

Global meta-analysis of how marine upwelling affects herbivory

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Abstract

Aim: Nutrient subsidies support high primary productivity, increasing herbivore abundance and influencing their top-down control of producers. Wind-driven upwelling events deliver cold nutrient-rich water to coastlines, supporting highly productive marine environments. Results from studies comparing ecological processes across upwelling regimes are mixed: some reveal weaker herbivory in upwelling regions, while others report a positive relationship between upwelling and herbivory. In this synthesis we examine the influence of upwelling on top-down control of producers across the globe.

Location: Global; marine ecosystems.

Time period: 1978–2017.

Major taxa studied: Marine herbivores and algae.

Methods: We used data from herbivory studies focusing specifically on the influence of upwelling activity (upwelling studies), and a broader collection of herbivore exclusion studies dating back four decades. For the upwelling studies we compared herbivore effects between experiments replicated across sites for which upwelling conditions were described by the authors. Meanwhile, for the broader collection of experiments we used externally sourced oceanographic data to characterize upwelling activity, and examined how herbivory changed along a gradient of upwelling activity.

Results: Our results consistently reveal that upwelling weakens herbivore effects on producers. Herbivory was, on average, four times weaker in upwelling sites relative to sites under weak upwelling or downwelling regimes in studies that specifically examined upwelling. The analysis of the broader herbivory literature revealed a similar weakening influence of upwelling on herbivory; however, the effect size was smaller and varied across producer functional groups.

Main conclusions: Nutrient subsidies from upwelling events reduce top-down control by herbivores in coastal ecosystems; however, the negative relationship between upwelling intensity and herbivory is likely the result of a combination of co-occurring processes. First, increased primary production overwhelms consumption by herbivores. Second, cold water reduces herbivore metabolism and activity. Finally, surface currents associated with upwelling activity transport herbivore larvae offshore, decoupling secondary production from herbivory.

KEYWORDS

algae, bottom-up, grazer, nutrients, oceanography, subsidies, top-down

1 | INTRODUCTION

Ecosystems are often connected by flows of organisms and materials that represent important resource subsidies, influencing trophic interactions and ecosystem function (Polis, Anderson, & Holt, 1997). The regulatory effects of resource flows have become a fundamental feature of ecological theory (Loreau & Holt, 2004), providing insights into connections between ecosystems across large spatial scales (Loreau, Mouquet, & Holt, 2003) and allowing for a more complete understanding of ecosystem function (e.g., Baxter, Fausch, & Saunders, 2005). Nutrient subsidies, in particular, can influence food-web structure and dynamics. Ecological theory predicts that producers are generally limited by their resources (Hairston, Smith, & Slobodkin, 1960), and primary productivity determines trophic connectivity and the ability of herbivores to reduce plant biomass (Fretwell, 1987). Nutrient imports can increase primary productivity, which in turn supports high secondary production, leading to strong consumption and top-down control of autotrophs (Shurin, Gruner, & Hillebrand, 2005). In this meta-analysis we examine how nutrient subsidies delivered by marine upwelling, a widely occurring oceanographic phenomenon, influence herbivory across the globe.

In marine systems, wind-generated upwelling events deliver deep, cold, nutrient-rich water to shallow coastlines. Upwelling activity supports some of the planet's most productive marine environments. In fact, the four major eastern boundary upwelling regions generate one fifth of the global fish catch (Fréon, Barange, & Aristegui, 2009). Coastlines exposed to strong upwelling activity are associated with high benthic algal growth rates, cover, nutrient content, and productivity (Blanchette, Broitman, & Gaines, 2006; Bustamante et al., 1995; Vinueza, Menge, Ruiz, & Palacios, 2014). While this demonstrates a positive influence of upwelling activity on marine producers, its influence on secondary production and top-down control may be more complex.

First, high benthic primary productivity in sites exposed to strong upwelling does not always translate into increased densities of benthic herbivores. While high food availability and quality in upwelling sites can increase the reproductive potential of herbivores (Pulgar et al., 2013), offshore currents transport larvae away from the coast, reducing invertebrate recruitment to sites under strong upwelling regimes (Blanchette et al., 2006; Broitman, Navarrete, Smith, & Gaines, 2001). Second, studies examining the effects of upwelling activity on herbivory have yielded mixed results. Experiments in Chile revealed that the strength of herbivore effects did not vary across contrasting upwelling regimes; however, per-capita herbivore effects (total grazer effect divided by the number of grazers) were stronger in upwelling sites (Nielsen & Navarrete, 2004). Similarly, experiments in New Zealand revealed that herbivore effects did not differ between the upwelled western coast and the downwelling eastern coast, but reported stronger herbivory during initial succession in upwelled areas (Menge et al., 1999). However, another study found weaker herbivore effects along the upwelled coast, but those authors examined the effects of herbivores on later successional stages potentially generating different conclusions (Guerry &

Menge, 2017). A similar weakening effect of upwelling activity on herbivory was reported along the west coast of North America, but the authors also suggested that upwelling may indirectly strengthen benthic herbivory via shading effects from phytoplankton blooms (Freidenburg, Menge, Halpin, Webster, & Sutton-Grier, 2007). Less research has been devoted to understanding the influence of upwelling in tropical coasts; however, strong upwelling activity in the Galapagos Islands weakened grazer impacts (Vinueza et al., 2014). Such variation in outcomes among studies merits further analysis to identify general patterns of influence of upwelling on herbivory, and potential factors that could explain the variation in reported effect-sizes.

Here, we synthesize data from published experiments in a meta-analytic framework to examine the influence of upwelling on herbivore effects. First, we compare effect-sizes among replicated herbivore-exclusion experiments, designed specifically to examine the influence of upwelling events on herbivory. We then go beyond the upwelling literature, expanding the geographical scale past regions traditionally studied (i.e., western coast of South and North America, and New Zealand). For this, we relied on a broader set of published herbivore-exclusion experiments and examined how the strength of herbivory varies along a gradient of upwelling intensity defined by the Bakun upwelling index (BUI; Bakun, 1973). The temporal dynamics of upwelling activity can also influence the delivery of resources and larvae to coastlines (Menge & Menge, 2013). Thus, we incorporated both upwelling intensity and variability in our global analysis. By expanding our synthesis beyond field-specific studies we seek to reduce the 'file-drawer effect', a well-known issue with meta-analyses (Arnqvist & Wooster, 1995) wherein significant effects are more likely to be published than null results. As the studies in the broader collection of literature focused on a variety of research questions, publication biases should not be specifically associated with upwelling effects.

We test the general hypothesis that upwelling weakens the top-down effects of herbivores across broad geographical scales. Classic theory linking bottom-up and top-down control predicts that higher productivity linked to stronger upwelling activity should strengthen herbivore effects via increases in consumer abundance (Oksanen, Fretwell, Arruda, & Niemela, 1981). However, recent meta-analyses of marine herbivory reveal weak herbivore effects in productive systems (Burkepile & Hay, 2006; Hillebrand, 2002). Further, the offshore advection of larvae in upwelling sites may decouple herbivore larval production from recruitment (Blanchette et al., 2006; Broitman et al., 2001), likely weakening herbivore effects by limiting herbivore abundance. Thus, a combination of increased algal growth and reduced herbivore recruitment could lead to weak herbivore effects at upwelling sites. While our primary goal is to examine relationships between upwelling activity and herbivory, we also explore how upwelling intensity interacts and may covary with other factors known to influence productivity and top-down control (i.e., day length, temperature, turbidity, latitude, habitat type, and producer functional group).

2 | METHODS

2.1 | Marine herbivory literature search

We compiled studies that measured the response of marine producers to the removal or exclusion of herbivores in intertidal and subtidal environments by searching the Institute for Scientific Information's Web of Science using the following terms: (graz* OR herbiv*) AND (exclud* OR exclus* OR fenc* OR cage* OR remov*) AND (macrophyte* OR alga* OR seagrass* OR eelgrass* OR seaweed*). We also included studies cited by other meta-analyses of marine herbivory (Burkepile & Hay, 2006; Poore et al., 2012). To meet our criteria, authors must have reduced herbivore densities in exclusion treatments via manual removal, by installing cages or fences, or through chemical means such as copper-based paints and pesticides. At the end of each experiment, authors measured producer percent cover, biomass, density, or growth inside exclusion and unmanipulated (control) treatments. Lastly, all studies reported the mean producer abundance inside the exclusion and control plots, and their respective number of replicates and measure of variance. A list of the data sources is found in the Appendix and Supporting Information Appendix S2.

2.2 | Response variable and moderators

We calculated herbivore effects as: $y_i = \log\left(\frac{\bar{X}_e}{\bar{X}_c}\right)$ where \bar{X}_e is the mean producer abundance in the exclusion treatment, and \bar{X}_c is the mean abundance in the control treatment. Thus, y_i measures the proportional change resulting from the experimental removal of herbivores, such that $y_i > 0$ when herbivore removal results in an increase in producer abundance relative to the control, and $y_i < 0$ when producer abundance is lower in the exclusion relative to the control. We obtained means and standard deviations from each study. When data were reported as time series, we used the data from the end of the experiment. If a procedural control was used to test for methodological artifacts, we recorded that treatment's mean, deviation, and sample size. Effect-sizes calculated using the mean from the procedural control treatment as the denominator were strong predictors of the effect-sizes calculated using the control treatment means (ANOVA: $F_{1,196} = 5.16, p < .05$), suggesting that artifacts associated with the exclusion method had little effect on the outcome of experiments. Thus, we used the control means to calculate y_i for the rest of our analysis.

For each experiment, we recorded information regarding habitat type, herbivore type, and the method used to exclude them. If enough taxonomic information was provided, we also classified the producer according to functional groups proposed by Steneck and Dethier (1994). Light availability is a determinant of primary productivity, so we estimated the mean day length (MDL) in hours for the duration of each experiment using the 'geosphere' package (Hijmans, Williams, & Vennes, 2017) from the R statistical software environment (R Core Team, 2018), and used it as a covariate in the analysis. Water clarity may also influence light availability, so we obtained

data for diffuse attenuation coefficients of the photosynthetically available radiation (K_d PAR). The K_d PAR provides an indicator of turbidity (Son & Wang, 2015), and is available through the National Oceanographic and Atmospheric Administration's (NOAA's) portal for remotely sensed oceanographic data (<https://coastwatch.pfeg.noaa.gov/erddap/index.html>).

We quantified the intensity and variation of upwelling at each experimental site using BUI data (Bakun, 1973) obtained from NOAA. The BUI reflects the water flux (cubic metres per second per 100 m of coastline) away from the coast (upwelling; positive values) or towards it (downwelling; negative values). NOAA generates upwelling indices worldwide at 0.5° intervals and a temporal resolution of 6 hr; we obtained the data using the "xtractomatic" package for R (Mendelssohn & Wilson, 2018). This index has been used to characterize upwelling activity in previous studies (e.g., Freidenburg et al., 2007; Menge et al., 1999; Menge & Menge, 2013); however, it is unreliable for locations in latitudes below 25°, complex coastlines, and small islands (Bakun & Agostini, 2001). We therefore excluded experiments that matched those criteria, as well as studies in estuaries to avoid confounding effects from terrestrial processes. To characterize upwelling regimes, including within year variation, we calculated the mean (BUI_M) and standard deviation (BUI_{SD}) of the 6-hourly upwelling indices across 2 years following the initiation of each experiment.

The global distribution of BUI data (Figure 1) reflects known geographical patterns of upwelling activity. The data predict a gradient of upwelling intensity along the west coast of North America (Figure 1), where upwelling increases in strength and frequency from Oregon to California (Huyer, 1983). The data also predicted strong upwelling activity in central Chile and along the western coast of South Africa, matching published descriptions of upwelling activity in those regions (Lutjeharms & Meeuwis, 1987; Montecino & Lange, 2009). Localized upwelling centres were also represented in the data, predicting positive BUI_M values along the west coast of New Zealand's South Island (Menge et al., 1999), and in Brazil's Cabo Frio (Valentin, Andre, & Jacob, 1987). Although the BUI quantifies upwelling activity, it does not provide a measure of resource availability. To examine links between the BUI, productivity, and nutrient availability we obtained daily chlorophyll-a mean concentrations from the SeaWiFS dataset, accessed via the 'xtractomatic' package. Data from SeaWiFS was available from September 1997 to December 2010. We also recorded nutrient concentration data from publications when available, focusing on nitrate because it was the most commonly reported nutrient.

2.3 | Statistical analyses

We used three analytical approaches to assess the robustness of our analysis and consistency of our inferences regarding upwelling's influence on herbivory. First, we focused on the upwelling literature, comparing herbivore effect-sizes between experiments replicated across contrasting upwelling regimes. We used a linear mixed effects (LME) model with each study's classification of upwelling regime as

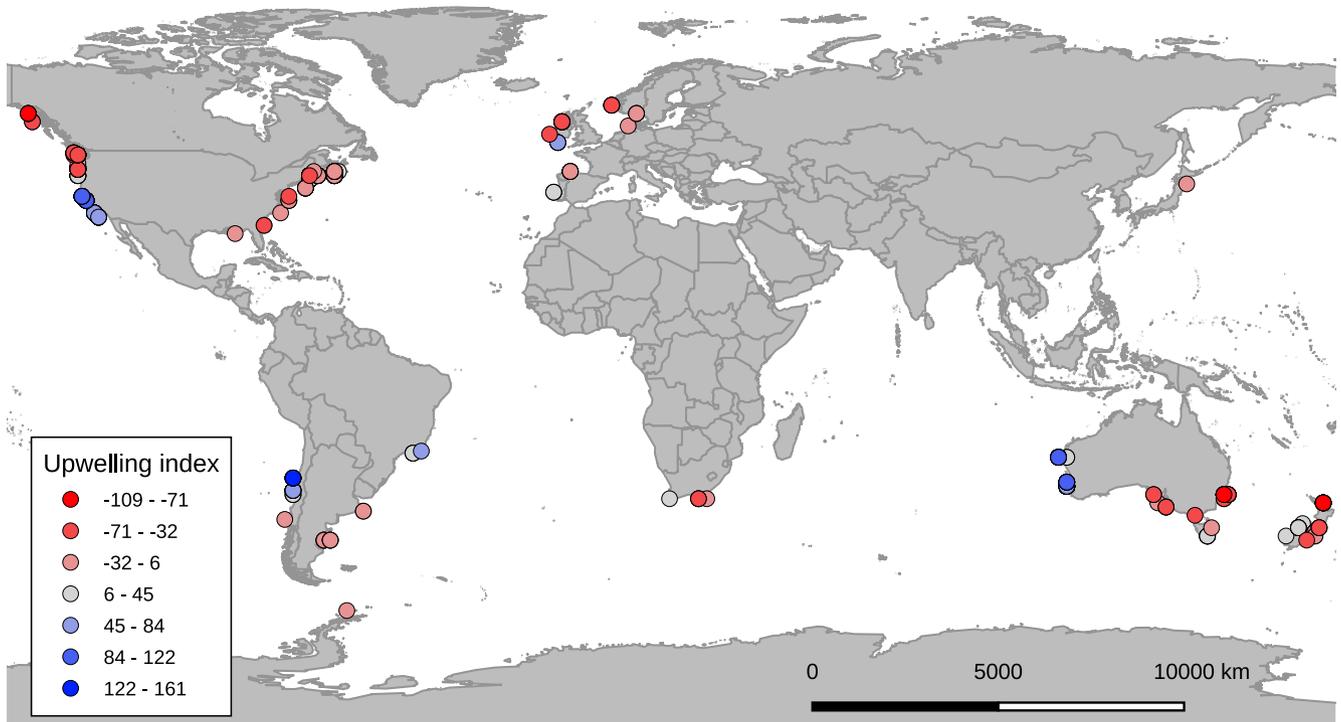


FIGURE 1 Global distribution of experimental sites for studies included in the analysis. The colour of each point reflects the mean Bakun upwelling index (BUI_M) values for studies conducted in that location. Positive BUI_M , indicating upwelling sites, are represented by cooler colours (i.e., blues). Meanwhile, negative BUI_M values, indicating downwelling, are represented by warmer colours (i.e., pinks and reds)

a fixed categorical factor, and the replicate measurements or sites within each study as a nested random factor. We also examined the fixed effect of the BUI_M and BUI_{SD} on effect-sizes using a LME model with the same nested random factor described above.

For our second analysis, we examined the influence of BUI_M and BUI_{SD} on herbivore effects reported by the broader set of herbivory studies, including upwelling studies. While this approach allowed us to broaden the scope of our analysis and reduce potential publication bias, it also led us to consider other factors that could alter the relationship between upwelling activity and herbivory. As a preliminary step, we used a LME with individual experiments as random factors to analyse the fixed effects of: producer functional group, herbivore type (macrograzer versus mesograzers), habitat type, substrate type (plate versus naturally available surface), and the season when the experiment was terminated. Based on that analysis we excluded levels of factors for which there were insufficient data to compare across upwelling regimes. We then ran a LME model to examine the fixed effect of BUI_M and BUI_{SD} while considering the individual experiments as a random effect. We included MDL as a covariate because it is an important driver of primary productivity; however, we excluded sea surface temperature and nutrient concentrations as they are themselves influenced by upwelling activity. The K_dPAR dataset's earliest available measurements date back to 2012, thus we were only able to examine the relationship between herbivore effects and the diffuse attenuation coefficient for a subset of the experiments ($n = 14$). We examined the effect of K_dPAR on herbivore effects separately for that subset of experiments using a

LME model with each experiment as a random effect and K_dPAR as a continuous fixed variable.

For our third approach we used an alternative analysis to further control for variation introduced by the factors discussed above. We applied a nearest-neighbour algorithm, using the 'optmatch' package for R (Hansen, 2007), to pair individual experiments according to contrasting upwelling regimes (positive and negative BUI_M), and equivalent producer functional group, grazer type, habitat type, and region. For each pair, one experiment was associated with positive mean BUI_M and the other with negative values, but both experiments within each pair were associated with the same region, habitat type, producer functional group, and grazer type. We compared the effect-sizes between upwelling regimes using a Student's paired *t* test.

The BUI is a useful measure of upwelling activity, but it does not quantify the delivery of nutrient subsidies or primary productivity. Thus, we used a linear regression to examine relationships between log-transformed nitrate concentrations and the BUI_M . The chlorophyll-*a* data did not meet assumptions of normality after transformations, so we used a nonparametric Spearman's rank correlation analysis to examine the effect of BUI_M on chlorophyll-*a* concentrations. We performed all statistical analyses using the R statistical software. Mixed effects models for meta-analyses were generated using the "metafor" package (Viechtbauer, 2010). We estimated individual mean effect-sizes and 95% confidence intervals for fixed moderators using restricted maximum likelihood, and used those values in graphs depicting results.

3 | RESULTS

3.1 | Analysis of upwelling literature

Studies designed specifically to compare herbivore effects across upwelling gradients revealed the strongest results. Herbivore effects were on average four times weaker in sites exposed to upwelling activity relative to those where upwelling was weak or absent [LME: -2.20 ($-2.34, -2.06$); $p < .001$; Figure 2]. We also examined the relationship between BUI_M and herbivory, which revealed a negative effect of upwelling intensity on herbivore effects [LME: -0.13 ; ($-0.13, -0.11$); $p < .001$; Figure 3a]. Notably, the BUI data we obtained coincide with the authors' classification of upwelling activity in their respective study sites. In other words, BUI_M values from experiments conducted in 'upwelling sites' were consistently higher than values from experiments in 'non-upwelling sites' (Wilcoxon rank sum test: $W = 11$, $p < .001$), providing an additional validation for the metric of upwelling activity. While BUI_M had an important effect on herbivory, effect-sizes were not influenced by BUI_{SD} [LME: -0.02 ; ($-0.03, 0.01$); $p = .13$]. Meanwhile, herbivore effects strengthened with longer days [LME: 9.03 ($7.89, 10.16$); $p < .001$]. We could not examine the relationship between K_dPAR and herbivory for the upwelling literature because those experiments were conducted before the earliest K_dPAR data were archived in NOAA's database: 2012.

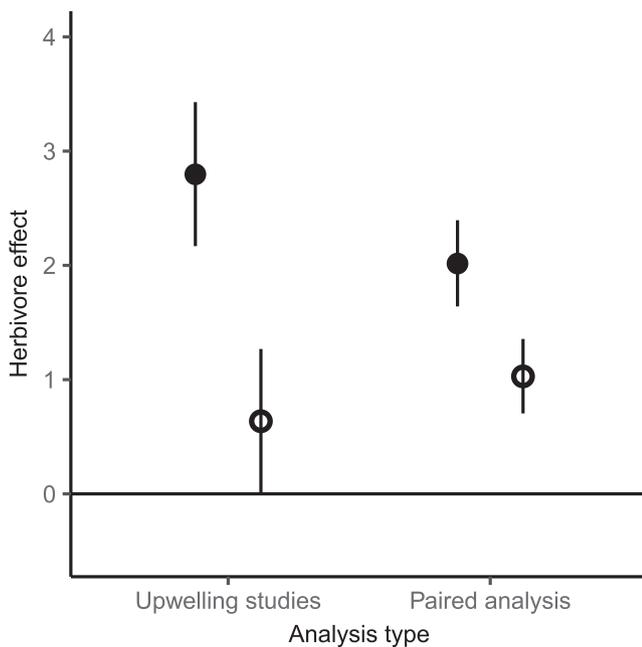


FIGURE 2 Comparison of herbivore removal effect in sites under contrasting upwelling activity. Filled circles correspond to experiments conducted in non-upwelling zones, while open circles correspond to experiments in upwelling areas. The comparison labelled 'Upwelling studies' corresponds to results from studies designed to examine the influence of upwelling on herbivory. The results labelled 'Paired analysis' were those obtained by conducting a pairwise analysis on experimental pairs generated using a pairing algorithm. Circles represent herbivore effects averaged within each group, and vertical bars represent 95% confidence intervals (CI)

3.2 | Analysis of broader herbivory literature

We examined the effects of different factors known to influence herbivory prior to our main analysis of the broader literature. Herbivore effects varied among producer functional groups: leathery macrophytes, corticated foliose algae, foliose algae and microalgae experience the strongest effects from herbivores, meanwhile herbivore effects on crustose algae were weak and negative (see Supporting Information Appendix S1: Figure S1.1). There was also variation in effect-size among habitat type, wherein herbivore effects were strongest in rocky subtidal and intertidal reefs, and highly variable for subtidal soft sediments, which were underrepresented in the data (see Supporting Information Figure S1.2). Finally, macrograzers exerted stronger top-down control on producers when compared to mesograzers (see Supporting Information Figure S1.3), and effect-sizes did not vary significantly among experiments terminated in different seasons (see Supporting Information Figure S1.4). Based on those results we focused our subsequent analysis on the following reduced dataset: we excluded data on crustose algae (10 experiments) because changes in crustose cover following the exclusion of herbivores was often the result of competitive interactions with faster growing non-calcified algae, rather than consumption. We also removed experiments performed in subtidal soft sediments because they were poorly represented in the data, and were only associated with negative BUI_M values. Given that our analysis revealed that mesograzers exert weaker effects on producers than macrograzers, we analysed the data for the two consumer groups separately. The resulting dataset for macrograzers consisted of 81 studies, including 228 experiments spanning all continents (see Supporting Information Appendix S2; Figure 1). Meanwhile, the dataset for mesograzers consisted of 9 studies, including 11 experiments performed in North America, Australia, and New Zealand.

The analysis of the broader collection of herbivory experiments manipulating macrograzers revealed a negative influence of BUI_M on herbivore effect-size [LME: -0.019 ($-0.024, -0.014$); $p < .001$; Figure 3b]. In nine experiments, changes in algal cover were indirectly caused by the exclusion of a predator, rather than the action of a grazer. We repeated the analysis without those data to remove potential bias and again found a significant negative effect of mean BUI_M on herbivory [LME: -0.018 ; ($-0.02, -0.01$); $p < .001$]. Upwelling activity weakened herbivory on two functional groups in particular: foliose algae [LME: -0.06 ($-0.07, -0.04$); $p < .001$; Figure 4a] and corticated foliose algae [LME: -0.03 ($-0.04, -0.01$); $p < .001$; Figure 4b]. Neither the BUI_{SD} [LME: 0.002 ; ($0.001, 0.006$); $p = .22$], nor MDL [LME: 0.08 ($-0.10, 0.27$), $p = .39$] influenced herbivore effects among the broader collection of studies. The analysis of K_dPAR 's influence on herbivore effects, however, revealed a nearly significant positive effect [LME: 11.97 ; ($-1.64, 25.58$); $p = .06$]. Our analysis of the mesograzers data did not reveal an effect of BUI_M [LME: -0.0025 ($-0.0140, 0.0089$); $p = .66$] or BUI_{SD} [LME: -0.0006 ($-0.0042, 0.003$); $p = .73$] on herbivory. Longer days (MDL), however, were associated with stronger mesograzers effects [LME: 0.17 ($0.041, 0.31$); $p < .01$]. We could not examine the influence of K_dPAR on herbivory by mesograzers because those data were only available for three experiments.

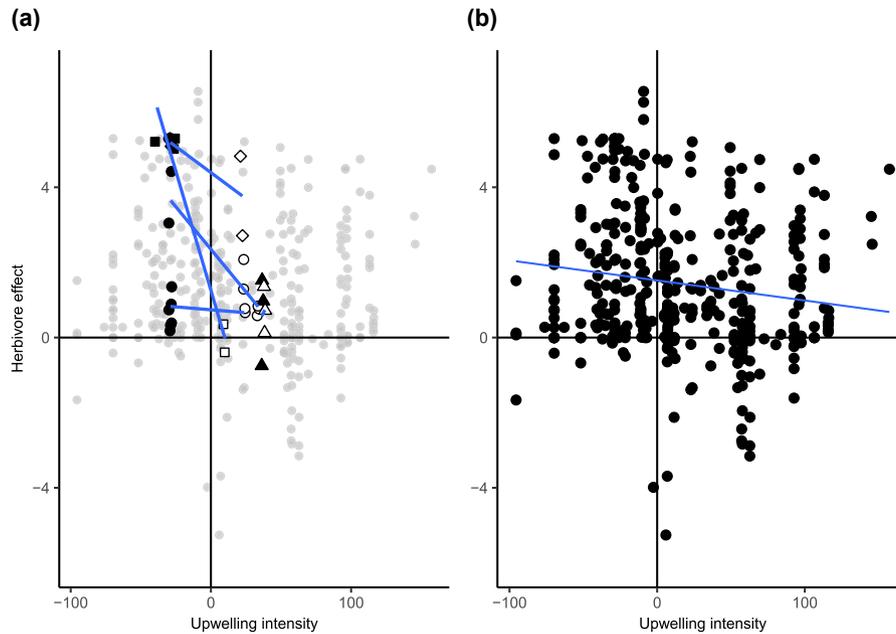


FIGURE 3 (a) Relationship between upwelling intensity (mean Bakun upwelling index, BUI_M) and herbivore effects, highlighting results from the upwelling literature. Open symbols depict effect sizes from experiments performed in sites exposed to upwelling activity, while filled symbols represent results from experiments performed in sites sheltered from upwelling activity, exposed to weak upwelling or in areas of active downwelling. Each shape represents a specific study: o = Freidenburg et al., (2007); \diamond Menge et al., (1999); \square = Guerry and Menge, (2017); Δ = Nielsen and Navarrete, (2004). Best fit lines were fitted for each experimental group from a given study. Grey circles in the background represent herbivore effects from the broader collection of studies. (b) Relationship between upwelling intensity (BUI_M) and herbivore effects for experiments in the broader selection of studies, including results from upwelling studies. Each circle represents the effect size reported by an individual experiment [Colour figure can be viewed at wileyonlinelibrary.com]

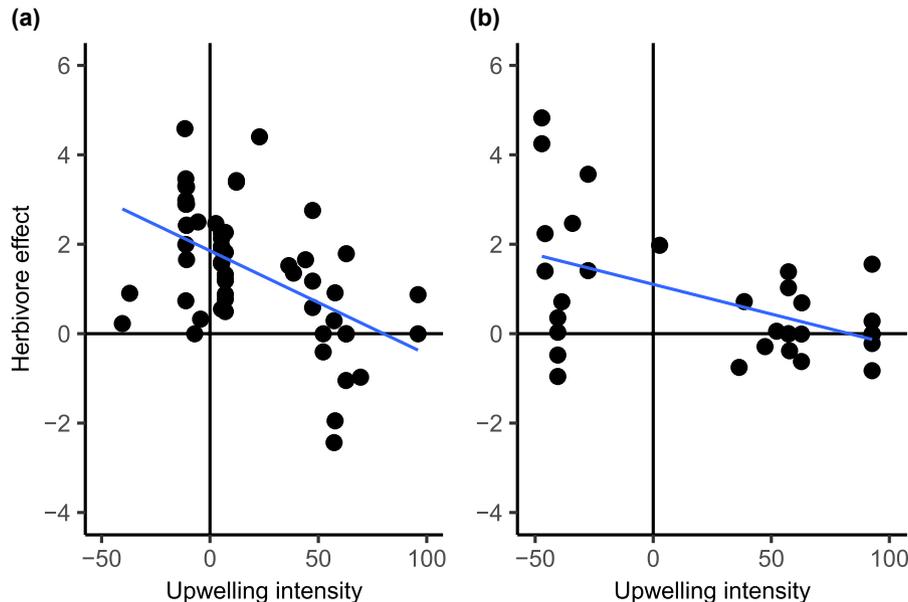


FIGURE 4 Relationship between upwelling intensity (mean Bakun upwelling index, BUI_M) and herbivore effect for (a) foliose algae and (b) corticated foliose algae. Each point depicts the result of an individual experiment performed in a given study, and best-fit lines are fitted to each functional group [Colour figure can be viewed at wileyonlinelibrary.com]

3.3 | Analysis of paired experiments

Our third approach, that is pairing independent studies using a nearest-neighbour algorithm, yielded results consistent with the analysis of the upwelling literature: the effect of herbivores was significantly

weaker in sites associated with positive BUI_M values relative to sites associated with negative values (Student's t test: mean difference = -0.99 ; $t = -3.87$; $p < .001$). While the two analytical approaches produced similar results, the analysis of the upwelling literature revealed a stronger effect of upwelling activity on herbivory than the

pairing approach (Figure 2). The distribution of negative and positive upwelling values was uneven, and so was the distribution of experiments across grouping variables. Thus, this pairing procedure excluded multiple studies, and the resulting dataset was composed of 108 experimental pairs of high versus low upwelling sites.

3.4 | Relationship between upwelling intensity and environmental parameters

Upwelling activity differentially influenced nutrient and chlorophyll concentrations. Across the studies that reported nutrient availability, nitrate concentrations increased with upwelling intensity (linear model: $F_{1,22} = 23.14$; $R^2 = .49$; $p < .01$; Supporting Information Appendix S3: Figure S3.1). Chlorophyll concentrations followed the opposite trend, however, and decreased with higher BUI_M (Spearman's rank correlation: $\rho = -.42$, $p < .001$; Supporting Information Figure S3.2).

4 | DISCUSSION

Our synthesis supports the hypothesis that upwelling activity weakens top-down control of marine producers. All three analytical approaches consistently reveal a negative relationship between upwelling intensity and herbivore effects. Studies designed to compare herbivory across upwelling gradients (upwelling studies) revealed the strongest effects of upwelling; however, the generality of those results is limited by low research effort and a narrow geographical breadth. By considering the broader herbivory literature and using open sourced oceanographic data (Bakun index), we were able to draw more general conclusions regarding the relationship between upwelling activity and top-down control by herbivores. This broader analysis also helped us address potential publication bias resulting from upwelling studies publishing null results at consistently lower rates than positive or negative results. While upwelling studies revealing the strongest effects could suggest the presence of a publication bias, this may be the result of careful site-selection and experimental replication by the authors of those studies. While we attempted to address potential publication bias within the upwelling literature, bias could still arise from the selective publication of significant herbivore removal effects over null results among the broader herbivory literature (i.e., studies not focused on upwelling). However, if weak or non-significant herbivore effects are more likely in strong upwelling conditions, but less likely to be published, then our results would be a conservative estimate of the effect of upwelling on herbivory.

While the different analytical approaches discussed above consistently revealed a weakening effect of upwelling on the effects of macrograzers, the analysis of the mesograzers data revealed an overall weak effect, which was not influenced by upwelling activity. This is consistent with previous experimental work revealing weak herbivore effects by mesograzers (Poore, Campbell, & Steinberg, 2009); however, the low number of studies manipulating those herbivores makes it difficult to draw general conclusions.

The weakening effect of upwelling intensity on top-down control revealed by our results is contrary to ecological theory, which predicts that increased primary productivity should support high herbivore densities, leading to stronger top-down control on autotrophs (Oksanen et al., 1981). Results from previous studies examining the influence of upwelling on trophic structure also reveal inconsistencies with theory linking top-down and bottom-up control: in Chile the cover of long-lived algae is highest in sites exposed to strong upwelling activity while the density of herbivores varies independently of oceanographic patterns (Broitman et al., 2001). Similarly, there are no consistent differences in herbivore densities between sites under contrasting upwelling regimes in South Africa or New Zealand (Bosman, Hockey, & Seigfried, 1987; Guerry & Menge, 2017), and studies in California and central Chile reported higher densities in non-upwelling sites (Blanchette et al., 2006; Nielsen & Navarrete, 2004). Those contrasts with theoretical predictions can be explained by a combination of processes linked to upwelling activity. First, upwelled nutrients increase primary productivity and producer growth rates (Blanchette et al., 2006; Bustamante et al., 1995), overwhelming top-down control by herbivores. Second, the offshore advection of larvae by surface currents in strong upwelling areas limits consumer recruitment (Connolly, Menge, & Roughgarden, 2001; Gaines, Brown, & Roughgarden, 1985). Thus, increased primary productivity combined with reduced herbivore recruitment could explain the association between strong upwelling and weak herbivory. While offshore transport can decouple herbivore larval production from recruitment, higher food availability and quality in upwelling zones can support larger herbivores (Bosman, Hockey, & Siegfried, 1987; Pulgar et al., 2013). In turn, larger individuals may have stronger effects on producers relative to smaller individuals, suggesting that per-capita herbivore effects (i.e., herbivore effect divided by herbivore abundance) could be stronger in upwelling zones (as described by Nielsen & Navarrete, 2004). We lacked the data to examine this mechanism; however, a better understanding of how upwelling influences herbivore demography would generate valuable insights into linkages between oceanographic and ecological processes.

The advection of surface water away from the coast may also explain why nutrient and chlorophyll concentrations exhibit different patterns along an upwelling gradient. The offshore flow of water in upwelling centres allows deep water to rise to the surface, increasing the concentration of nutrients along the coast. This increase in nutrient availability should lead to high planktonic primary productivity; however, numerical responses by phytoplankton may lag behind the delivery of upwelled nutrients, and planktonic producers are swept offshore. Indeed, according to the intermittent upwelling hypothesis, the supply of phytoplankton is greatest in sites exposed to intermittent upwelling activity, and decreases with increasing upwelling frequency and intensity (Menge & Menge, 2013). That study focused on the phytoplankton–invertebrate sub-web in intertidal communities, concluding that resource supply and predation pressure should be strongest in sites exposed to intermittent upwelling. The authors also speculated that nutrient supply should increase along a gradient of persistent downwelling to persistent upwelling, while herbivore

effects should decrease along the same gradient (Menge & Menge, 2013), consistent with our results. The intermittency index used in that study was based on ecological and environmental data that were collected previously by the authors in their study sites. Given our meta-analytical approach, we lacked the necessary information to calculate such an index.

In addition to increases in nutrient availability, upwelling events also reduce water temperature along coastlines, and cold upwelled water should decrease metabolic rates, dampening top-down control (Bruno, Carr, & O'Connor, 2015). Research shows that low temperatures indeed lead to reduced grazing rates (Polunin & Klumpp, 1992), and can weaken top-down control on producers (Kishi, Murakami, Nakano, & Maekawa, 2005). While cold temperatures linked to upwelling activity can reduce the activity of consumers (Sanford, 1999), it would be difficult to disentangle the relative influence of cooling and nutrient enrichment on top-down control as both occur simultaneously and are driven by the same process (i.e., upwelling). This is an important interaction to consider in future research as rising ocean temperatures should increase primary productivity and reduce the metabolic constraints imposed by cold upwelled waters (O'Connor, 2009), potentially altering food-web structure and dynamics (Bruno, Carr, & O'Connor, 2015).

The influence of climate change on upwelling activity goes well beyond warming oceans. Changes to coastal pressure gradients due to atmospheric greenhouse gas loading can increase the intensity and duration of equatorward winds and upwelling activity (Bakun, 1990). Stronger and more persistent upwelling can also reduce invertebrate recruitment to coastlines by increasing offshore larval advection (Iles et al., 2012), potentially leading to declines in consumer populations. Increases in greenhouse gas concentrations can alter oceanographic processes at even larger scales by increasing the frequency of El Niño-like conditions (Timmerman et al., 1999). Strong El Niño events can weaken and even cause the cessation of upwelling activity, leading to large declines in edible algal forms and herbivore populations (Vinueza, Branch, Branch, & Bustamante, 2006).

Our coverage of tropical regions was limited by low research effort and the lack of BUI data for low latitudes. Despite the lack of research near the equator, major eastern boundary upwelling regions extend into tropical latitudes where upwelling intensifies and becomes nearly constant (Bakun, 1990). Upwelling centres at low latitudes are ideal systems to examine the ecological processes structuring marine communities in the tropics. Seminal research suggested that shores near the equator are largely devoid of benthic algae due to the strong and persistent action of a diverse suite of herbivores (Menge & Lubchenco, 1981); however, a recent study in the Galapagos archipelago reveals that upwelling activity can relax that top-down control promoting higher algal cover (Vinueza et al., 2014). Warmer surface temperatures in the tropics may also lead to large thermal contrasts between cold upwelling centres and warm adjacent water masses. Such contrasts in environmental conditions raise questions regarding the adaptation of tropical herbivores to cold temperatures. Those questions are particularly intriguing in

seasonal tropical upwelling areas, such as those located along the Central American isthmus (O'Dea, Hoyos, Rodríguez, De Gracia, & De Gracia, 2012), where surface water temperature can vary by 10°C or more (D'Croz & O'Dea, 2007).

Several variables other than upwelling intensity also explained significant variation in herbivore effect among studies. Mean day length had a positive influence on herbivore effects. We included that variable in our analysis to account for relationships between light availability and primary productivity, expecting weaker herbivore effects with higher primary productivity. The positive influence of day length on herbivore effects may instead reflect seasonal patterns of temperature and herbivore activity in which grazing rates are strongest during warmer months (Polunin & Klumpp, 1992), when days are longer. Turbidity also influences light availability in aquatic systems, and the nearly significant positive relationship between turbidity (K_d PAR) and herbivore effects suggests that low light penetration may limit producer growth, leading to increased herbivory (Freidenburg et al., 2007).

The effect of herbivore removal varied among producer functional groups, and the strength of the interaction between upwelling intensity and herbivore effects varied accordingly. Sheet-like algae (foliose and corticated foliose groups) responded strongly to the removal of grazers, and herbivory on those forms was significantly reduced by upwelling activity. Low morphological complexity and a lack of structural defences of foliose and corticated foliose algae may increase their susceptibility to herbivory. However, their high productivity and growth rates may allow those algae to increase their cover rapidly, swamping herbivore effects when nutrient levels are high (Littler, Taylor, & Littler, 1983; Steneck & Dethier, 1994), such as in upwelling conditions. Leathery macrophytes also responded strongly to the exclusion of grazers, but upwelling did not weaken herbivory on that group. The data for leathery macrophytes were dominated by kelps (nearly 75%), which can store nutrients in the form of amino-acids enabling growth during nutrient-poor periods (Zimmerman & Kremer, 1986). As a result, kelps may respond weakly to increases in nutrient supply (Pfister & Van Alstyne, 2003). Thus, variation in the supply of upwelled nutrient subsidies may have little effect on kelp growth rates, leading to weak effects of upwelling activity on top-down control of kelps.

Our results demonstrate that upwelling activity reduces the strength of top-down control by herbivores. The seeming contradiction between ecological theory and our results suggests that the direction of the relationship between primary productivity and top-down control can depend on system-specific processes. In this case, the increases in primary productivity associated with upwelling activity may not generate the strong herbivore effects that theory predicts due to the recruitment and metabolic limitations imposed by the offshore advection of larvae and surface cooling in upwelling areas. Understanding how upwelling influences global patterns of productivity and top-down control of herbivores is crucial for predicting future changes to the structure and dynamics of marine ecosystems. Given the importance of upwelling systems for fisheries (Fréon et al., 2009) such changes could have serious repercussions to human societies.

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DATA AVAILABILITY STATEMENT

The data used in the analysis are available online publicly through the Dryad archive.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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APPENDIX. DATA SOURCES

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