

American coast between 37°N in winter and 41°N in summer, paralleling seasonal shifts of Φ_{crit} (fig. S4A). Eastern cod migrate vertically, moving from cool temperatures in surface waters in winter to deeper waters in summer, in parallel with Φ_{crit} (fig. S4B). Seasonal migrations of benthic Atlantic rock crab also coincide with variations in Φ_{crit} in bottom waters (Fig. 3B). On the continental shelf, the latitudinal limits of seasonal crab populations in the mid-Atlantic Bight and of year-round populations north of 40°N are both delineated by a common Φ_{crit} . Deeper waters of the continental slope (100 to 400 m) have a metabolic index above Φ_{crit} , thus providing refugia for populations migrating from shallower shelf environments during summer (10).

Projected climate changes by this century's end (2071 to 2100) will affect the distribution of the metabolic index and thus of marine animals (Fig. 4). Climate models predict substantial warming and deoxygenation throughout most of the upper ocean (fig. S5 and table S4) (10). This implies global reductions in the metabolic index (Fig. 4A) throughout the upper water column (0 to 400 m), with a model-average decline of 21% (intermodel range 17 to 25%). Only ~1/3 of this reduction is attributable to O_2 loss, indicating that future marine hypoxia will be driven primarily by rising temperature, not by declining O_2 (3). The decline in Φ , and the relative contribution of temperature versus O_2 , vary geographically (fig. S6). In mid-latitude Northern Hemisphere oceans—where fisheries are often highly productive—the metabolic index, and thus habitat suitability, should decline dramatically (~50%). The Pacific is prone to some of the largest reductions in Φ , driven by its larger projected fractional decrease in O_2 (figs. S5 and S6).

The focal species studied here illustrate how projected warming plus O_2 loss should shift metabolically viable habitats by century's end (Fig. 4, B to E). Habitable zones will often be vertically compressed and habitable seasons shortened throughout geographic ranges, but overall habitat losses are projected to be greatest near the equatorward edge of ranges, where Φ is low. For example, in the western subtropical Atlantic, where a wide swath of benthic habitat of rock crab is already close to Φ_{crit} , a 30% reduction in Φ would force a poleward retreat of slope populations from ~25°N to ~35°N. For other focal species, the average cumulative loss of habitat, measured as the reduction in currently occupied water volume with $\Phi > \Phi_{crit}$, ranges from 14 to 26% (table S5) (intermodel range 9 to 42%). These losses in aerobic habitat may be partially offset by habitat expansions where species ranges are now limited by cold tolerance.

Our results suggest that climate constraints on aerobic energy provision are the primary factors governing the equatorward range limit for diverse marine ectotherms. Thus, the metabolic index provides a simple but powerful metric linking physiology and biogeography with current and future environmental conditions. Even so, climate-forced ecosystem shifts will be complex, because changes in the metabolic index may be

exacerbated by declines in net primary productivity (20), ocean acidification, and pollution (1), or ameliorated by acclimation and genetic adaptation (21). Biotic interactions will be altered because currently interacting species—if they have different metabolic sensitivities—will show noncoincident range contractions. Polar species may face increased competition caused by the invasion by lower-latitude species. Shallow-water predators may benefit from upwelling migrations of deeper water prey (22), and prey may benefit if their predators move away (23). Thus, climate shifts in the metabolic index may alter species ecologies even where metabolic indices exceed critical limits. Predictions of differential responses of ecologically interacting species to future shifts in metabolic indices will require more studies of temperature-dependent hypoxic tolerances, especially those of interacting and potentially interacting species.

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SUPPLEMENTARY MATERIALS

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Materials and Methods
Supplementary Text
Figs. S1 to S6
Tables S1 to S5
References (24–51)

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CORAL REEFS

Limited scope for latitudinal extension of reef corals

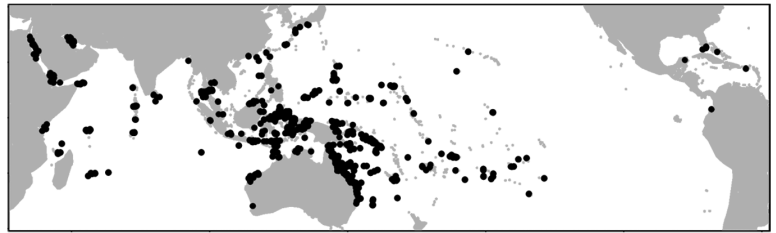
Paul R. Muir,^{1*} Carden C. Wallace,¹ Terence Done,^{1,2} J. David Aguirre^{3,4}

An analysis of present-day global depth distributions of reef-building corals and underlying environmental drivers contradicts a commonly held belief that ocean warming will promote tropical coral expansion into temperate latitudes. Using a global data set of a major group of reef corals, we found that corals were confined to shallower depths at higher latitudes (up to 0.6 meters of predicted shallowing per additional degree of latitude). Latitudinal attenuation of the most important driver of this phenomenon—the dose of photosynthetically available radiation over winter—would severely constrain latitudinal coral range extension in response to ocean warming. Latitudinal gradients in species richness for the group also suggest that higher winter irradiance at depth in low latitudes allowed a deep-water fauna that was not viable at higher latitudes.

The growth of phototrophic corals, those that rely on energy from endosymbiotic algae or “zooxanthellae,” is determined by three primary latitude-correlated environmental factors (solar radiation, temperature,

aragonite saturation) and by a number of factors not related to latitude (e.g., nature and depth of the substratum, wave climate, salinity, water quality, siltation regime) (1, 2). Among the primary drivers of coral growth, only one—the amount of

Fig. 1. Sampling sites used in the study. The global database (16) comprises 14,235 records of latitude, longitude, and depth of 104 staghorn coral specimens collected at 1397 sites. For inclusion at a site, a species is recorded only if at least one specimen was collected for taxonomic verification.



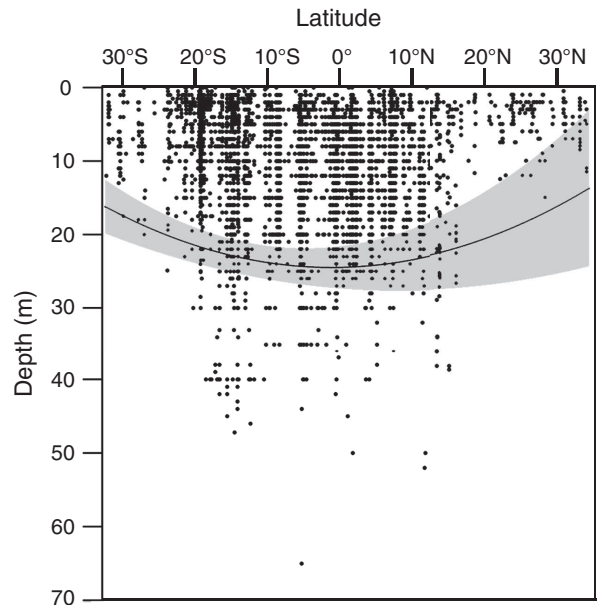
solar radiation that penetrates into the ocean and fuels photosynthesis—is unlikely to change substantially with climate change. Solar radiation at the sea surface diminishes with increasing latitude as winter day length and solar elevation decrease (3); solar radiation further attenuates through the water column, thereby limiting the depth at which phototrophic corals can survive (4, 5).

These findings have led to the hypothesis that phototrophic corals should be restricted to shallower depths at higher latitudes (2, 6, 7). Here, we tested this hypothesis using an extensive specimen-based global data set of the depth and latitudinal distributions of 104 species of reef corals of the genera *Acropora* and *Isopora* (the “staghorn” corals; Fig. 1). High diversity of growth forms in these genera provides by far the greatest variety among corals of microhabitats for fishes (8) and invertebrates (9). However, staghorn corals, which make up a large proportion of coral species richness and cover of the world’s richest coral reefs (2, 10), are under threat (11), particularly from increasing sea surface temperatures, which cause corals to bleach, succumb to disease, and die en masse (12). Nonetheless, there is contemporary (13, 14) and fossil (15) evidence for poleward range expansions of staghorn corals associated with increasing sea temperatures. We show here that local daily winter insolation will ultimately limit any such poleward expansion made possible by contemporary ocean warming, and hence will limit the expansion of associated biota.

In the global data set (Fig. 2), the maximum depth limit (0.975 quantile) of staghorn corals was deepest (26 m) at the equator (5°S to 5°N) and shallowest at their latitudinal extremes (11 m ≥ 30°N; 9 m ≥ 30°S). A polynomial quantile regression mixed model (16) revealed a strong latitudinal gradient in depth limits, both for all species combined and for latitudinally widespread species only (Fig. 2 and table S1). This suggests that the latitudinal gradient in maximum depth was driven not by changes in species composition but by an environmental driver that affects all species. Using species distribution models (MaxEnt), we showed (16) that temperature, aragonite saturation, and salinity in well-mixed reef waters were relatively poor pre-

Fig. 2. Latitudinal gradient in the maximum depth limits of staghorn corals.

Polynomial quantile regression mixed model (0.975 quantile) is indicated by solid line, with 95% confidence intervals shaded. Accurate depth data were available for 104 species and 14,235 specimens. Analysis of latitudinally widespread species only (22 species) produced an almost identical model, indicating that the latitudinal gradient was not driven by changes in species composition (tables S1 and S5).



dictors of the maximum depth of occurrence of staghorn corals: None of these three factors was limiting at any depth at the poleward limit of staghorn coral distribution (Fig. 3, A to C, and table S3). In contrast, photosynthetically available radiation (PAR; wavelengths 400 to 700 nm), modeled for clear reef waters (16) and specifically winter PAR (17, 18), was a strong predictor of the limits to depth across the latitudinal distribution (Fig. 3 and table S4). Daily PAR decreases gradually with latitude (3), and the greatest differential between low and high latitudes occurs during winter. Declines in winter irradiance are further amplified underwater by additional surface reflection and long subsurface path length, both associated with low winter Sun angles. Our modeling (16) showed that during local midwinter (17) at latitude 0° daily PAR at 20 m depth is 43% of surface PAR, whereas at 34°N it is only 35%. We found that winter PAR constrains the depth of occurrence of staghorn corals, accounting for the latitudinal gradient in depth distribution, and that it could in principle exclude staghorn corals from shallow substrata otherwise deemed suitable for corals on the basis of temperature and aragonite saturation alone (19).

The geographic or depth limit beyond which coral growth is vigorous enough for reef building or growth of carbonate platforms, termed the “Darwin point,” has been shown to be de-

termined by aragonite saturation, temperature, and light (1, 4, 6, 19–21). Modeling indicates that reef building mainly occurs for aragonite saturation greater than 3.4, annual minimum temperature greater than 18°C, and on substrata where PAR is greater than 250 $\mu\text{E m}^{-2} \text{s}^{-1}$ (equivalent to 7 to 8 mol photons $\text{m}^{-2} \text{day}^{-1}$), (6, 19–21). However, reef corals commonly occupy non-reef habitats such as rocky shores or shallow embayments well beyond the latitudinal limits of reef building (2, 10); the determinants of their distributional limits have not been quantified, although it is commonly held that they are constrained latitudinally mainly by temperature [reviewed in (2)] and vertically mainly by light (3, 4, 20). We found that winter PAR of 5.2 mol photons $\text{m}^{-2} \text{day}^{-1}$ is a strong predictor of the depth and latitudinal limits of distribution of staghorn corals (16), which have a high dependence on a steady supply of photosynthate produced by their zooxanthellae (22). We posit that the 5.2 mol photons $\text{m}^{-2} \text{day}^{-1}$ isolume represents a key threshold for coral physiology below which their zooxanthellae’s photosynthetic production does not meet their basal metabolic needs. In this respect, staghorn corals are like some marine plants, whose limits of depth and latitude are also determined by daily hours of irradiance above a threshold basal compensation point (20), and they are unlike other growth forms of corals

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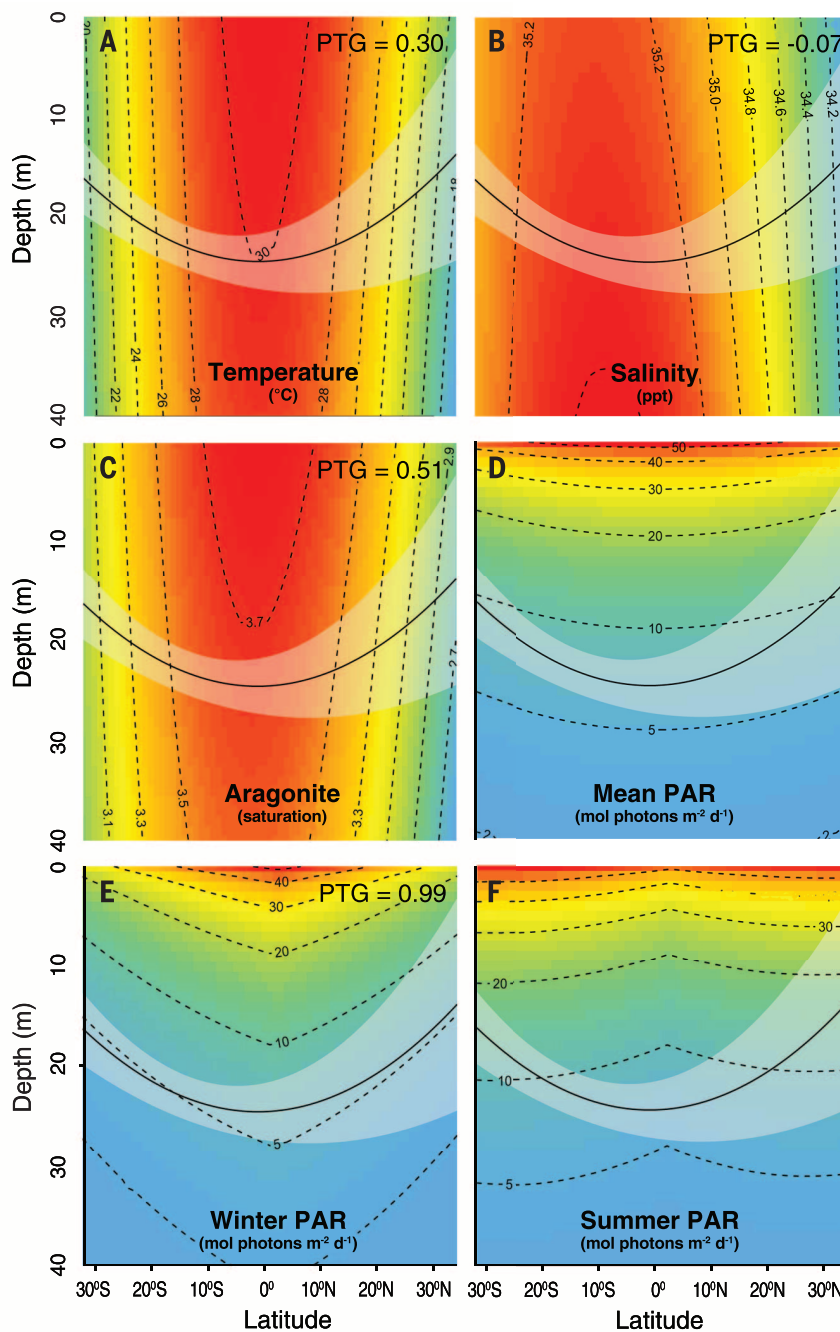


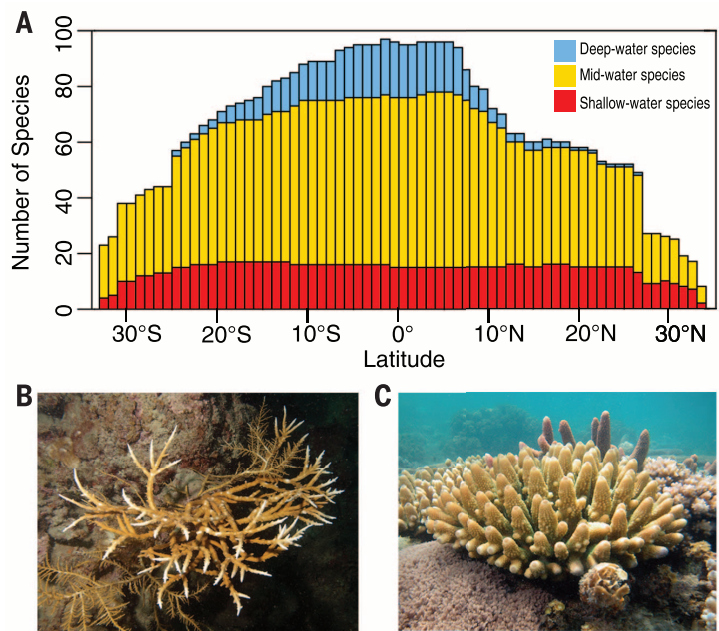
Fig. 3. Analysis of environmental predictors of maximum depth limits. (A to C) Mean annual temperature (A), salinity (B), and aragonite saturation (C). (D to F) Mean daily dose of photosynthetically available radiation (PAR) over an entire year (D), winter (17) (E), and summer (16, 17) (F). Solid line in each panel indicates maximum staghorn coral depth limits (0.975 quantile regression), with 95% confidence interval shaded. PTG (proportion of total gain) values represent the proportional contribution of each factor, in isolation, to the predictive power of the full species distribution model; that is, $PTG = [\text{gain (single predictor)}] / [\text{gain (full model)}]$. The strongest predictor of the depth and latitudinal distribution of staghorn corals was winter PAR (PTG = 0.99). A threshold of $5.2 \text{ mol photons m}^{-2} \text{ day}^{-1}$ best accounted for the predicted maximum depth limits (16).

that can substantially supplement winter nutritional shortfalls through stored energy reserves and/or heterotrophy (22). We showed that there is a factor of 4 variation in winter PAR requirement among the 104 staghorn coral species reported on here (16), likely reflecting species-specific adaptations, including a number of attributes associated with reduced light at depth: flattened branch morphologies to maximize interception of light (2, 10), changes in the density and type of zooxanthellae (23), and some capacity for heterotrophic nutrition (24). However, their efficacy as specific adaptations to seasonally low light at high latitudes has not been reported.

The depth-limiting effects of winter PAR also appear to contribute to a strong latitudinal gradient in species richness in staghorn corals (Fig. 4A). This pattern is consistent with reef corals overall (2, 25) and many other marine and terrestrial taxa (26–28). Categorizing species by their maximum depth limits, we found that the richness gradient was largely driven by a deep-water fauna restricted to low latitudes (Fig. 4A). By contrast, mid-water species richness remained relatively constant to mid-latitudes, whereas shallow water species richness was retained until latitudes 27° to 28° . We contend that the low-latitude combination of high winter irradiance and suitable substrata at depth

constitutes a niche for staghorn corals that does not exist at higher latitudes. This niche is occupied by a central Indonesia–west Pacific fauna typically with fragile and laterally flattened skeletal morphology that limits its members to deep, calm waters well below the influence of waves and swell (29); suitable substrata in deep calm waters at higher latitudes receive insufficient winter irradiance to support this fauna. This mechanism, and the emergent latitudinal patterns of richness of staghorn corals, are aspects of the topography–environment relationships that are not addressed in biogeophysical models of reefs and carbonate platforms (1, 19, 20). Moreover, although factors

Fig. 4. Latitudinal trends in staghorn coral species richness. (A) Categorization of species according to their maximum depth limits (0.975 quantile) (16) (table S5). The deep-water species account for much of the latitudinal gradient in species richness. Species richness was calculated for 1° latitude bins. (B) Example of a deep-water species (*Acropora pichoni*) restricted to low-latitude habitats. (C) A widely distributed shallow-water species (*A. gemmifera*).



such as habitat availability, evolutionary history, vicariance events, and sea surface temperature undoubtedly contribute to patterns of species richness in reef corals overall (2, 25, 28–30), this study makes a compelling case for the overriding importance of light in controlling the poleward attenuation of species richness in a major coral group.

Recent observations of poleward range extensions in corals suggest there is potential for corals to colonize higher latitudes as sea surface temperatures increase (13–15, 31). However, to meet their current winter light requirements, staghorn corals would need to decrease their maximum depth by a predicted (16) 0.6 m for each degree of latitude that their range extended beyond their present northern and southern limits. Species currently at their poleward limits of distribution, their depth range already restricted (Fig. 2), have little scope for further shallowing, or consequently, latitudinal extension. For tropical shallow and mid-water fauna (Fig. 4), contraction into shallower depths would bring into play potentially range-limiting parameters of shallow microenvironments such as damage from waves and swells, extremes of temperature and salinity, competition with shallow corals and macroalgae (2), and ultimately, subaerial exposure at low tide (7). Deep-water species currently restricted to depth at low latitudes (Fig. 4) are also unlikely to colonize shallow waters for the same reasons and would therefore remain latitudinally constrained by winter PAR requirements. In addition, constraints on staghorn coral depth distribution and potential for latitudinal extension may be exacerbated by factors that increase the attenuation of light in the water column and thus reduce winter PAR, such as increased phytoplankton and sediment associated with agricultural runoff, urban develop-

ment, and dredging (32, 33). Until now, two climate-sensitive environmental variables, aragonite saturation and temperature, have been emphasized as the main contemporary drivers of latitudinal limits to the growth of coral reefs (1, 20, 21). Here, we have shown how winter irradiance regime—a climatic constant—may be the ultimate limiter of any potential latitudinal extension of the range of staghorn corals made possible by anthropogenic warming of temperate seas.

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SUPPLEMENTARY MATERIALS

www.sciencemag.org/content/348/6239/1135/suppl/DC1
Materials and Methods
Figs. S1 to S5
Tables S1 to S5
References (34–45)

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