Trophic cascades and connectivity in coastal benthic marine ecosystems: a meta-analysis of experimental and marine reserve research

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Abstract: Predators often exert top-down control on lower trophic levels, such that their removal or addition can trigger trophic cascades. Despite coastal ecosystems containing well known trophic cascades, the abiotic and biotic factors governing the occurrence and strength of these cascades are still unclear. We worked to explain the variability of trophic cascades in benthic marine ecosystems by conducting a meta-analysis of experimental (N = 17) and observational (N = 22) studies that recorded herbivore and producer populations in the presence and absence of a first level predator. From these data (147 predator-herbivore-producer measurements), we show that, although not as strong as previously estimated, the presence of predators decreased herbivore populations between 2.1 to 4.76 times and increased producer populations by 1.62 to 2.83 times. Biotic factors related to species' body size were most influential in determining herbivore population response to predator presence, while abiotic factors, including nutrient concentration, best determined the producer population response. Our results also show producers responded more intensely to changes in herbivore populations in high nutrient and low temperature environments. Looking at populations in marine reserves we found that herbivore populations in reserves were 3.00 times lower on average, compared to areas outside the reserve, while producer populations were on average 1.84 times higher. Overall, this work advances our understanding of the factors modulating trophic cascade strength, demonstrates that reserves can have ecosystem wide impacts, and establishes a new baseline of trophic cascades in benthic marine systems.

1. INTRODUCTION

Marine predator populations often play important roles in maintaining the ecological functioning and economic services of coastal ecosystems. First level predators such as lobsters (Ling et al. 2009), fishes (Caselle et al. 2018), and sea otters (Estes & Palmisano 1974) exert top down control on herbivores and indirectly support foundation species, such as kelp, seagrasses, and other macroalgae, which are often controlled by the herbivores (Shurin et al. 2010). As a result of this indirect trophic interaction, known as a trophic cascade (Svenning et al. 2016), predator populations, aquatic or terrestrial, can support and shape entire ecosystems and their associated ecosystem services (Larkum et al. 2006, Clark & Johnston 2017, Wernberg et al. 2019). Additionally, marine predators provide direct ecosystem services when used for human consumption or material use (Smith & Addison 2003, Myers & Worm 2005). Because of their high ecological and socio-economic value, predators are not only depleted in many systems (Heithaus et al. 2008), but in some cases reintroduced or conserved via complex management strategies, e.g. marine reserves, reintroductions, or legal protections (Halpern 2003, Davis et al. 2019). As humans become increasingly involved in either removing, introducing, or enhancing marine predator populations, it is important that we understand the ecosystem-wide implications of these manipulations, intentional or otherwise. Theory and practice suggest that predators can structure consumer and producer populations in the ocean, but there is considerable variability within these observations (Borer et al. 2005, Shears et al. 2008, Baum & Worm 2009). It is therefore important to consider the generality of trophic cascades as well as how we can make better predictions about which ecosystem attributes or conditions result in the greatest changes in herbivores and producers following a predator addition or removal.

Despite coastal marine ecosystems containing some of the best-known trophic cascades (e.g. Estes & Duggins 1995, Shears & Babcock 2002, Moksnes et al. 2008) the drivers of their variability are not well synthesized, (but see work on quantifying their magnitude in Atwood & Hammill (2018), and ecosystem and region specific work in He & Silliman (2016) and Östman et al. (2016)). Previous syntheses on the determinants of trophic cascades (Shurin et al. 2002, Borer et al. 2005) contained very few data points from coastal marine systems (8 / 102 data points in Shurin et al. (2002) work and 18 / 210 in Borer et al.'s (2005) updated analysis), and demonstrated a high degree of variability in the strength of those cascades, with strength defined as the amount of negative change in the herbivore population or positive change in the producer population caused by the presence of a predator. Since these publications, researchers have made more progress in analyzing the factors that influence the direct trophic interactions of herbivory (Poore et al. 2012) and predation (Griffin et al. 2013, Katano et al. 2015). These studies can be used to make inferences about trophic cascades, but we remain limited in our ability to predict the indirect ecosystem consequences of continued removal of marine predators, reintroductions, or to what extent marine reserves, which often restore predator populations, have cascading effects through ecosystems (Hessen & Kaartvedt 2014, He & Silliman 2016).

Marine reserves are well recognized as a tool to restore fish populations (Molloy et al. 2009), but there is less evidence to support their effect on non-extracted species such as herbivores and algae (Gilby & Stevens 2014, Woodcock et al. 2017). Although unharvested species may not directly benefit from marine reserves, they could be indirectly affected through trophic interactions, specifically by resurgent predator populations or indirect effects of the marine reserve (Shears & Babcock 2002, McClanahan & Muthiga 2016). Such positive effects could increase the resilience of foundation species (e.g. kelp) to climate, competition, and consumption based disturbances (Olds et al. 2014). Within an ecological theory context, researchers can use marine reserves to test ecological principles at the spatial scale of natural ecosystems, a detractor levelled against small scale experimental studies (Meentemeyer & Box 1987). To test for the ability of marine reserves to restore trophic relationships in an ecosystem, herbivore and producer populations within the reserve (with predators) are compared to herbivore and producer populations outside the reserve (without predators). Because they are not directly manipulated, we expect that populations shifts in the protected area studies will be smaller than in controlled, experimental research (Hillebrand 2009), but could never-the-less prove to be a viable management option for reversing the trophic effects of marine predator declines. Within reserves, it is also expected that cascade strength will amplify with reserve age as predators have longer to recover from overexploitation (Molloy et al. 2009), but not size, as found with predator return (Lester et al. 2009).

The occurrence and strength of trophic cascades are likely context dependent and hinge on various biotic and-or abiotic factors, as well as the methodological pretexts present in that ecosystem or study (Borer et al. 2005, Cebrian et al. 2009, Shurin et al. 2010). Research into the abiotic drivers of trophic cascades has been limited and we focus our investigation on two potentially key factors 1) temperature, which regulates metabolism and determines how predator or consumers populations can grow and reproduce, and 2) nutrient levels (nitrate and phosphate), which influence a producer's growth rate with a reduced consumer pressure. While past investigation on biotic factors has focused on species diversity and degrees of omnivory, our work investigates the role of body size, which influences consumption pressure (Vucic-Pestic et al. 2010), predator-prey mass ratio, which influences the probability of predation (DeLong et al. 2015), and trophic connectivity which examines the link between a shift in one trophic level and an adjacent one, i.e. how a shift in the herbivore populations results in a shift in a linked producer population (Duffy 2002).

In this study, we conducted a global meta-analysis of the peer-reviewed literature on coastal benthic marine trophic cascades to synthesize current understanding of 1) their strengths, 2) their biotic and abiotic drivers, 3) how the implementation of marine reserves influences these food web interactions. Specifically, we hypothesized that trophic cascades would be stronger in high temperature environments, which necessitate higher energy demands and consumption pressures (Bruno et al. 2015); in high nutrient environments, where systems are less nutrient limited and more likely to be top-down controlled (Oksanen et al. 1981, Jeppesen et al. 2003, Östman et al. 2016); when larger bodied species, with higher consumption rates, are involved (DeLong et al. 2015); when predator-prey mass ratios are intermediate and species are likely to interact (Vucic-Pestic et al. 2010); and when trophic connectivity is high, such that changes in herbivore populations reflect changes in producer populations (Duffy 2002). We also compared our results to the two most closely related previous meta-analyses (Shurin et al. 2002, Borer et al. 2005) to assess how additional data from studies conducted over the past decade have influenced our understanding of trophic cascades in coastal marine ecosystems. As marine predators continue to decline (Christensen et al. 2014) and the oceans become increasingly managed (Edgar et al. 2014), such knowledge is vital not only to ecological theory but for marine management.

2. METHODS

2.1. Literature search and study selection

We used SCOPUS Web of Science (WOS) to conduct two distinct searches of the primary literature related to marine trophic cascades. The first search sought studies that had examined trophic cascades using experimental methods and combined the terms: ("top down" or trop* or cascad* or contr* or indirect*) AND (exclus* or enclos* or remov* or cage* or fenc* or mesocosm) AND (marine or sea or ocean) AND (pred* or prey) AND (primary or producer or *grass or *phyte or alga* or seaweed). The second search targeted trophic cascade studies based upon natural experiments and observations surrounding marine reserves, and used the search terms: ("top down" or trop* or cascad* or contr* or indirect*) AND (reserve* or MPA or park or protect*) AND (marine or sea or ocean) AND (pred* or prey) AND (primary or producer or *grass or *phyte or alga* or seaweed). The first searches were conducted between February 23, 2016 and March 10th, 2016, and we conducted renewed searches to update the results between September 22nd and 26th, 2018. The WOS searches cumulatively and respectively yielded 821 and 1931 studies and contained studies published between the years 1990 and 2017. Additional papers were added from the references of the past meta-analyses on the subject.

We evaluated the titles and abstracts of our search results to determine if the papers were relevant to our research questions. We first read the title and abstract of each search result and marked studies for potential inclusion if it appeared that they recorded a three level trophic cascade in a coastal benthic marine environment; following this process we had 223 publications remaining. We then read the full publication in greater detail to determine if the study measured the mean and variance of herbivore and producer populations with and without a primary predator population. In addition to these criteria, we excluded studies based on the following criteria to ensure that we only included comparable data points in our analysis. We excluded a study if it explicitly examined an omnivorous predator that fed on both the herbivores and producers and would confound the effects of the predator “treatment” (Heck Jr et al. 2000). Additionally, we excluded studies that: only reported values for grazing rate or tissue damage because they are not direct measures of producer populations (Shurin et al. 2002, Borer et al. 2005), recorded the predator effect when mixed with another treatment (e.g. nutrient addition), used cages that excluded both herbivorous and predatory species, or only provided modeled results, each of which would either confounded the effect being tested or not have provided empirical evidence. We attempted to ensure temporal synchronicity in the measurements and therefore excluded studies if they recorded predator, herbivore, or producer populations greater than one month apart from each other. Specific to marine reserves, we excluded studies that used fisheries landings as a proxy for biomass because they are not representative of the entire community or if the study reported herbivores that were part of an active fishery, as they too would directly benefit from the protection of the reserve.

From each of the 39 papers that met our final selection criteria, we extracted data on the mean herbivore and producer populations with and without predator populations (N = 147). We also made additional considerations on how to record the data. We recorded the primary producer populations using biomass, density, percent cover, or chlorophyll-a concentrations as the units, while we used density, biomass, or abundance for the herbivore populations. If a study recorded both biomass and abundance, we used biomass as the metric of measurement because it is more comparable across species. If a study had multiple time points, we used the point at the end of the study because it was furthest from any manipulation and most likely to represent natural conditions. If a study manipulated a predator and recorded more than one herbivore or primary producer, we considered each species response individually while acknowledging that they were not independent events (see effect size calculation). Similarly, we recorded separate entries from the same study if it examined multiple locations or distinct time points (see effect size calculation). Finally, to accommodate the use of the log response ratio, if zero values were present in either the herbivore or the producer metric, we substituted the lowest reasonable value that could have been recorded (e.g. 1 if abundance was measured or 1% if percent cover was measured, (Poore et al. 2012). To extract these data, we used the software graphClick 3.0.3 (Arizona Software Inc., USA) to extract all the data from the qualifying studies (full data in Supplement Table S1).

2.2. Predictor variables

In addition to the population data, we collected a variety of potential quantitative and qualitative predictor variables (Supplement Table S2**)**. First, we recorded the following categorical factors related to the species involved, e.g. predator type (invertebrate N = 43, vertebrate N = 86), herbivore type (invertebrate N = 136, vertebrate N = 11), and primary producer type (macro algae N = 127, epiphytic algae N = 17, seagrass N = 3) from the study. Next, we used the World Ocean Atlas dataset, atlas resolution 1˚ x 1˚ (Levitus et al. 2013) and the site's geographic coordinates to extract: sea surface temperature (SST), nitrate concentrations, and phosphate concentrations for each data point. We excluded mesocosm studies from this analysis because the field variables, SST, nitrate concentration, and phosphate concentration, would not necessarily be representative of the conditions in the mesocosm. We recorded the body size of predators and herbivores as the maximum length in any dimension (cm) and collected the information either from the study or extracted it from the online sources (Supplement Table S1). If multiple species were present, we used the mean body size. We calculated the marine reserve age as the survey year minus the reserve foundation year. We sourced the reserve size data from the publication or the web (Supplement Table S1).

2.3. Calculation and analysis of the effect sizes

We used a meta-analytic approach to examine the direction and magnitude of the herbivore and primary producer effect sizes (i.e. strength) with and without predators. To facilitate comparison with past studies on this subject (Shurin et al. 2002, Borer et al. 2005, Poore et al. 2012, Griffin et al. 2013, Katano et al. 2015), we used the log-response ratio as the measure of effect size (Borenstein et al. 2009). However, we diverged from the two major prior studies (Shurin et al. 2002, Borer et al. 2005), and included measures of variance while calculating the effect size. It was previously thought that too much data is lost by requiring measures of variance but this is no longer the case, as only 24 data points were removed due to a lack of variance data. We used the R programming environment 3.3.3 (R Core Team 2017), the package metafor (Viechtbauer 2010) to calculate the effect sizes, and the package ggplot2 (Wickham & Chang 2008) to plot the results.

We calculated two effect sizes: 1) the herbivore effect size, which quantifies the change in the herbivore population in response to the removal or addition of a predator population, 2) the producer effect which quantifies the change in the producer population in response to the removal or addition of a predator population. A positive herbivore or producer effect size indicates an increase in the population in the presence of the predator and a negative effect size indicates a decrease. A significant herbivore effect size had a 95% CI less than 0 and a significant producer effect size had a 95% CI greater than 0. We calculated the “times” increase or decrease of the effect size by exponentiating the log-response ratio.

We analyzed the statistical significance of the predictor variables using linear mixed effects models with the rma.mv function, also found in the metafor package (Viechtbauer 2010). We used linear mixed effects models to account for the number of repeated measures used in the analysis (e.g. same study, different geographic location or species considered, N = 67). If a factor had a P value < 0.05, we tested it for significant within-group differences (e.g. study method or vertebrate Vs. invertebrate predator) using a Tukey Honest Significance test with a Bonferroni correction by using the R package multcomp (Hothorn et al. 2008). We found no statistical difference between the effect sizes of observational and experimental studies, so we analyzed all studies together. Lastly, we used the *funnel* function in metafor to test for publication bias.

2.4. Strength of trophic connection and cascades

We determined the trophic connectivity to be the relative change in the producer population given a change in the herbivore population. We calculated this metric by taking the residuals of a 1:1 regression line with the producer effect sizes greater than zero on the y-axis and the herbivore effect sizes less than zero on the x-axis. A value of 0 indicates that for every unit change in the herbivore metric, there was a proportional change in the producer metric. A negative residual signifies a smaller increase in the producer metric relative to the herbivore and a positive value indicates the opposite. We tested these values for significance using the same methods as above except using the nlme package (Pinheiro et al. 2012) in R.

Similarly, we used the nlme package in R to test whether the effect sizes from this study are significantly different than those found in Shurin et al. (2002) and Borer et al.'s (2005) work across terrestrial and aquatic systems.

3. RESULTS

Our meta-analysis yielded 147 herbivore and producer effect sizes from 39 studies, in 67 independent locations, from 13 different countries (Appendix Fig. A1).

3.1 Effect sizes

Overall, the presence of predators had significant negative effects on herbivore populations and significant positive effects on primary producer populations: herbivores decreased an average of 3.16 times (95% CI, 2.10 – 4.76, Fig. 1, Table 1) in the presence of predators, while producers increased an average of 2.13 times (95% CI, 1.62 – 2.83, Fig. 1, Table 1). We found no significant difference ($P > 0.05$, Appendix Table A1) between the effect sizes of the experimental and observational studies.

Examining the effect sizes for various subsets of our data (e.g. vertebrate VS invertebrate herbivore; Table 1), we found that the majority of these within group category effect sizes had the expected outcome, that is, herbivore declines and producer increases in the presence of predators. There were, however, three exceptions: 1) the methodology category, specifically studies that used an enclosure cage to test trophic cascades had non-significant herbivore (95% CI > 0) and producer effect sizes (95% CI < 0) (Table 1), 2) studies that had vertebrate herbivores also had non-significant herbivore effect sizes (Table 1), 3) thereafter, the only within group categories to have a non-significant producer effect size were studies in which the primary producers were either epiphytes or seagrass (Table 1).

3.2. Predictors of herbivore and primary producer effect sizes

Four factors were significant predictors of the herbivore effect size. Herbivore populations were more reduced by predators in higher temperature ecosystems ($P = 0.04$, $N = 108$, Fig. 2, Appendix Table A1), when predators were more similar in size to the herbivores, as indicated by a lower predator to herbivore size ratio ($P < 0.01$, $N = 147$, Fig. 2, Appendix Table A1), when larger bodied herbivores, such as fishes, were involved in the interaction ($P < 0.01$, $N = 147$, Fig. 2, Appendix Table A1). Finally, the study method used, whether a mesocosm, cage enclosure, enclosure, marine reserve, or observation was a statistically significant categorical predictor ($P = 0.02$, $N = 147$, Appendix Table A1), despite there being no significant within group differences ($P > 0.05$, Appendix Table S4).

Both significant predictors of the producer effect size were abiotic. Producer populations increased more when predators were present in ecosystems that had higher phosphate and nitrate levels ($P = 0.02$ and $P < 0.01$, respectively, $N = 108$, Fig. 2, Table 1). We found no significant relationship between the herbivore effect size and the producer effect size ($P > 0.05$, Fig. 2).

Within marine reserves, herbivore populations were on 3.00 times smaller and primary producer populations 1.84 times larger, on average, compared to areas outside the reserve. The size of a marine reserve did not influence the herbivore or producer effect size, whereas older marine reserves had greater reductions in herbivores compared to non-reserve areas ($P = 0.04$, $N = 59$, Fig. 4, Table 1), but had no effect on the change in the producer population.

3.3. Strength of trophic connectivity

Biotic and abiotic predictor variables affected the strength of the trophic connection, defined as the change in producer effect size given a change in the herbivore effect size. Specifically, trophic connectivity was strongest when the predator to herbivore body size ratio was high (P = 0.02, N = 82, Fig. 3, Supplement Table S3), in lower temperature environments (e.g. below 15 °C, P = 0.04, N = 82, Fig. 3, Supplement Table S3), and in systems with high phosphate and nitrate concentrations (P = 0.03 and P = 0.04, respectively, N = 82, Fig. 3, Supplement Table S3).

3.4 Comparison to past studies and systems

We found no significant difference between either the herbivore or producer effect sizes in our study and those estimated for coastal marine ecosystems in previous trophic cascade meta-analyses (P > 0.05, Fig. 5, Supplement Table S5; Shurin et al. 2002; Borer et al. 2005). However, comparing the effect sizes from our marine benthic meta-analysis to the effect sizes from other ecosystems (including marine, freshwater, and terrestrial ecosystems; Shurin et al. 2002; Borer et al. 2005), we found that the estimated herbivore effect was only significantly stronger in marine benthic than in lentic benthic ecosystems (P < 0.01, N = 12, Fig. 5, Supplement Table S5). We did not detect significant differences between ecosystems (P > 0.05) for the producer effect size.

4. DISCUSSION

Our meta-analysis, which assesses over a decade of new research compared to the two most related previous studies, provides evidence that trophic cascades have occurred in nearly all the marine systems and contexts examined, and have a variety of drivers, with differing implications for marine food web alterations. We found that whereas top-down control of herbivores was most influenced by biotic variables, control of producer populations was most influenced by abiotic factors, such as nutrients. Counter to our expectations, however, we found that changes in herbivore populations did not translate into proportional changes in producer populations. Evaluating studies involving marine reserves, a common conservation tool to increase predator populations, we found that reserve effects on predators often cascaded down to both herbivore and producer populations. Lastly, by using updated sample sizes to compare the effect sizes of our study to past work, we found that trophic controls in benthic marine systems were not as strong as previously reported. However, even with our increased dataset, there are still major geographic and taxonomic gaps that require addressing in future trophic cascade research.

4.1. Determinants of the herbivore effect size

Most of the significant predictors of herbivore effect size were biotic variables related to the size of the herbivore species involved. Our finding that larger herbivores decreased more than smaller herbivores in the presence of a predator could have arisen because larger organisms have longer generation times (Fenchel 1974), and thus may be slower to recover from predation events, such that there are larger resultant effect sizes. A second, more methodological explanation, is that when larger individuals are removed, more biomass is taken from the system and when comparing between treatment and control data points, this stark contrast between predated and non-predated data, could also have led to larger effect sizes. This explanation, however, is only correct if biomass is considered and only 24% (35 / 147) of our data points recorded herbivore populations as biomass. Nevertheless, future trophic interaction research could standardize predation events by body size to help account for this potentially confounding factor. As predicted, we found that predators reduced herbivores more when they were similar in size (as indicated by a smaller predator-prey mass ratio). Previous research (Vucic-Pestic et al. 2010) suggests species similar in size are more likely to have a trophic interaction than those that are significantly different. Past trophic cascade meta-analyses have not examined this relationship so we cannot compare our results in this context. However, predator size, a component of the ratio, had no significant influence on the herbivore effect size, suggesting that herbivore body size is more influential in this interaction. Consequently, we would expect that larger herbivores, that are more similar in size to their predators will be most affected by any future predator introductions. Past studies (Griffin et al. 2013, Gamfeldt et al. 2015) also found that biotic factors, including predator species richness (which we were unable to include due to limited sample size), were better predictors of the predator-herbivore connection than abiotic factors.

We also found that herbivores were most affected by predators in high temperature environments, likely due to increased metabolic demands and consumption rates. Consequently, herbivores are more likely to increase following a predator removal in warmer waters but as we see in our study, changes in herbivore populations have more effect on producers in cooler waters. Other meta-analyses have shown that increased temperatures can increase the strength of trophic cascades in aquatic ecosystems (Kratina et al. 2012) but that the strength will increase proportionately more in colder ecosystems (Marino et al. 2018). Therefore, increased temperatures should result in higher predator impacts on herbivores, and potentially mixed predator effects on producer populations.

4.2. Determinants of the producer effect size

Contrary to herbivores, we found that abiotic factors were the best predictors of the effect size for producers. As predicted (Oksanen et al. 1981, Jeppesen et al. 2003, Östman et al. 2016), predator presence had the most positive effect on producer populations in high nutrient environments, where nutrients are not limiting, and producer populations are more likely top down controlled. Moreover, these conditions are often found in ecosystems with lower species diversity (Edgar et al. 2017), where the manipulation of a single species should have a greater effect (Rodríguez-Castañeda 2013). Poore et al. (2012) found the same result for the herbivore-producer trophic link and hypothesized that it was due to greater primary productivity and higher standing stock producer biomass. As a result, the rate of production outpaces the rate of consumption and there is a greater contrast between the grazed and un-grazed plots. These explanations are not mutually exclusive but as with the herbivore effect size, future research should seek to standardize measures of producer populations by growth or production rates. Therefore, we would expect predator introductions or marine reserves to have the most positive effects in high nutrient ecosystems and we may expect strong trophic cascades in regions with increased nutrient loading, such as those near cities, agricultural areas, or aquaculture facilities (Gowen 1994, Bennett et al. 2001).

4.3. Trophic connectivity

Contrary to expectation, the strength of herbivore and primary producer responses to predator presence was unrelated. As a result, some minor modifications to food webs had large reverberations, and conversely, large shifts in herbivore populations did not always proportionately influence producer populations. What determines the former as opposed to the latter will depend on the trophic connection between the herbivore and producer (Duffy et al.

2007, van Veen & Sanders 2013, Heath et al. 2014). Using a new trophic connectivity metric, we showed strong trophic connectivity in high nutrient systems and weak connectivity in high temperature ecosystems. As such, we expect there to be greater increases of producer populations in response to herbivore population declines in estuarine systems, which receive large inputs of nutrients from land runoff and river outflow (Cloern et al. 2014). With regards to temperature, warmer marine ecosystems typically have more fish and invertebrate species (Tittensor et al. 2010) and as a result, there are potentially more trophic connections and less reliance on a single interaction which should result in lower connectivity (Griffin et al. 2013). These inferences are speculative, but the trophic connectivity metric provides a new approach to analyzing trophic cascade data and assessing ecological controls.

4.4. Marine reserves and trophic cascades

While numerous studies have reported positive effects of marine reserves on restoration of predatory fish populations (e.g. Lester et al. 2009, Edgar et al. 2014), few studies have examined the effect of marine reserves on herbivores and primary producer populations. Our work counters the results of Gilby & Stevens (2014), which had limited sample sizes for temperate kelp ecosystems (N = 5 for producers) and found no effect of reserves on either herbivore or algae populations. Instead, we found herbivores decreased on average 3.00 times, and producers increased 1.84 times within reserves compared to outside, numbers that are comparable to studies that used enclosure cages, exclusion cages, or mesocosms to directly manipulate predator populations. Moreover, if potential confounding variables, such as spillover benefits to herbivore populations (e.g. higher habitat quality or lower pollution levels inside reserves; Jamieson & Levings 2001) and illegal poaching from the reserve (Byers & Noonburg

2007) are considered, it is even more notable that reserves have such a significant effect on producer populations. Despite the importance of producer or habitat forming species in marine ecosystems, the planning process for marine reserves does not typically consider producer populations and instead tends to focus on fishes and macroinvertebrates (Woodcock et al. 2017). As a result, there is space to incorporate a more complex ecosystem perspective and begin to plan and evaluate reserves based upon their ability to protect critically important primary producer populations. Nevertheless, we want to emphasize that a marine reserve is not necessarily a solution to habitat loss in all marine systems, only in those linked to predator loss and those absent of other stressors. Within these contexts, marine reserves may be more effective in low temperature, high nutrient ecosystems. Future efforts to restore marine species in warmer temperature or lower nutrient concentration environments could focus on both installing the marine reserve to restore predator populations and working on active restoration to restore the producer populations (Eger et al. 2020).

The mechanisms that make marine reserves more or less effective at restoring populations is the subject of ongoing research (Lester et al. 2009, Molloy et al. 2009, Di Franco et al. 2016), and our work provides some insight into the reserve characteristics that influence trophic interactions. We found that reserve size had no influence on effect size, while reserve age was significantly and positively correlated with the herbivore effect size. Consequently, and as has been found with predator populations (Lester et al. 2009), when seeking to restore predator-herbivore dynamics, bigger is not necessarily better. And while we found strong evidence that marine reserves also impact the herbivore and producer populations, these effects increased over time so managers should not expect immediate effects. Because we found no connection between the size of the herbivore effect size and the size of producer effect size, it is not necessarily surprising that there were marginal benefits to the producer populations as the reserve age increased. It is also possible, that because of their extremely quick growth rates (Ramus 1992, Reed et al. 2009), algae may quickly respond to reduced herbivory rates, and thus there is no relationship with time. Past work has shown that no-take reserves are most effective at restoring fished populations, (Sala & Giakoumi 2018) and this finding could theoretically extend to lower trophic levels. Unfortunately, there was limited variation in the protection levels of marine reserves in our analysis so that we were unable to robustly test this question.

4.5. Trophic cascades in marine systems

Our findings were qualitatively consistent with previous marine meta-analyses, including those focused on coastal marine ecosystems specifically, of trophic controls and cascades (Shurin et al. 2002, Borer et al. 2005, Griffin et al. 2013, Katano et al. 2015, Östman et al. 2016). However, our estimate of herbivore declines in the presence of predators (3.16 times on average) was larger than that of Katano et al. (2015; 2.50 times decrease), and our estimate of producer increases (2.14 times) was smaller than the 3.1 times estimated in Poore et al's (2012) examination of coastal marine systems when herbivores were directly removed. Katano et al.'s (2015) study had a much higher sample size (N = 293) than our study because its selection criteria only required there to be data on herbivore responses to predators, which could account for the lower overall effect size, as we found when comparing our work to previous studies (see below). Poore et al. (2012) focused on the direct trophic link between herbivores and producers, and we suggest our results may be lower because of the "trophic trickle" (Halaj & Wise 2001), meaning that trophic effects are attenuated with the addition of trophic levels. Contrary to earlier cross-ecosystem studies (Shurin et al. 2002, Borer et al. 2005), and a more recent but limited analysis (Atwood & Hammill 2018), we found very little differentiation within different categories, such as invertebrates compared to vertebrates. Only four within-group factors, typically with low sample sizes, had non-significant effect sizes (producer effect size 95% CI < 0 or herbivore effect size 95% CI > 0), and categorical factors were not predictors of cascade strength. Consequently, our findings suggest that trophic cascades are important ecological interactions in most coastal benthic marine ecosystems, regardless of species taxonomy. There are, however, some exceptions to our work as we did not include studies with omnivorous predators, which can dampen the strength of cascades (Bruno & O'Connor 2005), or trait-mediated cascades which are non-consumptive (Burkholder et al. 2013).

Our synthesis is, to the best of our knowledge, the first to show that trophic cascades in coastal marine systems are not inherently stronger than those in other ecosystems. We suggest that this finding is a result of an increased sample size and additional ecological contexts of the synthesized studies compared to earlier work. For example, we included data from a variety of habitats (coral reef, kelp, mudflat, rocky intertidal saltmarsh, seagrass, and shallow benthic), a wide range of geographic locations (Appendix Fig. A1), and a mix of observational and experimental research (79 and 68 data points, respectively). These additional contexts are significantly expanded from the initial syntheses by Shurin et al. (2002), and Borer et al. (2005). It is also plausible that the increased sample size, which added several studies with null or negative results, resulted in a lower overall effect size (Fig. 5). As a result, we can conclude that while strong trophic cascades appear to be common in coastal marine systems, they are not guaranteed and counter-intuitive results can still arise. For example, Cardona (2006) found that temporal patterns in predation and size dependent predation relationships could “uncouple” trophic cascades, and producer populations were reduced in the presence of predators in a coastal marsh ecosystem.

4.6. Observational versus experimental studies

Interestingly, we found no significant difference between the effect sizes of experimental and observational studies. While previous studies have suggested that observational studies are too complex or contain too many confounding variables to allow for robust testing of theoretical principles (Sagarin & Pauchard 2012) our results suggest that natural experiments and observations can provide similar conclusions compared to those from traditional experimental research. Our findings provide additional support for natural experiments (Davies & Gray 2015) and should increase the confidence with which ecologists can test an ecological theory at large scales and with little or no experimental manipulation.

4.7. Data gaps

Despite synthesizing the results from 147 data points, there remain significant gaps in multiple data categories that prevent the synthesis of a truly balanced dataset. Whereas experimental study locations were all located in Europe and the United States of America (USA), most observational studies occurred in other regions of the world (namely the Caribbean, SE Australasia, and E Africa). No studies were recorded in South America, Asia, or Antarctica (Appendix Fig. A1). Future studies should seek to address these geographical biases. Naturally, these biases also extend to the abiotic variables associated with those regions. More work should be conducted in regions with high nutrient concentrations or high sea surface temperatures (Fig.

2). Two notable biotic gaps exist as well. First, as was the case with Borer et al.'s (2005) analysis, very few vertebrate herbivores such as fish were examined in this study (11 / 147), and the majority of the studies examined macroalgae as the producer (127 / 147), with seagrass particularly under-examined (3 / 147) (see Table S1; for all sample sizes). Because of these gaps, we present our results as an update of our understanding of cascades in coastal marine systems and challenge future research to work to address these limitations.

4.8. Conclusion

We are in a period of unprecedented human activity in our world's oceans and much of this activity impacts predator populations. Our work advances understanding of the consequences of predator loss and the circumstances under which predator removals or additions will have the greatest ecosystem effects. Marine protected areas, which are often aimed at restoring predatory species, can also positively affect lower trophic levels and can aid in full ecosystem recovery. Our study updates our understanding of trophic connections in marine systems, which are often understudied compared to terrestrial ecosystems, and indeed it counters the concept that marine trophic cascades are stronger than those on land. As such we highlight the importance of revisiting ecological paradigms with updated data sets and note several important data gaps within our study. Future research can build on this study not only by filling the data gaps denoted above, but also by evaluating more nuanced predator effects, such as varying predator densities (instead of simply presence vs. absence) and species numbers, and including non-consumptive effects, thereby allowing for even more informed management decisions about coastal marine food webs.

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Figure 1: Schematic showing three trophic levels with examples of marine predators, herbivores, and primary producers, with positive (blue) and negative (dashed red) relationships amongst them. Numbers are the 95% confidence intervals of the mean herbivore decrease and mean producer increase in the presence of predators as found in the meta-analysis.

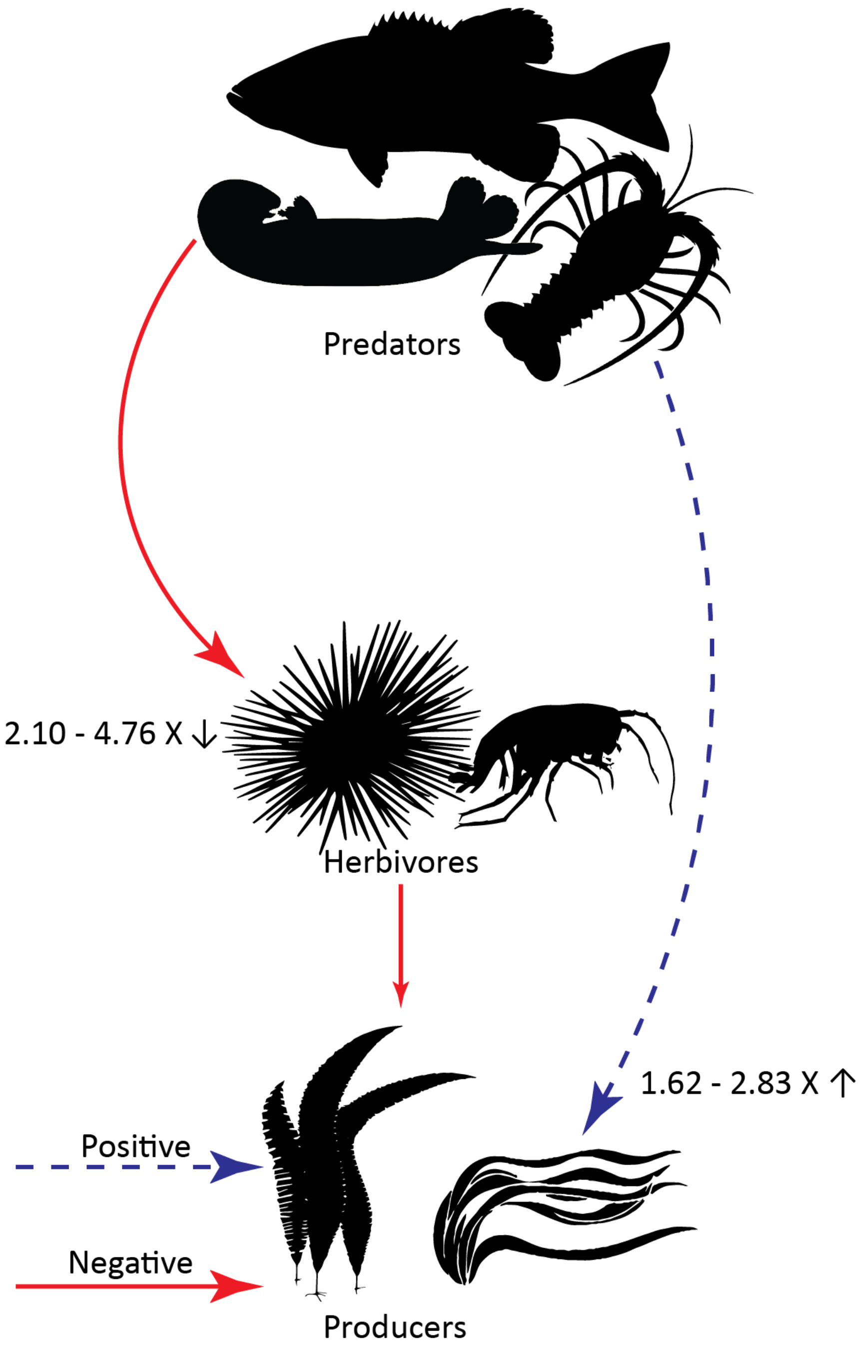


Figure 2: Herbivore (left) and producer (right) effect sizes versus explanatory variables, significant ($P < 0.05$) relationships are indicated with the black lines. In each panel, the solid line is the predicted value and the thin dashed lines are twice the standard error for significant relationships. The thick dashed line in the bottom right panel represents the 1:1 ratio between the herbivore and producer effect size. *Indicates a variable that was log-transformed for analysis.

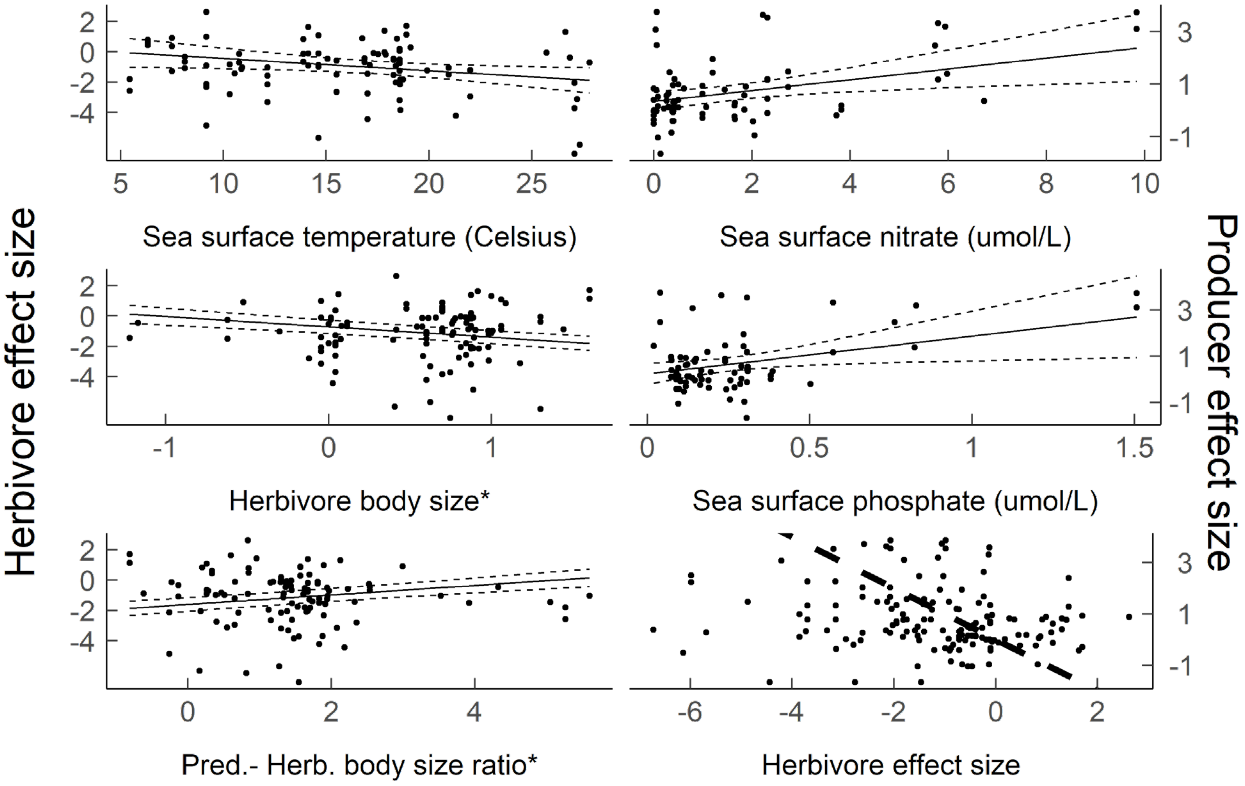


Figure 3: Trophic connectivity versus significant explanatory variables. In each panel, the solid line is the predicted value and the dashed lines are twice the standard error for significant relationships ($P < 0.05$). *Indicates a variable that was log-transformed for analysis.

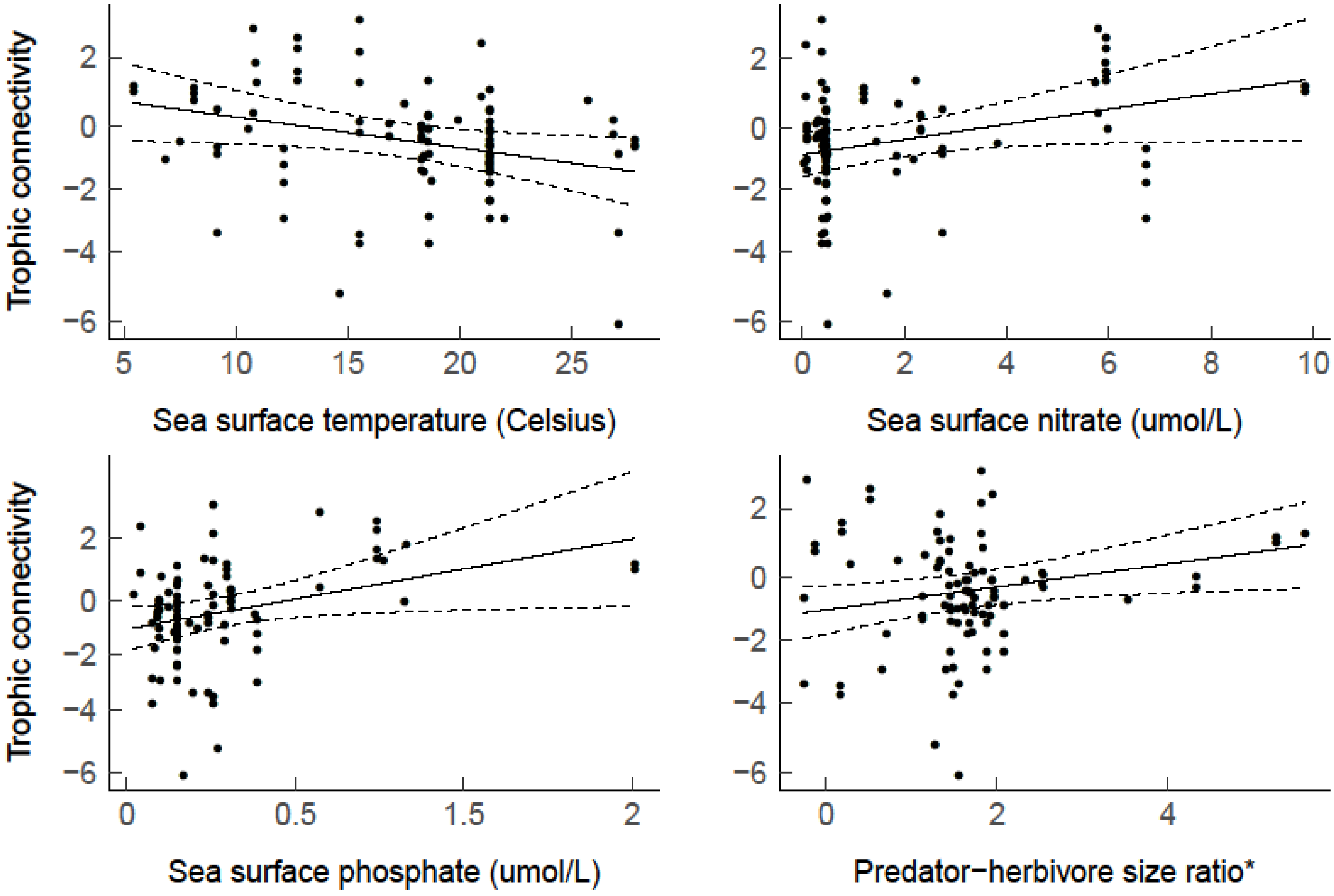


Figure 4: Herbivore (top) and producer (bottom) effect sizes versus marine reserve age and size. The solid line is the predicted value and the dashed lines are twice the standard error for significant relationships ($P < 0.05$). *Indicates a variable that was log-transformed for analysis.

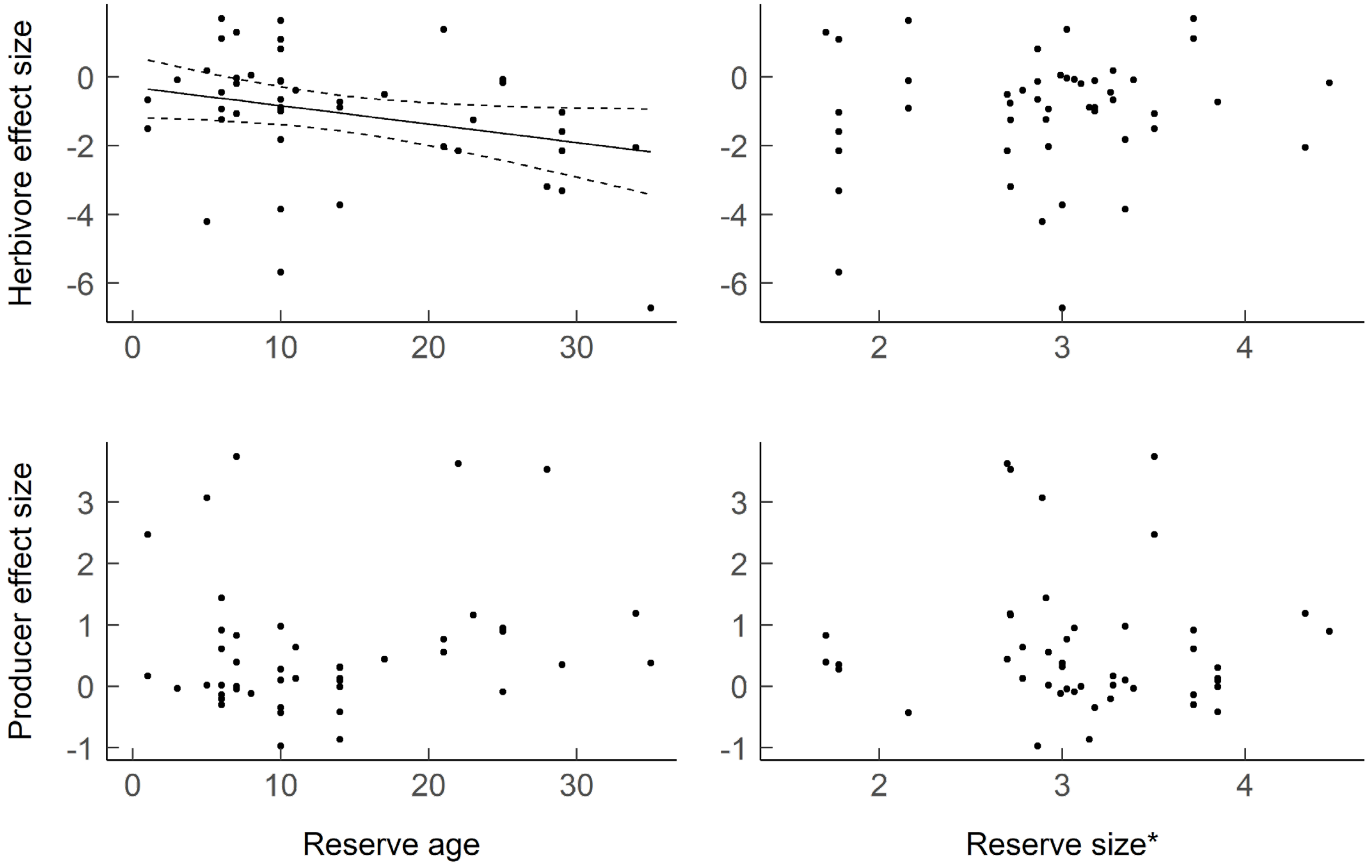


Figure 5: Histograms of the effect sizes from the current study and the effect sizes of the benthic marine studies used in Shurin et al.'s (2002) and Borer et al.'s (2005) work. Dashed grey lines indicate the non-significant effect size, while the solid black line is the mean effect size from the present study and the dashed black line is the mean effect size from previous related meta-analyses (top: Shurin et al. (2002); bottom: Borer et al. (2005)). N equals the number of measurements.

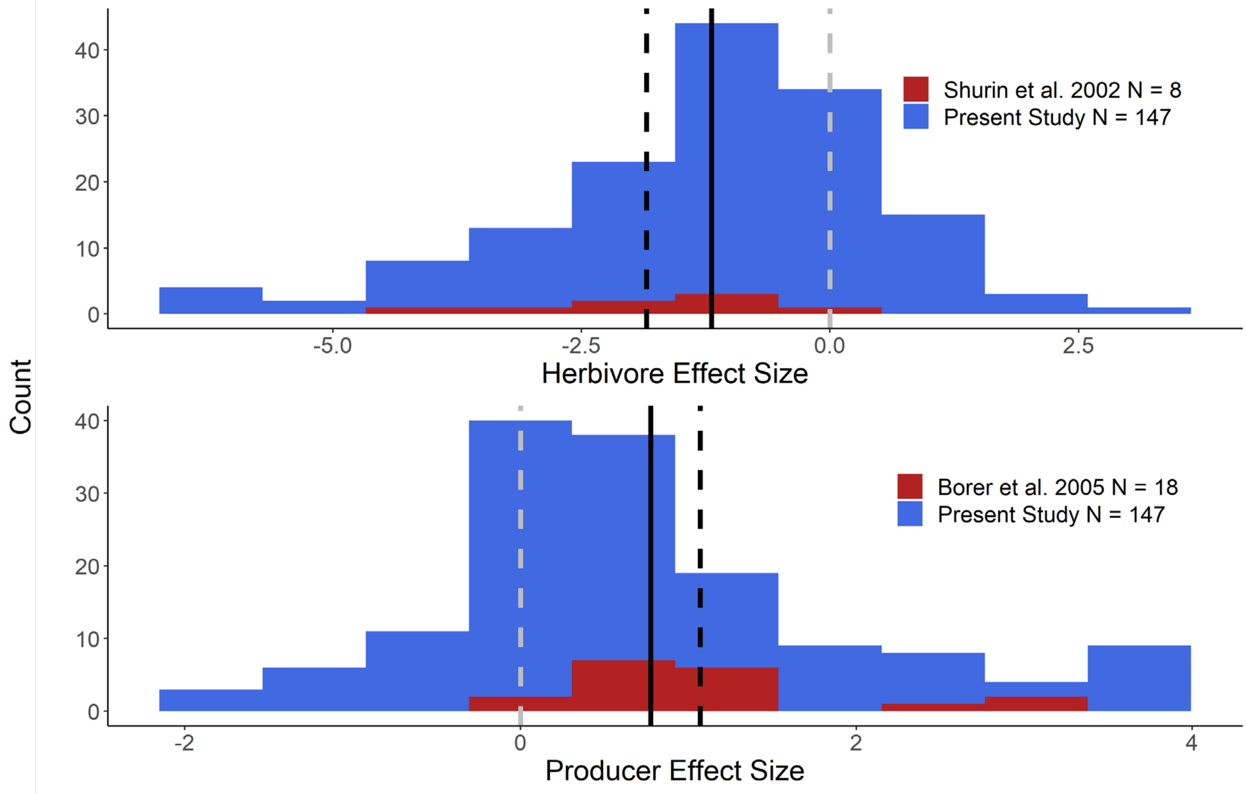
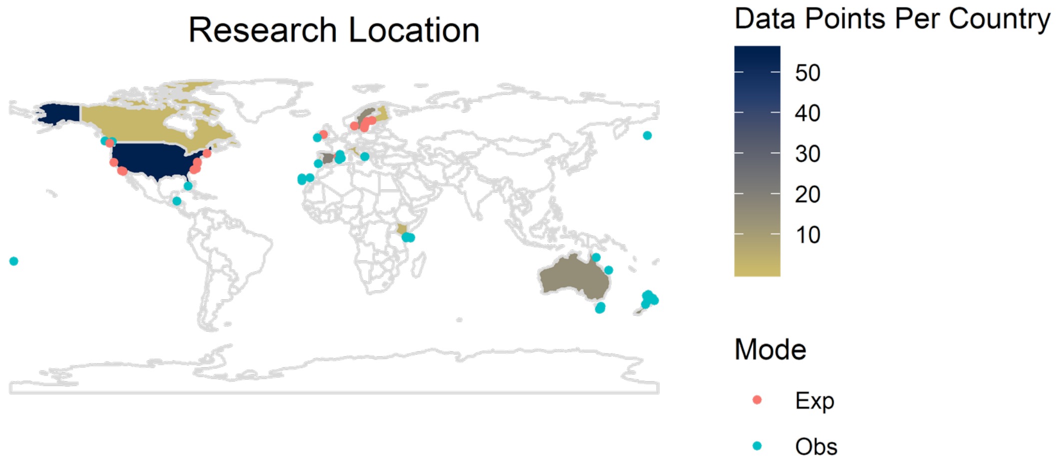


Table 1: Mean effect sizes (herbivore and producer) with the upper (Ub) and lower (Lb) boundaries of 95% confidence intervals as broken down by within-group categories. An italicized value indicates a non-significant effect size.

	Producer effect size			Herbivore effect size		
Factor	Mean	Ub	Lb	Mean	Ub	Lb
Species Types						
Predator: invertebrate	0.80	1.30	0.3	-1.25	-0.52	-1.98
Predator: vertebrate	0.74	1.08	0.4	-1.10	-0.60	-1.60
Herbivore: invertebrate	0.76	1.04	0.48	-1.18	-0.77	-1.60
Herbivore: vertebrate	0.76	1.07	0.46	*-0.62*	*0.68*	*-1.93*
Producer: epiphyte	*0.43*	*1.12*	*-0.25*	-1.15	-0.63	-1.67
Producer: macro	0.81	1.10	0.52	-1.14	-0.73	-1.55
Producer: seagrass	*0.53*	*1.71*	*-0.64*	-1.26	-0.67	-1.85
Study Method						
Enclosure	*0.47*	*1.14*	*-0.19*	*0.07*	*1.14*	*-1.01*
Exclusion	0.83	1.50	0.16	-1.69	-0.58	-2.79
Marine reserve	0.61	0.98	0.24	-1.10	-0.52	-1.68
Mesocosm	1.29	1.99	0.59	-1.63	-0.56	-2.70
Observation	0.98	1.88	0.08	-1.47	-0.05	-2.89
Study Type						
Experimental	0.93	1.40	0.46	-1.14	-0.46	-1.82
Observational	0.67	1.01	0.32	-1.15	-0.63	-1.67
Overall	0.76	1.04	0.48	-1.15	-0.74	-1.56

APPENDIX

Appendix Figure A1: Location of the studies included in this analysis. The dark to light color scale shows the number of studies per country while the red or blue dots indicate an observational (Obs) or experimental (Exp) study. N is the number of measurements, 147 in total.



Appendix Table A1: Results of the linear mixed-effects models between the various predictor variables and the herbivore and producer effect sizes. Bolded entries are statistically significant (P < 0.05), SE = standard error, "Int." indicates the model intercept.

		Producer effect size			Herbivore effect size		
Factor	N	Estimate	SE	P value	Estimate	SE	P value
Biotic and Abiotic							
Herbivore: invertebrate (Int.)	136	0.82	0.16	0.90	-1.28	0.23	0.63
Herbivore: vertebrate	11	0.01	0.07	0.90	0.39	0.82	0.63
Herbivore size	147	0.01	0.04	0.91	**-0.69**	**0.12**	**< 0.01**
Nitrate	108	**0.20**	**0.08**	**< 0.01**	< 0.001	0.12	1.00
Phosphate	108	**1.63**	**0.71**	**0.02**	-0.502	0.99	0.61
Predator-herbivore size ratio	147	0.00	0.02	0.98	**0.01**	**0.00**	**< 0.01**

Predator: invertebrate (Int.)	43	0.80	0.25	0.85	-1.50	0.43	0.51
Predator: vertebrate	86	-0.06	0.31	0.85	0.34	0.51	0.51
Predator size	147	0.13	0.23	0.58	0.10	0.48	0.84
Producer: epiphyte (Int.)	17	0.40	0.38	0.53	-1.27	0.28	0.97
Producer: macro	127	0.48	0.38	0.53	0.01	0.18	0.97
Producer: seagrass	3	0.18	0.72	0.53	-0.10	0.30	0.97
Study duration	75	0.07	0.59	0.91	0.53	0.74	0.47
Temperature	108	-0.04	0.03	0.15	**-0.09**	**0.04**	**0.04**
Study Method							
Enclosure (Int.)	24	0.48	0.34	0.28	**-0.07**	**0.55**	**0.02**
Exclusion	16	0.35	0.25	0.28	**-1.76**	**0.55**	**0.02**
Marine reserve	60	0.14	0.39	0.28	**-1.17**	**0.62**	**0.02**
Mesocosm	39	0.82	0.50	0.28	**-1.70**	**0.77**	**0.02**
Observation	8	0.51	0.57	0.28	**-1.54**	**0.91**	**0.02**
Study Type							
Experimental	79	0.93	0.24	0.37	-1.14	0.35	0.98
Observational	68	-0.27	0.30	0.37	-0.01	0.44	0.98
Reserve Characteristics							
Reserve age	59	0.43	0.322	0.42	**-0.05**	**0.03**	**0.04**
Reserve size	59	0.11	0.45	0.74	0.44	0.45	0.32