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Smooth and Spiky: The Importance of Variability in Marine Climate Change Ecology

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Abstract

Greenhouse gas emissions are warming the ocean with profound consequences at all levels of organization, from organismal rates to ecosystem processes. The proximate driver is an interplay between anthropogenic warming (the trend) and natural fluctuations in local temperature. These two properties cause anomalously warm events such as marine heatwaves to occur with increasing frequency and magnitude. Because warming and variance are not uniform, there is a large degree of geographic variation in temporal temperature variability. We review the underappreciated interaction between trend and variance in the ocean and how it modulates ecological responses to ocean warming. For example, organisms in more thermally variable environments are often more acclimatized and/or adapted to temperature extremes and are thus less sensitive to anthropogenic heatwaves. Considering both trend and variability highlights the importance of processes like legacy effects and extinction debt that influence the rate of community transformation.

INTRODUCTION

For most of the last 10,000 years, the physical conditions in marine ecosystems have been nearly stationary. Stationarity does not mean unchanging (Ryo et al. 2019). It means that you can think of each year's temperature as being drawn from a probability distribution with a stable mean and standard deviation. Changes occur, but they occur through natural variation around the mean. These variations can come from daily shifts in the weather and longer-term, large-scale modes of climate variability like the El Niño Southern Oscillation (ENSO) or, the Pacific Decadal Oscillation (PDO).

Marine communities are made up of species that are adapted to the prevailing local conditions. Thermal conditions can be characterized by the mean temperature, the amplitude of the annual cycle, and the interannual variability. These characteristics of ocean temperature strongly influence countless aspects of the physiology and ecology of marine organisms, the composition and diversity of marine communities, and even the structure and dynamics of marine food webs.

To characterize these features globally, we used monthly sea surface temperature data from the National Oceanic and Atmospheric Administration extended reconstructed sea surface temperature data set to identify the month for every location where the maximum temperature is typically observed. The difference in temperature between the warmest and coolest month shows a strong latitudinal gradient, with seasonal amplitude increasing from the equator to the poles (**Figure 1*a***). The seasonal amplitude is then further elevated in the northwest Pacific and northwest Atlantic due the influence of the continents on the weather. A similar latitudinal pattern exists in the interannual variability over the period 1982–2020 during the locally warmest month (**Figure 1*b***). However, regions like the eastern tropical Pacific stand out as a region of elevated variance, reflecting the strong influence of ENSO.

The community of species at a location reflects the region's inherent natural variability. For example, in the absence of intense fishing, Atlantic and Pacific cod are large and long lived. Their large body size allows them to produce huge quantities of eggs (Barneche et al. 2018), and their long life spans give them many years of attempted reproduction. These traits allow them to be successful in the highly variable, boom-or-bust conditions of their subpolar environments (Pershing & Stamieszkin 2020).

Climate change is now shattering any assumptions of stationarity. Since 1900, the oceans have absorbed 3×10^{23} J of energy trapped by human-caused greenhouse gas emissions (Cheng et al. 2021). At the surface, the spatial fingerprint of ocean warming is not uniform. Since 1982, the regions around the North Atlantic subpolar gyre have warmed at an above average rate while the center of the gyre has cooled (**Figure 1*c***). This pattern has been linked to a slowdown in the Atlantic meridional overturning circulation (Caesar et al. 2018, 2021). The Mediterranean and North Pacific have also warmed rapidly. At the same time, the Southern Ocean and eastern tropical Pacific have cooled somewhat. The cooling in the Southern Ocean is likely due to an increase in wind-driven transport of sea ice (Haumann et al. 2020), while the pattern in the tropical Pacific is most likely due to the fact that the last few years of data collection occurred during the cool phase of the PDO.

The purpose of this review is to advance our understanding of how marine ecosystems have changed and will change in response to climate change. We are specifically interested in understanding the limitations of current approaches and identifying experimental, conceptual, and theoretical approaches necessary to understand the new ocean. A key theme of our review is that climate change in the ocean is both smooth and spiky. By smooth, we mean that there are clear temperature trends driving change. For example, Harris et al. (2022) interpreted warming as a press perturbation. By spiky, we mean that there is natural, inherent variability on top of the trend. The smooth trends and spikes from variability interact, and understanding how processes

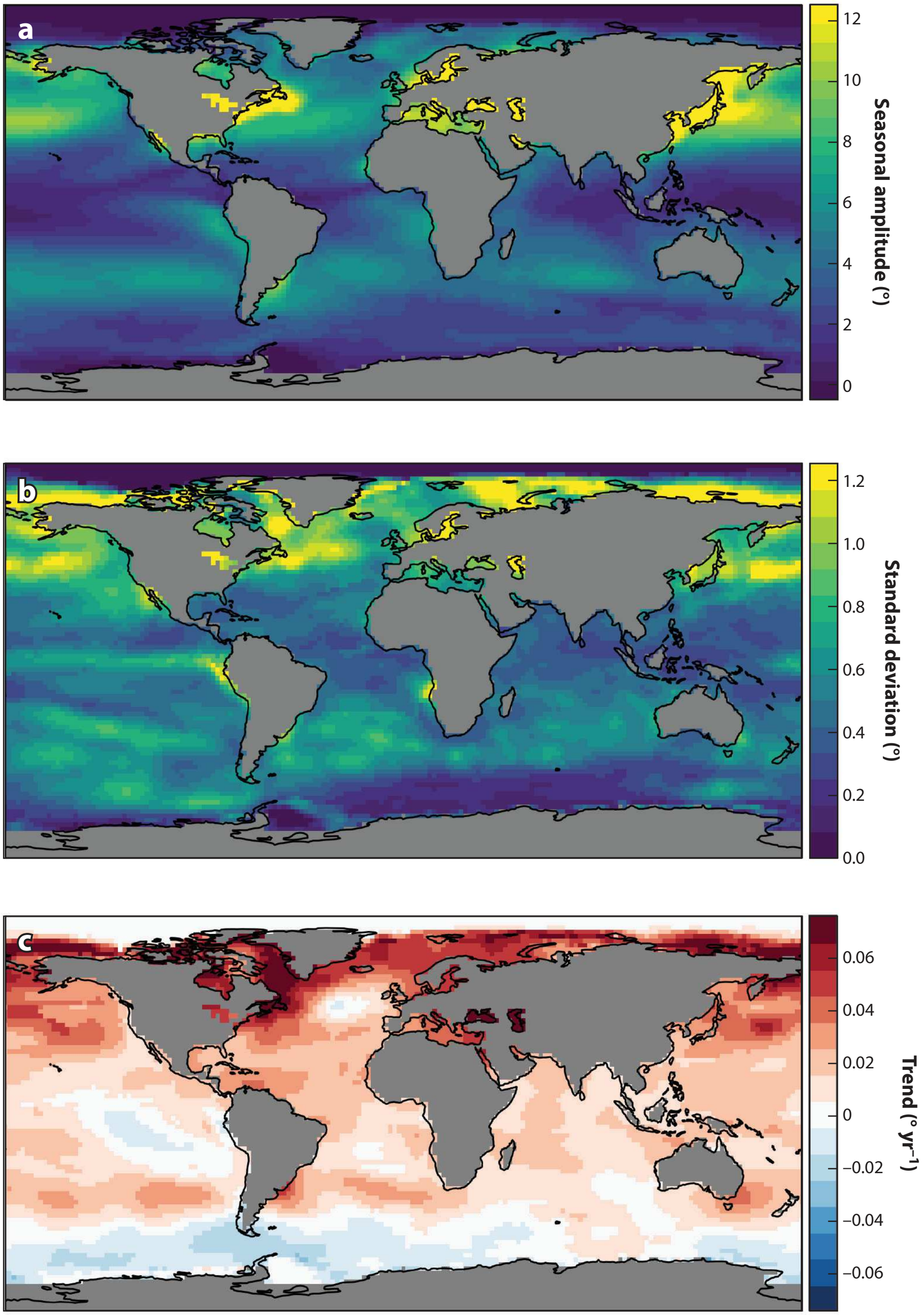

Figure 1

Sea surface temperature conditions (°C) around the world. (*a*) Seasonal amplitude defined as the difference between the warmest and coolest months at each location in the 1982–2011 climatology. (*b*) Standard deviation of annual temperatures in the warmest month over the period 1982–2020. (*c*) Linear trend in temperature in the warmest month. Methods based on Pershing et al. (2019) and described further in the **Supplemental Material**.

Supplemental Material >

within organisms and communities filter these interactions is the key to understanding how marine ecosystems will change over the next century.

We begin by considering how organisms and communities adapt or adjust to both smooth and spiky changes. We then review processes including legacy effects and extinction debt that influence the rate at which communities adjust to changes in the physical environment. We consider processes that serve as constraints that limit the ability of species to move horizontally or vertically to track changes. Finally, we conclude with a synthesis and research recommendations.

HEATWAVES, ADAPTATION, AND THE CENTRAL ROLE OF VARIABILITY

One of the fundamental aspects of evolution is that organisms are adapted to the historical conditions in their environment. Traditionally, ecologists have been able to focus on variability in the physical conditions in their systems of study. Variability is one factor that influences the combination of species and traits in a community. Variability also introduces the possibility of extremes or spikes that function as pulse perturbations and can have an outsized impact on communities (Yang et al. 2008, Harris et al. 2022). This suggests that we need to think about warming and other smooth changes relative to the variability inherent in the system.

The upward trend due to global warming is making extreme events ever more likely. Pershing et al. (2019) considered how trend and variability interact to produce unusual temperatures. They considered the variability as an inherent feature of the ecosystem and the warming trend as an external driver of change. The same temperature trend will lead to a greater chance of an extreme in a lower variability ecosystem than in a high variability environment. Most ocean locations have warming trends near 0.02°C/y and variance around the trend near 0.3° during their warmest months of the year (**Figure 2*a***). These conditions, which currently exist off South Africa, mean that an extreme temperature (defined as monthly temperature exceeding the 95th percentile relative to the 30 year mean) should occur four times more frequently in today's climate than in the past (20% instead of 5%). Regions like the Galapagos and the Channel Islands, United Kingdom, that have weak trends and historically high variability had little change in the probability of these extremes over the time period considered. Several regions with strong trends had very high probabilities of extremes. The Gulf of Maine (trend = 0.054°/y, variability = 0.9°) should experience an extreme 30% of the time. While the Eastern Caribbean and Eastern Mediterranean have lower trends (0.034°/y and 0.045°/y, respectively), their relatively low temperature variability (0.5° and 0.6°, respectively) lead to a higher (36%) chance of extremes.

Thermal stress has led to the mortality of benthic foundation species in each of these three regions with a high probability of temperature extremes. For example, populations of seagrass (*Posidonia oceanica*) endemic to the Mediterranean experienced leaf necrosis and shoot mortality during a period of high sea surface temperature in summer 2021 (Stipcich et al. 2022). Future losses of up to 75% of seagrass habitat in the Mediterranean are projected from climate models (Chefaoui et al. 2018). Mass mortalities of gorgonians and 24 other sessile invertebrate species coincided with anomalously high temperatures across 6 areas of the Mediterranean Basin in 2003 (Garrabou et al. 2009). In the Caribbean, coral reefs have been subjected to more than a century of warming (Bove et al. 2022) and thus multiple episodes of coral bleaching and mortality beginning in the mid-1980s (Eakin et al. 2009, Selig et al. 2010, Muniz-Castillo et al. 2019). In the Gulf of Maine, die-offs of kelp were observed at an offshore ledge during heatwaves in 2012 and 2016 that contributed to a decline in kelp density (Witman & Lamb 2018). Overall, the exceptional pace of warming in the Gulf of Maine has led to an increase in temperate species and a loss of subarctic species (Pershing et al. 2021).

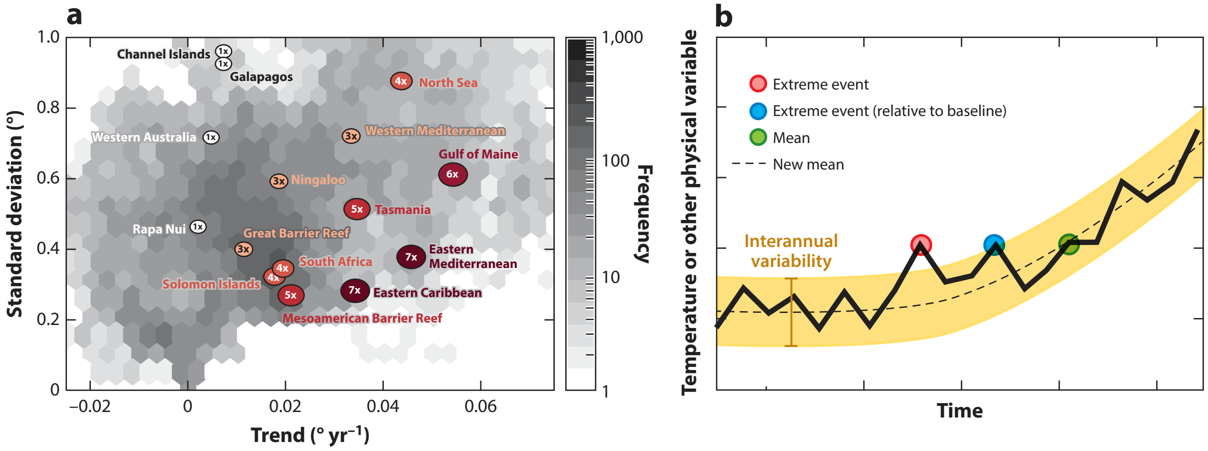

Figure 2

Interaction between trends and events. (*a*) Distribution of interannual standard deviation in sea surface temperature (°C) during the warmest month plotted against trend over the period 1982–2020. The shaded hexagons indicate the number of 2°-by-2° ocean regions with the combination of standard deviation and trend. The ovals highlight the conditions in specific regions of interest. The shading and size of the ovals indicate the change in the probability of a 5% event assuming a static baseline. For example, the strong trend and low variance mean that the Eastern Mediterranean currently has a 36% chance of exceeding this threshold. Methods are based on Pershing et al. (2019) and described further in the **Supplemental Material**. (*b*) Diagram depicting how trend and variability interact to produce events. The yellow region represents the interannual variability around the mean (*dashed line*). The solid black line indicates the actual temperature in each year. The three events highlighted by colored circles all have the same temperature. Initially, this is an extreme such as a heatwave that is well outside the variance (*red circle*). The onset of warming brings the second event (*blue circle*) to the edge of the variance, and continued warming means that the third event (*green circle*) corresponds to the expected mean.

One of the ways that the trend and variability are currently interacting in the ocean is in the formation of marine heatwaves. Marine heatwaves are commonly defined as five or more consecutive days above the 90th percentile temperature for that day (Hobday et al. 2016). This definition has been applied by more than 800 studies referring to marine heatwaves. For temperature, there is strong evidence that variability is not changing (Alexander et al. 2018) and that the increase in marine heatwaves is not being driven by an increase in variance (Oliver et al. 2021).

Supplemental Material >

The biggest challenge of using the Hobday et al. (2016) definition is determining how to define the baseline that is used to define the temperature thresholds. In most studies, the baseline is based on a fixed 30-year reference period (for example, 1981–2010). When compared to a fixed baseline period, the number of heatwave days increases as the local mean temperature increases (Oliver et al. 2018). The increase in heatwaves defined in this way is particularly prominent in climate projections. For example, Frölicher et al. (2018) estimated that a marine heatwave that would occur with probability 0.01 in a preindustrial baseline climate would occur with probability 0.4 in 2080 under high CO_2 emissions.

Jacox (2019) argued that a fixed-baseline approach muddies the understanding and interpretation of marine heatwaves. They point out that at present, El Niño events are a major driver of marine heatwaves in the eastern Pacific. However, under a fixed baseline approach, eventually La Niña conditions could produce heatwave conditions. Understanding the consequences of a baseline is particularly important when considering the biological impacts of marine heatwaves or ecological surprises (Oliver et al. 2018, Pershing et al. 2019). A short baseline period that is updated frequently would identify events that are likely to have an impact on a system that can adjust quickly, while a longer baseline period may be appropriate for slower-adjusting systems or for long-lived species (Oliver et al. 2021).

We show an idealized interaction between a smooth warming trend and variability (**Figure 2*b***). In this conceptual model, we assume that variability does not change. This assumption is consistent with analyses based on observations and models that suggest that temperature distributions do not change in response to warming (Alexander et al. 2018) and that the increase in marine heatwaves is not being driven by an increase in variance (Oliver et al. 2021). While temperatures are likely best approximated solely by a shift in the mean, this is not true for all environmental variables. For example, ocean warming increases the probability of tropical cyclones reaching higher storm categories (Kossin et al. 2020). This will potentially lead to increased variance in storm-driven disturbance. In the model shown in **Figure 2*b***, a temperature spike or heatwave occurs at the first labeled point. These conditions push the system beyond the historical range. This event is likely to have a strong impact on the system, especially if it comes during a critical season or during the warmest part of the year. Because of the trend, this temperature extreme is likely to occur again in a few years. Under a fixed baseline model, we would expect this event to have the same impact as the first event. However, it is possible that the first extreme event altered the system, for example, by extirpating a previously common species, so that it leads to less noticeable changes. Finally, within a few years of additional warming, what was once an extreme is now the mean.

The process by which organisms and thus communities respond to repeated events is central to understanding the ecology of climate change in the ocean. Changes to species composition in response to frequent disturbance can lead to increased resistance to future events. If the return time of heatwaves and other disturbances is shorter than the time needed for population recovery, impacts can decline as disturbance-sensitive individuals and species are weeded out of the community.

Individuals, populations, and communities that inhabit locations where environmental conditions are inherently variable are often more resistant to acute, extreme events. This hardening via exposure to extreme conditions can arise from a wide variety of mechanisms. At the individual level, acclimatization or hormetic priming (Costantini 2014) to environmental extremes can occur (simultaneously) via numerous pathways including epigenetic mechanisms, such as DNA methylation, and changes in the associated microbiome of an organism (Stillman 2003, Putnam 2021, Somero 2010). These phenotypic changes can sometimes, to a limited degree, be passed onto offspring (Byrne et al. 2020, Putnam 2021). Populations can become less sensitive to extremes via the cumulative acclimatization of constituent individuals and also through selection for genotypes that are phenotypically plastic or less sensitive to the stressor (Somero 2010). Natural selection for resistant genotypes is also a widely demonstrated mechanism that can reduce population-level sensitivity to extremes.

At the community level, acute events can reduce the abundances of sensitive species through selective mortality based on their physiological, morphological, or life history traits. Such selection of resistant species is a common community-level response to severe disturbance that simultaneously increases resistance and alters species and trait composition (and subsequently ecosystem functioning). The combination of these (and other) mechanisms that underlie increased resistance following a disturbance event or period of variable conditions is sometimes referred to as a legacy effect or ecological memory. An example is the reduced sensitivity of tropical coral communities to subsequent events following hurricanes or heatwaves (Witman 1992, Stuart-Smith et al. 2018, Edmunds 2019, Hughes et al. 2019). The implications of this adaptation to environmental variability—essentially made possible by ecological variability (i.e., acclimatization, adaptation, changes in species composition, etc.)—are that ecological history matters and thresholds change over time. This means that the impact of the same temperature (e.g., the three events in **Figure 2*b***) becomes less noticeable with each successive occurrence.

RATE PROCESSES PREDICTING GLOBAL CHANGES IN MARINE BIODIVERSITY

Temperature extremes are causing local extinctions and colonizations that are subsequently leading to rapid changes in the geographic ranges of marine species. Typically, species ranges are shifting toward higher latitudes, away from warmer areas where heat waves have exceeded organismal thermal thresholds (causing local extirpations). Cumulatively, ongoing range shifting of many (and possibly most) marine species is changing regional-to-global patterns of species richness and composition.

A variety of approaches have been used to forecast changes in global patterns of marine biodiversity in the near- to mid-term future (i.e., 2050–2300) under different emissions scenarios. All published models assume a smooth future of gradual change, they assume that species declines are due to the trend rather than infrequent extremes (variance), they do not consider geographic variability in temporal variability (spatiotemporal variance), and they assume that dispersal and range expansion is smooth (and largely unlimited). These shortcomings—all based on a gradual change mindset in which past and future variance is regionally homogeneous—may have substantially affected study outcomes.

Most projections of future changes in species distribution or community properties like richness are based on models that are fundamentally equilibrium theories. Species distribution models based on thermal niches assume that species track their preferred temperature conditions as they move poleward during warming. While these models may be appropriate for end-of-century conditions (an assertion that is fundamentally untestable), they are clearly inadequate for predicting the response to marine heatwaves. For example, many squid species are able to rapidly track changes in temperature. Longfin squid moved into the Gulf of Maine during the 2012 heatwave (Mills et al. 2013), and Humboldt squid extended their range 1,000 km during the series of El Niño events in the early 2000s (Zeidberg & Robison 2007). However, many benthic invertebrates do not have this ability. Their distributions shift due to differential reproductive success and mortality combined with dispersal. This process is much slower and may be constrained by other ecosystem changes. The difference in the rate at which species can move is creating novel communities with properties that have not been studied or even predicted.

Other equilibrium theories such as macroecological predictions relating diversity to temperature or even the distribution of biomes face similar problems (e.g., Allen et al. 2002, Rombouts et al. 2011). These concepts or relationships were based on observations of ecosystems that had experienced a long period of stationary conditions (bounded variability on top of a stable mean). The community of organisms had the opportunity to adjust to the prevailing conditions. These theories suggest where the community at a location may be headed under a certain temperature change, but they do not indicate how long it will take to get there or what the community will look like in the intervening years. For example, several climate scenarios such as Shared Socioeconomic Pathways (SSP) 1–2.6, reach a stable global mean temperature later in the century. We would expect communities to reach the ideal conditions envisioned by equilibrium theories years to decades after the temperature stabilizes. Scenarios like SSP3–7.0 project continued warming throughout the century. Theories that assume stationarity or equilibrium conditions should be used cautiously in these conditions, yet most projections include them.

All published efforts to forecast future geographic patterns of species richness essentially predict the future distributions of real or simulated species from current estimated thermal tolerances or observed or expected rates of migration. Although these environmental niche models (ENMs) or bioclimate envelope models are powerful and appealing, they have several limitations. For example, species-specific thermal sensitivities are based on extant distributions, geographic affiliation with temperature, and the assumption that temperature is largely controlling population distributions. Additionally, species migrations are sometimes assumed to match the climate velocity (i.e., changes in surface isotherms) of temperature or other factors. It is clear that for many species, resource limitation, enemies (predators, competitors, parasites, etc.), the presence of mutualists, and myriad other factors strongly influence distributions and colonization success. ENMs generally also fail to account for adaptation or acclimatization, thereby overestimating local extinction. Thus, some approaches probably overestimate both extinction and migration success and likely exaggerate changes in richness and turnover (i.e., compositional shifts).

Historically, marine species richness was highest in warm equatorial seas, especially in the western equatorial Pacific. Generally, marine biodiversity forecasts predict declines in species richness in at least part of the equatorial seas and gains in higher latitudes (Chaudhary et al. 2021). Species invasions and extinctions are both generally predicted to be greatest in the Arctic. Although local extinctions for tropical marine species are predicted to be high, most models predict that a substantial fraction will shift their ranges to higher latitude, thereby avoiding global extinction. All published studies forecast a rapid global redistribution of marine species and consequently high degrees of turnover and compositional change. In all cases, the degree of change is strongly dependent on the emissions pathway and magnitude of environmental change. However, the timing, extent, direction, and geographic patterns of changes in marine species richness are surprisingly study specific and highly dependent on assumptions about specific factors causing mortality (e.g., deoxygenation versus thermal stress), the capacity of species to shift their ranges poleward, and possibly other aspects of study design.

The first global-scale effort to model the geographic redistribution of species (Cheung et al. 2009) was based on an ENM that used known ranges and temperature affinities combined with climate models to forecast future distributions of commercially harvested fishes and the resulting geographic patterns of extinctions and invasions. The model is relatively sophisticated in that it incorporated population dynamics and projected larval dispersal based on known current patterns and pelagic larval duration and estimated dispersal distance. The Cheung et al. (2009) model predicted that invasions will be far more likely in the Arctic and in areas of the Southern Ocean. Extinction frequency was more spatially variable but generally highest in the Southern Ocean, warm equatorial seas (especially the central and western Pacific), and the North Atlantic. Thus, the greatest species turnover and changes in richness were predicted to occur in the fastest warming and coolest marine region.

A follow-up study (Jones & Cheung 2015) using a similar approach but based on an ensemble of ENMs predicted similar patterns of extinction and colonization for 802 commercially harvested species. Under the high emissions scenario [representative concentration pathway (RCP) 8.5] extinction probability by 2050 was 12% in tropical seas (between 10 N and 10 S latitude) and 4% globally. Indicative of the model's high confidence in species' capacity to shift their ranges poleward, 97% of species did so at a median rate of 26 km per decade.

García Molinos et al. (2015) expanded on this work, using an ENM to project the future distributions of 12,796 species from 23 phyla, most of which were not commercially harvested (**Figure 3**). The study included sessile species such as bryozoans, bivalves, and corals. Although it was dominated by fishes (9,475 of the 12,796 species) some, including butterflyfishes, wrasses, and other benthic species, are relatively site attached. Like the models in Cheung et al. (2009) and Jones & Cheung (2015), the García Molinos et al. (2015) model projected high extinction frequencies in tropical seas, especially the coral triangle region around Indonesia. They also found extensive and rapid poleward range shifts and high invasion frequency by 2100 under RCP 8.5, especially in the Arctic but also in the tropical western Pacific.

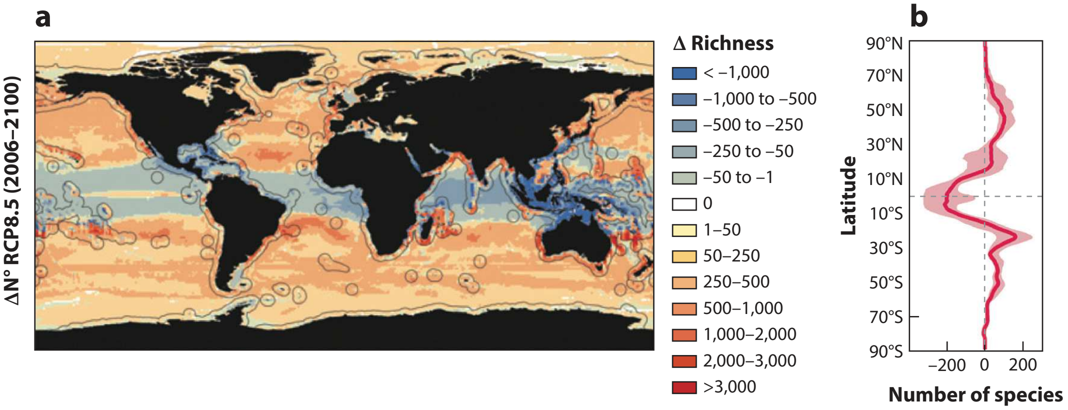

Figure 3

Projected changes in global marine species richness through 2100 based on RCP 8.5. (*a*) Spatial distribution of richness change showing decreasing richness in the tropics and increasing richness at higher latitudes. Black lines on the map are the limits of exclusive economic zones. (*b*) Zonal average richness change. Abbreviations: RCP, representative concentration pathway. Figure reproduced with permission from García Molinos et al. (2015).

The challenge of viewing ocean ecosystem changes through a smooth or equilibrium view can be illustrated using the concept of climate velocity. Pinsky et al. (2013) documented range shifts in commercial fish and invertebrates associated with temperature changes. They concluded that these species are following isotherms, meaning they are moving at the climate velocity. The challenge with interpreting this result is in understanding exactly the timescales involved. By considering the climate velocity and distribution shifts over many decades, their study takes a smooth view of ocean ecology. Studies of the same data that consider higher frequency variability find a diversity of responses to temperature, with some species tracking conditions and others lagging (Schuetz et al. 2019).

It is also worth considering whether the smooth view of species distribution changes will continue to hold. The conclusions of Pinsky et al. (2013) apply to a period (1968–2011) when global temperatures were rising at 0.16°/decade (see **Supplemental Material**). Over the following decade, the rate of global warming increased to 0.22°/decade. A key question is, At what rate of change can key species assemblages move together? Revisiting some of the foundational papers on range shifts and climate change as global warming accelerates would provide insights into these mechanisms.

Supplemental Material >

In essence, the ENMs project the state that ecosystems should tend toward, assuming past processes are still valid. What they are unable to capture is whether communities will be able to keep up with the idealized state. This is especially true under the high CO_2 scenarios like RCP 8.5 in which change is rapid and continues throughout the century. Understanding the processes that determine the rate of community transformation is therefore critical to understanding when or even whether these long-range projections actually apply. The rate of change in ecosystems is closely tied to the history in that community.

TEMPORAL DYNAMICS

Ecosystem history is encapsulated in the temporal dynamics of communities, with an effect emerging sometime after prior exposure to a stressor described as a legacy effect and the length of time between the exposure and the effect as a time lag (Essl et al. 2015, Ryo et al. 2019). Ecological memory refers to the ability of past experiences to explain present or future responses of an ecological system (Ryo et al. 2019), while extinction debt is a type of a legacy effect leading to the local extinction of species (Tilman et al. 1994, Kuussaari et al. 2009).

Long-lived organisms experience multiple temperature anomalies (spikes) superimposed on a trend of increasing temperature (**Figure 2*b***). The initial exposure to a temperature anomaly may have a greater impact than subsequent anomalies. At the individual level of organization, shocks from initial temperature anomalies could lead to reduced growth and reproduction and higher mortality relative to subsequent anomalies (spikes). This may result in demographic changes such as reduced population growth rates and recruitment and smaller population sizes. The effect of winnowing individuals of different species killed by the initial anomaly may be manifested in changes in species composition and diversity at the community level. Since regional marine ecosystems vary widely in terms of the magnitude of temperature anomalies and the frequency at which they recur (**Figures 1** and **2*a***), it is possible that regional variation may underlie legacy effects.

The frequency of disturbance from episodic temperature anomalies defines the return time of the stressor and the capability to recover (White & Jentsch 2001, Witman & Dayton 2001). Organisms living in ecosystems experiencing a high frequency of temperature anomalies may experience residual effects of antecedent anomalies. Time lags can vary from days to years depending on the physiology and thermal sensitivity of the organism and level of ecological organization. Physiological stress may be imposed with the shortest time delay, such that mortality and its ultimate effects on community change (Pratchett et al. 2008, Rhoades et al. 2023) and range shifts (Hiddink et al. 2015) may be lagged by weeks to years from the event.

Although multiple large temperature anomalies are typically attributed to negative ecological effects (Garrabou et al. 2022), there is some evidence that multiple anomalous warming events closely spaced (clustered) in time have less-deleterious effects than randomly spaced ones (Dal Bello et al. 2017) or than those that recur at low frequency. Indeed, ecological legacy effects may be positive from an evolutionary standpoint if they precondition individuals to environmental change, leading to acclimation, adaptation, or rapid evolution. Recent studies of thermal shocks in coral reefs (Pratchett et al. 2008, Hughes et al. 2019, Hackerott et al. 2021) highlight legacy effects. For example, in a review of ecological memory in corals, Hackerott et al. (2021) found that colonies with prior stress exposure (temperature shocks, bleaching) bleached less severely during subsequent periods of anomalously high temperatures. This type of positive legacy effect varies by coral species and the composition of the coral symbiont community (Claar et al. 2020) and with the magnitude and duration of the thermal anomaly. However, the generality of positive legacy effects of temperature spikes remains unknown, as prior exposure to high temperatures can also lead to coral mortality on the second exposure (Grottoli et al. 2014) or have no effect (Hughes et al. 2017). Species-specific legacy effects may influence coral diversity and dominance in the long run by winnowing sensitive species or by increasing the abundance of species responding positively to prior thermal anomalies. The loss of reef structures from coral bleaching creates legacy effects in reef fish communities (Garpe et al. 2006, Pratchett et al. 2008), with declines in the abundance and diversity of coral-reef fishes lagging by 3 years or more after the initial thermal disturbance. These studies attributed changes in reef fish assemblages to the delayed effect of structural collapse of dead corals, which reduces overall topographic complexity of coral-reef habitats, particularly on Indo-Pacific reefs formerly dominated by acroporid corals.

Extinction debt is typically studied as a consequence of disturbance-generated loss of a physical habitat created by a foundation species such as trees, seagrass beds, or corals for those species associated with the habitat structure (Tilman et al. 1994, Jackson & Sax 2010). The magnitude of and time to species loss following a temperature anomaly or disturbance depends on whether the associated species are habitat specialists or generalists, their dispersal ability, and the size of the focal habitat that is disturbed (Kuussaari et al. 2009, Hylander & Ehrlén 2013, Watts et al. 2020). In contrast to terrestrial plant communities, knowledge of extinction debt in marine communities is limited (Stone et al. 1996, Lefcheck et al. 2016). Anomalously low temperatures during the 2007–2008 La Niña event killed structurally complex finger coral foundation species, which led to an extinction debt of 32–49 months for the communities of mobile invertebrates associated with the coral habitat (Rhoades et al. 2023). Some of the most well documented examples of the impacts of recurrent high temperature anomalies come from Mediterranean subtidal ecosystems where heat waves occurred during the summers of 1999, 2003, and 2006 (Garrabou et al. 2019, 2022). The heat waves created mass mortalities of gorgonian foundation species, sponges, and other sessile invertebrate species. However, extinction debt is presently not a central focus of research on marine heat waves (Harris et al. 2022, Smith et al. 2023).

CONSTRAINTS ON CHANGE

In the previous section, we argued that state-dependent processes like legacy effects can interact with the variability in the system and either accelerate or slow the rate of change. A fundamental unanswered question concerns whether the changes envisioned by models that assume smooth change or rest on equilibrium assumptions are even possible. In other words, what are the constraints or barriers—physical or biological—that species and communities will encounter as the environment changes?

Light is a fundamental barrier that is not generally included in many ENMs. Organisms that move poleward will encounter greater amplitudes of seasonal changes in day length and reduced light intensity during the summer. This effect is most extreme near the poles and could provide a fundamental limit for algae and for visual predators like fish (Pershing & Stamieszkin 2020). Light levels decline exponentially with depth, making the vertical contrasts even more extreme (Caves & Johnsen 2021). No matter what the temperature is, the vertical range of organisms like algae or zooxanthellate corals that are dependent on photosynthesis is limited to the euphotic zone.

How temperature trends and temperature variability change in the vertical dimension along depth gradients in the ocean has implications for the potential of deep habitats to serve as refuges from warming surface waters (**Figure 4**). The depth refuge hypothesis (Glynn 1996, Bongaerts et al. 2010, Thatje 2021) has three elements, predicting (*a*) that the survival of deep dwelling organisms will be greater than that of shallow ones in a warming ocean, (*b*) that organisms can escape stressful warm shallow waters by colonizing or migrating to deep cooler habitats, and (*c*) that deep-dwelling populations represent a reproductive source for shallow ones (Hughes & Tanner 2000, Lesser et al. 2009). The hypothesis is set up by the vertical structure of the water column, with a surface mixed layer of warmer water overlying deeper, cold water with a transitional thermocline in between (Fiedler 2010) during stratified conditions (**Figure 4*a***).

A majority of the studies supporting the depth refuge hypothesis concern sessile species such as corals, generally finding reduced coral bleaching at depth, consistent with the cooler thermal environments of deep reefs. Studying local oceanographic conditions in the Bahamas and South Africa (Riegl & Piller 2003) and at three island groups across the Pacific, Wyatt et al. (2020) found that upwelling areas can provide a thermal refuge for corals. Internal waves were the likely upwelling driver in the Bahamas (Riegl & Piller 2003) and in Panama, French Polynesia, and Okinawa (Wyatt et al. 2020). Milleporid hydrocorals at 11 m depth survived warming from two El Niño events, while those at shallow, warmer depths (2–5 m) were driven to local extinction in the Gulf of Chiriqui, Panama (Smith et al. 2014). Similarly, bleaching-induced mortality of acroporid corals was lower at 6–8 m depths than at shallower ones (Bridge et al. 2013). In a comprehensive study of 153 coral species responses to bleaching in the Maldives, Muir et al. (2017) discovered that nearly three-quarters of the shallow (3–5 m deep) species had deep (24—30 m) individuals with

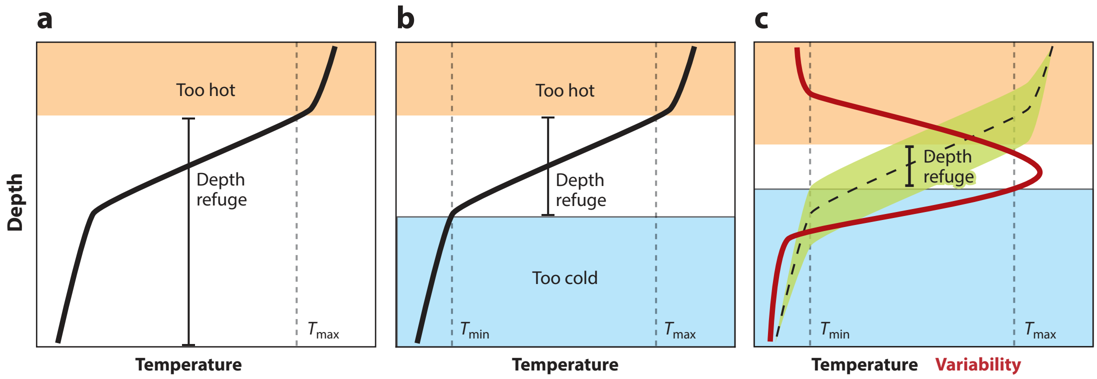

Figure 4

(*a*) Conceptual diagram of temperature depth refuge under mean conditions, with additional constraints of (*b*) deep cold water, and (*c*) variable conditions. (*a*) The solid black curve represents a typical summer temperature profile with a distinct thermocline. The dashed vertical lines indicate the upper and lower temperature limits of a species. In the first scenario (panel *a*), warming has made the surface waters too hot (*orange*). Deep cold waters (*blue*) are below the species thermal tolerance, and with no other limitations, a broad depth refuge is created (*white*). (*b*) Adding a lower temperature limit (T_{min}) (*dashed line*) means that deep waters are too cold (*blue*) and a temperature refuge exists in the middle depths (*white*). (*c*) The same environment with daily temperature variability from internal waves or other high frequency processes. The green region depicts the range of temperatures around the mean condition, with the red curve showing the overall variability. Because of variability, the upper depth limit moves deeper and the lower limit is slightly shallower. The depth refuge coincides with the zone of maximal temperature variability, which could make the refuge either more unstable or beneficial to organisms inhabiting it via acclimation (ecological hardening). Abbreviations: T_{max}, upper temperature limit of a species; T_{min}, lower temperature limit of a species.

lower incidences of bleaching from the 2016 El Niño event. A nonlinear decline of bleaching with depth on the Great Barrier Reef was documented for 62.5% of coral species, while shallow reefs experienced higher thermal stress than deep ones (Baird et al. 2018).

With the added ability to change their depth distribution by migration, mobile species are moving deeper. For example, Dulvy et al. (2008) reported that 28 species of demersal fish were moving at a rate of 3.6 m/decade down to cooler depths. Phytoplankton can achieve a refuge in deep tropical and subtropical regions (Jorda et al. 2019). However, not all target depth refuge environments are within an organism's fundamental niche, as modeling emissions scenarios predicted that pelagic organisms will encounter novel shallow and deep thermal boundaries by 2080–2100, challenging their capacity to adapt (Santana-Falcón & Séférian (2022). Considering mobile ectotherms, Thatje (2021) argued that their ability to escape warming, shallow environments by changing their bathymetric distribution requires acclimation to temperature and pressure in order to meet their oxygen demands. In crustaceans and mollusks, acclimation leads to increased pressure and temperature tolerances (Thatje 2021). Generally, there is more support for the first two predictions of the depth refuge hypothesis than for deep reefs as a reproductive source for shallow populations (Bongaerts et al. 2017).

Whether deeper, cooler water habitats actually provide a refuge from shallow warming is controversial. In addition to studies supporting the hypothesis, there are investigations that have found either limited support or no support (Bongaerts et al. 2017, Frade et al. 2018, Venegas et al. 2019). For example, bleaching does not decline with depth universally for all coral species, leading Bongaerts et al. (2017) to state that it should not be considered an ecosystem-wide hypothesis. In broad surveys of coral reefs at 457 reef sites across the central and western Pacific, Venegas et al. (2019) found no depth refuge from heat stress for corals down to 38 m. An evaluation of the deep refuge hypothesis on the Great Barrier Reef by Frade et al. (2018) provided insight that may partially reconcile the opposing views of the depth refuge hypothesis, as they found that the ability of the deep reef to serve as a refuge from warming varies temporally. There was a lower incidence of bleaching on deep (40 m) versus shallower (5–25 m) reef sites during the 2016 El Niño event, but this effect was transient, as it disappeared when the upwelling season ended (Frade et al. 2018).

Moving deeper to escape warm surface water (**Figure 4*a***) may not work if the ambient temperature at depth is below the organism's thermal tolerance (T_{min}) (**Figure 4*b***) or if its bathymetric distribution is constrained by factors other than temperature. Light is a key limiting factor for all photosynthesizing organisms including corals with zooxanthellae. Due to the absorption of light in sea water, illumination decreases exponentially with depth, so a cool habitat in the mesophotic zone may not be a suitable depth (**Figure 4*b*,*c***) for zooxanthellate corals if light levels are too low. Oxygen saturation, another limiting factor, declines from the surface to the oxygen minimum zone at depths ranging from 200 to 1,000 m (Levin 2003), challenging organisms to meet their metabolic demands (Thatje 2021). The availability of hard-substrate habitat required for the settlement and persistence of epifaunal invertebrates may be an additional constraint, as it declines with depth as the substrate of rocky coastal areas, islands, and carbonate reefs grades into the sediment-covered habitats of the deep ocean (Weissburg et al. 2014).

Temperature variability and its influence on organisms seeking bathymetric refuges changes with depth. The characterization of temperature variability along depth gradients depends on the range of depths considered and the physical driver. A synthesis of published studies of depth-dependent temperature variability suggests a curvilinear pattern across a broad bathymetric range (**Figure 4*c***). Variability increases from the surface mixed layer to a maximum associated with a range of thermocline depths and then ultimately declines to the comparatively isothermal environment of the deep sea (**Figure 4*c***). For example, temperature variability at 15 and 28 m depth was greater than at 6 m above a pinnacle in the Gulf of Maine where the thermocline was regularly downwelled by internal waves (Witman et al. 1993). In an exceptionally broad thermocline (50–200 m) over coral reefs in Palau, the range of temperatures in an internal wave regime was 1–2°C at 2–35 m, increasing to 2 to 4.5°C at 55—90 m depth (Wolanski et al. 2004). Similarly, the thermal environment generated by internal waves on the deep slopes of coral reefs generated a broader temperature range at 35 than at 7 m depth (Leichter et al. 1996) and at 25 m than at 5 m depth (Sheppard 2009). Conductivity, temperature, and depth (CTD) profiles in the Gulf of Chiriqui indicated a narrow temperature standard deviation in surface waters, a maximal standard deviation at 40 m depth, and a narrow deviation again at 60 m (Smith et al. 2014). In the Mediterranean, the coefficient of variation of summer temperatures from 5–40 m increased with depth at one out of four sites and displayed the curvilinear pattern (**Figure 4*c***) at two out of four sites (Bensoussan et al. 2010). CTD profiles from four oceanic regions displayed the lowest temperature variability at the greatest depths (Fiedler 2010).

A depth refuge superimposed on the vertical structure of the water column (**Figure 4**) shows that the size of the potential thermal refuge, i.e., depths below the organism's maximum temperature tolerance, T_{max}, (**Figure 4*a***) is larger than the realized depth refuge, which is constrained by deep water that is colder than the organism's lower physiological tolerance limit (T_{min}) (**Figure 4*b*,*c***). This indicates there is a limit to how deep an organism can disperse to achieve greater survival in deeper thermal environments. Superimposing the curvilinear pattern of temperature variability across depth on **Figure 4*c*** suggests that shallow populations and communities living at thermocline depths will experience high temperature variance (**Figure 4*c***) and likely an unstable depth refuge compared to those at subthermocline depths. Whether living at thermocline depths represents a cost (instability) or a benefit (hardening, acclimation with repeated variability) to organisms seeking a thermal refuge remains an important topic for future investigation. It stands to reason that organisms living in low temperature variability environments at subthermocline depths will be more affected by the trend than the variance in temperature as the ocean warms (**Figure 2**).

CONCEPTUAL MODEL

Our review highlights the need to understand how marine ecosystems respond to the interaction of smooth climate trends and spiky natural variability. We now present a conceptual model that synthesizes the processes outlined above to show the value in this approach.

We envision an ecosystem experiencing a warming trend (**Figure 5*a***). As in **Figure 1**, we depict the trend as an envelope of conditions around the mean. The actual temperature time series is drawn from the distribution. We represent the community as a distribution of species across

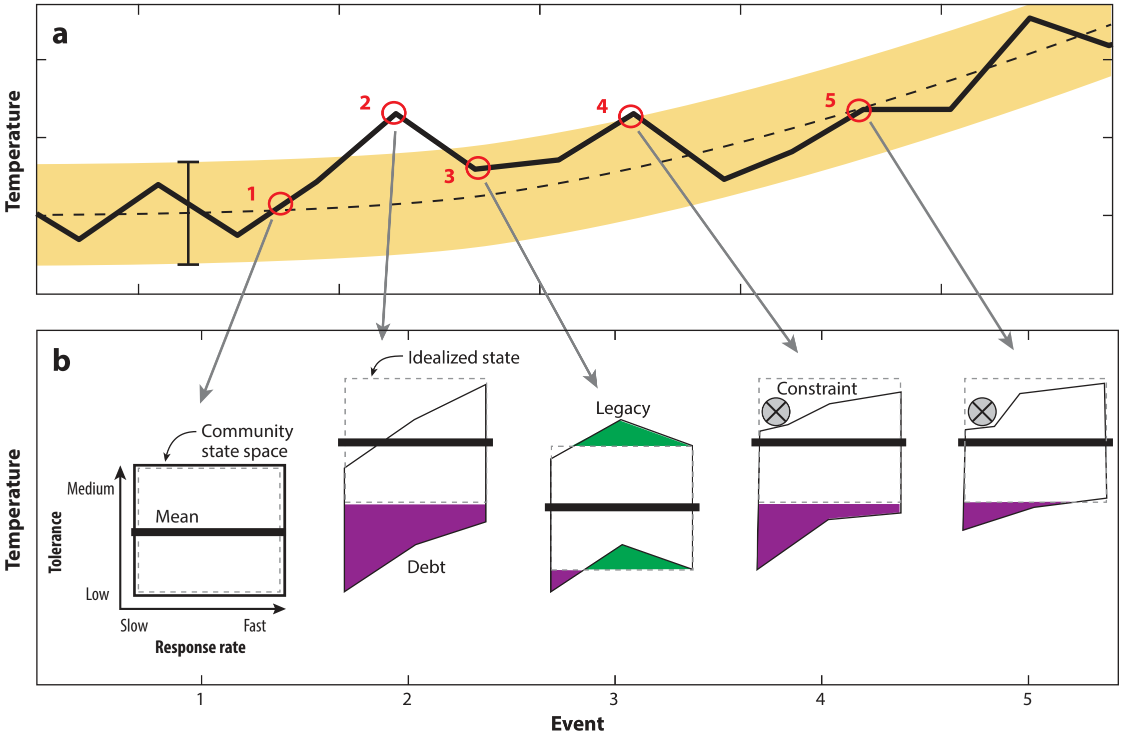

Figure 5

Conceptual diagram of ecological processes in response to both mean and variability. (*a*) A portion of the temperature time series from **Figure 1** with observed values (*solid line*), mean (*dashed line*), and variability (*yellow shading*), along with five annual events highlighted with red circles. (*b*) The state of a community during the five highlighted events. For each event, we depict the community in the location as a distribution of species across two trait axes. The vertical axis indicates the temperature tolerance of species in the community, and the horizontal axis indicates the response rate (for example, through population growth or mobility). For each event, we show the mean temperature (*dark line*) and the idealized community state (*dashed square*) that would occur if the ecosystem were held at that temperature for many years. During Event 1, the realized community (*black polygon*) is similar to the idealized community because conditions have been stationary. During Event 2, the idealized state has shifted in response to a heatwave, but only portions of the idealized state space have been occupied. Species in the purple shaded region are outside the idealized state. They are present but declining, indicating extinction debt. During Event 3, the temperature has declined, but portions of the community (*green shading*) remain at the previous levels. These are legacy effects that accelerate movement of the state during the next warm event. During Event 4, portions of the community encounter constraints (*gray circles*) that keep a portion of the state space from being filled. These constraints and extinction debt keep the state from matching the idealized distribution even though the ecosystem conditions are at the mean. The discrepancy will depend on the rate of change and the rates of the ecological processes depicted.

two trait axes (**Figure 5*b***). The vertical axis indicates the temperature tolerance of species in the community, and the horizontal axis indicates the response rate (for example, through population growth or mobility). We assume that if the mean is held steady for several years and the variance is fixed (i.e., the system is stationary) that the community will approach an idealized state depicted as a dashed square. At the beginning (**Figure 5**, Event 1), the mean conditions have been steady, and we expect that the realized community would be similar to the idealized community.

As warming commences, the ecosystem experiences a heatwave (Event 2), with temperatures well above the historical variance. The idealized state tracks the temperature; however, the processes in the community are not fast enough to perfectly track the conditions. This means that only portions of the idealized state space have been occupied. Species outside the idealized state are present but declining, indicating extinction debt.

During Event 3, the temperature has declined and the idealized state shifts, but portions of the community remain at the previous levels. These are legacy effects that accelerate movement of the state during the next warm event.

The final two events both have temperatures comparable to Event 2, though these are increasingly common conditions. Due to the legacy effects, the community in Event 4 is closer to the idealized state than during the first heatwave. During Event 4, portions of the community encounter constraints that keep a portion of the state space from being filled. The final event has a temperature that is now the new mean of the system; however, because the system is constantly changing due to the trend, it does not yet match the idealized state. Extinction debt and the presence of constraints keep the state from matching the idealized distribution. The discrepancy will depend on the rate of change and the rates of the ecological processes depicted.

SUMMARY POINTS

1. The trend of increasing mean temperature interacting with natural temperature variability results in anomalous warming events such as heat waves that are deleterious to marine life. It is important to recognize that temperature variance per se is not generally increasing. Rather, the anthropogenic trend is extending the peaks of natural variability beyond ecological thresholds.
2. There is a large degree of geographic variability in temperature trends and temperature variability. The interplay between the two parameters is an overlooked component of climate change. It highlights regions where the rising trend underlies high (Gulf of Maine, Caribbean and Mediterranean Seas) probabilities of exceptional warming events and ecological surprises. Foundation species in these regions have experienced substantial climate-related changes.
3. Temperature events like heatwaves must be defined against a baseline. The choice of the baseline period, and whether the baseline is updated, changes our view of marine heatwaves or ecological surprises (fitness loss, population declines, diversity loss, community shifts). A longer baseline period may be suitable for long-lived species or slower-adjusting systems, while shorter baseline periods that are updated frequently would tend to identify events impacting a system that can adjust quickly.
4. In terms of temperature change, we now live in a nonstationary world. A primary objective of climate change ecology is to document, understand, and forecast ecological responses to climate change with an equilibrium mindset. Yet communities are in a nonequilibrium state in response to heatwaves and other disturbances.

5. Models of species distributional changes in horizontal (i.e., latitude, longitude) and vertical (depth) dimensions in the ocean emphasize species following isotherms with little attention to other constraints besides temperature on species responses. These other limiting factors include light, oxygen, and substrate type. Failure to acknowledge these limitations may overestimate the ability of species to escape stressful temperatures and may underestimate extinctions and losses of ecosystem functions.
6. Aspects of temporal variation such as the frequency of repeated temperature anomalies and delays in ecological changes (legacy effects) following anomalies are central to understanding the different ecological impacts of climate change. These processes can either accelerate or slow the rate of change and adaptation. There is growing evidence that sessile organisms like corals in more variable thermal habitats are more resistant to thermal anomalies via ecological hardening.
7. Temperature variability and its influence on organisms seeking bathymetric thermal refuge changes with depth. The relationship between depth and sensitivity to heatwaves depends on the extent of depths considered and the type of oceanographic driver and is highly location dependent. Locations conducive to internal waves are commonly, but not always, associated with depth refuges.

FUTURE ISSUES

1. Future marine climate change ecology should consider both the temperature trend and inherent temperature variability, how they interact to exceed thresholds producing extreme events (**Figure 5**), and how they vary regionally to affect individuals, populations, and communities.
2. A key question in models forecasting future species distributions is at what rate of change can key species assemblages move together? The difference in the rate at which species can move is creating novel communities with properties that have not been studied or even predicted.
3. Published models of species range changes assume a smooth future of gradual change where species declines are due to the trend rather than infrequent extremes (variance), they do not consider geographic variability in temporal variability, and they assume that dispersal and range expansion are smooth (and largely unlimited). Future modeling efforts need to incorporate these aspects in order to make more realistic predictions.
4. Current studies tend to focus on the immediate or short-term impacts of temperature anomalies. There is a need for comprehensive research on the ecological consequences of temporal variation in temperature anomalies including cumulative negative (fitness loss) and positive (acclimation, ecological hardening) effects of repeated events and lagged responses of varying duration, including extinction debt. Ignoring extinction debt can lead to underestimates of biodiversity loss following heat waves and other thermal anomalies.
5. Most models of the ecological consequences of marine climate change concern horizontal range shifts (latitudinal, longitudinal) and do not consider that organisms may shift their ranges vertically, with depth, to avoid thermal stress in shallow water. The

depth refuge hypothesis frames these vertical changes, yet more research is needed to rigorously evaluate it, including field measurements of organism fitness, seasonal variation in thermal regimes, and temperature variability across broad ranges of depth.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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LITERATURE CITED

Alexander MA, Scott JD, Friedland KD, Mills KE, Nye JA, et al. 2018. Projected sea surface temperatures over the 21st century: changes in the mean, variability and extremes for large marine ecosystem regions of Northern Oceans. *Elem. Sci. Anthropocene* 6:9

Allen AP, Brown JH, Gillooly JF. 2002. Global biodiversity, biochemical kinetics, and the energetic-equivalence rule. *Science* 297:1545–48

Baird A, Madin J, Álvarez-Noriega M, Fontoura L, Kerry J, et al. 2018. A decline in bleaching suggests that depth can provide a refuge from global warming in most coral taxa. *Mar. Ecol. Prog. Ser.* 603:257–64

Barneche DR, Robertson DR, White CR, Marshall DJ. 2018. Fish reproductive-energy output increases disproportionately with body size. *Science* 360(6389):642–45

Bensoussan N, Romano J-C, Harmelin J-G, Garrabou J. 2010. High resolution characterization of northwest Mediterranean coastal waters thermal regimes: to better understand responses of benthic communities to climate change. *Estuar. Coast. Shelf Sci.* 87(3):431–41

Bongaerts P, Ridgway T, Sampayo EM, Hoegh-Guldberg O. 2010 Assessing the 'deep reef refugia' hypothesis: focus on Caribbean reefs. *Coral Reefs* 29:309–27

Bongaerts P, Riginos C, Brunner R, Englebert N, Smith SR, Hoegh-Guldberg O. 2017. Deep reefs are not universal refuges: Reseeding potential varies among coral species. *Sci. Adv.* 3(2):e1602373

Bove CB, Mudge L, Bruno JF. 2022. A century of warming on Caribbean reefs. *PLOS Clim.* 1(3):e0000002

Bridge TCL, Hoey AS, Campbell SJ, Muttaqin E, Rudi E, et al. 2013. Depth-dependent mortality of reef corals following a severe bleaching event: implications for thermal refuges and population recovery. *F1000Res.* 2:187

Byrne M, Foo SA, Ross PM, Putnam HM. 2020. Limitations of cross- and multigenerational plasticity for marine invertebrates faced with global climate change. *Glob. Chang. Biol.* 26(1):80–102

Caesar L, McCarthy GD, Thornalley DJR, Cahill N, Rahmstorf S. 2021. Current Atlantic meridional overturning circulation weakest in last millennium. *Nat. Geosci.* 14(3):118–20

Caesar L, Rahmstorf S, Robinson A, Feulner G, Saba V. 2018. Observed fingerprint of a weakening Atlantic Ocean overturning circulation. *Nature* 556(7700):191–96

Caves EM, Johnsen S. 2021. The sensory impacts of climate change: bathymetric shifts and visually mediated interactions in aquatic species. *Proc. R. Soc. B* 288:20210396

Chaudhary C, Richardson AJ, Schoeman DS, Costello MJ. 2021. Global warming is causing a more pronounced dip in marine species richness around the equator. *PNAS* 118(15):e2015094118

Chefaoui RM, Duarte CM, Serrão EA. 2018. Dramatic loss of seagrass habitat under projected climate change in the Mediterranean Sea. *Glob. Chang. Biol.* 24(10):4919–28

Cheng L, Abraham J, Trenberth KE, Fasullo J, Boyer T, et al. 2021. Upper ocean temperatures hit record high in 2020. *Adv. Atmos. Sci.* 38(4):523–30

Cheung WWL, Lam VWY, Sarmiento JL, Kearney K, Watson R, Pauly D. 2009. Projecting global marine biodiversity impacts under climate change scenarios. *Fish Fish*. 10(3):235–51

Claar DC, Starko S, Tietjen KL, Epstein HE, Cunning R, et al. 2020. Dynamic symbioses reveal pathways to coral survival through prolonged heatwaves. *Nat. Commun.* 11:6097

Costantini D. 2014. Does hormesis foster organism resistance to extreme events? *Front. Ecol. Environ.* 12(4):209–10

Dal Bello M, Rindi L, Benedetti-Cecchi L. 2017. Legacy effects and memory loss: how contingencies moderate the response of rocky intertidal biofilms to present and past extreme events. *Glob. Chang. Biol.* 23(8):3259–68

Dulvy NK, Rogers SI, Jennings S, Stelzenmüller V, Dye SR, Skjoldal HR. 2008. Climate change and deepening of the North Sea fish assemblage: a biotic indicator of warming seas. *J. Appl. Ecol.* 45(4):1029–39

Eakin CM, Lough JM, Heron SF. 2009. Climate variability and change: monitoring data and evidence for increased coral bleaching stress. In *Coral Bleaching: Patterns, Processes, Causes, and Consequences*, ed. MJH van Oppen, JM Lough, pp. 41–67. Berlin: Springer

Edmunds PJ. 2019. Three decades of degradation lead to diminished impacts of severe hurricanes on Caribbean reefs. *Ecology* 100(3):e02587

Essl F, Dullinger S, Rabitsch W, Hulme PE, Pyšek P, et al. 2015. Historical legacies accumulate to shape future biodiversity in an era of rapid global change. *Divers. Distrib.* 21(5):534–47

Fiedler PC. 2010. Comparison of objective descriptions of the thermocline. *Limnol. Oceanogr. Methods.* 8(6):313–25

Frade PR, Bongaerts P, Englebert N, Rogers A, Gonzalez-Rivero M, Hoegh-Guldberg O. 2018. Deep reefs of the Great Barrier Reef offer limited thermal refuge during mass coral bleaching. *Nat. Commun.* 9(1):3447

Frölicher TL, Fischer EM, Gruber N. 2018. Marine heatwaves under global warming. *Nature* 560(7718):360–64

García Molinos J, Halpern BS, Schoeman DS, Brown CJ, Kiessling W, et al. 2015. Climate velocity and the future global redistribution of marine biodiversity. *Nat. Clim. Chang.* 6(1):83–88

Garpe K, Yahya S, Lindahl U, Öhman M. 2006. Long-term effects of the 1998 coral bleaching event on reef fish assemblages. *Mar. Ecol. Prog. Ser.* 315:237–47

Garrabou J, Coma R, Bensoussan N, Bally M, Chevaldonné P, et al. 2009. Mass mortality in northwestern Mediterranean rocky benthic communities: effects of the 2003 heat wave. *Glob. Chang. Biol.* 15(5):1090–103

Garrabou J, Gómez-Gras D, Ledoux J-B, Linares C, Bensoussan N, et al. 2019. Collaborative database to track mass mortality events in the Mediterranean Sea. *Front. Mar. Sci.* 6:707

Garrabou J, Gómez-Gras D, Medrano A, Cerrano C, Ponti M, et al. 2022. Marine heatwaves drive recurrent mass mortalities in the Mediterranean Sea. *Glob. Chang. Biol.* 28:5708–25

Glynn PW. 1996. Coral reef bleaching: facts, hypotheses and implications. *Glob. Chang. Biol.* 2(6):495–509

Grottoli AG, Warner ME, Levas SJ, Aschaffenburg MD, Schoepf V, et al. 2014. The cumulative impact of annual coral bleaching can turn some coral species winners into losers. *Glob. Chang. Biol.* 20:3823–33

Hackerott S, Martell HA, Eirin-Lopez JM. 2021. Coral environmental memory: causes, mechanisms, and consequences for future reefs. *Trends Ecol. Evol.* 36(11):1011–23

Harris RMB, Beaumount LJ, Vance TR, Tozer CR, Remenyi TA, et al. 2022. Biological responses to the press and pulse of climate trends and extreme events. *Nat. Clim. Chang.* 8:579–87

Haumann FA, Gruber N, Münnich M. 2020. Sea-ice induced Southern Ocean subsurface warming and surface cooling in a warming climate. *AGU Adv*. 1(2):e2019AV000132

Hiddink JG, Burrows MT, García Molinos J. 2015. Temperature tracking by North Sea benthic invertebrates in response to climate change. *Glob. Chang. Biol.* 21(1):117–29

Hobday AJ, Alexander LV, Perkins SE, Smale DA, Straub SC, et al. 2016. A hierarchical approach to defining marine heatwaves. *Prog. Oceanogr*. 141:227–38

Hughes TP, Kerry JT, Alvarez -Noriega M, Alvarez -Romero JG, Anderson KD, et al. 2017. Global warming and recurrent mass bleaching of corals. *Nature* 543:373–77

Hughes TP, Kerry JT, Connolly SR, Baird AH, Eakin CM, et al. 2019. Ecological memory modifies the cumulative impact of recurrent climate extremes. *Nat. Clim. Chang.* 9(1):40–43

Hughes TP, Tanner JE. 2000. Recruitment failure, life histories, and long-term decline of Caribbean corals. *Ecology* 81(8):2250–63

Hylander K, Ehrlén J. 2013. The mechanisms causing extinction debts. *Trends Ecol. Evol.* 28:341–46

Jackson ST, Sax DF. 2010. Balancing biodiversity in a changing environment: extinction debt, immigration credit and species turnover. *Trends Ecol. Evol.* 25(3):153–60

Jacox MG. 2019. Marine heatwaves in a changing climate. *Nature* 571(7766):485–87

Jones MC, Cheung WWL. 2015. Multi-model ensemble projections of climate change effects on global marine biodiversity. *ICES J. Mar. Sci.* 72(3):741–52

Jorda G, Marbà N, Bennett S, Santana-Garcon J, Agusti S, Duarte CM. 2019. Ocean warming compresses the three-dimensional habitat of marine life. *Nat. Ecol. Evol.* 4(1):109–14

Kossin JP, Knapp KR, Olander TL, Velden TS. 2020 Global increase in major tropical cyclone exceedance probability over the past four decades. *PNAS* 117:11975–80

Kuussaari M, Bommarco R, Heikkinen RK, Helm A, Krauss J, et al. 2009. Extinction debt: a challenge for biodiversity conservation. *Trends Ecol. Evol.* 24(10):564–71

Lefcheck JS, Marion SR, Lombana AV, Orth RJ. 2016. Faunal communities are invariant to fragmentation in experimental seagrass landscapes. *PLOS ONE* 11(5):e0156550

Leichter JJ, Wing SR, Miller SL, Denny MW. 1996. Pulsed delivery of sub-thermocline water to Conch Reef (Florida Keys) by internal tidal bores. *Limnol. Oceanogr.* 41:1490–501

Lesser MP, Slattery M, Leichter JJ. 2009. Ecology of mesophotic coral reefs. *J. Exp. Mar. Biol. Ecol.* 375(1–2):1–8

Levin LA. 2003. Oxygen minimum zone benthos: adaptation and community response to hypoxia. *Oceanogr. Mar. Biol.* 41:1–45

Mills K, Pershing A, Brown C, Chen Y, Chiang F-S, et al. 2013. Fisheries management in a changing climate: lessons from the 2012 ocean heat wave in the Northwest Atlantic. *Oceanography* 26(2):191–95

Muir PR, Marshall PA, Abdulla A, Aguirre JD. 2017. Species identity and depth predict bleaching severity in reef-building corals: Shall the deep inherit the reef? *Proc. R. Soc. B* 284(1864):20171551

Muñiz-Castillo AI, Rivera-Sosa A, Chollett I, Eakin CM, Andrade-Gómez L, et al. 2019. Three decades of heat stress exposure in Caribbean coral reefs: a new regional delineation to enhance conservation. *Sci. Rep.* 9(1):11013

Oliver ECJ, Benthuysen JA, Darmaraki S, Donat MG, Hobday AJ, et al. 2021. Marine heatwaves. *Annu. Rev. Mar. Sci.* 13:313–42

Oliver ECJ, Donat MG, Burrows MT, Moore PJ, Smale DA, et al. 2018. Longer and more frequent marine heatwaves over the past century. *Nat. Commun.* 9(1):1324

Pershing AJ, Alexander MA, Brady DC, Brickman D, Curchitser EN, et al. 2021. Climate impacts on the Gulf of Maine ecosystem. *Elem. Sci. Anthropocene* 9(1):00076

Pershing AJ, Record NR, Franklin BS, Kennedy BT, McClenachan L, et al. 2019. Challenges to natural and human communities from surprising ocean temperatures. *PNAS* 116(37):18378–83

Pershing AJ, Stamieszkin K. 2020. The North Atlantic ecosystem, from plankton to whales. *Annu. Rev. Mar. Sci.* 12:339–59

Pinsky ML, Worm B, Fogarty MJ, Sarmiento JL, Levin SA. 2013. Marine taxa track local climate velocities. *Science* 341(6151):1239–42

Pratchett M, Munday P, Wilson S, Graham N, Cinner J, Bellwood D. 2008. Effects of climate-induced coral bleaching on coral-reef fishes, ecological and economic consequences. *Oceanogr. Mar. Biol. Annu. Rev.* 46:251–96

Putnam HM. 2021. Avenues of reef-building coral acclimatization in response to rapid environmental change. *J. Exp. Biol.* 224(Suppl. 1):jeb239319

Rhoades O, Brandt M, Witman JD. 2023. La Niña -related coral death triggers biodiversity loss of associated communities in the Galápagos. *Mar. Ecol.* **https://doi.org/10.1111/maec.12767**

Riegl B, Piller WE. 2003. Possible refugia for reefs in times of environmental stress. *Int. J. Earth Sci.* 92(4):520–31

Rombouts I, Beaugrand G, Ibanez F, Chiba A, Legendre L. 2011. Marine copepod diversity and the metabolic theory of ecology. *Oecologia* 166:349–55

Ryo M, Aguilar-Trigueros CA, Pinek L, Muller LAH, Rillig MC. 2019. Basic principles of temporal dynamics. *Trends Ecol. Evol.* 34(8):723–33

Santana-Falcón Y, Séférian R. 2022. Climate change impacts the vertical structure of marine ecosystem thermal ranges. *Nat. Clim. Chang.* 12(10):935–42

Schuetz JG, Mills KE, Allyn AJ, Stamieszkin K, Bris AL, Pershing AJ. 2019. Complex patterns of temperature sensitivity, not ecological traits, dictate diverse species responses to climate change. *Ecography* 42(1):111–24

Selig ER, Casey KS, Bruno JF. 2010. New insights into global patterns of ocean temperature anomalies: implications for coral reef health and management. *Glob. Ecol. Biogeogr.* 19:397–411

Sheppard C. 2009. Large temperature plunges recorded by data loggers at different depths on an Indian Ocean atoll: comparison with satellite data and relevance to coral refuges. *Coral Reefs* 28(2):399–403

Smith KE, Burrows MT, Hobday AJ, King NG, Moore PJ, et al. 2023. Biological impacts of marine heatwaves. *Annu. Rev. Mar. Sci.* 15:119–45

Smith TB, Glyn PW, Mate JL, Toth LT, Gyory J. 2014. A depth refugium from catastrophic coral bleaching prevents regional extinction. *Ecology* 95:1663–73

Somero GN. 2010. The physiology of climate change: how potentials for acclimatization and genetic adaptation will determine 'winners' and 'losers.' *J. Exp. Biol.* 213(6):912–20

Stillman JH. 2003. Acclimation capacity underlies susceptibility to climate change. *Science* 301(5629):65

Stipcich P, Marín-Guirao L, Pansini A, Pinna F, Procaccini G, et al. 2022. Effects of current and future summer marine heat waves on *Posidonia oceanica*: plant origin matters? *Front. Clim.* 4:844831

Stone L, Eilam E, Abelson A, Ilan M. 1996. Modelling coral reef biodiversity and habitat destruction. *Mar. Ecol. Prog. Ser.* 134:299–302

Stuart-Smith RD, Brown CJ, Ceccarelli DM, Edgar GJ. 2018. Ecosystem restructuring along the Great Barrier Reef following mass coral bleaching. *Nature* 560(7716):92–96

Thatje S. 2021. Climate warming affects the depth distribution of marine ectotherms. *Mar. Ecol. Prog. Ser.* 660:233–40

Tilman D, May RM, Lehman CL, Novak MA. 1994. Habitat destruction and the extinction debt. *Nature* 371:65–66

Venegas RM, Oliver T, Liu G, Heron SF, Clark SJ, et al. 2019. The rarity of depth refugia from coral bleaching heat stress in the western and central Pacific Islands. *Sci. Rep.* 9(1):19710

Watts K, Whytock RC, Park KJ, Fuentes-Montemayor E, Macgregor NA, et al. 2020. Ecological time lags and the journey towards conservation success. *Nat. Ecol. Evol.* 4(3):304–11

Weissburg M, Helmuth B, Witman J. 2014. The physical context of marine communities. In *Marine Community Ecology and Conservation*, ed. MD Bertness, BB Silliman, J Stachowicz, pp. 11–36. Sunderland, MA: Sinauer Press

White PS, Jentsch A. 2001. The search for generality in studies of disturbance and ecosystem dynamics. In *Progress in Botany*, Vol. 62, ed. K Esser, U Lüttge, JW Kadereit, W Beyschlag, pp. 399–450. Berlin, Heidelberg: Springer

Witman JD. 1992. Physical disturbance and community structure of exposed and protected reefs: a case study from St. John, U.S. Virgin Islands. *Am. Zool.* 32:641–54

Witman JD, Dayton PK. 2001. Rocky subtidal communities. In *Marine Community Ecology*, ed. MD Bertness, SD Gaines, M Hay, pp. 339–66. Sunderland, MA: Sinauer Press

Witman JD, Lamb RW. 2018. Persistent differences between coastal and offshore kelp forest communities in a warming Gulf of Maine. *PLOS ONE* 13(1):e0189388

Witman JD, Leichter JJ, Genovese SJ, Brooks DA. 1993. Pulsed phytoplankton supply to the rocky subtidal zone: influence of internal waves. *PNAS* 90:1686–90

Wolanski E, Colin PL, Naithani J, Deleersnijder E, Golbuu Y. 2004. Large amplitude, leaky, island-generated, internal waves around Palau, Micronesia. *Estuar. Coast. Shelf Sci.* 60:705–16

Wyatt ASJ, Leichter JJ, Toth LT, Miyajima T, Aronson RB, Nagata T. 2020. Heat accumulation on coral reefs mitigated by internal waves. *Nat. Geosci.* 13(1):28–34

Yang LH, Bastow JL, Spence KO, Wright AN. 2008. What can we learn from resource pulses? *Ecology* 89:621–34

Zeidberg LD, Robison BH. 2007. Invasive range expansion by the Humboldt squid, *Dosidicus gigas*, in the eastern North Pacific. *PNAS* 104(31):12948–50

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