REPORT

COMMUNITY ECOLOGY

Predator control of marine communities increases with temperature across 115 degrees of latitude

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Early naturalists suggested that predation intensity increases toward the tropics, affecting fundamental ecological and evolutionary processes by latitude, but empirical support is still limited. Several studies have measured consumption rates across latitude at large scales, with variable results. Moreover, how predation affects prey community composition at such geographic scales remains unknown. Using standardized experiments that spanned 115° of latitude, at 36 nearshore sites along both coasts of the Americas, we found that marine predators have both higher consumption rates and consistently stronger impacts on biomass and species composition of marine invertebrate communities in warmer tropical waters, likely owing to fish predators. Our results provide robust support for a temperature-dependent gradient in interaction strength and have potential implications for how marine ecosystems will respond to ocean warming.

The strength of species interactions, such as predation and competition, is thought to peak at low tropical latitudes and decline toward the poles (*1*). Such geographic variation in interaction strength is invoked frequently as both a major cause and consequence of the latitudinal diversity gradient, one of the most robust patterns of life on Earth (*2–5*). However, studies available to date across large spatial scales and multiple habitats provide conflicting support for increased predation intensity in the tropics and have been mostly limited to measuring rates of prey loss. For example, predation intensity (consumption rate) on seeds (*6*) and terrestrial insect mimics (*7*) was greater in the tropics than at higher latitudes. By contrast, attacks on open ocean long-line fishing hooks baited with natural prey peaked at mid-latitudes instead of the tropics (*8*), as did consumption of squid baits in shallow coastal waters (*9*).

Currently, it remains largely unknown whether global gradients in predation intensity produce associated gradients in the magnitude of effects on prey communities, especially across latitudes. Such a gradient in community-level effects is likely to have profound consequences for patterns of biodiversity (*10*), ecosystem function (*11*, *12*), and resilience to global change (*13*). Although some studies have found evidence for stronger effects of predation on community composition at tropical versus temperate sites, primarily in shallow-water marine benthic habitats (*14–17*), these were restricted to spatial scales of 20° to 45° latitude and usually along single coastlines. Other regional-scale studies in similar marine habitats did not detect this latitudinal pattern in community effects of predators (*18*, *19*). Where latitudinal trends in predation intensity and impact have been observed at regional spatial scales, a number of environmental factors that follow a latitudinal gradient have been proposed as drivers of this pattern, including time since glaciation, lack of freezing winters, day length, and temperature (*20*). Ambient temperature is likely important because it strongly influences metabolic rates and underpins organism functioning and the ecology of populations, communities, and ecosystems (*21*). Although temperature generally declines with latitude, the relationship varies among regions (Fig. 1). Thus, including in situ temperature as an independent predictor could help to explain the mixed results from previous studies. Clarifying the relationship between predation intensity, impacts on prey communities, and temperature could also facilitate prediction of community response to future ocean warming.

We tested whether intensity of predation and its community-level effects decrease from tropical to subpolar latitudes in coastal marine ecosystems. Specifically, we assessed the impact of fish and other large, mobile predators on sessile marine invertebrate communities. We used standardized and replicated experiments at 36 nearshore sites across 115° of latitude, along both Pacific and Atlantic coasts of the Americas (Fig. 1 and table S1). We conducted three complementary experiments to test whether predation intensity and top-down control of prey communities vary consistently along latitudinal and temperature gradients in both hemispheres. We focused on coastal subtidal communities of sessile invertebrates on hard substrates for multiple reasons. These communities are widely distributed throughout the world and are especially conducive to experiments, responding rapidly to manipulation and allowing for robust tests of general ecological processes (*3*, *22*). There is also evidence that top-down control is stronger in the tropics than in temperate regions for these hard-substrate communities at some regional scales (*14–16*, *18*, *23*). We expanded on this past work to test with high replication whether results are consistent on an extensive geographic scale, across the Americas in two oceans (*24*).

Our experiments measured three separate components of predation: (i) consumption of a standard bait as a measure of predation intensity, (ii) effects of sustained predation on the development of benthic community composition and biomass over 3 months, and (iii) the effects of short-term predation on already developed benthic communities (table S2) (*24*). The three complementary predation measures were colocated in space and time at each site. To compare predator consumption rates on a broadly palatable prey for the first component, we used dried squid as a standardized bait at all sites and recorded bait loss after 1 hour as a measure of predation intensity (*25*). For the second and third components, we allowed natural communities to develop on standardized substrates for 3 months (*15*) and manipulated predator access at different time points in community assembly, to evaluate the effect of predation on composition and biomass of sessile invertebrate communities (*24*). Cages were designed and used in both experiments to selectively exclude and evaluate effects of large (>1 cm) mobile predators, especially fishes, which are major consumers of benthic invertebrate prey in shallow subtidal habitats and can affect their community composition (*14–18*, *23*). The second component contrasted communities developed continuously under caged versus uncaged control conditions for

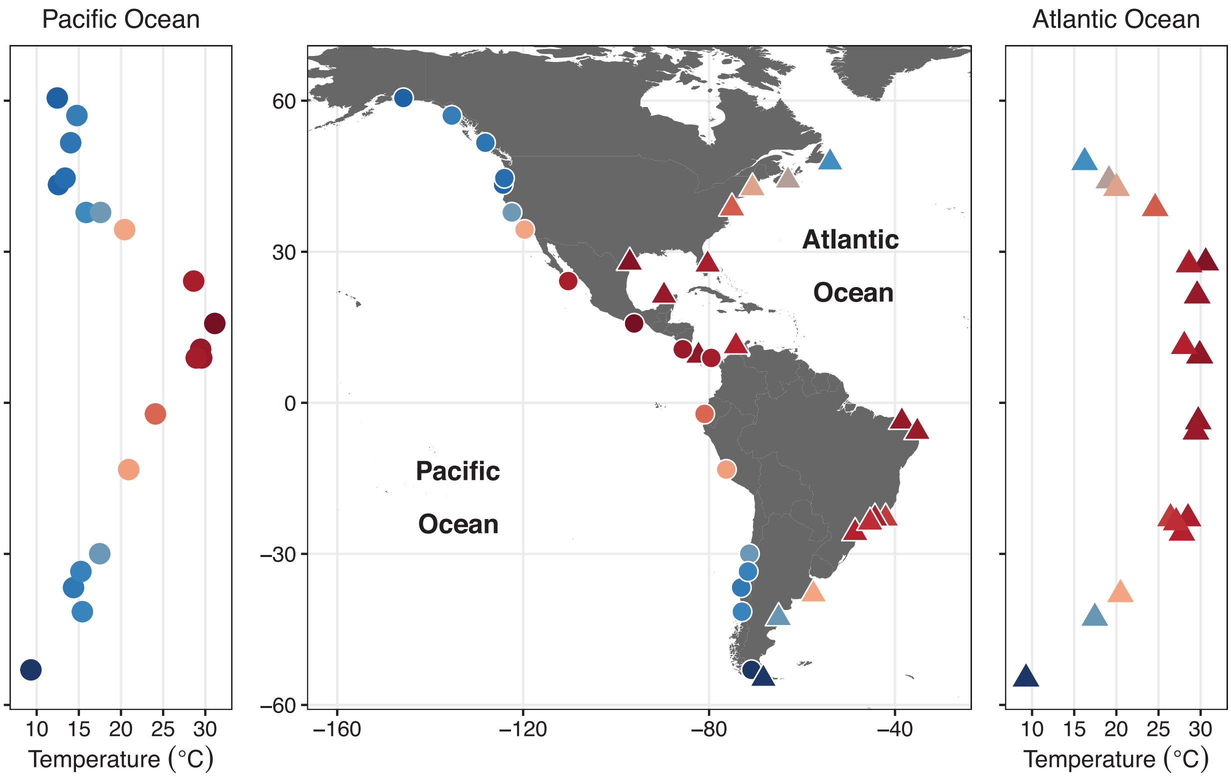

Fig. 1. Site location and mean temperatures. Location, latitude, and mean temperature recorded at experimental sites on Atlantic (triangle) and Pacific (circle) coastlines of the Americas. Color scale indicates gradient in temperature recorded across latitudes during the experiment (dark blue, ~9°C; dark red, ~31°C).

12 weeks. For the third component, we allowed communities to develop for 10 weeks in cages and then uncaged half of these, comparing effects of predator exposure on these established communities after 2 additional weeks. We also measured temperature at each site throughout the experiments using dataloggers (*24*).

We analyzed the results with mixed effects models and a model selection approach, with separate global models estimating the responses of bait consumption; sessile community biomass; and community composition to variation in seawater temperature or latitude, ocean basin, hemisphere, caging treatment, and interactions among all these terms. We explicitly compared alternate models that included either latitude or temperature recorded during the experiment to evaluate which was a better predictor of predator effects (*24*).

Our results provide robust experimental evidence that top-down control of community

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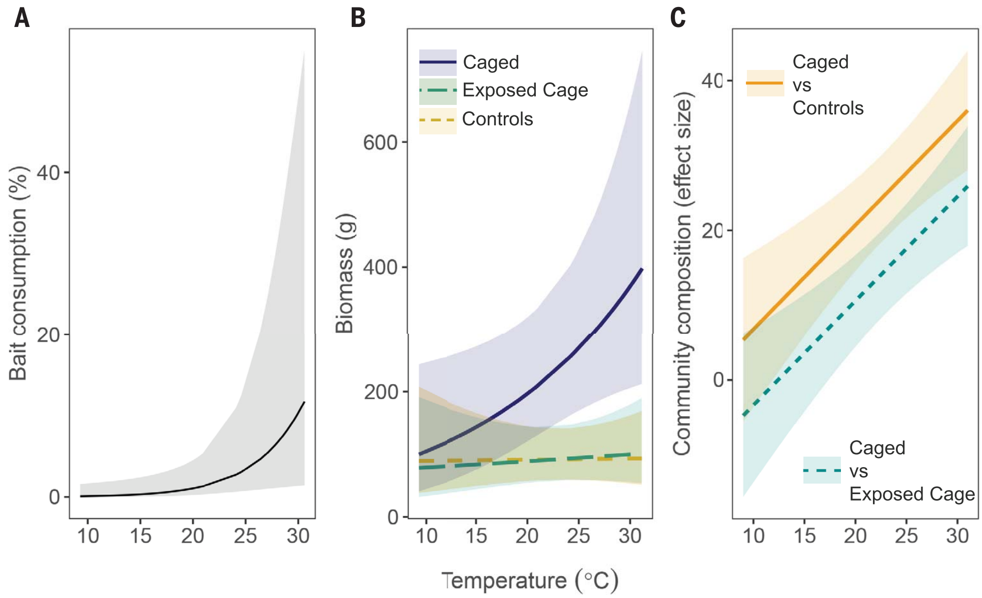

Fig. 2. Modeled variation in predation intensity and responses of biomass and community composition to predation with increasing temperature. (**A**) Predation measured as bait loss increased with in situ temperature along Atlantic and Pacific coastlines of the Americas. The line indicates predictions from a generalized linear mixed effects model [conditional coefficient of determination (R^2) = 0.79]. (**B**) The effect of predation on biomass accumulation increased with temperature. Dark blue indicates predators were excluded throughout the experiment; green indicates predators were excluded until the last 2 weeks of the experiment and then the experiment was exposed to predators; and yellow indicates open to predators throughout the experiment (model conditional R^2 = 0.89). Predators consumed significantly more biomass as temperature increased between 9° and 31°C. (**C**) Effect of predation on community composition increased along the latitudinal temperature gradient. Exclusion of predators throughout the 3-month experiment (gold, caged versus controls) had a greater impact on community composition than 2-week exposure (blue, caged versus exposed cage) of the late-stage community to predators. Lines show effect size as predictions from linear models of square roots of the estimated component of variation for each contrast within each site. Shaded areas show 95% confidence intervals (CIs) (*24*).

structure consistently increases with temperature and is strongest in the tropics, supporting a major tenet in ecology and evolutionary biology. Predation intensity and its effects on marine hard-substrate communities increased from colder high-latitude to warmer tropical waters (Fig. 2). Seawater temperature and latitude were strongly correlated [correlation coefficient (r) = 0.84], and although results were qualitatively similar for seawater temperature and absolute latitude, the models with seawater temperature were more strongly supported for both predation intensity and community responses (*24*). Predation intensity, as measured in the first experiment with bait consumption, was greatest in the warm tropics and approached zero at sites where mean summer sea surface temperature was below ~20°C (Fig. 2A, fig. S2, and table S3). Whereas the bait loss assay provides a short-term (1 hour) measure of predation intensity, the two caging experiments integrate longer-term impacts of predators on community attributes, revealing that predators had consistently larger effects on communities at higher temperatures and during multiple stages of community development. Specifically, in the second experiment, the effect of predators increased with temperature for both biomass accumulation (wet-weight) (Fig. 2B, fig. S3, and table S4) and community composition (Fig. 2C, figs. S4 to S6, and tables S5 to S7). In the third experiment, predators reduced prey community biomass in warmer tropical waters during the 2-week exposure, compared with communities that remained caged, and biomass of these exposed communities converged on uncaged control treatments across all temperatures (Fig. 2B and table S4). Community composition also responded more strongly to this later-stage predation at warmer sites (Fig. 2C and table S6). Thus, results of these three complementary experiments provide strong and consistent evidence that predation intensity by mobile predators is higher on average, and shapes community composition more strongly, in warm tropical waters.

The organisms that changed most in response to predators were solitary tunicates and encrusting bryozoans; dominance of these groups diverged among treatments with increasing temperature (fig. S4). At warm water sites, encrusting bryozoans were most prevalent on open control panels, whereas solitary tunicates occurred most frequently on caged panels that restricted predator access (Fig. 3 and table S7, C and D). This pattern may result from competitive release of less palatable bryozoans when spatially dominant tunicates are removed by predators during community assembly (*19*, *26*). When later-stage tropical communities were exposed to predators, solitary tunicate dominance was reduced (compared with caged panels), with a coincident increase in bare space (Fig. 3). Bare space decreased toward the tropics in all treatments. It is likely that prevalence of large solitary tunicates drove the observed higher biomass in treatments protected from predators at most sites (Fig. 2B).

Although we found a strong overall increase in predation intensity and top-down control at warmer temperatures, the scale of the responses varied among ocean basins and hemispheres. For example, bait loss and community composition responses were more marked in the northern hemisphere (figs. S2, A and B, and S6B), whereas the biomass response of prey communities was more apparent in the North Atlantic and South Pacific than other regions (fig. S3B). This variation likely derives from regional differences in the species and functional characteristics of predators and prey, environmental conditions other than temperature, and/or biological factors beyond those measured here (such as productivity) (*23*). Fundamental differences in oceanography exist at the ocean basin scale (for example, equatorial upwelling on the Pacific coastline is largely absent from the Atlantic sites) that would be expected to have effects on the observed latitudinal patterns (*27*). More broadly, the variation among sites underscores the need for high replication and broad geographic coverage to thoroughly evaluate both regional and global patterns.

This study provides new insights into the macroecological pattern of biotic interactions. We show that intensity of predation indeed declines consistently with latitude, as expected, but is better predicted by mean summer temperature experienced during the experiment than by latitude, hinting at underlying mechanisms. We demonstrate that this gradient in predation intensity produces a parallel gradient in top-down control of marine community

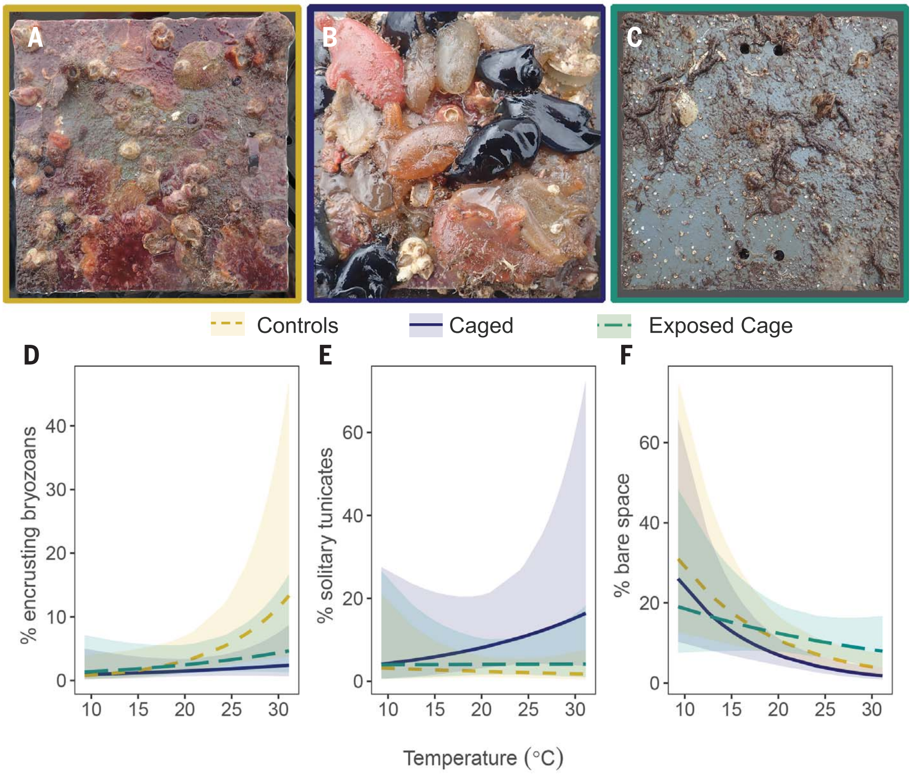

Fig. 3. Effects of predator treatments on community composition at a tropical Atlantic site and response of key functional groups from models based on all sites. (**A** to **C**) Photographs illustrate differences among experimental treatments at Bocas del Toro, Panama. At this and other warm water sites, encrusting bryozoans predominated in (A) control panels (exposed to predators), (B) solitary tunicates in caged panels (predators excluded), and (C) bare space in exposed cage panels [as in (B) but exposed to predators for the last 2 weeks through cage removal]. (**D** to **F**): Modeled percent cover across all sites of (D) encrusting bryozoans, (E) solitary tunicates, and (F) bare space, which together explained most of the variation in community composition among treatments (yellow, controls; dark blue, caged; green, exposed cage) in warm water sites. Shaded areas show 95% CIs (*24*).

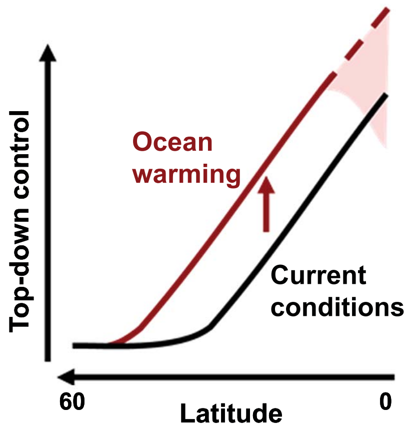

Fig. 4. Conceptual illustration of the hypothesized impact of ocean warming on future trends in top-down control of marine communities. Predation intensity was low and had little or no effect on benthic communities at cold latitudes and increased toward the equator with temperature, above an inflection point (~20°C). The black line describes a simplified view of the current latitudinal pattern of top-down control in our study. The solid red line describes the hypothesized effect of future ocean warming, which may shift this inflection point poleward, increasing predation effects at higher latitudes. The dashed red line describes a region of uncertainty in the tropics, where increased temperatures exceed our current observations and possibly thermal tolerance of some predators, so that top-down control may increase or decline within this region (shaded to suggest a range of possible responses).

biomass and composition that has been long suspected but not rigorously tested at this scale. As predicted, predation intensity in our shallow hard-substrate communities increased with temperature, similar to the patterns of bait loss in terrestrial and marine environments over an expansive latitudinal range (*7*, *9*). Our results were likely driven by highly mobile fish that can exert strong effects on epibenthic invertebrates in warm tropical water (*14*–*18*, *23*). We recognize that predation effects may differ for marine communities in other habitat types, including those where macroinvertebrates exert strong predation effects (*3*, *27*). More specifically, other studies in marine systems have shown a variety of patterns (*8*, *9*, *28*), which may reflect physical differences among habitats, taxonomic composition of predator or prey groups, smaller spatial scales, or less replication.

Overall, our analyses demonstrate a strong temperature-dependent gradient of increasing predator impacts on community biomass and composition and support prior predictions of stronger interaction strengths at warmer latitudes based on regional-scale studies [for example, (*15*, *17*)]. This study, completed at a large spatial scale, contributes to mounting evidence that temperature is a key predictor of global gradients, not only in diversity (*29*) and a suite of biological processes (*21*) but also in the strength of interactions among species (*30*, *31*) and the resulting effects of those interactions on communities.

Our results imply that climate change may have predictable effects on the regulation of nearshore communities along the world's shorelines. Our finding of a fundamental relationship between temperature and predation effects across large geographic scales suggests that, in addition to shifting species' distributions (*32*), ocean warming may cause the intensity of top-down control to expand poleward (Fig. 4). Specifically, the observed temperature-predation relationship exhibits an inflection point at ~20°C (Fig. 2) (*19*) that will likely move poleward with warming (Fig. 4), both promoting top-down control at high latitudes and increasing predation effects at mid- to high latitudes through time (*33*). The response to warming is less certain in the tropics, where predation may increase or decrease, because projected temperature increases are beyond our current range of observations and may exceed thermal tolerances of existing predators. Such broad-scale shifts in top-down control could have far-reaching consequences, given the key role of species interactions in maintaining ecosystem structure, diversity, biogeochemical processes, and the provision of critical ecosystem services to human communities (*3*, *13*).

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SUPPLEMENTARY MATERIALS

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Science

Predator control of marine communities increases with temperature across 115 degrees of latitude

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More predation in warmer seas
Species richness of many taxa is higher near the equator, and ecologists have long hypothesized that this pattern is linked to stronger interactions between species (e.g., competition and predation) in the tropics. However, empirical evidence showing that the strength of species interactions varies with latitude is limited. Ashton *et al.* tested whether predation on benthic marine communities is higher at lower latitudes. Using a standardized experiment at 36 sites along the Pacific and Atlantic coasts of North and South America, the authors found both greater predation intensity (consumption rate) and stronger impacts on benthic communities nearer the equator. These trends were more strongly related to water temperature than to latitude, suggesting that climate warming may influence top-down control of communities. —BEL

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