

1 **Global meta-analysis of how marine upwelling affects herbivory**

2 **Running Title:** Upwelling effects on marine herbivory

4 **Abstract**

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

11 Location: Global; marine ecosystems.

13 Time period: 1978-2017.

14 Major taxa studied: Marine herbivores and algae.

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

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

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

32
33 **Keywords:** algae, bottom-up, grazer, nutrients, oceanography, subsidies, top-down

36 **Introduction**

37 Ecosystems are often connected by flows of organisms and materials that represent important
38 resource subsidies, influencing trophic interactions and ecosystem function (Polis, Anderson, & Holt,
39 1997). The regulatory effects of resource flows have become a fundamental feature of ecological theory

40 (Loreau & Holt, 2004), providing insights into connections between ecosystems across large spatial
41 scales (Loreau, Mouquet, & Holt, 2003) and allowing for a more complete understanding of ecosystem
42 function (e.g. Baxter, Fausch, & Saunders, 2005). Nutrient subsidies, in particular, can influence food-
43 web structure and dynamics. Ecological theory predicts that producers are generally limited by their
44 resources (Hairston, Smith & Slobodkin, 1960), and primary productivity determines trophic
45 connectivity and the ability of herbivores to reduce plant biomass (Fretwell, 1987). Nutrient imports can
46 increase primary productivity, which in turn supports high secondary production, leading to strong
47 consumption and top-down control of autotrophs (Shurin, Gruner, & Hillebrand, 2006). In this meta-
48 analysis we examine how nutrient subsidies delivered by marine upwelling, a widely occurring
49 oceanographic phenomenon, influences herbivory across the globe.

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

58 First, high benthic primary productivity in sites exposed to strong upwelling does not always
59 translate into increased densities of benthic herbivores. While high food availability and quality in
60 upwelling sites can increase the reproductive potential of herbivores (Pulgar et al., 2013), offshore
61 currents transport larvae away from the coast, reducing invertebrate recruitment to sites under strong
62 upwelling regimes (Blanchette et al., 2006; Broitman, Navarrete, Smith, & Gaines, 2001). Second, studies
63 examining the effects of upwelling activity on herbivory have yielded mixed results. Experiments in Chile
64 revealed that the strength of herbivore effects did not vary across contrasting upwelling regimes,
65 however, per-capita herbivore effects (total grazer effect divided by the number of grazers) were
66 stronger in upwelling sites (Nielsen & Navarrete, 2004). Similarly, experiments in New Zealand revealed
67 that herbivore effects did not differ between the upwelled western coast and the downwelling eastern
68 coast, but reported stronger herbivory during initial succession in upwelled areas (Menge et al., 1999).
69 However, another study found weaker herbivore effects along the upwelled coast, but those authors
70 examined the effects of herbivores on later successional stages potentially generating different
71 conclusions (Guerry & Menge, 2017). A similar weakening effect of upwelling activity on herbivory was
72 reported along the west coast of North America, but the authors also suggested that upwelling may
73 indirectly strengthen benthic herbivory via shading effects from phytoplankton blooms (Freidenburg,
74 Menge, Halpin, Webster, & Sutton-Grier, 2007). Less research has been devoted to understanding the
75 influence of upwelling in tropical coasts, however, strong upwelling activity in the Galapagos Islands
76 weakened grazer impacts (Vinueza, Menge, Ruiz, & Palacios, 2014). Such variation in outcomes among
77 studies merits further analysis to identify general patterns of influence of upwelling on herbivory, and
78 potential factors that could explain the variation in reported effect-sizes.

79 Here we synthesize data from published experiments in a meta-analytic framework to examine
80 the influence of upwelling on herbivore effects. First, we compare effect-sizes among replicated
81 herbivore-exclusion experiments, designed specifically to examine the influence of upwelling events on
82 herbivory. We then go beyond the upwelling literature, expanding the geographical scale past regions
83 traditionally studied (i.e. western coast of South and North America, and New Zealand). For this, we
84 relied on a broader set of published herbivore-exclusion experiments and examined how the strength of
85 herbivory varies along a gradient of upwelling intensity defined by the Bakun Upwelling Index, or BUI
86 (Bakun, 1973). The temporal dynamics of upwelling activity can also influence the delivery of resources
87 and larvae to coastlines (Menge & Menge, 2013). Thus, we incorporated both upwelling intensity and

88 variability in our global analysis. By expanding our synthesis beyond field-specific studies we seek to
89 reduce the 'file-drawer effect', a well-known issue with meta-analyses (Arnqvist & Wooster, 1995)
90 wherein significant effects are more likely to be published than null results. Since the studies in the
91 broader collection of literature focused on a variety of research questions, publication biases should not
92 be specifically associated with upwelling effects.

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

106 107 108 109 **Methods**

110 111 *Marine herbivory literature search*

112 We compiled studies that measured the response of marine producers to the removal or
113 exclusion of herbivores in intertidal and subtidal environments by searching ISI's Web of Science using
114 the following terms: (graz* OR herbiv*) AND (exclud* OR exclus* OR fenc* OR cage* OR remov*) AND
115 (macrophyte* OR alga* OR seagrass* OR eelgrass* OR seaweed*). We also included studies cited by
116 other meta-analyses of marine herbivory (Burkepille & Hay, 2006; Poore et al., 2012). To meet our
117 criteria, authors must have reduced herbivore densities in exclusion treatments via manual removal, by
118 installing cages or fences, or through chemical means such as copper-based paints and pesticides. At the
119 end of each experiment, authors measured producer percent cover, biomass, density, or growth inside
120 exclusion and unmanipulated (control) treatments. Lastly, all studies reported the mean producer
121 abundance inside the exclusion and control plots, and their respective number of replicates and
122 measure of variance. A list of the data sources is found in Appendix 1 and Appendix S2.

123 124 *Response variable and moderators*

125 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
126 the exclusion treatment, and \bar{X}_c is the mean abundance in the control treatment. Thus, y_i measures the
127 proportional change resulting from the experimental removal of herbivores, such that $y_i > 0$ when
128 herbivore removal results in an increase in producer abundance relative to the control, and $y_i < 0$ when
129 producer abundance is lower in the exclusion relative to the control. We obtained means and standard
130 deviations from each study. When data were reported as time-series, we used the data from the end of
131 the experiment. If a procedural control was used to test for methodological artifacts, we recorded that
132 treatment's mean, deviation, and sample size. Effect-sizes calculated using the mean from the
133 procedural control treatment as the denominator were strong predictors of the effect-sizes calculated
134 using the control treatment means (ANOVA: $F_{1,196} = 5.16$, $p < 0.05$), suggesting that artifacts associated

135 with the exclusion method had little effect on the outcome of experiments. Thus, we used the control
136 means to calculate y_i for the rest of our analysis.

137 For each experiment, we recorded information regarding habitat type, herbivore type, and the
138 method used to exclude them. If enough taxonomic information was provided, we also classified the
139 producer according to functional groups proposed by Steneck & Dethier (1994). Light availability is a
140 determinant of primary productivity, so we estimated the mean day length (MDL) in hours for the
141 duration of each experiment using the 'geosphere' package (Hijmans, Williams, & Vennes, 2017) from
142 the R statistical software (R Core Team, 2018), and used it as a covariate in the analysis. Water clarity
143 may also influence light availability, so we obtained data for diffuse attenuation coefficients of the
144 photosynthetically available radiation (K_d PAR). The K_d PAR provides an indicator of turbidity (Son &
145 Wang, 2015), and is available through the National Oceanographic and Atmospheric Administration's
146 (NOAA) portal for remotely sensed oceanographic data
147 (<https://coastwatch.pfeg.noaa.gov/erddap/index.html>).

148 We quantified the intensity and variation of upwelling at each experimental site using BUI data
149 (Bakun, 1973) obtained from NOAA. The BUI reflects the water flux (cubic meters per second per 100 m
150 of coastline) away from the coast (upwelling; positive values) or towards it (downwelling; negative
151 values). NOAA generates upwelling indices worldwide at 0.5° intervals and a temporal resolution of 6
152 hours; we obtained the data using the 'xtractomatic' package for R (Mendelssohn, Bessey, & Foley,
153 2018). This index has been used to characterize upwelling activity in previous studies (e.g. Menge et al.,
154 1999; Freidenburg et al., 2007; Menge & Menge, 2013), however, it is unreliable for locations in
155 latitudes below 25°, complex coastlines, and small islands (Bakun & Agostini, 2001). We therefore
156 excluded experiments that matched those criteria, as well as studies in estuaries to avoid confounding
157 effects from terrestrial processes. To characterize upwelling regimes, including within year variation, we
158 calculated the mean (BUI_M) and standard deviation (BUI_{SD}) of the six-hourly upwelling indices across two
159 years following the initiation of each experiment.

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

173 174 *Statistical analyses*

175 We used three analytical approaches to assess the robustness of our analysis and consistency of
176 our inferences regarding upwelling's influence on herbivory. First, we focused on the upwelling
177 literature, comparing herbivore effect-sizes between experiments replicated across contrasting
178 upwelling regimes. We used a linear mixed effects (LME) model with each study's classification of
179 upwelling regime as a fixed categorical factor, and the replicate measurements or sites within each
180 study as a nested random factor. We also examined the fixed effect of the BUI_M and BUI_{SD} on effect-sizes
181 using a LME model with the same nested random factor described above.

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

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

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

216
217

218 **Results**

219

220 *Analysis of upwelling literature*

221 Studies designed specifically to compare herbivore effects across upwelling gradients revealed
222 the strongest results. Herbivore effects were on average four times weaker in sites exposed to upwelling
223 activity relative to those where upwelling was weak or absent (LME: -2.20 [-2.34, -2.06]; $p<0.001$; Fig. 2).
224 We also examined the relationship between BUI_M and herbivory which revealed a negative effect of
225 upwelling intensity on herbivore effects (LME: -0.13; [-0.13, -0.11]; $p<0.001$; Fig. 3a). Notably, the BUI
226 data we obtained coincides with the author's classification of upwelling activity in their respective study
227 sites. In other words, BUI_M values from experiments conducted in 'upwelling sites' were consistently
228 higher than values from experiments in 'non-upwelling sites' (Wilcoxon rank sum test: $W=11$, $p<0.001$),
229 providing an additional validation for the metric of upwelling activity. While BUI_M had an important

230 effect on herbivory, effect-sizes were not influenced by BUI_{SD} (LME: -0.02; [-0.03, 0.01]; $p=0.13$).
231 Meanwhile, herbivore effects strengthened with longer days (LME: 9.03 [7.89, 10.16]; $p<0.001$). We
232 could not examine the relationship between K_dPAR and herbivory for the upwelling literature because
233 those experiments were conducted before the earliest K_dPAR data was archived in NOAA's database:
234 2012.

235 236 *Analysis of broader herbivory literature*

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

256 The analysis of the broader collection of herbivory experiments manipulating macrograzers
257 revealed a negative influence of BUI_M on herbivore effect-size (LME: -0.019 [-0.024, -0.014]; $p<0.001$;
258 Fig. 3b). In nine experiments, changes in algal cover were indirectly caused by the exclusion of a
259 predator, rather than the action of a grazer. We repeated the analysis without those data to remove
260 potential bias and again found a significant negative effect of mean BUI_M on herbivory (LME: -0.018; [-
261 0.02, -0.01]; $p<0.001$). Upwelling activity weakened herbivory on two functional groups in particular:
262 foliose algae (LME: -0.06 [-0.07, -0.04]; $p<0.001$; Fig. 4a), and corticated foliose algae (LME: -0.03 [-0.04,
263 -0.01]; $p<0.001$; Fig. 4b). Neither the BUI_{SD} (LME: 0.002; [0.001, 0.006]; $p=0.22$), nor MDL (LME: 0.08 [-
264 0.10, 0.27], $p=0.39$) influenced herbivore effects among the broader collection of studies. The analysis of
265 K_dPAR 's influence on herbivore effects, on the other hand, revealed a nearly significant positive effect
266 (LME: 11.97; [-1.64, 25.58]; $p=0.06$). Our analysis of the mesograzer data did not reveal an effect of BUI_M
267 (LME: -0.0025 [-0.0140, 0.0089]; $p=0.66$) or BUI_{SD} (LME: -0.0006 [-0.0042, 0.003]; $p=0.73$) on herbivory.
268 Longer days (MDL), however, were associated with stronger mesograzer effects (LME: 0.17 [0.041, 0.31];
269 $p<0.01$). We could not examine the influence of K_dPAR on herbivory by mesograzers because that data
270 was only available for three experiments.

271 272 *Analysis of paired experiments*

273 Our third approach, that is pairing independent studies using a nearest-neighbor algorithm,
274 yielded results consistent with the analysis of the upwelling literature: the effect of herbivores was
275 significantly weaker in sites associated with positive BUI_M values relative to sites associated with
276 negative values (Student's T-test: mean difference= -0.99; $t=-3.87$; $p<0.001$). While the two analytical
277 approaches produced similar results, the analysis of the upwelling literature revealed a stronger effect

278 of upwelling activity on herbivory than the pairing approach (Fig. 2). The distribution of negative and
279 positive upwelling values was uneven, and so was the distribution of experiments across grouping
280 variables. Thus, this pairing procedure excluded multiple studies, and the resulting dataset was
281 composed of 108 experimental pairs of high versus low upwelling sites.

282

283 *Relationship between upwelling intensity and environmental parameters*

284 Upwelling activity differentially influenced nutrient and chlorophyll concentrations. Across the
285 studies which reported nutrient availability, nitrate concentrations increased with upwelling intensity
286 (linear model: $F_{1,22}=23.14$; $R^2=0.49$; $p<0.01$; Fig. S3.1). Chlorophyll concentrations followed the opposite
287 trend, however, and decreased with higher BU_{IM} (Spearman's rank correlation: $\rho=-0.42$, $p<0.001$; Fig.
288 S3.2).

289

290

291 **Discussion**

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

309 While the different analytical approaches discussed above consistently revealed a weakening
310 effect of upwelling on the effects of macrograzers, the analysis of the mesograzers revealed an
311 overall weak effect which was not influenced by upwelling activity. This is consistent with previous
312 experimental work revealing weak herbivore effects by mesograzers (Poore, Campbell, & Steinberg,
313 2009), however, the low number of studies manipulating those herbivores makes it difficult to draw
314 general conclusions.

315 The weakening effect of upwelling intensity on top-down control revealed by our results is
316 contrary to ecological theory which predicts that increased primary productivity should support high
317 herbivore densities, leading to stronger top-down control on autotrophs (Oksanen et al., 1981). Results
318 from previous studies examining the influence of upwelling on trophic structure also reveal
319 inconsistencies with theory linking top-down and bottom-up control: in Chile the cover of long-lived
320 algae is highest in sites exposed to strong upwelling activity while the density of herbivores varies
321 independently of oceanographic patterns (Broitman et al., 2001). Similarly, there are no consistent
322 differences in herbivore densities between sites under contrasting upwelling regimes in South Africa or
323 New Zealand (Bosman, Hockey, & Seigfreid, 1987; Guerry & Menge, 2017), and studies in California and
324 central Chile reported higher densities in non-upwelling sites (Nielsen & Navarrete, 2004; Blanchette et

325 al., 2006). Those contrasts with theoretical predictions can be explained by a combination of processes
326 linked to upwelling activity. First, upwelled nutrients increase primary productivity and producer growth
327 rates (Bustamante et al., 1995; Blanchette et al., 2006), overwhelming top-down control by herbivores.
328 Second, the offshore advection of larvae by surface currents in strong upwelling areas limits consumer
329 recruitment (Gaines, Brown, & Roughgarden, 1985; Connolly, Menge, & Roughgarden, 2001). Thus,
330 increased primary productivity combined with reduced herbivore recruitment could explain the
331 association between strong upwelling and weak herbivory. While offshore transport can decouple
332 herbivore larval production from recruitment, higher food availability and quality in upwelling zones can
333 support larger herbivores (Bosman et al., 1987; Pulgar et al., 2013). In turn, larger individuals may have
334 stronger effects on producers relative to smaller individuals, suggesting that per-capita herbivore effects
335 (i.e. herbivore effect divided by herbivore abundance) could be stronger in upwelling zones (as
336 described by Nielsen & Navarrete, 2004). We lacked the data to examine this mechanism, however, a
337 better understanding of how upwelling influences herbivore demography would generate valuable
338 insights into linkages between oceanographic and ecological processes.

339 The advection of surface water away from the coast may also explain why nutrient and
340 chlorophyll concentrations exhibit different patterns along an upwelling gradient. The offshore flow of
341 water in upwelling centers allows deep water to rise to the surface, increasing the concentration of
342 nutrients along the coast. This increase in nutrient availability should lead to high planktonic primary
343 productivity, however, numerical responses by phytoplankton may lag behind the delivery of upwelled
344 nutrients, and planktonic producers are swept offshore. Indeed, according to the intermittent upwelling
345 hypothesis, the supply of phytoplankton is greatest in sites exposed to intermittent upwelling activity,
346 and decreases with increasing upwelling frequency and intensity (Menge & Menge, 2013). That study
347 focused on the phytoplankton-invertebrate sub-web in intertidal communities, concluding that resource
348 supply and predation pressure should be strongest in sites exposed to intermittent upwelling. The
349 authors also speculated that nutrient supply should increase along a gradient of persistent downwelling
350 to persistent upwelling, while herbivore effects should decrease along the same gradient (Menge &
351 Menge, 2013), consistent with our results. The intermittency index used in that study was based on
352 ecological and environmental data that was collected previously by the authors in their study sites.
353 Given our meta-analytical approach, we lacked the necessary information to calculate such an index.

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

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

372 even cause the cessation of upwelling activity, leading to large declines in edible algal forms and
373 herbivore populations (Vinueza, Branch, Branch, & Bustamante, 2006).

374 Our coverage of tropical regions was limited by low research effort and the lack of BUI data
375 for low latitudes. Despite the lack of research near the equator, major eastern boundary upwelling
376 regions extend into tropical latitudes where upwelling intensifies and becomes nearly constant (Bakun,
377 1990). Upwelling centers at low latitudes are ideal systems to examine the ecological processes
378 structuring marine communities in the tropics. Seminal research suggested that shores near the equator
379 are largely devoid of benthic algae due to the strong and persistent action of a diverse suite of
380 herbivores (Menge & Lubchenco, 1981), however, a recent study in the Galapagos archipelago reveals
381 that upwelling activity can relax that top-down control promoting higher algal cover (Vinueza et al.,
382 2014). Warmer surface temperatures in the tropics may also lead to large thermal contrasts between
383 cold upwelling centers and warm adjacent water masses. Such contrasts in environmental conditions
384 raise questions regarding the adaptation of tropical herbivores to cold temperatures. Those questions
385 are particularly intriguing in seasonal tropical upwelling areas, such as those located along the Central
386 American isthmus (O'Dea, Hoyos, Rodríguez, De Gracia, & De Gracia, 2012), where surface water
387 temperature can vary by 10°C or more (D'Croz & O'Dea, 2007).

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

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

411 Our results demonstrate that upwelling activity reduces the strength of top-down control by
412 herbivores. The seeming contradiction between ecological theory and our results suggests that the
413 direction of the relationship between primary productivity and top-down control can depend on system-
414 specific processes. In this case, the increases in primary productivity associated with upwelling activity
415 may not generate the strong herbivore effects that theory predicts due to the recruitment and
416 metabolic limitations imposed by the offshore advection of larvae and surface cooling in upwelling
417 areas. Understanding how upwelling influences global patterns of productivity and top-down control of
418 herbivores is crucial for predicting future changes to the structure and dynamics of marine ecosystems.

419 Given the importance of upwelling systems for fisheries (Fréon et al., 2009) such changes could have
420 serious repercussions to human societies.

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544 **Data accessibility statement:**

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

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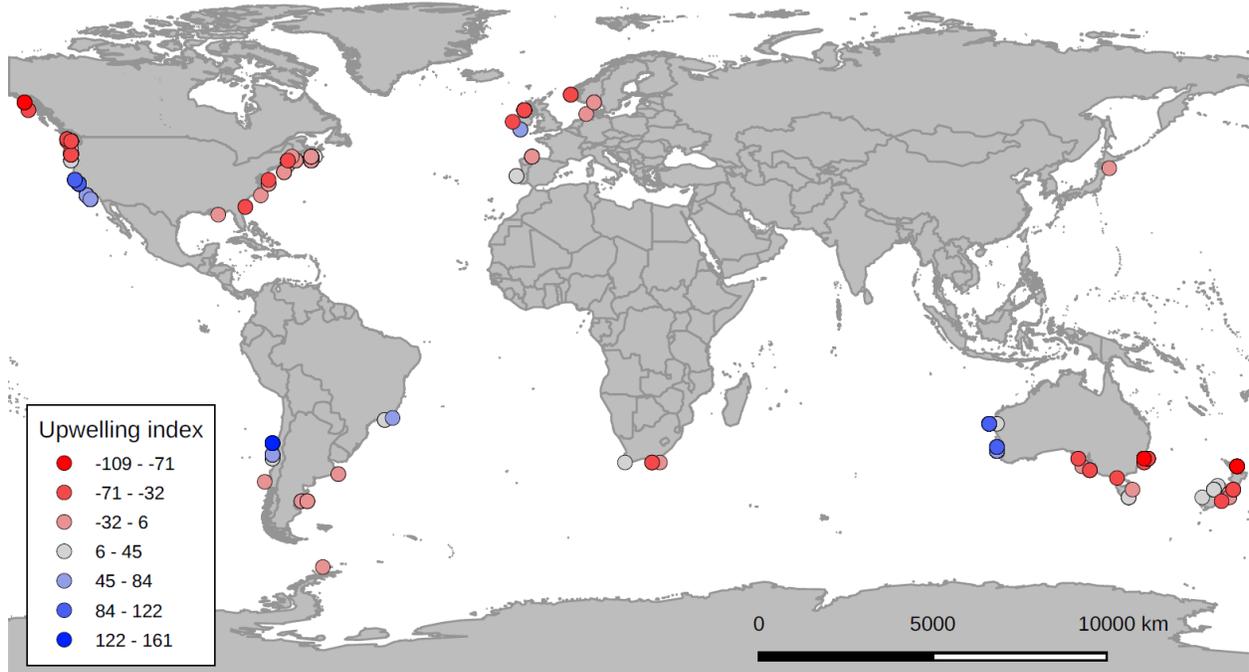
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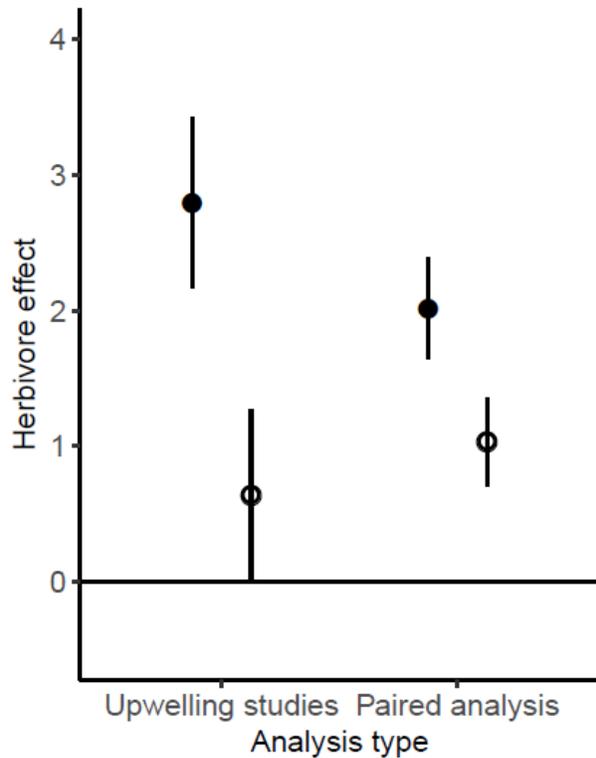
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583 **Figures**
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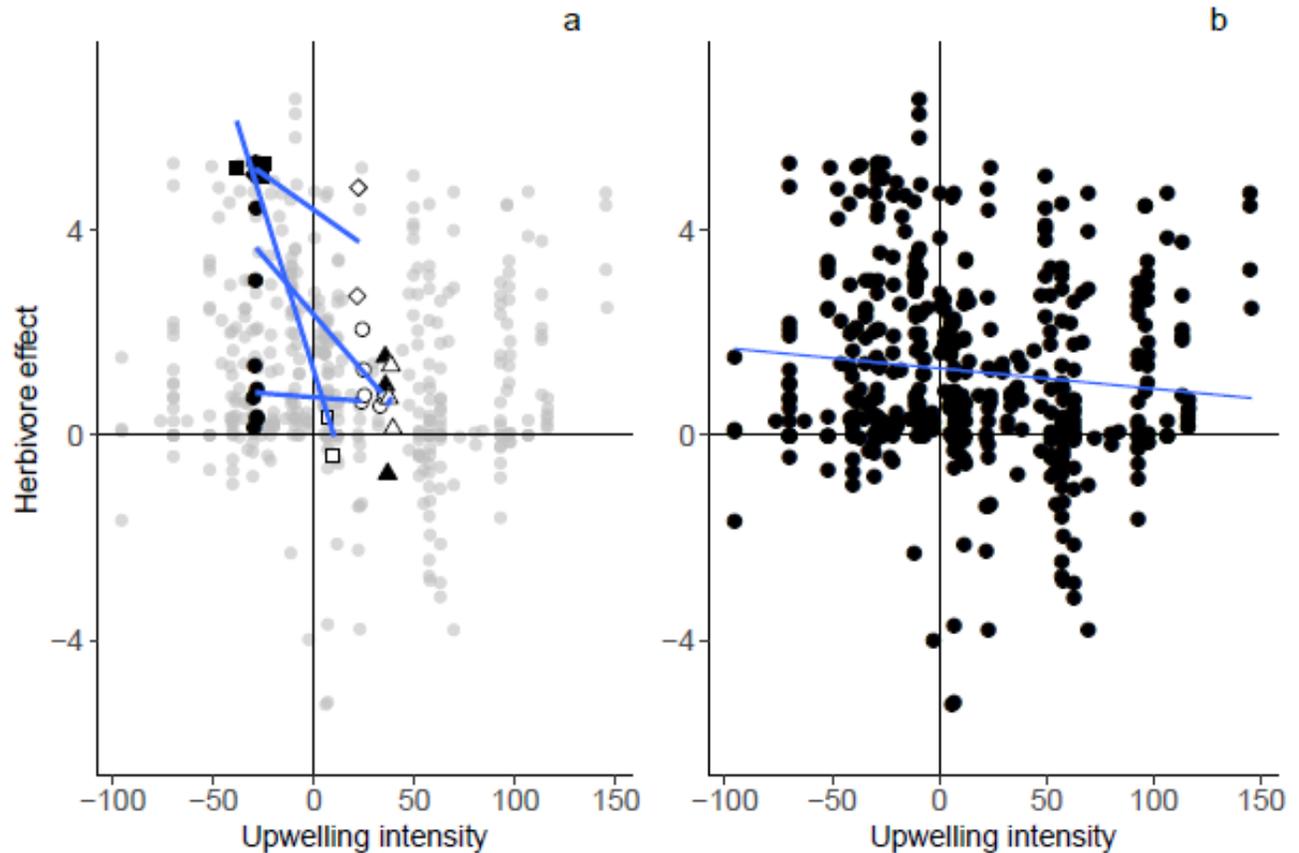


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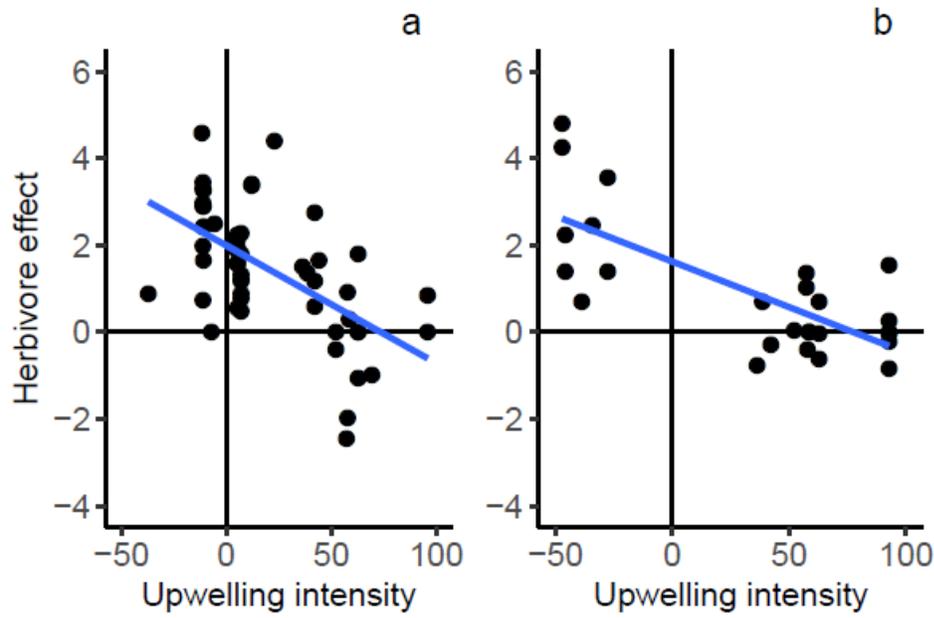
Figure 1. Global distribution of experimental sites for studies included in the analysis. The color of each point reflects the BUI_M values for studies conducted in that location. Positive BUI_M , indicating upwelling sites, are represented by cooler colors (i.e. greens and blues). Meanwhile, negative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



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 597 Figure 2. Comparison of herbivore removal effect in sites under contrasting upwelling activity. Filled
 598 circles correspond to experiments conducted in non-upwelling zones, while open circles correspond to
 599 experiments in upwelling areas. The comparison labeled 'Upwelling studies' corresponds to results from
 600 studies designed to examine the influence of upwelling on herbivory. The results labeled 'Paired
 601 analysis' were those obtained by conducting a pairwise analysis on experimental pairs generated using a
 602 pairing algorithm. Circles represent herbivore effects averaged within each group, and vertical bars
 603 represent 95% CI.
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 607 Figure 3: (a) Relationship between upwelling intensity (BU_M) and herbivore effects, highlighting results
 608 from the upwelling literature. Open symbols depict effect sizes from experiments performed in sites
 609 exposed to upwelling activity, while filled symbols represent results from experiments performed in
 610 sites sheltered from upwelling activity, exposed to weak upwelling, or in areas of active downwelling.
 611 Each shape represents a specific study: o Freidenburg, Menge, Halpin, Webster, & Sutton-Grier, (2007);
 612 ◇ Menge et al., (1999); □ Guerry & Menge, (2017); Δ Nielsen & Navarrete, (2004). Best fit lines were
 613 fitted for each experimental group from a given study. Gray circles in the background represent
 614 herbivore effects from the broader collection of studies. (b) Relationship between upwelling intensity
 615 (BU_M) and herbivore effects for experiments in the broader selection of studies, including results from
 616 upwelling studies. Each circle represents the effect size reported by an individual experiment.
 617



618
 619 Figure 4: Relationship between upwelling intensity ($BUIM$) and herbivore effect for (a) foliose algae and
 620 (b) corticated foliose algae. Each point depicts the result of an individual experiment performed in a
 621 given study, and best-fit lines are fitted to each functional group.

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649 Appendix S1: Results of test of moderators

650 Appendix S2: Summary of data sources

651 Appendix S3: Analysis of relationship between BUI, nutrient concentration and chlorophyll-a
652 concentration.

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