

Stronger predation intensity and impact on prey communities in the tropics

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Abstract. The hypothesis that biotic interactions strengthen toward lower latitudes provides a framework for linking community-scale processes with the macroecological scales that define our biosphere. Despite the importance of this hypothesis for understanding community assembly and ecosystem functioning, the extent to which interaction strength varies across latitude and the effects of this variation on natural communities remain unresolved. Predation in particular is central to ecological and evolutionary dynamics across the globe, yet very few studies explore both community-scale causes and outcomes of predation across latitude. Here we expand beyond prior studies to examine two important components of predation strength: *intensity* of predation (including multiple dimensions of the predator guild) and *impact* on prey community biomass and structure, providing one of the most comprehensive examinations of predator–prey interactions across latitude. Using standardized experiments, we tested the hypothesis that predation intensity and impact on prey communities were stronger at lower latitudes. We further assessed prey recruitment to evaluate the potential for this process to mediate predation effects. We used sessile marine invertebrate communities and their fish predators in nearshore environments as a model system, with experiments conducted at 12 sites in four regions spanning the tropics to the subarctic. Our results show clear support for an increase in both predation intensity and impact at lower relative to higher latitudes. The predator guild was more diverse at low latitudes, with higher predation rates, longer interaction durations, and larger predator body sizes, suggesting stronger predation intensity in the tropics. Predation also reduced prey biomass and altered prey composition at low latitudes, with no effects at high latitudes. Although recruitment rates were up to three orders of magnitude higher in the tropics than the subarctic, prey replacement through this process was insufficient to dampen completely the strong impacts of predators in the tropics. Our study provides a novel perspective on the biotic interaction hypothesis, suggesting that multiple components of the predator community likely contribute to predation intensity at low latitudes, with important consequences for the structure of prey communities.

Key words: *biotic interaction hypothesis; Eastern Pacific Ocean; experimental macroecology; fish; invertebrates; latitudinal gradient; marine biogeography; predator–prey interactions; recruitment.*

INTRODUCTION

The biotic interaction hypothesis suggests that species interactions are stronger at lower compared to higher latitudes (Schemske et al. 2009). This hypothesis has roots in classic evolutionary predictions that the benign and stable climate of the tropics leads to strong and

specialized interactions, which may increase diversification rates and help explain the origin of high tropical biodiversity (Dobzhansky 1950, Fischer 1960, Mittelbach et al. 2007). Beyond evolutionary expectations, however, lies a fundamental ecological prediction that stronger interactions at lower latitudes could shape global patterns of community assembly, community structure, and ecosystem functioning, rendering latitudinal variation in species interactions a principal tenet of contemporary community ecology.

Predator–prey interactions are central to ecosystem dynamics, and a change in predation strength with latitude is likely to have significant implications for how communities are structured over ecological and

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evolutionary time across the globe (Menge and Lubchenco 1981, Albouy et al. 2019, Silvestro et al. 2020). Although evidence continues to accrue in support of the prediction that predation intensity is stronger at lower latitudes (e.g., Schemske et al. 2009, Roslin et al. 2017, Reynolds et al. 2018), debate on its generality persists (Roesti et al. 2020). Further, variation in predation strength across latitude likely has important ecological consequences for prey communities, yet studies that document such community-scale effects, or impacts of predation, are rare (but see Freestone et al. 2011, Lavender et al. 2017, Dias et al. 2020, Freestone et al. 2020). Testing the prediction that both predation *intensity* and *impacts* on prey communities are greater at lower latitudes requires standardized experiments and observations on multiple components of a system across continental scales. Few studies employ such approaches, however, given the challenges associated with standardizing meaningful measures of interaction strength and prey community attributes across wide latitudinal ranges and distinct biogeographic regions.

To quantify predation *intensity*, studies that span biogeographic scales often assess predation rates (Jeanne 1979, Bertness et al. 1981, Heck and Wilson 1987, Roslin et al. 2017, Hargreaves et al. 2019, Longo et al. 2019, Roesti et al. 2020, Whalen et al. 2020), which have clear value in estimating top-down forcing in a community. Multiple dimensions of the predator community, however, contribute to predation intensity beyond predation rates and can vary among regions. Functional attributes of predators, such as body size, can influence predation intensity (Longo et al. 2019), as larger-bodied predators are likely to increase consumption to meet metabolic demands (Brown et al. 2004). More diverse predator communities, as are expected to occur at lower latitudes (Hillebrand 2004), can also increase top-down control of prey density through either the increased likelihood of including a strong predator or niche complementarity among predators (Menge et al. 1986, Griffin et al. 2013). Further, the more time predators spend interacting with focal prey communities during foraging periods, or the interaction duration, may indicate tighter species associations or a high local density of predators, which can have ecological consequences for prey (Griffen and Williamson 2008). Therefore, a challenge lies in integrating detailed experimentation and observation to understand how attributes of predator communities affect interaction intensity across latitude.

Variation in predation intensity can also result in significant *impacts* on prey communities, which can have clear ecological importance. Community-scale biomass removal of prey, for example, is critical to aggregate processes like trophic transfer and ecosystem functioning (Gamfeldt et al. 2015). Predation can further influence fundamental processes of prey community assembly and stability, thereby shaping multiscale patterns of prey composition and diversity (Chase et al. 2009, Jurgens et al. 2017). Intense predation may not always result in

substantial community impact, however, depending on the extent of biomass removal per predation event, the relative abundance of impacted species, the diet breadth of predators, and compensatory dynamics in prey growth or recruitment (Vieira et al. 2016, Zvereva et al. 2020). Prey recruitment rates in particular can vary substantially across latitude (Menge 1991, Connolly et al. 2001, Freestone et al. 2009), with the potential to replace prey after predation and even swamp predator effects (Cheng et al. 2019). Understanding the extent to which multiple dimensions of predation intensity correspond to impacts on prey communities across continental scales is largely unexplored.

Using standardized and replicated experiments in nearshore marine habitats across 47 degrees of latitude, from the subarctic to the tropics, we tested the hypothesis that predation pressure is stronger and shapes prey communities at lower latitudes. We focused on both key dimensions of predation *intensity* (i.e., predation rates, predator body size and diversity, and interaction duration) and community-level *impacts* of the interaction (i.e., effects of predation on prey biomass and community structure). To assess predation intensity, we used direct in situ observations of predators interacting with our experimental prey communities, and to quantify predation impact, we used two independent experiments. We further tested for latitudinal patterns in prey recruitment to explore the potential for this process to mediate predation impacts. This suite of coordinated experiments and observations represents the most detailed data to date on latitudinal gradients in predation intensity and community-level impacts, providing an integrative and novel test of the biotic interaction hypothesis.

METHODS

Study system

Sessile marine invertebrate communities and their predators provide an exceptional model for understanding predator–prey interactions across latitude. These invertebrate prey communities consist of a diverse multi-phyletic group (including ascidians, bryozoans, sponges, polychaete worms, barnacles, mollusks, and cnidarians) that colonize both natural and artificial substrates and exhibit a wide variety of growth forms, reproductive strategies, feeding behaviors, and predator defense adaptations. Further, these hard-bottom marine systems are especially conducive to experimental manipulations on meaningful temporal and spatial scales (e.g., Connell 1961, Paine 1966). A diverse guild of vertebrate and invertebrate predators consume these invertebrate prey, but we concentrate on fish as an important component of this guild.

We focused our study of subtidal marine systems on the Pacific coast of North America and Central America, contrasting subarctic, temperate, subtropical, and tropical communities across 47 degrees of latitude

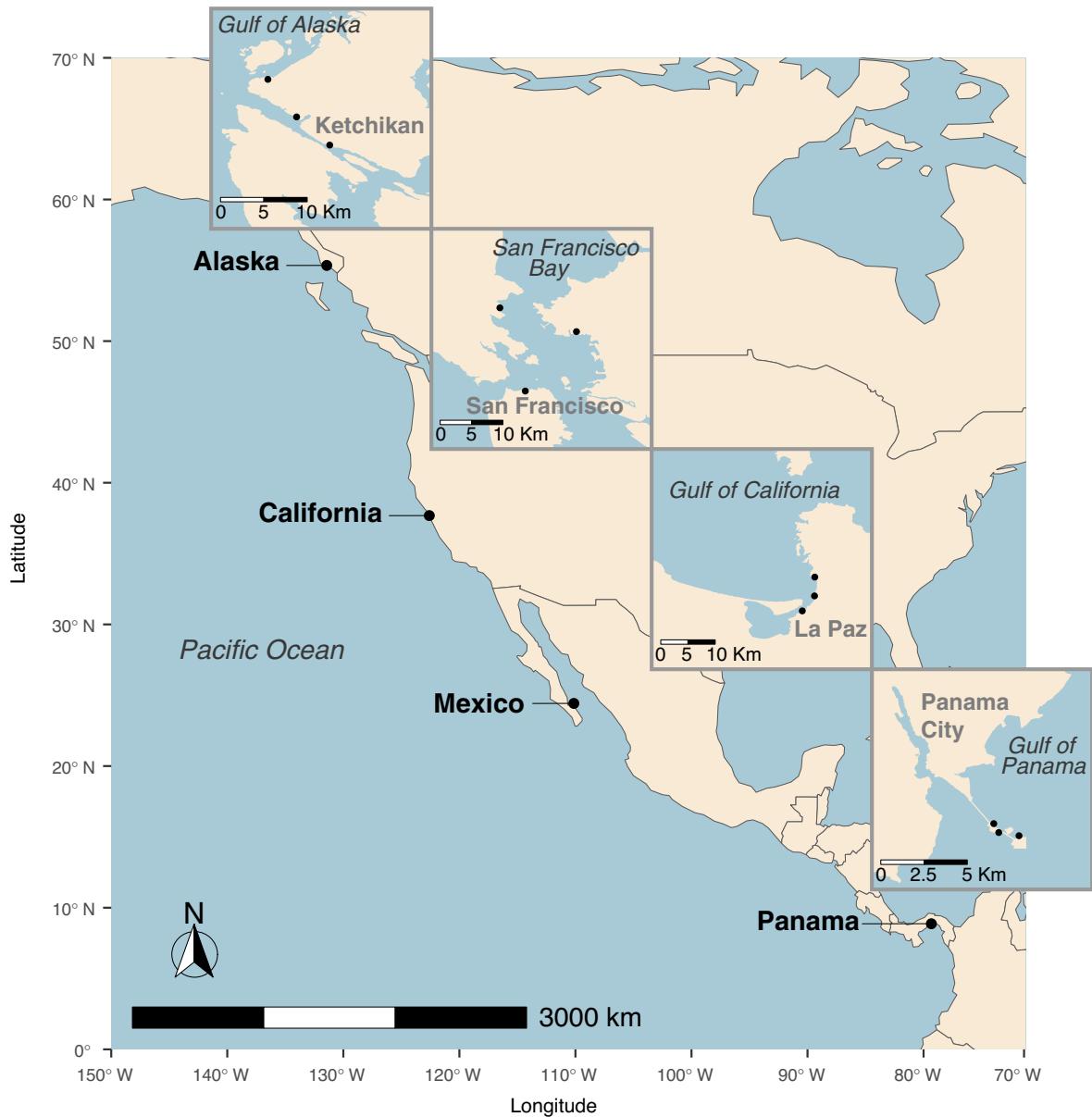


FIG. 1. Experiments were conducted at three sites (locations shown as black dots in insets) in each of four regions, for 12 study sites across the latitudinal gradient.

(~7,000 km; Fig. 1). This coastline is ideal for latitudinal comparisons given its continuity from the equator to the Arctic. We conducted experiments at three sites in each of four study regions, for 12 sites across the latitudinal gradient (Fig. 1). Focal regions were (1) subarctic Ketchikan, Alaska (55° N, 131° W), (2) temperate San Francisco, California (37° N, 122° W), (3) subtropical La Paz, Mexico (24° N, 110° W), and (4) tropical Panama City, Panama (8° N, 79° W). Each site was a marina in high salinity (mean >20 ppt) habitat with low exposure to wave activity, and was selected within these

abiotic constraints without regard to the biological communities present. Sites were independent in that distances among marinas and shoreline topography were sufficient to limit larval dispersal of many invertebrates among sites. Therefore, we included three sites to capture the local-scale biological variation present in each region and provide a robust test of our experimental treatments given this random variability. Further, marinas can be useful as model habitats with which to explore biogeographic patterns in coastal marine communities that parallel patterns in more natural systems (Rodemann and Brandl 2017).

One challenge to large-scale comparative studies is standardizing key variables, such as habitat type, among biogeographically distinct regions. Thus, we used uniform prey habitats to reduce confounding variability that could result from differences in substrate type, depth, area, and complexity, or community age or history. We deployed PVC settlement panels as a simplified model habitat, which allowed for hundreds of standardized replicate communities to develop in situ as planktonic larvae of the invertebrates settle and grow on the panels. These communities assembled naturally and are subjected to similar ecological dynamics as communities on natural substrates. In particular, predation pressure observed on these experimental substrates can mimic dynamics on natural substrates (Freestone et al. 2020), and use of settlement panels allows for the direct quantitative comparison of community dynamics across biogeographic regions (Freestone and Osman 2011, Freestone and Inouye 2015, Lavender et al. 2017).

We further standardized experimental deployment protocols and timing across the latitudinal gradient. Panels were 14 cm × 14 cm × 0.95 cm, and the surfaces were sanded to facilitate invertebrate recruitment. Experimental panels were hung from floating docks at 1-m depth. By hanging the panels, we limited access to our prey communities by benthic predators to more clearly focus on the contributions of predatory fish as a component of the predator guild. Panels were at least 1 m apart, and the experimental surface was oriented horizontally facing the sea floor to deter algal growth. Panels were assigned at random to experimental treatments, as outlined below. Experiments were deployed in Alaska in June 2015, California in May 2016, Mexico in June 2017, and Panama in December 2015. Like most biological systems in the Northern Hemisphere, high-latitude regions undergo strong seasonality, with growth and reproduction peaking in the warmer summer months and tapering off substantially in colder months. Growth and recruitment can occur year-round in the tropics, but on the Pacific coast of Panama, primary productivity generally peaks during periods of upwelling in the dry season (December–April; Sellers et al., 2021). Therefore, experiments in all regions were conducted during seasons of high productivity and recruitment that extended throughout our experiments.

Predator exclusion experiment

To test the hypothesis that predation *impact* on prey communities is stronger at lower latitudes, we conducted a 3-month predator exclusion experiment on prey community assembly. Three exclusion treatments were used: (1) low predation treatment (caged), (2) ambient predation control (no cage), and (3) ambient predation procedural control (partial cage). Cages and partial cages (18 cm × 18 cm × 7 cm) were constructed out of marine-grade plastic with a 6.35-mm mesh, which effectively excluded our focal predators but was unlikely to

eliminate all predation (i.e., micropredators; Freestone et al. 2011). Partial cages had four sides but no front, which faces the seafloor when deployed, to control for shading and alteration of flow dynamics due to the caging material while allowing full access to the predator community. Panels were deployed independently; therefore, each cage or partial cage had a single panel. Each of the three treatments was replicated five times at each of three sites within the four regions, for 180 panels across the latitudinal experiment. Cages were cleaned (to prevent overgrowth) and maintained every 2 weeks. Panels were retrieved after 3 months of community assembly and weighed for a measure of biomass (wet weight [g] of prey community including standardized panel). Communities were then examined under a stereoscope to estimate total richness of sessile invertebrates, with individuals identified to the lowest taxonomic resolution possible, or assigned a consistent morphospecies identifier. Abundance was measured as percent cover across 50 points (7 × 7 grid plus one random point). Specimens of each species/morphospecies observed at each site were collected, and taxonomic experts and DNA barcodes verified field identifications whenever possible.

Predator exposure experiment

To test the hypothesis that predation *intensity* and *impact* are stronger at lower latitudes, we conducted a short-term, 3-d predator exposure experiment on mature prey communities after a 3-month assembly period. This experiment provided an independent assessment of predation impact, to complement the predator exclusion experiment that measured impact on prey community assembly. The exposure experiment further provided opportunity for paired measurements of predation intensity. We deployed 10 caged panels at each site ($N = 120$) at the onset of the exclusion experiment to allow prey communities to develop under low predation. Cages were cleaned and maintained every 2 weeks as in the exclusion experiment. After 3 months, panels were retrieved, weighed for biomass, and redeployed in their initial locations. For redeployment, cages were removed from five random panels per site to expose those communities to ambient predation, and the remaining five panels were recaged as controls. After a 3-d exposure period, panels were retrieved and again weighed for biomass.

To observe predator–prey interactions in situ directly and assess predation *intensity*, we used high-definition GoPro underwater cameras to film diurnal predation on exposed communities (five panels/site, $N = 60$). Small racks held the cameras a fixed distance (0.4 m) from the panel, with the panel oriented vertically in the water column to maximize ambient light. Racks were deployed at 1-m depth as above. Experiments and cameras were deployed simultaneously on the first morning of exposure once sufficient ambient light enabled filming.

Filming continued for approximately 2+ h and was repeated each subsequent morning of the 3-d experiment. We processed the first four hours of footage for each prey community as a sample of predator activity, generally 2 h from the first and second days of exposure, rendering a total of 240 h of observation across the latitudinal gradient. Predation rates (i.e., strikes/exposure hour) per predator taxa, interaction duration (i.e., the total duration that predators were adjacent to the prey community and feeding, per exposure hour), and mean predator size (estimated length based on size relative to panel, cm) were recorded for each panel.

Recruitment experiment

We conducted a detailed assessment of prey recruitment at each site to understand biogeographic variation in recruitment rates and the *impact* of predators on abundance of recruits through postsettlement mortality. Clean panels were deployed and then retrieved at each site every 2 weeks during the 3-month experimental period. Two weeks is sufficient to observe both early recruitment dynamics as well as postsettlement mortality due to predation in this system (Stachowicz et al. 2002, Osman and Whitlatch 2004, Freestone et al. 2020). Recruitment sampling continued until completion of all experimental retrievals as outlined above, for up to eight 2-week recruitment periods per region. To provide a measure of recruitment under reduced and ambient predation pressure, three panels were deployed in each of the three treatments that were used in the exclusion experiment (caged, no cage, partial cage). This design yielded nine panels per 2-week recruitment interval at each site and 792 panels across the latitudinal gradient. Cages were cleaned and maintained every 2 weeks. Upon retrieval, we recorded the total number of invertebrate recruits on a 10 × 10 cm standardized subsection of each panel using a stereoscope.

Data analysis

To test for predation *impacts* from the exclusion experiment, we measured four attributes of prey communities: biomass, taxonomic richness, taxonomic diversity (Shannon diversity index, H'), and composition. For richness, which had integer response data, we compared an ordinary least-squares linear mixed model with a Gaussian distribution (hereafter, OLS model) to generalized linear mixed models (GLMMs) with Poisson and negative binomial distributions. Comparisons were made via model selection with Akaike's information criterion (AIC) values, and the OLS model performed best. Treatment differences for continuous responses (biomass and diversity) were also modeled with OLS. Biomass was natural logarithm (LN) transformed to meet model assumptions. Models included fixed factors of region, treatment, and their interaction. Random factors nested in region were site and the interaction between site and

treatment. Including these random factors in the model ensured that any significant main effects of treatment exceeded this random variability. To test the principal hypothesis that predation would have a stronger effect at low latitudes, treatment effects were calculated as a contrast to compare prey community attributes under ambient predation (treatment and procedural controls: no cage and partial cage, respectively) versus low predation (predator exclusion cage) for each region (Holm tests).

To test for predation *impacts* on prey community composition, we analyzed abundance data using multivariate mixed models (PERMANOVA, Anderson 2001) on Bray–Curtis similarity measures. Given the number of species unique to each region, analyses were conducted separately for each region. Models had a fixed factor of treatment with the focal contrast (caged vs. controls), a random factor of site, and their interaction. Models were computed from 9,999 permutations, and Monte Carlo tests were used to calculate P values.

The predator exposure experiment provided measurements of both predation intensity and impact. To test for interaction impact, we compared differences in biomass before and after either exposure to predation or being recaged as controls. Biomass (LN transformed) data were modeled with an OLS model with fixed effects of region, exposure treatment (exposed or control), sampling interval (before or after redeployment), and all interactions. Random effects nested in region were site and the interactions between site and exposure treatment, sampling interval, and panel. Contrasts were used to test for differences in biomass before and after redeployment (sampling interval) for each treatment and region combination (Holm tests).

To assess key dimensions of predation *intensity*, we evaluated four attributes of the predator community: (1) regional diversity of observed predators, (2) total predation rates (i.e., number of strikes for all predator taxa combined) at local and regional scales, (3) total interaction duration, and (4) mean predator size. Total richness of observed predators and the diversity of strikes (Shannon diversity index, H' , calculated using strike frequency per predator taxa) of the regional pool of predators were calculated. We observed a clear increase in variation in the local (panel) scale predator strike, interaction duration, and size data at low latitudes. Because maximum predation intensity can have substantial ecological effects on prey communities, we used linear quantile mixed model regression to model the relationship between latitude and five quantiles of the data (10th, 25th, 50th, 75th, and 90th quantiles). Models included effects of latitude (fixed) and site (random).

To explore biogeographic patterns in recruitment rates under both ambient and low-predation conditions, we modeled total recruitment (number of individuals of all taxa combined). Model selection with AIC indicated a GLMM with negative binomial distribution and a log link function performed best relative to Poisson GLMM or OLS. Fixed factors were region, treatment, and their

interaction. Random effects nested in region were site and the interactions between site and treatment, sampling date, and treatment \times sampling date. Contrasts were used to test for differences among treatment groups (caged vs. controls) in each region, and Holm tests were used to test for differences among regions.

The OLS, GLMM, and quantile regression models were computed with R statistical software version 3.5.2 (R Development Core Team 2018). The OLS models were evaluated with the mixed function from the afex package version 0.22-1 (Singmann et al. 2018), GLMMs were evaluated with glmmTMB package (Brooks et al. 2017), and multiple comparisons were completed with the multcomp package version 1.4-8 (Hothorn et al. 2008). Assumptions of OLS models were evaluated with plots of residuals versus fitted values, normal quantile plots, and Shapiro-Wilk goodness-of-fit tests of normality. Assumptions of GLMM models were evaluated with plots of Pearson residuals versus fitted values and estimation of the overdispersion parameter (Zuur et al. 2009). Quantile regression models were completed with the qrLMM package for R (Galarza and Lachos 2017). PERMANOVAs were calculated with Primer v7.0.13 (Quest Research Limited, Auckland, New Zealand).

RESULTS

Predator exclusion experiment

Over a 3-month community assembly experiment, predation had a strong *impact* on prey community biomass in the tropics, but not at higher latitudes. Biomass was higher in the predator exclusion (caged) treatment relative to controls (no cage and partial cages), but only in tropical Panama (Fig. 2a; Region \times Treatment: $F_{6/16,0} = 9.12$, $P = 0.0002$; contrasts: Panama: $t = 5.12$, $P = 0.0004$, Alaska and Mexico: $P > 0.05$). In California, caged communities had lower biomass than both controls (contrast: $t = -5.04$, $P = 0.0004$) because of treatment artifacts (i.e., heavy fouling on the cages despite regular cleaning) that reduced growth in that region. Nevertheless, ambient predation reduced biomass in the tropics, a pattern that was not observed in any higher-latitude region, consistent with stronger impacts of predation on prey communities at low latitudes.

Predation also had a stronger *impact* on prey composition at lower latitudes (Fig. 3a). Predator exclusion had a strong and consistent effect on community composition in Panama (Fig. 3b; treatment contrast: pseudo- $F_{1/2} = 10.2$, $P = 0.0013$) and Mexico (Appendix S1: Fig. S1; treatment contrast: pseudo- $F_{1/2} = 3.19$, $P = 0.019$), but not at higher latitudes (treatment contrast: $P > 0.05$). We observed random spatial variability in composition, and treatment effects on composition, among sites in all regions ($P < 0.05$), but predator exclusions resulted in consistent effects in Panama and Mexico beyond this random variability.

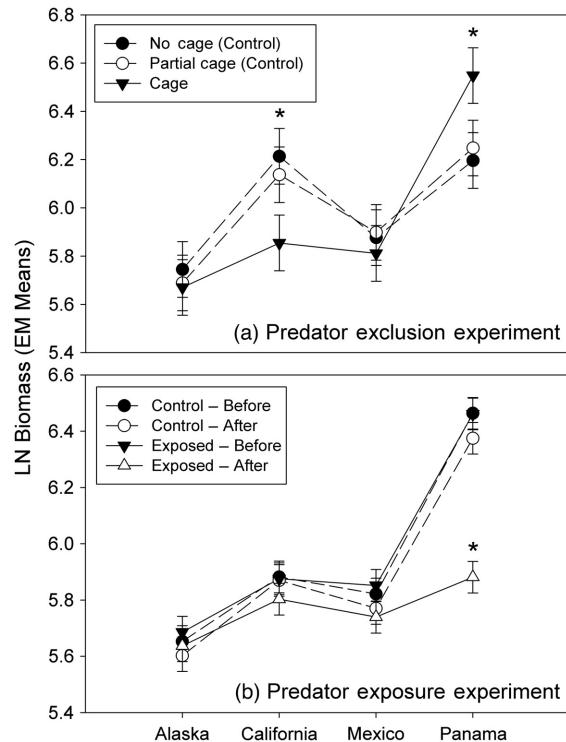


FIG. 2. Effects of (a) predator exclusion and (b) predator exposure on prey community biomass (LN biomass, g) expressed as estimated marginal means from mixed models (\pm SE). Asterisks indicate significant treatment contrasts ($\alpha = 0.05$).

Predator exclusion did not have an effect on either prey community richness or diversity (contrasts: $P > 0.05$), but differences in both measures were observed among regions with local richness peaking in subtropical Mexico (Appendix S1: Fig. S2; Richness: $F_{3/8} = 23.8$, $P = 0.0002$; Diversity: $F_{3/8} = 9.63$, $P = 0.005$). Across the 12 sites in our four study regions, we detected 193 sessile taxa representing Anthozoa, Ascidiacea, Bivalvia, Bryozoa, Cirripedia, Gastropoda, Hydrozoa, Porifera, Sabellidae, Serpulidae, and Spirorbidae. We observed 60 taxa in Alaska, 55 in California, 99 in Mexico, and 94 in Panama.

Predator exposure experiment

After the 3-d exposure period, we again observed strong *impacts* of predators on prey communities only in the tropics, providing results that were consistent with the predator exclusion experiment. Exposure to predation caused a clear reduction in prey community biomass, but only in the tropics (Fig. 2b; Region \times Exposure Treatment \times Sampling Interval: $F_{3/103,0} = 43.3$, $P < 0.0001$). In Panama, prey communities that were exposed to predation underwent a marked loss of biomass ($t = 13.5$, $P < 0.0001$), whereas control

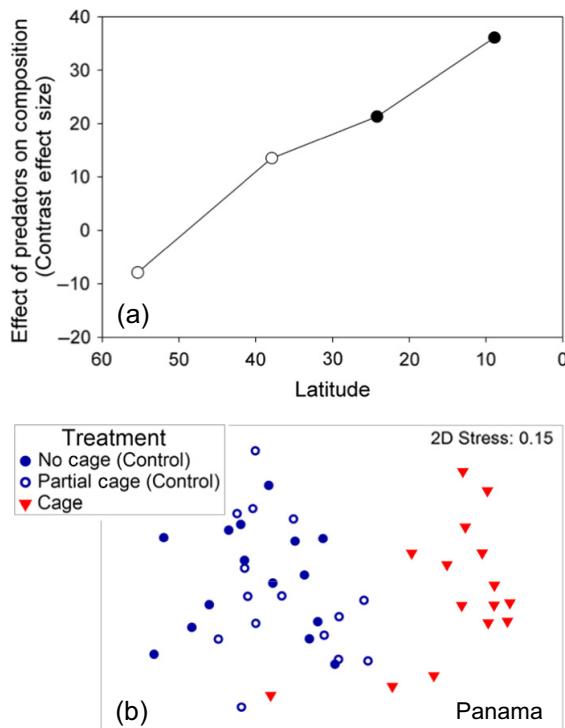


FIG. 3. (a) Effect of predator exclusion on prey composition across latitude. Effect sizes reported as the estimates of components of variation (square root) (Anderson et al. 2008) from treatment contrasts in multivariate models for each region. Significant treatment contrasts are represented by filled circles, and open circles indicate nonsignificant effects. (b) Multidimensional scaling plot for prey communities in Panama. Symbols indicate treatments. Communities across three sites are shown. Each point is a single prey community on a panel, and closer relative proximity among points indicates greater compositional similarity.

treatments in Panama and exposure and control treatments in all higher-latitude regions showed no differences ($P > 0.05$).

Observed predation, which was exclusively by fish, was more *intense* in the tropics. The total number of fish strikes observed in Panama was over twice that of Mexico and over an order of magnitude higher than California or Alaska (Fig. 4a). At a local (panel) scale, maximum (75th and 90th percentile) strike rates and interaction durations increased toward lower latitudes, with up to a tenfold difference in strike rates and a sixfold difference in interaction durations between Panama and Alaska (Fig. 4b, c). Mean predator size was also larger at lower latitudes in nearly all data quantiles (25th, 50th, 75th, 90th) with maximum size varying across the latitudinal gradient by up to fourfold (Fig. 4d). Sixteen fish species were observed to strike the prey communities across the gradient, with 3 species in Alaska, 1 in California, 3 in Mexico, and 11 in Panama (Appendix S1: Table S1). Regional diversity of strikes per fish taxa was over five times higher in Panama

($H' = 1.3$) than in Mexico ($H' = 0.18$), California ($H' = 0$), or Alaska ($H' = 0.22$; Fig. 4a).

Recruitment experiment

Over the 3-month experimental period and across the 12 study sites, recruitment rates varied by three orders of magnitude and ranged from zero invertebrate individuals to over 2,800 per 2-week sampling interval. Recruitment was highest in Panama and California, and lowest in Alaska (Appendix S1: Fig. S3; Region: $\chi^2 = 43.8$, $P < 0.0001$). Note that measurements represent peak recruitment in the seasonal higher latitudes and do not imply annual rates. Predator exclusion treatments did not affect recruitment rates in any region ($P > 0.05$).

DISCUSSION

Two independent lines of evidence from nearshore marine ecosystems spanning 47 degrees of latitude support the hypothesis that both predation intensity and impact are strongest in the tropics. First, direct observations of predators interacting with prey communities revealed a more diverse fauna of diurnal fish predators at low latitudes, with higher predation rates, longer interaction durations, and larger predator body sizes, each suggesting stronger predation intensity in the tropics. Second, predator impacts on prey communities were more severe at low latitudes. Predation reduced prey community biomass in the tropics over a 3-month time frame of community assembly, as well as during a short-term 3-d exposure, indicating consistently strong predation impacts emerging at substantially different temporal scales and stages of community development. In contrast, predation did not affect patterns of biomass at higher latitudes at either temporal scale. Predation also shaped prey composition more strongly at low latitudes, with the effect of predation nearly 70% stronger in tropical Panama than even subtropical Mexico, while predation had no observable effect on composition at higher latitudes. These combined results support the biotic interaction hypothesis, but also provide the most robust data to date demonstrating a clear link between predation intensity and impact on prey communities across latitude.

Although we observed the highest maximum predation rates and the longest predator interaction durations in the tropics, variability was also higher in the tropics. This variability has important implications for predicting predator-prey interactions. Maximum measures likely have particular ecological importance given that predator impacts can be additive through time. With high variability coupled with high maximum rates, extreme predation effects are more likely to be observed across large spatial and temporal scales. Nevertheless, strong and consistent impacts of predation occurred over both a 3-month assembly time scale and a 3-d exposure period in the tropics, despite this variability in

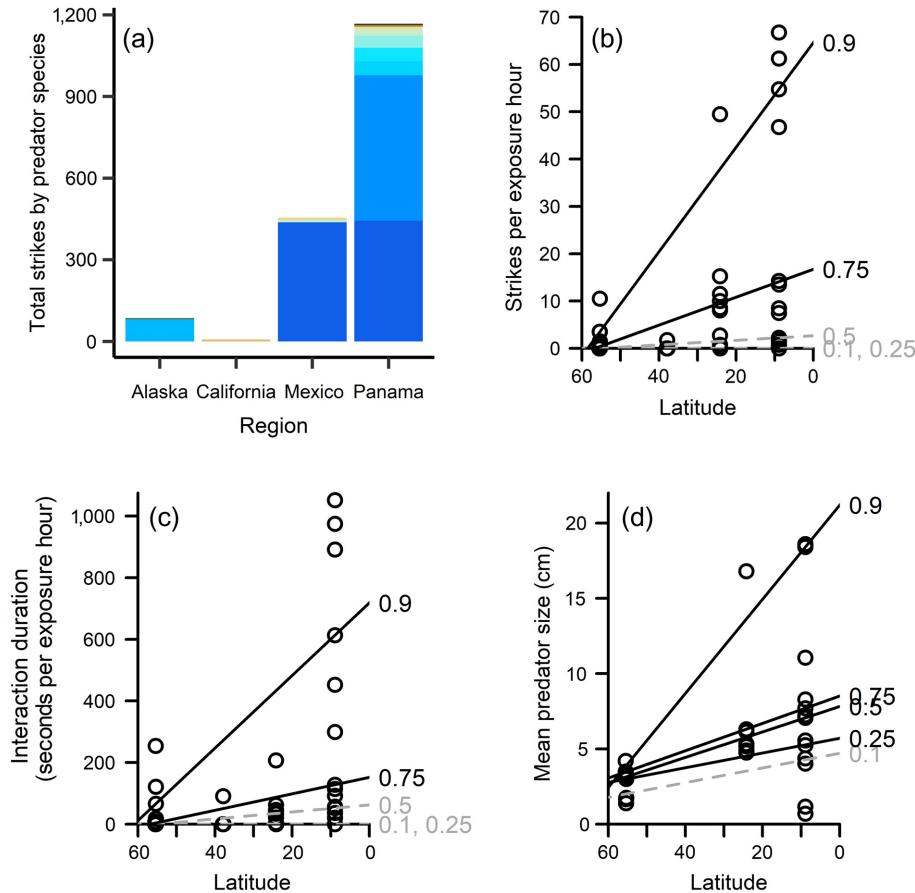


FIG. 4. Predation intensity results from the predator exposure experiment: (a) total predator strikes by region, shaded by predator taxa (Appendix S1: Table S1); and results of the quantile mixed model regression for (b) total strikes, (c) total interaction duration, and (d) mean predator size. In (b)–(d), each point represents a predator community observed interacting with a single exposed prey community (panel). Fitted lines represent the slope and intercept for each quantile, overlaid on these data. Numbers next to the fitted lines represent the quantile (0.1, 0.25, 0.5, 0.75, 0.9). Solid black lines have slopes different from zero ($\alpha = 0.05$), indicating a relationship with latitude. Gray dashed lines do not have a significant slope.

predation rates. Beyond the spatial and temporal scales studied here, intra- and interannual shifts in predator and prey composition, as well as abiotic conditions (Cloern et al. 2007, Carr et al. 2018, M. F. Repetto, A. L. Freestone, M. E. Torchin et al., *unpublished manuscript*), may contribute further to temporal variability in the tropics. Both seasonal upwelling events as well as interannual environmental patterns shaped by El Niño Southern Oscillation (ENSO) could influence consumer interactions over longer time scales. Indeed, an ENSO event occurred during our experiment in 2015–2016; however, the extent to which these longer-term interannual temporal fluctuations govern aggregate measures of consumer pressure in the tropics is not well resolved (Sellers et al., 2021). It is also important to note that our direct observations of predators included only diurnal fish, which represent an important predator guild in this system. Although nocturnal predation certainly occurred during our experiments, diurnal fish predators appear to have strong impacts; the largest decline in prey

biomass during predator exposures can occur directly after deployment during the first diurnal period (M. F. Repetto, A. L. Freestone, M. E. Torchin et al., *unpublished data*). Further, studies that include both fish and benthic predators show qualitatively similar results (Freestone et al. 2011, Papacostas and Freestone 2019, Freestone et al. 2020). Recognizing the variability inherent in predator–prey interactions is central to predicting outcomes across broad spatial and temporal scales.

Similarly, we observed the largest and most variable predator body sizes in the tropics, and functional traits of both predators and prey can shape predation intensity and impact. A predator’s body size, or mass, can predict its metabolic rate, which in turn can predict ecological processes including predation rates (Brown et al. 2004). The warmer ocean waters of the tropics likely magnify metabolic demands of larger predators (Iles 2014), and indeed, temperatures can predict consumer pressure in marine communities (Reynolds et al. 2018, Longo et al. 2019). Body size diversity in particular can increase the

strength of predator–prey interactions through resource partitioning (Rudolf 2012, Ye et al. 2013), and may more fully reflect functional variation than measures of species diversity (Brucet et al. 2018). Furthermore, although prey taxonomic composition shifted in response to predation in the tropics, the effects of predators on individual prey taxa will likely depend on prey functional traits, such as those related to defense and palatability (Sheppard-Brennand et al. 2017, López and Freestone 2021). Functional groups of prey can vary systematically in these traits, rendering some groups more susceptible to predation than others (L. J. Jurgens, A. L. Freestone, G. M. Ruiz et al., *unpublished data*, Lavender et al. 2017, Dias et al. 2020). Indeed, some prey functional groups (e.g., solitary tunicates) can be consumed to the point of exclusion in these communities in the tropics (Freestone et al. 2013, Torchin et al., 2021), highlighting the potential for trait-specific impacts on prey.

In addition, regional species diversity of the predator guild was over three times greater in the tropics than at higher latitudes, likely contributing to strong predation impacts at low latitudes. More diverse predator communities can increase top-down control of prey communities through the chance inclusion of strong predators (Douglass et al. 2008) and niche complementarity among predators (Griffin et al. 2013). Occurrences of strong predators at a local scale can result from stochastic colonization processes (i.e., sampling effect, sensu Tilman et al. 1997), but at larger scales, species distributions shape the regional species pool of predators from which local communities are composed. At a regional scale, the fish taxa that had the highest strike rates also have distributions that are restricted to low latitudes, demonstrating that low-latitude predator guilds were not only more diverse, but also included taxa, such as tetraodonts (pufferfish), that were key predators in this system. Further, the extent to which predator and prey diversity enhances trophic niche opportunities, and therefore, predation impacts on prey, likely hinges on the degree of predator specialization (Duffy et al. 2007). Given that interactions are expected to be both strong and specialized in the tropics (Dobzhansky 1950, Schemske et al. 2009), an increase in predator diversity may allow for complementary pairwise interactions that can vary across temporal and spatial scales and may contribute to stronger predation impacts in the tropics (M. F. Repetto, A. L. Freestone, G. M. Ruiz et al., *unpublished manuscript*).

Finally, prey recruitment has the potential to moderate observed interaction outcomes. Observed predator effects could intensify with low recruitment, as consumed individuals are not replaced, or dampen, with high recruitment that exceeds predator diet requirements (i.e., predator swamping; Cheng et al. 2019). High recruitment in Panama, however, was insufficient to dampen the observed predator effects completely. Further, even though our sampling overlapped with peak

seasonal recruitment at high latitudes, consistently low recruitment in Alaska did not appear to amplify predation effects. Interestingly, although micropredators, which can easily enter the cages used in this experiment, can have a large impact on invertebrate recruitment (Osman et al. 1992, Nydam and Stachowicz 2007), particularly at low latitudes (Freestone et al. 2011), the larger predators excluded by our cages did not have a systematic effect on recruitment rates in the tropics or elsewhere. Nevertheless, patterns of recruitment across latitude are likely to have important impacts on community assembly, given the high variability in recruitment rates and composition in space and time (M. Bonfim, C. Schlöder, and A. L. Freestone, *unpublished manuscript*).

Our study provides a novel integration of large-scale experimental and observational approaches to explore interactions among communities of predators and prey. Our results expand the growing literature that shows stronger predation at lower latitudes in both marine and terrestrial systems (Schemske et al. 2009, Freestone et al. 2011, Roslin et al. 2017, Reynolds et al. 2018, Hargreaves et al. 2019, Longo et al. 2019, Freestone et al. 2020), but contrast with studies that find consumption rates of standardized bait can peak at midlatitudes for some groups of marine predators (Musri et al. 2019, Roesti et al. 2020, Whalen et al. 2020). Subsets of predators may demonstrate different consumption patterns across latitude because of differences in abundance and composition of specific predator taxa or geographic variation in abiotic patterns along different coastlines. Latitudinal trends in consumption can be further dampened, or even inverted, by biogeographic variation in prey composition or local ecological factors (Torchin et al. 2015, Zvereva et al. 2020). Together, studies to date demonstrate the complexity of predicting predator–prey dynamics across latitude and the need for integrative approaches to identify emergent patterns.

Using such approaches, spanning the subarctic to the tropics, our results demonstrate that both predation intensity and impact can show parallel patterns across latitude, with peak interaction strength in the tropics. Our detailed data on two trophic guilds show high but variable predation rates, predator body sizes, and interaction durations at low latitudes. These attributes, coupled with high predator diversity, can result in strong predation impacts in the tropics, despite high rates of prey recruitment. We note that our experiments measured predation intensity and impact during periods of high biological activity in these regions, and cumulative annual and interannual effects may further magnify these patterns, as predator activity likely declines in winter at higher latitudes and may fluctuate in the tropics as well. Although the scope of this experimental study is unprecedented, additional research will need to test the generality of these results as they relate to other ocean basins with different temperature and oceanographic regimes and ecosystems that contain different guilds of predators and prey. As we uncover how fundamental

interactions shape natural communities across latitude, we move closer to integrating the fields of community ecology and macroecology, recognizing that the relative influence of local community processes can hinge on biogeography.

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