

Seasonal upwelling reduces herbivore control of tropical rocky intertidal algal communities

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Abstract. Communities are shaped by a variety of ecological and environmental processes, each acting at different spatial scales. Seminal research on rocky shores highlighted the effects of consumers as local determinants of primary productivity and community assembly. However, it is now clear that the species interactions shaping communities at local scales are themselves regulated by large-scale oceanographic processes that generate regional variation in resource availability. Upwelling events deliver nutrient-rich water to coastal ecosystems, influencing primary productivity and algae–herbivore interactions. Despite the potential for upwelling to alter top-down control by herbivores, we know relatively little about the coupling between oceanographic processes and herbivory on tropical rocky shores, where herbivore effects on producers are considered to be strong and nutrient levels are considered to be limiting. By replicating seasonal molluscan herbivore exclusion experiments across three regions exposed to varying intensity of seasonal upwelling, separated by hundreds of kilometers along Panama’s Pacific coast, we examine large-scale environmental determinants of consumer effects and community structure on tropical rocky shores. At sites experiencing seasonal upwelling, grazers strongly limited macroalgal cover when upwelling was absent, leading to dominance by crustose algae. As nutrients increased and surface water cooled during upwelling events, increases in primary productivity temporarily weakened herbivory, allowing foliose, turf and filamentous algae to replace crusts. Meanwhile, grazer effects were persistently strong at sites without seasonal upwelling. Our results confirm that herbivores are key determinants of tropical algal cover, and that the mollusk grazing guild can control initial stages of macroalgal succession. However, our focus on regional oceanographic conditions revealed that bottom-up processes regulate top-down control on tropical shorelines. This study expands on the extensive body of work highlighting the influence of upwelling on local ecological processes by demonstrating that nutrient subsidies delivered by upwelling events can weaken herbivory in tropical rocky shores.

Key words: bottom-up control; community assembly; Eastern Pacific; mollusks; nutrient subsidies; oceanography; spatial; temporal; top-down control.

INTRODUCTION

Community structure varies across space and time, and understanding the processes that drive that variation is fundamental to ecology. Early top-down models highlighted the importance of local consumer effects, and predicted that plant biomass was regulated by herbivores (Hairston et al. 1960). Those models eventually incorporated bottom-up regulatory effects, positing that trophic structure and the strength of top-down control

vary along gradients of primary productivity (Oksanen et al. 1981, Fretwell 1987), which is itself influenced by both biotic and abiotic factors (Hunter and Price 1992).

Increasingly, ecologists have recognized that regional-scale processes influence community structure and species interactions by regulating flows of materials and organisms across ecosystems, and supplying resource subsidies to recipient communities (Loreau and Holt 2004). Nutrient subsidies generate strong bottom-up effects by supporting high primary productivity (Polis et al. 1997), which can alter top-down control by increasing producer abundance and herbivore density (Shurin et al. 2006). Thus, primary productivity and the local effects of herbivores may hinge on the supply of nutrient subsidies.

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Classic research on rocky shores highlights the role of local species interactions as determinants of community assembly (Connell 1972, Paine 1974, Menge and Lubchenco 1981), whereas later studies demonstrate that nutrient subsidies delivered by upwelling events support high primary productivity along temperate shorelines (Menge 1992, Bustamante et al. 1995, Blanchette et al. 2006), thereby altering local algae–herbivore interactions across broad geographic scales (Hacker et al. 2019). A recent meta-analysis linking oceanographic data with results from published herbivory experiments found that upwelling events weaken herbivore effects (Sellers et al. 2020). Tropical marine communities may be particularly sensitive to pulses in primary productivity because nitrogen is limiting in warm tropical surface waters (Moore et al. 2013). Indeed, tropical upwelling can alter predator–prey interactions on submerged rock walls (Witman et al. 2010), and influences the distribution of coral and algae (Glynn and Stewart 1973, de Guimaraens and Coutinho 2000), but few studies examine how upwelling influences herbivory across tropical shores (Sellers et al. 2020). In the Galapagos Archipelago, nearly persistent upwelling shapes intertidal communities characterized by high foliose algal cover and weak herbivory (Vinueza et al. 2014). However, upwelling events and the associated nutrient subsidies are often limited to a few months in other tropical regions (e.g., O’Dea et al. 2012), and seasonal pulses in primary productivity may destabilize consumer–resource interactions (Oksanen 1990). Thus, we hypothesized that short-term increases in primary productivity driven by seasonal upwelling events are sufficient to boost producer abundance and weaken top-down control, even in tropical rocky shores where herbivory is generally thought to strongly limit algal growth (Menge and Lubchenco 1981).

To test this hypothesis, we replicated seasonal herbivory experiments along the Pacific coast of Panama, which was the setting for foundational research that helped establish the prevailing perspective that strong top-down control limits macroalgal abundance on tropical rocky shores (Menge and Lubchenco 1981, Lubchenco et al. 1984). That research highlighted the role of fish as determinants of intertidal community structure in the tropics, however, different species or guilds may acquire functional relevance during the initial stages of

macroalgal succession (Aguilera and Navarrete 2012). Slow-moving molluscan grazers, in particular, strongly limit algal recruitment and abundance during initial succession (Menge et al. 1986). In this study we compare the effects of herbivorous mollusks on intertidal algal recruitment and abundance during initial succession between regions exposed to contrasting seasonal upwelling regimes along the Pacific coast of Panama. Upwelling varies seasonally and regionally along that coast (D’Croz and O’Dea 2007), making it an ideal location to test how temporal and spatial variability in oceanographic conditions influence top-down control on tropical coastal ecosystems. Specifically, we address the following questions: (1) can seasonal upwelling events increase macroalgal abundance in tropical rocky intertidal communities? And, (2) is top-down control by tropical intertidal grazers weakened during upwelling events?

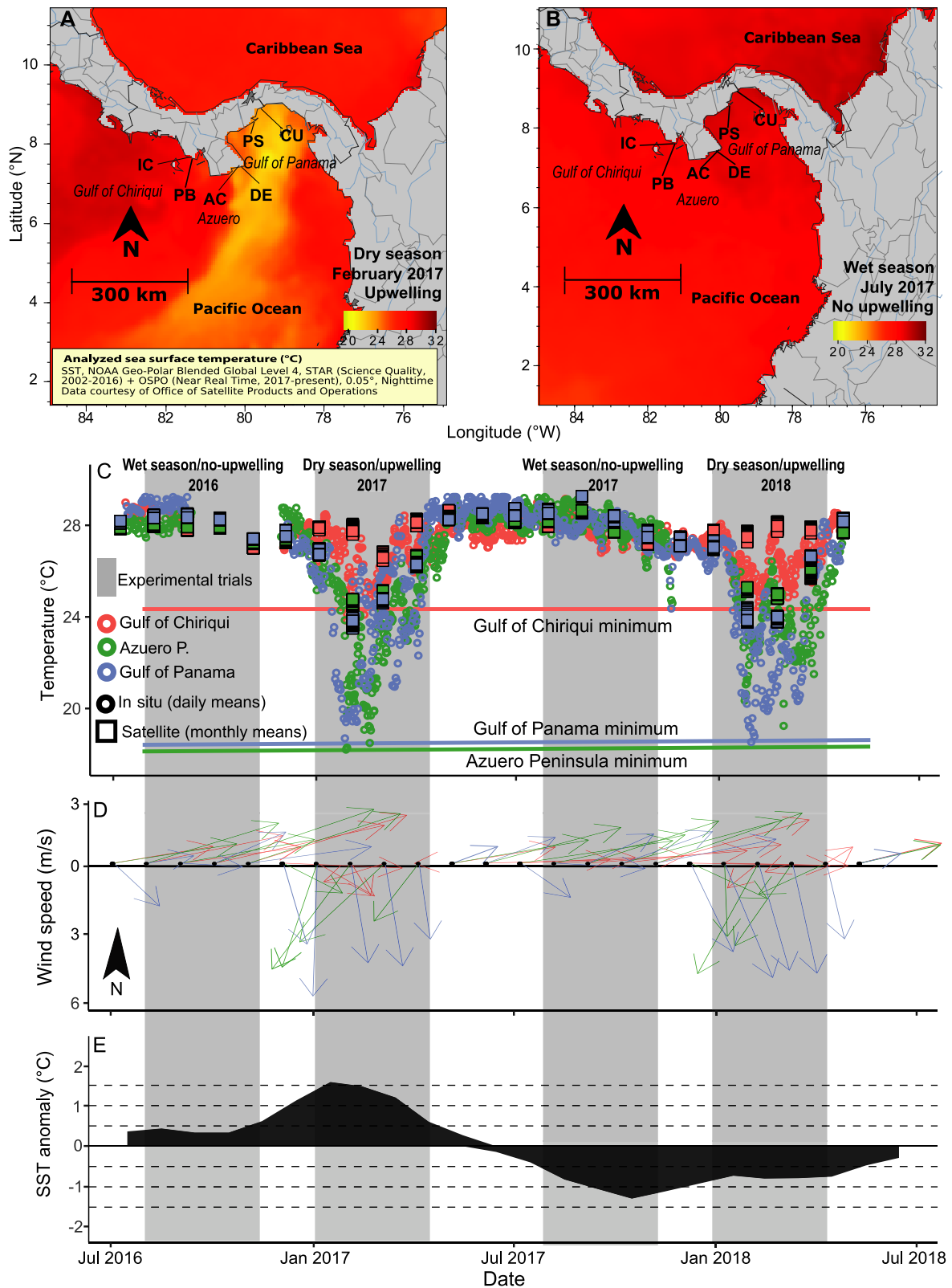
METHODS

Study sites

Panama’s Pacific coast is divided by the Azuero Peninsula into the Gulf of Chiriqui to the west, and the Gulf of Panama to the east (Fig. 1A and B). The Gulf of Panama features a continental shelf that spans 27,175 km², has an average depth of 65 m, and is enclosed to the north, east, and west (D’Croz and O’Dea 2007, Reijmer et al. 2012). Our sites in that region were ~145 km north from the 200-m isobath. In contrast, the continental shelf south of Azuero Peninsula is narrow (<30 km) and shallow (30–50 m; Okaya and Ben-Avraham 1987), and our sites were ~15 km north from the 200-m isobath. The Gulf of Chiriqui features a continental shelf spanning 13,119 km², is enclosed to the north and east, and has an average depth of 110 m (Reijmer et al. 2012). Our sites there were ~45 km north from the 200-m isobath. Tectonic activity in the Gulf of Chiriqui has created a topographically complex bottom compared to the uniform shelf in the Gulf of Panama (Kolarsky et al. 1995).

Weather in Panama is characterized by a dry season between December and April with strong northerly winds and clear skies, and a wet season between May and November with variable winds and frequent rain

FIG. 1. (A) Satellite image of SST along Panamanian coasts during dry season (15 February 2017), and (B) wet season (15 July 2017). Study sites are identified from west to east: Isla Catalina (IC) and Punta Brava (PB) in the Gulf of Chiriqui, Achotines (AC) and Destiladeros (DE) in Azuero, and Culebra (CU) and Playa Serena (PS) in the Gulf of Panama. Maps were generated using NOAA’s GeoPolar data set (<https://coastwatch.pfeg.noaa.gov/data.html>) and downloaded on 21 August 2020. (C) Temporal patterns of water temperature across regions. Circles correspond to mean daily surface water temperature calculated from hourly in situ measurements from iButton sensors. Squares correspond to monthly sea-surface temperature means downloaded for each site from NOAA’s GeoPolar data set. Symbol color corresponds to region: Gulf of Chiriqui in red, Azuero in green, and Gulf of Panama in blue. The same color pattern is used in all figures. Horizontal bars indicate the lowest mean daily temperature for each region, and shaded rectangles indicate each experimental trial. (D) Wind vectors indicating mean wind speed and direction by region. The direction of the arrow represents the cardinal direction to which the wind was blowing. The length of the arrow indicates wind speed, and negative wind speeds are northerly winds (i.e., blowing from north to south). (E) Three-month running mean of monthly SST anomalies for ENSO region 1 + 2, spanning the length of our study. Thresholds for El Niño and La Niña conditions are 0.5 and –0.5 respectively.



(Glynn and Stewart 1973). Northerly dry season winds generate upwelling in the Gulf of Panama and Azuero Peninsula, leading to declines in water temperature (Fig. 1A) and increases in nutrient concentration. Upwelling ceases in all regions during the wet season (Fig. 1B), as winds subside, waters warm, and nutrient concentrations decline (Owen 1997, D'Croz and O'Dea 2007). Mountains to the north of the Gulf of Chiriqui block northerly winds, restricting upwelling in that region (O'Dea et al. 2012). Panama's Pacific coast experiences semi-diurnal tides with an ~6 m tidal range, exposing intertidal organisms to stress from heat and desiccation (Lubchenco et al. 1984).

In each region, we selected two exposed south-facing rocky outcrops composed primarily of basalt, with moderate slopes ($<30^\circ$), few cobbles, and little sand (Fig. 1A, B; Appendix S1: Table S1). We set up our experiments in the low intertidal zone, located 0.5–1 m above mean lowest low water (MLLW), where space availability is high and macroalgal cover is low (Menge and Lubchenco 1981). A diverse suite of consumers regulates algal and invertebrate cover in Panama's Pacific intertidal assemblages (Lubchenco et al. 1984). Upright algae are largely absent, but patches of filamentous and turf algae are sporadic (Earle 1972). Sessile invertebrate cover on the upper surface of rocks is patchy in the Gulf of Panama, and dominated by barnacles, such as *Cthamalus fissus* and *Amphibalanus* sp., and bivalves, including *Ostrea* sp. and *Chama echinata* (Menge and Lubchenco 1981). While past intertidal surveys focused on the Gulf of Panama, our observations while selecting sites in June 2016 indicated that crustose algae dominated all sites, while macroalgae and sessile invertebrates were patchy.

Monitoring environmental conditions

We regularly measured water temperature, dissolved nutrients, and chlorophyll *a* (chl *a*) concentration at every site to characterize nearshore oceanographic conditions. Water temperature was recorded hourly using one or two Thermochron iButtons (Embedded Data Systems, Lawrenceburg, Kentucky, USA) per site secured to the substrate ~1 m below MLLW with Z-spar Splashzone compound (Carboline Company, St. Louis, Missouri, USA). The temperature loggers were submerged except for brief periods (~2 h) during spring tides, and data corresponding to aerial exposure periods were removed from analyses. Nutrient and chl *a* concentrations were measured every two to three weeks throughout each experimental period (see *Herbivore exclusion experiment*). We measured nitrate, phosphate, and ammonium concentration in two to three replicate water samples collected in acid-washed 125-mL high-density opaque polyethylene bottles from roughly 1 m below the surface during the rising tide. The samples were kept on ice for ~12 h before filtering them through 25-mm pre-combusted Whatman glass-fiber filters with

a 0.7 μm pore size. The filtrate remained frozen at -20°C until processing. Nitrate and ammonium concentration was quantified by automated flow injection colorimetry using a Lachat Quikchem autoanalyzer (Hach, Loveland, Colorado, USA). We measured phosphate concentration by molybdate colorimetry using a Trilogy fluorometer (Turner Designs, San Jose, California, USA) following standard protocols (Parsons 2013). We estimated chl *a* concentration from five 25-mL samples that were kept in a dark bag for <30 minutes until analysis with an Aquaflash handheld fluorometer (Turner Designs).

To link local environmental conditions at our sites to regional oceanographic and atmospheric processes, we examined relationships between in situ environmental measurements and remote-sensing data. We downloaded monthly averages of wind speed and direction at a spatial resolution of 0.25° from the Advanced Scatterometer aboard the MetOp-A satellite (Gelsthorpe et al. 2000), within 1° by 1° grids located ~30 km south from each site. We obtained monthly averages of sea-surface temperature (SST) from the National Aeronautics and Space Agency's High Resolution SST Level 4 analysis (JPL MUR MEaSUREs Project 2015), and sourced monthly chl-*a* concentration from the agency's Moderate Resolution Imaging Spectroradiometer (MODIS) on board the Aqua satellite (Minnett et al. 2004). The SST and chl *a* data's resolution were 0.025° and 0.01° , respectively, and were measured within $0.5^\circ \times 0.5^\circ$ grids located ~5 km south of each site. Both cool and warm phases of the El Niño Southern Oscillation (ENSO) cycle have environmental consequences throughout the TEP (Glynn and Colgan 1992). We characterized ENSO conditions corresponding to our experiments by calculating 3-month running means of SST anomalies for ENSO regions 1 and 2 from the Extended Reconstructed Sea Surface Temperature data set (Huang et al. 2017).

Herbivore exclusion experiment

To examine temporal and spatial variation in algal cover and herbivore effects we performed a three-month grazer exclusion experiment, replicated at the six study sites during two wet (August–November, 2016 and 2017) and two dry seasons (January–April, 2017 and 2018). We initiated each trial by clearing the benthic biota from $21 \times 25 \times 25$ cm plots using metal scrapers and wire brushes, then burned the substrate with a propane torch. This allowed us to examine grazer effects during the initial stages of community assembly, when effects of mollusks on algal cover are strongest (Menge et al. 1986). It also enabled us to compare results across seasons and regions, without potential artifacts generated by different initial communities.

We grouped the plots at each site into seven blocks of three plots, and randomly assigned one of three treatments to each plot. The grazer exclusions deterred molluscan grazers (henceforth grazers) with a barrier of

copper strips (Corry's Slug and Snail Copper Tape Barrier, Atlanta, Georgia, USA) and synthetic grass cemented to the rock around the plot's perimeter with Z-spar Splashzone compound. Copper treatments are common and effective in molluscan exclusion experiments (Range et al. 2008). The artificial grass excluded keyhole limpets, which are undeterred by copper (Nielsen and Navarrete 2004). Open controls allowed access to grazers and corners were marked with a dab of epoxy. Procedural controls tested for potential artifacts of our exclusion method, and consisted of discontinuous copper and grass barriers epoxied around 50% of the perimeter. We included a fourth unmanipulated and uncleared treatment to each block to track seasonal changes in the existing sessile assemblages. Procedural and uncleared controls were not included in our first trial: wet season 2016.

Every two to three weeks, we characterized benthic cover, counted mobile consumers inside all plots, and removed any that had infiltrated exclusion plots. Grazer activity increased during nighttime low tides, so we counted consumers at night in September 2016 and February 2017 in three accessible sites: Culebra, Playa Serena, and Punta Brava (Fig. 1A). To quantify sessile growth inside plots, we placed a metal grid with 100 random points and identified the organism under each point to the lowest taxonomic level possible. Algae were grouped into functional groups according to common classifications: foliose, corticated, crustose, filamentous, and articulated coralline (Steneck and Dethier 1994). We collected sessile growth inside each plot when the trials ended to measure algal biomass, however, we did not use those data because it was difficult to remove barnacle fragments prior to weighing samples, making the data unreliable. Thus, our analysis of algal abundance focused on percent cover data.

Molluscan grazer surveys

Differences in grazer density among sites can drive spatial variation in herbivory, thus, in addition to monitoring the abundance of grazers in our plots, we also estimated herbivore density at each site by counting all individuals inside 15–20 0.25-m² quadrats haphazardly placed in the low intertidal. Surveys took place during daytime low tides between April and June 2016 (wet season), and between January and March 2018 (dry season).

Statistical analysis

We used the R statistical software for all analyses (R Core Team 2014). We examined the fixed effect of the interaction between region and season on in situ and satellite temperature, while accounting for the random effect of site, using a linear mixed-effect model (LME) from the lme4 package (Bates et al. 2019). The factor "season" consisted of two levels: dry and wet. We then used Tukey's pairwise analysis from the emmeans

package (Lenth et al. 2019) to test for regional and seasonal contrasts. Nutrient and chl *a* data (in situ and satellite) did not meet normality assumptions after transformation, so we used a Kruskal-Wallis test and a Dunn's test to examine regional and seasonal pairwise contrasts. To examine relationships between in situ and satellite chl *a* measurements, we used Spearman's rank correlation given violations to normality assumptions in the data.

We calculated grazer effects as the difference in non-crustose algal cover between the exclusion and open control plots. We used it in our analyses, instead of percent cover, because it simplified our models by removing a factor for treatment. We used an LME model to test the fixed effect of the interaction between region and season, and a random term for site. We then examined paired spatial and temporal contrasts in herbivore effects using Tukey's pairwise test.

To identify potential experimental artifacts of our exclusion method we compared algal cover between open and procedural controls for each block using an LME model with a fixed term for the interaction between season and treatment, and a random term of block nested within site. We assessed the effectiveness of our exclusion method by comparing the number of grazers inside open controls and exclusion plots using a generalized LME model (GLMM) with a Poisson error distribution, and a random term of block nested within site. We also included a fixed term for season to determine if the number of grazers in our plots varied between contrasting upwelling conditions. To examine spatial and temporal patterns of herbivore density we examined the molluscan survey data using a LME model with a fixed term for the interaction between region and survey period (wet season 2016 and dry season 2018), and a random term for site.

To compare our results to similar studies in temperate shores, we used data from a meta-analysis of studies comparing herbivory across upwelling regimes (Sellers et al. 2020). Following their methods, we recalculated our herbivore effects as $\log(\text{EX}/\text{OC})$, where EX is mean algal cover in exclusion treatments, and OC is the cover in the open controls. Then, we used mixed-effects meta-analytical models from the metaphor package (Viechtbauer 2010) to examine the interaction between latitude (tropical vs. temperate) and upwelling regime.

To test for differences in the abundance of sessile taxa inside uncleared plots between regions and seasons we used a permutation analysis of variance (PERMANOVA; Anderson 2001) from the vegan package (Oksanen et al. 2019), and examined regional pairwise contrasts using pairwise.adonis (Martinez Arbizu 2020). We calculated Bray-Curtis dissimilarities on the squared-root transformed abundance to limit leverage by dominant taxa. To visualize the PERMANOVA results we used nonmetric multidimensional scaling (nMDS), and calculated similarity percentages (SIMPER) to determine the contribution of each taxa to regional contrasts.

RESULTS

Oceanographic conditions

Northerly winds blew over the Gulf of Panama (mean speed $\pm$ SE = 5.96 ± 0.18 m/s) and Azuero Peninsula (5.07 ± 0.13 m/s) in the dry season, while winds in the Gulf of Chiriqui were weaker (1.99 ± 0.09 m/s) and more variable in their direction (Fig. 1D). Greater wind velocity coincided with lower temperatures (Fig. 1C and D), but there was a significant interaction between region and season ($F_{2, 61,701} = 6091$, $P < 0.001$). Pairwise contrasts revealed larger temperature declines during the dry season in the Gulf of Panama (mean seasonal difference $\pm$ SE = $4.23 \pm 0.02^\circ\text{C}$, $P < 0.001$) and Azuero Peninsula ($4.25 \pm 0.02^\circ\text{C}$, $P < 0.001$), than in the Gulf of Chiriqui ($1.37 \pm 0.02^\circ\text{C}$, $P < 0.001$). Daily temperatures reached minima of 18°C in the Gulf of Panama and Azuero Peninsula, but remained above 24°C in the Gulf of Chiriqui. Nitrate concentration increased only in the Gulf of Panama and Azuero Peninsula in the dry season (Fig. 2A; AP vs. GC: Dunn's test: $z = 3.57$, $P < 0.001$; GP vs. GC: $z = 3.19$, $P < 0.01$). In the wet season, southwesterly winds predominated, with average speeds ranging between 2.97 ± 0.12 m/s (Gulf of Panama) to 4.29 ± 0.07 m/s (Azuero Peninsula; Fig. 1D), and water temperature averaged 28°C in all regions (Fig. 1C). Nitrate concentration declined in the Azuero Peninsula and Gulf of Panama in the wet season, but remained higher in the Gulf of Panama than other regions during that period (Fig. 2A; Dunn's test, GP-AP, $z = 2.97$, $P < 0.05$; GP-GC, $z = 2.02$, $P = 0.06$). Ammonium and phosphate concentrations followed similar seasonal and regional patterns as nitrate (Appendix S2: Figs. S1 and S2). Seasonality in chl *a* was limited to the Gulf of Panama (seasonal

contrast = 0.91 ± 0.09 , $P < 0.001$), where concentrations doubled during upwelling events in the dry season (Fig. 2B).

In situ water temperature and chl *a* measurements reflected environmental conditions captured at larger spatial scales using remote sensing tools. Satellite SST data was correlated with in situ temperature ($R^2 = 0.83$, $P < 0.001$), and both data sets followed similar temporal and regional patterns. Satellite SSTs declined in all regions in the dry season ($F_{1,2} = 62.83$, $P < 0.001$), but declines were larger in the Azuero Peninsula and Gulf of Panama (Fig. 1C). In situ and satellite chl *a* measurements were also correlated (Spearman rho = 0.65, $P = 0.001$), and both data sets revealed that chl *a* increases during upwelling months were limited to the Gulf of Panama (Fig. 2B).

The dry season experiments in 2017 coincided with an ENSO warm phase, and was followed by a cool phase that spanned the wet season of 2017 and dry season of 2018 (Fig. 1E). Shifts in ENSO conditions led to small changes in water temperature in all regions. In the Gulf of Chiriqui, in situ dry season water temperatures were higher in the 2017 ENSO warm phase than in the 2018 cool phase ($0.19^\circ \pm 0.04^\circ\text{C}$, $P < 0.05$). We also observed declines in wet season temperatures between 2016 and 2017, as conditions shifted to a cool phase ($-0.53^\circ \pm 0.04^\circ\text{C}$, $P < 0.001$). In the Azuero Peninsula and Gulf of Panama, declines of in situ temperatures between ENSO phases were limited to the wet season (GP $-0.29^\circ \pm 0.03^\circ\text{C}$, $P < 0.05$; AP $-0.34^\circ \pm 0.04^\circ\text{C}$, $P < 0.05$), when upwelling was absent. Nitrate concentration in the Azuero Peninsula and the Gulf of Panama did not vary between the dry season of 2017 (warm phase) and the dry season of 2018 (cool phase; GP, $z = 1.33$, $P = 1.00$; AP, $z = 0.98$, $P = 1.00$).

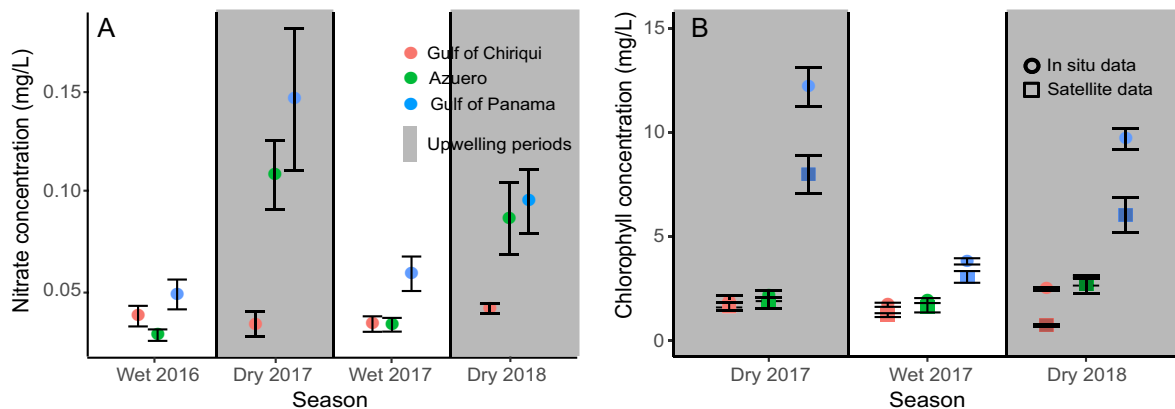


FIG. 2. (A) Nitrate concentration in mg/L across regions and seasons. Points and vertical lines represent means and standard error (SE) at a given region and season. Samples for nutrients and in situ chlorophyll *a* (chl *a*) were collected every two to three weeks during each experimental trial: wet season (August–November) and dry season (January–April). (B) Mean chl *a* concentrations across regions and seasons. Circles are mean in situ chl *a*, while squares are means of chl *a* measurements obtained from MODIS. Vertical bars are SEs.

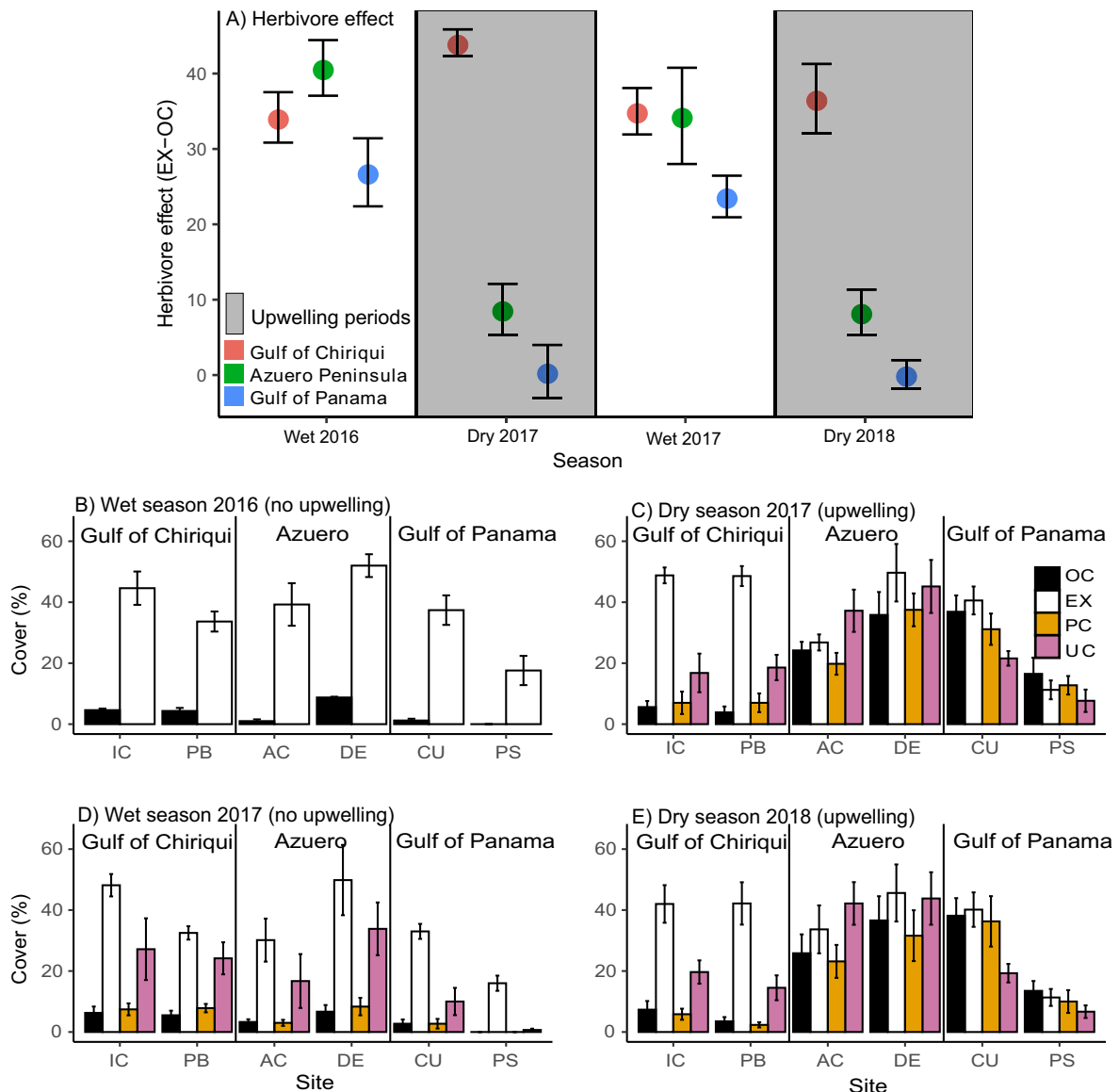


FIG. 3. (A) Effect of grazer exclusion on non-crustose macroalgal cover compared between regions across two dry seasons (2017 and 2018), and two wet seasons (2016 and 2017). Herbivore effect was calculated as the difference between the algal cover in the exclusion and open control plots at the end of each experimental trial. Circles represent mean herbivore effect, and vertical bars are standard errors. Panels B–E show mean percent cover of non-crustose macroalgae inside each treatment at each site at the end of the wet season in (B) 2016 and (D) 2017 and (C) dry season in 2017 and (E) 2018. The color of the bar represents a specific treatment: open control (OC), herbivore exclusions (EX), procedural control (PC), and unmanipulated control (UC). The sites are arranged from west to east, starting with IC and PB in the Gulf of Chiriqui, followed by AC and DE in the Azuero Peninsula, and PS and CU in the Gulf of Panama. PC and UC treatments were added after our first seasonal trial. Vertical lines above bars represent standard errors.

Herbivore experiments

During the wet season, when conditions did not favor upwelling, grazers had strong effects on non-crustose macroalgae (henceforth “macroalgae”) in all regions (Fig. 3A; “Regional contrasts” in Appendix S3). Control plots remained bare, except for increases in crustose algae (Appendix S4: Fig. S1), and macroalgal cover was

less than 5% in all sites. Macroalgal cover in exclusion plots was higher than in open controls (Fig. 3B and D), and the assemblage composition varied regionally. In the Azuero Peninsula and Gulf of Chiriqui, exclusion treatments were settled by algal turf (Appendix S4: Fig. S1) composed by *Jania* sp., small corticated algae (*Gelidiella* sp. and *Hypnea spinnella*), and unidentified filaments. Exclusion plots in the Gulf of Panama were settled by

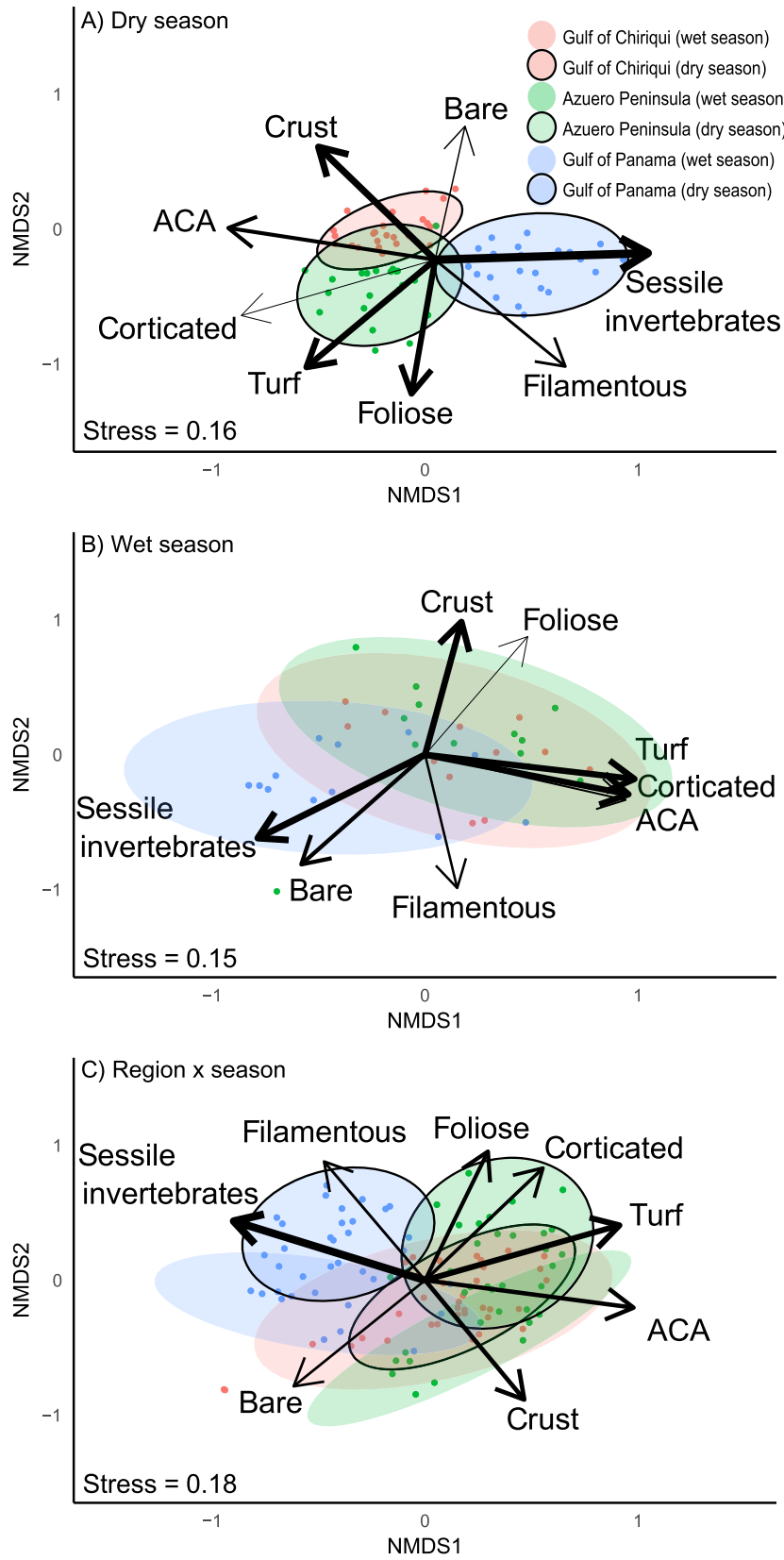


FIG. 4. Nonmetric multidimensional scaling (NMDS) of a Bray-Curtis distance matrix describing regional dissimilarities among assemblages in uncleared plots during (A) dry and (B) wet seasons. (C) NMDS illustrating seasonal and regional contrasts in the functional composition in uncleared plots. Blue points and ellipses correspond to the Gulf of Panama, green to Azuero Peninsula, and red for the Gulf of Chiriqui. Ellipses are 95% confidence intervals around the regional centroids. Ellipses with black borders indicate upwelling, while those without borders correspond to non-upwelling periods. Each point represents one uncleared plot. The stress value in the bottom left of each panel is a measure of the disagreement between the rank order in the original data set and that in the NMDS. Black arrows indicate the contribution of functional groups to dissimilarities among assemblages, where arrow thickness increases with the magnitude of the group's relative contribution (Appendix S7: Tables S1–S3).

turf and filamentous algae, and also by barnacles. Other macroalgae, such as foliose and corticated, were rare in all treatments across all sites during the wet season (Appendix S4: Figs. S1, S2).

In the dry season, when conditions favor upwelling, herbivore effects declined sharply in the Gulf of Panama and Azuero Peninsula, but remained strong in the Gulf of Chiriqui (Fig. 3A; see “Seasonal contrasts” in Appendix S3: Table S1). In the Gulf of Panama and Azuero Peninsula, algal cover increased in all treatments between wet and dry seasons (Fig. 3B–E). In the Azuero Peninsula, turf cover was ~20% in open control and exclusion treatments during the dry season, and foliose algae, which was rare in wet season, established rapidly in all treatments (Appendix S4: Fig. S1). Foliose algae dominated assemblages in the Azuero Peninsula in the first weeks of the dry season trials, but declined in March, as algal turf increased (Appendix S4: Fig. S1). In the Gulf of Panama, foliose algae and barnacles settled in our plots during the dry season (Appendix S4: Fig. S1). Macroalgal cover was higher than 20% in all treatments in the Gulf of Panama and Azuero Peninsula during dry season, however, one site in the Gulf of Panama was an exception: Playa Serena (Fig. 3C, E). Macroalgal cover was below 20% in plots from that site, while barnacles covered ~45% of the substrate. Grazer effects in the Gulf of Chiriqui did not vary seasonally: macroalgal cover was low in open control plots, while turf settled in herbivore exclusion plots (Fig. 3; Appendix S4: Fig. S1). The regional contrasts in herbivore effects we observed during dry season disappeared in the wet season when upwelling ceased (see “Regional contrasts” in Appendix S3: Table S1). We did not observe interannual differences in grazer effects within regions across consecutive wet or dry seasons (Fig. 3A: Table S1; “Seasonal contrasts” in Appendix S3: Table S1), despite contrasting ENSO regimes (Fig. 1E).

Barnacles were the most abundant sessile invertebrate in our plots, and recruited more heavily in the Gulf of Panama than in other regions (Appendix S4: Fig. S1). However, recruitment pulses of the mussel *Brachydontes* sp. occurred at the end of dry season in both years, when upwelling conditions subside in the Gulf of Panama (Appendix S4: Fig. S2).

Non-crustose macroalgal cover was comparable in open and procedural controls, ($F = 0.26$, $P = 0.77$; Fig. 3B–E), indicating the absence of experimental artifacts. Algal cover increased in all controls during the dry

season in the Gulf of Panama and Azuero Peninsula, but not in the Gulf of Chiriqui (Fig. 3B–E).

Our exclusion method was effective in reducing access to molluscan grazers: more were present in open controls than in the exclusion plots during nighttime low tides (open control, mean $\pm$ SE = 7.50 ± 0.52 ; exclusion, 0.03 ± 0.01 ; $z = 5.60$, $P < 0.001$). Differences among treatments were smaller during daytime low tides, when grazers were less active on emergent rocks, but abundance in exclusion plots remained lower (open control, 1.23 ± 0.13 ; exclusion, 0.04 ± 0.03 ; $z = 11.09$, $P < 0.001$). Grazers abundance in open controls was similar during dry and wet seasons (seasonal contrast = 0.2 ± 0.1 , $z = 0.31$, $P = 0.30$). Surveys indicated that grazer densities did not vary consistently across regions ($F_{2,3} = 0.32$, $P = 0.75$), but did vary across sites ($F_{3,105} = 7.90$, $P < 0.001$; Appendix S5). Grazer densities were similar in 2016 and 2018 ($F_{1,2} = 0.86$, $P = 0.35$, Appendix S5). All taxa counted in our plots and surveys are listed in Appendix S6.

Seasonal and regional variation in assemblages of unmanipulated plots

Multivariate analysis of the assemblages in uncleared plots revealed that higher algal cover in the Azuero Peninsula and Gulf of Panama in the dry season led to strong regional contrasts that accounted for 54% of the dissimilarity among assemblages ($F_{2,3} = 39.8$, $P < 0.001$; Fig. 4A). Pairwise contrasts were significant among all three regions ($P < 0.001$, Appendix S7: Table S4). The cover of foliose and turf algae was highest in uncleared plots in the Azuero Peninsula, while algal filaments and sessile invertebrates were most abundant in the Gulf of Panama. Crustose algal cover was highest in the Gulf of Chiriqui (Appendix S7: Table S1, Fig. S1A).

The wet season regional contrasts in uncleared assemblages were weaker than in the dry season (32%, $F_{2,3} = 8.2$, $P < 0.001$, Fig. 4B). Only comparisons between the Gulf of Panama and other regions were significant ($P < 0.001$, Appendix S7: Table S4). Regional differences were driven by a high sessile invertebrate cover in the Gulf of Panama (Appendix S7: Fig. S1B, Table S2). The composition of uncleared assemblages in the Gulf of Chiriqui and Azuero Peninsula overlapped considerably and were dominated by crustose algae (Appendix S7: Fig. S1B).



FIG. 5. Picture of the low zone in our site in Culebra, Gulf of Panama during (A) dry season in February 2019 (B) and wet season in September 2019. The green alga in the top panel is *Ulva* sp., while the yellow algae are *Colpomenia* sp. Photo credit: A. J. Sellers.

Dissimilarities among regions were stronger during the dry season because assemblage composition in the Gulf of Panama and Azuero Peninsula varied seasonally (Fig. 4C). Foliose, turf, and corticated algae increased during dry season in the Azuero Peninsula, while articulated corallines and crusts declined. In the Gulf of Panama, filamentous and foliose algae increased in uncleared plots during dry

season, but barnacles remained common throughout the year (Appendix S7: Fig. S1, Table S3). Assemblage composition did not change significantly between seasons in the Gulf of Chiriqui (Fig. 4C, Appendix S7: Table S3). Seasonal changes in the overall sessile community surrounding our study plots were readily apparent at our upwelling sites (Fig. 5).

Comparison to other upwelling studies

Our reanalysis of the data presented in Sellers et al. (2020), including the results from the present study, revealed that upwelling significantly weakened herbivore effects regardless of latitude (LME, $F_{1,2} = 19.14$, $P < 0.001$). Indeed, we did not find a significant interactive effect of latitude and upwelling regime on herbivore effects ($F_{1,2} = 0.24$, $P = 0.62$).

DISCUSSION

Consumer control was generally strong across our study sites, consistent with previous intertidal work in the tropics (Menge and Lubchenco 1981). However, high nutrient availability and low water temperature during upwelling events in the dry season coincided with increased algal accumulation that outpaced consumption by grazers in upwelled regions. Upwelling events led to temporary shifts in dominance where foliose and turf algae became prominent in sessile assemblages. Grazing was consistently strong in the Gulf of Chiriqui, where nutrient availability and water temperature changed little between dry and wet seasons. While the highest nitrate concentrations we recorded were often an order of magnitude lower than those reported by studies in upwelled temperate shores (e.g., Nielsen and Navarrete 2004), our results indicate that even temporarily limited seasonal upwelling events boost primary productivity and subsequently reduce top-down control in tropical shores.

Algal accumulation and weak herbivory during upwelling periods are likely the result of high nutrient availability as well as metabolic constraints imposed on grazers by low temperatures. Although high nutrient availability may allow algal growth to exceed consumption by grazers, we did not measure algal growth because individual algal thalli were too small to track in the field. Transplant experiments using larger macrophytes in Chile, however, show that *Mazzalaea laminaroides* can grow up to 2.5 times faster under strong upwelling conditions (Nielsen and Navarrete 2004). Cold upwelled waters may also weaken top-down control by slowing consumer metabolic rates (Bruno et al. 2015). Even small changes in water temperature due to upwelling can slow consumer activity (Sanford 1999), however, it is unclear how changes in metabolic rates are linked to top-down control. While disentangling the effects of surface cooling and nutrient increases in field studies is difficult, carefully designed mesocosm experiments may shed light on the relative contribution of each parameter to the weakening of grazer effects.

We assessed the effect of intertidal molluscan grazers on algal cover during initial succession, when molluscan grazers strongly limit algal establishment (Menge et al. 1986) by feeding on microalgae and algal spores (Underwood 1979). Our exclusion experiments confirm that molluscan grazers strongly limit algal cover during initial succession. However, other herbivores such as crabs

and fish were not excluded from our plots, and they are known to control ephemeral algae in tropical shores (Menge et al. 1986). Crabs and fish may have reduced algal biomass in our study by cropping algal growth, or altered cover by removing entire algal thalli. While this implies that our experiments underestimated herbivore effects, it also suggests that the exclusion of even one grazer group can alter community assembly in tropical rocky shores. Our ongoing work aims to experimentally compare the effects of different herbivore guilds, and how they vary between contrasting upwelling regimes.

The interannual and seasonal water temperature patterns we describe are consistent with a contemporaneous study showing that upwelling in the Gulf of Panama acted as a thermal buffer against increases in temperature during the 2016–2017 El Niño (Randall et al. 2020). Our results indicate that as ENSO conditions shifted from a warm phase to a cool phase, wet season and dry season water temperatures declined in the Gulf of Chiriqui. In the Gulf of Panama and the Azuero Peninsula, those declines were limited to the wet season, and dry season temperatures did not change between ENSO phases. Thus, upwelling temperatures in the Gulf of Panama and Azuero Peninsula were not influenced by shifting ENSO conditions. El Niño events can severely weaken equatorial upwelling, causing algal declines and grazer mortalities in the Galapagos (Vinueza et al. 2006). We did not observe significant changes in community assembly between contrasting ENSO phases, however, we lack the long-term data needed to disentangle the ecological consequences of seasonal upwelling from those of interannual ENSO cycles.

Seasonality in water temperature, nutrient availability, and algal cover were similar in both seasonally upwelled regions, whereas dry season increases in chl *a* were limited to the Gulf of Panama where sessile invertebrate cover was highest. We hypothesize that differences in the width of the continental shelf and coastal morphology (upwelled headland vs. bay) between the Azuero Peninsula and Gulf of Panama contribute to such differences. Weak cross-shelf currents over gulfs with wide shelves (e.g., Gulf of Panama) may favor larval retention, phytoplankton blooms, and larval recruitment. In contrast, offshore transport in upwelled headlands with narrow shelves (e.g., Azuero Peninsula) may limit recruitment and sessile invertebrate cover (Kirincich et al. 2005, Pfaff et al. 2011). Further studies are needed to understand the mechanisms underlying the apparent persistent differences in recruitment between these regions, and how they are influenced by topographic modulation of coastal flows.

The intermittent upwelling hypothesis (IUH) predicts that strong and persistent upwelling supports high macroalgal cover, while frequent upwelling relaxation periods favor high chl *a* concentrations, larval recruitment, and sessile invertebrate cover (Menge and Menge 2013). The IUH has not been tested in the tropics, but our results and those from studies in the Galapagos allow us to coarsely evaluate the hypothesis' predictions

in tropical shores. Results from intertidal research in the Galapagos are consistent with the IUH: intertidal sites exposed to strong and nearly persistent upwelling are dominated by macroalgae and have low barnacle cover. Meanwhile, algal cover is lower and barnacle cover increases in sites exposed to weaker and more irregular upwelling (Vinueza et al. 2014). Our results indicate that sessile invertebrates are more abundant in the Gulf of Panama, where short upwelling seasons are followed by prolonged upwelling relaxation periods. Together, the two studies suggest that the IUH may help explain regional differences in intertidal community structure across the TEP. However, in contrast, an earlier study indicated barnacle cover and recruitment increase with upwelling intensity and frequency (Witman et al. 2010). In order to reconcile these seemingly contradictory results, and properly test the predictions of the IUH in the TEP, it is necessary to carefully define the spatial scales of variability in surface advection across upwelling regimes over the dispersal scales of the dominant species involved, and then establish replicated experiments, surveys, and environmental monitoring efforts across the region.

Tropical marine algae are considered to be strongly regulated by herbivores (Menge and Lubchenco 1981, Longo et al. 2014). Our experimental results from Panama support these predictions, however, by comparing the effects of grazers on community assembly across contrasting upwelling regimes we demonstrate that large-scale oceanographic processes can alter the outcome of algal-herbivore interactions on tropical shores. Our findings confirm those of a recent meta-analysis of herbivore exclusion experiments from largely temperate regions showing that upwelling weakens herbivory (Sellers et al. 2020). By reanalyzing their data with results from our experiments on tropical locations we show that upwelling's weakening effect on herbivory is similar across latitudes. Thus, even on tropical shores, where herbivore effects are thought to be strongest, large-scale oceanographic processes such as upwelling can temporarily overwhelm top-down control of marine primary producers.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecy.3335/supinfo>

DATA AVAILABILITY

The raw data for the experimental results, molluscan grazer counts inside the plots, and grazer surveys (Sellers et al. 2021) are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.br15dv7n>.