Contribution to the Theme Section 'The ecology of temperate reefs in a changing world'

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

Aaron M. Eger[1,2,*], Julia K. Baum[1]

[1]University of Victoria, Department of Biology, PO Box 1700 STN CSC, Victoria, BC, V8W 2Y2, Canada

[2]*Present address:* School of Biological, Earth, and Environmental Sciences, University of New South Wales, Sydney, NSW 2033, Australia

ABSTRACT: Predators can exert top-down control on lower trophic levels, such that their removal or addition may trigger trophic cascades. Despite coastal ecosystems containing well known trophic cascades, there remains uncertainty about the abiotic and biotic factors governing the occurrence and strength of these cascades. Here, we sought 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 predator. From these data (147 predator–herbivore–producer measurements), we show that predators decreased herbivore populations between 2.1–4.76 times and increased producer populations by 1.62–2.83 times their original biomass, abundance, or density. Contrary to past research, these values are comparable to other ecosystems. Biotic factors related to species body size were most influential in determining herbivore population responses to the presence of predators, while abiotic factors, including nutrient concentration, best determined producer population responses. Our results also show that producers responded more strongly to changes in herbivore populations in high-nutrient and low-temperature environments. We found that herbivore populations in marine reserves were 2.83 times lower on average compared to areas outside the reserve, while producer populations were on average 1.90 times higher. Overall, this work advances understanding of factors modulating trophic cascade strength, demonstrates that reserves can have ecosystem-wide impacts, and provides new information about the average strength of trophic cascades in benthic marine ecosystems.

KEY WORDS: Trophic cascade · Marine ecology · Meta-analysis · Marine reserve · Trophic control

1. INTRODUCTION

Marine predator populations often play important roles in maintaining the ecological function and ecosystem services of coastal systems. Predators such as lobsters (Ling et al. 2009), fishes (Caselle et al. 2018), and sea otters (Estes & Palmisano 1974) can exert top-down control on herbivores and indirectly support foundation species such as kelp, seagrasses, and other macroalgae, if these were being 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 harvested 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 are reintroduced or conserved via management strategies such as 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 of 102 data points in Shurin et al.'s 2002 work and 18 of 210 in Borer et al.'s 2005 updated analysis) and found 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 progress in analyzing 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, predator reintroductions, or to what extent marine reserves, which often restore predator populations, cause cascading effects in ecosystems (Hessen & Kaartvedt 2014, He & Silliman 2016).

Marine reserves are a well-recognized 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 change, competition, and consumption-based disturbances (Olds et al. 2014). In the context of ecological theory, researchers can use marine reserves to test ecological principles at the spatial scale of natural ecosystems, a criticism that is sometimes levelled at small-scale experimental studies (Meentemeyer & Box 1987). To test 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 population shifts in the protected-area studies will be smaller than in controlled, experimental research (Hillebrand 2009), but could nonetheless 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 previously found with predator recoveries (Lester et al. 2009).

The occurrence and strength of trophic cascades are context-dependent and may hinge on various biotic and/or abiotic factors, as well as the ecosystem type or study design (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 focused our investigation on 2 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. While past investigations on biotic factors have focused on predator diversity and degrees of omnivory (Bruno & O'Connor 2005, Katano et al. 2015), 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 is the link between a shift in one trophic level and an adjacent one, i.e. how a shift in the herbivore population results in a shift in a linked producer population (Duffy 2002).

In this study, we conducted a global meta-analysis of peer-reviewed literature on trophic cascades in

coastal benthic marine ecosystems to synthesize current understanding of (1) their strengths, (2) their biotic and abiotic drivers, and (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 2 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 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 2 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 23 February and 10 March 2016,

with renewed searches conducted between 22 and 26 September 2018 to update the results. The WOS searches cumulatively and respectively yielded 821 and 1931 papers 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 3 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 a study if it explicitly examined an omnivorous predator that fed on both herbivores and producers and would confound the effects of the predator 'treatment' (Heck 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 have either confounded the effect being tested or not 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 1 mo 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 for the mean and standard deviation of herbivore and producer populations with and without predator populations. 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 Section 2.3). Similarly, we recorded separate entries from the same study if it examined multiple locations or distinct time points (see Section 2.3). 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 v.3.0.3 (Arizona Software) to extract all the data from the qualifying studies (full data in Table S1 in the Supplement at www.int-res. com/articles/suppl/m656p139_supp.xlsx).

2.2. Predictor variables

In addition to the population data, we collected a variety of potential quantitative and qualitative predictor variables (Table S2). First, we recorded the following categorical factors related to the study species involved, e.g. predator type (invertebrate, n = 51; vertebrate, n = 96), herbivore type (invertebrate, n = 136; vertebrate, n = 11), and primary producer type (macro algae, n = 127; epiphytic algae, n = 17; seagrass n = 3). Next, we used the World Ocean Atlas data set, atlas resolution 1 × 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 (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 (Table S1).

2.3. Calculation and analysis of 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 2 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 would be lost by requiring measures of variance, but this is no longer the case: we found that only 24 data points needed to be removed because they lacked an estimate of variance (and 147 remained). We used the R v.3.3.3 (R Core Team 2017) package metafor (Viechtbauer 2010) to calculate the effect sizes and the package 'ggplot2' (Wickham & Chang 2008) to plot the results.

We calculated 2 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, and (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 < 0 and a significant producer effect size had a 95% CI > 0. We calculated the 'times' increase or decrease (e.g. 2 times the original abundance) of the treatment compared to the control (i.e. 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 in which the 'observation ID' was a random effect, 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 p < 0.05, we tested it for significant within-group differences (e.g. study method or vertebrate vs. invertebrate predator) with a Tukey's HSD 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.
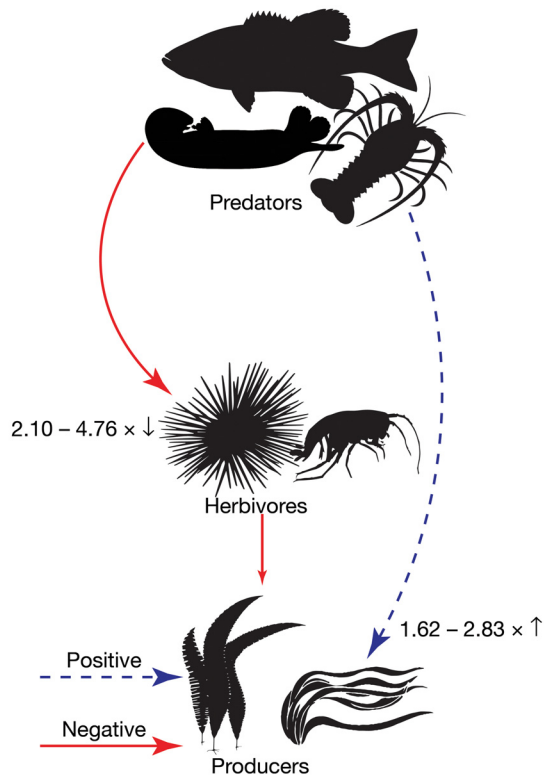
Fig. 1. Schematic showing 3 trophic levels with examples of marine predators, herbivores, and primary producers, with positive and negative relationships amongst them. Numbers are the 95% CIs of the mean herbivore decrease and mean producer increase in the presence of predators as found in the meta-analysis

work across terrestrial and aquatic systems. Our data and code are available open access at https://github.com/baumlab/Eger_etal_2020_MEPS_TrophicCascadesMetaanalysis.

3. RESULTS

Our meta-analysis yielded 147 herbivore and producer effect sizes that met all of our data extraction requirements. These data came from 39 studies in 67 independent locations from 13 different countries (Fig. A1 in the Appendix).

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 2.14 times (95% CI, 1.62–2.83; Fig. 1, Table 1). We found no significant difference ($p > 0.05$; Table A1) between the effect sizes of the experimental studies and observational marine reserve studies.

We found that the majority of within-group effect sizes (e.g. vertebrate vs. invertebrate herbivore;

2.4. Strength of trophic connection and cascades

We determined the trophic connectivity (Polis 1991, Duffy 2002) 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 >0 on the y-axis and the herbivore effect sizes <0 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; 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 were significantly different than those found in Shurin et al. (2002) and Borer et al.'s (2005)

Table 1. Mean effect sizes (herbivore and producer) with the upper (Ub) and lower (Lb) boundaries of 95% CIs as broken down by within group categories. **Bold** values indicate a non-significant effect size

Factor	Producer effect size			Herbivore effect size		
	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	**0.48**	**1.15**	**−0.20**	**0.06**	**1.13**	**−1.00**
Exclusion	0.83	1.50	0.16	−1.68	−0.58	−2.78
Marine reserve	0.64	1.02	0.27	−1.04	−0.45	−1.62
Mesocosm	1.29	2.00	0.59	−1.63	−0.57	−2.69
Observation	0.78	1.62	0.05	−1.72	−0.41	−3.02
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

Table 1) had the expected outcome of herbivore declines and producer increases in the presence of predators. There were, however, 3 exceptions: (1) 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), and (3) studies in which the primary producers were either epiphytes or seagrass were the only within-group categories to have a non-significant producer effect size (Table 1).

3.2. Predictors of herbivore and primary producer effect sizes

Four factors were significant predictors of herbivore effect size. Herbivore populations were more reduced by predators in higher temperature ecosystems (p = 0.04, n = 108; Fig. 2a, 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. 2e, Table A1), and when larger bodied herbivores, such as fishes, were involved in the interaction (p < 0.01, n = 147; Table A1). Finally, the study method used, whether a mesocosm, cage enclosure, enclosure, marine re-

serve, or observation was a statistically significant categorical predictor (p = 0.02, n = 147; Table A1), despite there being no significant within-category differences (p > 0.05; Table S4).

Both significant predictors of the producer effect size were abiotic nutrients. 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. 2b,d, Table A1). We found no significant relationship between the herbivore effect size and the producer effect size (p > 0.05; Fig. 2f).

Within marine reserves, herbivore populations were 2.83 times smaller and primary producer populations 1.90 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. However, older marine reserves had greater reductions in herbivores compared to non-reserve areas (p = 0.047, n = 59; Fig. 3a, Table A1), despite reserve age not affecting the producer population.

3.3. Strength of trophic connectivity

Biotic and abiotic predictor variables affected trophic connectivity strength, defined as the change in producer effect size given a change in herbivore
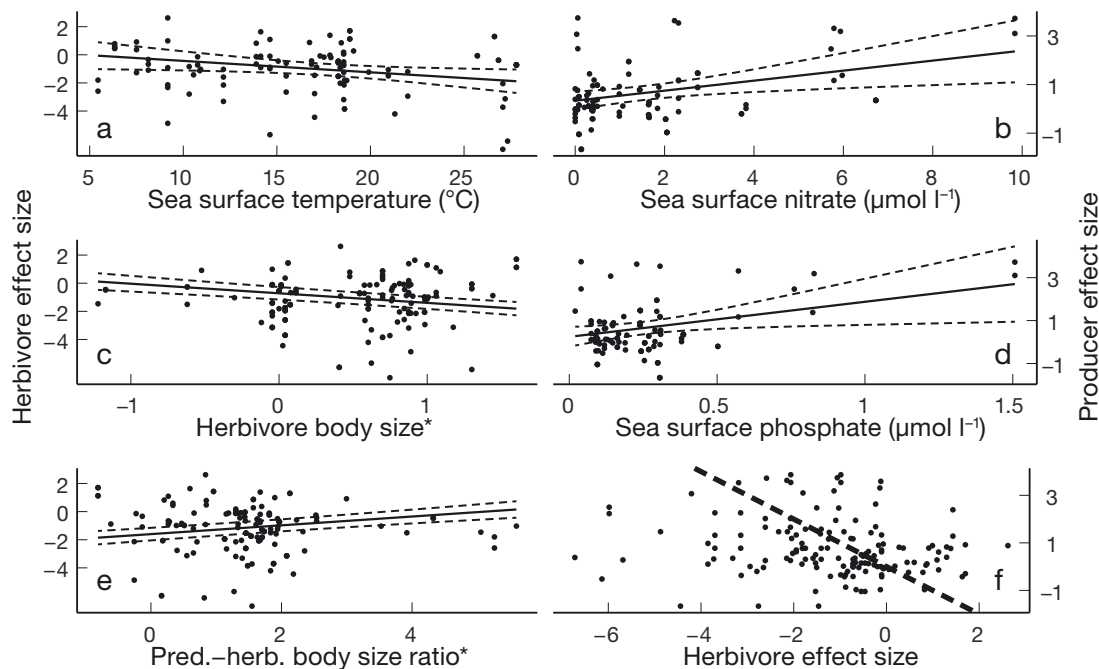

Fig. 2. (a,c,e) Herbivore and (b,d,f) producer effect sizes versus explanatory variables. Black lines: significant (p < 0.05) relationships; solid lines: predicted values; thin dashed lines: twice the standard error for significant relationships. Thick dashed line in (f): the 1:1 ratio between the herbivore and producer effect size. (*) Indicates a variable that was log-transformed for analysis
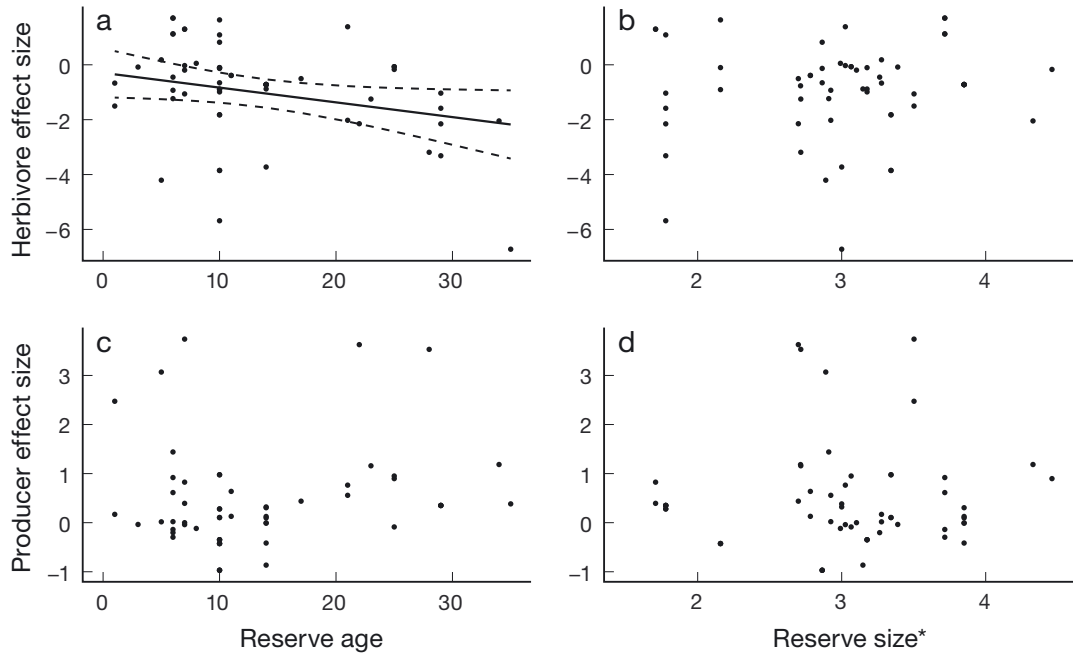
Fig. 3. (a,b) Herbivore and (c,d) producer effect sizes versus marine reserve age and size. Solid line: predicted value; dashed lines: twice the standard error for significant relationships (p < 0.05). (*) Indicates a variable that was log-transformed for analysis

effect size. Specifically, trophic connectivity was strongest when the predator to herbivore body size ratio was high (p = 0.03, n = 91; Fig. 4d, Table S3), in lower temperature environments (e.g. below 15°C,

p = 0.04, n = 91; Fig. 4a, Table S3), and in systems with high phosphate and nitrate concentrations (p = 0.03 and p = 0.04, respectively, n = 91; Fig. 4b,c, Table S3).
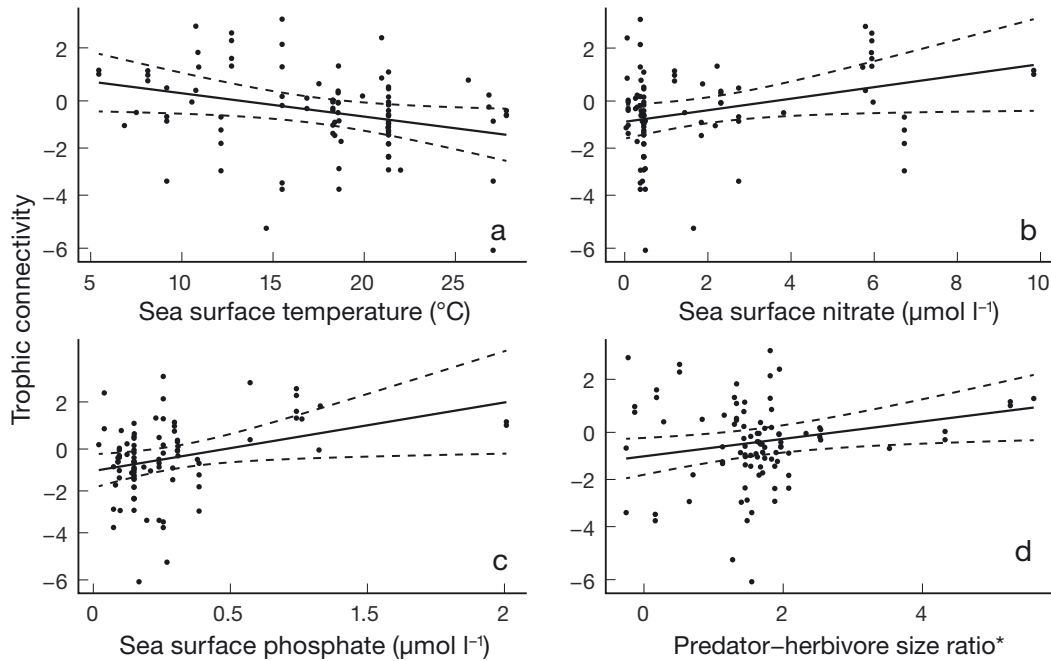

Fig. 4. Trophic connectivity versus significant explanatory variables: (a) sea surface temperature, (b) sea surface nitrate, (c) sea surface phosphate, and (d) predator–herbivore size ratio. Solid lines: predicted value; dashed lines: twice the standard error for significant relationships (p < 0.05). (*) Indicates a variable that was log-transformed for analysis
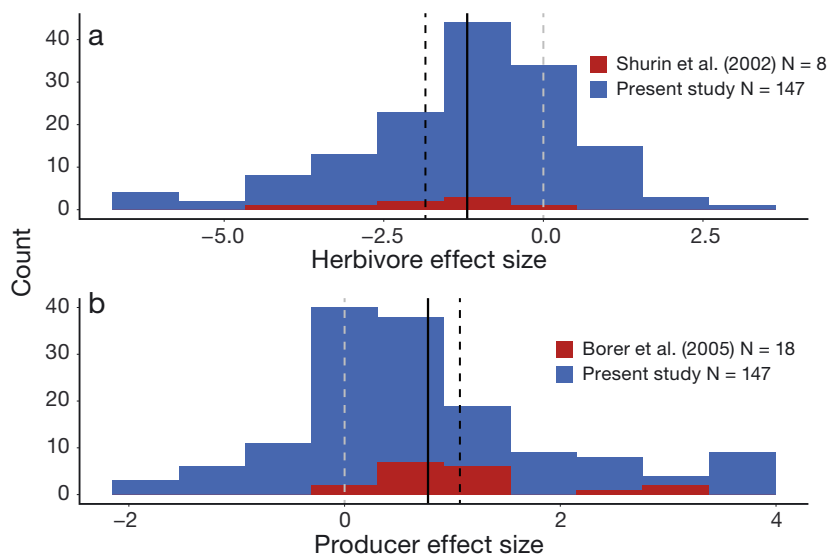
Fig. 5. Effect sizes from the current study and the effect sizes of the benthic marine studies used in (a) Shurin et al. (2002) and (b) Borer et al. (2005). Dashed grey lines: non-significant effect size; solid black lines: mean effect size from the present study; dashed black lines: mean effect size from previous related meta-analyses. N: number of measurements

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 data set, there are still major geographic and taxonomic gaps that require addressing in future trophic cascade research.

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. 5a,b, Table S5; Shurin et al. 2002, Borer et al. 2005). 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 compared to lentic benthic ecosystems (p < 0.01, n = 12; Fig. 5a,b, Table S5). We did not detect significant differences between ecosystems (p > 0.05) for the producer effect size.

4. DISCUSSION

Our meta-analysis, which assessed over a decade of new research compared to the 2 most closely related previous studies, provides evidence that trophic cascades have occurred in nearly all the coastal 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

4.1. Determinants of herbivore effect size

The majority of 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 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 predation and non-predation data could also have led to larger effect sizes. This explanation, however, is only relevant when biomass is considered in the study, and only 24% (35 of 147) of our data points recorded herbivore populations in this manner. 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 suggests species similar in size are more likely to have a trophic interaction than those that are significantly different (Vucic-Pestic et al.

2010). 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 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 predators had a greater impact on herbivore populations in high-temperature environments, likely because of increased metabolic demands and consumption rates. Consequently, our results suggest that herbivores are more likely to increase following a predator removal in warmer waters. In contrast, our analyses revealed that changes in herbivore populations have more effect on producers in cooler waters (see below). 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 producer effect size

Contrary to herbivores, which were strongly influenced by biotic factors, we found that producer populations were only influenced by abiotic factors. As predicted, 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 (Oksanen et al. 1981, Jeppesen et al. 2003, Östman et al. 2016). 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 outpaced the rate of consumption and there was a greater contrast between grazed and un-grazed plots. These explanations are not mutually exclusive but, as with 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 on producers 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 were unrelated. As a result, while some minor modifications to food webs had large reverberations across both trophic levels, large shifts in herbivore populations did not always proportionately influence producer populations, and conversely, small shifts in herbivore populations sometimes were accompanied by large changes in producer populations. What determines the difference is 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), only Gilby & Stevens (2014) previously reviewed the effect of marine reserves on herbivores

and primary producer populations. Our work counters their results, which had limited sample sizes (e.g. n = 5 for producers in temperate marine ecosystems), and found no effect of reserves on either herbivore or algae populations. Instead, we found that herbivores decreased on average 2.83 times, and producers increased 1.90 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 best able to restore producer populations 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 while working to actively restore 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 older reserves had stronger reductions in herbivore populations. 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 the 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 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 ecosystem 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 study categories, such as invertebrates compared to vertebrates. Only 4 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 cas-

cade 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 (Fig. A1), and a mix of observational and experimental research (79 and 68 data points, respectively). These additional contexts significantly expand 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. 5ab). 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 of almost 150 data points, there are significant gaps in multiple data categories that prevent the synthesis of a truly balanced data set. Whereas experimental study locations were all located in Europe and the USA, most observational studies occurred in other regions of the world (the Caribbean, southeast Australasia, and eastern Africa). No studies were recorded in South America, Asia, or Antarctica (Fig. A1). Future studies should seek to address these geographical biases. 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 SSTs (Fig. 2a,b,d). 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 of 147), and the majority of the studies examined macroalgae as the producer (127 of 147), with seagrass particularly under-examined (3 of 147) (see Table A1 in the Appendix 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. Conclusions

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 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 noted 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.

LITERATURE CITED

Atwood TB, Hammill E (2018) The importance of marine predators in the provisioning of ecosystem services by coastal plant communities. Front Plant Sci 9:1289

Baum JK, Worm B (2009) Cascading top-down effects of changing oceanic predator abundances. J Anim Ecol 78: 699–714

Bennett EM, Carpenter SR, Caraco NF (2001) Human impact on erodable phosphorus and eutrophication: a global perspective: increasing accumulation of phosphorus in soil threatens rivers, lakes, and coastal oceans with eutrophication. Bioscience 51:227–234

Borenstein M, Hedges LV, Higgins JPT, Rothstein HR (2009) Effect sizes based on means. In: Introduction to meta-analysis. Wiley & Sons, West Sussex, p 21–32

Borer ET, Seabloom EW, Shurin JB, Anderson KE and others (2005) What determines the strength of a trophic cascade? Ecology 86:528–537

Bruno JF, O'Connor MI (2005) Cascading effects of predator diversity and omnivory in a marine food web. Ecol Lett 8: 1048–1056

Bruno JF, Carr LA, O'Connor MI (2015) Exploring the role of temperature in the ocean through metabolic scaling. Ecology 96:3126–3140

Burkholder DA, Heithaus MR, Fourqurean JW, Wirsing A, Dill LM (2013) Patterns of top-down control in a seagrass ecosystem: Could a roving apex predator induce a behaviour-mediated trophic cascade? J Anim Ecol 82: 1192–1202

Byers JE, Noonburg EG (2007) Poaching, enforcement, and the efficacy of marine reserves. Ecol Appl 17:1851–1856

Caselle JE, Davis K, Marks LM (2018) Marine management affects the invasion success of a non-native species in a temperate reef system in California, USA. Ecol Lett 21: 43–53

Cardona L (2006) Trophic cascades uncoupled in a coastal marsh ecosystem. Biol Inv 8:835

Cebrian J, Shurin JB, Borer ET, Cardinale BJ, Ngai JT, Smith MD, Fagan WF (2009) Producer nutritional quality controls ecosystem trophic structure. PLOS ONE 4:e4929

Christensen V, Coll M, Piroddi C, Steenbeek J, Buszowski J, Pauly D (2014) A century of fish biomass decline in the ocean. Mar Ecol Prog Ser 512:155–166

Clark GF, Johnston EL (2017) Australia state of the environment 2016: coasts. Department of the Environment and Energy, Canberra

Cloern JE, Foster SQ, Kleckner AE (2014) Phytoplankton primary production in the world's estuarine−coastal ecosystems. Biogeosciences 11:2477–2501

Davies GM, Gray A (2015) Don't let spurious accusations of pseudoreplication limit our ability to learn from natural experiments (and other messy kinds of ecological monitoring). Ecol Evol 5:5295–5304

Davis RW, Bodkin JL, Coletti HA, Monson DH, Larson SE, Carswell LP, Nichol LM (2019) Future directions in sea otter research and management. Front Mar Sci 5:510

DeLong JP, Gilbert B, Shurin JB, Savage VM and others (2015) The body size dependence of trophic cascades. Am Nat 185:354–366

Di Franco A, Thiriet P, Di Carlo G, Dimitriadis C and others (2016) Five key attributes can increase marine protected areas performance for small-scale fisheries management. Sci Rep 6:38135

Duffy JE (2002) Biodiversity and ecosystem function: the consumer connection. Oikos 99:201–219

Duffy JE, Cardinale BJ, France KE, McIntyre PB, Thébault E, Loreau M (2007) The functional role of biodiversity in ecosystems: incorporating trophic complexity. Ecol Lett 10:522–538

Edgar GJ, Stuart-Smith RD, Willis TJ, Kininmonth S and others (2014) Global conservation outcomes depend on marine protected areas with five key features. Nature 506:216–220

Edgar GJ, Alexander TJ, Lefcheck JS, Bates AE and others (2017) Abundance and local-scale processes contribute to multi-phyla gradients in global marine diversity. Sci Adv 3:e1700419

Eger AM, Marzinelli E, Gribben P, Johnson CR and others (2020) Playing to the positives: using synergies to enhance kelp forest restoration. Front Mar Sci 7:544

Estes JA, Duggins DO (1995) Sea otters and kelp forests in Alaska: generality and variation in a community ecological paradigm. Ecol Monogr 65:75–100

Estes JA, Palmisano JF (1974) Sea otters: their role in structuring nearshore communities. Science 185:1058–1060

Fenchel T (1974) Intrinsic rate of natural increase: the relationship with body size. Oecologia 14:317–326

Gamfeldt L, Lefcheck JS, Byrnes JEK, Cardinale BJ, Duffy JE, Griffin JN (2015) Marine biodiversity and ecosystem functioning: What's known and what's next? Oikos 124: 252–265

Gilby BL, Stevens T (2014) Meta-analysis indicates habitat-specific alterations to primary producer and herbivore communities in marine protected areas. Glob Ecol Conserv 2:289–299

Gowen RJ (1994) Managing eutrophication associated with aquaculture development. J Appl Ichthyology 10:242–257

Griffin JN, Byrnes JEK, Cardinale BJ (2013) Effects of predator richness on prey suppression: a meta-analysis. Ecology 94:2180–2187

Halaj J, Wise DH (2001) Terrestrial trophic cascades: How much do they trickle? Am Nat 157:262–281

Halpern BS (2003) The impact of marine reserves: Do reserves work and does reserve size matter? Ecol Appl 13:117–137

He Q, Silliman BR (2016) Consumer control as a common driver of coastal vegetation worldwide. Ecol Monogr 86:278–294

Heath MR, Speirs DC, Steele JH (2014) Understanding patterns and processes in models of trophic cascades. Ecol Lett 17:101–114

Heck KL Jr, Pennock JR, Valentine JF, Coen LD, Sklenar SA (2000) Effects of nutrient enrichment and small predator density on seagrass ecosystems: an experimental assessment. Limnol Oceanogr 45:1041–1057

Heithaus MR, Frid A, Wirsing AJ, Worm B (2008) Predicting ecological consequences of marine top predator declines. Trends Ecol Evol 23:202–210

Hessen DO, Kaartvedt S (2014) Top-down cascades in lakes and oceans: Different perspectives but same story? J Plankton Res 36:914–924

Hillebrand H (2009) Meta-analysis of grazer control of periphyton biomass across aquatic ecosystems. J Phycol 45: 798–806

Hothorn T, Bretz F, Westfall P (2008) Simultaneous inference in general parametric models. Biom J 50:346–363

Jamieson GS, Levings CO (2001) Marine protected areas in Canada: implications for both conservation and fisheries management. Can J Fish Aquat Sci 58:138–156

Jeppesen E, Jensen JP, Jensen C, Faafeng B and others (2003) The impact of nutrient state and lake depth on top-down control in the pelagic zone of lakes: a study of 466 lakes from the temperate zone to the Arctic. Ecosystems 6:313–325

Katano I, Doi H, Eriksson BK, Hillebrand H (2015) A cross-system meta-analysis reveals coupled predation effects on prey biomass and diversity. Oikos 124:1427–1435

Kratina P, Greig HS, Thompson PL, Carvalho-Pereira TSA, Shurin JB (2012) Warming modifies trophic cascades and eutrophication in experimental freshwater communities. Ecology 93:1421–1430

Larkum AWD, Orth RJ, Duarte CM (2006) Seagrasses: biology, ecology and conservation. Springer, Dordrecht

Lester SE, Halpern BS, Grorud-Colvert K, Lubchenco J and others (2009) Biological effects within no-take marine reserves: a global synthesis. Mar Ecol Prog Ser 384:33–46

Levitus S, Antonov J, Baranova O, Boyer T and others (2013) The world ocean database. Data Sci J 12: WDS229–WDS234

Ling SD, Johnson CR, Frusher SD, Ridgway KR (2009) Overfishing reduces resilience of kelp beds to climate-driven catastrophic phase shift. Proc Natl Acad Sci USA 106: 22341–22345

Marino NDAC, Romero GQ, Farjalla VF (2018) Geographical and experimental contexts modulate the effect of warming on top-down control: a meta-analysis. Ecol Lett 21:455–466

McClanahan TR, Muthiga NA (2016) Geographic extent and variation of a coral reef trophic cascade. Ecology 97: 1862–1872

Meentemeyer V, Box EO (1987) Scale effects in landscape studies. In: Turner MG (ed) Landscape heterogeneity and disturbance. Ecological Studies, Vol 64. Springer-Verlag, New York, NY, p 15–34

Moksnes P, Gullström M, Tryman K, Baden S (2008) Trophic cascades in a temperate seagrass community. Oikos 117: 763–777

Molloy PP, McLean IB, Côté IM (2009) Effects of marine reserve age on fish populations: a global meta-analysis. J Appl Ecol 46:743–751

Myers RA, Worm B (2005) Extinction, survival or recovery of large predatory fishes. Philos Trans R Soc B 360:13–20

Oksanen L, Fretwell SD, Arruda J, Niemela P (1981) Exploitation ecosystems in gradients of primary productivity. Am Nat 118:240–261

Olds AD, Pitt KA, Maxwell PS, Babcock RC (2014) Marine reserves help coastal ecosystems cope with extreme weather. Glob Chang Biol 20:3050–3058

Östman Ö, Eklöf J, Eriksson BK, Olsson J, Moksnes P, Bergström U (2016) Top-down control as important as nutrient enrichment for eutrophication effects in North Atlantic coastal ecosystems. J Appl Ecol 53:1138–1147

Pinheiro J, Bates D, DebRoy S, Sarkar D, Team RC (2012) nlme: linear and nonlinear mixed effects models. R package version 3. https://cran.r-project.org/package=nlme

Polis GA (1991) Complex trophic interactions in deserts: an empirical critique of food-web theory. Am Nat 138:123–155

Poore AGB, Campbell AH, Coleman RA, Edgar GJ and others (2012) Global patterns in the impact of marine herbivores on benthic primary producers. Ecol Lett 15:912–922

R Core Team (2017) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Ramus J (1992) Productivity of seaweeds. In: Falkowski PG, Woodhead AD (eds) Primary productivity and biogeochemical cycles in the sea. Environmental Science Research, Vol 43. Springer, New York, NY, p 239–255

Reed D, Rassweiler A, Arkema K (2009) Density derived estimates of standing crop and net primary production in the giant kelp *Macrocystis pyrifera*. Mar Biol 156:2077–2083

Rodríguez-Castañeda G (2013) The world and its shades of green: a meta-analysis on trophic cascades across temperature and precipitation gradients. Glob Ecol Biogeogr 22:118–130

Sagarin R, Pauchard A (2012) Is observation-based ecology scientific? In: Observation and ecology: broadening the scope of science to understand a complex world. Springer, Washington, DC, p 109–130

Sala E, Giakoumi S (2018) No-take marine reserves are the most effective protected areas in the ocean. ICES J Mar Sci 75:1166–1168

Shears NT, Babcock RC (2002) Marine reserves demonstrate top-down control of community structure on temperate reefs. Oecologia 132:131–142

Shears NT, Babcock RC, Salomon AK (2008) Context-dependent effects of fishing: variation in trophic cascades across environmental gradients. Ecol Appl 18:1860–1873

Shurin JB, Borer ET, Seabloom EW, Anderson K and others (2002) A cross-ecosystem comparison of the strength of trophic cascades. Ecol Lett 5:785–791

Shurin JB, Markel RW, Mathews B (2010) Comparing trophic cascades across ecosystems. In: Terborgh J, Estes JA (eds) Trophic cascades: predators, prey, and the changing dynamics of nature. Island Press, Washington, DC, p 319–336

Smith MT, Addison JT (2003) Methods for stock assessment of crustacean fisheries. Fish Res 65:231–256

Svenning JC, Pedersen PBM, Donlan CJ, Ejrnæs R and others (2016) Science for a wilder Anthropocene: synthesis and future directions for trophic rewilding research. Proc Natl Acad Sci USA 113:898–906

Tittensor DP, Mora C, Jetz W, Lotze HK, Ricard D, Vanden Berghe E, Worm B (2010) Global patterns and predictors of marine biodiversity across taxa. Nature 466:1098–1101

van Veen FJF, Sanders D (2013) Herbivore identity mediates the strength of trophic cascades on individual plants. Ecosphere 4:64

Viechtbauer W (2010) Conducting meta-analyses in R with the metafor package. J Stat Softw 36:1–48

Vucic-Pestic O, Rall BC, Kalinkat G, Brose U (2010) Allometric functional response model: body masses constrain interaction strengths. J Anim Ecol 79:249–256

Wernberg T, Krumhansl K, Filbee-Dexter K, Pedersen MF (2019) Status and trends for the world's kelp forests. In: Sheppard C (ed) World seas: an environmental evaluation, Vol 3: ecological issues and environmental impacts. Elsevier, Amsterdam, p 57–78

Wickham H, Chang W (2008) ggplot2: an implementation of the grammar of graphics. R Package version 07. https:// CRAN.R-project.org/package=ggplot2

Woodcock P, O'Leary BC, Kaiser MJ, Pullin AS (2017) Your evidence or mine? Systematic evaluation of reviews of marine protected area effectiveness. Fish Fish 18:668–681
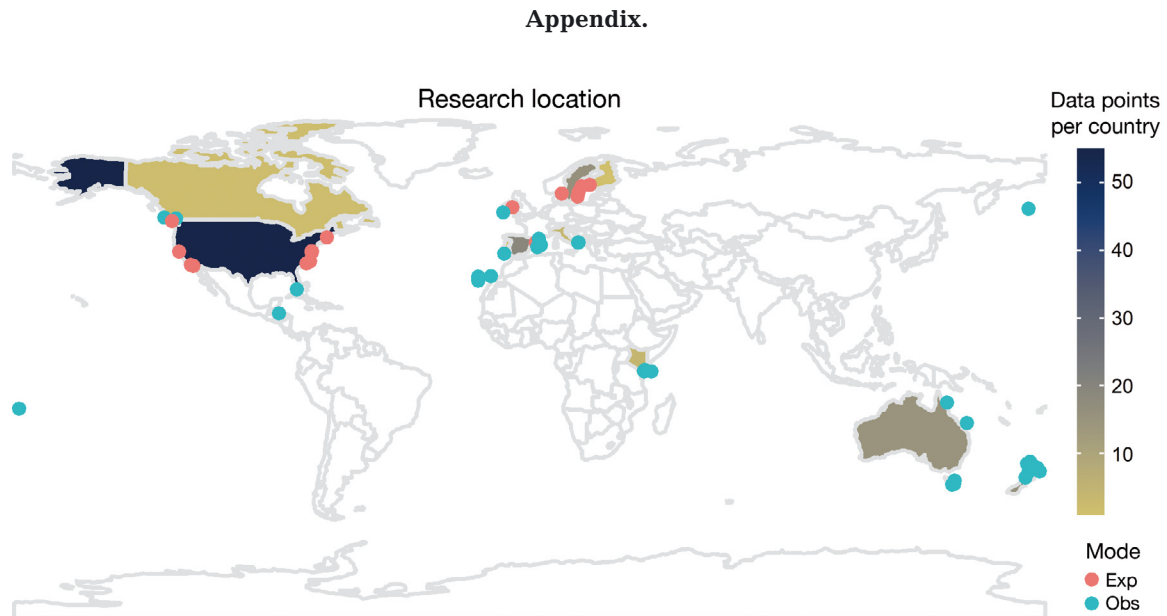
Appendix.

Fig. A1. Location of the studies included in this analysis. Dark to light color scale: number of studies per country; red or blue dots: observational (Obs) or experimental (Exp) study; N: number of measurements (total: 147)

Table A1. Results of the linear mixed-effects models between the various predictor variables and the herbivore and producer effect sizes. **Bold** entries are statistically significant (p < 0.05); Int.: the model intercept

Factor	n	Producer effect size			Herbivore effect size		
		Estimate	SE	p	Estimate	SE	p
Biotic and abiotic							
Herbivore: invertebrate (Int.)	136	0.76	0.14	0.94	−1.18	0.21	0.41
Herbivore: vertebrate	11	0.01	0.07	0.94	0.56	0.68	0.41
Herbivore size	147	0.00	0.04	0.94	**−0.68**	**0.11**	**<0.01**
Nitrate	108	**0.21**	**0.08**	**<0.01**	0.01	0.11	0.90
Phosphate	108	**1.63**	**0.71**	**0.02**	−0.75	0.94	0.43
Predator-herbivore size ratio	147	0.00	0.02	0.98	**0.31**	**0.05**	**<0.01**
Predator: invertebrate (Int.)	51	0.80	0.25	0.85	−1.25	0.37	0.73
Predator: vertebrate	96	−0.06	0.31	0.85	0.15	0.45	0.73
Predator size	147	0.13	0.23	0.58	0.48	0.43	0.27
Producer: epiphyte (Int.)	17	0.43	0.35	0.53	−1.15	0.26	0.87
Producer: macro	127	0.37	0.36	0.53	0.01	0.18	0.87
Producer: seagrass	3	0.10	0.69	0.53	−0.11	0.29	0.87
Study duration	75	0.07	0.59	0.91	0.51	0.75	0.50
Temperature	108	−0.04	0.03	0.15	**−0.08**	**0.04**	**0.03**
Study method							
Enclosure (Int.)	24	0.48	0.34	0.33	**0.07**	**0.55**	**0.02**
Exclusion	16	0.35	0.25	0.33	**−1.75**	**0.55**	**0.02**
Marine reserve	59	0.17	0.39	0.33	**−1.11**	**0.62**	**0.02**
Mesocosm	39	0.82	0.50	0.33	**−1.70**	**0.77**	**0.02**
Observation	9	0.31	0.55	0.33	**−1.78**	**0.86**	**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	0.02	0.02	0.42	**−0.05**	**0.03**	**0.047**
Reserve size	59	0.11	0.32	0.74	0.44	0.45	0.33