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Biological Impacts of Marine Heatwaves

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Abstract

Climatic extremes are becoming increasingly common against a background trend of global warming. In the oceans, marine heatwaves (MHWs)—discrete periods of anomalously warm water—have intensified and become more frequent over the past century, impacting the integrity of marine ecosystems globally. We review and synthesize current understanding of MHW impacts at the individual, population, and community levels. We then examine how these impacts affect broader ecosystem services and discuss the current state of research on biological impacts of MHWs. Finally, we explore current and emergent approaches to predicting the occurrence and impacts of future events, along with adaptation and management approaches. With further increases in intensity and frequency projected for coming decades, MHWs are emerging as pervasive stressors to marine ecosystems globally. A deeper mechanistic understanding of their biological impacts is needed to better predict and adapt to increased MHW activity in the Anthropocene.

1. INTRODUCTION

Living organisms function between certain temperature limits determined by the typical thermal conditions they have experienced over evolutionary timescales (i.e., their thermal niche). Beyond these limits, performance declines, and without mitigating action, mortality may eventually occur. As Earth's atmosphere and oceans warm, organisms' upper temperature thresholds are being exceeded more frequently and by greater magnitudes (Frölicher et al. 2018, Oliver et al. 2018). Responses to warming have been observed across biological scales, from genes to ecosystems, in many regions around the world (Doney et al. 2012), with major consequences for human societies (Smith et al. 2021). It is increasingly apparent that biological responses to short-term thermal extremes are wide-ranging and pervasive, and the combination of gradual warming trends and extreme events can drive unprecedented ecosystem change (Harris et al. 2018).

The term marine heatwave (MHW)—referring to a discrete period of unusually high seawater temperatures—was coined following an unprecedented warming event off the west coast of Australia in the austral summer of 2011, which led to a rapid dieback of kelp forests and associated ecosystem shifts along hundreds of kilometers of coastline (Pearce & Feng 2013, Wernberg et al. 2013). Since then, a number of high-intensity events have occurred (Sen Gupta et al. 2020) (**Figure 1**; **Supplemental Table 1**), including low-latitude MHWs linked to the El Niño of 2015–2016 in the central/eastern tropical Pacific and multiple MHWs in the Coral Sea (in 2016, 2017, and 2020), all of which led to widespread coral bleaching and mortality (Pears et al. 2017, Pratchett et al. 2021). The longest (non–El Niño) MHW on record, the Blob, covered much of the northeastern Pacific from 2014 to 2016 and has been linked to major ecosystem impacts—including extreme low productivity (Hart et al. 2020), mass mortality events for mammals and seabirds (Cavole et al. 2016), and harmful algal blooms (McCabe et al. 2016)—that in turn affected the delivery of ecological goods and services for human society (Smith et al. 2021).

Supplemental Material >

While several definitions have been proposed to quantitatively describe MHWs, the most widely used approach defines them as periods when temperatures exceed the 90th percentile of the local climatology for five days or more (Hobday et al. 2016; this definition is adopted here), with MHWs of increasing severity identified using an associated categorization scheme (Hobday et al. 2018a). Other definitions include those based on higher percentiles that identify more extreme events (e.g., Sen Gupta et al. 2020); fixed temperature limits corresponding to known organism thresholds (Frölicher et al. 2018); or accumulated heat stress, such as those used to assess coral bleaching risk (Kayanne 2017). The frequency and intensity of MHWs have increased significantly over the last century, with the proportion of time the global ocean is subject to MHW conditions increasing by more than 50% from 1925 to 2016, relative to a fixed baseline (Oliver et al. 2018, Masson-Delmotte et al. 2021). As MHW intensification is primarily due to anthropogenic ocean warming, these patterns show no sign of abating, and the frequency of MHWs is predicted to increase over the remainder of this century (Frölicher et al. 2018, Oliver 2019).

Marine heatwave (MHW): a discrete, prolonged (five days or more) period of anomalously high sea temperature (e.g., >90th percentile relative to local climatology) for any given location and season

It should be noted that short-term extreme warming events are a natural component of ocean climate variability, and MHWs (although not defined as such) and their associated impacts have

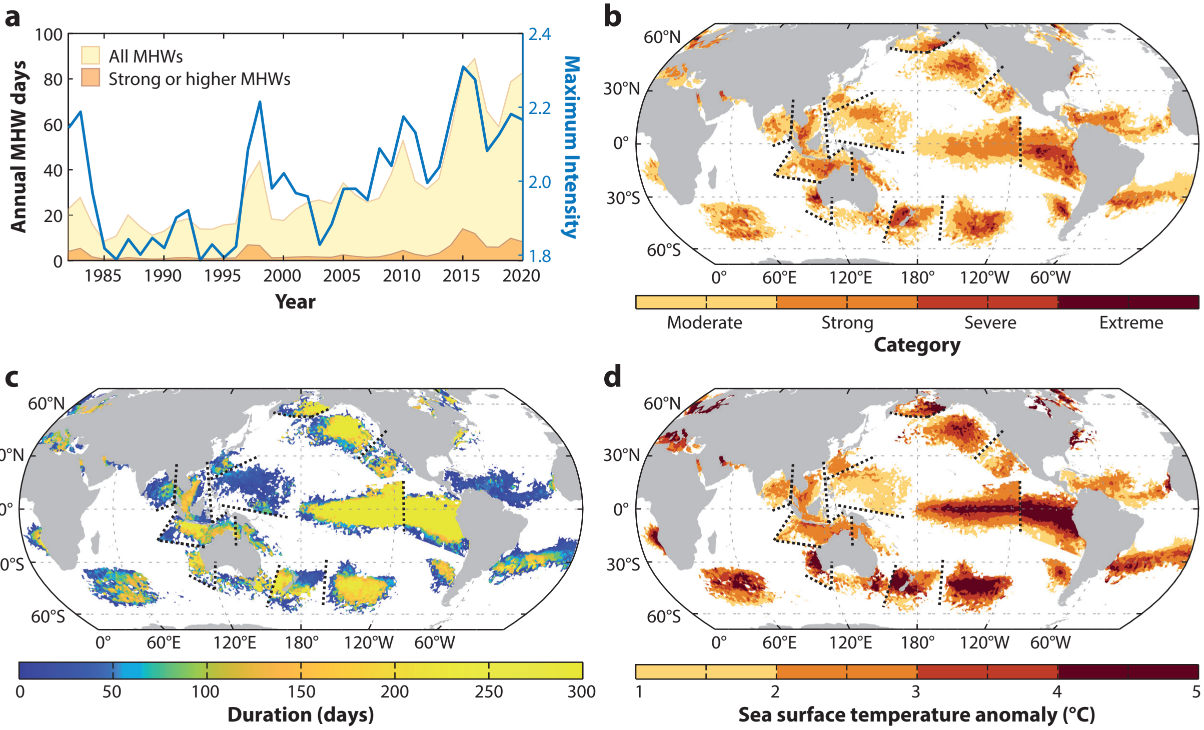


Figure 1

Extreme MHW characteristics. (*a*) Time series of the number of days annually that had MHW conditions of any severity level (*yellow*) and that had MHW conditions categorized as strong or higher (*orange*), as defined by Hobday et al. (2018a), with the associated maximum intensity superimposed (*blue*). (*b*–*d*) Snapshots of MHW category (panel *b*), total duration (panel *c*), and maximum sea surface temperature anomaly (panel *d*) for a selection of extreme MHWs identified by Smith et al. (2021). Abbreviation: MHW, marine heatwave.

been characterized and reported on for several decades (e.g., Hart & Scheibling 1988). However, recent rapid warming trends across much of the global ocean have increased the likelihood of thresholds being exceeded (relative to a fixed climatology) and, as such, the occurrence of MHWs. In defining MHWs, the choice of whether to use a fixed or moving climatological baseline will influence metrics, trends, and forecasts and should be tailored to the research question (Oliver et al. 2021). In ecological impact studies, where the rate of acclimatization or adaptation to warmer conditions is generally assumed to be lower than the current rate of ocean warming for most ecosystems, fixed climatological baselines are more commonly adopted (Oliver et al. 2021). While fixed baselines are more sensitive to changes in mean sea temperature over time, moving baselines are more influenced by changes in the variability in a system, and so a combination of the two approaches can be complementary.

Our understanding of the characteristics, trends, local drivers, and predictability of MHWs and their links to large-scale climate patterns or climate change has risen rapidly over the last decade. The increase in MHW research has been motivated by (*a*) the increasing frequency and severity of events, including high-profile case studies that have documented severe ecological impacts (e.g., Wernberg et al. 2016); (*b*) the development of freely available computer codes (e.g., Schlegel & Smit 2018) that produce easy-to-calculate, quantitative, and standardized metrics (Hobday et al.

2016, 2018a); (*c*) the release of free, high-quality, multidecadal satellite sea surface temperature data sets (Beggs 2020); and (*d*) improved physical and biological monitoring, including, in some cases, near-real-time monitoring (Holbrook et al. 2020). As a result, researchers can now quantify the atmospheric and ocean fluxes of heat and mixing processes that are the proximate causes of MHW evolution (and decay) and how these are modulated by the ocean state (Holbrook et al. 2019, Sen Gupta et al. 2020). Attribution techniques have also been applied to individual MHWs to estimate the influence of climate change (e.g., Oliver et al. 2017, Benthuysen et al. 2018, Laufkötter et al. 2020). There is also a growing appreciation of how and why recurrent climate patterns such as the El Niño–Southern Oscillation or the Madden–Julian Oscillation can trigger distant MHWs via atmospheric or oceanic teleconnections (Feng et al. 2013, Di Lorenzo & Mantua 2016) and how this may inform prediction of MHWs (Holbrook et al. 2020).

Ecosystem services: the outputs and processes that nature provides to human societies

Cellular stress response: molecular changes that cells undergo in response to environmental stressors

Here, we examine the current state of knowledge of the biological impacts of MHWs from individual to whole-ecosystem levels and evaluate the effects of these impacts on ecosystem services. We focus primarily on the responses of fully marine species and habitats, rather than transitional species found at the land–sea interface (e.g., mangroves, salt marshes, and intertidal habitats), which are influenced by MHWs but often more so by atmospheric heatwaves and other climatic events (e.g., Sippo et al. 2018). Finally, we explore contemporary approaches to understanding and predicting the current and future impacts of MHWs and discuss adaptation and management approaches.

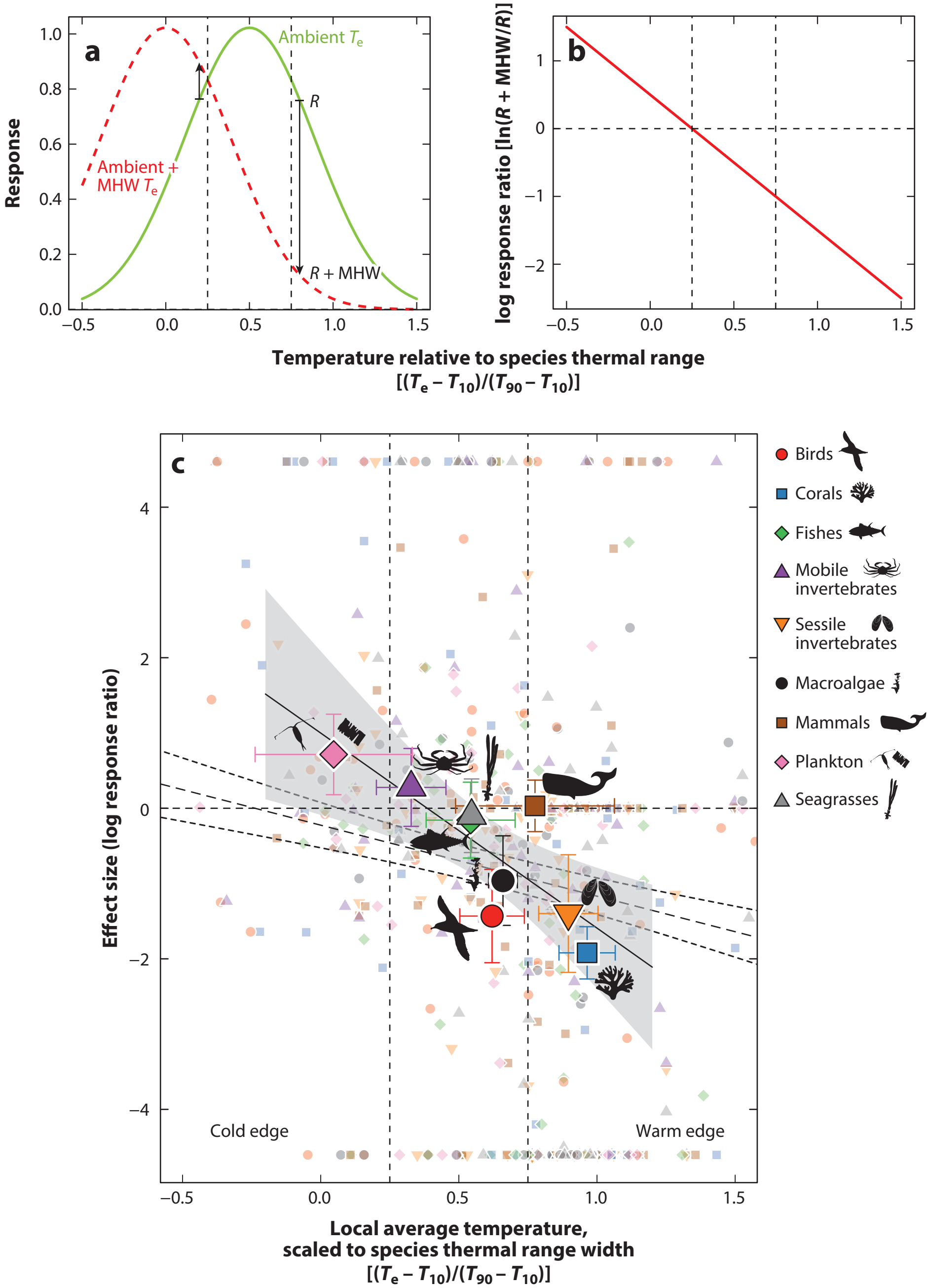
2. ECOPHYSIOLOGICAL AND INDIVIDUAL-LEVEL IMPACTS

The latitudinal distributions of most marine species are typically a projection of their thermal niche in space (Sunday et al. 2012). Temperature exerts a profound influence over all physiological processes (e.g., photosynthesis and respiration) and therefore governs ecological performance (e.g., growth, reproduction, phenology, and survival) (Seibel & Drazen 2007). Within a species range, performance is generally greatest toward the range center, where temperatures are optimal, and decreases with increasing proximity to range margins (Angilletta 2009) (**Figure 2*a***). As such, individuals found between the cool leading range edges and the center of their distribution may benefit from MHW exposure, as increasing temperatures alleviate cold stress and improve performance (**Figure 2*a***). Conversely, because thermal safety margins (the buffer between experienced temperatures and the species maximum thermal limits; Sunday et al. 2014) are usually smallest for individuals found toward the warm trailing edges of their distribution, it is here that thermal niches and critical thresholds are most likely to be exceeded (Wiens 2016, Smale et al. 2019) (**Figure 2**).

Negative responses of individuals to MHWs vary from sublethal effects on core physiological processes to mortality. Elevated temperatures increase basal metabolic rates, and the energy demand can exceed the metabolic capacity of the species (Lemoine & Burkepile 2012). At higher MHW intensities, short-term stress responses are employed. Under high thermal stress, the cellular stress response—a multisystem, graded, energetically expensive response—is activated to protect and repair the cellular macromolecular systems (proteins, RNA, DNA, and lipoproteins) (reviewed in Somero 2020). In addition, individuals may make other physiological adjustments to depress their metabolism and conserve energy for cellular protection and repair (Guppy & Withers 1999). Consequently, energy deficits develop that generally increase with MHW intensity and duration. Where these debts are not matched by increased energy acquisition, other aspects of performance will be negatively impacted (Begon & Townsend 2020). In such cases, individuals may modify their behavior, relocate, and/or adjust their physiology. However, if such buffering capacity is exceeded, MHWs can have severe consequences for individual performance.

2.1. Thermoregulatory and Physiological Modifications

Thermoregulatory behaviors, such as relocation to thermal refugia, is an immediate strategy to avoid thermal stress before physiological adjustments are required. However, unlike terrestrial and intertidal landscapes, which offer a mosaic of microclimates, subtidal seascapes often lack local thermal refugia (Pinsky et al. 2019). Consequently, behavioral responses are limited to highly



(*Caption appears on following page*)

Figure 2 (*Figure appears on preceding page*)

Meta-analysis of MHW studies, showing that MHW effects depend on the location of the impact within each species' thermal range. (*a*) The effects of increased temperature during an MHW can be predicted from species thermal response curves under average temperatures (ambient T_e; *green line*) and heatwave conditions (ambient + MHW T_e; *dashed red line*). Performance is enhanced (*upward black arrow*) during MHWs in the cooler part of the thermal range and negatively impacted in the warmer part (*downward black arrow*). T_e is the temperature at the effect location, and R is the species response. (*b*) If the thermal performance curves are Gaussian (Bonachela et al. 2021), then the expected effect of an MHW expressed as the log response ratio declines linearly with location in the thermal range. (*c*) This predicted pattern is seen in a meta-analysis of literature data (Smale et al. 2019). MHW effects on species (*small symbols*) depend on the local average temperature (T_e) relative to the species thermal range [$\mathrm{SRL} = (T_e - T_{10}) / (T_{90} - T_{10})$, where SRL is the species range location and T_{10} and T_{90} are the 10th and 90th percentiles of temperatures in the geographical range of the species, respectively]. Species' MHW effects tend to be more negative toward the warm edges of ranges (*dashed regression line*: $R^2 = 0.06$, log response ratio $= -0.224 \pm 0.153 - 0.944 \pm 0.156 \times \mathrm{SRL}$, parameter estimate ± standard error, $n = 540$, $P < 0.001$). Differences in responses to MHWs among taxa (group averages ± standard errors shown as *large symbols with error bars*) are also strongly related to the average range locations of studies of each taxa (*dotted regression line*: $R^2 = 0.61$, log response ratio $= 0.999 \pm 0.460 - 2.591 \pm 0.702 \times \mathrm{SRL}$, parameter estimate ± standard error, $n = 7$, $P = 0.008$). Strong negative impacts of MHWs on corals and positive effects on corals derive from the locations of the original studies. Abbreviation: MHW, marine heatwave. Figure adapted from Smale et al. (2019).

mobile species. For example, pelagic species may track suitable temperatures over hundreds of kilometers, and when MHWs are restricted to shallow surface waters, demersal species may seek refuge in nearby cooler, deeper waters (e.g., Freitas et al. 2016). Where relocation is not possible, individuals may seek to balance resulting energy deficits through increased feeding (Gunderson & Leal 2016) or decreased reproductive investment (Caputi et al. 2016, Barbeaux et al. 2020). Reduced energy availability can also interfere with metabolism-linked behaviors that affect neuromuscular and physiological function. Whatever the mechanism, behavioral modifications can in turn impact higher-order ecological processes such as predator–prey interactions. For example, increased foraging of reef fish during MHWs to offset higher energy demands can increase vulnerability to predation and catchability from fisheries (Bacheler & Shertzer 2020, Brown et al. 2020), and neuromuscular interference occurring because of energy shortfalls can compromise the efficacy of camouflage behavior in urchins (Brothers & McClintock 2015).

Where behavioral modifications are ineffective, and particularly for sessile or sedentary species, physiological adjustments may be necessary for individuals to survive elevated temperatures. As MHWs occur over much shorter time frames (typically within a single generation for many species), during an event, individuals must rely on physiological alterations mediated through phenotypic plasticity. Most commonly, this involves adjustments to the composition of proteins in the cell, to the fluidity of cell membranes, and to small molecules in the cytoplasm to maintain homeostasis. While the temperatures that cause thermal damage to the macromolecular components of the cell are generally conserved, the cellular stress response harbors considerable plasticity that may allow individuals to modify their vulnerability to the early stages of thermal stress (Somero 2020). For example, repeated exposures to thermal stress can lead to key proteins being frontloaded (e.g., heat shock proteins) in the cell, allowing a more rapid response (Gleason & Burton 2015). However, while this may reduce energy consumption during MHWs and increase resistance to cumulative heat exposure, it may also incur other, longer-term ecological trade-offs, such as fecundity or growth (Bay & Palumbi 2017).

Phenotypic plasticity: the ability of an organism to change its phenotype in response to environmental change

2.2. Growth and Reproduction

If metabolic demands increase and individuals cannot match elevated energy requirements with behavioral modifications, then reduced performance (e.g., growth and reproduction), and ultimately decreased fitness, will occur following depletion of internal energy reserves. As reserves are accessed to balance energetic shortfalls, net body mass is typically reduced, resulting in decreases in growth, reproductive capacity, performance, and potentially survival. The complex life cycles of most marine species, combined with the timing and duration of MHWs relative to reproductive cycles, means that reproductive responses to MHWs are also likely to differ with individual circumstances. Most marine species broadcast gametes into the water column for external fertilization, with subsequent development involving several ontogenetic stages. These developmental stages often occur within a narrow subset of the species' thermal niche and may follow their own thermal performance curve (Pandori & Sorte 2019), leading to multiple potential pressure points. For example, MHWs that stress reproductive adults may result in lower reproductive investment and subsequently fewer, smaller, and lower-quality gametes (e.g., Shanks et al. 2020), whereas individuals benefiting from MHWs may increase reproductive effort and even generate offspring primed for future events (Jueterbock et al. 2021). Alternatively, events occurring while gametes are in the water column may positively or negatively impact fertilization success, metamorphosis, and subsequent development (Smith et al. 2013, Gall et al. 2021).

Thermal performance curve: a species-specific curve describing changes in rates of biological processes within a thermal niche

The impacts of MHWs on individuals range in severity depending on biogeographical context, inherent species traits, life history stage, and previous exposures. Moreover, differing MHW characteristics (i.e., rate of onset/decline, intensity, frequency, and duration) will likely induce differing physiological responses, with consequent impacts on fitness. Importantly, MHWs do not occur in isolation but interact, often synergistically, with other stressors, such as elevated turbidity (Tait et al. 2021), desiccation stress (Thomsen et al. 2019), harmful algal blooms, and anoxia (Gruber et al. 2021), meaning effects on individuals may be more complex than simple temperature reaction norms. Greater understanding of how individual responses cascade through to populations, communities, ecosystems, and human society will facilitate a more comprehensive understanding of the biological impacts of MHWs.

3. SPECIES- AND POPULATION-LEVEL IMPACTS

While the severity of impacts caused by MHWs varies among species and populations, and with event characteristics (e.g., Straub et al. 2022), several commonalities have emerged. Species with a narrow thermal niche (stenotherms) are more likely to be negatively affected by MHWs than those with broader thermal tolerances (eurytherms), but populations may also respond differently to one another depending on disturbance history (Hughes et al. 2021). Moreover, selection pressure can lead to local adaptation either over many generations in response to gradual warming or much more rapidly through exposure to acute thermal stress (King et al. 2018, Coleman & Wernberg 2020). As explored above, populations found towards a given species trailing range edge may be more susceptible to MHW activity. Responses include mass mortality events (Pearce et al. 2011, Garrabou et al. 2019, Genin et al. 2020), reproductive failure (Caputi et al. 2016, Shanks et al. 2020), range shifts (Cavole et al. 2016, Lenanton et al. 2017), and establishment of nonnative species (Thomsen & South 2019, Verdura et al. 2019) and vary across species ranges and with MHW characteristics. While effects on foundation species are clearly important (e.g., habitat-forming species such as corals; see Section 4), in this section we first focus on nonfoundational species.

3.1. Benthic Invertebrates (Excluding Corals)

Benthic invertebrates are typically sessile or sedentary as adults, limiting their ability to relocate to less stressful environments during MHWs. Responses range from reproductive failure or mass mortalities to range expansion/contraction and increased abundance. Significantly reduced reproduction or total reproductive failure was observed in dozens of benthic invertebrates across at least five taxa for two consecutive years during the 2014–2016 Blob MHW (Shanks et al. 2020). This level of reproductive failures may devastate local populations for years or even decades. For example, during the 2011 Western Australia MHW, elevated temperatures led to low recruitment in scallops (*Ylistrum balloti*) and blue swimmer crabs (*Portunus armatus*), resulting in significant population-level declines and fishery closures ranging from 18 months to 5 years (Caputi et al. 2016, 2019). Impaired growth and poor condition (i.e., low muscle mass) were also reported for scallops, suggesting low adult fitness. At the same time, recruitment in king prawns (*Penaeus latisulcatus*) was geographically variable, with record high recruitment in southern, cooler-water populations but reduced recruitment in more northern, warmer-water populations (Caputi et al. 2016).

Tropicalization: a shift in community composition toward a greater dominance of lower-latitude (warmer-water) species

A database of mass mortality events occurring in the Mediterranean Sea (Garrabou et al. 2019) highlights the severe impacts MHWs can have on benthic invertebrates. Between 1979 and 2020, more than 2,300 mass mortality events, relating to more than 90 species, were recorded for benthic invertebrates in the Mediterranean, the majority of which were associated with periods of anomalously warm temperatures (Garrabou et al. 2019). Mass mortality events have also been recorded as an indirect response to MHWs. For example, an MHW in the Tasman Sea in 2015–2016 was linked to Tasmania's first outbreak of Pacific oyster mortality syndrome (Oliver et al. 2017). During the 2011 Western Australia MHW, the abalone *Haliotis roei* suffered catastrophic mortality caused by deoxygenation of the water from a combination of high temperatures and calm conditions (Pearce et al. 2011); mortality rates reached 99.9% in populations near the warm range edge but were only 10% in cooler-water populations (Caputi et al. 2016). Off the west coast of the United States, low productivity linked to the 2014–2016 Blob MHW resulted in food limitation that led to starvation in populations of the red abalone (*Haliotis rufescens*) (Hart et al. 2020), and the same MHW accelerated mortality rates from sea star wasting disease, contributing to the population collapse of a keystone predator, *Pycnopodia helianthoides* (Harvell et al. 2019).

MHWs can also lead to increased growth rates and range expansions of mobile benthic invertebrates. In 2012, an MHW in the northwestern Atlantic resulted in an earlier migration to shallow-water areas and earlier molts in American lobsters (*Homarus americanus*), leading to individuals reaching legal landing size earlier in the year (Mills et al. 2013). In the northeastern Pacific, poleward shifts or increases in abundance were reported for a number of benthic invertebrates during the 2014–2016 Blob (Sanford et al. 2019), and during the 2011 Western Australia MHW, tropicalization of benthic kelp forest invertebrates was reported (Wernberg et al. 2016). Here, there were clear winners and losers; while species adapted to warmer water showed range expansion, range contraction was reported for species adapted to cooler water.

3.2. Marine Fish

Mass mortality events linked to MHWs have been reported in wild and farmed fish populations (**Figure 3**), often in association with harmful algal blooms (Clement et al. 2016, Trainer et al. 2020), deoxygenation of water (Mendez et al. 2015), and disease (Genin et al. 2020). For example, during an MHW in the Red Sea in 2017, mass mortalities of more than 40 species of coral reef fish were reported, likely caused by a combination of thermal stress and increased bacterial infection (Genin et al. 2020). In 2016, an MHW in the southeastern Pacific led to two independent harmful algal blooms in Chilean inland marine waters that resulted in mass mortalities of farmed Atlantic and coho salmon and trout, a catastrophic loss for the aquaculture industry (Clement et al. 2016, Trainer et al. 2020).

Not all MHW-associated algal blooms produce toxins, and increases in primary productivity following MHWs may alternatively stimulate zooplankton and fish production. For example, an

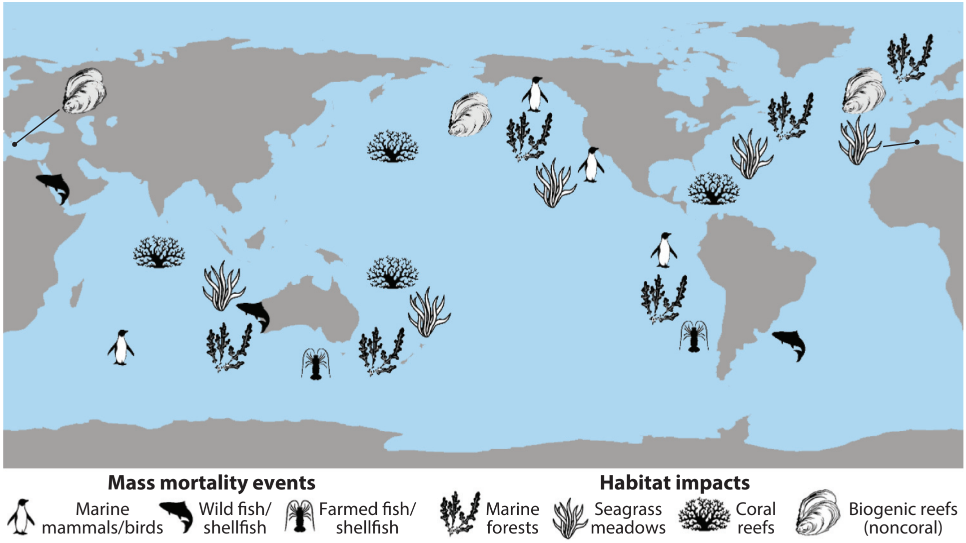


Figure 3

Population-level mass mortality events and habitat impacts of MHWs referenced in this review. Abbreviation: MHW, marine heatwave. All icons are from the Noun Project (**https://thenounproject.com**): penguin created by Christy Presler; fish and shrimp created by Ker'is; seaweed created by Kevin; seagrass created by James Smith; coral created by Agne Alesiute; oyster created by Buckley Powell.

MHW in the Canadian Arctic in 2009 led to an increase in cod reproduction driven by early ice breakup and favorable feeding conditions (Bouchard et al. 2017, LeBlanc et al. 2020). However, MHW-induced responses in reproduction and recruitment may also be negative, and in the northeastern Pacific during the 2014–2016 Blob, reduced food availability combined with increased metabolic demand resulted in an energetic mismatch that caused recruitment failure in Pacific cod (*Gadus microcephalus*), leading to population collapse and closure of commercial fisheries (Barbeaux et al. 2020).

Both temporary and semipermanent range shifts have been reported for fish species during and following MHWs. During the 2011 Western Australia MHW, several small tropical fish species extended their ranges poleward, some of which were followed by successful recruitment and overwintering populations (Lenanton et al. 2017). Similarly, during the 2014–2016 Blob, several game fish species either proliferated at the poleward range edge or, in some cases, extended their range as much as thousands of kilometers poleward (Cavole et al. 2016). Conversely, in the Coral Sea in 2016, an increase in the catch per unit effort of coral trout during an MHW indicated an apparent increase in population size. Studies suggest, however, that increased catchability was an indirect effect related to the impacts of warming on physiological and behavioral traits (e.g., increased feeding activity making bait and lures more attractive) rather than greater abundances (Brown et al. 2020), highlighting the need to better understand the physiological responses of complex organisms to MHW events.

3.3. Marine Megafauna

The impacts of MHWs on marine megafauna range from sharks and sea turtles temporarily extending their ranges hundreds to thousands of kilometers outside of typical limits to reproductive failure and mass strandings and mortalities of seabirds, pinnipeds, and cetaceans (Bost et al. 2015, Cavole et al. 2016, Kendrick et al. 2019, Nowicki et al. 2019, Wild et al. 2019, Smith et al. 2021). Many seabird and pinniped species exhibit high fidelity toward their breeding grounds and, as such, are vulnerable to climate-driven shifts in prey abundances or distributions. In 1997–1998, MHWs associated with a strong El Niño event led to reproductive failure and mass mortalities of Galápagos sea lions (*Zalophus wollebaeki*) in the southeastern Pacific (Salazar & Bustamante 2003) and king penguins (*Aptenodytes patagonicus*) in the southern Indian Ocean (Bost et al. 2015), largely due to shifts in prey distribution. More recently, during the 2014–2016 Blob MHW, shortages of invertebrate and fish prey and toxins from harmful algal blooms (which magnified through the food web), both of which were related to extreme warming, led to reproductive failure, starvation, strandings, and ultimately mass mortality events from California to Alaska, in species including California sea lions (*Zalophus californianus*), Guadalupe fur seals (*Arctocephalus townsendi*), Cassin's auklets (*Ptychoramphus aleuticus*), and common murres (*Uria aalge*) (Cavole et al. 2016, Piatt et al. 2020). By contrast, in 2014, during the early stages of the Blob, increased reproduction was reported in the endangered southern resident killer whale populations in Puget Sound, and a shift in prey distribution brought a variety of whale species unusually close to the Californian coast, providing a boost for the whale-watching industry (Cavole et al. 2016). The influx of whales into coastal waters, however, led to an increase in entanglements as the spatial overlap increased between fishing gear and whale habitat (Santora et al. 2020).

3.4. Nonnative Species

MHWs may offer periods of thermally favorable conditions for species to extend their distributions outside of their established ranges, at least temporarily. For nonnative species, MHWs may lead to an extension of the already-established nonnative range or facilitate successful establishment in a newly hospitable location, most likely following translocation via human activities. Nonnative invaders are often characterized by having broad thermal tolerance, and consequently, MHWs and background climate change can facilitate their establishment (e.g., Papacostas et al. 2017). For example, the Pacific oyster (*Crassostrea gigas*) was introduced to Europe as an aquaculture species under the premise that local temperatures were within its range for growth but too low for temperature-sensitive reproduction (Ruesink et al. 2005). However, high summer temperatures, often associated with MHWs, have provided new spawning opportunities, facilitating the establishment of wild populations (Ruesink et al. 2005, Herbert et al. 2016). Such opportunities are predicted to accelerate as MHWs become more frequent and intense (King et al. 2021).

MHW-assisted introductions of nonnative species may, however, be short-lived. For example, following the 2011 Western Australia MHW, a founder population of the nonnative Asian green mussel (*Perna viridis*) was identified on the hull of a boat, believed to have originated from an adult hitchhiker from Southeast Asian waters that spawned in Australian waters during the MHW (McDonald 2012). Although the MHW enabled a spawning event, *P. viridis* has apparently not established self-sustaining populations. Finally, the establishment or spread of nonnative species may be facilitated by MHWs through competitive release, whereby dominant native competitors exhibit reduced fitness or mortality and allow nonnatives to proliferate. For example, the nonnative seaweed *Caulerpa cylindracea* in the Mediterranean Sea has proliferated following competitive release from the MHW-affected gorgonian *Paramuricea clavata* (Verdura et al. 2019), and invasive Japanese kelp (*Undaria pinnatifida*) has proliferated in New Zealand, where native southern bull kelp was lost after the 2017–2018 Tasman Sea MHW (Thomsen & South 2019). Clearly, MHW intensification and the continued global spread of nonnative species will increasingly interact to alter ecological structure and functioning.

4. FOUNDATION SPECIES AND ASSOCIATED COMMUNITIES

Community- and ecosystem-level impacts of MHWs have been reported across many regions when shifts in foundation species occur (Smale et al. 2019). Often, loss or replacement of habitat-forming foundation species (e.g., reef-building corals, seagrasses, and seaweeds) cascades to community and ecosystem impacts, such as altered primary productivity, trophic disruption, and altered biodiversity and ecological functioning. Specific responses include range shifts that lead to restructuring of entire habitats (Johnson et al. 2003, Wernberg et al. 2016, Eakin et al. 2019, Kendrick et al. 2019, Verdura et al. 2019), altered community composition (Stella et al. 2011, Vergés et al. 2014, Wernberg et al. 2016, Gómez-Gras et al. 2021a, Serrano et al. 2021), biodiversity loss (Grilo et al. 2011, Stella et al. 2011, Verdura et al. 2019), and declines in abundance or shifts in behavior of large, iconic top consumers (Kendrick et al. 2019). The impacts, however, are not uniform across all species, times, or regions, but can reverberate throughout the food web, directly or indirectly affecting species across multiple trophic levels. Widespread losses of habitat-forming foundation species driven by MHWs have been reported in many regions (**Figure 3**), often with consequences for entire communities and ecosystems.

4.1. Marine Forests

Marine forests—formed by kelp and other large seaweeds—represent some of the most widespread and productive habitats on Earth (Steneck et al. 2002). MHWs are often identified as contributing directly or indirectly to declines in marine forests globally (Filbee-Dexter & Wernberg 2018, Straub et al. 2019, Smale 2020), precipitating some of the most spectacular marine ecosystem reconfigurations in recent times (e.g., Wernberg et al. 2016, Filbee-Dexter et al. 2020, McPherson et al. 2021). As kelps are foundation species, the effects of MHWs on kelp forests generally lead to substantial impacts on associated communities. Often it is difficult to distinguish between the effects of losing the foundational kelp species and the direct effects of MHWs on the associated species (Thomsen & South 2019).

There have been several examples globally where MHW-driven losses of kelp forests have ultimately resulted in community-wide shifts to alternative states, often persisting for many years after the MHWs have subsided. As with other species, impacts vary across the species ranges and are typically more pronounced at the warm range edges of distribution (but see Bennett et al. 2015, Thomsen et al. 2019, Tait et al. 2021). For example, in central California, the 2014–2016 Blob MHW induced moderate declines in giant kelp (*Macrocystis pyrifera*) and negative effects on some associated invertebrates and fish (Reed et al. 2016), whereas in the warmer waters of Baja California, Mexico, loss of giant kelp forests was more pronounced, driving marked shifts in associated community structure at some locations (Arafeh-Dalmau et al. 2019).

During the 2011 Western Australia MHW, marine forests formed by kelp (*Ecklonia radiata*) and fucoids (*Scytothalia dorycarpa*) underwent range contractions and functional extinction along 100 km of coastline at their equatorward (warm) limit (Smale & Wernberg 2013, Wernberg et al. 2016), while cooler marine forests remained largely unimpacted (Wernberg et al. 2013, 2016). The collapse of marine forests led to a concurrent community-wide shift in seaweed, invertebrate, and fish assemblages (Smale & Wernberg 2013, Wernberg et al. 2016), which have not recovered more than 10 years later (Wernberg 2021). Similar community shifts have also been observed following loss of southern bull kelps (*Durvillaea* spp.) in New Zealand, which have remained regionally extinct in some areas since the 2017–2018 Tasman Sea MHW (Thomsen & South 2019, Thomsen et al. 2021). While the response of associated species such as turf algae (Filbee-Dexter et al. 2020, Thomsen et al. 2021), smaller fucoid seaweed (Thomsen & South 2019), sea urchins (Rogers-Bennett & Catton 2019), and herbivorous fish (Bennett et al. 2015, Zarco-Perello et al. 2017) may not be directly related to the initial response of the kelp forest to the MHW, they often drive feedback processes that may prevent recovery and lock the ecosystem into a persistent alternative state.

4.2. Seagrass Meadows

Heat stress caused by MHWs can alter seagrass competitive hierarchies or lead to seagrass loss, with knock-on effects for associated communities and entire ecosystems. Increased shoot mortality, flowering intensity, leaf necrosis, and respiration, coupled with increased susceptibility to herbivory, may result in reductions in seagrass species and facilitate nonnative or opportunistic species (Hernán et al. 2017). For example, during MHWs associated with the 1997–1998 El Niño, eelgrass (*Zostera marina*) declined in California and was replaced by opportunistic widgeon grass (*Ruppia maritima*), which proliferated and continued to dominate for at least a year after warming subsided (Johnson et al. 2003). In the Mediterranean Sea, high levels of shoot mortality and flowering induction in the seagrass *Posidonia oceanica* in 2003 and 2006 were attributed to thermal stress caused by MHWs (Diaz-Almela et al. 2007, Marbà & Duarte 2010). Sustained ocean warming combined with MHW intensification in the Mediterranean has facilitated large-scale decline of *P. oceanica* meadows and enabled expansions of nonnative seaweed and seagrass competitors, with significant reduction in biodiversity and carbon stocks (Marbà et al. 2014, Pergent et al. 2014).

Direct loss of seagrass, or shifts from large temperate species to small tropical species, leads to a decline in habitat complexity (and therefore quality), productivity, and available resources, indirectly impacting the associated community, ranging from benthic invertebrates to large, iconic top consumers. In North America, an MHW in Chesapeake Bay in 2005 led to a >50% loss of *Z. marina*, indirectly causing declines in three commercially important fishery species supported by the meadows (Lefcheck et al. 2017, Kendrick et al. 2019). To date, the best-documented impacts of MHWs on seagrass habitats are from Shark Bay, a United Nations Educational, Scientific, and Cultural Organization (UNESCO) World Heritage site where the 2011 Western Australia MHW caused the collapse of approximately 1,300 km^2 of seagrass meadows previously dominated by the large temperate species *Amphibolis antarctica* and *Posidonia australis* (Arias-Ortiz et al. 2018, Kendrick et al. 2019, Strydom et al. 2020). While approximately 1,000 km^2 remain lost, small, fast-growing tropical seagrasses such as *Halodule uninervis* rapidly expanded into other unvegetated areas (Kendrick et al. 2019). The reduction in habitat volume and complexity, loss of predation refugia, and declining food availability had severe cascading effects, leading to declines in the abundance and fitness of several species of sea snakes, dugongs (*Dugong dugon*), bottlenose dolphins (*Tursiops aduncus*), green turtles (*Chelonia mydas*), and pied cormorants (*Phalacrocoraz varius*) (Nowicki et al. 2019). Some predators, such as dolphins, modified their behavior and habitat use, increasing their risk of predation (Wild et al. 2019). Conversely, populations of several apex predators, including tiger sharks (*Galeocerdo cuvier*), and generalist consumers, such as loggerhead turtles (*Caretta caretta*), were relatively stable over the MHW (Matich et al. 2011, Kendrick et al. 2019, Nowicki et al. 2019). Overall, these observations suggest that generalist and opportunistic consumers are less susceptible to the indirect effects of MHWs compared with seagrass-associated specialists.

4.3. Coral Reefs

One of the most globally recognized impacts of ocean warming is the mass bleaching (loss of endosymbiotic dinoflagellates from coral hosts) and mortality (heat-induced loss of coral tissue) of reef-building corals. Since global mass bleaching events were first reported in 1998 (Wilkinson 2000), they have become increasingly common and severe, with the longest, most widespread, and most destructive event impacting more than half of the world's coral reef areas between 2014 and 2017 (Eakin et al. 2019). Furthermore, the rapid onset of warming that occurs during MHWs can exceed thermal thresholds in corals, resulting in immediate heat-induced mortality followed by dissolution of the skeleton and loss of three-dimensional structure (Leggat et al. 2019). Loss of reef habitat complexity and structure directly impacts the diversity and abundance of reef-associated organisms. On the Great Barrier Reef alone, major episodes of bleaching were reported in 2016, 2017, and 2020 (Pratchett et al. 2021). During the 2016 event, high temperatures led to the catastrophic die-off of fast-growing staghorn and tabular corals, leading to a shift in ecological functioning and reduction in three-dimensionality that impacted approximately one-third of the reef (Hughes et al. 2018). Along the warmer equatorial Great Barrier Reef, where reef degradation was particularly severe, parallel declines in abundances of coral-eating (corallivores) and herbivorous fish, increases in planktivorous fish abundances, and shifts in invertebrate communities were reported, highlighting widespread ecosystem-level impacts (Stuart-Smith et al. 2018).

As with many ecosystems, the impacts of MHWs on coral reefs vary with the severity and duration of the event, along with experience of previous events. The aforementioned 2016 MHW disproportionately affected the equatorial section of the Great Barrier Reef, where warming was more severe and the reef system had not been subjected to such conditions for more than a decade. Responses of corals along the reef to the subsequent 2017 and 2020 warming events indicated that across a period of 1–3 years following a bleaching event, reefs were more resilient as thermal thresholds for bleaching temporarily increased (Hughes et al. 2021). Regardless of this apparent increased resilience with recurring MHW events, the capacity of reefs to recover to previous states following MHWs has also deteriorated due to the differential heat tolerance of different coral size classes. Larger coral colonies are often less heat tolerant than smaller individuals and, consequently, are disproportionately affected by MHWs. For example, during an MHW in the central Pacific in 2019, mortality was most commonly observed in the largest colonies. Larger corals are disproportionately more fecund than smaller individuals (Speare et al. 2022), and as the reproductive capacity of a reef deteriorates, so does its ability to successfully produce coral recruits to facilitate recovery. Furthermore, larger colonies typically have a larger three-dimensional structure than smaller cohorts, so a shift to smaller size classes may have cascading negative impacts on associated biodiversity.

4.4. Biogenic (Noncoral) Reefs

Sessile invertebrates such as bivalves, octocorals, and tube worms can form complex structures that offer habitat for a wide range of associated species. In the Mediterranean Sea, biogenic reefs are often characterized by dense colonies of octocorals and other coralligenous species that function as foundation organisms and underpin local biodiversity and community structure (Ponti et al. 2018). Many of these colonies have suffered mass mortalities from successive MHWs (e.g., in 1999, 2003, and 2006; Garrabou et al. 2021, Smith et al. 2021), resulting in shifts in the structure and function of entire ecosystems (Gómez-Gras et al. 2021a). For example, in Cabrera National Park, Spain, an MHW in 2011 caused widespread mortality of the gorgonian *P. clavata*, leading to reduced biomass and density. Subsequently, local biodiversity declined as complex coralligenous habitat was replaced by simplified algal turfs, with associated loss of species diversity (Verdura et al. 2019). Similarly, in the Scandola marine protected area, Corsica, *P. clavata* and the coral *Coralliun rubrum* have shown a progressive reduction in density and biomass since a severe MHW in 2003, with recovery thought to be hindered by recurrent MHWs in this area (Gómez-Gras et al. 2021b).

The impacts of MHWs on biogenic reefs can be both beneficial and detrimental for associated fauna. For example, summer MHWs have facilitated the wild establishment of nonnative *C. gigas* around Europe (see Section 3.4). Resulting outcomes range from increased habitat complexity and associated species richness to displacement of native species such as reef-forming mussels and polychaete worms (Herbert et al. 2016 and references therein). Off the coast of France, the formation of *C. gigas* reefs has led to an increase in species richness and abundance when compared with adjacent mud or rock (Lejart & Hily 2011). Conversely, in the Wadden Sea, the oysters have partially displaced the native mussel species, converting *Mytilus edulis* reefs to mixed reefs dominated by 95% *C. gigas*. The impacts of this displacement on associated fauna have been varied: Overall species richness, diversity, biomass, and abundance were higher on the mixed reef; mussels continued to settle on the reef using the larger oysters as protection against predation; and the feeding rates of oystercatchers and curlews increased. At the same time, bird species that previously fed on the mussels were expected to be detrimentally impacted as their food source decreased (Herbert et al. 2016 and references therein).

5. ECOSYSTEM SERVICE–RELATED IMPACTS

The oceans support many ecosystem services that human societies depend upon. Over the past 25 years, provisioning, regulating, habitat (or supporting), and cultural ecosystem services have been impacted by at least 34 MHWs, often resulting in economic losses in the region of millions (sometimes billions) of US dollars (Smith et al. 2021). The impacts of MHWs on ecosystem services significantly hinder our ability to achieve several of the United Nations Sustainable Development Goals (SDGs), including zero hunger (SDG 2), decent work and economic growth (SDG 8), climate action (SDG 13), life below water (SDG 14), and peace, justice, and strong institutions (SDG 16). The associated socioeconomic consequences have likely been severely underreported for many regions and events, particularly where research, reporting (e.g., of commercial fishery landings), and wider communication channels are less well established.

5.1. Provisioning and Cultural Services

A recent review of the socioeconomic impacts of MHWs highlighted that a disproportionate number of impacts relate to provisioning services, in particular fisheries and aquaculture (Smith et al. 2021). Losses or gains of provisioning services can directly influence employment, food availability, and other ecosystem services, as well as affecting global market values. For example, an MHW in the southeastern Pacific in 2016 led indirectly to the largest fish farm mortality event ever recorded globally. The MHW caused two concurrent harmful algal blooms in Chilean inland marine waters, together known as the Godzilla red tide event, which resulted in the mortality of 100,000 metric tons of Atlantic and coho salmon and trout, equivalent to US$800 million, or 15% of annual production for Chile (Clement et al. 2016, Trainer et al. 2020). In turn, this led to the loss of 4,500 jobs and a >50% increase in the cost of salmon exported to the United States (González 2016).

The opposing outcomes of two recent MHWs in the Gulf of Maine highlight how management practices can alleviate impacts on ecosystem services. In 2012, an MHW led to early inshore migration of the commercially fished American lobster (*Homarus americanus*) followed by early molt to legal size. Commercial landings during spring were unexpectedly high, and supply exceeded processing capacity, resulting in a drop in lobster value along with blockades, protests, and civil unrest as fishermen attempted to export lobsters from the United States to Canada for processing (Mills et al. 2013, Holbrook et al. 2020). While this led to a loss of US$38 million in 2012, proactive management strategies employed following the event enabled fishermen to profit during a second MHW in 2016 (Pershing et al. 2018). A combination of increased processing capacity and the development of seasonal forecasts enabled fishermen to broker deals to sell early landings, ultimately resulting in a gain of US$108 million.

Impacts of MHWs on provisioning services are often directly associated with impacts on cultural services (by directly affecting tourism) and indigenous and recreational fisheries. For example, an MHW in the Southeast Asian seas in 2010 led to bleaching and mass mortality of corals that collectively resulted in an estimated US$49–74 million loss in tourism (Doshi et al. 2012). Comparatively, during the 2014–2016 Blob, shifts (increases and decreases; see Section 3.3) in iconic marine megafauna resulted in both positive and negative impacts on tourism, while harmful algal blooms related to the MHW led to the multiyear closures of fisheries along the west coast of the United States. Closures of the commercial Dungeness crab (*Metacarcinus magister*) fishery affected both indigenous and nonindigenous fishermen (Moore et al. 2019), while closures of the recreational razor clam (*Siliqua patula*) and abalone (*Haliotis* spp.) fisheries reduced tourist spending by a combined ~$84 million per annum (Ferriss et al. 2017, Rogers-Bennett & Catton 2019).

5.2. Regulating and Habitat Services

Changes to regulating services (e.g., through nutrient cycling, carbon capture, and storm protection) and habitat services (e.g., by offering biogenic structure for a diverse range of species) during MHWs are often linked to shifts in foundation species. For example, marine and coastal vegetated habitats (e.g., seagrass beds and salt marshes) act as blue carbon ecosystems, storing carbon in their biomass and underlying sediments (McLeod et al. 2011). By storing carbon, some coastal vegetated habitats may mitigate climate change driven by anthropogenic carbon dioxide emissions. A major consequence of MHWs is the broad-scale destruction of these systems. For example, widespread loss of seagrass meadows from Shark Bay following the 2011 Western Australia MHW resulted in the release of approximately 2–9 Tg of carbon dioxide into the atmosphere over the following three years (Arias-Ortiz et al. 2018). Seagrass loss also led to reduction in biogenic habitat and food for a variety of species, ranging from commercially important invertebrates to iconic megafauna (Kendrick et al. 2019) (see also Section 4.2), collectively resulting in a loss of ecosystem services valued at US$3.1 billion per year for multiple years (Smith et al. 2021). Loss of kelp forests represents one of the most pervasive response to recent MHWs. Among other locations, significant declines in kelp forests following MHW events have been reported off Western Australia (Wernberg et al. 2016), New Zealand (Thomsen et al. 2019), Mexico (Arafeh-Dalmau et al. 2019), the west coast of the United States (Rogers-Bennett & Catton 2019), and both sides of the North Atlantic (Filbee-Dexter et al. 2020). In these examples, declining kelp forests resulted in loss of regulating services, including reductions in carbon standing stock and transfer, lower nutrient turnover, and diminished habitat quality and extent.

In terms of ecosystem service value, the most precious biomes on Earth per unit area are coral reefs (Costanza et al. 2014). These ecosystems provide storm protection to coastlines (preventing an estimated US$4 billion of damages annually), offer important habitat for a rich and diverse range of species, and are fundamental for nutrient cycling and carbon fixation (Woodhead et al. 2019 and references therein). Consequently, degradation of coral reefs caused by MHWs has significant impacts on regulating and habitat ecosystem services. For example, the 2016 MHW in the Coral Sea, which caused severe degradation to the Great Barrier Reef, led to a broad-scale homogenization and reduced diversity of fish communities (Stuart-Smith et al. 2018). Similarly, in the western Indian Ocean, MHWs in 1998 and 2016 both caused a >70% decline of branching corals around the Seychelles, habitat loss, and reduced abundance and richness of reef fish. Here, although two-thirds of reefs had recovered to pre-1998 coral abundances by 2011, the remaining third underwent a regime shift from coral- to algae-dominated ecosystems (Graham et al. 2015, Wilson et al. 2019) and a complete shift in habitat services. As MHWs intensify, their impacts on ecosystem services will likely increase, with major implications for human societies.

6. RESEARCH APPROACHES TO MARINE HEATWAVE IMPACTS

The volume of research relating to both the drivers of and biological responses to MHWs has increased dramatically in recent years (Hobday et al. 2018a). Research on the impacts of MHWs has utilized a range of complementary approaches, including observational studies in natural systems, controlled experiments in both field and laboratory settings, and modeling studies (Bass et al. 2021). This recent research effort has significantly advanced our understanding of MHW impacts.

The majority of research has stemmed from field-based observations of natural systems to elucidate responses to MHW events. Various forms of time series data have been used to generate reliable pre-MHW baselines, including fishery catch data (e.g., Barbeaux et al. 2020), habitat and biodiversity monitoring (e.g., Gómez-Gras et al. 2021b), remotely sensed data (e.g., Arias-Ortiz et al. 2018), and citizen-led wildlife counts (e.g., Piatt et al. 2020). Information may be collected at the population, species, community, or ecosystem level and typically spans multiple years (or, in exceptional cases, decades) prior to the MHW event to capture natural baseline variability. The advantage of field approaches is that they provide real-world observations, in that natural communities of interacting species are responding to actual warming events in the oceans. Such studies integrate the effects of extreme temperatures across biological scales, from genes to ecosystems, to advance understanding of MHW impacts.

Where field observations benefit from realism, however, they may lack in mechanistic understanding. Marine ecosystems are highly variable and complex, and effects of MHWs are not observed in isolation. Other factors, such as nutrient, light, and oxygen availability; UV light; desiccation and turbidity stress; pollution; fishing pressure; and disease may interact additively, synergistically, or antagonistically with temperature to mediate MHW impacts (e.g., Rogers-Bennett & Catton 2019, Tait et al. 2021, Thomsen et al. 2021). Similarly, species interactions are highly complex and prevalent in marine ecosystems, and responses of certain species can disproportionately influence community- and ecosystem-level effects. Finally, observational field-based research relies on robust and reliable baselines against which to detect change. Given that monitoring in the marine environment is often costly and challenging, reliable baseline data are not always available for the particular location or time of an MHW event. The need for reliable monitoring data, along with ecological and oceanographical contexts, has likely led to a pronounced geographical bias in MHW research, with the majority of impact studies originating from Australia, Europe, and the United States (e.g., Caputi et al. 2016; Cavole et al. 2016; Wernberg et al. 2016; Barbeaux et al. 2020; Gómez-Gras et al. 2021a,b).

While observational studies of responses to MHWs are correlative, experimental approaches can instead infer causation and improve mechanistic understanding of impacts. Experimental research on marine climate change impacts has intensified dramatically in recent decades, with an increasing number of studies focused on MHWs (Bass et al. 2021). Controlled manipulations can be used to determine cause–effect relationships for single stressors (in this case, MHWs) in isolation, helping to disentangle their effects from those of other stressors in the marine environment. Characteristics of MHWs, such as intensity, duration, and return period, can be manipulated to gain a deeper understanding of their relative importance. Moreover, under controlled conditions, a wider range of response variables can be measured, particularly at the molecular and physiological levels, again offering insights into the mechanisms underlying observed responses.

In marine ecology, the majority of climate change experiments focus on a single species in isolation and/or manipulate a single stressor (e.g., temperature or ocean acidification; Bass et al.

2021), even though species interact within complex communities and are often responding to multiple stressors simultaneously. While significant progress toward more ecologically relevant controlled experiments has been made, many laboratory-based experiments suffer from experimental artifacts and low realism. Some attempts have been made to shift the experimental venue from the laboratory to the field, to test for impacts on natural communities and incorporate ambient environmental variability (e.g., Smale et al. 2017), but manipulating temperature in the marine environment remains challenging. A compromise between laboratory and field research is the use of mesocosms, which incorporate the natural variability of most environmental parameters (e.g., light) while controlling key variables such as temperature. Sophisticated mesocosm systems can allow for the study of multiple species simultaneously, enabling community-level experiments to be carried out under realistic near-natural conditions (e.g., Pansch et al. 2018), although due to the cost of setup, this experimental approach is rare.

More recently, studies have combined climate models with ecophysiological and/or biogeographical information to predict future responses to MHWs (Koerich et al. 2021). While still in its infancy, this predictive approach has great potential to assist conservation and management of marine species faced with MHW intensification in coming decades. Nevertheless, the disparity in scale between climate models and ecological processes that structure communities and ecosystems remains a challenge.

7. PREDICTING THE IMPACTS OF FUTURE EVENTS

Given the dramatic effects of MHWs on ecosystems and human societies (Cavole et al. 2016, Smith et al. 2021), advance warning of events would aid managers in many marine sectors (Holbrook et al. 2020, Spillman et al. 2021). Such warnings can provide information on the likelihood, intensity, duration, or frequency of events, and potentially their subsequent biological or human impacts. Predictions of MHWs is a focus of intense research activity, spanning a range of timescales that correspond to a different decision set (Hobday et al. 2016). MHW projections on decadal to centennial timescales rely on IPCC-class models and provide information on how the statistical properties of extreme events (e.g., frequency, mean duration, and maximum intensity) are likely to evolve based on different plausible future emissions scenarios (e.g., Frölicher et al. 2018, Oliver et al. 2019). Long-term projections are highly sensitive to the rate of emissions prescribed in these scenarios, while nearer-term decadal-scale forecasts are more sensitive to initial ocean conditions. An increased likelihood of detrimental biological impacts is expected with more intense MHW category events (Hobday et al. 2018a), leading to greater biological and human disruption (Oliver et al. 2021).

Near-term MHW forecasts (lead time of less than seven days) are being developed in Australia and New Zealand (Moana Proj. 2022) that predict the evolution of specific events, using a framework similar to weather forecasts. Seasonal MHW forecasts (lead time of weeks to a few seasons) are also in development in Australia (CSIRO 2022), although forecast skill varies (e.g., Benthuysen et al. 2021). For example, forecast skill on seasonal timescales depends on ocean memory (i.e., the persistence of temperature anomalies) and the occurrence of large-scale climate modes, such as the El Niño–Southern Oscillation, Interdecadal Pacific Oscillation, and North Atlantic Oscillation. Other studies have retrospectively developed and tested forecasts of specific events, such as the 2014–2016 MHW in the California Current system, spawned by the Blob (Jacox et al. 2019). Different climate modes have been associated with significant changes in the likelihood of MHWs in different regions (Holbrook et al. 2019). Even so, recent developments have facilitated skillful forecasts of up to one year of the onset and persistence of MHWs across the global ocean (Jacox et al. 2022).

The potential biological impacts of future MHWs have largely been inferred from impacts observed during historical events. However, a growing body of literature based on experiments that examine responses to plausible future conditions is providing new insights into species survival (e.g., Minuti et al. 2021, Straub et al. 2022) and ecosystem outcomes (e.g., Atkinson et al. 2020). These experimental results and historical observations can be incorporated into ecosystem models (Plagányi et al. 2011) to predict MHW impacts. For example, using such models, Babcock et al. (2019) compared the multidecadal response of Australian coastal ecosystems to (*a*) a single MHW and (*b*) episodic MHW-driven mortality events every 5 years. Recovery times for individual functional groups after the single event ranged from 4 to 60 years. While the median recovery time was typically 10–15 years, lower biomass of primarily slower-growing or longer-lived groups persisted for many decades. With repeat events, there was limited recovery, resulting in parts of the system remaining in a permanently altered state. Much less is currently known about adaptation (either through acclimation or adaptation) of ecosystems to changes in extreme events, and models have rarely accounted for these processes. Babcock et al. (2019) examined the effect of adaptation to MHWs in the Atlantis ecosystem model for southeastern Australia. Modifying demographic parameters to simulate adaptation lessened the effect of extreme climatic events, halving the magnitude of biomass declines and shortening recovery times, but did not negate all impacts.

Compound events: multiple extreme events of different natures occurring simultaneously or in close succession

To date, the impact of future MHWs on human societies that depend on the ocean for livelihoods has only been inferred based on historical observations (Smith et al. 2021). In the future, these complex impacts can be explored in socioecological system models (e.g., Atlantis; Fulton et al. 2011), as has been done for climate impacts on fishery-dependent communities (e.g., Dunstan et al. 2018, Pethybridge et al. 2020). It is now also clear that MHWs can co-occur with other stressors (Gruber et al. 2021, Tait et al. 2021), and so investigation of these compound events will require holistic ocean monitoring (e.g., oxygen, pH, turbidity, and temperature) to detect interactions and feedbacks. Multifactorial experiments will play a role (e.g., Boyd et al. 2018), but unlike single-stressor experiments, they cannot eliminate all caveats.

8. MANAGEMENT AND ADAPTATION OPTIONS: FUTURE-PROOFING THE OCEAN

With MHW intensification, a range of tools and approaches will be needed to maintain ecological functioning and safeguard provision of ecosystem services. Improved forecasting will inform short-term management actions to reduce the risk to ecosystems or related services on timescales of days to seasons (Spillman et al. 2021). On longer timescales, societal or biological adaptation measures can help alleviate negative impacts in the future. For example, changing fishery management and practices, including ad hoc fishery closures (Caputi et al. 2019), catch limits (Pershing et al. 2018), and targeting of alternative species (Hobday et al. 2018b), can allow impacted stocks time to recruit and recover while exploiting new resources. Similarly, changes in aquaculture practices (e.g., target species, site selection, harvest timing, and translocation) could be informed through improved MHW predictions at both short and longer timescales.

A variety of techniques aimed at increasing species' thermal tolerances in order to increase the resilience of populations, communities, and ecosystems are currently being investigated. These include priming, whereby early life stages are exposed to heat before outplanting to populations for restoration or aquaculture, in order to induce latent heat tolerance in adults (Jueterbock et al. 2021), and assisted evolution, whereby heat-tolerant strains are identified and deliberately bred into natural or farmed populations (e.g., Coleman et al. 2020). Similarly, restoration efforts using heat-tolerant individuals to recolonize temperate and tropical reefs are showing some success (e.g., Layton & Johnson 2021).

Additionally, combining predictive forecasting with experimental approaches that identify species-level physiological tipping points, across a species distributional range, may increase our ability to predict responses to future MHWs. Developing such an understanding will enable identification of both high-risk areas and potential climatic refugia, which will be fundamental for conservation actions such as building climate-resilient marine protected areas and protecting range-shift corridors (Burrows et al. 2014, Verdura et al. 2021). Beyond this, building a mechanistic understanding of species responses to individual MHWs, multiple consecutive MHWs, or compound events, along with different MHW characteristics, will further increase our ability to predict the outcomes of isolated and combined/consecutive stressors. Ultimately, to mitigate future impacts of MHWs, which will intensify as a result of anthropogenic climate change (Frölicher et al. 2018, Oliver et al. 2018), rapid measures to reduce greenhouse gas emissions or increase rates of carbon capture and storage are needed.

Climatic refugia: areas of the marine environment where some or all variables affected by climate change are stable or changing the least

SUMMARY POINTS

1. Marine heatwaves (MHWs) have become longer, more intense, and more frequent over the past half century, a trend that is predicted to continue into the future.
2. Biological responses to MHWs occur at the individual, population, and community levels and typically intensify toward the warm trailing range edges of species distributions.
3. Within a species, responses vary not only with MHW event characteristics (e.g., rate of onset/decline, intensity, and duration) but also among populations and individuals based on disturbance history and local adaptations.
4. The knock-on effects of MHWs on ecosystem services can result in economic losses in the region of millions to billions of US dollars and considerable societal impacts.

FUTURE ISSUES

1. Field-based observational research would be improved with better monitoring of a range of ecological response variables across wider geographical scales, with a focus on regions that are poorly studied but likely affected by MHWs.
2. The usefulness of controlled experiments would benefit from more sophisticated manipulations involving multiple stressors, simulations of MHWs with different properties, and a greater diversity and number of experimental organisms.
3. Clear reporting of MHW metrics and characteristics, using widely accepted definitions (e.g., Hobday et al. 2016, 2018a), is necessary to facilitate comparisons across regions, events, and experiments.
4. Further development of approaches to future-proof marine ecosystems faced with MHW intensification is needed to alleviate the impacts of extreme warming events in the coming years and decades.

DISCLOSURE STATEMENT

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Errata

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