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Review article

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Marine heatwaves as hot spots of climate change and impacts on biodiversity and ecosystem services

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Abstract

Intensifying marine heatwaves (MHWs) are pervasive and destructive manifestations of anthropogenic climate change. Over the past two decades, MHWs have driven biological, ecological and socioeconomic change in almost all oceans and seas. In this Review, we assess the impacts of MHWs on marine organisms and the benefits they provide to people, highlight knowledge gaps and consider opportunities to mitigate MHW impacts. Globally, MHWs have become increasingly intense and frequent, and result in mortality or movement of species when acute temperature thresholds are exceeded. Vulnerability and resilience to MHWs vary among species, but these mortality events have been prominent for habitat-forming foundation species such as corals, kelp and seagrass, causing many cascading indirect impacts on ecosystem functioning and biodiversity. Poleward species shifts produce novel and complex species interactions and altered ecosystem functions, which have considerable consequences for people and their livelihoods. Reducing greenhouse gas emissions remains essential and urgent to address impacts long term, but increases in MHW intensities and duration will be unavoidable and prominent for the foreseeable future. As such, closing the current knowledge gaps around MHWs and their impacts on biodiversity, as well as proactive management strategies, are urgently needed to mitigate further damage to ecosystems and people, and to build resilience into the future.

Sections

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Key points

- Marine heatwaves (MHWs) are periods of unusually warm oceans. Globally, MHWs are a natural phenomenon but have become stronger, longer, and more frequent since ~1980, driven by anthropogenic climate change. The oceans are now experiencing record-high temperatures as warming and large-scale climate phenomena combine to intensify and prolong MHW conditions.

- Temperature influences biological processes from cells to biomes. Species have evolved specific temperature tolerances that match their latitudinal distributions. MHWs cause acute temperature stress, where species and populations with narrow distributions, limited mobility and proximity to their warm distribution limits are most vulnerable.

- MHWs have direct impacts on species productivity and distribution, and indirect impacts through altered species interactions. Impacts on foundation or keystone species result in cascading changes to communities, food webs and ecosystem functioning. Impacts of MHWs are often exacerbated by co-occurring stressors.

- MHWs have affected ocean ecosystem services. Loss of fisheries, nutrient cycling, carbon storage, ecotourism and cultural values have followed shifts in species' abundance and distribution, decimation of seagrasses, corals and kelps, and megafauna mortality. In a few cases, new opportunities have arisen.

- Reducing greenhouse gas emissions is the only long-term solution against increasingly severe MHWs. In the short term, preparation for increasing impacts of MHWs is required. Emerging adaptation approaches include flexible fisheries management and swift conservation to protect vulnerable species. Future research should integrate effects of temperature and compounding stressors.

Introduction

Increasing atmospheric and ocean temperatures are perhaps the most pervasive manifestation of anthropogenic climate change, the evidence for which is unequivocal[1]. This global warming is driving increasingly frequent and severe extreme weather events, including storms, floods and heatwaves[2], that affect both human and ecological systems[3–7].

Temperature has a fundamental influence on biology, from cells to biomes[8]. Indeed, variations in temperature explain many of the spatial and temporal patterns observed in the performance, distribution, and abundance of species[9,10]. Temperature is highly dynamic and has changed throughout Earth's history, during which species have responded to ice ages and warm interglacial periods – generally over millennia-long timescales. However, species now face rapid warming and temperature variability that has occurred over the past ~50 years. Gradual increases in mean temperature can lead to slow behavioural and adaptive responses over generations, but acute thermal events often lead to rapid responses and potentially strong selection[11] because they push organisms beyond their thermal limits[12].

Marine heatwaves (MHWs; Box 1) have been increasing in intensity, duration and frequency as a direct consequence of anthropogenic climate change[13]. MHWs have affected species around the world, from microorganisms[14,15] to whales[16], and have caused mass die-offs of habitat-forming species such as kelp, seagrass and corals; widespread redistribution and mortality of fishes, birds and mammals; disruption to food webs; and shifts in ecosystem structure, all of which have imperilled the provision of ecosystem services such as fisheries and aquaculture, carbon storage and nutrient cycling, and recreation and tourism[5,7,17,18]. MHWs are now recognized by both national and international reporting and policy bodies as critical marine ecosystem stressors. As MHWs will continue to intensify at least until 2100 (refs. 19,20), improved understanding of their physical drivers and biological impacts to inform approaches to adaptation and management is urgently required. However, biological responses to extreme temperatures during MHWs are complex and often nonlinear[21], as these responses are mediated by both the ecological and geographic context of the affected species as well as the physical properties of the events themselves[22,23]. Capacity to predict MHWs is improving[24] and, although reliably predicting the impacts of these events remains challenging, an essential starting point is understanding their past effects.

Previous reviews on MHWs have predominantly focused on the physical science including MHW definitions, analytical methods, patterns in space and time, and their underlying drivers[25–28], and to a lesser extent on biological responses[5,17,21]. In this Review, we explore global ecological impacts, challenges and solutions to highlight how MHWs can provide insight into future warming scenarios, as well as future MHW events. We also consider how MHWs can drive selective pressure to increase future climate resilience. Specifically, we first briefly summarize the increasing physical manifestation of MHWs over the past 100 years, before discussing in detail how MHWs have affected populations and ecosystems. We separately assess 'direct' effects related to temperature stress, 'indirect' effects in which species interactions are modified by different temperature responses and compounding stressors, and impacts on ecosystem services and the benefits humans derive from the oceans. Finally, we consider challenges and future research directions to better understand and possibly mitigate impacts from MHWs.

MHWs on the rise

The frequency and intensity of MHWs have increased since the early twentieth century[13,20]. These changes are predominantly due to long-term ocean warming, which has shifted the temperature variability distribution upwards[29]. Background warming caused by anthropogenic climate change is projected to continue, and increasing MHW trends are therefore also expected to persist and possibly accelerate in the coming decades[19,20]. Indeed, the continued upwards trend in MHWs has characterized the past decade (Fig. 1a), with 2023 and 2024 breaking all records in terms of spatial extent and overall intensity[30].

Long, strong and everywhere

In 2016, the global annual MHW occurrence (that is, the number of MHW days) had increased by 54% since 1925 (ref. 13). The frequency and duration of MHWs had also increased by 34% and 17%, respectively[13], and between 1982 and 2016 every quarter-degree grid cell of the global ocean had experienced at least one strong, severe or extreme MHW relative to a 1983–2012 baseline. For most of the ocean, the maximum intensity and duration of these events ranged from ~2.5 to ~3.7 °C, and 40 to 160 days. However, for 4–5% of the global ocean, daily sea surface temperature anomalies exceeded 5 °C and events lasted >250 days (ref. 31). Extending this data into 2024, further increases are apparent. Particularly in the past 2 years, a considerable increase in MHWs has occurred – especially moderate and strong events (Fig. 1a). High-frequency satellite data have revealed that, on particular days, MHWs extended across 120 million km^2

Box 1 | MHW drivers and definitions

Drivers of MHWs

Marine heatwaves (MHWs) are discrete periods of unusually warm ocean temperatures, driven by many atmospheric and oceanic processes (figure part **a**). For example, high-pressure systems can locally reduce cloud cover and wind speeds, leading to increased solar heating and supressed evaporative cooling. Warm Ekman or boundary currents, and suppressed coastal upwelling or mixing of deep cool waters, are important drivers of MHWs. These local processes are modulated by climate oscillations including the El Niño–Southern Oscillations, Interdecadal Pacific Oscillations, North Atlantic Oscillation and Madden–Julian Oscillations.

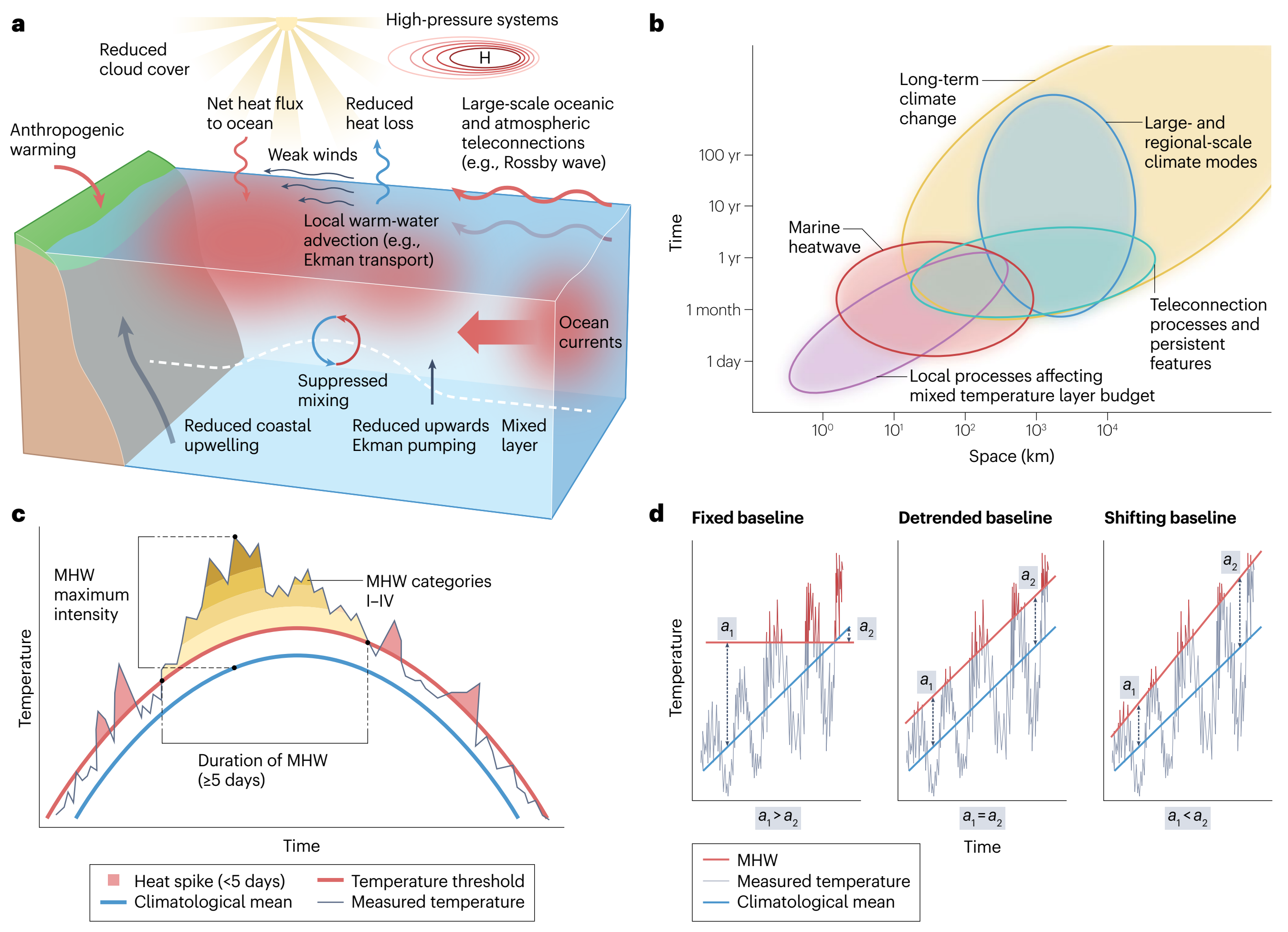
Scale of MHWs

The drivers of MHWs manifest across a broad range of spatiotemporal scales (figure part **b**). For example, weather systems or mesoscale ocean eddies that affect local heat fluxes typically operate on scales from tens to hundreds of kilometres and on timescales of days to months. By comparison, regional climate modes and associated teleconnections can affect these local phenomena across or between ocean basins on subseasonal to decadal timescales.

On multidecadal and longer timescales, anthropogenic climate change raises the background temperature increasing MHW frequency and temperatures against historical baselines but can also alter local processes, climate modes and teleconnections modifying temperature variability.

Defining MHWs

The most commonly used framework defines a MHW as a warm-water event at a location lasting five or more days, where observed ocean temperatures exceed the 90th percentile of observations in a fixed long-term (usually 30 years or more) climatological record for that time of year (figure part **c**). MHW categories can also be defined based on the relative exceedance of that baseline. This definition was motivated by a need to understand biological impacts and acknowledges that MHWs and their impacts can occur at different times of year. A clear definition for MHWs has been instrumental in identifying patterns and trends in MHWs historically and into the future as well as in comparing their various metrics, facilitating comparisons of ocean temperature anomalies and their biological and human impacts across the globe.



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Temperature baselines

MHWs are departures from normal ('baseline') temperature conditions and several contrasting approaches exist to identifying MHWs, depending on the type of baseline applied (figure part **d**). Most MHW studies use a fixed baseline, comparing contemporary temperatures with a historical climatological mean that does not change as time passes. As a consequence, MHWs become more frequent as the oceans warm. By contrast, detrended and shifting baselines account for (that is, remove) background warming. The detrended baseline adjusts MHW thresholds to account for slow changes in climatological temperatures and thereby isolates changes in MHW characteristics related to changes in temperature variability. The shifting baseline continuously updates the MHW threshold based on a recent climatological period and, therefore, ensures that MHW frequency remains stationary even if variability increases. Both approaches emphasize changes in temperature variability over total heat exposure and are less likely to report that MHWs have become stronger, longer and more frequent since the Industrial Revolution. Compared to a fixed baseline they are, perhaps, most relevant for understanding changes in the climate system and less relevant for understanding biological impacts.

Part **a** of figure adapted from ref. 26, Springer Nature Limited. Part **b** of figure adapted from ref. 25, CC BY 4.0. Part **c** of figure adapted from ref. 37, CC BY 4.0, and with permission from ref. 236, Elsevier. Part **d** of figure adapted from ref. 28, CC BY 4.0.

(33%) of the oceans, strong MHWs across 33 million km^2 (9%), and severe and extreme events combined across 400,000 km^2 (0.1%) (Fig. 1a). Nearly all global ocean locations have experienced a MHW (Fig. 1b). The main cause of these increases in MHW intensity, frequency and duration are increases in the average background temperature. For example, MHW duration and intensity in the East Asian seas are primarily related to background warming[32]. However, important changes in the characteristics of temperature variability have also occurred in some regions. For example, in the Mediterranean Sea, regional MHW trends have additionally been related to increases and decreases in sea surface temperature variability in western and eastern regions, respectively, driving regional differences in MHW occurrence. These changes are related to changes in atmospheric high pressure, the primary driver of MHWs in this region[33]. Another important driver of MHWs and their trends relates to preconditioning of the ocean. When winds are weak the upper layer of the ocean becomes thinner, and is therefore heated (or cooled) more easily. Long-term shallowing of mixed layers in the northeast Pacific, for example, probably had an important role in the development of the prominent MHW 'Blob 2.0'[34], and coastal regions exhibit stronger trends in summer MHW metrics, when mixed layers are shallower[35]. Additionally, in the Arctic, intense surface warming melts the sea ice, causing the mixed layer to shoal and intensify the MHW signal[36].

Into the future

Future projections indicate that MHW frequency, duration and intensity are expected to continue on an upwards trajectory, even under scenarios involving substantial mitigation of greenhouse gas emissions[13,20]. Specifically, under current national policies for the reduction of global carbon emissions, an estimated average warming of ~3.5 °C by 2100 would increase the probability of MHW occurrence by 41 times and their spatial extent by 21 times compared with pre-industrial times[20]. The high-emissions scenario (RCP8.5) is projected to result in >90% of the entire globe entering a permanent MHW state by the end of the twenty-first century, in which up to 70% of events are extreme. Under the RCP4.5 scenario, 50% of the ocean would be in a permanent MHW state, strong and severe events would increase dramatically[19,37].

Most of the projected changes (for example, ~90% of change in MHW intensity) are simply related to an increase in the mean ocean temperature, consistent with past studies[29,38]; however, in some regions, changes in variability are more important. Up to 80% of projected change in MHW intensity in high latitude regions, and 40% in the tropical Pacific, are related to changes in internal variability[38]. The dominant factor controlling these variability-induced changes relates to shifts in characteristics of the El Niño–Southern Oscillation (ENSO), highlighting the critical importance of improving ENSO projections to better understand future MHWs. Projected increases in stratification and long-term shoaling of the mixed layer[39] are likely to have important roles in controlling regional and seasonal trends in future MHW metrics.

Complex drivers

Drivers of MHWs in the upper ocean have been extensively studied[25]. An upper-ocean or mixed-layer heat budget is commonly used to analyse local processes that cause MHWs. The most important processes differ across MHW events but typically include reduced evaporative cooling resulting from anomalously weak winds, enhanced solar radiation, changes in ocean circulation – especially in strong boundary current regions – and changes in vertical ocean mixing that affects the mixed layer and the volume of water being heated. Large-scale modes of climate variability (such as ENSO) and their teleconnections often modulate these local processes[25,40].

Modelling and observational research suggests that regional and seasonal variations exist in the dominance of different drivers and potential MHW predictability[26]. For example, sensible air–sea heat fluxes become more important during winter in the extra-tropics, whereas in tropical regions vertical mixing in the ocean is particularly important year round[41] and, in high-energy regions, mesoscale eddies contribute substantially to the build-up and decay of smaller events[42].

Growing interest is being shown in subsurface MHWs, which often have higher intensities than their surface counterparts and can affect marine life in different parts of the water column[43,44]. Subsurface events can be related to multiple processes, which include shifts in deep frontal structures, eddies or strong currents, including the movement of boundary currents onto the shelf and the mixing of heat below the mixed layer. Often, subsurface MHWs result from the vertical displacement of the water column through coastal downwelling, wind-driven Ekman pumping in the open ocean, or the passage of downwelling planetary waves that act to depress warm water, particularly near the thermocline[43–46]. The depth structure of subsurface MHWs can evolve through time; for example, subduction from mixed-layer MHWs can give rise to MHWs below the mixed layer without a surface signature, and these subsurface MHWs will occasionally re-emerge later and facilitate the development of new surface-trapped MHWs[47,48]. So far, research on the biological impacts of subsurface MHWs is limited, but modelling suggests substantial overlap

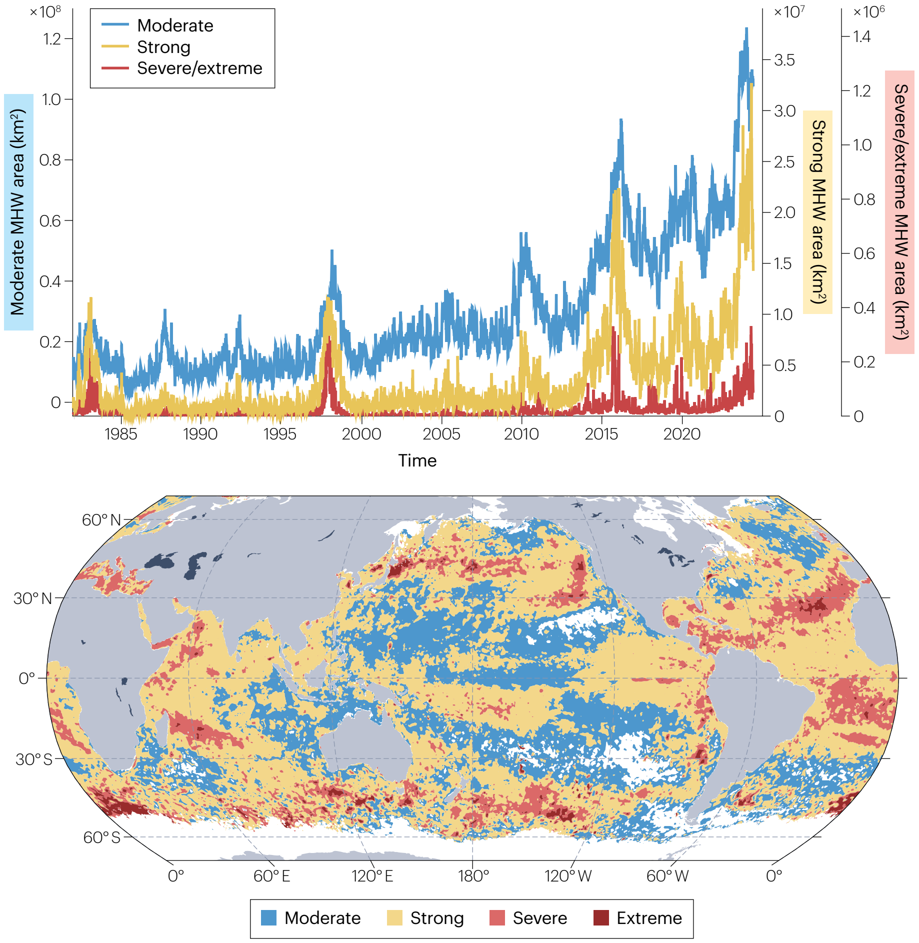

Fig. 1 | MHWs in time and space. a, A time series of the area of ocean covered by the different categories of marine heatwaves (MHWs) (moderate, strong, and severe and extreme combined) for each day during 1982–2023 (1-year running mean, updated from ref. 13). **b**, A map of the maximum category attained by a MHW at each location between 1 July 2023 and 30 June 2024. MHWs calculated from the National Oceanic and Atmospheric Administration Optimum Interpolation Sea Surface Temperature v1.1 (ref. 235) following MHW and category definition from refs. 37,236.

between high cumulative MHW intensity and range edges of deep water (>50 m) biota, putting species at risk across >20% of the ocean area[43]. Interestingly, many subsurface events, measured at a fixed points in space, are associated with the horizontal and vertical movements of temperature gradients, a process known as 'heave'. Heave might have little effect on freely moving pelagic marine species (such as phytoplankton and zooplankton) that shift with the prevailing circulation.

Direct effects from expansion to extinction

Increasingly frequent and intense MHWs introduce a new dimension of acute thermal stress that affects organisms directly, leading to decreased growth, reproduction and/or competitive ability[17,49,50], as well as increased vulnerability to other stressors[51,52]. If sufficiently prolonged or severe, acute thermal stress can lead to mortality, local extinction or shifts in species distributions[49,53–55]. Although MHWs occur in all seasons[35], most studies have focused on biological effects from summer MHWs because extreme absolute (high summer) temperatures generally affect physiology (for example, exceeding survival thresholds and causing dramatic changes) more than elevated temperature during colder winter months (increasing metabolic rates).

Typically, physiological performance improves as temperature increases until an optimum point is reached, beyond which performance declines rapidly, eventually surpassing the upper thermal threshold of an organism (Fig. 2a). Thermal optimum and performance breadth vary: some species are cold-adapted or warm-adapted thermal specialists that have narrow range distributions (known as stenotherms), whereas others are thermal generalists (eurytherms) that have wide range distributions (Fig. 2b). These traits can influence species' vulnerability to thermal stress and lead to disproportionate impacts on performance and survival for species living close to or above their optimum temperature[56].

At the cellular level, increased temperature can substantially alter metabolic processes, aerobic scope and oxygen demand[57,58]. Energy-intensive cellular stress responses work to protect and repair vital macromolecules such as DNA, RNA and proteins[59]; however, as thermal stress increases, the associated energy deficits negatively affect performance[60]. These small-scale processes are evident in broader biogeographic patterns of marine species[61], such that latitudinal ranges are primarily determined by species' thermal tolerances, whereas longitudinal ranges are influenced by a combination of factors including ocean currents, dispersal mechanisms and geological barriers[62,63]. Typically, organisms will perform best around the centre of their latitudinal range where temperatures are optimal, and show declining performance towards the range edges[64].

Species-specific impacts of MHWs

A range of responses to MHWs have been observed in a wide variety of species, as high temperatures affect different indicators of ecological

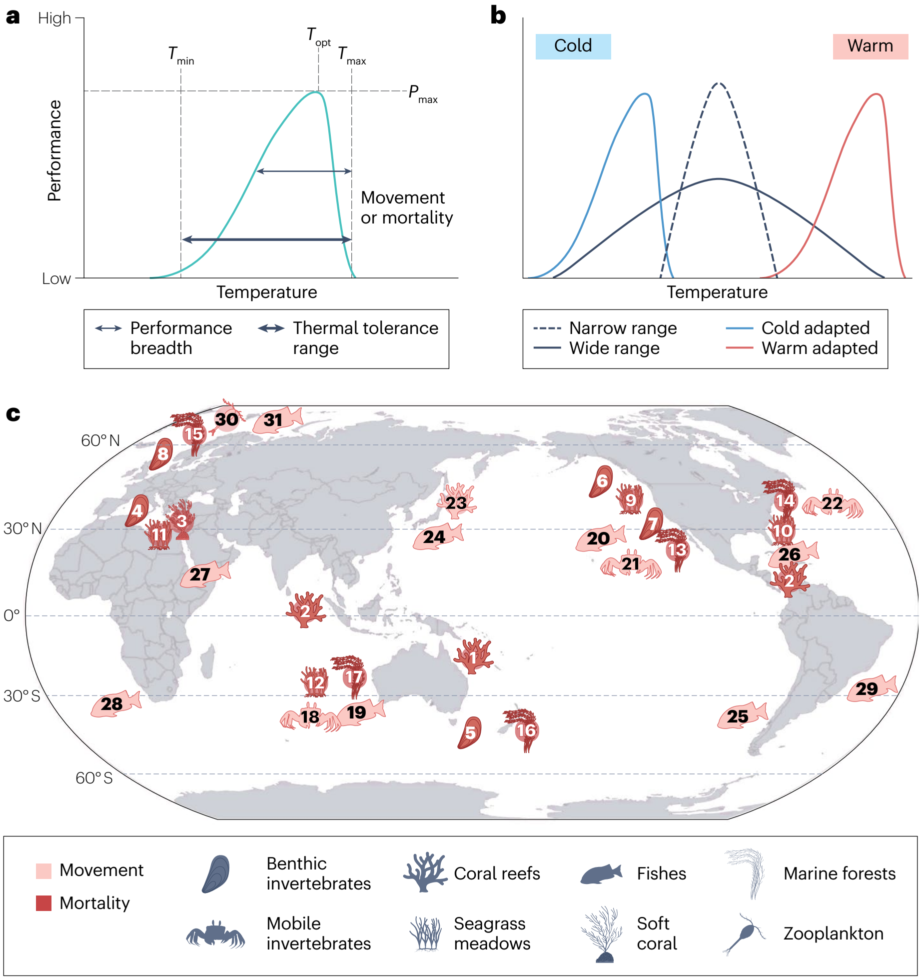

Fig. 2 | Exceeding acute temperature thresholds causes rapid mortality and distribution shifts. **a**, Species live within the lower (T_{min}) and upper (T_{max}) temperature limits of their thermal tolerance range. When temperature stress from a marine heatwave (MHW) exceed a species' acute limit and it cannot maintain homeostasis or adapt, it will either have to move or it will die. Note that the performance curve – the temperature (T_{max}) at which they perform best (P_{max}) – is rightly skewed, implying relative high sensitivity to MHWs upwards of the species' optimal temperature zone (T_{opt}). **b**, Species can have a wide or a narrow temperature tolerance, which can be optimized to cool or warm environments (here illustrated as narrow cool and narrow warm adapted, respectively). **c**, Many case studies have described rapid mortality events (dark red) and shifting distributions (light red) during or shortly after MHWs. When mortality has been observed for foundational and abundant perennial sessile species, such as corals, kelp, seagrass and reef-forming bivalves, rapid loss of ecosystem functions (for example, productivity, resilience and wave dampening) and loss of habitat-associated flora and fauna often follows. All case studies numbered on the map are discussed in the text (see also Fig. 4 for examples of MHW-driven alterations to specific species interactions).

performance – including birth and death rates, resource acquisition, movements and behaviour[5,17,65]. At the individual level within a species, responses to MHWs can differ owing to genotypic and phenotypic plasticity, which can increase thermal tolerance and reduce impacts during an event. Plasticity in thermal tolerance can be transferred across events and generations via epigenetic processes, 'priming' future generations to better withstand thermal stress, as reported for individuals and populations of many taxa including corals[66], seagrasses and macroalgae[67–70]. MHWs can also drive selection for thermally tolerant genotypes[71], as these events filter out cold-adapted individuals and shift the genetic composition of populations[71], thereby increasing the chance of survival during future MHWs[22]. For example, in Western Australia, an extreme MHW decreased genetic diversity of seaweed populations, even though no conspicuous changes to abundances or phenotypic appearance occurred[72,73]. The ability to adapt genetically can also affect recovery following MHWs; for example, populations that have higher genetic diversity might have a higher probability of developing thermal tolerance over generations[11,74–76].

Net negative effects of MHWs are consistently observed, and by far dominate species responses[23]. However, the severity and direction of impact (that is, positive or negative) can depend on whether the species are thermal specialists or generalists, cold adapted or warm adapted, where in their range the MHW occurs, and whether the species are sessile or mobile[21,23]. Acute thermal anomalies typically have severe negative effects on cold-adapted species that have narrow temperature tolerances, especially when these events occur near their warm-range edges. Populations at these boundaries often have smaller thermal safety margins than elsewhere in their range, making them vulnerable even to moderate temperature increases that can push them beyond their physiological limits[77]. Although warm-adapted species and species with broad temperature ranges can also suffer from acute thermal anomalies, the effects are often distributed more broadly across their range. For example, pup mortality of the cold-adapted narrow-range southern elephant seal (*Mirounga leonina*) increased during El Niño years in the Bellingshausen Sea, and high temperature combined with sea ice retreat compromised foraging and reduced breeding success of elephant seals at King George Island – a population located near the species' warm-range edge[78]. The cold-adapted narrow-range snow crab (*Chionoecetes opilio*) also experienced substantial population declines after MHWs in the Bering Sea[79]. The warm-adapted narrow-range surgeonfish achilles' tang (*Acanthurus achilles*) declined in abundance after MHWs[80], and elkhorn coral (*Acropora palmata*) and head coral (*Favia favus*) experienced reduced survival after El Niño MHW events[81,82]. The thermal generalist golden kelp (*Ecklonia radiata*) experienced reduced abundance across much of its distribution ranges following an extreme MHW in Western Australia[83,84]. Similarly, another thermal generalist giant kelp (*Macrocystis pyrifera*) showed declines in both abundance and biomass along much of the northeast Pacific in response to MHWs[85–87]. Finally, eelgrass (*Zostera marina*) suffered reduced density broadly across its range after MHWs[88].

Mortality events

If temperature stress from a MHW exceeds a species' thermal limit and it cannot maintain homeostasis or adapt, the species will have to either move or die (Fig. 2a,b). This has led to major mortality events throughout the world (Fig. 2c). Importantly, thermal performance curves of species are typically right skewed, implying relatively high sensitivity to temperature increases from the species' optimal to acute temperature zone (Fig. 2a,b). Rapid mortality events and distribution shifts during or immediately after MHWs are increasingly observed[17,89]. More specifically, MHWs can cause rapid shifts in the distribution of species by facilitating or inhibiting populations near their cold or warm distribution edges, respectively. In some cases, these rapid shifts in distribution can lead to persistent range shifts (Fig. 2c), for example, where recolonization is limited to new arrivals from poleward sites. However, MHWs can also cause localized mortality and even localized extinctions within a species range[55,84].

Mortality events are particularly conspicuous for dominant sessile species, such as corals[90,91], seagrasses[92,93] and kelps[55,84,94,95], but have also been reported for mobile species unable to move, such as fish in aquaculture pens[96,97]. The mortality of dominant large and long-lived sessile species is especially problematic because these organisms form the essential three-dimensional structure that shapes ecosystem function and supports productivity, resilience and biodiversity, while offering food and shelter for numerous habitat-dependent species[98].

Reef-building hard corals (Scleractinia) have been severely affected by MHWs, leading to the loss of their endosymbiotic dinoflagellates (that is, bleaching). Prolonged warming results in heat-induced mortality, followed by gradual skeleton dissolution, increased susceptibility to breakage, and loss of three-dimensional reef structure with cascading adverse impacts on myriads of reef-associated species[99]. On the Great Barrier Reef, Australia, large-scale coral bleaching has been observed with increasing frequency[100]. This bleaching has caused major die-off of staghorn and tabular corals, resulting in a shift in ecological function and reduction in three-dimensionality[101] (Fig. 2c, case study 1). Global mass bleaching has become increasingly common since the late 1990s, and the most destructive event affected >50% of the world's coral reefs between 2014 and 2017 (refs. 102,103) (Fig. 2c, case study 2).

Other habitat-forming sessile invertebrates have also suffered from MHWs. For example, gorgonian soft corals (*Paramuricia clavata*) and other calcareous species have suffered mass mortalities from repeated MHWs in the Mediterranean Sea (Fig. 2c, case study 3), for example, in 1999, 2003 and 2006 (refs. 5,104), resulting in reduced biodiversity and shifts in the structure and function of communities to simpler and smaller ephemeral algal turfs[105–107]. Indeed, more than 2,300 mass mortality events relating to more than 90 benthic invertebrate species have been recorded in the Mediterranean Sea since 1979, many linked to MHWs[89] (Fig. 2c, case study 4). In New Zealand, subtidal sponge gardens have been decimated following years of repeated MHWs, which have particularly impacted the Fjordland region, a World Heritage Site[108,109] (Fig. 2c, case study 5).

In British Columbia, northeast Pacific, intertidal barnacles experienced large-scale die-off in 2021 after exposure to both extreme air and high-water temperatures, leading to wide-ranging impacts on a diverse associated intertidal community[110] (Fig. 2c, case study 6). Similarly, in California, extreme oceanic and atmospheric temperatures caused mass mortality of intertidal mussels (*Mytilus californianus*) in 2004 (ref. 111) (Fig. 2c, case study 7). Still, MHW-induced mortality of intertidal species can be highly variable on small scales, typically being highest for sessile organisms exposed to equatorwards-facing dark rocks and on the top layers of aggregated colonies[111]. However, MHWs can also promote the establishment of warm-adapted species, such as non-native Pacific oysters (*Crassostrea gigas*) around Europe. In the German and Danish Wadden Sea, this warm-tolerant species has displaced cool-tolerant native reef-forming mussels and polychaete worms[112] (Fig. 2c, case study 8).

MHWs have affected habitat-forming plants dramatically. For example, the 1997–1998 El Niño, caused high mortality of eelgrass (*Zostera marina*) in California (Fig. 2c, case study 9) leading to its replacement by opportunistic widgeon grass (*Ruppia maritima*)[113]. On the east coast of North America, in Chesapeake Bay, the same seagrass species suffered >50% loss after a MHW in 2005 (refs. 114,115) (Fig. 2c, case study 10). High mortality of Neptune grass (*Posidonia oceanica*) was also observed in the Mediterranean Sea after extreme thermal stress from MHWs in 2003 and 2006 (refs. 93,116). In this region, intensified MHWs caused by ocean warming have led to large-scale declines in seagrass meadows and expansion of invasive species, ultimately resulting in a net loss of biodiversity[117,118] (Fig. 2c, case study 11). Finally, in Western Australia, >1,000 km^2 of temperate seagrass meadows (*Amphibolis antarctica* and *Posidonia australis*) were lost from Shark Bay, another World Heritage Site, after the Ningaloo Niño MHW in 2010–2011 (refs. 92,115,119) (Fig. 2c, case study 12). Here, this loss was followed by rapid expansion of the much smaller warm-water narrow-leaf seagrass (*Halodule uninervis*)[115]. This dramatic habitat transition resulted in loss of sediment-stored carbon and declines in charismatic megafauna such as sea snakes (Elapidae), dugongs (*Dugong dugon*), bottlenose dolphins (*Tursiops aduncus*), green turtles (*Chelonia mydas*) and pied cormorants (*Phalacrocoraz varius*)[120].

Many kelp forests have also been decimated by MHWs. For example, in the warm waters of Baja California, Mexico, loss of giant kelp (*M. pyrifera*) was pronounced and northern bull kelp (*Nereocystis luetkeana*) collapsed entirely along large stretches of coastlines from California to Washington after the 2014–2016 'Blob' MHW[95]. These losses resulted in dramatic changes to diverse kelp-associated communities[85,121,122] (Fig. 2c, case study 13). Similarly, sugar kelp forests (*Saccharina latissima*) have been decimated in both the northeastern USA and southern Norway after repeated MHWs around the early 2000s[94] (Fig. 2c, case studies 14 and15). Around Christchurch, New Zealand, the intertidal southern bull kelp (*Durvillaea* spp.) went regionally extinct following the extreme 2017–2018 Tasman Sea MHW, which co-occurred with midday low spring tides, calm days, clear skies and high atmospheric temperatures[55,123] (Fig. 2c, case study 16). Even more dramatic cases have been documented for golden kelp (*Ecklonia radiata*) and strapweed (*Scytothalia dorycarpa*), which experienced severe physiological stress, leading to regional extinction near their warm range limits following the extreme Ningaloo Niño in Western Australia in 2010–2011. This event caused a rapid 100 km range contraction of kelp forests[84,124] (Fig. 2c, case study 17) and a concurrent community-wide tropicalization with a shift in seaweed, invertebrate and fish assemblages towards warm-water species[84,124] (Fig. 2c, case studies 18 and 19). Almost 15 years later, these kelp forests have not recovered, as limited propagule availability and the dominance of turf-forming species and herbivores inhibit recolonization[125].

Shifts towards the poles and into deeper water

Numerous temperature-driven poleward distribution shifts have been reported for all forms of marine species around the world[126–129]. Most of these shifts have been reported in the context of gradual ocean warming, although it is likely that many, if not most, of these would have been instigated or accelerated by MHWs. However, owing to a lack of high-resolution temporal sampling, linking changes observed over decades to specific short-term temperature events is difficult. MHWs facilitate fast episodic arrivals of warm-adapted species into cooler regions and reduce performance, or even decimate, existing cool-adapted species to create novel communities comprising an increased mix of warm-water species relative to the original community. This process is known as 'tropicalization' (or 'borealization' where temperate species increase at arctic latitudes). So far, hundreds of examples of tropicalization, representing almost all phyla from microorganisms to megafauna, have been documented from marine ecosystems[130], highlighting that oceans have fewer barriers to dispersal than terrestrial systems[131]. Similarly, many introduced non-native warm-adapted species can establish themselves and spread faster and further because of warming and stronger MHWs[132]. However, not all species in a community can move polewards as expected. For example, although 87% of coastal species in Australia have been found to have shifted polewards, 13% did not[133]. This example illustrates how processes other than temperature responses affect distributions, including complex indirect effects such as competitive release, in which competitively inferior (but temperature-tolerant) species can expand their ranges if competitively superior species are more sensitive to MHWs.

Regions with continuous tropical–temperate coastlines are hot spots for these changes, as mobile organisms such as fish and some invertebrates can respond rapidly to warm temperatures. For instance, in the northeastern Pacific, the 1997–1998 El Niño resulted in a northwards shift across 29 families of tropical fishes[134] (Fig. 2c, case study 20). In the same region, the 2014–2016 MHWs caused polewards shifts of fishes from Mexico into southern California[135] and shifts of at least 37 species from Oregon into northern California[136], including nine species of pelagic mobile invertebrates (Fig. 2c, case study 21). In the northwest Atlantic, longfin squid (*Doryteuthis pealeii*) shifted polewards to Maine as a result of the 2012 North Atlantic MHW, resulting in a new local fishery and market opportunity during the summer season[137] (Fig. 2c, case study 22). Other examples of range shifts by fishes have been attributed to underlying temperature increases and the intensification of polewards boundary currents that transport warm tropical water into temperate regions. For example, in Japan, warming driven by the dominant polewards-flowing Kuroshio Current is facilitating the expansion of corals and herbivorous fishes into temperate macroalgal communities[138] (Fig. 2c, case studies 23 and 24). This warming has led to the intrusion of tropical species such as rabbitfish (*Siganus fuscescens*) and parrotfish (*Calotomus japonicus*), resulting in severe overgrazing of kelp[139]. A similar influx of warm-water fishes from lower latitudes was reported in central and southern Patagonia[140] (Fig. 2c, case study 25). In southeastern USA, range-shifting parrotfish (*Nicholsina usta*) considerably increased seagrass herbivory compared with native grazers[139] (Fig. 2c, case study 26) and, in the Mediterranean Sea, the opening of the Suez Canal allowed the northwards movement of two herbivorous rabbitfishes (*Siganus rivulatus* and *Siganus luridus*) from the Red Sea in response to warming[139] (Fig. 2c, case study 27). Finally, shifts in surgeonfish (*Acanthurus* spp.) and parrotfish (*Scarus* spp. and *Sparisoma amplum*) have also been observed in southeastern Africa (surgeonfish only) and eastern South America[139] (Fig. 2c, case studies 28 and 29). By comparison, far fewer examples of borealization have been documented, although rapid movement of temperate zooplankton and fish into the Arctic has been observed[141,142] (Fig. 2c, case studies 30 and 31).

Deeper and cooler vertical layers could theoretically provide thermal refugia from MHWs in stratified waters (a 'deepening' process). Vertical shifts in species distributions to follow the deepening of isoclines[143] is analogous to altitudinal shifts up mountain sides in terrestrial systems. Deepening is possible for most marine animals where substrate conditions, food and sediment loads are suitable; however, very clear waters are required for primary producers – including corals – to maintain photosynthesis while shifting to depths with lower light levels. Deepening is, therefore, much more restricted for primary producers than for marine animals[144,145]. Model predictions and preliminary observations suggest deepening distribution shifts are occurring and will continue for mobile species, particularly fishes[127,146], whereas virtually nothing is known about vertical temperature refugia for sessile species.

Tropicalization increase the community temperature index

Individual species can be facilitated or inhibited by MHWs, depending on their thermal niche (often approximated by their thermal range), the ambient temperature and the elevated temperature stress from MHWs. Assuming temperature is the main variable affecting co-occurring species, the community-wide impacts from MHWs can be quantified and simplified into a single metric, the community temperature index (CTI), by averaging individual responses across the species pool[147] – although species variability to temperature and uncertainties in distribution data can complicate analyses[148,149]. Increases in CTI have been widely documented (Fig. 2c), in particular for fish and rocky reef organisms, as communities slowly shift from being dominated by cool-adapted species to warm-adapted species in response to background warming[150–156]. However, CTI has also been shown to increase on short timescales during or shortly after MHWs, such as for microbial communities after the Tasman Sea MHW[14] and for phytoplankton and zooplankton communities during the 'Blob'[157]. By contrast, MHWs might not affect demersal (benthic) fish communities or their CTI[158].

Vulnerability to MHWs

The impacts of MHWs can differ among species owing to diverging evolutionary pathways and life histories that result in different physiological adjustments or thermoregulatory behaviours underpinning widely different temperature tolerances. For example, behavioural responses such as temporarily relocating to areas with more suitable temperatures[159] or increasing foraging time to offset higher energy deficits[160] are limited to mobile species that might be able to track favourable isotherms[161]. During El Niño years, when MHWs are prevalent off the west coast of South America, Peruvian anchovies (*Engraulis ringens*) track temperature gradients, temporarily shifting their ranges[162]. Increased foraging efforts have been reported for coral trout on the Great Barrier Reef and for seabirds in the North Pacific during MHWs to offset increased energy demands[160,163]. By contrast, physiological adjustments are more likely to occur in sessile or sedentary species than in highly mobile species, or as a secondary response in mobile species if behavioural modifications are ineffective or not possible (for example, within enclosed seas where relocation is not possible). For these species, the observed impacts vary from sublethal changes in physiological or reproductive performance to mortality[17]. Further, although considerable plasticity has been observed in some species of fish[164], others have demonstrated only limited phenotypic plasticity in response to warming[165].

Meta-analyses have revealed that species living closer to their warm-range edge overall are more negatively affected by MHWs than those living towards their cooler-range edge[21,23] (Fig. 3a). Sessile species have also been shown to be more negatively affected by MHWs than mobile species[21] (Fig. 3a). Interestingly, in contrast to widespread reports of changes in fish distribution (Fig. 2c) and fish mortality in aquacultural pens[96,166], limited impacts have been documented for demersal fishes from bottom water MHWs on continental shelves in North America and Europe[158]. This could reflect that the distribution of demersal fishes might be less affected by temperature than many other species or that MHWs are difficult to measure in deeper waters. However, although community-wide time-series analyses do not explicitly focus on the negative effects of MHWs on individual, high-profile species (thereby reducing the risk of publication bias), averaging positive and negative net effects across many species can cancel out impacts, and weaken apparent responses to MHWs[167]. Using annual time-series data to detect shifts in fish abundance caused by MHWs is also challenging, owing to difficulties in isolating MHW effects from those of changing average temperatures and other events. Furthermore, many fish species are not represented in data until they reach a sufficient size to be caught in survey trawls, introducing a delay in understanding the influence of past MHWs on year-class strength. Understanding the responses of fish assemblages to temperature changes might be improved by examining how individual species relate to thermal limits rather than simply considering temperature differences from a presumed optimal mid-range temperature[158]. Finally, species with slow reproductive rates (for example, large predatory fish and marine mammals) face greater difficulty in recovering from population losses due to MHW events than species that reproduce quickly.

MHW characteristics (such as intensity or duration) can result in different impacts to marine organisms across biological scales. For example, intense, short-duration MHWs can cause acute stress and mortality in sensitive or vulnerable species, whereas longer, less-intense MHWs can lead to sublethal stress responses such as reduced growth or reproduction[49]. Highly mobile species might be more vulnerable to large and long-lasting MHWs than to short and small events because they cannot reach refugia. By contrast, sessile species must cope with the conditions in their immediate vicinity and are equally vulnerable to small and large MHWs, meaning the severity of a species response is determined by both the MHW characteristics and the biological risk factors described (such as thermal history and specific geographical location)[17]. Indeed, regions that support a high proportion of species found near their warm-range edge will be most vulnerable to future MHWs and can therefore be identified as 'key risk areas'. Community-wide MHW risk areas (that is, where >10% of species in the region are near their warm edge) include the eastern Mediterranean, the southern Red Sea, the Caribbean Sea, the Mexican region of the North Pacific and much of the tropical west Pacific[21] (Fig. 3b). Furthermore, locally, higher proportions of warm-edge species are also seen along the coastlines of Europe, western USA and Canada, northern Africa and in the Yellow Sea (Fig. 3b). Future MHWs in these regions can

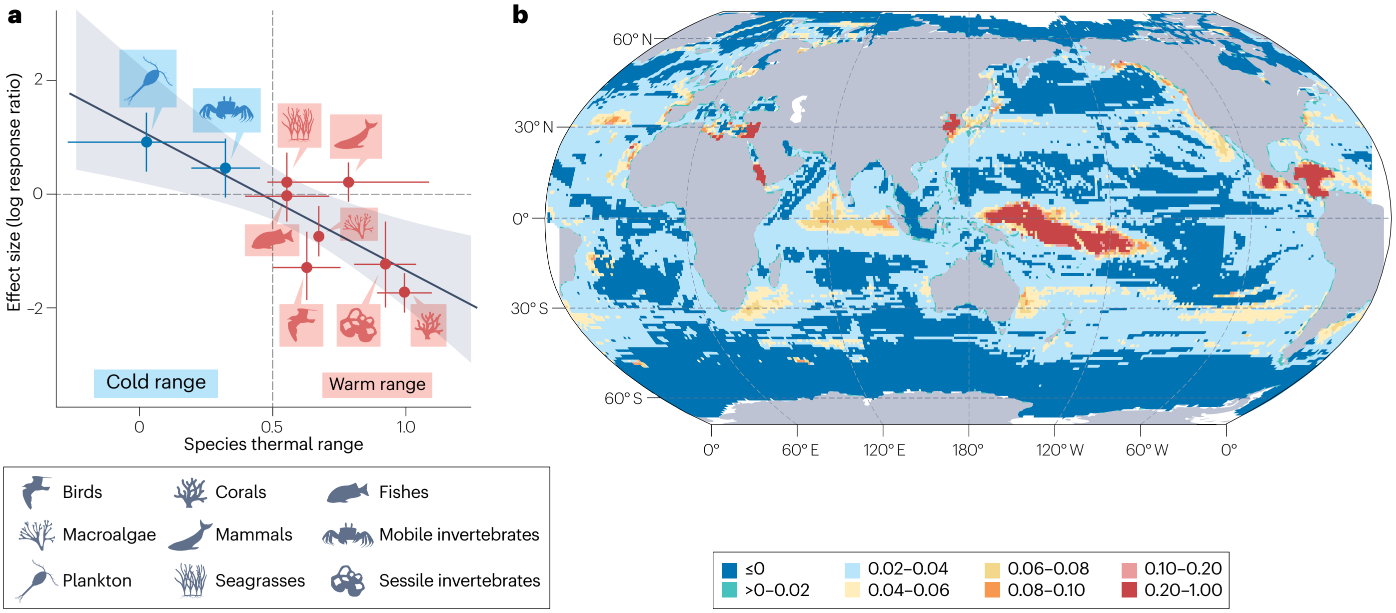

Fig. 3 | Range position and vulnerability to MHWs. a, Previous meta-analysis[17] has shown that species-specific impacts from marine heatwaves (MHWs) are often negative (negative log-response ratio) near the species' warm range (red icons) and positive near its cold range (blue icons). These effects vary between taxonomic groups (mean effect size per taxa group shown with standard errors). In some cases, positive impacts on taxa have been observed near their warm range edges (red icons). **b**, A global map showing regions with higher proportions of species at their warm-range edge (blue, low proportion; pink, high proportion); that is, regions that have particularly high vulnerability to future MHWs. Specifically, the proportion of species in the local species pool that were near their warm range edge (PGT90) were calculated to determine locations where MHWs might be more likely to have a strong negative effect. The map is based on 16,582 species global distribution maps from the Aquamaps project. For each 1° latitude/longitude grid cell, the proportion of species present was calculated where the sea surface temperature, defined as the average annual temperature from 1960 to 2009 using the Hadley Centre HadISST v.1.1 dataset[237], exceeded the 90th percentile of each species' temperature range. This value was then divided by the total number of species present in the grid cell. Part **a** adapted from ref. 17, CC BY 4.0. Part **b** adapted from ref. 21, Springer Nature Limited.

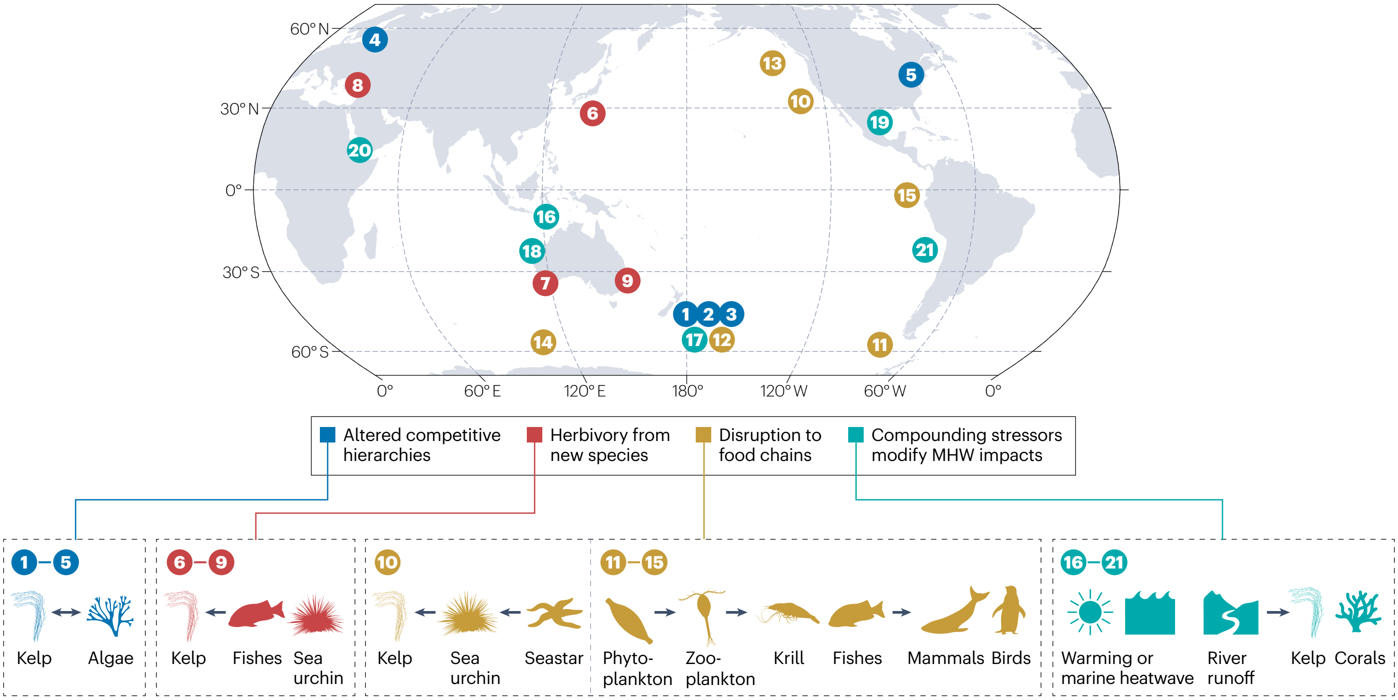

Fig. 4 | Compounding stressors and species interactions modify MHW impacts. In addition to affecting species' thermal performance (Figs. 2 and 3) marine heatwaves (MHWs) also modify direct species interactions such as competition, indirect interactions such as facilitation cascades, and entire communities. Case studies from around the world (1–21) have documented altered species interactions that have been modified by MHWs, including two-species interactions such as competition (blue, numbers 1–5) and herbivory (red, numbers 6–9), three-to-four species food chains (yellow, numbers 11–15) and those involving compounding stressors (teal, numbers 16–21). The arrows indicate the direction of impact cascades resulting from MHWs. All case studies numbered on the map are discussed in the text.

therefore be expected to have particularly strong community-wide effects, and to cause localized extinctions and range contractions.

Indirect effects from species interactions and compounding stressors

Biological impacts of MHWs caused by direct species responses to acute temperature stress are relatively easy to observe and interpret. However, as species compete with, disturb, facilitate and predate on one another, impacts on one species can lead to complex indirect knock-on effects on other species and the communities they exist in. Moreover, impacts can differ along environmental stress gradients and depending on compound (co-occurring) anthropogenic stressors such as biological invasions, coastal turbidity, and pollution or storminess. Although temperature-driven impacts on communities can be anticipated from individual species' temperature tolerances, altered species interactions and compounding stressor complicate such predictions.

Altered species interactions lead to complex community impacts

Biological communities are complex aggregates of many species that are structured by local abiotic conditions (such as temperature), resource levels (such as nutrients), simple two-species interactions (competition and predation), and more complex indirect ≥3-species interactions (trophic cascades)[168,169]. As temperature affects the fitness of individual species in a community differently, MHWs alter species interactions and can cause unexpected impacts on communities. Such community impacts are prominent when MHWs cause abrupt loss of habitat-forming foundation species such as corals, kelp and seagrasses, and particularly so if they are replaced by rocky 'barrens' or smaller turf (ephemeral opportunistic) species[18,54,92,95,170–173]. These new smaller species can sometimes initiate feedback loops that prevent re-establishment of the original foundation species and cause persistent ecosystem-wide regime shifts[84,174]. For example, a MHW off New Zealand led to decreased fitness of a dominant foundation species, southern bull kelp (*Durvillaea antarctica/poha*), and increased fitness of warmer-adapted brown algae, including the invasive Japanese kelp (*Undaria pinnatifida*), and red algae competitors[123,172,175]. The resulting shift in competitive hierarchies had knock-on effects for more complex three-species competition cascades, as encrusting, foliose and epiphytic algae that normally live beneath healthy bull kelp canopies were outcompeted by the new dominant species[175]. The combined effects of the altered competitive hierarchies, loss of bull kelp propagules and altered substrate conditions resulted in a persistent regime shift and little chance of future recovery for the original bull kelp habitat[172,175].

Similarly complex community-wide impacts of MHWs have been observed in many places around the world (Fig. 4). In addition to New Zealand (Fig. 4, case studies 1–3), altered competitive hierarchies after MHWs have been documented in the northeast Atlantic, where kelps were outcompeted by turfs of small fast-growing heat-tolerant algae[94,176] (Fig. 4, case study 4). Similarly, in the northwest Atlantic, kelp have been affected simultaneously by MHWs and competition from more heat-tolerant invasive epibiotic bryozoans that obstruct kelp photosynthesis and nutrient uptake, resulting in increased blade rigidity and susceptibility to wave breakage[177,178] (Fig. 4, case study 5). In some places, MHWs have also resulted in stronger trophic top-down control on primary producers, following mass immigration of warm-adapted herbivores. For example, off Japan and Western Australia, and in the Mediterranean Sea, MHWs reduced canopies of kelp and seagrass, a loss that was markedly accelerated by elevated grazing pressure following rapid influxes of warm-water herbivorous fish from lower latitudes[54,83,139,179] (Fig. 4, case studies 6–8, see also Fig. 2c). Similarly, the warm-tolerant invasive long-spined urchin (*Centrostephanus rodgersii*) has accelerated MHW-associated loss of the giant kelp (*M. pyrifera*) off southeastern Australia and Tasmania, to the point where giant kelp now is rare in many places[180,181] (Fig. 4, case study 9).

Effects of MHWs on two-species interactions such as competition and herbivory can cause complex indirect knock-on effects by, for example, altering competition cascades, keystone predation and tropic cascades (Fig. 4, case studies 10–13), ultimately modifying interaction webs[175,182–184]. For example, in the northeast Pacific, seastar mortality from wasting disease has been linked to extreme MHWs and caused population explosions of their sea urchin prey (*Strongylocentrotus purpuratus*), resulting in increased grazing pressure on temperature-stressed northern bull kelp (*Nereocystis luetkaena*)[95,185,186] (Fig. 4, case study 10). MHWs, El Niño events, and altered upwelling and associated nutrient supply have also been linked to reduced phytoplankton primary production, altered plankton blooms, range shifts in zooplankton and, ultimately, cascading impacts on food chains. For example, changes to phytoplankton have been linked to fewer krill and reduced survival of Adélie penguins (*Pygoscelis adeliae*) in Antarctica[187] (Fig. 4, case study 11) as well as to altered foraging by whales after ‘the Blob’ along the US west coast[121,188] and around New Zealand[16] (Fig. 4, case study 12). Furthermore, a combination of changes to phytoplankton and zooplankton communities and their productivity in the northeast Pacific might have contributed to collapse of the Pacific cod (*Gadus macrocephalus*) population[189] and mass mortality of seabirds[190,191] (Fig. 4, case study 13), and to declines in reproductive success in king penguins (*Aptenodytes patagonicus*) in Antarctica (Fig. 4, case study 14) and Galapagos sea lions (*Zalophus wollebaeki*) (Fig. 4, case study 15) in the eastern Pacific[192,193]. However, in other cases, MHWs have increased phytoplankton[194] and might thereby have facilitated higher levels in the food web; in the Arctic in 2009, MHWs and ice melting resulted in increased cod feeding and reproduction[195,196]. These examples highlight that seemingly innocuous effects of MHWs on microscopic pelagic plankton can cause complex indirect impacts across communities and up the food web to iconic megafauna such as birds, seals and whales.

Compounding stressors modify impacts from MHWs

In addition to direct temperature effects and complex community effects from altered species interactions, impacts from MHWs are also complicated by variation in species tolerances and interactions along environmental gradients and with compounding stressors[22,197]. That is, MHWs rarely occur in isolation and can instead be accompanied by compounding stressors and perturbations, potentially causing antagonistic or synergistic effects.

Altered catchment usage and elevated river runoff increases coastal turbidity and sediment loads to coral reefs, reducing photosynthesis by zooxanthella and clogging coral polyps, thereby increasing susceptibility to MHWs and bleaching[198,199] (Fig. 4, case study 16). Similarly, in New Zealand, poor water quality increased the susceptibility of giant kelp (*M. pyrifera*) to MHW stress, particularly towards the species' warm-range edge[200] (Fig. 4, case study 17). Extreme freshwater inflow after stronger storms in tropical and temperate regions, or from accelerated melting of glaciers and icesheets in polar regions, can also exacerbate MHW impacts. Such elevated freshwater flow increases turbidity and sediment smothering of reefs and lowers nearshore salinity, increasing osmotic stress on marine species. For example, increased riverine flow might have exaggerated die-off of seagrasses (*Posidonia* and *Amphibolis*) in Shark Bay (Western Australia)[92] that had cascading negative impacts on herbivorous megafauna such as turtles and dugongs[120,201] (Fig. 4, case study 18). Global warming and stronger MHWs can also fuel stronger storms and hurricanes that increase biomechanical stress and damage to nearshore sessile species such as mangroves and corals, the latter of which are also severely stressed by the elevated MHW temperatures[7,18,202] (Fig. 4, case study 19). Sea level rise can also modify impacts from MHWs, particularly for mangroves and salt marshes that are susceptible to drowning, although these intertidal habitats are more stressed by stronger storms and extreme air temperature than extreme water temperature[18].

Several instances have been documented in which impacts of MHWs have been exacerbated by invasive species (Fig. 4, case study 5), harmful algal blooms and pathogens[203,204]. For example, numerous coral reef fishes were killed in the Red Sea in 2017 from a combination of bacterial diseases and a MHW[205] (Fig. 4, case study 20), and in the southeast Pacific Ocean a combination of harmful algal blooms and MHWs in 2016 caused mass mortalities of farmed salmon and trout[203,204] (Fig. 4, case study 21). Furthermore, altered currents can break down barriers to dispersal and, in concert with range-shifting herbivores, modify impacts from MHWs. Finally, MHWs can increase vertical stratification by warming surface waters, thereby affecting subsurface currents and altering food supplies for deeper suspension-feeders such as gorgonians, bryozoans, and hydroids[206,207].

Overall, global changes to oceanographic systems, non-native species introductions, altered species interactions, localized extinctions, polewards range extensions, and compounding stressors create novel interactions and communities, affecting ecosystem in unprecedented ways and increasing the challenges of predicting MHW impacts.

Impacts from MHWs on ecosystem services

The global oceans provide a wealth of benefits to humans, supporting industries including fisheries, aquaculture and tourism, and offering a variety of natural contributions through provisioning, regulating, supporting and cultural services[208] (Fig. 5). Over the past three decades, impacts on ecosystem services from MHWs have included loss of fisheries, impacts to nutrient cycling and carbon storage, and mass mortalities of charismatic megafauna[5]. Although impacts are predominantly negative for humans, a few positive responses have also been recorded, for example, through new tourism opportunities or successful management interventions[65,209].

Food security, fisheries and aquaculture industries

Some of the most visible impacts of MHWs are those affecting fisheries and aquaculture, which sustain more than 3 billion people globally[210]. In the northeast Pacific Ocean, MHWs in 2013–2016 and 2019–2020 collectively led to single or multiyear closures of at least five commercial fisheries along the west coast of the USA (Fig. 5, case study 1), amounting to losses in excess of hundreds of millions of US $ (ref. 211). Similarly, following a MHW in the southeast Indian Ocean in 2011, some shellfish fisheries were closed for 1.5–5 years to allow stock recovery,

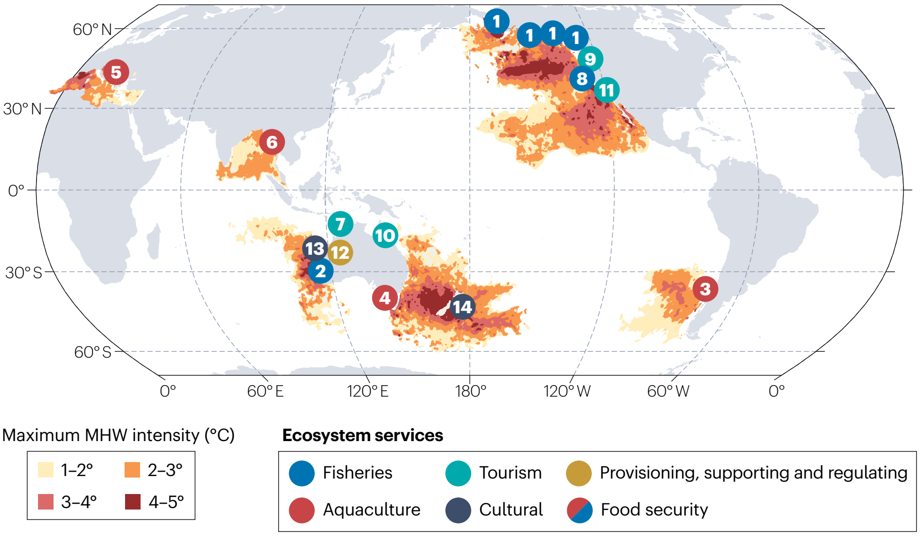

Fig. 5 | Impacts of MHWs on ecosystem services. Marine heatwaves (MHWs) affect a range of ecosystem services that provide a wealth of benefits to humans, including commercial and recreational fisheries (blue) and aquaculture (red) that ensure food security; tourism opportunities (green), and a variety of natural contributions including cultural (black), provisioning, supporting and regulating services (yellow). Locations of ecosystem services affected by MHWs are overlain on the maximum temperature of the event. All case studies numbered on the map are discussed in the text.

resulting in industry losses valued at ~US $43 million (refs. 212,213) (Fig. 5, case study 2). The aquaculture industry has also been affected by MHWs. Mass mortality of farmed salmon and trout following a MHW in the southeast Pacific Ocean in 2016–2017 led to Chilean export losses of ~US $800 million (ref. 204) (Fig. 5, case study 3). Loss of farmed shellfish due to MHWs has been reported in a variety of areas, including the Tasman Sea in 2016 (ref. 214) (Fig. 5, case study 4) and the Mediterranean Sea in 2022 (ref. 215) (Fig. 5, case study 5). MHWs have also been observed to cause harmful algal blooms that subsequently have killed fish in enclosed pens[166,216].

Mitigation strategies to reduce impacts of MHWs on fisheries and aquaculture include delayed seeding, early harvest, relocating pens or preparation for disease outbreaks in aquaculture, as well as applying quotas, temporary closures or targeting alternative species for fisheries to preserve stock levels[17,209,212,217]. Such interventions were successfully implemented in the lobster industry in the Gulf of Maine. Following a US $38 million loss during a MHW in 2012 in which early record landings led to a drop in lobster value, proactive management and quotas limiting monthly catch during an event in 2016 led instead to gains of US $108 million (ref. 209). Opportunistic commercial fisheries have also been reported in multiple countries globally as species shift their distribution during MHWs[218], although the gains made by these small-scale fisheries are typically minor compared with losses to previously established fisheries[5].

Tourism industry

The tourism sector has experienced both losses and gains from MHWs. Coral bleaching caused by MHWs in southeast Asia in 2010 led to a loss of US $49–74 million for the diving and snorkelling industry[219] (Fig. 5, case studies 6 and 7) and, in 2015, MHWs caused harmful algal blooms off the west coast of the USA that led to closures of recreational razor clam and abalone fisheries and a resulting loss of ~US $84 million in tourist spending[95,220] (Fig. 5, case studies 8 and 9). Harmful algal blooms can also be dangerous to people and pets, and have therefore also led to beach closures and lost cultural, recreational and economic benefits[221,222]. Conversely, bleaching on the Great Barrier Reef in 2016–2017 led to increasing 'last chance tourism' motivating visitors[223] (Fig. 5, case study 10), and the MHW off California in 2015 brought warm-water species such as tuna and several whale species further north than usual, boosting sports fishing and whale-watching industries[65] (Fig. 5, case study 11). Tourism enterprises can mitigate impacts by reducing staff, moving boats to cheaper moorings or modifying activities to take advantage of temporary opportunities such as the arrival of warmer-water megafauna[217].

Impacts to non-industry-based ecosystem service

In addition to supporting various industries, the global oceans provide a vast range of other ecosystem services that are valuable to human societies, many of which have been affected by MHWs[5]: mass mortality events, coral bleaching, and loss of foundation species affect cultural and supporting services; harmful algal blooms caused by MHWs affect regulating services; and species range shifts and tropicalization affect provisioning services[5]. In some cases, single events have led to losses of all four main types of ecosystem services (regulating, provisioning, supporting and cultural). For example, the Ningaloo Niño in the southeast Indian Ocean in 2011 led to the loss of 1,300 km^2 of seagrass from the Shark Bay world heritage area, Western Australia[92]. This loss, in turn, led to the release of stored carbon dioxide (loss of a regulating service)[119] (Fig. 5, case study 12), and the affected seagrass was slowly replaced by tropical seagrass species with lower habitat and nutritional value (loss of supporting and provisioning services) (Fig. 5, case study 12). Finally, the associated loss of habitat led to a decline in a variety of species including iconic megafauna (loss of a cultural service)[115] (Fig. 5, case studies 12 and 13). Collectively, the loss of ecosystem services from Shark Bay seagrass was valued at US $3.1 billion per annum[5], and more than a decade later, only limited recovery has been observed[115]. Similar supporting and cultural ecosystem services have been affected by MHWs in New Zealand following substantial loss of endemic southern bull kelp[123] (Fig. 5, case study 13). For example, Indigenous tribes make 'poha' bags of southern bull kelp (*Durvillaea poha*), used for cultural collections and storage of mutton birds, and the loss of bull kelp disrupts this cultural service. Similarly, dramatic loss of kelp forests along the west coasts of the USA and Australia has diminished ancient connections between coasts, cultural practices and food collections for the Indigenous people of North America and Australia[211,224]. In the USA alone, more than 200 tribes were affected by the Blob, resulting in >US $100 million being appropriated to support tribal fishing[211].

Recent increases in MHW activity have prompted proactive management attempts to protect ecosystem services. For example, in Tasmania, critically endangered red handfish (*Thymichthys politus*) were removed from the wild and maintained in aquaria for several months in 2023 in an attempt to preserve the species during a MHW[24]. Other approaches that have been suggested but not applied or even fully investigated include habitat restoration using warm-adapted species and genotypes, pumping cool water to the surface from depth or artificial shading to protect against solar radiation[217].

Future directions, challenges and solutions

MHWs are intensifying with climate change, posing severe risks to marine ecosystems, biodiversity and coastal economies. Advances in forecasting and early warning systems provide crucial predictions to help coastal communities and industries to prepare for MHWs. However, challenges remain in detecting MHWs in real time, particularly in remote or subsurface waters where satellite data fall short. Effective responses require a mix of proactive measures directly aimed at responding to MHWs, such as temporarily adjusting aquaculture practices and reactive interventions such as species relocation. Additionally, emerging technologies – including remote sensing and genetic analysis – and cross-sectorial collaborations offer promising approaches to monitor, understand, and adapt to the impacts of increasingly frequent and intense MHWs.

Forecasting and responding to MHWs

Improved forecasting systems, early warning models for MHWs[24,217] and real-time impacts on indicator species, such as range-shifting megafauna, can help stakeholders to implement proactive management measures to protect vulnerable species, ecosystems and activities. Yet detection of MHWs in real time can be challenging and very little predictive capability exists for impacts. Data collection is typically limited to satellite-based remote sensing of surface temperatures, which can be obstructed by cloud cover, does not reveal subsurface events, and might not accurately capture water temperatures in coastal regions that are strongly influenced by upwelling or land. Moorings and autonomous sensors, such as those deployed on gliders, can collect real-time data and could supplement the wide coverage afforded by satellites[225,226], and real-time observations of sensitive species, including range-shifting megafauna, could provide early warnings.

Short-term forecasts that predict MHWs days to months in advance are now available in some regions[227,228]. However, forecasting impacts is difficult owing to limited causal evidence and, as some regions remain difficult to forecast accurately, industries and coastal communities in these regions are vulnerable to unexpected events. Developing increasingly skilful, localized forecasting models and strengthening the mechanistic understanding of links between MHW characteristics and their biological impacts is therefore a priority (Table 1). Knowledge of the vulnerability of different species to MHWs is critical to predict biological impacts but is also scarce. In this context, adapting climate vulnerability assessments[229] and other tools that generally address long-term gradual warming to more explicitly assess vulnerability to short-term MHW events could help to close this gap.

Once observations or forecasts indicate a MHW is occurring or likely to occur, effectively communicating risks is essential to enable communities and industries to prepare and respond. Regular briefings can have a key role in removing the 'surprise' element[24]. Through these briefings, marine stakeholders (such as coastal communities, conservation managers, aquaculture, tourism operators and fisheries) can gain insights into predicted risks, potential impacts and recommended actions, fostering a proactive response culture[24,228].

In Australia, several states have developed MHW response plans to assist communication planning, policy responses and impact management. Plans can include proactive actions such as altering aquaculture practices, or reactive actions such as emergency harvesting of at-risk aquaculture species. The plans' scope also extends to include species-specific strategies, habitat restoration and ecosystem support initiatives, which can help to buffer local ecosystems against the worst effects of MHWs. By preparing comprehensive response plans, marine managers can better respond to and recover from MHW impacts, helping to protect both ecosystems and economies[24]. Importantly, to be efficient these response plans must be targeted explicitly at the risks from MHWs and not at risks generically associated with gradual climate change.

Several types of interventions have been attempted with limited success as they are not universally effective and can face substantial challenges. For example, annual efforts to rescue endangered species can lead to policy fatigue unless companion actions, such as preparation of more suitable translocation sites, are taken in parallel. Efforts to pump cool water over coral reefs during peak heat stress would be effective only at a small scale and are not possible nor practical to implement across large areas. Likewise, restoration of marine habitats is still a small-scale and resource-intensive activity that would be difficult or impossible to implement across the scales of habitat damage caused by MHWs[230,231]. Over-reliance on these 'emergency' responses can be costly and will probably be limited to a small number of species or a small area of habitat. These limitations pose a substantial challenge, as management efforts must balance immediate needs with long-term sustainability. Thus, increasing protection and building resilience into marine ecosystems and urgently addressing climate change – the root cause of the increase in events – rather than relying solely on repetitive and questionable post hoc interventions, is crucial for limiting the impacts on MHWs on marine species and ecosystem services.

Challenges to understanding impacts

Although our understanding of vulnerability to MHWs and the mechanisms behind their impacts on ocean biodiversity is growing, many MHW events remain unreported as vast areas of ocean contain unmonitored ecosystems and species, as well as thermal conditions that can obscure ecological consequences of these events (Table 1). In particular, impacts on pelagic and highly mobile species, polar species, long-lived species and species living in deep water are not well understood, despite reported MHWs affecting these regions and species. Moreover, further research is required into how species and communities are affected by MHWs that occur in colder seasons[35], during which mortality and altered migration might be less common. These 'cool MHWs' could potentially still have important impacts, such as by affecting recruitment pulses, increasing metabolic rates and energy demands, and modifying species interaction rates. Additionally, the effects of MHWs are generally only published when impacts are observed, and often only focusing on specific species of interest, thus resulting in publication bias and limiting our understanding of ecological thresholds and resilience. A greater focus on also publishing studies showing lack of impacts in response to documented MHWs would help to address the publication bias and provide better information

Table 1 | Knowledge gaps challenging our understanding of marine heatwave (MHW) impacts on species and ecosystems

Knowledge gap	Consequence	Recommendation
Ocean–coast mismatch	MHWs are predominantly assessed by remote sensing of surface water in the open ocean, and temperatures are poorly resolved in shelf and coastal areas where most MHW impacts have been recorded This mismatch challenges our ability to link observed and predicted temperature stress and impact	Further work is required to resolve oceanography on the coast (for example, <100 m depth), and ecology on the open ocean (pelagic biodiversity and highly mobile marine megafauna); both require long-term monitoring and process studies
Reporting bias	Effects of MHWs are only reported (published) where impacts are observed, and for subsets of species of particular interest This creates a bias against situations (species, locations and so on) where MHWs are not observed, where they have little/no impact, or where impacts are inherently difficult to observe (for example, rare species), limiting understanding of thresholds and resilience	Use long-term biological monitoring data and datasets not originally collected to detect impacts of MHW's matched up with time-series of MHWs[23] Include information on multiple species, especially non-target species[14]
Correlative evidence	Most of the current knowledge of biological impacts of MHWs is based on correlations and unreplicated observations, and little underlying mechanistic understanding exists of ultimate drivers of change This gap in understanding adaptation, resilience or vulnerability to MHWs makes separating the relative contributions from different factors during compound events difficult, challenging attribution and mitigation	Undertake multispecies, multifactor experiments testing effects of different MHW characteristics on different organismal responses[234] Extrapolate experimental evidence to geographically relevant scales through model simulations and meta-analyses Anticipate MHWs through emerging forecasts[227,228] and undertake natural experiments
Geographic gaps	Considerable geographical disparity exists in the evidence for impacts of MHWs in different ecoregions, and the majority of examples come from a few high-profile events in the developed world (for example, 'the blob' affecting the west coast of North America) Although this disparity is due to a combination of data availability and where events have occurred and been recorded, it precludes a full assessment of the magnitude of MHW impacts on biodiversity and the costs to humans	Target under-represented areas Enable biodiversity monitoring by local scientists in disadvantaged regions Target areas of biological and environmental activity (upwelling regions, areas of glacial melt and freshwater inflow, areas prone to cycle impact[7], and areas with megafisheries and other human interests), biodiversity and endemicity hot spots as well as areas with species at risk (Fig. 3)
Overlooked biology	Impacts have mainly been reported where biodiversity information is available (including well-monitored regions) for targeted species (relating to fisheries, tourism and so on). Direct effects of temperature (for example, mortality) also dominate the recorded impacts in contrast to indirect effects and compound effects. Observations of recovery processes are also obscured by spatial and temporal scales of observation As a result, understanding of resilience is limited, particularly for long-lived habitat-forming species	Work is required to understand responses of specialized organisms such as polar endemics and deep sea species, and the impacts of polar and subsurface MHWs Research on the role of organismal history in species vulnerability to MHWs are needed to better under potential 'priming' and resilience of organisms facing MHWs Work is needed on compound effects and indirect effects, and experimental work is required on interactions between factors (biological experiments) Expand scales of observation in both space and time Undertake ecological modelling to combine direct and indirect effects including predation, competition and facilitation, as these have been shown to be important Improve modelling frameworks, such as species distribution models, to include MHWs for prediction of changes in distribution

for predicting when impacts might occur. Even when the immediate impacts of MHWs are understood, a longer-term perspective is needed to comprehend the extent to which species can recover, especially in the context of repeated events, or whether MHWs can drive long-term adaptation to thermal conditions and change the genetic make-up of populations over time. MHWs are known to drive long-lasting regime shifts through flipping ecological systems, but future research should integrate extreme thermal conditions (including repeat events) into evolutionary models and genetic studies of resilience. These challenges are particularly acute for very large and long-lived species that require observations over decades or more. Such eco-evolutionary models can help to disentangle whether marine heatwaves are agents of evolution that can prime species for climate change by placing individuals under selective pressure to withstand acute thermal stress, or simply one of many additional stressors in the ocean that increase mortality and reduce overall diversity. Importantly, even if MHWs do drive evolutionary adaptation, the ongoing environmental changes might be too profound and rapid for species to respond. In any case, understanding these dynamics is essential for predicting the resilience and future composition of marine ecosystems under climate change.

New opportunities for detecting impacts

Advances in technology are unlocking new opportunities for monitoring and understanding the biological impacts of MHWs at the temporal (days to months) and spatial (regional) scales where these effects are felt. Remote sensing technologies – such as autonomous underwater vehicles, gliders and high-frequency satellite data – are transforming observations and responses to MHWs. Although observation capacity must be urgently expanded, many of these tools already provide continuous, large-scale and high-resolution data, enabling researchers to monitor biodiversity, temperature anomalies and ecosystem shifts with unprecedented accuracy and reach. This automation enables the timely detection of MHW impacts on marine species and ecosystems, from population declines to shifts in species distributions. By expanding our monitoring capacity, remote sensing helps to capture the range of direct and indirect effects of MHWs as they unfold, enabling improved assessments of both acute and long-term ecological impacts.

Genomic tools are rapidly advancing, further enhancing our capacity to monitor rare and cryptic species, and inaccessible places[232], as well as assess, predict and potentially manipulate species resilience to heat stress[233]. Environmental DNA sampling, for example, enables the detection of species from tiny amounts of DNA in water or sediments without direct observation of the organisms themselves[232]. Similarly, genomic analyses allow researchers to investigate the genetic basis for thermal tolerance across species. Some species can express heat shock proteins that help them to withstand extreme temperatures, whereas others lack this capability. Understanding these genetic adaptations allows us to predict which species or populations are more likely to endure future MHWs and informs conservation strategies for temperature-sensitive species. By applying these genomic techniques to past and present MHW events, researchers can assess how species' genetic diversity influences their recovery and resilience, providing essential data for conservation decisions.

Although new technology will be instrumental to our ability to upscale detection of MHW impacts, cross-sectorial networks, collaborations and citizen science also provide powerful new possibilities for expanding our observations. For example, commercial and recreational fishers and scuba divers are on the water far more often than scientists, and could be valuable for alerting scientists and managers to unusual species occurrences as potential indicators of larger oceanographic anomalies. This could be especially valuable where the capacity for monitoring does not exist.

Conclusions

Increasingly severe MHWs have emerged as threatening and destructive manifestations of anthropogenic climate change in our oceans. Over the past decade, documentation of how MHWs have been at the core of environmental, biological, ecological and socioeconomic change in marine ecosystems in virtually all oceans and seas has increased exponentially. All projections indicate that the frequency, intensity and duration of these extreme events will continue to increase with climate change. The resulting acute thermal stress and increased extreme conditions will profoundly reshape life in our oceans, and have profound socioeconomic and environmental consequences into the future. Although reducing greenhouse gas emissions remains essential to address these impacts long term, these impacts will be an unavoidable and prominent part of the foreseeable future. Closing the current knowledge gaps around MHWs and their impacts on biodiversity, as well as proactive management strategies, are therefore urgently needed to mitigate further damage to ecosystems and people, and to build resilience into the future.

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