13, $F_{1,128} = 2.91$, $P = 0.09$). When grouping the experiments at even larger spatial scales, average grazer impacts varied among biogeographical regions only for intertidal rocky reefs (7 realms contrasted, $F_{6,361} = 5.71$, $P < 0.001$) where the difference was due to low grazer impact in the two tropical regions (Central Indo-Pacific and Tropical Eastern Pacific). There were no differences among regions for subtidal rocky reefs (5 realms contrasted, $F_{4,54} = 0.27$, $P = 0.89$), coral reefs (4 realms contrasted, $F_{3,175} = 2.21$, $P = 0.09$) or seagrass beds (3 realms contrasted, $F_{2,25} = 0.72$, $P = 0.50$).

Variation in impacts with grazer type and size

Given the uneven distribution of herbivore taxa among habitats, we contrasted taxa within the four major habitats represented (i.e. those for which there were > 5 experiments per grazer type) (Table S2). On intertidal rocky reefs, molluscs had the highest grazing impacts (Fig. 3a, $F_{2,294} = 8.74$, $P = 0.002$), with these impacts not differing significantly from urchins, but higher than experiments that excluded multiple groups. Molluscs and urchins had the highest impacts on subtidal rocky reefs (Fig. 3a, $F_{3,100} = 3.66$, $P = 0.02$). On coral reefs, the highest effect sizes were observed for experiments that excluded fish and multiple taxa (Fig. 3a, $F_{2,170} = 5.60$, $P = 0.004$), whereas no differences among herbivore taxa were observed in seagrass beds (Fig. 3a, $F_{3,11} = 0.76$, $P = 0.54$).

We contrasted the impacts of macrograzers (fishes, urchins and large molluscs) with those of the smaller mesograzers (amphipods, isopods and small molluscs) to test whether mesograzers can significantly impact marine vegetation. Macrograzers more strongly impacted producer abundance than mesograzers ($F_{1,745} = 15.42$, $P < 0.001$), with the pattern largely explained by differences among mollusc size classes (Fig. 3b). Quantitative comparison with the grazing effects of macrograzers, however, is complicated by the fact that the small mesh sizes needed to exclude mesograzers in caging experiments will also exclude local macrograzers if present. In experiments aimed at excluding mesograzers, the abundance of primary producers was significantly increased by grazer exclusion in all

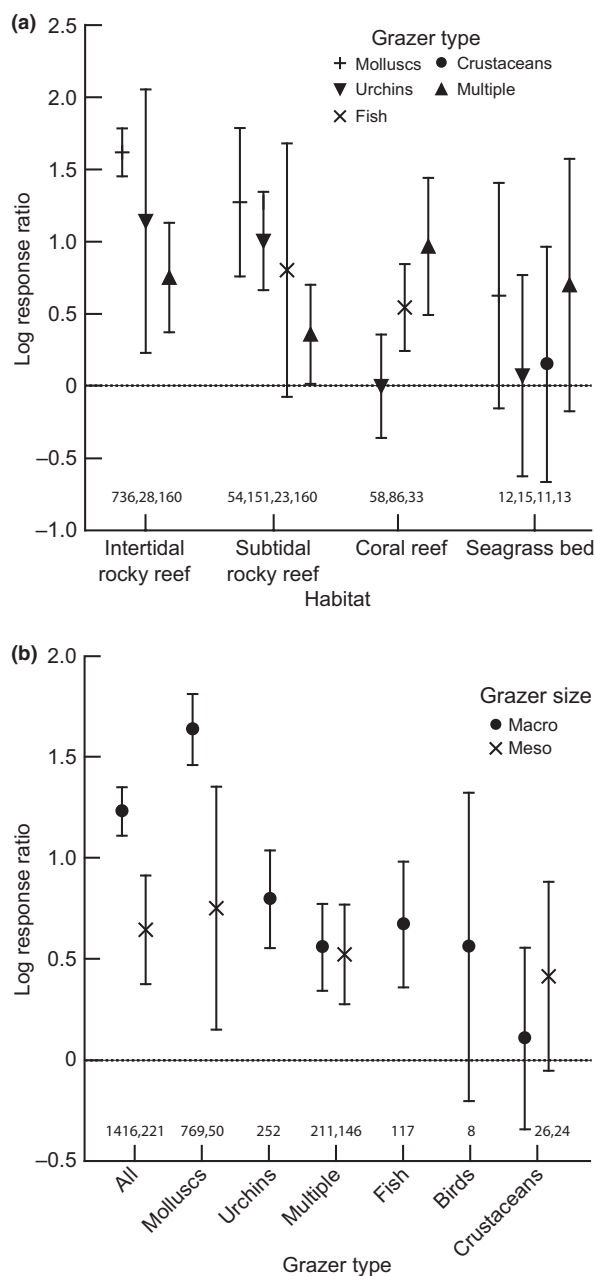


Figure 3 Variation in the effects of excluding grazers among major taxonomic groups of grazers within (a) each major habitat type, and (b) between macrograzers and mesograzers within each of the grazer types. The means, error bars, dotted line at zero and sample sizes are as explained for Fig. 2.

habitats examined (Fig. 3b, mean LRR = 0.64, equivalent to plots exposed to mesograzers having 47% of the producer abundance of exclusion plots, on average).

Variation in grazer impact with primary producer traits

Strong variation was evident among functional groups of primary producers (Fig. 4a, $F_{9,863} = 16.69$, $P < 0.001$). Grazers had strongest effects on leathery macrophytes and foliose algae. On average, filamentous, corticated foliose and micro-algae all declined with grazer presence, whereas calcareous algae (crustose and articulated),

corticated macrophytes, seagrasses and salt marsh vegetation were not significantly affected by grazers (Fig. 4a).

Among experiments that reported the identity of primary producers, herbivores most strongly depressed brown and green algae, with significantly lower impacts on red algae, seagrasses and cyanobacteria (Fig. 5a, $F_{4,752} = 19.3$, $P < 0.001$). At a finer level of taxonomic resolution, grazing impacts varied strongly among orders of primary producers (Fig. 4b, $F_{17,726} = 10.22$, $P < 0.001$). Across all habitats, algae from the orders Fucales, Laminariales, Palmariales, Dasycladales, Ulvales, Cladophorales and Dictyotales were most impacted (negatively) by grazers (Fig. 4b). The remaining orders were, on average, unaffected by the exclusion of herbivores with the exception of cyanobacteria in the order Nostocales, which increased in the presence of herbivores (Fig. 4b).

Given the uneven distribution of producer functional groups, phyla and orders across habitats, we contrasted groups separately within each habitat using only those with more than five replicate observations per group. Strong differences among functional groups remained within intertidal ($F_{6,537} = 21.62$, $P < 0.001$) and subtidal ($F_{6,153} = 2.76$, $P = 0.01$) rocky reefs, with the strongest grazing impacts on leathery macrophytes. There were strong differences in grazer impacts among producer phyla (excluding seagrasses) in intertidal rocky reefs, subtidal rocky reefs and coral reefs (Fig. 5a, Table S2). The strong differences observed among algal orders across all habitats (Fig. 4b) were also present within habitats (Fig. 5b, Table S2). Impacts were strongest on algae from the orders Fucales and Ulvales on intertidal rocky reefs ($F_{8,396} = 18.24$, $P < 0.001$), and on Fucales, Ulvales and Laminariales on subtidal rocky reefs ($F_{9,144} = 5.09$, $P < 0.001$). On coral reefs, grazer impacts were highest on algae from the Fucales (Fig. 5b, $F_{3,252} = 15.57$, $P < 0.001$).

Multiple regression modelling using a subset of variables within intertidal and subtidal rocky reefs (mean sea surface temperature, phosphate concentration, grazer type, producer order, starting conditions, experimental duration and plot size) demonstrated that producer order was associated with a higher proportion of the variation (43% intertidal, 31% subtidal) than any other variables (all others < 13%) (Table S3). The most strongly supported models selected differed little from the model with all terms, thus failing to isolate a more parsimonious selection of predictor variables (Table S3).

Grazers are often hypothesised to benefit macrophytes by removing epiphytes. Only nine experiments measured both epiphytes and macrophytes, and among these, there was no evidence for differences in impacts between epiphytes and macrophytes (paired t -test, $t_8 = 1.25$, $P = 0.25$). From the 16 experiments that presented data on the abundance of epiphytic algae, the removal of grazers did increase epiphytes 2.3-fold (mean LRR = 0.84, 95% confidence interval: 0.12–1.55) and we found no difference between mesograzers and macrograzers in effectiveness of epiphyte removal ($t_{14} = 0.14$, $P = 0.89$).

Influence of experimental method

We conducted a series of additional tests to confirm that the results obtained were not confounded by differences in experimental methods (fully detailed in the Appendix 3 in the Supporting Information and Table S2). Effect sizes increased weakly with plot size (Figure S4, $F_{1,386} = 5.17$, $P = 0.02$, $R^2 = 0.01$), and only dif-

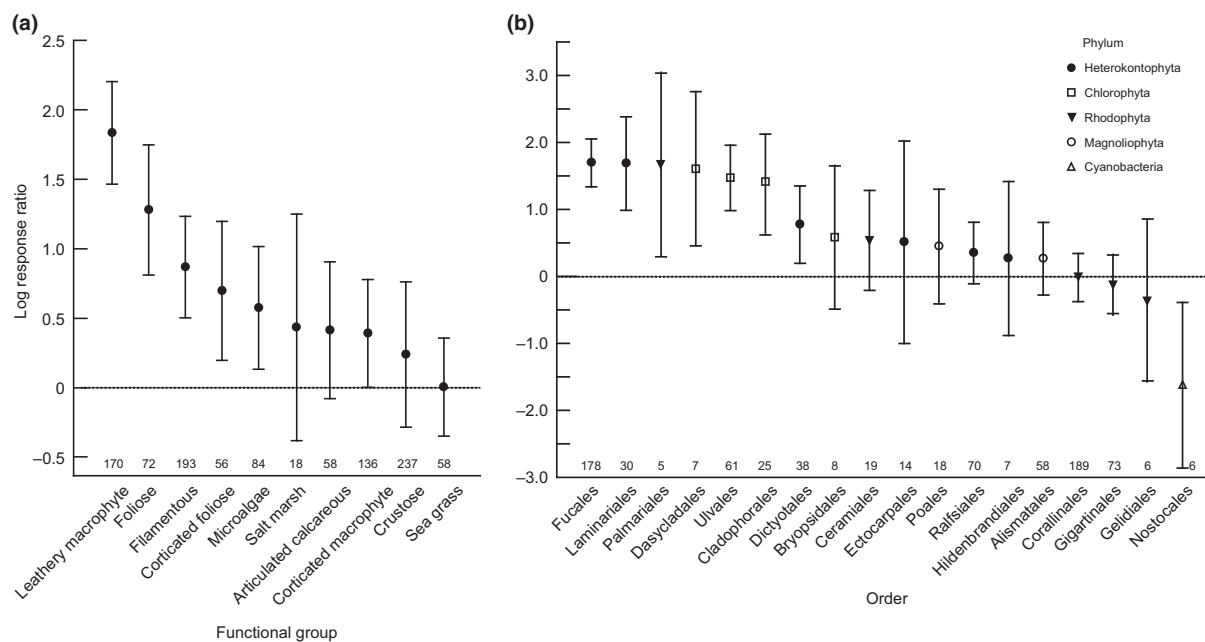


Figure 4 Variation in the effects of excluding grazers among (a) functional groups, and (b) orders (labelled by phylum) of primary producers. The means, error bars, dotted line at zero and sample sizes are as explained for Fig. 2. Orders and functional groups with fewer than five replicate observations are excluded from the figures.

ferred among methods of exclusion for molluscs (Figure S3b, Table S2). Effect sizes increased with experimental duration for measures of total producer abundance (Figure S6a, $F_{1,280} = 51.45$, $P < 0.001$), but not, on average, for measures of single species (Figure S6b, $F_{1,260} = 0.03$, $P = 0.86$).

DISCUSSION

Our analysis of over 600 controlled field experiments presents the largest and most coherent synthesis of experimentally measured herbivore impacts in nature. Across the global range of environments, herbivore impact on marine benthic primary producers is intense, reducing producer abundance by 68% on average, compared with 49–59% estimated from previous analyses of aquatic systems (Gruner *et al.* 2008; Hillebrand 2009), and consistently higher than estimates from terrestrial vegetation (Cebrian 1999). Our results, thus confirm that consumers exert strong control on benthic producers throughout the world's oceans. These impacts are exerted not only by large herbivores, such as fishes and urchins, but also by mesograzers (small crustaceans and molluscs) whose role has been rarely recognised (Duffy & Hay 2000; Poore *et al.* 2009) with the exception of gastropods in the rocky intertidal. Unexpectedly, we found little influence of latitude, mean annual water temperature, nutrient availability or major herbivore taxon on grazing impacts, which were also similar among the major habitat types (except for particularly intense herbivory on intertidal rocky reefs) and largely consistent among different biogeographical regions (except for limited grazing impacts on tropical intertidal rocky reefs). Instead, impacts differed most consistently among producer taxa (orders) and morphologically based functional groups, suggesting stronger control by phylogeny and morphology than by environment, and a previously unrecognised degree of phylogenetic conservatism in algal susceptibility to consumption.

Long-standing arguments that consumer pressure is higher in the tropics (Gaines & Lubchenco 1981) are supported by limited experimental evidence (e.g. Coley & Barrone 1996; Pennings & Silliman 2005), stronger defences of some taxa at lower latitudes (Bolser & Hay 1996; Rassmann & Agrawal 2011; Pearse & Hipp 2012), and the paucity of herbivorous vertebrates at higher latitudes (Floeter *et al.* 2005). However, we found no evidence that potentially stronger herbivory translates to stronger impacts on aggregate abundance of tropical marine producers. The generality of latitudinal gradients in biotic interactions has remained unresolved due to few studies being conducted on appropriate scales, and a wide variety of metrics used to quantify interaction strengths. Our analysis overcomes these limitations by focusing on a common, rigorous methodology that directly measures consumer impacts at natural densities in the field, across a broad range of habitats, herbivores and producers. The lack of stronger herbivore impacts in the tropics, or on coral reefs, was unexpected but is consistent with recent meta-analyses across marine and terrestrial environments that similarly found no or variable latitudinal gradients in consumer effects on primary producer abundance (Gruner *et al.* 2008; Hillebrand 2009; Moles *et al.* 2011).

Herbivore impact in field experiments is measured as the difference in abundance (standing biomass or cover) of a multi-species producer assemblage between an exclusion treatment (E) and a control (C) exposed to herbivores (summarised in our analysis as $\ln[E/C]$ (Coleman *et al.* 2006). Abundance, in turn, reflects the outcome of production, interaction among producer species, and removal by herbivores (and other losses). Thus, high rates of herbivory may not necessarily translate to changes in aggregate producer abundance. Moreover, all these processes may be influenced by the environment and traits of both producers and herbivores. Despite the well-known variation in feeding behaviour among species within a taxonomic group (e.g. Poore *et al.* 2008), our analyses identified variation among major taxa and size classes of

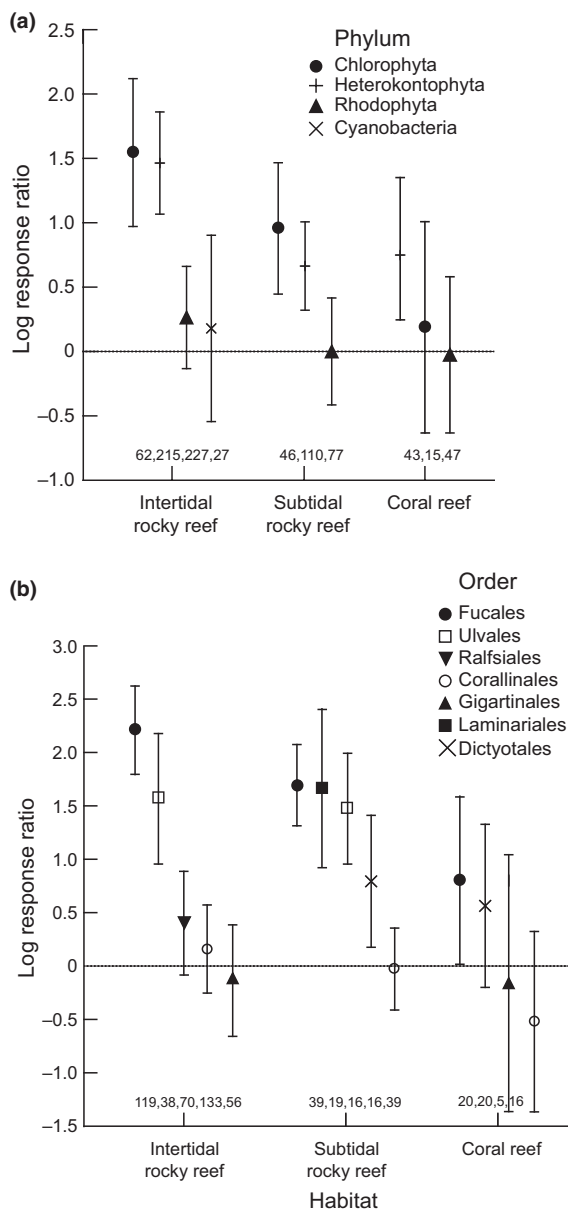


Figure 5 Variation in the effects of excluding grazers among (a) phyla and (b) orders of primary producers within each major habitat types. The means, error bars, dotted line at zero and sample sizes are as explained for Fig. 2. In (b), the orders presented in each habitat are the five orders with the highest number of replicate observations per habitat.

herbivores, with particularly intense herbivory recorded from molluscs on intertidal rocky reefs. It should be noted, however, that the field exclusion experiments in this data set record population-level impacts (i.e. integrating naturally occurring variation in herbivore abundance, composition, body size distributions and per-capita grazing rates) and are not always able to partition impacts among herbivore taxa (e.g. the ‘multiple’ category when more than one taxon is excluded). Our contrasts among herbivore taxa assume that the original experiments manipulated the taxa they intended to. This will certainly be true in the 28% of observations that come from experiments where the investigators manually removed herbivores of known identity, as well as those caging experiments where taxa other than those manipulated are absent or deemed unimportant (e.g.

caging experiments in high latitude kelp forests manipulating urchins, where herbivorous fishes are largely absent). In cases where multiple taxa are excluded simultaneously, alternative experimental designs (e.g. enclosure experiments with known grazers) are needed to better partition impacts among herbivore taxa (e.g. Burkipile & Hay 2008). Below, we consider how global patterns in herbivore impact may be mediated by temperature, nutrients, producer traits and cascading impacts of higher predators.

Temperature is a fundamental driver of biological processes and varies systematically with latitude. Both photosynthesis and respiration increase with temperature, resulting in both faster plant growth and higher consumption by herbivores, on average, at warmer temperatures and at lower latitudes. As consumption tends to increase with temperature faster than does photosynthesis (Allen *et al.* 2005), herbivore control might be expected to be stronger at warmer temperatures. However, faster plant growth may also enhance tolerance to grazing (Wise & Abrahamson 2007). Consistent with both these hypotheses, tropical coral reefs have very low algal biomass, yet are highly productive, evidently because herbivores can crop nearly all daily production and maintain the dominant filamentous algae in a state of rapid growth free of resource limitation (Carpenter 1986).

Given the expectations of more intense herbivory in the tropics, and known positive relationships between grazing rates and temperature (e.g. aquatic grazing on periphyton, Hillebrand 2009), why then does herbivore exclusion not cause large increases in algal biomass there relative to temperate regions? One contributor may be the latitudinal gradients in nutrient availability. Stratification of the warmer water column at low latitudes maintains generally lower nutrient availability in tropical surface waters. Perhaps in part for this reason, large nutrient-hungry kelps (Laminariales and Fucales) are less common in the tropics, and tropical algae tend to be smaller than temperate algae. If producers typically reach higher biomass in exclusion plots in nutrient-rich temperate waters, this may translate to a greater scope for increase in algal abundance when herbivores are removed in temperate areas, counteracting any trend driven by stronger herbivory in the tropics. This hypothesis is supported by our findings that the percentage cover of producers in the exclusion plots (i.e. potential standing biomass) increases with distance from the equator and increasing nutrient availability. Similarly, effect sizes of grazer impacts on aquatic periphyton correlate positively with standing biomass (Hillebrand 2009). The weak positive correlations between grazing effect sizes and nutrient availability observed in our data contrast with previous large scale syntheses that have found either no variation in top-down control (Borer *et al.* 2005; Hillebrand 2009), or declines in marine herbivore impacts (Burkipile & Hay 2006) with increasing ecosystem productivity. Alternatively, the most impacted orders of algae (Fucales, Ulvales, Laminariales) may have few tropical representatives precisely because these species suffer most from herbivory and herbivory is more intense in the tropics. Thus, it is possible that strong selection by herbivores has eliminated many susceptible species from the tropics or prevented their invasion from temperate regions. In this case, the lack of impact of latitude on present day impact of herbivores on producer abundance could be thought of as the ‘ghost of herbivory past’.

For intertidal species, contrasts across gradients in productivity, and simple predictions of increased per capita grazing rates with increased water temperature, are complicated by the variation in thermal and desiccation stresses. For tropical intertidal species that live close to

their thermal maxima (Somero 2011), grazing activity may be more strongly limited by air temperatures than by water temperatures. This hypothesis is consistent with our finding of low grazer impacts, on average, for tropical, intertidal rocky shores (the only habitat in which effect sizes varied among biogeographical regions).

The most striking feature of our analysis was strong and consistent variation among producer groups in vulnerability to herbivores. The strong variation among producer orders implies that major patterns in vulnerability were established early in the evolution of producer taxa and have persisted despite hundreds of millions of years of dynamic consumer-prey interactions. Notably, herbivore impacts were especially low in salt marshes and seagrass beds, which are dominated by vascular plants that are less nutritious than algae (Cebrian *et al.* 2009) and generally little grazed. There was, however, relatively little available data from field exclusion experiments on the importance of grazing of epiphytes and benthic microalgae in those plant-dominated systems. Superimposed on the taxonomic pattern is one of strong variance among morphologically based functional groups. Our results, however, differed from the predictions of classical models of algal functional group vulnerability (Steneck & Dethier 1994). For example, leathery macrophytes were among the most strongly impacted by herbivory, even when compared with microalgal and filamentous groups which are expected to be more palatable (Fig. 4). This contrasts with arguments that grazing favours fast-growing 'weedy' species (Gruner *et al.* 2008), and a previous meta-analysis that found upright algae are only moderately grazed in temperate systems (Burkpile & Hay 2006). Our results may reflect the fact that kelps are often controlled by heavy grazing at small life history stages whereas filamentous taxa continue to grow rapidly and produce under heavy grazing. Although the experiments with kelps that we reviewed were generally conducted over long time scales (mean = 525 days), and thus should have allowed grazing on all life stages, measurements of kelp populations are dominated by adult stages. Thus, our data are unable to confirm whether the observed high grazer impacts on this functional group persist beyond the early life stages.

The high resistance of crustose algae to herbivory, as predicted by functional form models and extensive field data (Steneck & Dethier 1994), is confirmed by our analyses. Our only evidence for herbivores facilitating the abundance of producer taxa is for the abundance of crustose algae to increase under fish and urchin grazing – the well-known phase shift between kelp forests and crustose dominated 'barrens'. The few other examples of grazers facilitating producer groups were grazing by crustaceans benefitting seagrasses (Figure S3, assumed to result from grazers removing epiphytes) and grazing increasing the abundance of the chemically defended cyanobacteria (Fig. 4b). The fact that certain producer taxa are unaffected, or benefit from, grazing is also evident from the increasing variance in effect sizes (both positive and negative) with experimental duration when measures of single species are analysed (Figure S7). In addition to structural defences, herbivory is strongly influenced by algal chemical defences (Paul *et al.* 2001), and higher rates of metabolism, evolution and herbivory in the tropics may generate stronger, diffuse coevolution between consumers and prey defences in tropical regions (Strauss *et al.* 2005). If chemical defences are indeed stronger in the tropics (as evident in some systems, e.g. Bolser & Hay 1996; but not others, Moles *et al.* 2011), they could offset the greater numbers or activity of herbivores there. On the other hand, tropical herbivores could have evolved greater tolerance for seaweed

defences than temperate herbivores, and thus, there is no straightforward prediction from the evolutionary history of strong plant-herbivore interactions on the current interaction strength.

Finally, in addition to these bottom-up effects, spatial variation in predation intensity might also help explain the weak relationships with latitude, temperature and nutrients, and our findings of the strongest herbivore impacts in the intertidal. The grazed (control) plots in most field experiments allow predator access, potentially inhibiting herbivore activity such that the log response ratio underestimates potential grazing impacts. Thus, we suspect that the characteristically strong trophic cascades in aquatic communities (Shurin *et al.* 2002; Estes *et al.* 2011) may contribute to some of our findings. The strong seasonality in temperate latitudes can generate up to 100-fold fluctuations in herbivore densities (e.g. Korpinen *et al.* 2010), which typically peak in autumn after summer recruitment, and may promote periodic escapes from predator control as predator responses lag behind those of herbivores. This may explain our finding that the increasing effect of herbivores with latitude is strongest for experiments concluded in winter, which would have thus experienced greater herbivory during autumn. Our finding of highest herbivore impacts in the intertidal may also be explained by relaxed predation if predators are less tolerant than herbivores of the physiologically stressful intertidal environment as envisioned in the consumer stress model (Menge & Olson 1990).

Our results confirm the central importance of herbivores in marine benthic ecosystems and provide the strongest test yet in any system of latitudinal and environmental variation in the impact of herbivory on producers on a global scale. The data strongly contradict the commonly accepted notion that herbivores have stronger impacts on producer biomass in tropical regions, and demonstrate that producer traits (i.e. algal identity) explain substantially more variation in herbivore impacts than consumer identity or large-scale variation in habitat, temperature or nutrient availability. Challenges for future research include (1) better clarifying the mechanistic bases for the strong variance in vulnerability among orders and functional groups of producers and (2) understanding how large-scale variance in environmental forcing and the strength of biotic interactions mediates expression of herbivore and producer functional traits, both at the physiological level and over the long span of evolutionary time. From the perspective of conservation and management, our finding of consistently strong top-down impacts throughout the world's oceans provide further support that alterations of marine food webs through fishing and exotic invasions can be expected to ripple through marine ecosystems and influence the base of the food web and the biogeochemical processes mediated by primary producers.

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All authors designed the research, prepared the database and edited the article; AP, VJ, ES, RT and MV analysed data; and AP and JED wrote the article.

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