


Biogeochemical extremes and compound events in the ocean

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OCEAN BIOGEOCHEMICAL EXTREMES AND COMPOUND EVENTS

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Nicolas Gruber, December 15, 2021.

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1st paragraph

The ocean is warming, losing oxygen, and it is being acidified, primarily as a result of anthropogenic carbon emissions¹⁻⁴. With ocean warming, acidification, and deoxygenation projected to increase for decades^{5,6}, extreme events, such as marine heatwaves⁷, are likely to intensify, occur more often, persist for longer, and extend over larger regions⁸⁻¹¹. Nevertheless, our understanding of oceanic extreme events, associated with warming, low oxygen concentrations or high acidity, and their impacts on marine ecosystems remains limited^{7,10,12-15}. Of particular concern are compound events, multiple extreme events that occur simultaneously or in close sequence, because their individual effects may interact synergistically¹⁶. Here we assess patterns and trends in open ocean extremes based on the existing literature and global and regional model simulations. Furthermore, we discuss the potential impacts of individual and compound extremes on marine organisms and ecosystems. We propose a pathway towards an improved understanding of extreme events and the capacity of marine life to respond to them. The absolute conditions exhibited by today's extreme events may be a harbinger of what may become "normal" in the future¹⁰. In consequence, pursuing this research effort may also help better understand the responses of marine organisms and ecosystems to future climate change. (200 words)

MAIN

The direct and indirect impact of human -driven emissions of CO₂ on marine systems are pervasive (Fig. 1). By burning fossil fuels and altering land-use, human activities have increased atmospheric CO₂ by ~50% in the last 200 yrs¹⁷. The resulting change in the Earth's radiative balance generates excess heat, more than 90% of which is taken up by the ocean, thereby warming it⁴. This ocean warming leads to a loss of dissolved oxygen, i.e., deoxygenation¹⁸, through the reduction of the solubility of dissolved oxygen. This loss is greatly amplified by the warming-induced changes in upper ocean stratification and ventilation^{19,20} which tend to reduce the supply of oxygen from the surface ocean into the interior, where oxygen is continuously consumed through respiration and remineralization processes²¹. Furthermore, the rise in atmospheric CO₂ also drives a strong flux of additional, i.e., anthropogenic, CO₂ into the ocean²², leading to a reduction in the oceanic pH and in the saturation state, Ω, of seawater with regard to mineral CaCO₃, while the concentration of the hydrogen ion [H⁺] (i.e., the acidity) increases (corresponding to a decrease in pH = -log [H⁺]). Such changes are often summarized as "ocean acidification"²³. These chemical changes are known to substantially affect marine organisms^{24,25}, especially those forming shells made from mineral

CaCO₃ such as oysters, crabs, and corals as the lower saturation state impairs their ability to calcify²⁶. These three hazards, i.e., those associated with ocean warming, acidification and deoxygenation are likely to continue for the coming decades even under emission scenarios that incorporate stringent cuts in future greenhouse gas emissions^{2,5,6}.

As changes in ocean temperature, oxygen, and acidity unfold, extreme conditions in these properties are bound to change disproportionately (Fig. 1)²⁷. In the ocean, our knowledge about such extreme events, i.e., the normally rare occurrences when a system is far outside the norm, is relatively limited. This is especially the case when comparing this with the situation on land where extremes are known to severely impact humans and ecosystems^{28,29}. Best studied are marine heatwaves, where knowledge has grown rapidly in recent years^{7-9,11,15,30,31}. For example, between 1982 and 2016 the number of days with marine heatwaves, defined here as days when the sea-surface temperature (SST) exceeds its local 99th percentile, has doubled⁸, even though human-driven global warming caused the ocean surface to warm “only” by ~0.4°C over this period³². One of the most prominent heatwaves was the “Blob” in the Northeast Pacific that occurred between 2013 and 2015 with SST anomalies, relative to 2002-2012, of up to 6°C³³. This event had severe consequences for marine life, ranging from massive die-offs of marine birds, higher mortality of sea lions, reduced stocks of many commercially valuable fish, to pronounced shifts in zooplankton community structure^{12,34-37}. The trend toward more frequent marine heatwaves is projected to continue under global warming, with the ocean encountering 16-fold more marine heatwave days compared to preindustrial conditions under a global warming of 1.5°C⁸. For example, a marine heatwave at the scale of the “Blob” is projected to occur every 10 years under this level of global warming³⁸. Similar trends are expected for extreme events associated with ocean deoxygenation and ocean acidification, but so far, with few exceptions for ocean acidity^{13,14}, little is known about these extremes in terms of their distribution, intensity, or duration, primarily owing to the lack of observations. This is a serious gap, especially when considering the pervasive effects that extremes in any of these hazards might have on marine productivity, ecosystem structure and function, ecosystem services, and ultimately for humankind (Fig. 1), as has been demonstrated for marine heatwaves^{12,37}. The potential for substantial ecosystem impacts could be exacerbated by compound extreme events, i.e., extremes in different hazards occurring simultaneously or in close spatial/temporal sequence^{16,39-41}, owing to their potential for mutually reinforcing, i.e., synergistic, effects between the hazards⁴². Extreme events can rapidly push marine ecosystems and their constituents beyond the limits of their resilience and hence impair their capability to acclimate or adapt, especially due to their abrupt nature. Thus, extremes and especially the newly emerging ones could have worse effects than those emanating from the slow decadal-scale progression of the mean

state (e.g., warming, deoxygenation or acidification) in response to the human-driven climatic drivers (Fig. 1). Single and compound extremes could also trigger abrupt major reshuffling of community structure with potentially grave consequences for marine ecosystem services⁴³.

Here, we examine and discuss marine heatwaves and the biogeochemical extremes characterized by low oxygen and high acidity using existing literature and new results from global and regional model simulations. We thereby focus on the open ocean, where the largest gaps in knowledge exist, and do not include an assessment of potential extremes associated with losses of oxygen in nearshore areas driven by eutrophication processes^{3,44}. We assess the patterns and trends of these open ocean extremes including the underlying processes, with special emphasis on compound extremes. We then discuss the potential impacts of individual and compound extremes on marine organisms and ecosystems, recognizing that our understanding of these impacts is, beyond marine heatwaves, not yet well developed. In response, we propose a conceptual framework in order to guide much-needed discussions.

DISTRIBUTION AND TRENDS

Marine heatwaves, and biogeochemical extremes associated with low oxygen and high acidity occur everywhere in the ocean, with both commonalities and important distinctions between the three types of extremes. To illustrate these extremes in a consistent manner across the globe, we use results from an Earth system model^{45,46}. This global model was run for both preindustrial conditions as well as for the historical period up to 2020 under prescribed radiative forcing¹⁴. To define the extremes, we use a relative threshold approach with a fixed baseline based on a pre-industrial reference period (see Box 1). Specifically, we selected either the 1st (oxygen) or the 99th (temperature and $[H^+]$) percentile of the daily mean model output as our relative threshold, using results from a 500-yr long preindustrial control simulation as the reference. The choice of a preindustrial reference period provides us with statistically robust characteristics given the more than 180,000 days to sample from. Using a modern reference period (1982 – 2019) for the characteristics investigated here yields very comparable results, although with lower spatiotemporal coherence, owing to the much shorter reference period (see supplementary material for a comparison). Our choice is also consistent with the use of the preindustrial reference period to define the climate target in the Paris agreement⁴⁷. We opted to use a fixed relative threshold for all properties in order to ensure consistency across the three hazards for the purpose of this illustration. This approach assumes that organisms and ecosystems are well adapted to the local conditions, but are limited in their capabilities to deal with the extreme conditions that they

encounter episodically (see Box 1)¹⁶. An important implication of the choice of a fixed relative threshold is that the characteristics of the extremes are changing with time when the underlying distribution is changing, e.g., any trend in the variable of choice implies a trend in the extremes¹⁶. We fully acknowledge that other definitions, e.g., the use of an absolute threshold¹³, or a moving baseline^{7,14}, might be better choices depending on the questions being addressed and the biological impacts being investigated (see Box 1 for a discussion).

The spatial patterns of the mean intensity of the simulated extremes are remarkably coherent across the three investigated types of extremes within each depth level (Fig. 2a,b). But the spatial distribution of mean intensities shifts considerably between the surface and 200 m depth, i.e., the upper thermocline. At the surface, the most intense extremes of all types tended to occur in the mid to high latitudes (Fig. 2a), whereas at 200 m depth, the hotspot for the most intense extremes are the tropics (Fig. 2b).

At the ocean surface, marine heatwaves tend to have their maximum intensity in the temperate and subpolar latitudes and in the eastern equatorial Pacific, with intensities exceeding 1°C (Fig., 2a; note that the intensity refers to the annual maximal size of the peak over threshold, i.e., the associated SST anomalies or magnitudes are nearly everywhere at least 1°C larger and can be as large as 6°C), consistent with observations (see Supplementary Material). The surface ocean distribution of the intensity of the high acidity extremes is overall similar to that of the heatwaves (Fig. 2a), but with some notable differences. Most striking are the generally much higher intensities in the North Pacific relative to the North Atlantic.

At 200 m depth, the most intense heatwaves tend to occur in the tropics, especially in the Pacific, and along the boundaries of the subtropical gyres with mean intensities that are of the same order of magnitude compared to those at the surface (Fig. 2b). The strongest high acidity and low oxygen extremes also tend to occur in the tropics, although slightly displaced poleward relative to the heatwaves. In addition, rather strong high acidity extremes occur at 200 m depth in the North Pacific, and at very high southern latitudes.

In the global average, the simulated heatwaves and high acidity extremes at the surface last in the preindustrial only about 10 days (see Fig. S5). Observational analyses of modern heatwaves actually suggest that an even shorter duration, i.e., of the order of a few days^{8,9}. This difference remains even if we analyze the model results using the same modern reference period (1982-2019) as the observations (Figs. S1 and S2), suggesting that this is a model bias. Similar biases toward too long lasting events has been identified across all models analyzed so far⁴⁸, irrespective of resolution⁴⁹. However, it is conceivable that the observed durations are skewed on the short side,

owing to the presence of missing observations in the SST product that could lead to artefactual breaks in the heatwaves⁵⁰. Accepting this potential shortcoming, the model suggests that in the regions characterized by high intensity extremes, both types of extremes can persist for much longer than the average event, i.e., nearly two months, with individual events continuing for multiple months (for marine heatwaves) to years (for high acidity extremes). At 200 m depth, all types of extremes, including the low oxygen ones, last longer compared to the surface (Fig. S5). In the global mean, they persist for about 40 days, but with large regional differences. The intense extreme events near the equator endure for a few days only, while those at the edges of the tropics and in the higher latitudes can persist for more than 200 days.

Between 1861 and 2020, the simulated number of heatwaves and biogeochemical extremes increased substantially, both at the surface and at depth (Fig. 2c,d). Given our definition, the number of extreme days in preindustrial times is 3.65. Compared to that reference, the number of days characterized by a heatwave increased more than 10 fold to more than 40 days per year at both surface (see also⁸) and 200 m depth, and those with low oxygen extremes at 200 m depth have increased about 5 fold. For the high acidity events, the entire ocean at surface and at 200 m depth is approaching a state of near permanent extreme conditions relative to preindustrial conditions¹⁴. These strong trends in all three variables reflect the substantial amount of ocean warming, acidification, and loss of oxygen that have occurred over the 20th century (Fig. 1). These trends make the extremes not only last longer, but also more intense^{8,14}. The near-permanent extreme conditions for $[H^+]$ are a direct consequence of the major imprint of ocean acidification on the ocean's carbonate chemistry, which has shifted today's range of variability to lie nearly completely outside the range in preindustrial times. In such cases, when a trend pushes a system toward near permanent extreme conditions, other approaches, such as categories⁵¹, a shifting baseline¹⁴, or an absolute threshold may be better suited to characterize changes in extreme event characteristics, as well as their biological impacts (see also Box 1).

PROCESSES CAUSING EXTREMES

These temporal modulations in extremes are closely linked to the processes that give rise to them (Fig. 3). In general, the most intense extremes in our three variables of interest occur in the regions where variability is highest. This is largely a consequence of the fact that regions with high variability have broader distributions, which implies stronger exceedances (intensities) given our definition of extremes on the basis of relative thresholds. Studies using both observations and models have shown that most marine heatwaves (at least those occurring at the surface) occur either

by local atmosphere-ocean interactions and associated ocean processes, such as upwelling, or by a horizontal displacement of the large-scale sea-surface temperature gradient^{7,31} (Fig. 3a,b). The lateral displacement mechanism drives many of the heatwaves in the western boundary currents³¹ and those reported in the Southern Ocean, while atmosphere-ocean interactions and the associated ocean processes drive nearly all the tropical heatwaves as well as many of those in the temperate latitudes (e.g. those associated with El Niño⁵², the Pacific "Blob"³⁵ or the "Blob2.0" that emerged in 2019⁵³). Atmosphere-ocean interactions tend to cause warming through several processes, involving reduced cloudiness, decreased wind speeds reducing vertical mixing, shifting winds altering ocean circulation, and changes in sea-surface temperature altering the atmospheric conditions in return. Some of these processes occur at scales of less than a few tens of kilometers, and are thus not fully resolved by our global model simulations. For the high acidity extremes at the surface, the underlying drivers have not been well studied. Model studies suggest an important role for upwelling (equatorial Pacific and western boundaries of the continents¹³) as well as shifts in the rate of vertical mixing and their interplay with altered biological productivity (high latitudes,⁵⁴) (Fig. 3c,d,e). Unusually strong upwelling can cause a high acidity extreme event through the surface exposure of deeper waters with high $[H^+]$ concentrations. Similarly, high vertical mixing tends to bring high acidity waters toward the surface, which, when not opposed by the $[H^+]$ decreasing effect of elevated biological productivity or reduced temperature, can create a high acidity extreme.

Extreme events occurring at depth have not been analyzed systematically on a global scale, although the literature is expanding rapidly at regional levels⁵⁵⁻⁵⁷. The dynamics identified in these studies and in our simulations permit some attribution. For example, the model-simulated low oxygen extremes in the 10° to 20° latitudinal band (Figure 2b) are likely driven by the lateral movement of the sharp boundary between the ventilated (high oxygen) subtropical gyre and the unventilated (low oxygen) tropical waters. Such lateral displacements occur in models and observations on annual to decadal timescales and have been well studied in the eastern tropical Pacific (see e.g. ⁵⁸). In the higher latitudes, the modeled low oxygen extremes at 200 m depth tend to be more patchy, with some of these associated with the (partially resolved) eddies in the model (Fig. 3f). Based on full eddy-resolving simulations⁵⁹ as well as observations⁶⁰, we expect that eddies and other mesoscale processes give rise to more of these smaller-scale extremes than simulated by the relatively coarse-resolution model employed here.

Many of the identified mechanisms can lead to more than just one type of extreme, potentially causing dual or triple compound events (Fig. 3). In particular, low oxygen and high

acidity extreme events can be expected to co-occur frequently, since subsurface remineralization of organic matter simultaneously depletes oxygen and increases acidity⁶¹ (Fig. 3e). Similar co-occurrence can be expected in association with the lateral or vertical displacement of fronts, upwelling, thermocline heaving, and eddies, as all of these act on strongly anticorrelated gradients of oxygen and acidity (Fig. 3b,c,d,e,f). Under specific circumstances, e.g., during an atmospherically-forced heatwave, shifts of lateral gradients, upwelling, and thermocline heaving can cause even triple compound extremes, i.e., heatwaves co-occurring with low oxygen and high acidity extremes.

OCEAN EXTREMES IN FOUR DIMENSIONS

To date, most literature on ocean extremes has focused on the surface ocean only, even though extremes may occur anywhere in the water column. In addition, most prior studies, including our own analyses shown above, employed a Eulerian view, i.e., they focus on the evolution and properties of extremes at a fixed location. But ocean extremes often move laterally over many hundreds of kilometers during their lifetime, requiring a Lagrangian (i.e., a feature-following) perspective to fully capture their impact. For example, mesoscale eddies (Fig. 3f) have been observed to travel >1000 kilometers during their often multi-year lifetimes^{62,63}. Thus, any pelagic organisms trapped within such an eddy, especially free-drifting organisms (plankton), will be exposed to the (potentially extreme) conditions associated with it for much longer compared to e.g., a benthic organism that resides in one place, encountering the extreme only in passing, i.e., in a Eulerian manner^{60,64}. Moreover, in order to understand the impact and consequences of ocean extremes on marine organisms, ecosystems, and biogeochemistry, one needs to give special attention to their vertical extent, i.e., take the four-dimensional (space-time) nature of the extremes in full consideration. Changes in the depth stratum are very important for the occurrence of habitat compression, i.e., the squeezing of a suitable habitat into a much smaller volume owing to the presence of an extreme anywhere in the water column^{65,66}.

To illustrate the four-dimensional nature of extremes, we use the example of the 2013-2015 “Blob” heatwave in the Northeast Pacific^{34,67,68}. Observations revealed that this event unfolded in a complex manner in space and time, with the first exceptionally warm conditions emerging in late 2013 in the central northwestern Pacific, but moving subsequently toward the North American Coast and then offshore before ending in late 2015. The “Blob” heatwave appears to have had its maximum warming near the surface, but the extremely elevated temperatures extended to depths beyond 100 m, although not uniformly so^{57,67}. Analyses of Argo profiling float data revealed that

the warming occurred at depth several months later, and subsequently propagated toward the North American continent with a lag relative to the anomalies at the surface of at least one year⁵⁶. Indeed, the deep-water temperature anomalies associated with the “Blob” appear to have persisted for at least two additional years, being conspicuous into 2018 along most of the North American western seaboard⁵⁶.

To investigate the Northeast Pacific 2013-15 “Blob” heatwave further, we use results from a hindcast simulation with a high resolution regional ocean biogeochemical model of the eastern Pacific [updated from⁶⁹]. The model successfully simulates the observed evolution of the “Blob” heatwave (Figs. S3 and S4), revealing the spatio-temporal progression of the marine heatwave (Fig. 4a,b). Indeed, Fig 4b shows clearly how throughout the event a substantial part (up to 50%) of the upper 100 m within the “Blob” encountered extremely high temperatures. This would be expected to force motile organisms that are sensitive to warming to greater depth, where temperatures are generally cooler. Similar habitat compressions can also occur laterally, i.e., by reducing the amount of cold-water habitat along the west Coast of the Americas⁶⁶. The model simulation also reveals that the “Blob” was not only an extreme event with respect to high temperatures, but also with regard to high acidity and low oxygen (Fig 4a,c&d). Both conditions extended to depth, potentially leading to a strong compounding habitat compression.

COMPOUND EXTREMES

Such dual or even triple compound extremes are of particularly high biological and/or ecological concern, especially when the hazards act synergistically⁴², as is the case, e.g., for oxygen and temperature⁷⁰⁻⁷² or pH and oxygen⁷³.

The regional model simulations for the 2013-2015 “Blob” event provide a window to explore the nature of such compound extremes (Fig. 4a,c&d). For example, the model simulations suggest that while high acidity and low oxygen dual extremes have occurred throughout the 1987 to 2016 period, the area affected by such dual extremes increased during the “Blob” more than ten-fold (Fig. 4a). Critically, the “Blob” is associated with the first occurrences of dual events involving high acidity conditions, and especially four episodes where all hazards are extreme, i.e., a triple (heatwave/low oxygen/high acidity) compound event. The strongest such triple event occurred at the peak of the “Blob” in July 2015, when nearly 25% of the eastern North Pacific (20°N-60°N, 115°W-155°W) was under heatwave conditions. The regional model simulates this triple event to occur offshore of the Northwest American Coast with many surrounding regions encountering the co-occurrence of at least two extreme conditions within the upper water column (Fig. 4c). The

average profile of the simulated conditions for July 2015 within the central northeastern Pacific (white box in Fig. 4b) reveals that this triple event extended from the surface to nearly 100 m, and that temperatures and acidity remained extremely high down to ~150 m (Fig. 4d).

Thus, the model simulations suggest that the “Blob” event was more than just a strong and persistent heatwave, it was a compound extreme event. It remains to be determined in what way these compound extreme characteristics of the “Blob” may have contributed to the myriad of observed biological impacts³⁴. Given the long-term trends in ocean warming, deoxygenation, and ocean acidification, such compound events defined on the basis of fixed baselines are bound to increase in number, intensity, and duration (Fig. 2c&d).

IMPACT ON ORGANISMS AND ECOSYSTEMS

The well documented responses of marine life to individual extremes^{15,34} have raised awareness of the threats posed by such events¹². Yet, our ability to translate these individual events into a generic causal framework to assess the impacts of extremes is currently very limited. This reflects our relatively poor understanding of the ramifications of extremes for marine life, especially when compared to terrestrial systems (e.g.⁷⁴). Best understood are the impacts of marine heatwaves, i.e., the thermal stress they impose on marine organisms^{12,75}, and especially on warm water corals⁷⁶⁻⁷⁸. In comparison, much less is known about the potential impact of low oxygen and high acidity extremes, with the exception of organisms living in coastal and nearshore habitats⁷⁹⁻⁸². Least understood in terms of biological impacts are the potential synergistic effects that can amplify hazards during compound extremes^{78,83-85}.

Even though our current knowledge about the biological impact of extremes is low, it is accumulating rapidly, with most coming from post-hoc analyses of time-series sites or impacted regions^{15,34,36,66,86-92} and increasingly from targeted lab and field-based experiments^{82-84,93,94}. The insight emerging from this growing body of work is that extremes represent a complex and multi-faceted threat to marine life (Boxes 1 and 2) that differs from that associated with the slow changes, decade by decade, by the stressors associated with climate change and increasing atmospheric CO₂^{95,96}. This is because when confronted with an extreme, organisms and ecosystems encounter additional challenges due to their exposure to the diverse characteristics of extremes ranging from abruptness, to magnitude, to heterogeneity along with the possibility of rapid recurrence (Box 2). Still, this does not imply we cannot learn from the large body of research conducted on the biological impact of the slowly-evolving hazards associated with ongoing ocean warming, acidification and deoxygenation and their interplay (e.g.⁹⁷⁻¹⁰¹). However, careful thought will be

required as to how best to apply these potentially informative datasets since their focus has been almost exclusively on biological responses to the magnitude of the hazard. At the same time, we have to recognize that not all extreme conditions will have a biological consequence. This is especially true for our statistical definition of extremes, i.e., our choice of a relative threshold approach. This caveat is perhaps most important for the high acidity and low oxygen extremes, but is also relevant for heatwaves.

In order to structure our understanding of the biological impact of extremes, we propose a framework spanned by two axes, i.e., the level of biological organisation and the timescale of the biological response to the key characteristics of extremes (Fig. 5). For the biological organisation, we commence with molecular and physiological responses within an individual cell (top), and extend this analysis up to the level of organisms and populations, and to ecosystems (bottom). For timescales, responses can occur from hours (left) to years and longer (right).

In the short-term, the impact of extremes, provided their absolute tolerance is not exceeded, depends critically on the plasticity of the organisms, i.e., physiological mechanisms that permit individual organisms to acclimatize in order to cope with environmental stress (Fig. 5). Also critical is the speed at which an organism can trigger these mechanisms relative to the abruptness of the event. For example, the activation of heat shock proteins (HSPs)¹⁰² is a common cellular-level response to the rapid onset of marine heatwaves¹⁰³. But this strategy has its physiological limits, such as that imposed by the level of temperature-dependent oxidative stress on DNA¹⁰², leading to some of the most detrimental effects of extremes on marine life¹⁰⁴.

On timescales of days to weeks, these intracellular acclimatization responses are associated with substantial costs^{83,102}. They affect the fitness of the organism with respect to its behaviour, growth and reproduction. Organisms could overcome this disadvantage via adaptation¹⁰⁵⁻¹⁰⁷, but the compressed timescales of extreme events, in conjunction with their high intensity, imposes strong limits on this strategy. An exception might be persistent and/or recurrent extremes, as they provide the near constancy of elevated temperatures that permitted coccolithophores to adapt to elevated temperatures in a one year long lab-based incubation experiment¹⁰⁷. Yet, in diatoms, adaptation to thermal stress has been shown to be limited under coincident nutrient stress due to physiological trade-offs¹⁰⁸. For longer lived organisms that cannot adapt so rapidly, including many marine metazoan ectotherms¹⁰⁹⁻¹¹¹, enforced movement to cooler waters^{112,113} is a viable alternative strategy¹¹⁴, although it may come with additional costs for rates of growth and/or reproduction⁸³. Such lateral migrations have been well documented for marine heatwaves for

several taxa^{37,88,112}. Often, the associated range changes cause a reshuffling of the species composition of the ecosystem. This can lead to increased competition among resident species¹¹⁵ and also may influence food web characteristics such as succession, functional diversity and redundancy¹¹⁶.

On time scales of months to years or more, ecosystems and their constituents may respond to extremes through various resilience mechanisms, including their capacity to resist change (resistance), to recover from damage, and to adapt to increasingly extreme environments¹¹⁷. Microevolutionary adaptation might actually be accelerated in response to extremes, especially in systems where an initial high genetic variability was substantially reduced owing to an extreme induced mass mortality¹¹⁸. At the level of entire ecosystems, compensatory dynamical processes¹¹⁹, such as the substitution of affected species with others of similar function in diverse or functionally redundant ecosystems are successful strategies to conserve biomass, productivity, ecosystem structure and/or function in the presence of perturbations. In addition, food-web interactions have been shown to be of critical importance for ecosystem resistance and resilience^{120–122}. Yet, there are numerous examples where extremes have led to transitions or even irreversible changes in ecosystem structure and composition^{12,75}. For instance, Indian Ocean coral reefs encountered a substantial reduction in coral coverage after a severe marine heatwave in 1998 with limited recovery thereafter^{90,91}, Australian temperate reef communities underwent an irreversible shift from kelp forests to communities typical for subtropical and tropical waters⁸⁸, and major changes in zooplankton and micronekton community structure have been observed after a heatwave in the California Current System³⁶. Rocky intertidal communities along a >1000 km stretch of the Gulf of Alaska went through substantial declines in diversity and a transition from macroalgal to mussel coverage over several years following the “Blob” heatwave⁹².

Some of these long-term ecosystem transitions^{92,123} might have emerged as the cumulative outcome of a series of cascading effects across the levels of biological organization¹²⁴. In such cascades, physiological or ecological effects at the organismal or species level are amplified within the food-web, thus leading to changes in biomass, productivity or foodweb stability and dynamics (Fig. 5). Such effects can emerge, for example, when species within a community have large differences with regard to their environmental tolerances⁷⁵ (see Fig. Box 1, panel b). The resulting differential sensitivity leads to a wide range of organismal fitness and subsequently changes in population sizes and community composition during extremes, potentially causing trophic mismatches¹²⁵ or collapses in predator-prey relationships¹²⁶. Such transitions can include trophic reorganizations, some of which have been found to result in shortened, ‘bottom-heavy’ food webs

in ecosystems where key stabilizing factors such as functional redundancy, trophic compensation and species substitution were absent¹²³.

In addition to the consideration of the timescale of the biological response, we also need to assess the biological ramifications of the temporal evolution of an extreme event, especially its heterogeneity, and the recurrence of events. But so far, no clear trend has emerged yet from the literature, as the reported responses to recurring extremes vary from positive to negative^{127,128}. This diverse range of responses may be linked to the degree and nature of strategies for resilience and resistance – for example, the role of high post-disturbance survivorship of recruits¹²⁷. However, the reported responses may be site specific⁷⁷, and dependent on the level of natural variability organisms and ecosystems encounter¹²⁹ as well as on the potential preconditioning prior to the extreme⁹³. Also, the response of biota to heterogeneity within a multi-month extreme (Fig. Box 2, Fig. 5) can be mixed. While these changes can induce even more stress on the organisms, they may also provide some temporary respite – for days to weeks - for residents to subsist/survive¹³⁰.

BIOLOGICAL RESPONSES TO COMPOUND EVENTS

Our conceptual framework in Fig. 5 also structures the discussion of the potential biological responses to compound events. At the physiological level, an energetic balance perspective such as embodied in the concept of oxygen and capacity limited thermal tolerances¹³¹ can provide a good starting point, at least for ectothermic marine animals (see also the work on the metabolic index^{132,133}). In this concept, it is assumed that the realized thermal niche of an animal is limited by the level of oxygen supply at both sides of the thermal window. Thus, low oxygen concentrations matter most when an animal is at its upper thermal limit, implying strongly synergistic effects during a compound event when a marine heatwave coincides with a low oxygen extreme. An extension of this concept to include the effect of CO₂, i.e., by considering hypercapnia¹³¹, predicts similar synergistic effects for a compound event characterized by a heatwave and high acidity (see also¹³⁴).

Multi-dimensional fitness-landscapes in stressor space¹³⁵, derived from either meta-analyses of species responses (e.g.⁹⁷), field observations of extreme events⁸³, targeted experiments¹⁰⁸, or based on novel adaptive models¹³⁶ may serve to provide equivalent metrics to the metabolic index and a better understanding of the biological mechanisms driving biological responses across ecological and spatio-temporal scales. The integration of empirical evidence with mechanistic relationships between stressors and their extremes derived based on first principles of

biology in novel adaptive marine ecosystem models¹³⁶⁻¹³⁸, or cell models¹³⁹ is likely to increase our fundamental understanding of ecosystem function – a key prerequisite for improved projections of responses to extremes.

However, in order to accurately predict the response of organisms and ecosystems to extremes in multiple dimensions, these novel approaches all rely on calibration against the available data. To date, there are only a handful of examples that report the biological responses to multiple hazards associated with compound events^{78,83,84}. In the California Current System, the combination of a marine heatwave and enhanced upwelling provided a ‘natural laboratory’ to explore the response of calcareous zooplankton (pteropods) to the triple hazards of high temperature and acidity, and low oxygen⁸⁴. A major biological response to this compound extreme was the need for metabolic compensation, which required the reallocation of energy within the investigated pteropods. Comparative physiology of the responses of crustacean and calcareous zooplankton to this Californian compound event indicated that copepods, due to a higher capacity antioxidant defense system and vertical migratory behavior, may be better at coping with such a triple threat event⁸³. Due to interactive effects, the multi-faceted responses of marine life to compound events is likely more complex than that for biota encountering individual extremes, and hence the conceptual framework in Figure 5 may present a useful point of departure to explore the cumulative effects on marine biota of compound extremes.

ADVANCING OUR UNDERSTANDING OF OCEAN EXTREMES

In the last few years, ocean extremes have emerged as an issue of great concern¹⁴⁰, especially given their potentially strong impact on marine life. Given the large socio-economic values (e.g. food security, tourism/employment) of the marine ecosystems under threat (e.g., the Great Barrier Reef¹⁴¹ or marine fisheries^{142,143}), this represents a substantial risk for society.

We recommend three focal threads to be followed in order to advance our understanding and to mitigate this risk. The first thread should focus on a better characterization of the high acidity and low oxygen extremes. Critically, the observational basis, including the links to consequent biological impacts, needs to be drastically improved, especially in subsurface waters. Indeed, the currently available observations of the oceans’ interior are often insufficient to even provide a robust baseline¹⁴⁴, against which extremes can be detected. The increasing number of autonomous observing platforms (such as Argo profiling floats, and moored systems), often with additional biogeochemical and biological sensors^{145,146}, provide a unique opportunity to substantially improve our ability to observe such events. These routine observations should be coupled with rapid

response investigations when an extreme event or compound event is unfolding (guided by real-time observations and early warning systems), involving more targeted means, involving gliders, moorings, and other tools. Improved and expanding modeling capabilities will also play an important role^{13,14,54}, especially also the establishment of catalogs of past events, for example using ocean reanalysis products¹⁴⁷, that can be used to search for and identify the potential impact in long-term timeseries. Also, novel data analysis and synthesis approaches involving machine learning approaches to, for example, to identify compound events in high dimensional data¹⁴⁸ can support a better characterization of extreme events.

The second thread should focus on the development of a more quantitative understanding of the processes that cause and maintain ocean extremes. A special effort will be needed to assess how the interactions between the ocean and atmosphere, and particularly their interplay at smaller scales, enhances the intrinsic variability of the system, thus generating the conditions conducive for the generation of extremes. This requires a combination of detailed analyses of observations and extensive modeling studies, especially with higher resolution models^{31,149}. Another essential contribution is the development of a predictive capability for ocean extremes¹⁵⁰ using both empirical as well as numerical approaches, so that impacted human communities, businesses, and leaders can prepare for extremes, by e.g., adapting strategies that reduce the exposure or minimize the magnitude of other stressors such as fishing pressure⁹⁰.

The third and perhaps most important thread should focus on the study of the impacts of ocean extremes on marine life. Especially critical is the need to address two major emerging challenges. First, teasing apart and better understanding the cumulative effects on biota of the multifaceted characteristics – from abruptness to recurrence - associated with individual extremes (Box 1 and Fig. 5). Due to the potential novel range of effects of these characteristics, we will need to analyse existing datasets on multiple stressors differently, e.g., by evaluating the response of ecosystems to perturbations as a function of time. Hence, we advocate a special effort to dissect the relative roles of the characteristics associated with extremes (Fig. 5) and to determine their relative importance. For example, will the effects of abruptness on the ability of organisms to acclimate determine their subsequent responses to duration, heterogeneity, and other properties? This question could be addressed via targeted experiments to explore the relative timescales of abruptness versus acclimatory responses⁹³.

The second challenge is the consideration of the role of the compounding effect of the different hazards, leading to a complex matrix of often novel conditions¹⁵¹ but further confounded by the many characteristics associated with the extremes. Approaches include manipulation experiments *in situ* or *in vitro*, and long-term monitoring, as well as new analysis methods to assess

the biological responses such as ‘early warning’ bio-markers⁸⁴ to provide routine *in situ* physiological assessments of the community. In addition, the existing large body of experimental evidence from multi-stressor research and meta-analyses (see e.g.,⁹⁷) could be exploited to interpret short- to intermediate-term, physiological, developmental or population level responses. In particular, multiple stressor studies that have been fostering a mechanistic understanding and jointly developed physiological modelling approaches to understand the interplay of stressors¹⁵² should be built upon and cautiously applied to compound extremes to assess biological responses to such events.

Such mechanistic models are critical to improve also our predictive capacity of marine ecosystem impacts. This requires the continued development of novel mechanistic models that assess population dynamics based on processes at the scale of the cell¹⁵³, take into account the plasticity of organisms and populations¹⁵⁴ or the adaptive capacity of ecosystems¹³⁶, and/or evaluate the dynamics of an ecosystem based on novel metagenomic and metatranscriptomic data that simultaneously provide an insight into ecosystem status and function¹³⁹. Furthermore, significant advances have to be made with regard to gaps in our understanding of the factors controlling biological and functional diversity, food-web interactions and relationships between different ecosystem constituents (trophic links, symbiosis, parasitism), and also with regard to the physiological states and trophic modes (mixotrophy) of populations, before these models can be operational in forecasting and future impact projection applications.

Policy instruments, such as climate change vulnerability assessments, that permit managers to better prepare and cope with the impacts of extremes will become more critical^{155,156}, especially when considering the expected increase in the frequency of extreme events (e.g.^{8,14}). Such appraisals can be pushed farther by developing extreme-based metrics that are specifically targeted at the assessment of ocean health and societal benefits, such as the Ocean Health Index¹⁵⁷. One option for such an index could be one that reflects the likelihood of occurrences of an extreme of a certain type and category, perhaps combined into a single metric across the three stressors. Such developments would permit the gauging of the socio-economic impact of potential changes in ocean ecosystem services emerging from extremes¹². Attribution studies in well-observed systems, such as coastal coral reefs world-wide, aimed at disentangling the effects of long-term climate change trends from those of extreme events, may further help to improve our quantitative understanding of the risk that extreme events may pose to marine ecosystems within the longer term climate change context^{38,90}. These insights may change our paradigms about what constitutes harmful/acceptable climate change⁹⁵.

Extreme events are a harbinger of the future by creating environmental conditions that the mean climate change will not generate for decades, and some recent extremes have been identified as the primary drivers of lasting, irreversible ecosystem change at the decadal scale^{88,91,158}. Extremes pose a potentially particularly strong threat to marine organisms, since a number of the characteristics of extremes (e.g., their abrupt onset, their short duration and their high intensities) can rapidly push organisms and entire ecosystems beyond their adaptive capacity. This may lead to critical ecological transitions⁴³ with potentially wide-reaching implications for the myriad of ecosystem services that the ocean is providing to humanity^{159,160}.

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AUTHOR CONTRIBUTIONS:

NG conceived this perspective, visualized and wrote it with strong conceptual and editorial input by all co-authors. PWB and MV led the writing of the biological impact section and TF led the analyses of the global model results.

DATA/CODE availability:

The model results presented in the paper are available through the ETH Research Collection (<https://www.research-collection.ethz.ch>).

Figure 1:

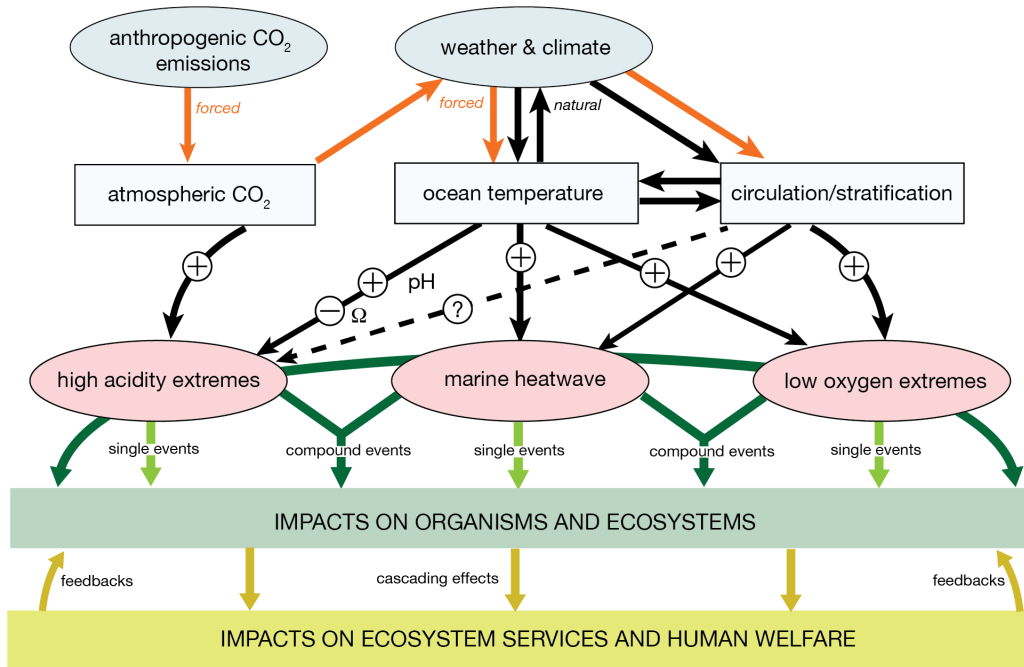


Figure 1: Drivers of marine heatwaves and ocean biogeochemical extremes and their impact. The three types of extremes considered here, i.e., marine heatwaves, low oxygen extremes and high acidity extremes, occur in part due to natural processes (black arrows), but their intensity, frequency, and duration is strongly impacted by the anthropogenic increase in atmospheric CO₂ and the resulting (human-forced) change in weather and climate (orange arrows). These three types of extremes can occur individually, but also together or in close sequence as so-called compound events. These extremes may have pronounced impacts on marine organisms and also the ecosystems that they form. Those changes, in turn, can affect key marine ecosystem services such as fisheries yields, and ultimately also human welfare through a series of cascading effects.

Figure 2:

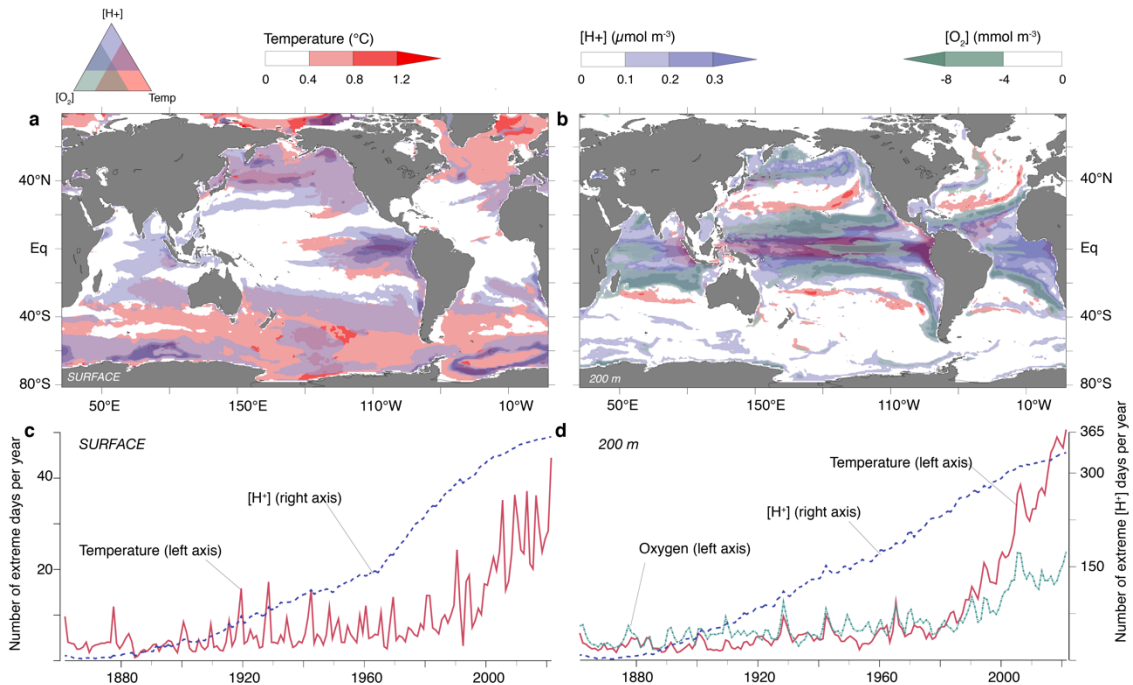


Figure 2: Global pattern and trends of marine heatwaves and biogeochemical extremes: (a) and (b) Mean intensities of all days when the thresholds are exceeded for heatwaves (red) (°C), high acidity extremes (blue) ($\mu\text{mol m}^{-3}$), and low oxygen extremes (green) (mmol m^{-3}). Shown are the intensities for (a) the surface layer, and (b) 200 m depth with the colors being mixed in regions of overlap. The extremes have been defined relative to a preindustrial control simulation. (c) and (d) Timeseries of the average number of extreme days per year at each location. Please note that the axis for the high acidity events is given on the right-hand side. All results are based on simulation results from the GFDL Earth System Model¹⁴.

Figure 3:

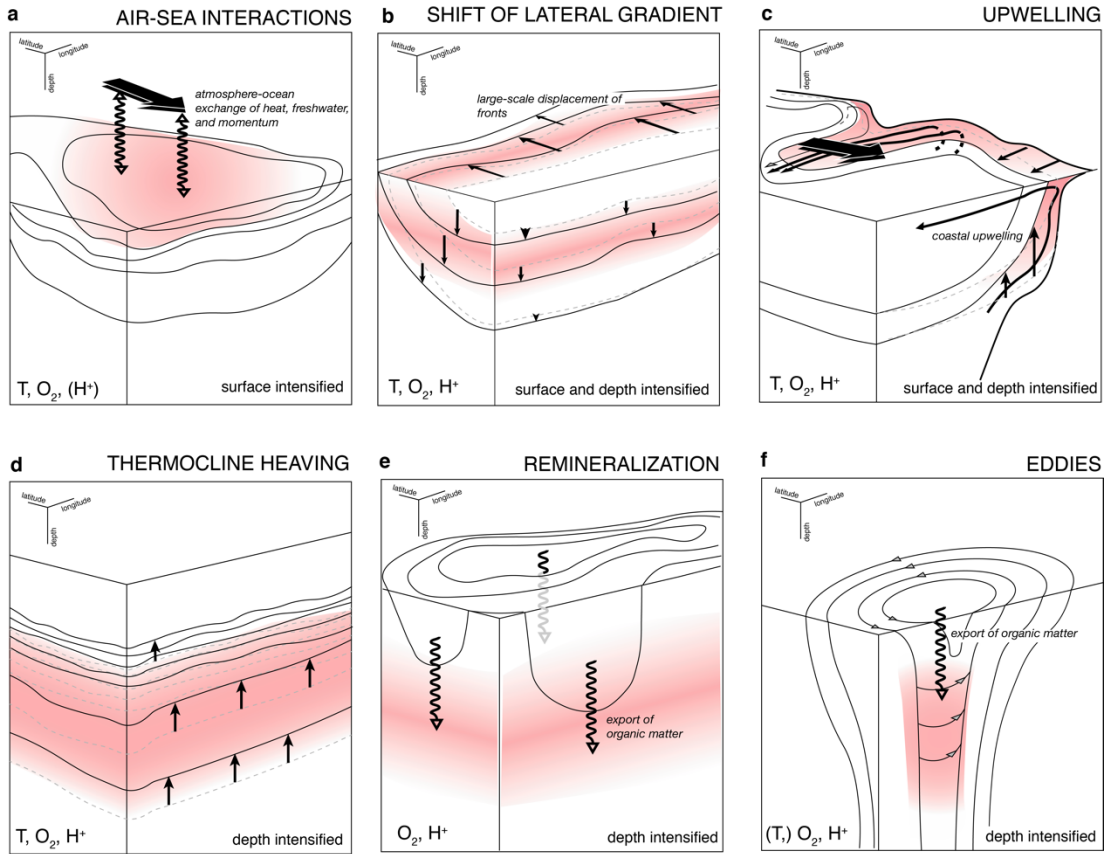


Figure 3: Idealized depictions of the mechanisms giving rise to extreme conditions in temperature, acidity, and oxygen. (a) Air-sea interactions, (b) lateral shifts of fronts (at the surface or at depth), (c) upwelling (shown here is coastal upwelling, but the same processes are at work also at the equator), (d) thermocline displacement, (e) enhanced remineralization of settling organic matter, and (f) eddy trapping. Not all variables are affected equally, as indicated on the bottom left of each panel.

Figure 4:

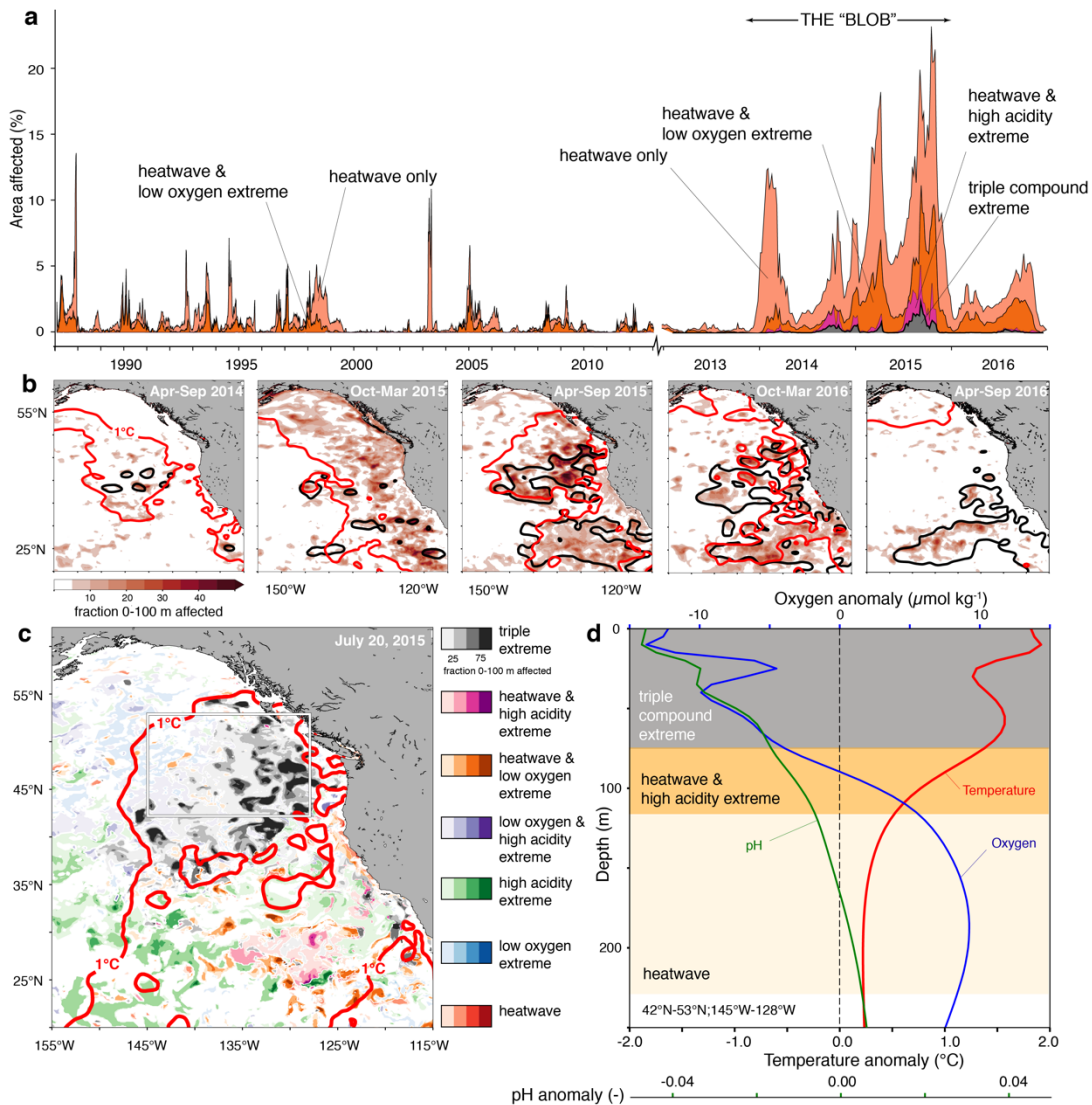


Figure 4: Illustration of the temporal evolution and four-dimensional nature of ocean extremes using model simulation results for the 2013-2015 “Blob”. (a) Temporal evolution of the fractional area (20°N-60°N, 115°W-155°W) that is subject to a marine heatwave or any compound event. An event contributes to this metric when at least 25% of the top 100 m of the water column is considered extreme for the considered properties. (b) Modeled spatial evolution of the temperature characteristics of the Blob event. The color filled contours depicts the average fraction of the top 100 m of the water column that is identified as a temperature extreme. The red and black contours represent the 1°C anomaly of temperature at the surface and at a depth of 100 m, respectively. They thus identify the extent of the “Blob”. (c) Snapshot of the modeled fields for July 20, 2015. The color indicates the type, while the saturation shows the fraction of the water column (0-100 m)

that is occupied by these extreme conditions. The white box off the western seaboard in panel (c) indicates the area over which the vertical profile show in (d) is averaged. All figures are based on a hindcast simulation using a regional ocean biogeochemical model⁶⁹ with the extremes being defined relative to a modern reference period (1986 to 2016).

Figure 5:

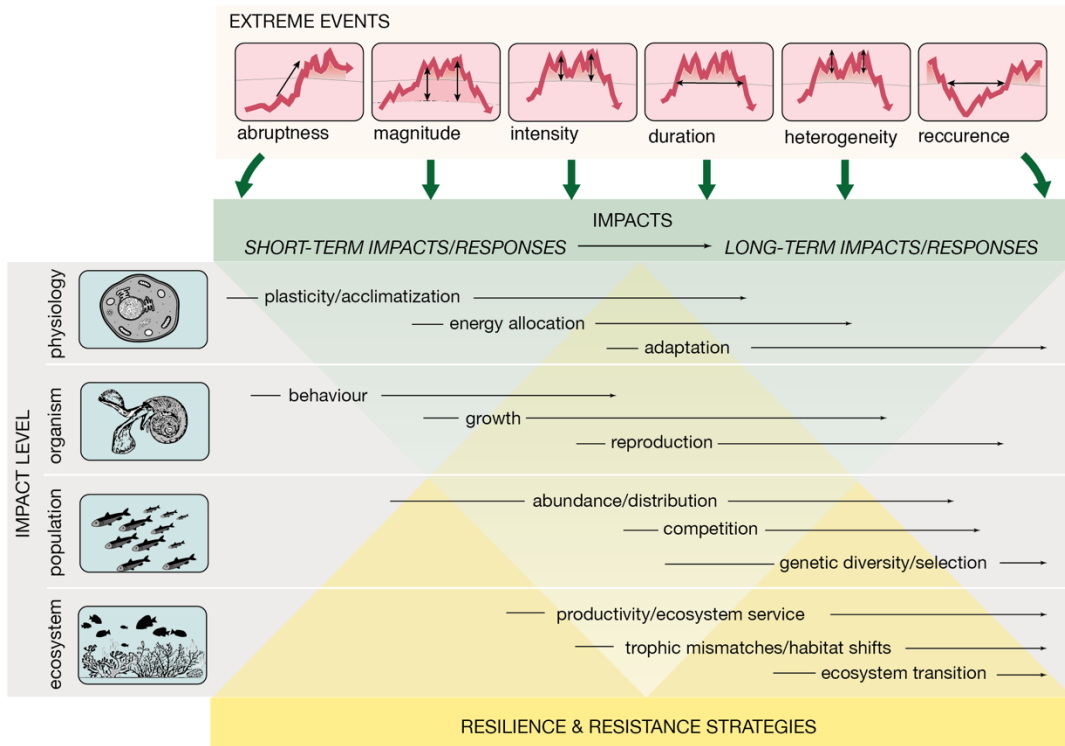


Figure 5: Conceptual framework to understand the impact of marine biogeochemical extremes and heatwaves on the functioning of marine life – from physiology through to ecosystems. The timescales of the biological impacts and responses relate also to the range of characteristics used to define extremes (Fig. Box 2) from short-term (days, abrupt onset of extremes) to long-term (years, recurring events, such as the 2016 and 2017 bleaching events of the Great Barrier Reef¹²⁸). Better understanding of the effectiveness of resilience and resistance strategies to extremes will be essential to more accurately project the range of biological responses, such as adaptive capacity, which may include two classes of responses, i.e., “persist in place” and “shift in space”¹¹⁴. A major unknown is the change in resilience of biota that may occur with the projected increase in the frequency of disturbances driven by extreme events¹¹⁷.

BOXES

BOX 1: Definition of extreme events

Any method used to identify extreme events needs to make several key choices based on the scientific question to be addressed (cf. 7). First, one needs to decide on the type of threshold, i.e., relative versus absolute (Fig. Box, panels a & b). Relative thresholds are based on the local variability in the stress variable (e.g., temperature percentiles). Their use is warranted in situations where one expects that organisms are adapted to cope with the normal range of variability, but challenged when the conditions move outside this range¹²⁹. In contrast, absolute thresholds are warranted in situations when the stress variable can move outside the physiological limits of marine organisms or can cross a physical or biogeochemical thresholds. (Fig. Box, panel b). The second decision, required only in the case of a relative threshold, is the reference period, i.e., the period that is used to construct the probability density function, and whether this reference period is fixed or moves with time, i.e., whether one uses a fixed or a so-called shifting baseline¹⁰. The third choice involves how seasonality is dealt with, i.e., whether the thresholds are determined from seasonally-varying data or from deseasonalized data. The fourth and final choice concerns the requirement of additional conditions, such as, for example, a certain minimum duration.

The basis for the decision about these choices rests primarily on the biological impact to be quantified – assessments of impacts at the ecosystem level have often taken a relative threshold approach, such as in the case of coral bleaching¹⁶¹. In contrast, physiological impacts at the organism level have often used absolute thresholds that reflect specific limits of metabolic processes. For marine heatwaves, most studies have used a relative threshold approach, but with varying choices with regard to the consideration of seasonality^{8,30}. Absolute thresholds tend to be more commonly used to study extremes with high acidity¹³ or low oxygen, although relative thresholds have also been used¹⁴. A typical absolute threshold is the saturation level with regard to mineral CaCO_3 , $\Omega=1$, i.e., when seawater changes from being supersaturated ($\Omega>1$) to becoming undersaturated ($\Omega<1$), thus leading to CaCO_3 shell dissolution. Analogous absolute thresholds for the definition of oxygen extremes would be the hypoxic limit ($\sim 60 \mu\text{mol kg}^{-1}$) or the suboxic/anoxic limit ($\sim 5 \mu\text{mol kg}^{-1}$), below which metabolic and physiological processes in heterotrophs are impaired.

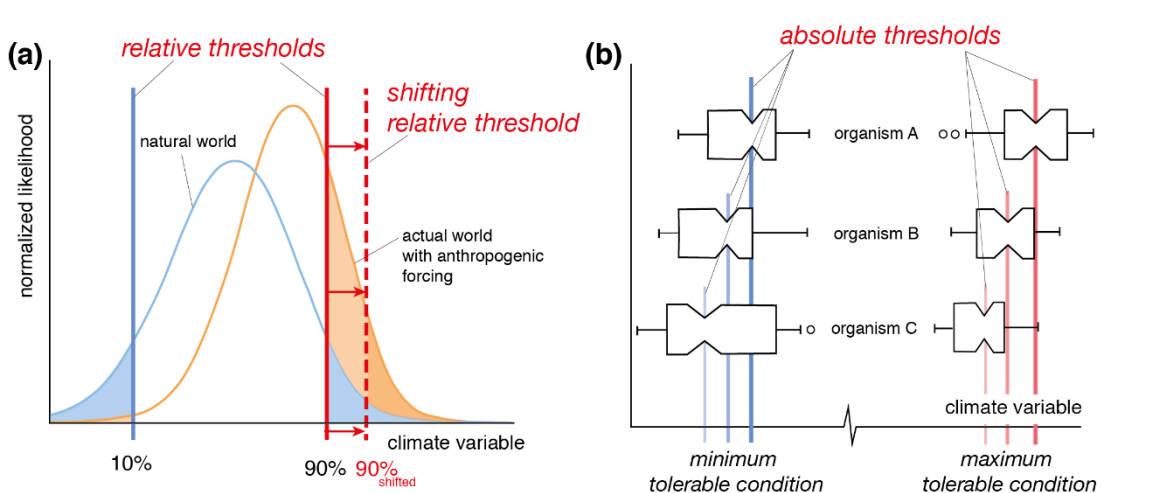
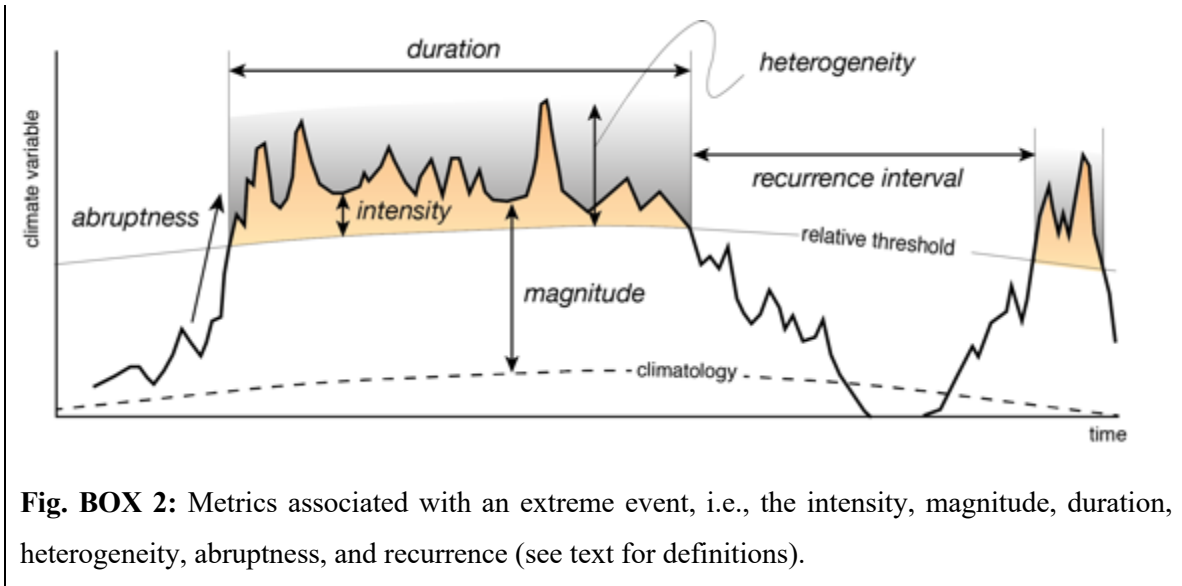


Fig. BOX 1: Concepts associated with the definitions of extreme events. (a) Relative thresholds determined from the perspective of the statistical distribution, here based on the 10th or 90th percentile. The relative thresholds are usually defined from the probability density function for a fixed reference period (fixed baseline). But the relative thresholds can also be defined from a probability density function that evolves with time, i.e., defining a shifting relative threshold (shifting baseline). (b) Absolute thresholds determined from the perspective of tolerable conditions for organisms, either near their estimated minimum or their maximum tolerable conditions. Here, a range of thresholds are shown for organisms A-C to reflect differences in their sensitivity to extremes⁷⁵.

BOX 2: Key characteristics of extreme events [currently 168 words]

Extreme events can be characterized by multiple characteristics (Fig. Box 2): The most commonly used ones are the *number of days* and the *duration*, i.e., the number of days and the time period during which this threshold was exceeded, and the *intensity*, i.e., how much the climate variable has remained, on average, above the threshold during the event. Closely related to the intensity is the *magnitude*, as it reflects the mean value of the climate variable during the event relative to its climatological mean. Less common, but physiologically and ecologically influential is the *abruptness* and the *heterogeneity*. The former describes the speed of the onset, while the latter reflects the variance of the intensity during an event. The final characteristics considered here is the *recurrence*, i.e., the average time between events at a particular location. Intensity and duration are sometimes combined to form an integrated metric, often referred to as cumulative intensity, degree heating weeks, or *severity* (defined as the product of mean intensity and duration). This metric plays an important role for coral bleaching, for example¹⁶². The *seasonal distribution* of extreme events will also be critical for the quantification of impacts at the population level (e.g. occurrence of extremes during reproductive periods), as the susceptibility to disruption can be life-stage dependent¹⁶³, and thus may vary seasonally.

The relevance of these extreme characteristics with regard to ecosystem impacts will depend on the taxa under study, but also on the level of biological organization at which these effects are evaluated. Whereas metrics such as intensity, duration or recurrence have been shown to correlate with impacts at both the organism and ecosystem level⁹³, abruptness will matter in relation to the rapidity of the acclimatory response of specific physiological processes¹⁰². Recurrence rate will have impacts at the population level such as reproductive success, or for the magnitude and permanence of adaptive responses¹⁴¹. The heterogeneity of events may be indicative of the degree to which refuges are created that provide a respite from stressful conditions^{85,127}. While relationships between event metrics and specific responses at the organism or population level can be quantified in targeted experiments, such dependencies may be challenging to disentangle in situ and at the ecosystem level due to a superimposition of multiple effects (ranging from acclimatory and competitive responses to community reshuffling and habitat shifts occurring at different spatio-temporal scales; Fig. 5).



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SUPPLEMENTARY MATERIAL:

Simulations with the global GFDL Earth system model

The global extreme event analysis was conducted with simulation results from the fully coupled Earth system model ESM2M developed at the Geophysical Fluid Dynamics Laboratory (GFDL) of the National Oceanic and Atmospheric Administration⁴⁵. The atmosphere has a horizontal resolution of 2° latitude x 2.5° longitude and the ocean has a nominal horizontal resolution of 1° latitude and 1° longitude, increasing toward the Equator to up to 0.3°. Ocean biogeochemistry is simulated by the Tracers Of Phytoplankton with Allometric Zooplankton version 2.0 (TOPAZ2). It represents 30 prognostic tracers, includes three phytoplankton functional groups and implicitly simulated zooplankton activity. The GFDL ESM2M captures the observed large-scale biogeochemical patterns and variability. We use a 500-yr preindustrial control simulation with prescribed atmospheric CO₂ concentrations at 286 ppm, as well as a historical simulation over the 1861-2005 period followed by a high (RCP8.5; RCP: Representative concentration pathway) simulation over the 2006-2100 period with prescribed atmospheric CO₂ and non-CO₂ greenhouse and natural forcing¹⁴. The RCP8.5 scenario is a high emission scenario without effective climate policies, leading to continued growth in greenhouse gas emissions.

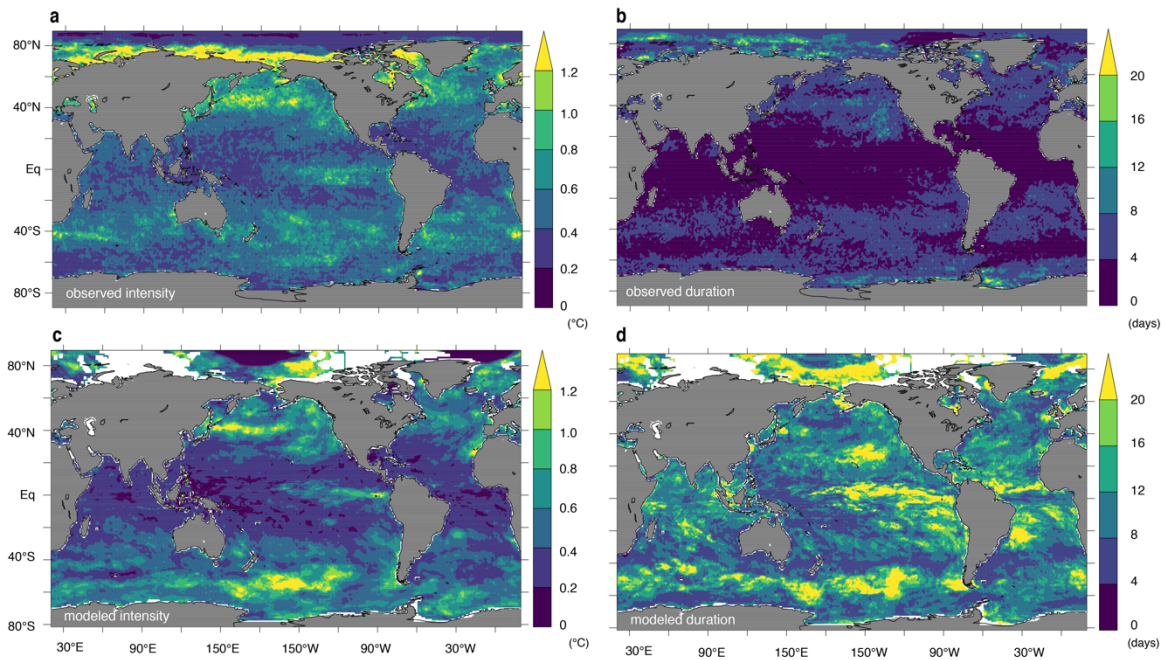
We limit the evaluation of the global model to the assessment of simulating marine heatwaves (Figs. S1 & S2). The fidelity of the model in simulating high acidity extremes¹⁴ and the mean state^{5,45} have been assessed elsewhere. We use NOAA's daily Optimum Interpolation SST (OISST) analysis product with a spatial resolution of 0.25°¹⁶⁴. This dataset provides a high-quality global record of SST observations obtained from satellites, buoys, and Argo floats on a regular grid. Before doing the analysis, we regridded the OISST dataset to a regular 1° grid to allow a direct comparison with the GFDL ESM2M model, which has a nominal horizontal ocean resolution of 1°. A marine heatwave is defined with a relative threshold of 99% using the OISST product from 1982 to 2019 as our baseline. Following this definition, marine heatwaves can be as short as one day, extend over only one grid cell and predominately occur in the warm season. Note that this definition differs from that used by ref⁽⁹⁾ on the basis of the definition of ref⁽³⁰⁾, leading to larger year-to-year variations compared to the results shown by ref⁽⁹⁾, since they consider heatwaves to occur any time during the year. This leads to a smoother distribution of heatwaves in time, and consequently a lesser degree of year-to-year variations.

The model simulates well the spatial pattern of maximum daily intensity of marine heatwaves with high intensity in the higher northern latitudes, the eastern equatorial Pacific and

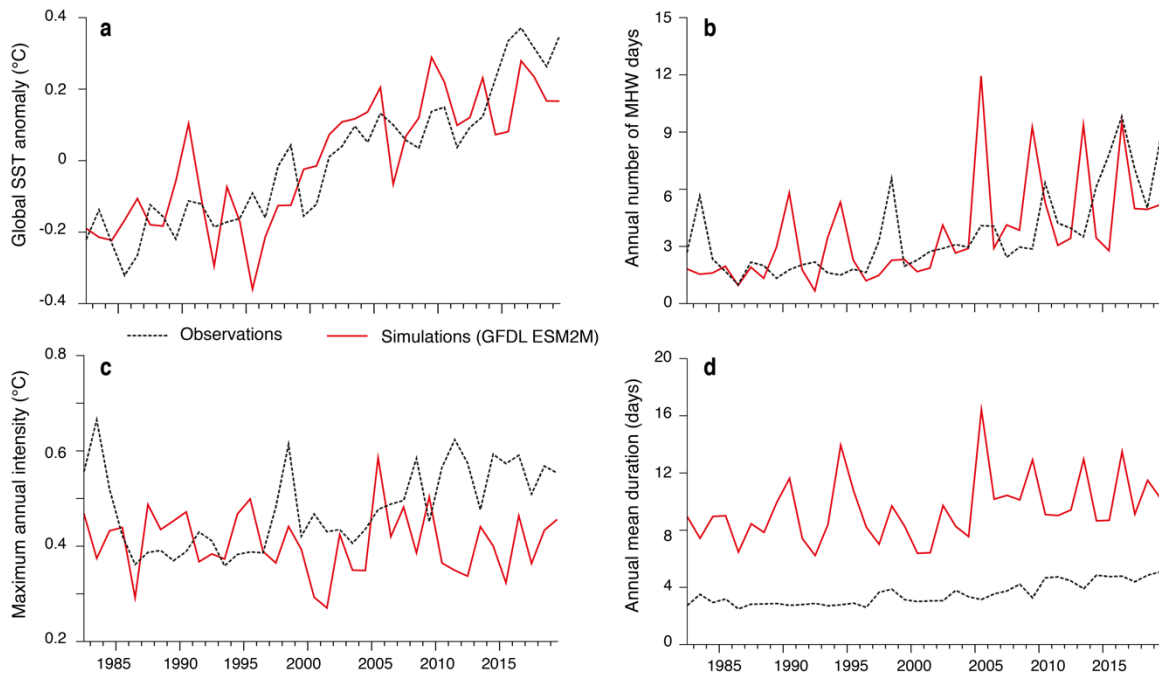
the northern part of the Southern Ocean (Fig. S1a,c). Lower intensities are simulated and observed in the subtropical gyres. Overall, the model simulates stronger differences in heatwave intensities between the different regions than seen in the observations. The modeled and observed durations differ more substantially, with the model overestimating the observed durations by about a factor of two to three (Fig. S1b,d). This is a well-known bias in CMIP-type of models (e.g.^{8,49}). The observed pattern of the duration is only marginally captured by the model, although there is a general tendency in both model and observations for longer heatwaves in the higher latitudes and shorter heatwaves in the mid latitudes. A striking difference is the model's simulation of relatively long heatwaves in the tropics, a feature not seen in observations.

The GFDL ESM2M model captures very well the positive long-term trends in global mean SST (Fig. S2a) and annual number of marine heatwave days (Fig. S2b). Global SST is simulated to increase by $0.13^{\circ}\text{C decade}^{-1}$ from 1982 to 2019. This is in very good agreement with the observed increase of $0.16^{\circ}\text{C decade}^{-1}$. Both the model and the observations indicate an increase in marine heatwave days per year of $1.3 \text{ days decade}^{-1}$ over the 1982-2019 period. Both maximum annual intensity and annual mean duration do not show any substantial trend over this period, whether in the GFDL ESM2M nor in the observational-based product. We do not expect that the model captures the phasing of the year-to-year variability in any of these metrics, as the fully coupled Earth system model simulates its own phasing of internal variability.

The very good agreement between modeled heatwave characteristic and the observational-based characteristics, apart from the duration, in addition to the model's high fidelity in simulating open ocean acidity extremes¹⁴ gives us great confidence in using this model for analyzing the mean state and trends in different characteristics of ocean biogeochemical extremes and heatwaves at the global scale.



Supplementary Figure S1. Evaluation of the model simulated heatwave characteristics with observations. Shown are the results from the simulations with the GFDL ESM2M model⁴⁵ and from the OISST product¹⁶⁴. (a) and (b) are the observed maximum daily intensity (°C) and average duration (days), respectively determined from the OISST product averaged over the period 1982 to 2019. (c) and (d) are the corresponding model simulated metrics from a combined historical (1982-2005) and RCP8.5 (2006-2019) simulation.



Supplementary Figure S2. Evaluation of the temporal dynamics of the model simulated heatwave characteristics in the global ocean. Shown are the results from the simulations with the GFDL ESM2M model¹⁴⁵ (red line) and from the OISST product¹⁶⁴ (black dashed line). (a) Timeseries of the global mean sea-surface temperature anomaly relative to the analysis period (1982 through 2019) (°C). (b) Timeseries of the global mean annual number of marine heatwave days. (c) Timeseries of the maximum annual intensity (°C). (d) Timeseries of the annual mean duration (days).

Simulations with the regional ROMS-BEC model

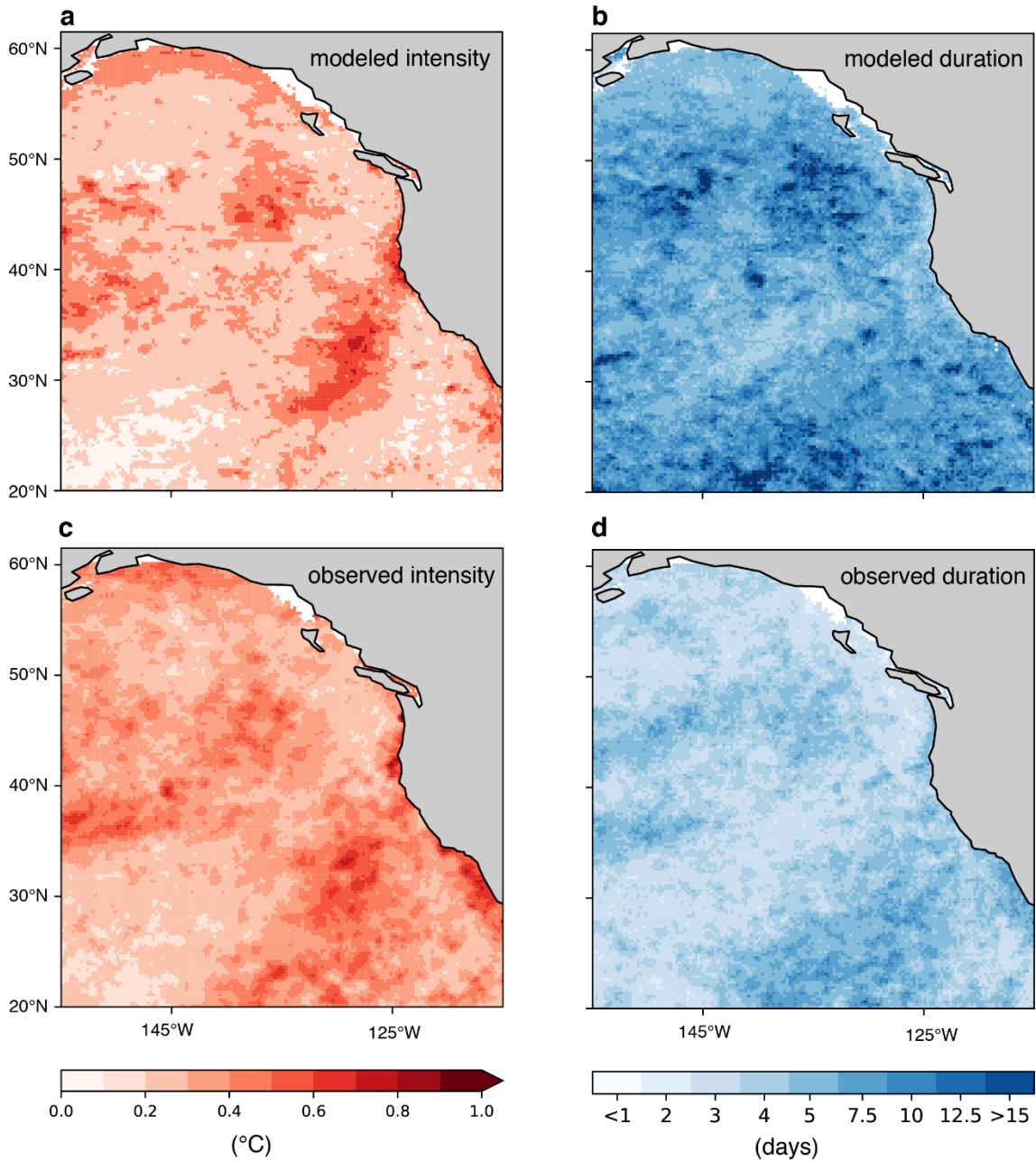
The 2013-2015 “Blob” event was analyzed using hindcast simulations of the telescopic North Pacific setup of ROMS-BEC by ref⁽⁶⁹⁾. Briefly, the model system consists of the Regional Oceanic Modeling System (ROMS)¹⁶⁵ coupled to an updated version of the Biogeochemical/Ecological Model (BEC)¹⁶⁶. BEC explicitly resolves the cycling of four nutrient elements, which limit the growth of three phytoplankton functional groups, which are being kept under control by the grazing of a single zooplankton functional group. The model domain covers the entire Pacific, but has a strong resolution refinement toward the U.S. West Coast, with most of the area of interest having a resolution of 10 kilometers or better. The model was initialized from observations, and then run through the period 1970 to 2016 using daily fields of wind stress, solar short-wave radiation, and fluxes of heat and freshwater from ERA Interim¹⁶⁷.

As was the case for the global model, we are limited in our evaluation to the assessment of the regional model’s fidelity in simulating marine heatwaves (Figs. S3 & S4) (For an evaluation of the mean state of the model, we refer to ref⁽⁶⁹⁾). For the observations, we use here OSTIA SST product of the U.K. MetOffice¹⁶⁸. This product is very similar to the OISST¹⁶⁴, with one of the differences constituting its focus on the foundation temperature, i.e., the temperature below the skin layer at the surface, which is a more suitable metric to compare to model results. As was done for the global model, we identified marine heatwaves using a relative threshold of 99% established from a daily climatology computed from daily data spanning the period January 1986 through December 2016 to establish our baseline. No additional requirements, such as minimum duration etc, were imposed. The comparison of the modeled marine heatwave intensities with the observed one reveals good agreement in magnitude and pattern, with a highly statistically significant pattern correlation of 0.49 across the entire analysis region (20°N-60°N, 155°W-115°W) (Fig S3a,c). The model captures well the regions of more intense heatwaves along the northern U.S. west coast, extending southwestward into the open ocean, and a region of more intense heatwaves in around 45°N and 140°W. Overall, the model exhibits slightly more contrast than the observations, leading to a slightly higher spatial standard deviation. The comparison is less favorable for the duration, where the modeled duration is nearly a factor of two longer than the observed one (Fig S3 b,d). At the same time, the pattern is similar, as evidenced by the positive spatial pattern correlation of 0.29. Broadly speaking, regions with higher heatwave intensities also tend to have longer heatwaves, although this is not the case for the marine heatwaves along the U.S. West coast, which tend to be short lived. The factor of two difference in duration between our high-resolution regional model and the observations mimics the factor of nearly three difference seen in the global, coarser-resolution model (Fig. S1 b&d, Fig. S2 d),

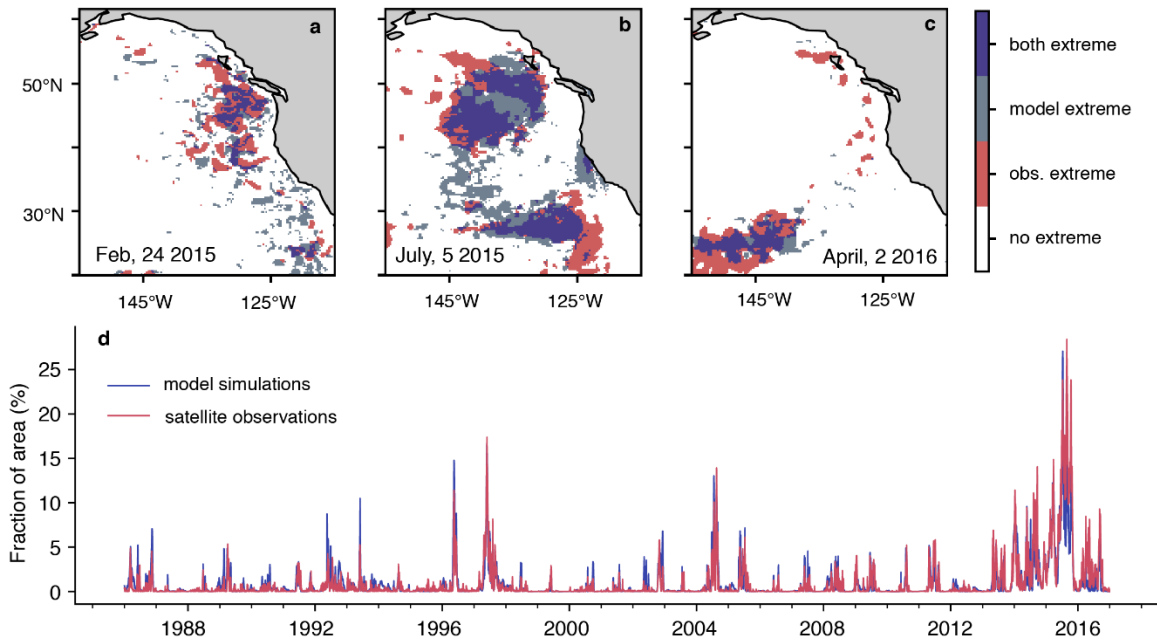
suggesting that it cannot be resolution alone that creates this difference.

The hindcast simulation captures very well the spatial and temporal dynamics of the 2015 “Blob” heatwave event in the Northeast Pacific (Fig. S4). The model is able to track the evolution of the SST anomalies with substantial detail, such that the space-time evolution of the location and extent of the “Blob” heatwave event is reproduced with high fidelity (Fig. S4a-c). Still, there are some differences, largely at the edges of the identified patches where the SST conditions are extreme. But the spatial extent of the heatwave is very accurately captured. This is confirmed in Fig. S4d for the entire analysis period (1986-2016) with the modeled and observed spatial extent of the heatwaves in the analysis region being practically indistinguishable.

The excellent comparison of the modeled heatwave characteristics with the observed one for the regional high-resolution model gives us confidence that the model is sufficiently suited for analyzing the “Blob” event. Fundamental physical processes associated with the “Blob” heatwave must be well represented by the regional model, suggesting that this model is also doing reasonably well with its representation of the oxygen and acidity conditions during the “Blob”.

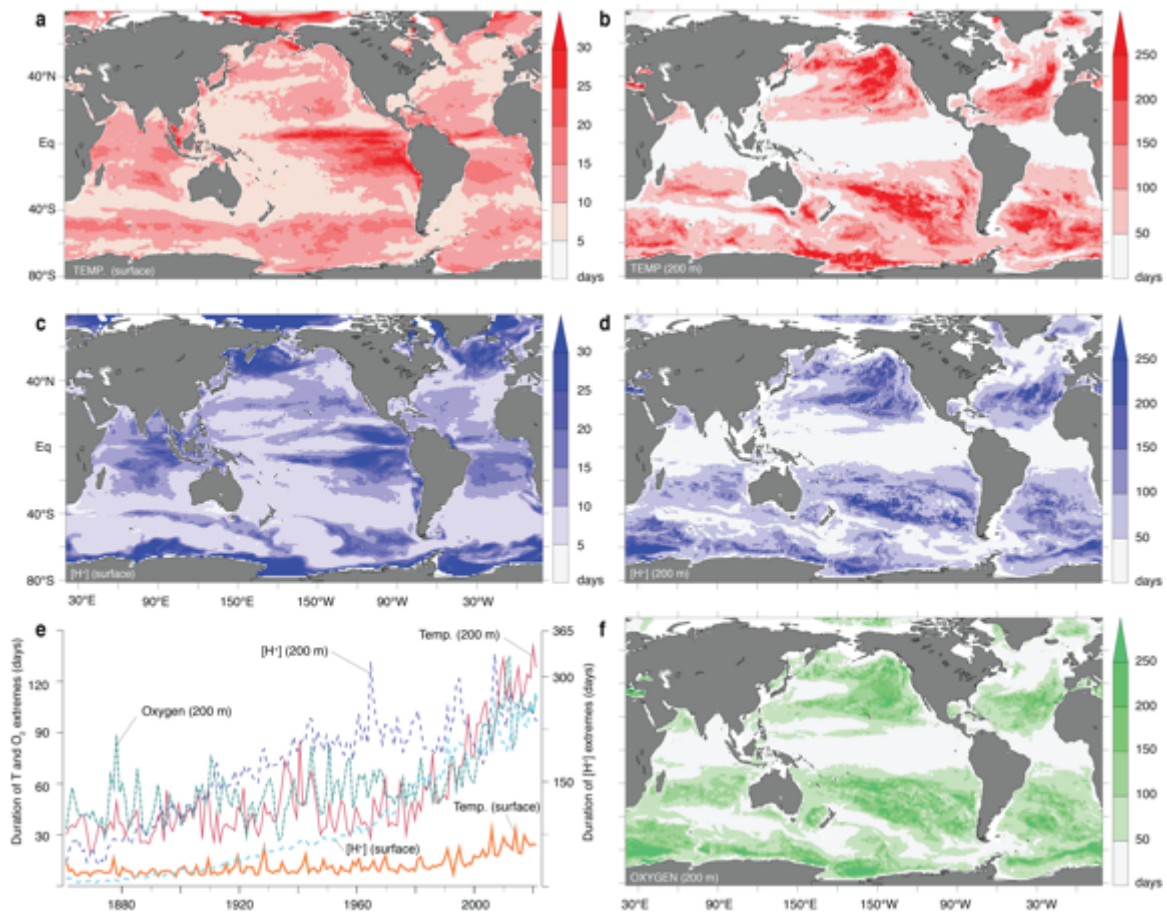


Supplementary Figure S3. Evaluation of model simulated heatwave characteristics in the Northeast Pacific with observations. Shown are the results from the regional model simulations with ROMS-BEC for the period January 1986 through December 2016 (a) for the average intensity ($^{\circ}\text{C}$), and (b) for the average duration of a heatwave. (c) and (d) show the corresponding metrics determined on the basis of the OSTIA sea-surface temperature product ¹⁶⁸.



Supplementary Figure S4. Evaluation of the model simulated spatial and temporal dynamics of marine heatwaves in the Northeast Pacific. (a – c) Maps of the evolution of the spatial extent of the “Blob” marine heatwave as simulated by the model in comparison with observations. The blue color indicates the area where both the observations and the model indicate the presence of a marine heatwave. Areas where the colors are red depict areas where the observations indicate the presence of a heatwave, but not the model. For grey, the opposite is the case. Shown are three snapshots for (a) Feb 24, 2015, (b) July 5, 2015, and (c) April 2, 2016. (d) Timeseries of the area within the Northeast Pacific that is occupied by a marine heatwave for the model (blue) and for the observations (red). Shown are the results from the regional model simulations with ROMS-BEC and the OSTIA sea-surface temperature product ¹⁶⁸.

Duration of events



Supplementary Figure S5. Spatial distribution and temporal evolution of the duration of extreme events. (a-d & f) Maps showing the average length of an extreme event during the preindustrial times. Marine heatwaves at (a) the surface and (b) at 200 m depth; High acidity extremes (c) at the surface and (d) at 200 m depth; (f) Low oxygen extremes at 200 m depth. (e) Timeseries showing the evolution of the global average duration of extreme events for the different types at the surface and at 200 m depth. All results are based on simulation results from the GFDL Earth System Model¹⁴.

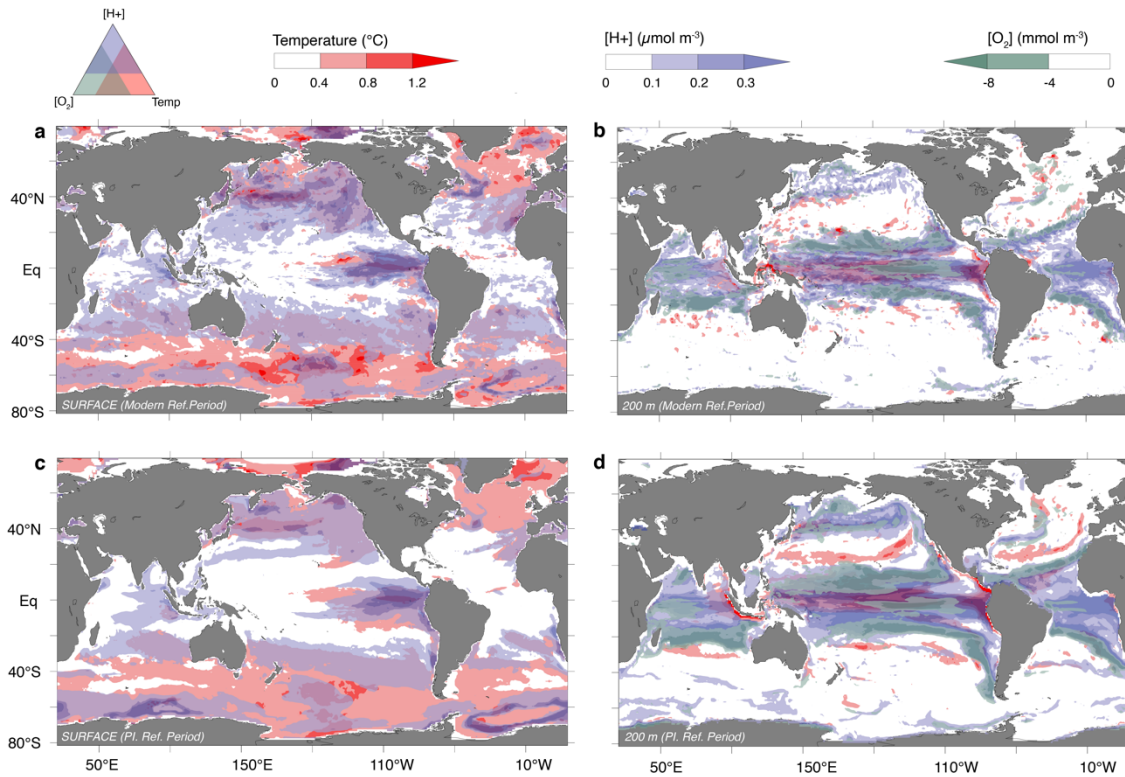
Preindustrial versus modern reference period

To assess the sensitivity of the results to our choice for the reference period, we recomputed the different metrics of the extremes for the global ocean using a modern reference period instead of the preindustrial reference period used in the text. Concretely, we used the model simulation results for the GFDL ESM2M model from the combined historical (1982-2005) and RCP8.5 (2006-2019) simulation to define the “modern” baseline and the thresholds. In order to take into consideration the strong trend in the $[H^+]$ over this period, we linearly detrended the data before computing the percentiles. We did the same for temperature and oxygen in order to be internally consistent, although the impact on the results for the latter two variables is relatively small. For $[H^+]$, this makes a large difference, since the changes in $[H^+]$ over the nearly four decades is larger than the difference between the 10th and the 90th percentile.

Overall, the sensitivity of the key metrics of extremes with respect to the choice of the reference period is small (with the exception, of course, of the temporal evolution of these metrics). Supplementary Fig. S6 shows the results for the intensity at the surface and at 200 m depth for heatwaves, high acidity, and low oxygen extremes for both the modern reference period (top row) and the pre-industrial reference period (bottom row) (as shown in Fig. 2 in the main text). The pattern and magnitude of the intensities of all types of extremes are very similar between the two reference periods, but with the results from the modern reference period being spatiotemporally less coherent. This is primarily a consequence of the much shorter reference period (38 years versus 500 years), which leads to statistically much less well defined thresholds for the modern period. As a consequence of this statistical imprecision, the results get patchier.

The results for duration (not shown) are similar, with the pattern for the preindustrial reference period being very similar for all variables to that obtained for the modern period, except for the higher level of patchiness. The duration itself is very similar at the surface, but for all variables about 30% shorter at depth for the modern period. We attribute this difference also to the short reference period, which tends to skew the distribution toward the shorter events since the very long events are truly rare.

The low sensitivity of the results to the choice of the reference period is the result of a relatively stationary variability of temperature, H^+ and oxygen over the historical period. This means that the changes in the extremes seen in the timeseries are primarily driven by a shift in the mean of the distribution, rather than by changes in variance, especially for temperature and oxygen and to a lesser extent of H^+ . This also implies that the results shown here would also be representative for those obtained using a shifting baseline.



Supplementary Figure S6. Sensitivity of the intensity of extremes to the reference period: (a) and (b) Mean intensities of all days when the thresholds are exceeded for heatwaves (red) ($^{\circ}\text{C}$), high acidity extremes (blue) ($\mu\text{mol m}^{-3}$), and low oxygen extremes (green) (mmol m^{-3}) given a modern reference period (1982-2019). Shown are the intensities for (a) the surface layer, and (b) 200 m depth with the colors being mixed in regions of overlap. (c) and (d) as (a) and (b) but for the extremes having been defined relative to a 500-yr long pre-industrial reference period (see also Fig. 2). All results are based on simulation results from the GFDL Earth System Model¹⁴.