millennial[5]. To understand the findings of Bordbar and colleagues that initial conditions had regionally differing effects on projections, we need to consider that the Atlantic and the Pacific exert distinct influences on internal variability. For oceans, long-term internal variability involves deep ocean processes, and the DSL is an integrated quantity throughout the entire ocean depth, including the deep layers. The North Atlantic is deep but relatively narrow, whereas the Pacific and tropical oceans are wide but can be considered as relatively shallow due to ocean stratification, which limits vertical mixing. This may explain why initial conditions exert more influence over DSL projections for the North Atlantic than the Pacific (Fig. 1a).

In addition to the single model approach using the Kiel Climate Model[3], Bordbar and colleagues[1] employed the multi-model ensemble approach by looking at similar projections from the CMIP5 models[6]. Their model-to-model comparison of the DSL signal and spread confirms that the Kiel Climate Model is representative of the latest-generation coupled climate models. With the CMIP5 ensemble and additional CO_2 emission scenarios such as RCP4.5 and RCP8.5, model uncertainty can be quantified, as well as the scenario uncertainty[7]. It turns out that all three uncertainty sources are important in centennial DSL projections (Fig. 1b).

This systematic analysis of DSL projections provides a comprehensive understanding of the associated uncertainty and suggests that oceanic initial conditions need to be taken into account for optimal DSL projections. This would require close collaboration between climate-modelling, data-assimilation and ocean-observation communities, particularly in light of the sparse observational data available for the deep ocean. In addition, we need to further and better assess the abilities of different models to reproduce centennial and longer-scale natural variability, as revealed by proxy records and long-term reanalysis data[5]. Filling in such gaps would allow seamless transitions from near-term predictions to long-term projections, and would provide more accurate climate and sea-level information to governments and societies. ❐

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MARINE BIOLOGY

The coral disease triangle

The underlying causes of biodiversity loss can be numerous and difficult to identify. Now evidence suggests that disease outbreaks triggered by warming oceans are a primary cause of the disappearance of Caribbean coral reefs.

John F. Bruno

Is a warmer world a sicker world? Disease is widely recognized as a primary cause of biodiversity loss and ecosystem degradation in aquatic and terrestrial ecosystems. Rapid, regional population declines in trees, amphibians, mammals and even sea-stars have all been linked to disease outbreaks. One explanation is global warming[1]. Higher than normal temperatures are thought to increase the occurrence and severity of disease outbreaks through several mechanisms, including increased pathogen virulence and weakened host immune systems owing to physiological stresses. Writing in *Nature Climate Change*, Randall and van Woesik[2] report that seemingly subtle increases in ocean temperature have completely altered the seascape of Caribbean reefs by triggering disease outbreaks in crucial, habitat-forming coral species.

Caribbean reefs are primarily built by two types of coral: massive, long-lived colonies of *Orbicella* species (formerly known as *Montastraea*) and fast-growing *Acropora* species, which form branching colonies (Fig. 1). Historically, these two taxa dominated Caribbean reefs, but populations of species from both genera have largely collapsed across the region. Their loss means flatter reefs that no longer provide hiding places for other organisms (including fishes that people eat), do not buffer coastal communities from storms, and cannot grow vertically in response to sea-level rise.

The proximate cause of the *Acropora* decline is white-band disease[3] — a tissue-degrading condition caused by an unknown pathogenic bacterium[4]. Outbreaks of this disease in the Caribbean appeared quite suddenly in the late 1970s and early 1980s, leading reef scientists to suspect that the causative pathogen was introduced to the region, perhaps via the Panama Canal or in ballast water carried by cargo ships. Until now, however, attempts to understand this disease focused almost entirely on the pathogen and largely failed to consider how changing environmental conditions might have facilitated this problem. To investigate these possible influences, Randall and van Woesik combined data from diver-conducted surveys for white-band disease from 473 Caribbean reefs with satellite records of ocean surface temperature. They found that higher temperatures are strongly related to the occurrence of disease — findings that directly link ocean warming with the transformation of an ecosystem at an enormous spatial scale.

Climate change ecologists evaluate how different aspects of temperature are changing to measure global warming. For example, are winters or summer nights less cool? Is the summertime peak a little higher each decade? Are heat waves getting longer or more intense? These different metrics have different potential consequences for people and wildlife. Moreover, for a given

Figure 1 | Colonies of *Orbicella* (left) and *Acropora* (right) corals in the Caribbean. Images courtesy of: left, © Vilainecrevette/Alamy; right, Christian Ziegler/Getty.

species, one metric might be benign while another is deadly. Ecologists rarely know which to investigate beforehand. Randall and van Woesik[2] assessed several 'thermal stress' metrics, including increases in winter minimums, summer maximums and 30-year warming trends, and found that these metrics successfully predicted the observed outbreaks. They also found strong evidence for temperature thresholds that, when exceeded, were likely to trigger disease. For example, colonies of *A. cervicornis* were more likely to be infected if winter ocean temperature was not cooler than 27.5 °C. For *A. palmata*, the winter threshold was 28.5 °C. White-band disease in *A. cervicornis* was also more common when temperature exceeded 33 °C and in *A. palmata* when the long term warming trend was greater than 0.015 °C per year. Increasing winter water temperatures have also been found to be correlated with increased severity of yellow band disease in *Orbicella* corals[1], possibly because cooler winter temperatures impair the pathogen or generally enable corals to recover from summer temperature stress and build up energy reserves.

Defining the relationship between ocean warming and coral disease can be difficult. Numerous aspects of ocean warming and potential response lags need to be considered, as do other factors that can influence where and when outbreaks occur, such as coral abundance, nutrient concentration and water depth[5,6]. If these factors are not accounted for, the fingerprint of temperature can be faint, potentially leading to a false-negative result. The concept that several factors are necessary — but alone are not sufficient — for an outbreak to occur, is called the 'disease triangle'. This idea, which stems from epidemiology, is that the host, the pathogen and the environment all play a part, and all three components need to be considered to understand and manage a disease. In many cases, the environment is itself a complex unit, comprising multiple triggers and other players, such as predators that can transmit the pathogen or create wounds that enable infections[7].

Although ocean warming had not been suspected to be the underlying cause of the observed decline of *Acropora* throughout much of its range — until now — one policy response had already recognized the importance of the environment to the decline of this species. *A. palmata* and *A. cervicornis* have been listed as threatened under the US Endangered Species Act, and the forward-thinking Draft Recovery Plan for these corals[8], released in 2014, recommends that we "curb ocean warming and acidification impacts to health, reproduction, and growth, and possibly curb disease threats, by reducing atmospheric greenhouse gas concentrations." However, the temperature-mitigation criterion (preventing temperature from exceeding 30 °C during spawning periods) was set to limit future or additional stress from bleaching and impaired reproduction, and Randall and van Woesik's findings[2] suggest that this season-specific limit will not prevent further disease outbreaks.

Although we might not be able to directly treat diseased corals or eradicate their pathogens, we can mitigate environmental conditions, such as thermal stress, that enable outbreaks. Randall and van Woesik's clear indication of the correlation between ocean warming and disease outbreaks in corals is further evidence that we need to get serious about our collective response to climate change. A coral-reef recovery plan that responds to their findings would require emissions reductions that would eventually return atmospheric concentrations of CO_2 to below 350 parts per million — the level considered to be the safe limit for coral reef survival[9] and roughly the concentration that had been reached when the white band disease outbreaks began. ❒

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