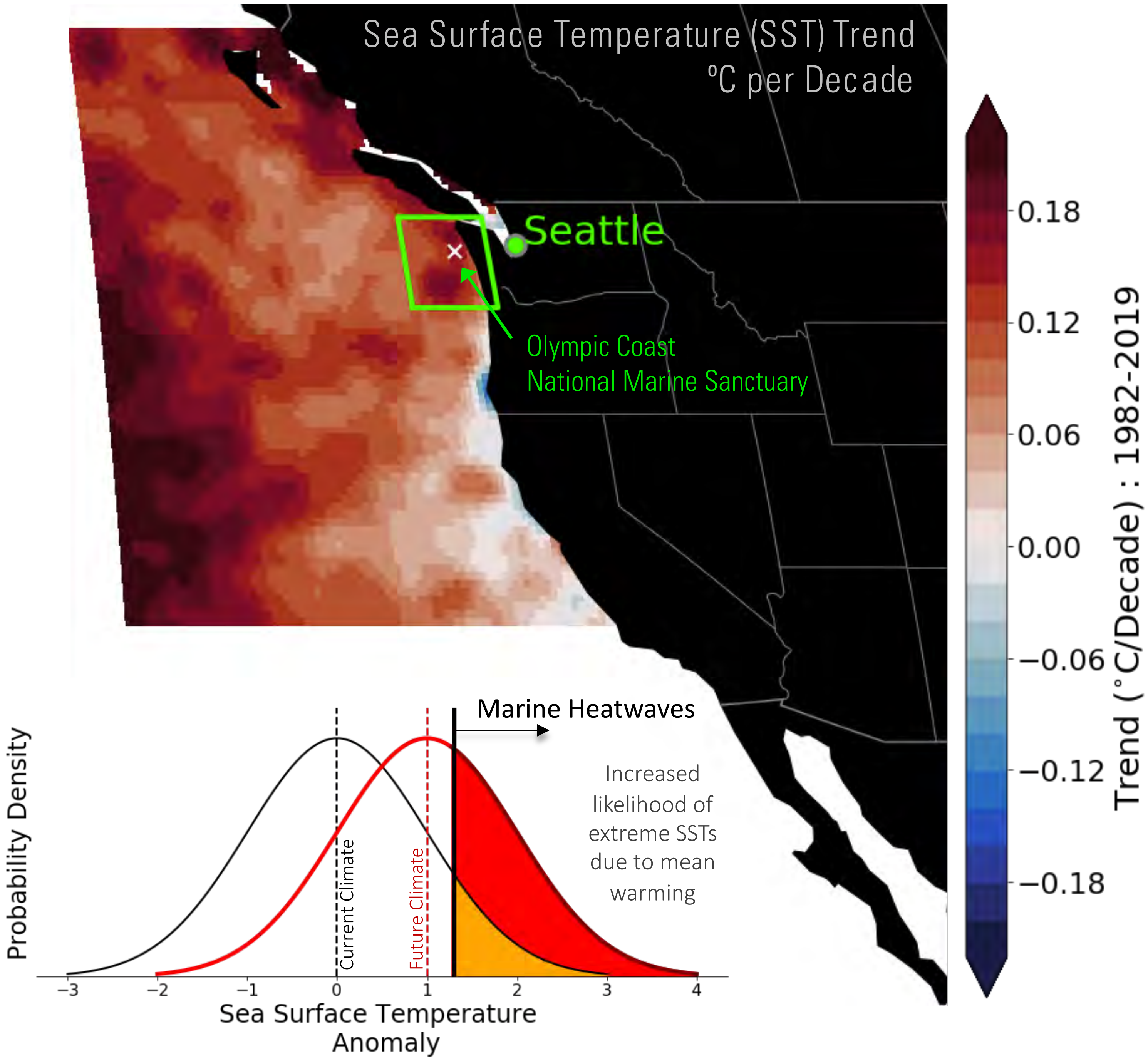

Photo Credit: Santa Barbara Coastal Long Term Ecological Research Project

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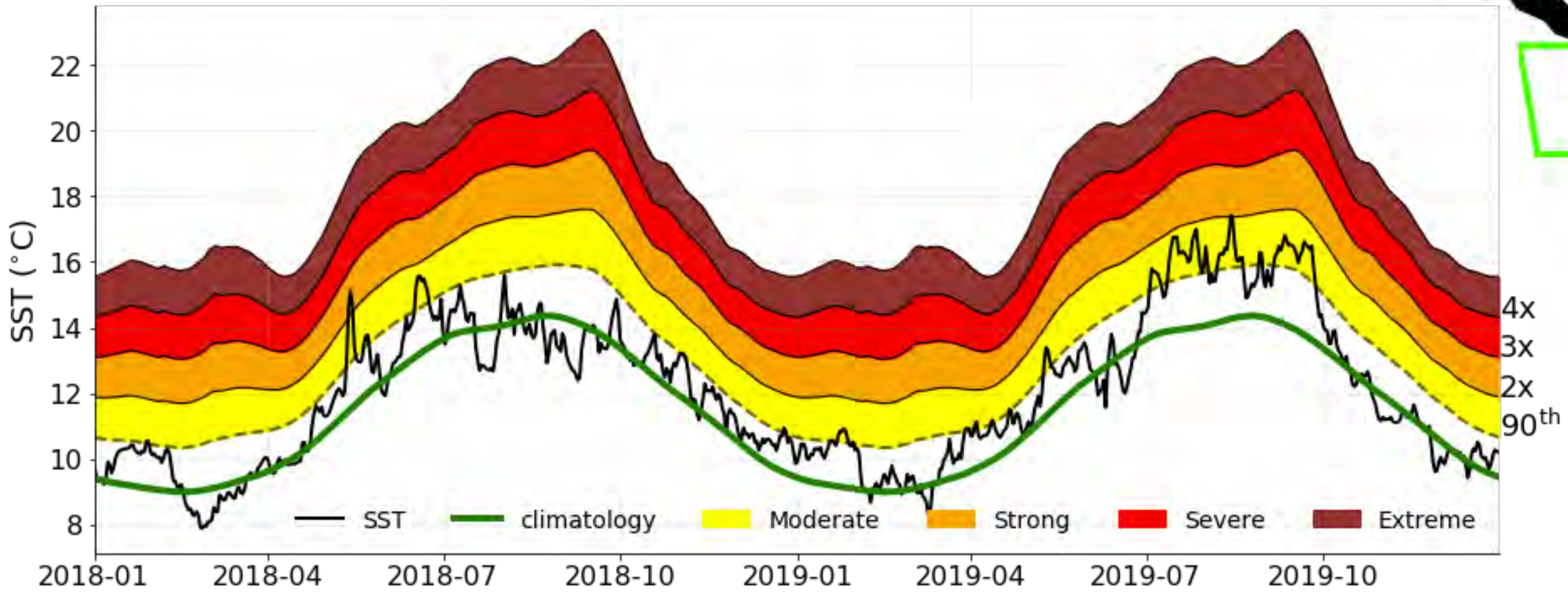
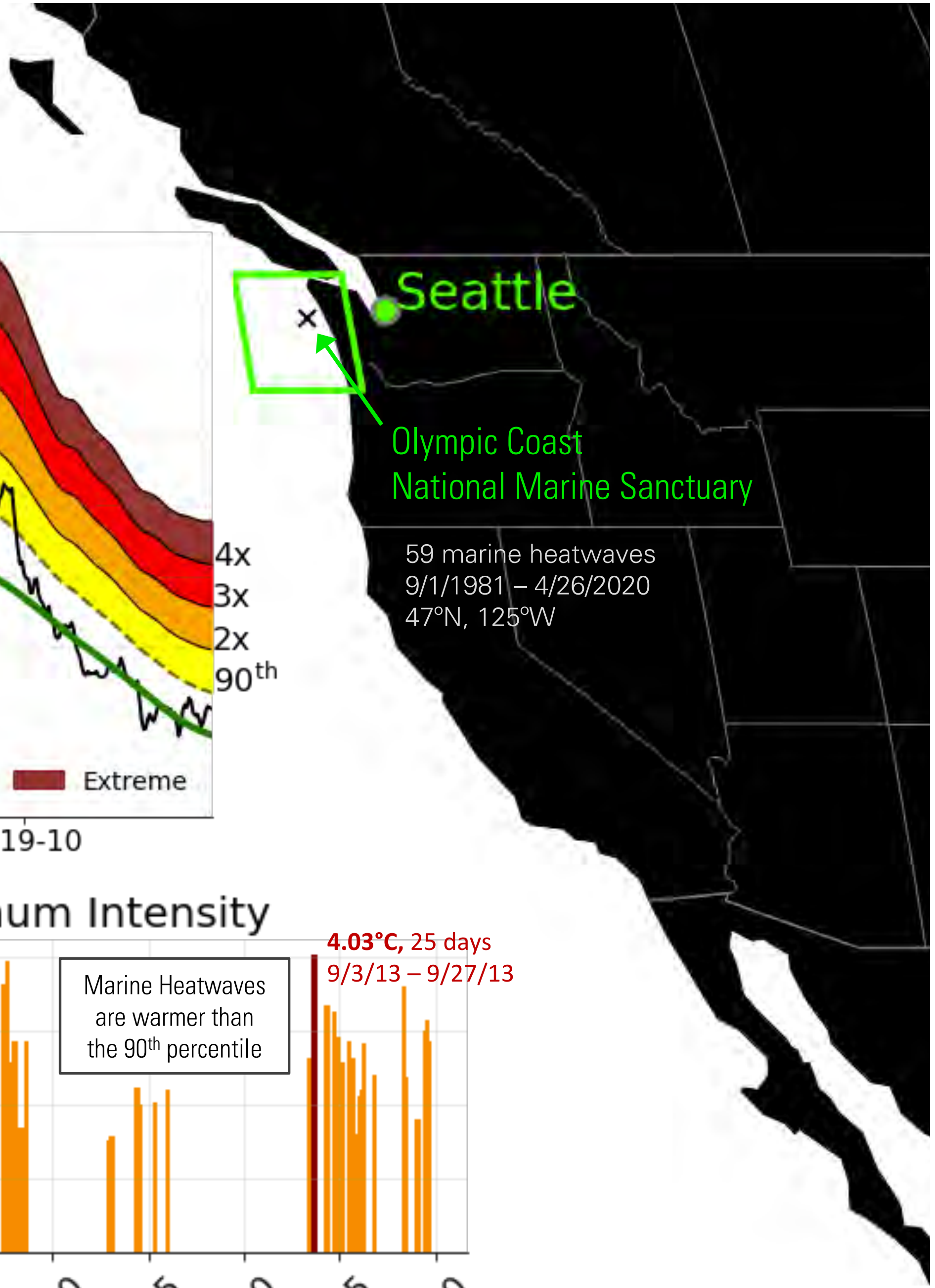
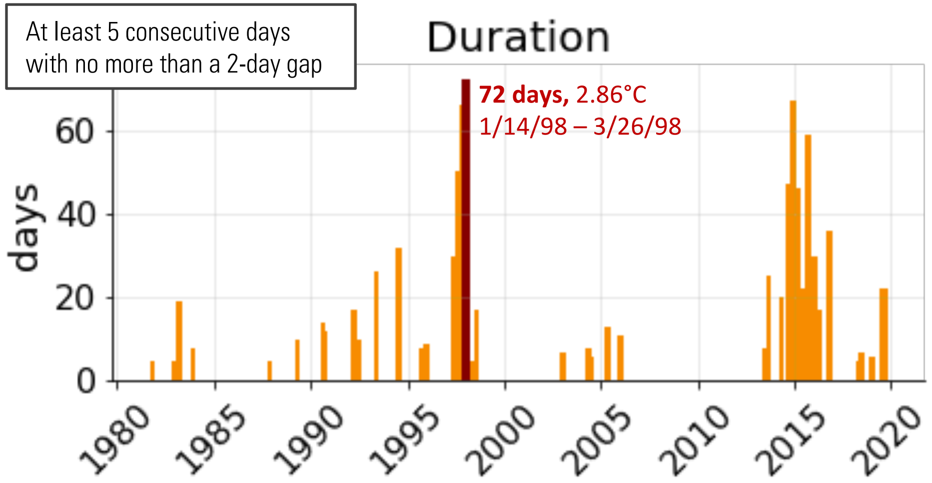
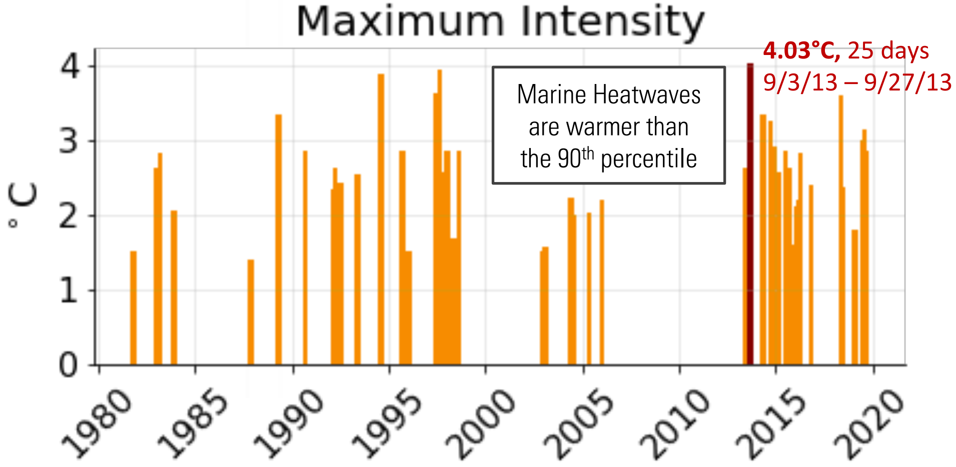
Marine Heatwaves

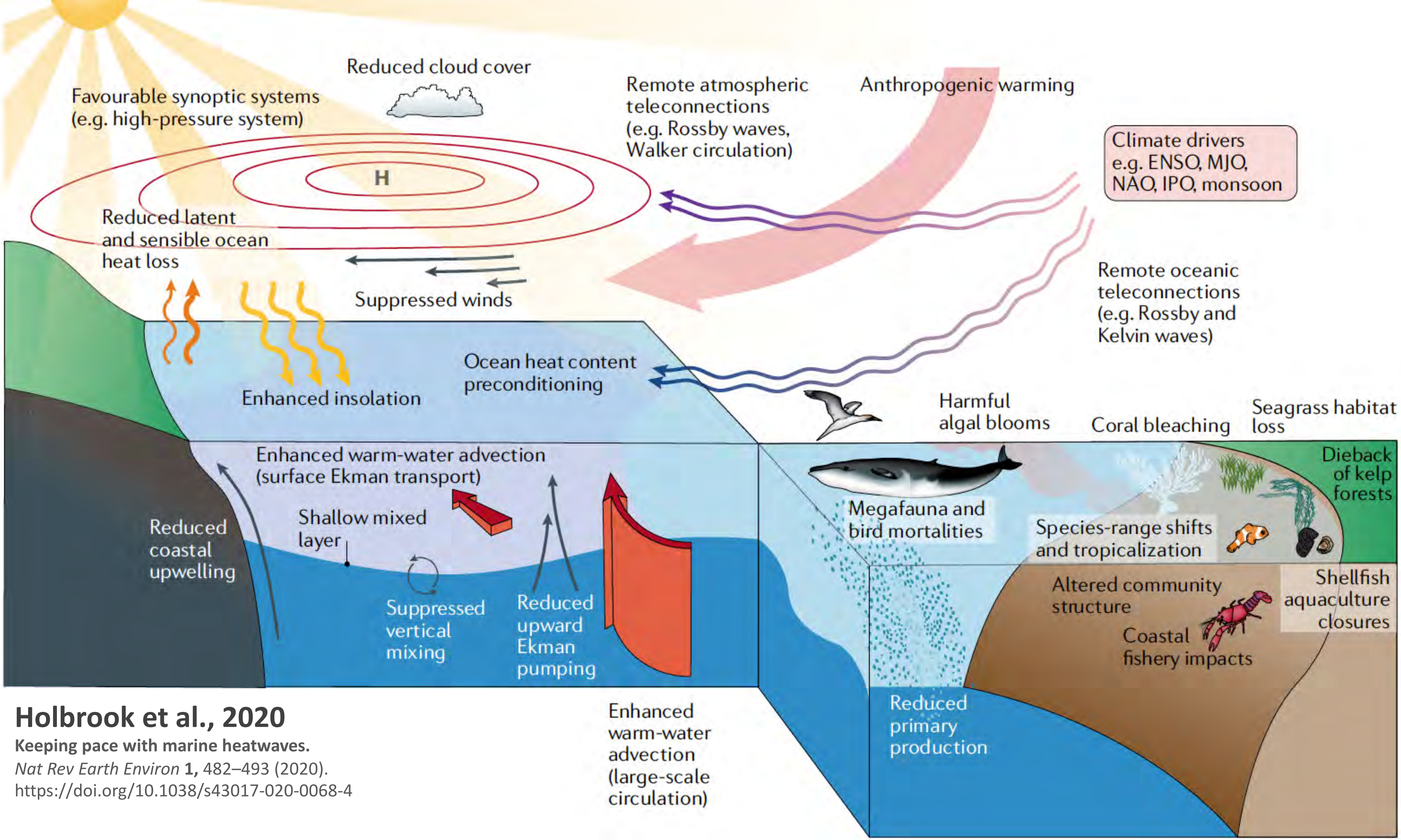
discrete, prolonged, & anomalously warm water events











Holbrook et al., 2020

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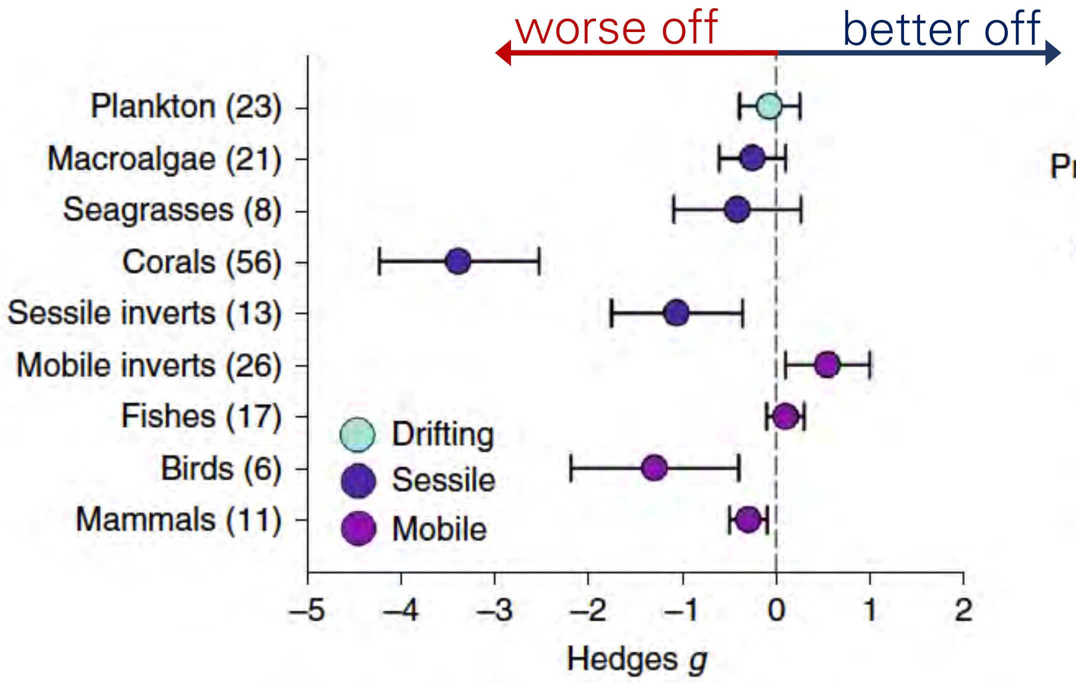

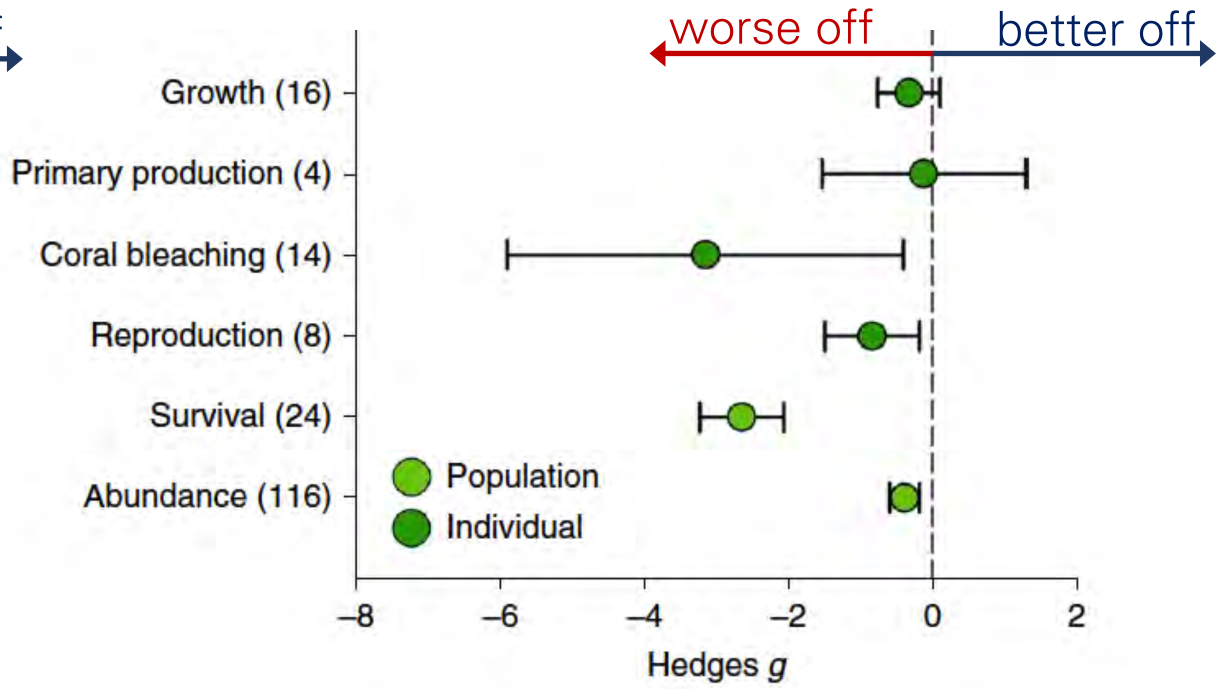

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***Marine heatwaves threaten global biodiversity and the provision of ecosystem services*.**

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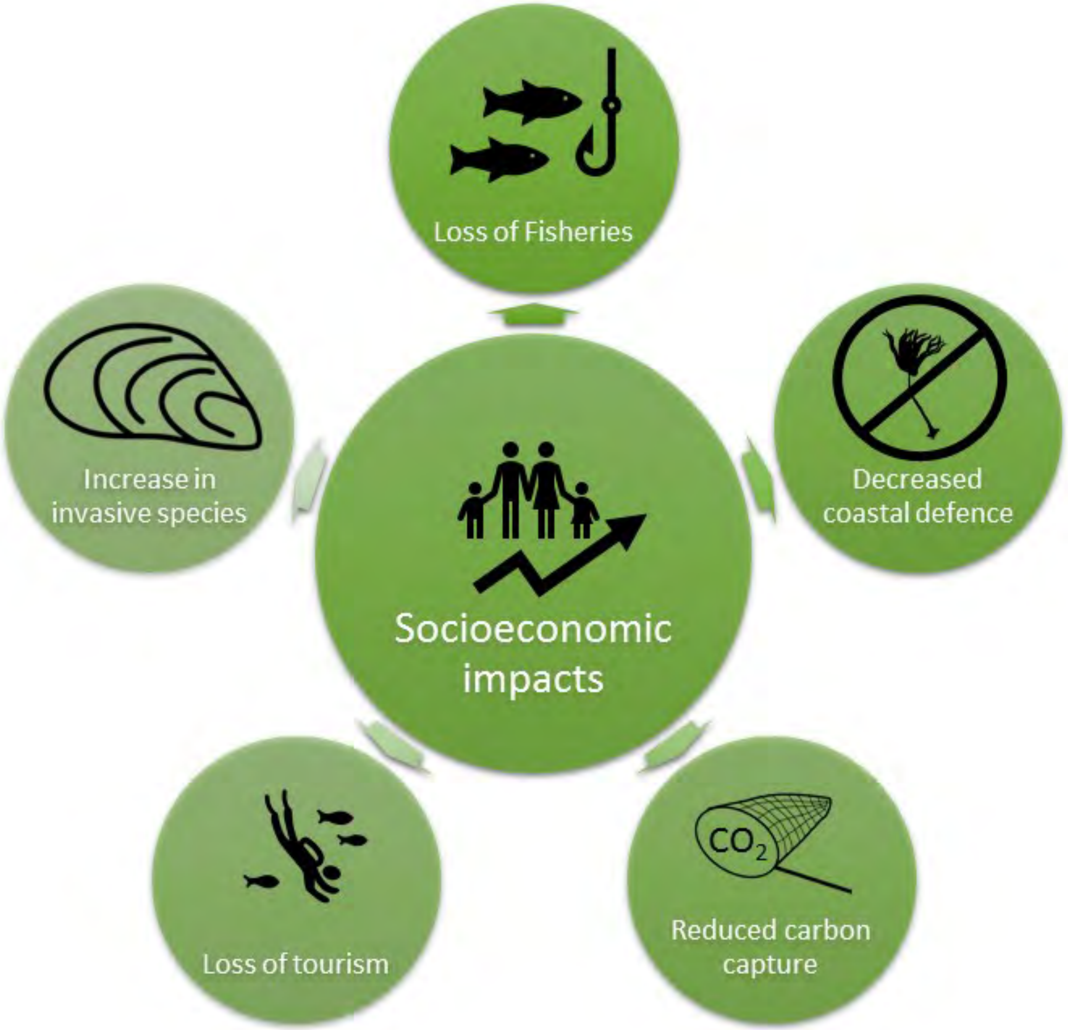
**Pictures from Vergés and Campbell (2020)*

Marine Heatwave Threats



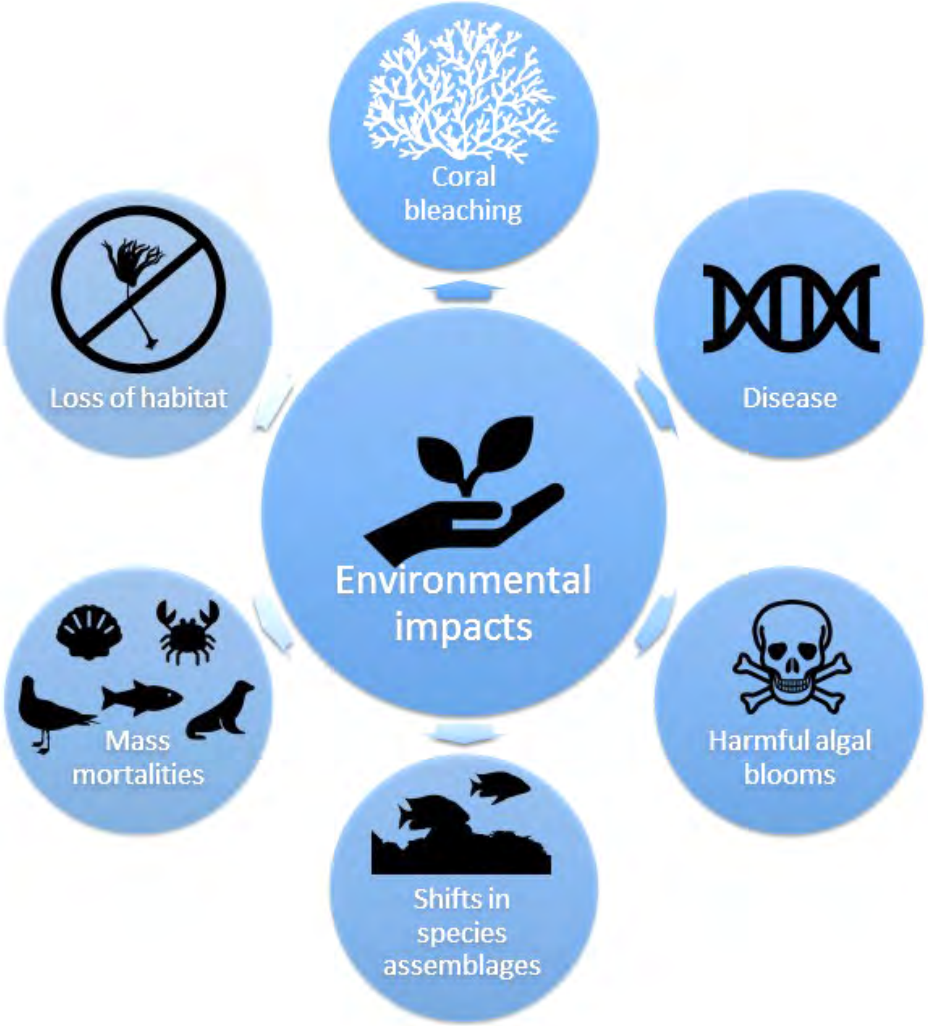


Image Credit: Katie Smith, The Marine Biological Association

Looking ahead 10 years

- Not if, but when
  - Forecast & Prediction
- Evolutionary Adaptation
  - Identify winners & losers
  - Anticipate species range shifts
- Compound Extremes & Whiplash Events
  - Multi-faceted monitoring of temperature, oxygen, nutrients, pH, etc.

Keeping pace with marine heatwaves

Neil J. Holbrook, Alex Sen Gupta, Eric C. J. Oliver, Alistair J. Hobday, Jessica A. Benthuysen, Hillary A. Scannell, Dan A. Smale and Thomas Wernberg

Abstract | Marine heatwaves (MHWs) are prolonged extreme oceanic warm water events. They can have devastating impacts on marine ecosystems — for example, causing mass coral bleaching and substantial declines in kelp forests and seagrass meadows — with implications for the provision of ecological goods and services. Effective adaptation and mitigation efforts by marine managers can benefit from improved MHW predictions, which at present are inadequate. In this Perspective, we explore MHW predictability on short-term, interannual to decadal, and centennial timescales, focusing on the physical processes that offer prediction. While there may be potential predictability of MHWs days to years in advance, accuracy will vary dramatically depending on the regions and drivers. Skilful MHW prediction has the potential to provide critical information and guidance for marine conservation, fisheries and aquaculture management. However, to develop effective prediction systems, better understanding is needed of the physical drivers, subsurface MHWs, and predictability limits.

Prolonged extreme oceanic warm water events — also known as marine heatwaves (MHWs) — can severely impact marine ecosystems and the services they provide[1–6]. Yet, despite their significance, dedicated and coordinated research into MHWs only became prominent following the extreme event off Western Australia in 2011 (REFS [7,8]). Indeed, it was during this event that the term 'marine heatwave' was first used to characterize an extensive, persistent and extreme ocean-temperature event[9] (BOX 1), spurring a new wave of research into their physical processes and corresponding impacts.

Since 2011, MHWs have been observed and analysed both retrospectively and contemporaneously and are now recognized to occur over various spatio-temporal scales. For example, given the ocean's heat capacity and dynamical scales, MHW events can persist for weeks to years[10–16]. They further vary in spatial extent and depth, depending on the processes that cause and maintain them, as well as the geometry of the regions in which they occur. For instance, MHWs can be locally confined to individual bays[17], around small islands or along short sections of coastline, or be broadly distributed over regional seas[10,18], ocean basins[15,19] or even spanning multiple oceans[20,21] (for a map of major MHW events, see FIG. 1).

As well as the physical drivers, the ecological impacts of MHWs have been studied in some depth. The effects include biodiversity loss and changes in species behaviour or performance[3,7], loss of genetic diversity and adaptive capacity[22], economic impacts from changes in fishery catch rates[1,23–25] and mortality or altered performance of farmed aquaculture species[13].The impacts of MHWs are particularly evident on coral reefs (promoting widespread bleaching, including pan-tropical events[26]), kelp forests (driving significant loss of kelp forest habitats off the coast of Western Australia, New Zealand, Mexico and the North Atlantic[7,27–29]) and seagrass meadows (wherein substantial declines have been observed[30]). At higher trophic levels, MHWs have impacted economically important species, including lobster and snow crab in the northwest Atlantic[1,31], lobster, crabs, abalone and scallops off Western Australia[24,32] and numerous species in the northeast Pacific[33]. In some cases, MHWs have even been linked with increased whale entanglements[34].

Given the evidence for potentially devastating impacts resulting from MHWs, there is a need for skilful prediction to inform effective response and adaptation strategies. This need is amplified by anthropogenic warming, which has increased MHW occurrences by 50% over the past several decades[35], a change that is also projected to increase in the future[36,37] (FIG. 2). However, despite improved process-based understanding[14], knowledge of MHW predictability and present MHW-prediction systems are in their infancy. Hence, there is a compelling need to understand and improve MHW predictability in order to guide marine conservation, fisheries management and aquaculture practices in a warming world.

In this Perspective, we explore the mechanisms and potential for MHW predictability across a range of timescales. We first consider the physical mechanisms that cause MHWs, before then exploring the importance of MHW-event monitoring as an activity to improve understanding of MHW precursors, processes and forecasts. Using this knowledge, we subsequently outline the potential for MHW predictability. Finally, we address future challenges and opportunities for MHW research, including those arising from climate change.

Physical mechanisms

A range of physical mechanisms can lead to anomalously warm ocean waters (FIG. 3). These include enhanced solar radiation into the ocean, suppressed latent and sensible heat losses from the ocean to the atmosphere, shoaling of the mixed layer from increased stratification, increased horizontal transport (advection) of heat, reduced vertical heat transport associated with suppressed mixing and reduced coastal upwelling or Ekman pumping (see REF. [14] for an in-depth discussion). Elevated upper ocean heat content, or the re-emergence of warm anomalies from the subsurface, can also precondition the ocean for increased likelihood of MHW occurrence. The amplification or suppression of these processes, either in isolation or collectively, can promote or inhibit MHW development driven by local air–sea interactions and feedbacks, and large-scale modes of climate variability acting locally or remotely. Here, we detail these physical processes, the

Box 1 | **Defining marine heatwaves**

'Heatwave' is a well-recognized term, broadly indicating to society the risks associated with thermal stresses on people and the environment. The atmospheric-research community uses qualitative descriptors and quantitative metrics to express heatwave events, with a widely used definition describing a heatwave as at least three consecutive days of air temperatures above the 90th percentile of climatological, seasonally varying norms[129].

In 2015, an analogous definition was developed for marine heatwaves (MHWs). Compared with the atmospheric definition, it was recommended that a threshold of at least 5 days above the seasonally varying 90th percentile[124] is needed to acknowledge longer thermal persistence timescales in the ocean. MHWs have also been defined as sea surface temperatures exceeding the 99th percentile[36,109] — a definition applied in the Intergovernmental Panel on Climate Change (IPCC) Special Report on the Ocean and Cryosphere (SROCC[117]). In fact, the SROCC defines a MHW as "an event at a particular place and time of the year that is rare and predominately, but not exclusively, defined with a relative threshold; that is, an event rarer than 90th or 99th percentile of a probability density function."

understanding of which has substantial bearing on MHW predictability, as discussed subsequently.

Coupled air–sea interactions and atmospheric preconditioning. Many of the iconic extratropical MHWs (for example, The Blob, central South Pacific) have been associated with persistent high-pressure systems (or blocking highs) over the ocean and their resulting air–sea interactions. Atmospheric blocking reduces cloud cover, enhances insolation and suppresses surface wind speeds, resulting in hot, dry weather. Collectively, these conditions reduce sensible and latent ocean heat loss and increase solar radiative heating, in turn, warming sea surface temperatures (SSTs)[14,19,38,39] (FIG. 3). Given that blocking highs have large spatial scales and can persist for weeks to months, they have the potential to substantially raise ocean temperatures over a large geographic region for a considerable duration, as reflected in the characteristics of MHWs they promote. For example, key events occurred during 2003 in the Mediterranean Sea[10,40], 2009/10 in the central South Pacific[19], 2012 in the northwest Atlantic[12,41], 2013/14 in the northeast Pacific[38] and 2017/18 in the Tasman Sea[42,43].

While these events are related to atmospheric blocking, the specific mechanisms vary. The 2009/10 MHW in the central South Pacific, for example, was generated by Rossby wave-related atmospheric anomalies arising from the central Pacific El Niño[19]. By contrast, the 2003 Mediterranean Sea[10,44] and 2017/18 Tasman Sea MHWs[42,43] formed through enhanced radiative heat fluxes caused by concurrent atmospheric heatwaves. For the 2012 northwest Atlantic[12,41] and 2013/14 northeast Pacific MHWs[15,38], atmospheric preconditioning was important. Specifically, persistent atmospheric weather patterns through the winter reduced wintertime heat loss from the ocean to the atmosphere, keeping the upper ocean warmer and preconditioning it to increased MHW likelihood in the following seasons. The 2013 North Pacific blocking pattern was so extreme and persistent that it was given the nickname the 'Ridiculously Resilient Ridge' (REF.[45]), referring to a large and unusual region of high sea-level pressure that was unprecedented since at least the 1980s[38].

Oceanic preconditioning. Oceanic preconditioning of warm temperature anomalies can result from the process of re-emergence[46]. If heat anomalies form during winter when the mixed layer is deep, subsurface anomalies can become uncoupled from the surface ocean in summer when the mixed layer shoals. When the mixed layer deepens again during the subsequent winter, the persistent subsurface anomalies are re-entrained into the mixed layer, making the surface ocean warmer[46]. Mixed-layer depths are also important for modulating the response of the surface ocean to heat fluxes. For example, when mixed layers are shallower than normal, they will warm more quickly for a given input of heat[47]. Indeed, an anomalously shallow mixed layer when net heat fluxes are into the ocean could increase the likelihood of summer MHWs, even in the absence of anomalously large surface heat fluxes[48]. Ocean circulation changes can also precondition the ocean for MHW development over longer timescales and at greater depths, whereby ocean heat content increases reduce surface heating requirements for MHW generation[49].

Modulation by climate modes and teleconnections. Modes of climate variability — which operate on timescales from intraseasonal (Madden–Julian Oscillation (MJO)), through interannual (El Niño–Southern Oscillation (ENSO), Indian Ocean Dipole), to decadal — are known to modulate the frequency, intensity and duration of MHWs[14,35,50]. These modes can influence ocean temperatures, including the development of regional MHWs, directly or remotely via atmospheric or oceanic teleconnections, which reverberate the effects globally[14,51].

On intraseasonal timescales, for instance, the MJO influences atmospheric circulation by suppressing convection and increasing Ekman pumping off northwest Australia, specifically during MJO phases 2–5 (REF.[52]). This process preferentially supports warmer SSTs and increases the likelihood of MHWs off Western Australia[53]. Conversely, the MJO has been associated with enhanced convection, capable of exciting a Rossby wave train through to the extratropics that effectively sets up a blocking high, which forces MHWs in the southwest Atlantic Ocean[39].

On interannual timescales, ENSO events play a substantial role in influencing MHW likelihood, not only in the tropical Pacific but also in regions remote to ENSO's centre of action. El Niño events are associated with increased SSTs in the central and eastern tropical Pacific, resulting in MHWs through the dynamic response of the thermocline to wind stress changes at the surface, Kelvin wave propagation across the Pacific and reduced upwelling[14]. El Niño events have also been associated with reduced strength of the subtropical north-easterly trade winds, which, in turn, reduce evaporation, increase local SSTs and trigger a positive thermodynamic wind–evaporation–SST feedback[15]. This feedback subsequently activates meridional modes, which propagate and amplify SST from the subtropics into the central equatorial Pacific. There, the positive SST anomalies favour the development of El Niño and tropical convection, exciting atmospheric Rossby waves that teleconnect to the extratropics, which aid persistence[15]. Conversely, La Niña events can remotely elevate SSTs off Western Australia via the propagation of oceanic Kelvin waves and by strengthening heat transport through the Leeuwin Current, increasing the likelihood of MHWs[47,54]. Thus, the phase of ENSO (along with other modes) is important in enhancing or suppressing MHWs in different regions across the globe[14,35].

On multi-year timescales, oceanic Rossby waves can propagate westwards for years to decades across ocean basins and modulate ocean heat content and the local vertical structure along their path. In particular, it has been shown that oceanic Rossby waves generated by wind changes in the interior South Pacific can modulate poleward transport through the Tasman Sea[55] and enhance MHW event likelihoods there[56]. This likelihood is increased despite the fact that the East Australian Current Extension region is eddy-rich, with eddy variability typically occurring on timescales of weeks to months. This oceanic Rossby wave teleconnection process provides an additional modulation mechanism to effectively 'load the dice' for increased MHW potential predictability in the Tasman Sea up to several years in advance.

Monitoring marine heatwaves

Coupled with understanding the physical processes contributing to MHW development, ocean temperature monitoring programmes are crucial for their identification and categorization. The near real-time monitoring of MHWs requires resources to deliver temperature data on a range of spatial scales and depths. In this regard, satellite sensors provide a suite of global and regional ocean surface information, including SST, sea level, currents and winds. Near real-time in situ data from Argo floats, gliders and moorings provide information on subsurface conditions, such as mixed-layer depth and heat content.

Integrated ocean data systems that incorporate these multiple data streams can offer region-specific information for monitoring MHWs. For example, Australia's Integrated Marine Observing System (IMOS) provides near real-time summaries of surface currents and SST, which, when referenced against climatology data, indicates the presence of MHWs around Australia — representing valuable information for the public, aquaculture industries, tourism operators in the marine environment and local communities.

Event-based monitoring. Event-based monitoring can offer targeted information for marine stakeholders once a MHW event has commenced. For example, identifying properties of a MHW, such as its vertical extent, can provide information on its persistence or potential disruption to marine ecosystems (TABLE 1); a shallow MHW might

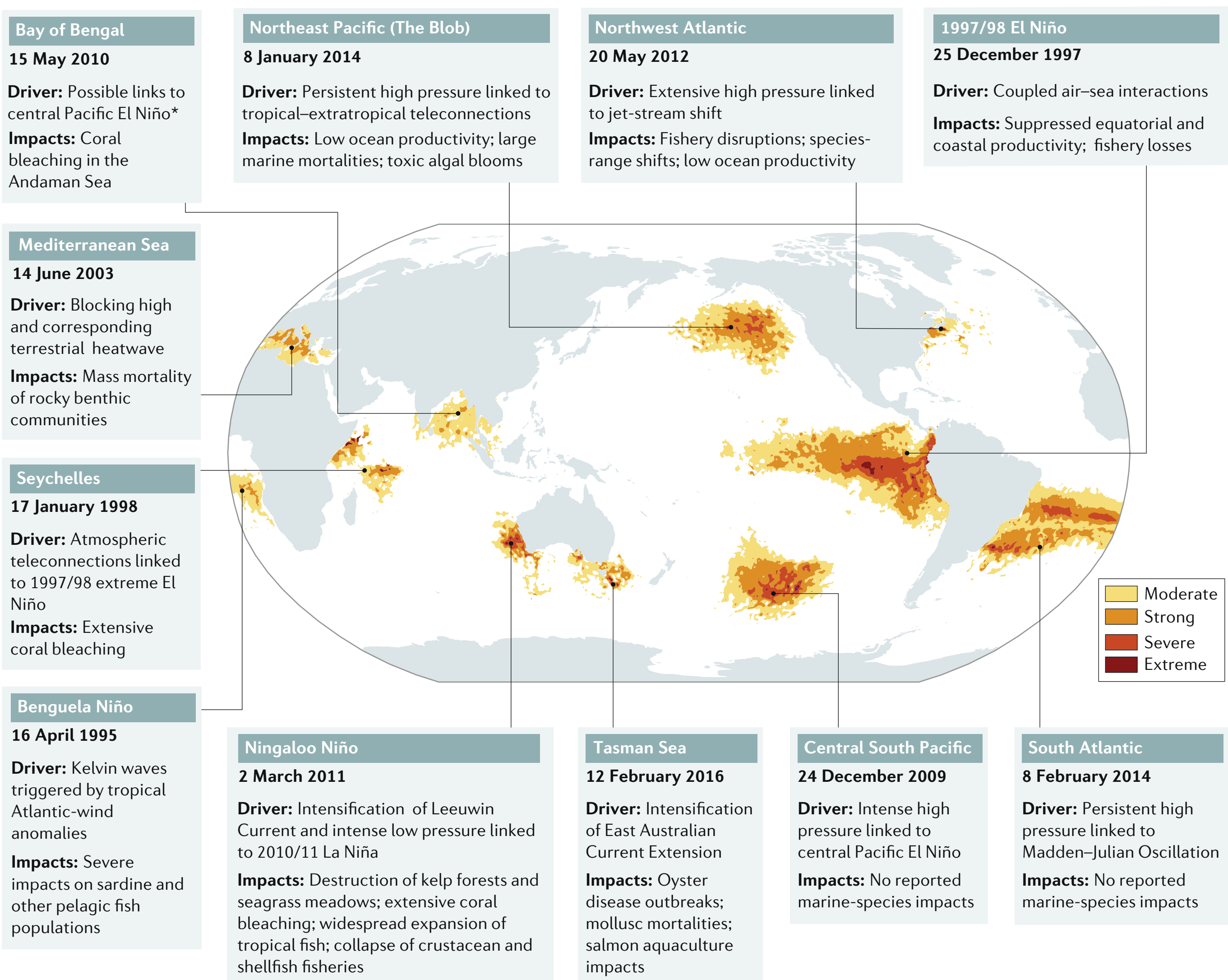


Fig. 1 | **Drivers and ecological impacts of major marine heatwave events.** A subset of major marine heatwave (MHW) events since 1995. The MHW intensity scale, from moderate to extreme, represents conditions corresponding to the peak date of the event, with categories identified successively as multiples of the 90th percentile[101]. The spatial scale, intensity and ecological impacts of MHWs can be substantial, as observed for the Benguela Niño[112], Seychelles[113], Ningaloo Niño[27,111], Tasman Sea[13], central South Pacific[19], South Atlantic[39], 1997/98 El Niño[114], northwest Atlantic[1,12], The Blob[15,38], Bay of Bengal[115,116] and the Mediterranean Sea[10,44]. Figure inspired by schematics in REFS[109,117,118]. *While the Bay of Bengal MHW co-occurred with a major central Pacific El Niño event, there have been no studies to confirm or reject a causal link.

be more likely to weaken if strengthening winds lead to deep mixing, whereas a deep MHW offshore would persist even if winds intensified.

During a MHW, rapid deployment of specific equipment can augment standard and integrated systems, and can target regions where infrastructure is not present or does not meet the needs for near real-time monitoring. For instance, existing technology such as autonomous underwater vehicles, vertical-profiling instruments and undulating towed vehicles can be manoeuvred to resolve a MHW's vertical structure and investigate contributing physical processes. An IMOS programme to examine the emergence, maintenance and decay phases of the 2018/19 Tasman Sea MHW, for example, revealed the potential for such monitoring approaches. During this programme, Slocum gliders deployed off Tasmania provided high temporal and spatial sampling over the continental shelf, informing the depth and characteristics of the anomalously warm-water event (FIG. 4). Near real-time data were shared with regional stakeholders, including local marine industries such as salmon and oyster aquaculture, stimulating interest and intensifying demand for predictive capability. Indeed, such real-time information, achieved through event-based monitoring, can inform adaptive management responses relevant

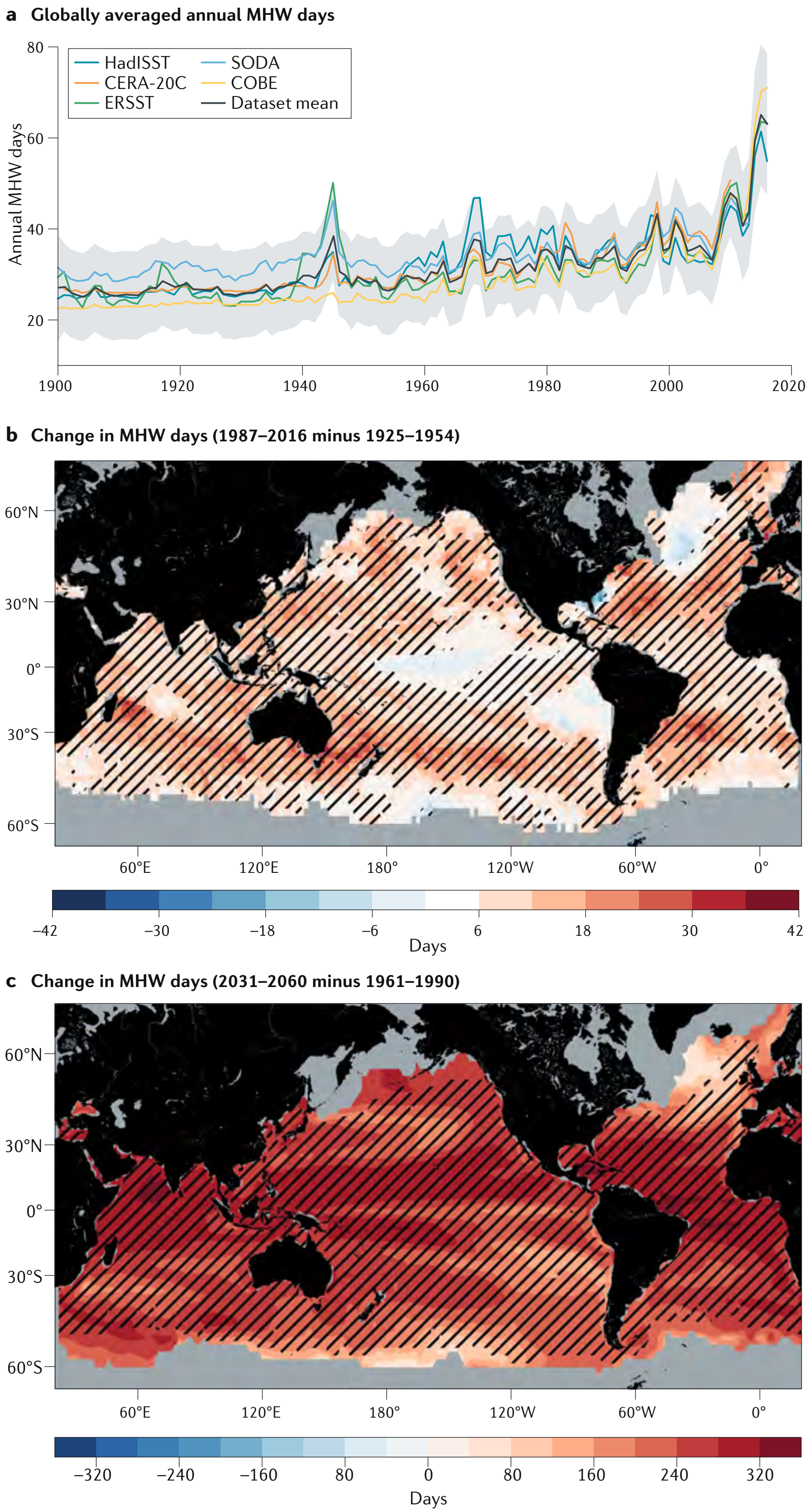


Fig. 2 | **Trends in global marine heatwave occurrence.** **a** | Globally averaged changes in the annual number of marine heatwave (MHW) days based on the Hadley Centre Sea Ice and Sea Surface Temperature (HadISST)[119], Extended Reconstructed Sea Surface Temperature (ERSST)[120], COBE[121], CERA-20C[122] and Simple Ocean Data Assimilation (SODA) datasets[123]. Grey shading indicates the 95% confidence interval. **b** | Changes in the annual number of MHW days from the period 1925–1954 to 1987–2016, based on the same data as in panel **a**. Hatching indicates statistically significant changes ($P < 0.05$). **c** | Changes in the annual number of MHW days from the period 1961–1990 to 2031–2060, based on six Climate Model Intercomparison Project (CMIP5) global climate models under the Representative Concentration Pathway (RCP) 8.5 emissions scenario. Hatching indicates grid points in which all six models agree on the sign of the change. Grey areas in panels **b** and **c** reflect missing data, primarily due to seasonal ice cover. In panels **a** and **b**, the effect of natural variability (the Atlantic Multidecadal Oscillation, Pacific Decadal Oscillation and El Niño–Southern Oscillation) has been removed following REF.[35]. MHW days are defined as the number of days when sea-surface-temperature anomalies exceed a daily climatological 90th percentile threshold, for at least 5 days[124]. The annual count of MHW days has increased substantially since the early twentieth century, and this increase has only accelerated up to the present day. This rise is projected to continue increasing in the future, with annual MHW days approaching a full year by the late twenty-first century. Panel **a** adapted from REF.[35], CC BY 4.0. Panel **c** reprinted from REF.[37], CC BY 4.0.

to multiple stakeholders, demonstrating the importance of translating raw data streams into visual results.

Monitoring subsurface marine heatwaves. While remote sensing, in combination with surface drifting buoys and ship underway data, provides high resolution SST data for both historical and real-time analyses of MHW surface characteristics, it is not only surface properties that need attention. MHWs can exhibit considerable depth penetration, or exist at depth with no surface expression, necessitating subsurface data[57,58]. Yet, the ability to characterize subsurface MHWs in both the open ocean[58] and coastal regions[57] is challenged by the sparsity of observations and the absence of continuous, long-term time series in the historical record (such as data from eXpendable BathyThermographs (XBTs), CTDs (conductivity, temperature and depth), gliders and Argo profiles).

These challenges hinder the development of robust and spatially complete subsurface temperature climatologies needed for statistical assessments of MHWs. Indeed, while some datasets exist[59,60], they do not extend to coastal regions, owing to an absence of Argo profiles[61]. Nevertheless, analyses of MHW vertical structure and corresponding processes have been attempted through the use of long-term mooring sites[20,57], autonomous floats in regional seas (such as the western Tasman Sea[58]) and dynamical ocean models or reanalyses that assimilate ocean observations[62,63]. Each of these approaches have known limitations; mooring sites provide information for single points in space and reanalysis data are based on model-synthesized sparse observations, meaning the products are only as good as the quality and quantity of observations they assimilate, and their distribution. Consideration of how to identify MHWs using suboptimal data is, therefore, important for future work[64]. Better understanding of the relevant timescales of subsurface MHWs, which can be longer than those at the surface[58], can alleviate some of the demands on high-frequency sampling. It is clear, however, that without improved subsurface characterization of MHWs — with bearing on surface recharge, heat storage and mixing — their prediction potential remains limited.

Predicting marine heatwaves

As discussed previously, MHW occurrences can depend on modes of climate variability[14,35,50], the background ocean state (heat content, mixed-layer depth)[48,49], ocean circulation[13], remote teleconnections[14,15,39,56] and the presence of weather systems such as atmospheric blocking[38,39,42]. In many instances, these drivers are themselves at least partially predictable, especially in regard to climate modes[65], suggesting that certain MHW events are potentially predictable many months ahead[14,18,56]. Here, we outline the need for understanding MHW predictability, their timescales and the development of forecast systems.

The benefit of and need for marine heatwave prediction. Skilful prediction of MHW events, and their intensity, duration, depth

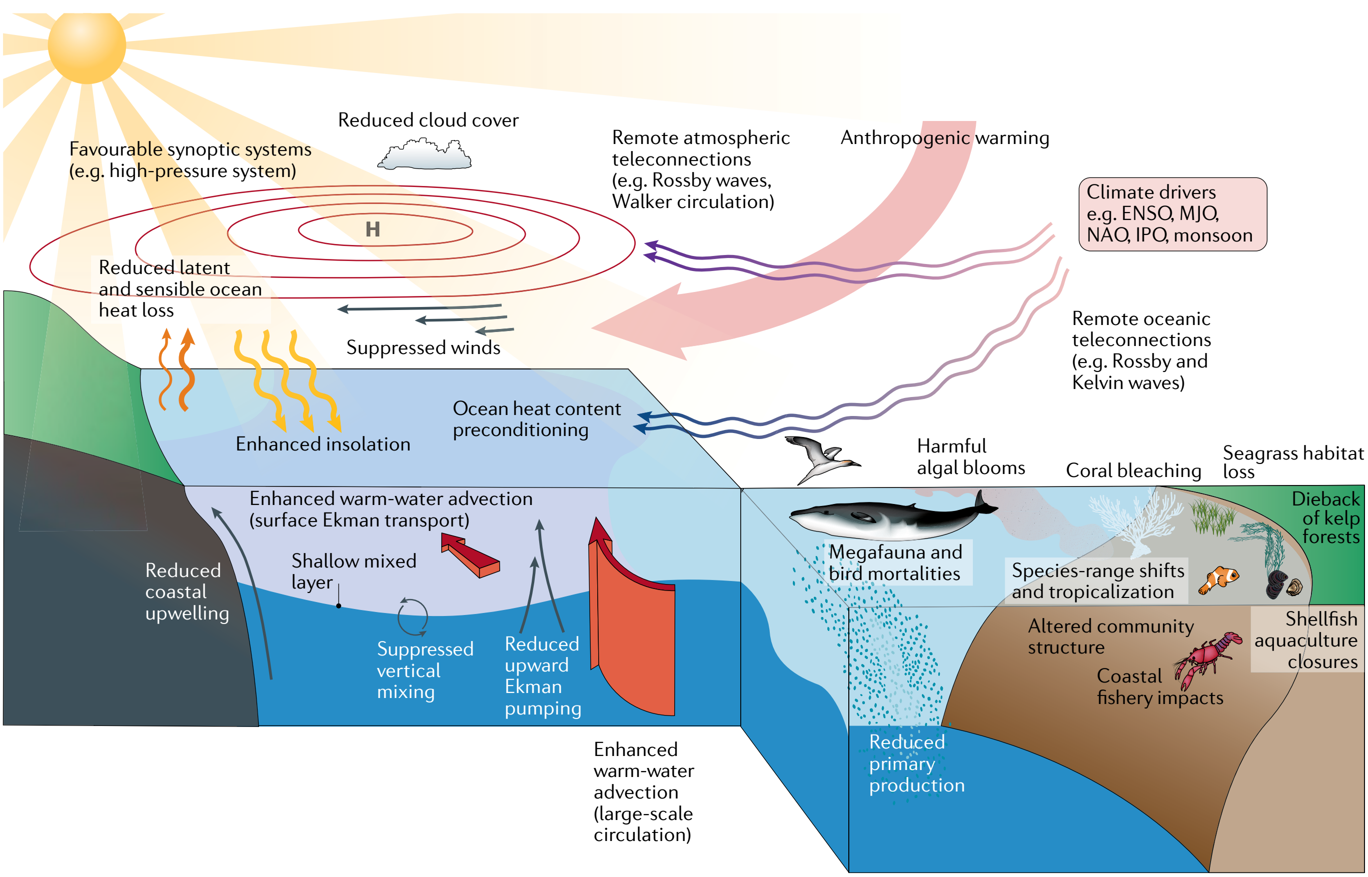


Fig. 3 | **Marine heatwave drivers and impacts.** Schematic of the drivers of marine heatwaves (left) and their impacts on oceanic and coastal ecosystems (right). Surface marine heatwaves are caused by local ocean and atmosphere heat fluxes affecting the surface mixed layer. These processes are controlled by local synoptic systems that can be modulated by large-scale climate oscillations and anthropogenic warming. Impacts range across trophic levels often affecting human systems. ENSO, El Niño–Southern Oscillation; H, high pressure; IPO, Interdecadal Pacific Oscillation; MJO, Madden–Julian Oscillation; NAO, North Atlantic Oscillation.

Table 1 | **Marine heatwave potential predictability lead times, scales, and potential and example impacts**

Condition	Predictability lead time	Predictability source	Persistence	Vertical scale	Horizontal scale	Impacted ecosystems	Impact severity	Example
Strong atmospheric and oceanic contributions[a]	Months (at least)	Local and remote climate forcing	Months	Up to 100s of metres	1,000s of kilometres	Surface to benthic (possibly)	Potentially substantial	2011 Western Australia MHW[47,111]
Strong atmospheric and weak oceanic contributions[a]	~1–2 weeks or season ahead	Atmospheric preconditioning and/or teleconnections	Months	Up to 10s of metres	1,000s of kilometres	Within mixed layer	Moderate to substantial	2014 NE Pacific + 2013/14 SW Atlantic + 2017/18 eastern Tasman Sea MHW[38,39,42,43]
Weak atmospheric and strong oceanic contributions[a]	Months to years	Oceanic preconditioning and/or teleconnections	Months	Up to 100s of metres	100s of kilometres	Surface to benthic (possibly)	Moderate to substantial	2015/16 Tasman Sea MHW[13,49,56]
Weak atmospheric and oceanic contributions[a]	Days	Transitory weather or eddies	Hours to days	Up to 10s of metres	Local	Minimal	Minor	Heat spikes

[a]Contributions refer to those from local atmospheric sources and those arising from oceanic advection. MHW, marine heatwave.

and spatial extent, is expected to be of great value to marine resource users and managers of fisheries, aquaculture and conservation[65–67]. For instance, short-term forecasts of a few days to weeks[68] would allow for active management strategies to be implemented, such as harvesting or relocating farmed species in aquaculture industries that would likely suffer mortality under MHW conditions. With predictive capabilities, it might be possible to ameliorate stressful conditions through short-term active interventions such as cooling or shading, as is currently implemented in Australian fishery and aquaculture sectors in response to seasonal forecasts of adverse conditions (for example, water temperature, rainfall and air temperature)[69]. Indeed, on seasonal timescales, forecasts can be used to inform strategic fisheries management decisions (target species, quotas and timings) or to implement temporary protected areas. While most applications of MHW predictions seek to support mitigation of detrimental ecological consequences, short-term to medium-term prediction of MHWs could also bring opportunities. For example, the 2011 MHW in Western Australia led to the temporary appearance of marine megafauna (whale sharks, manta rays, tiger sharks, turtles) and recreationally important fish species well outside their normal range[9], providing a short-term business opportunity for local tour operators.

Anticipating regions that might be affected by decadal and longer-term MHW intensification would also guide placement of fully protected areas[70], as well as inform fisheries management approaches by future-proofing target species for fisheries and aquaculture[24]. Moreover, longer-term prediction can help focus conservation efforts such as assisted evolution or early restoration in sensitive habitats and regions[30]. Skilful prediction can identify areas where mitigation strategies might have limited utility, as it may not be economically feasible or technically possible to mitigate all the impacts on marine ecosystems[71].

Predictability timescales. The degree to which MHWs are predictable requires knowledge of how the relevant physical drivers and processes interact in time, from days (SST persistence), to weeks (blocking systems and atmospheric teleconnections), to months (oceanic preconditioning) and years (low-frequency climate modes and oceanic teleconnections). Given that the heat capacity, persistence and propagation timescales of oceanic processes (such as from oceanic Rossby waves) are much greater than those for the atmosphere (for instance, from blocking), MHW development is expected to have longer predictability lead times in regions where oceanic processes dominate (TABLE 1, FIG. 5).

For example, MHW forecasts with lead times of 7–10 days might be possible when air–sea interactions (such as from a blocking event) dominate MHW development. However, at weeks-to-months leads, preconditioning factors from mixed-layer depth or ocean heat content enhance predictability potential[48,49]. For example, if the mixed-layer depth in boundary current and extension regions is relatively shallow leading into summer, anomalously warm SSTs might be expected in the summer season[48]. Information on ocean advection processes and internal variability (from large-scale eddies, for example) might improve MHW forecast potential on similar timescales, as has been found for seasonal forecasts[72] (TABLE 1). Atmospheric and oceanic circulations are recognized in describing MHW types along the eastern Tasmanian shelf region, where persistence and intensity are related to the relative contribution of the East Australian Current and atmospheric heat input[62].

Climate modes and their teleconnections are expected to influence MHW predictability on subseasonal to seasonal[18,39,53,73] and interannual to decadal timescales[14,56]. Most climate modes have some degree of predictability, or at least persistence, and can, therefore, provide potential sources of MHW predictability. For example, ENSO can be predicted ~6 months in advance, and, given strong connections to MHWs off Western Australia, some degree of predictability on seasonal timescales might be possible in that region.

Moreover, atmospheric blocking events at midlatitudes via remote teleconnections also offer some predictability, albeit at much shorter timescales[39]. While blocking can be influential to MHW development, the realistic simulation of blocking is a challenge, as is the forecasting of these blocking events[74–77]. Specifically, although atmospheric blocking can increase the likelihood of MHW event occurrence, other short-term oceanic processes can work against the blocking such that the event does not occur, creating significant uncertainty around MHW event likelihood.

Other processes can also offer predictive potential. The clustering of ocean eddies in western boundary currents[78], for example, contribute potentially predictable changes in ocean temperature extremes[62,79,80]. Remotely forced oceanic Rossby wave teleconnections — which take months to many years to propagate westwards across ocean basins — also hold considerable promise for multi-year prediction of MHW likelihood in the Tasman Sea region[56].

Developing forecast systems. Marine managers can gain valuable information from seasonal MHW forecasts. However, skilful forecasts are not easily achieved. For example, a recent assessment of seasonal forecast skill from the US National Centers for Environmental Prediction's Climate Forecast System in 'The Blob' region had little success[81]. Meanwhile, a separate assessment of seasonal MHW forecasts of the California Current System in eight global climate-forecast systems indicated that large ensemble forecasts were potentially beneficial, with MHWs being more or less predictable, depending on the forcing mechanisms[18]. In Australia, ocean 'weather' forecasts (7–10 days) are already available through Bluelink, but these have not yet specifically addressed MHWs.

Testing and developing the aforementioned relationships and timescales for forecast systems can benefit from using data-learning algorithms or through process-based ocean model experiments, including single-model or multi-model ensembles. Such examples have been shown for coral-bleaching events[82]. MHW-forecast systems that use large ensembles of weather and/or climate model simulations are expected to be the most promising, in line with similar ensemble numerical modelling techniques applied to forecast extreme events such as tropical cyclones. The use of machine learning to synthesize datasets is also a promising avenue towards sequential time series forecasting. For example, neural networks composed of gated recurrent units might hold promise for learning seasonal patterns in SST and predicting extremes when trained with MHW-relevant climate features[83]. Data to train such models should be relevant to the phenomena being forecasted, for example, the NINO3.4 index, regional sea-level pressure and upper ocean heat content. It is clear, however, that, whichever method is used, forecast systems must be developed for different regions given the spatial heterogeneity of predictability processes.

Forecasting MHWs comes with the opportunity and challenge of communicating these forecasts with stakeholders, including fishery managers and the public[84]. Choosing thresholds and timescales for forecasts that are relevant to marine ecosystem response and planning requires identifying who the forecast system will inform and the desired criteria or metrics that will facilitate decision-making, and will require considerable efforts towards stakeholder engagement.

Future perspectives

MHWs have emerged as one of the grand challenges facing marine ecosystems and the sustainability of marine resources, demanding progress in understanding the physical phenomena; improved prediction systems; increased collaboration between marine scientists, climate scientists, marine industries and managers; and the efficient, accessible and consistent dissemination of new knowledge. We expand here on specific areas that warrant attention.

Developing improved understanding of physical processes. Heat budgets provide a valuable tool for understanding processes that cause MHWs[13,14,41,47,48,73]. However, fixed-region budget approaches are limited toanalysing the drivers of MHWs locally, while remote forcing and atmospheric and oceanic teleconnections can also be important contributors to the development and decline of MHWs. Hence, there is merit in considering large-scale dynamical frameworks that connect remote drivers to MHW events, which might benefit predicting MHW onset, persistence, decay, spatial extent, depth and intensity. There has been some success in understanding the physical mechanisms of atmospheric heatwave development through Lagrangian back-trajectory analysis[85,86], a technique also used in the ocean to investigate the influences of microbial exposure to ocean-temperature variability as they drift[87]. A beneficial addition for the analysis of MHW predictability will be the use of adjoint models to explain the fundamental dynamics of back-trajectory teleconnections[88].

Marine ecosystem and fisheries-management implications. The management of marine species, habitats and ecosystems can be seriously affected by MHW impacts on

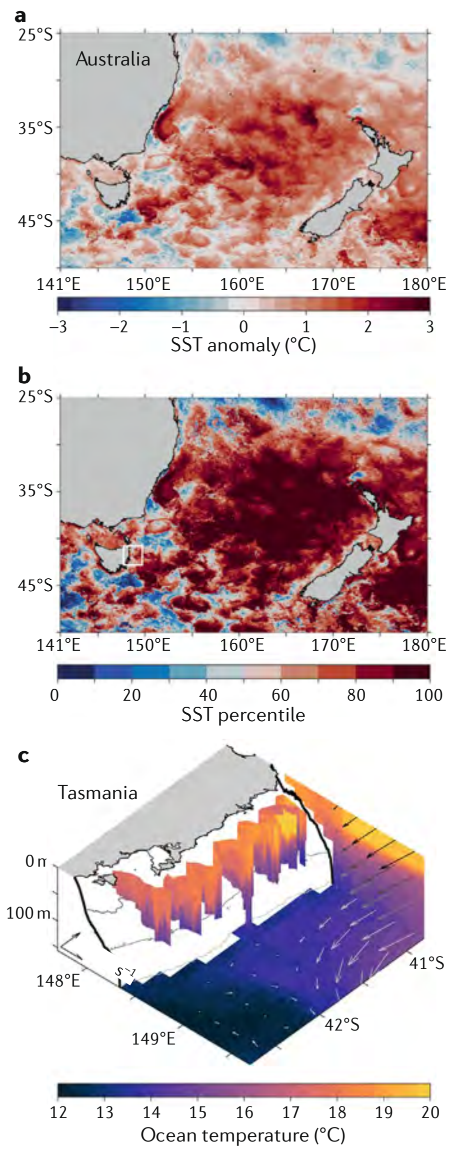


Fig. 4 | **Integrated approaches for monitoring marine heatwaves. a** | February 2019 mean sea surface temperature (SST)[125] anomalies during the 2018/19 Tasman Sea marine heatwave. SST represents monthly mean, multisensor, night-time-only readings at 0.2 m depth. Anomalies are calculated with respect to the 50th percentile February climatology from the SST Atlas of Australian Regional Seas (SSTAARS[126]). **b** | February 2019 SSTAARS SST percentiles, where the percentiles are centred on mid-February and constructed over 60 days. The region off eastern Tasmania is shown by a white box. **c** | Subsurface temperature measured by a Slocum glider, deployed 13 February 2019 in the north and recovered 9 March 2019 in the south. The temperatures and ocean-current velocities (subsampled) along 40.8°S and along 155 m depth are the 13–28 February 2019 means derived from the 10-km resolution Bluelink ReANalysis (BRAN)-2015 (REF.[127]). The current velocities are shaded according to their depth and consistent with the shading of isobaths plotted every 50 m (black to light grey). SST data in panel **a** and Slocum glider data in panel **b** are from the Australian Ocean Data Network (AODN) Portal (https://portal.aodn.org.au/). Coastline data in panel **c** are from REF.[128].

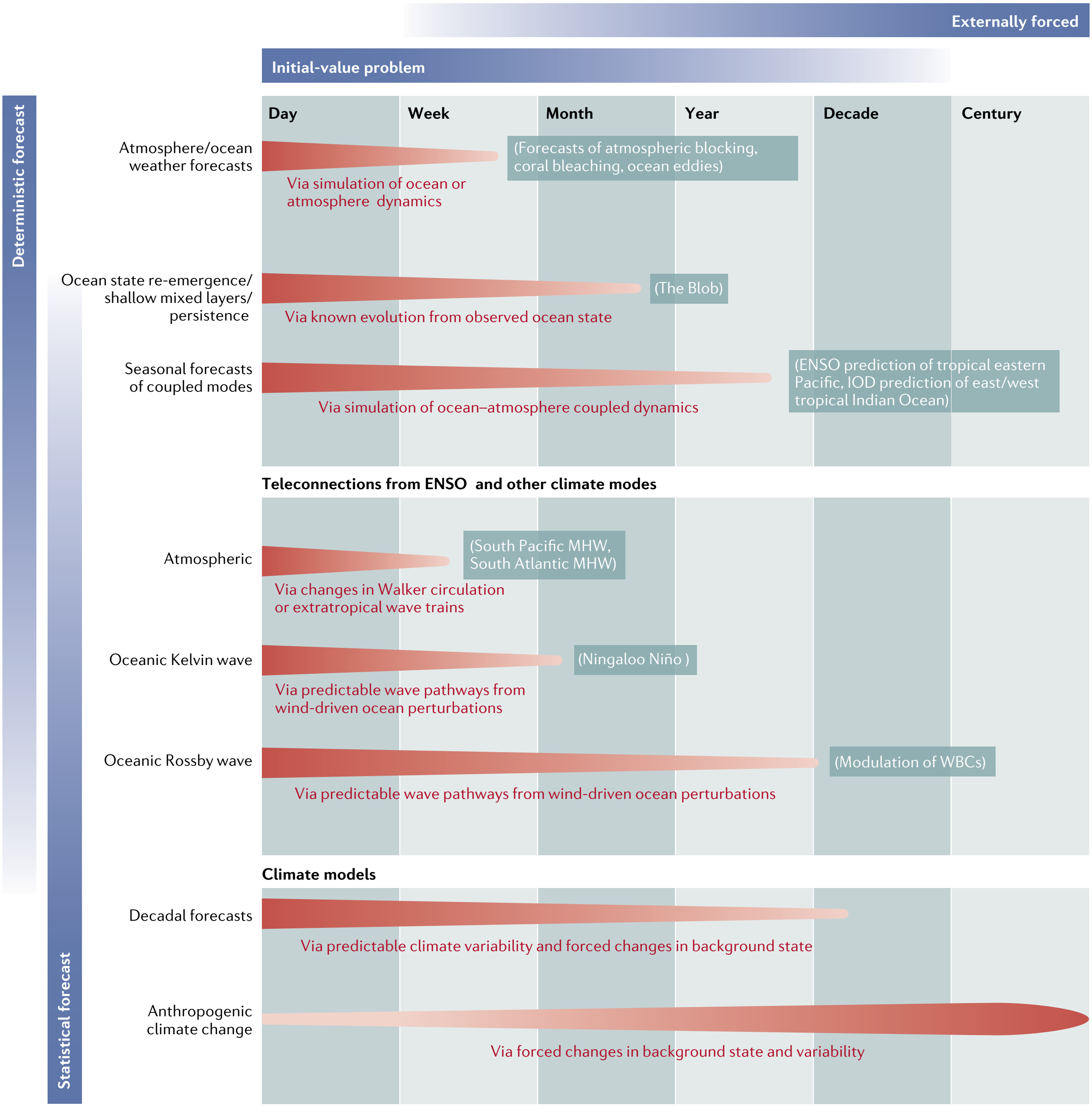


Fig. 5 | **Marine heatwave potential predictability and forecast timescales.** A spectrum of marine heatwave (MHW) prediction timescales and types ranging from initialized forecasts, which predict specific events (deterministic forecasts), through to externally forced projections, in which scenarios can be used to explore changed statistical probabilities of MHW likelihoods (statistical forecasts). The red horizontal bars provide indicative timescales of predictability for each prediction system type, where increasing opacity corresponds to increasing confidence in the prediction skill for that lead time. ENSO, El Niño–Southern Oscillation; IOD, Indian Ocean Dipole; WBCs, western boundary currents.

fisheries and aquaculture, recreational activities and biodiversity conservation[3]. However, marine governance and management practices for responding to a rapidly changing climate are in early stages of development[89], and a wider range of tools and strategies will be needed to adapt to and mitigate against future MHWs[90]. Although a reactive response can limit the damage to some industries, such as aquaculture, in other cases, it might be too late. For example, wild abalone in a MHW would likely be in poor condition and unable to be harvested.

Proactive responses to these extreme events — which include passive approaches such as catchment management, fishing restrictions and identification of marine protected areas — can be implemented by marine managers if sufficient warning is provided[91]. These approaches aim to increase the resilience of marine ecosystems by limiting exposure to stressors that compound the impact of warming, such as overfishing, eutrophication and pollution[92,93], or protecting natural ecological processes such as predation and herbivory, which confer ecosystem resistance to change[94,95]. However, passive approaches can be slow or inefficient[96].

By contrast, active interventions seek to maintain or re-establish ecosystems or key ecosystem services through direct manipulation, ranging from habitat rehabilitation and restoration through to assisted migration, species replacements and assisted evolution[97–99]. Although some of these options are ethically contentious, they may be essential for ensuring the long-term survival of vulnerable marine ecosystems[100], which are under threat from increased MHWs.

The performance of many marine industries is related to the occurrence of favourable environmental conditions, including suitable habitats. Aquaculture requires water temperatures to remain within tolerance limits of the farmed species, while fisheries often rely on species that relocate in response to changing environmental conditions. Warm waters can lead to the arrival of new species, providing opportunity for commercial and recreational fishers. Marine habitats that support fisheries and tourism activities might be damaged or enhanced by anomalous conditions, with coral bleaching a well-known detrimental example. Extreme conditions such as MHWs shock systems and present challenges for managing economic enterprises dependent on the ocean (BOX 2). Information about the likelihood of MHW occurrence is, therefore, valuable to a wide range of marine communities, and decisions can be made to take advantage of opportunities or minimize losses. Importantly, the availability of future environmental information can differentially advantage some groups over others, so decisions about information dissemination should be made with this in mind[84]. One way to minimize differences between stakeholders is to provide transparent and equitable access to information.

Experience to date suggests that three elements assist stakeholders in making the best decisions with forecasts. First, proactive planning of responses enables end users of the forecasts to evaluate different response options depending on factors such as lead time. This process can allow clear options to be considered when a forecast for undesirable conditions is issued and can be undertaken as part of business-planning cycles. Second, dedicated training and information sessions are essential to understand the skill and uncertainty requirements for users[84]. Such sessions could potentially involve simulation activities to explore different responses to extreme events to build the capacity of stakeholders, including those from industry. Finally, implementation of risk-based responses must be considered when skill is low and uncertainty is high. For example, a forecasted MHW that might impact production could be met with a partial early harvest of the vulnerable species, rather than a full harvest[84].

Communication and engagement. While awareness about MHWs is rapidly increasing in the scientific community,

Box 2 | **Marine heatwaves as a stress test for management systems**

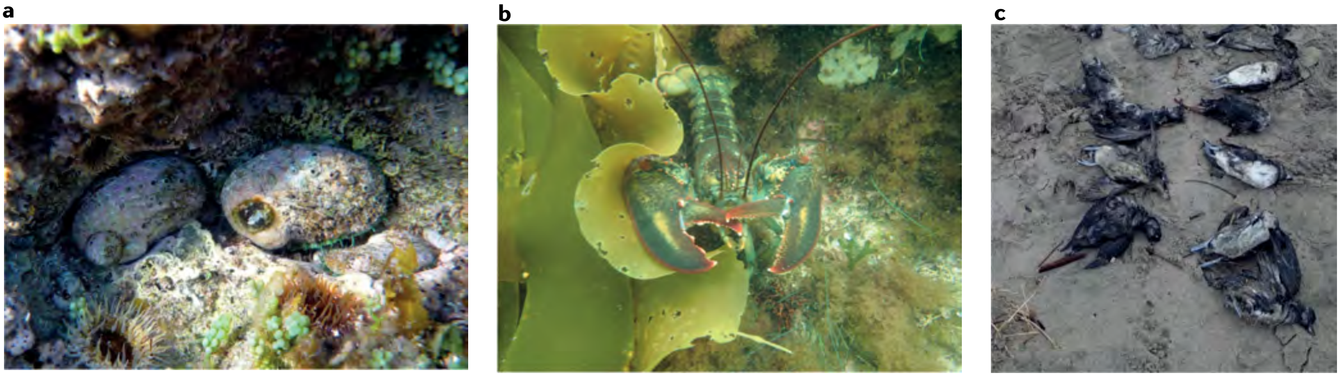
Three well-known marine heatwaves (MHWs) challenged existing management approaches owing to their intensity, duration and rapid onset. The 2011 Western Australia MHW resulted in mass mortality of Roe's abalone, and, in response, managers closed the fishery and instituted an outplanting approach in the years following the event. Scallop fisheries in the region affected by the MHW were closed for 3–5 years, while the Shark Bay crab fishery was closed for 18 months[24]. This event tested assessment and management responses and showed that flexible harvest strategies (as well as early detection and monitoring of the MHW) allowed for early management intervention[24].

The 2012 Gulf of Maine MHW revealed unexpected connections between the natural and human components of the ecosystem[130]. Early and above-average landings in a valuable lobster fishery led to a backlog in the supply chain and a drop in lobster price; exacerbating the supply chain bottleneck was the fact that the Canadian lobster fishery also had unusually high spring landings. The joint impact was low prices on both sides of the border, accompanied by Canadian protests and blockades of lobster imports coming from Maine. The management system was unable to respond to the 2012 event but made changes that meant another MHW in 2016 did not cause the same impacts. These changes included the development of seasonal forecasting approaches to provide warning of future events.

A large MHW in the northeast Pacific ('The Blob') appeared off the coast of Alaska in the winter of 2013/14 and subsequently stretched south to Baja California. This event persisted through to the end of 2015. Mass strandings of marine mammals and seabirds occurred along the west coast of the United States and Canada[33]. Several thousand California sea lions died on beaches following shortages of forage fish. More than 50,000 Cassin's auklets were estimated to have starved and been washed ashore beginning in September 2014. These dying and dead animals stressed animal-rescue arrangements, pathology testing and management responses.

All the examples of MHWs above required rapid and novel responses, which can be difficult if policy or legislative barriers exist. In the cases where flexible instruments were already in place, such as in Western Australia, the management system coped better, even under persistent impacts. In other cases, improvements were not realized until the next event. Learning from these stress tests will improve management under climate variability and change and better prepare marine managers for the future when more extreme ocean temperatures will be the 'new normal'.

a b c



Figure, part **a**, Roe's abalone: image courtesy of Anthony Hart, DPIRD-Mollusc Science; part **b** Maine lobster: image courtesy of Andrew Pershing-Gulf, Maine Research Institute; part **c** Cassin's auklets: image courtesy of L. Doyle/COASST, Julia Parrish.

much of the information can be considered technical and relatively inaccessible to stakeholders in fisheries, aquaculture, tourism and biodiversity conservation. The full potential of increased predictive capacity will be contingent on rapid dissemination and uptake across these relevant stakeholders. The first step towards rapid dissemination is streamlining and simplifying the information given. In this context, experience from other types of extreme events such as tropical cyclones and earthquakes shows that consistent naming conventions and intuitive classification schemes for attributing relative magnitude can be effective[101]. To this end, the MHW severity-classification scheme[101] and information provided by this approach is already seeing uptake[24,102], and we recommend that this framework be used in communicating MHWs to stakeholders. The second step towards dissemination is to generate a central repository for MHW information and news, which can serve as an interface between stakeholders and scientists. The MHW website is one such example, and other regional engagement websites are also emerging. Such initiatives need to be expanded to include information targeting specific stakeholders — so-called targeted forecasts. Finally, using available temperature products, near real-time visualization of ongoing MHWs allows intuitive understanding of the dynamics of near-future and ongoing MHWs. Although a 'Marine Heatwave Tracker' is currently available in a web-based format, additional stakeholder-suited delivery mechanisms, such as smartphone applications, may be needed. With all these elements in place, predictable MHW events will allow proactive responses by potentially affected marine stakeholders, leading to improved marine management.

Establishing baselines. Globally, the increased frequency of MHWs is due primarily to the warming trend[35,103]. It has been suggested that baselines should also shift when analysing MHW events under climate change[104]. While using a shifting baseline period can be beneficial for analysing the underlying variability in MHW occurrence over time and its dynamics, ecosystem impacts from climate change are likely to be best understood if we consider changes against a fixed baseline. A baseline that shifts in line with a species' adaptive capabilities may be suitable in some cases, as the impact of MHWs on marine species often critically depends on the rate of change in absolute temperature, above the species' thermal limits[105]. It might be that some species have no capacity to adapt on short timescales, given the rapidity of temperature change, while other species can adapt either fully or perhaps partially. These differences in adaptation rates should be taken into consideration when designing baselines as fixed or shifting, and when interpreting the impacts of rapid temperature change.

Conversely, future advances in our understanding of shifts in dynamical processes might require subsequent updates of the baseline period. One way of at least partially addressing these issues is the use of MHW categories[101], where the introduction of new extreme categories can be considered and analysed with respect to their drivers, even when the baseline remains fixed. Whether to fix or shift baselines depends on the key questions being asked and is the subject of ongoing discussion and debate[104], and remains a fertile area for research and consideration.

Keeping pace with climate change. The rapidly growing awareness of MHWs and their increasing impact is a harbinger of the pace of climate change. In the Tasman Sea alone, three of the four summers between 2015/16 and 2018/19 have seen substantial MHW events, two of which were driven by the presence of large and persistent high-pressure blocking events. Given that blocking events are apparently becoming more frequent and pervasive as a result of climate change[106,107], we can expect blocking to remain a critical mechanism for driving large-scale MHWs into the future.

Over the coming decades, MHWs will become more frequent, longer in duration and/or more intense across much of the globe[36,37]. These projected changes represent threats to the health and sustainability of marine ecosystems globally[3,108,109]. Addressing this challenge will require significant action. It will require not only coordinated global commitment to reduce greenhouse-gas emissions but also governance arrangements that support novel adaptation strategies, including protecting refugia for foundation marine species of coral, kelp and seagrass that provide essential habitats to marine ecosystems. Although skilful MHW prediction will require improved process-based understanding of MHWs and their drivers, forecasting ecosystem impacts[110] requires physiological understanding of species' thermal sensitivity and critical thresholds, and how these link to other stressors. Coupling action between mitigation and adaptation will require creative solutions, spanning traditional disciplinary boundaries to protect and sustain our marine ecosystems and the services they provide. The utility of proactive decision-making will be facilitated by skilful MHW prediction and approaches will need to be adaptive to keep pace with MHW changes in a warming world.

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Author contributions

N.J.H. led the overall conceptual design, led the activity and coordinated the writing. A.S.G. generated Figs 1, 3 and 5. E.C.J.O. generated Fig. 2. J.A.B. generated Fig. 4. A.J.H. led the conceptual design for Box 2 and Table 1. All authors discussed the concepts presented and contributed to the writing.

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LETTERS

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Marine heatwaves threaten global biodiversity and the provision of ecosystem services

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The global ocean has warmed substantially over the past century, with far-reaching implications for marine ecosystems[1]. Concurrent with long-term persistent warming, discrete periods of extreme regional ocean warming (marine heatwaves, MHWs) have increased in frequency[2]. Here we quantify trends and attributes of MHWs across all ocean basins and examine their biological impacts from species to ecosystems. Multiple regions in the Pacific, Atlantic and Indian Oceans are particularly vulnerable to MHW intensification, due to the co-existence of high levels of biodiversity, a prevalence of species found at their warm range edges or concurrent non-climatic human impacts. The physical attributes of prominent MHWs varied considerably, but all had deleterious impacts across a range of biological processes and taxa, including critical foundation species (corals, seagrasses and kelps). MHWs, which will probably intensify with anthropogenic climate change[3], are rapidly emerging as forceful agents of disturbance with the capacity to restructure entire ecosystems and disrupt the provision of ecological goods and services in coming decades.

Anthropogenic climate change is driving the redistribution of species and reorganization of natural systems, and represents a major threat to global biodiversity[4,5]. The biosphere has warmed considerably in recent decades with widespread implications for the integrity of ecosystems and the sustainability of the goods and services they provide[6,7]. In addition to the near ubiquitous long-term increases in temperature, the frequency of discrete extreme warming events (heatwaves) has increased[8,9] with projections indicating they will become more frequent, more intense and longer lasting throughout the twenty-first century[10]. While extremes occur naturally in the climate system, there is growing confidence that the observed intensification of heatwaves is due to human activities[11,12]. The twenty-first century has already experienced record-shattering atmospheric heatwaves[8,13], such as the 2003 European heatwave, the Australian 'Angry Summer' of 2012–2013 and the European 'Lucifer' heatwave in 2017, with devastating consequences for human health, economies and the environment[8].

Discrete and prolonged extreme warming events occur in the ocean as well as the atmosphere. MHWs are caused by a range of processes operating across different spatial and temporal scales, from localized air–sea heat flux to large-scale climate drivers, such as the El Niño Southern Oscillation[14]. Regional case studies have documented how MHWs can alter the structure and functioning of entire ecosystems by causing widespread mortality, species range shifts and community reconfiguration[15–17]. By affecting ecosystem goods and services, such as fisheries landings[18,19] and biogeochemical processes[20,21], MHWs can have major socioeconomic and political ramifications. Recent high-profile ocean warming events include the record-breaking 2011 'Ningaloo Niño' (2010–2011) off Western Australia[22], the long-lasting 'Blob' (2013–2016) in the northeast Pacific[23] and El Niño-related extreme warming in 2016 that affected most of the Indo–Pacific[24,25]. These events have increased awareness of MHWs as an important climatic phenomenon affecting both physical and biological processes. Until recently, the lack of a common framework to define MHWs[14] has hampered attempts to examine temporal trends or to compare physical attributes or biological impacts across different events, regions or taxa. However, by defining MHWs as periods when daily sea-surface temperatures (SSTs) exceed a local seasonal threshold (that is, the 90th percentile of climatological SST observations) for at least 5 consecutive days[14], Oliver et al.[2] showed that the frequency and duration of MHWs have increased significantly over the past century across most of

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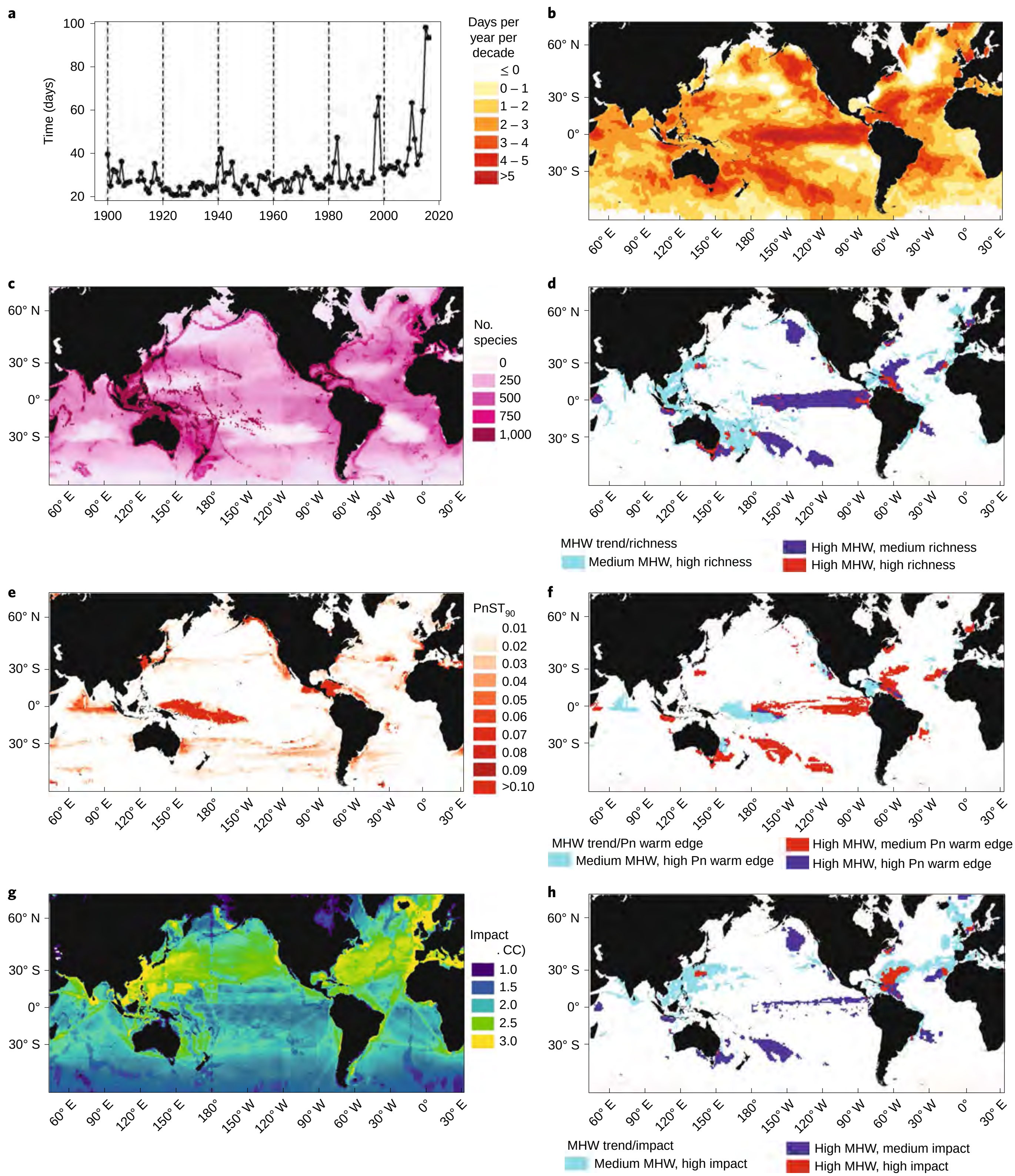

Fig. 1 | Global patterns of MHW intensification, marine biodiversity, proportions of species found at their warm range-edge and concurrent human impacts. a,**b**, Globally averaged time series of the annual number of MHW days and trends in the annual number of MHW days (in the periods 1925–1954 and 1987– 2016) across the global ocean. **c**,**e**,**g**, Existing data on marine biodiversity (**c**), the proportion of species within the local species pool found near their warm range edge (**e**) and non-climatic human stressors (**g**), were combined with trends in the annual number of MHW days (**b**). **d**,**f**,**h**, The resultant bivariate maps identify regions of high diversity value that may be affected by MHWs (**d**), high thermal sensitivity of species that may have been particularly vulnerable to increased MHWs (**f**) and high levels of non-climatic human stressors where MHW intensification has affected concurrently on marine ecosystems (**h**). Pn, proportion; $PnST_{90}$, proportion of species beyond 90% species thermal range; excl. CC, excluding climate change.

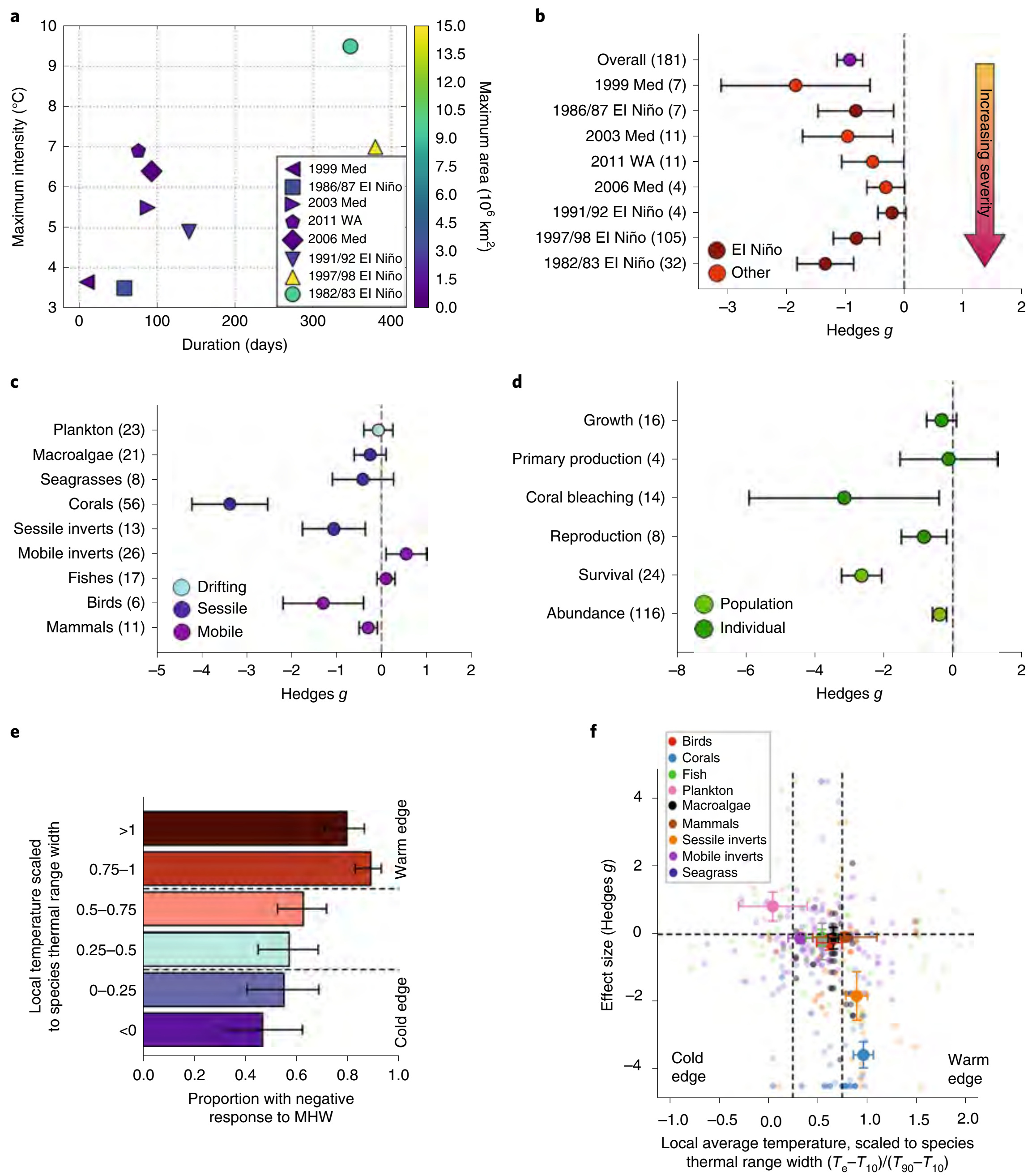

Fig. 2 | Ecological impacts of MHWs as determined by a meta-analysis of responses to eight prominent MHW events. a,**b**, The attributes of the eight MHW events used in the meta-analysis (**a**) and the overall effect of each MHW event across all ecological responses (**b**). **c**,**d**, The effect of MHWs on major taxonomic groups (**c**) and types of ecological response (**d**). The number of independent observations for each category are shown in parentheses and values represent mean (±95% CI) effect sizes (Hedges *g*, to account for bias associated with small sample sizes). **e**,**f**, Populations located towards the warm-water limit of species distributions tended to respond more negatively to MHWs (**e**) with effect sizes (Hedges *g*, ± 95% CI) generally becoming more negative for warmer equatorward range-edge populations (**f**). Plots are based on responses of 685 species-level observations; bold symbols in **f** indicate means for each major taxonomic group and faded symbols show individual studies (T_e, temperature at effect location; T_{10}, T_{90}, 10% and 90% species range temperatures). Horizontal (**e**) and vertical dashed (**f**) lines delineate the lower and upper quartiles of species thermal ranges. Med, Mediterranean; WA, Western Australia.

the global ocean. Here, we used the same MHW framework[14] to examine observed trends in the annual number of MHW days and the implications for marine ecosystems globally. We incorporated existing data on marine taxon richness, the proportion of species found at their warm range edges and non-climatic human impacts to identify regions of high vulnerability, where increased occurrences of MHWs overlap with areas of high biodiversity, temperature sensitivity or concurrent anthropogenic stressors. We also conducted a meta-analysis on the impacts of MHWs by examining ecological responses to eight prominent MHW events that have been studied in sufficient detail for formal analysis. We examined 1,049 ecological observations, recalculated to 182 independent effect sizes from 116 research papers that examined responses of organisms, populations and communities to MHWs. We also

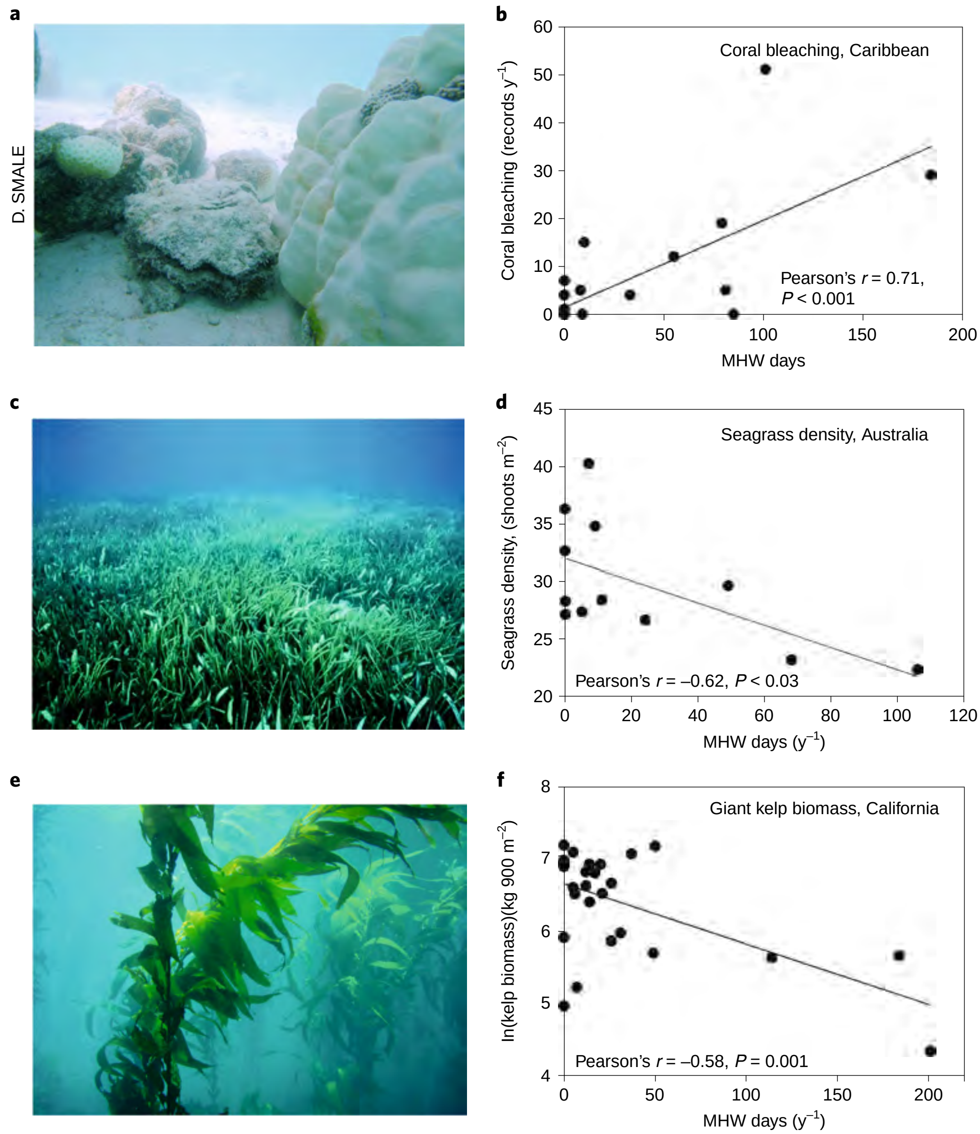

Fig. 3 | Impacts of MHWs on foundation species. a, Severe MHWs, such as those associated with the extreme El Niño events of 1997–1998 and 2015–2016, have caused widespread bleaching and mortality of reef building corals. **b**, Analysis of annual coral bleaching records from the Caribbean Sea/Gulf of Mexico region (1983–2010, data from NOAA Coral Reef Watch) showed that the number of MHW days per year was positively correlated with the frequency of coral bleaching observations. **c**, Seagrass meadows yield critical ecosystem services, including carbon sequestration and biogenic habitat provision, yet recent MHWs have affected seagrass populations in several regions. **d**, Monitoring data from independent sites in Cockburn Sound, Western Australia (2003–2014, data provided by Cockburn Sound Management Council) indicated that the number of MHW days recorded in the previous year was negatively correlated with seagrass (*Posidonia sinuosa*) shoot density. **e**, Kelp forests represent critical habitats along temperate coastlines but extreme temperatures experienced during MHWs can cause widespread mortality and deforestation. **f**, Satellite-derived estimates of giant kelp (*Macrocystis pyrifera*) biomass along the coastline of California/Baja California (1984–2011, data from Santa Barbara Coastal Long-term Ecological Research programme) showed that kelp biomass was negatively correlated with the number of MHW days recorded during the previous year. Credit: National Oceanic and Atmospheric Administration, US Department of Commerce (panels **c** and **e**).

explored relationships between the occurrence of MHWs and the health of three globally important foundation species (coral, seagrass and kelp) from three independent time series that were collected at sufficient spatiotemporal resolutions to explicitly link ecological responses to MHWs. Finally, we reviewed the literature on MHWs for evidence of impacts of these events on goods and services to human society.

The total number of MHW days per year, based on five quasi-global SST datasets, has increased globally throughout the twentieth and early twenty-first centuries (Fig. 1a). As a global average, there were over 50% more MHW days per year in the last part of the instrumental record (1987–2016) compared to the earlier part (1925–1954)[2], with most regions experiencing increases in the number of MHW days (Fig. 1b). Global patterns of marine taxon richness (Fig. 1c) overlaid with trends in annual MHW days reveal regions where increased MHW occurrences can influence biologically diverse regions; in particular, southern Australia, the Caribbean Sea and the coastline bounding the mid-eastern Pacific (Fig. 1d). Given that warm range-edge populations are likely to be the most affected by MHWs (as thermal tolerances are exceeded during anomalously high temperatures), regions that support a high proportion of species found near their warm range edge will be particularly vulnerable to increased MHW activity (Fig. 1e). Several regions were identified as having experienced marked

Table 1 | Impacts of MHWs on services provided by marine ecosystems.

Service type	Ecosystem service	Impacts	Refs.
Provisioning	Living resources (non-food)	Extreme temperatures caused widespread mortality, local extinctions and range contractions of a diversity of taxa[c,d,e]	15,17,40
	Food	Changes in the distributions and abundances of commercial fisheries species[b,e,f]	18,33,41
Regulating	Carbon sequestration and storage	Reduced carbon burial and sequestration due to decreased growth and high mortality of seagrasses[d,e]	36,42
	Moderation of extreme events	Complex, three-dimensional biogenic benthic habitat was replaced by simple poorly structured habitat, altering hydrodynamics and sediment transport and reducing natural coastal defence[a,b]	43,44
	Nutrient cycling	Increased stratification and extreme temperatures caused decreased phytoplankton production and nutrient turnover[b,g] Widespread loss of productive benthic habitats (seagrass, kelp forests) disrupting carbon and nitrogen cycling[d,e]	16,20, 36,45
	Biological control	Anomalous warming events associated with influx of invasive non-native species[e]	33
Habitat or supporting services	Habitats for species	Local extinctions, range contractions and high mortality rates of habitat-forming corals, seagrasses and macroalgae, resulting in simplified habitat structure and depleted local biodiversity[a,b,e,h]	34,42–44, 46–48
Cultural	Tourism and recreation	Locations affected by intense warming events are less attractive for recreational activities and have decreased socioeconomic value[d,g,h]	15,21, 49,50

Definitions of ecosystem services adapted from The Economics of Ecosystems and Biodiversity, TEEB, developed by UNEP[51]. Evidence of impacts was collated from specific MHWs: [a]1982/83 El Niño event; [b]1997/98 El Niño event; [c]1999 Mediterranean MHW; [d]2003 Mediterranean MHW; [e]2011 Western Australian MHW, [f]2012 Northwest Atlantic MHW; [g]the 2013–2016 Northeast Pacific 'Blob'; [h]the 2015/2016 El Niño event in northern Australia.

increases in MHW days and also supporting a high proportion of species found near their warm range edges (Fig. 1f), with marine ecosystems in the southwest Pacific and the mid-west Atlantic particularly at risk. Furthermore, regions where rapid increases in the annual number of MHW days overlap with existing high-intensity non-climate human stressors (Fig. 1g) include the central west Atlantic, the northeast Atlantic and the northwest Pacific (Fig. 1h). Here, existing regional pressures, including overfishing and pollution, have the potential to exacerbate MHW impacts and vice versa.

Examination of eight prominent (and sufficiently studied) MHWs showed they varied greatly with respect to spatial extent (by a factor of >15, Fig. 2a and Supplementary Fig. 1), duration (10–380 days) and maximum intensity (3.5–9.5 °C above climatological SST) (Fig. 2a). It should be noted that several MHWs were primarily driven by large-scale El Niño events that, by their nature, affected ocean climate at large spatial scales. Here, the largest contiguous MHW associated with each ENSO (El Niño Southern Oscillation) event was identified and characterized with MHW metrics. Our meta-analysis of ecological impacts (on the basis of Hedges g effect sizes to account for bias associated with small sample sizes[26]) detected an overall negative effect of MHWs on biota across research papers, events, taxa and response variables ($E = -0.93$; 95% CI $= 0.22$; $Q = 6303$, d.f. $= 181$; $p_{\text{heterogeneity}} < 0.001$, $I^2 = 97.13$; see Methods). All eight MHWs were associated with negative ecological impacts although the mean negative effect sizes were not significantly different from zero for the two events with lowest sample sizes (Fig. 2b). There was no clear relationship between the severity of the MHW (derived from normalized MHW intensity and duration) and their observed impacts (Fig. 2b). All taxonomic groups, with the exception of fishes and mobile invertebrates, responded negatively to MHWs with birds and corals being most adversely affected (Fig. 2c). The positive fish response was, in part, driven by new incursions of tropical species into affected temperate regions[16]. Corals were directly affected by these MHWs, as extreme absolute temperatures resulted in widespread bleaching and mortality[27,28], whereas birds were indirectly affected through changes in prey availability[29]. Birds and corals are also particularly sensitive to longer term increases in sea temperature associated with ocean warming[30]. Overall, our analyses suggest that sessile taxa were more affected by MHWs than mobile and planktonic taxa (Fig. 2c), perhaps because mobile taxa generally have higher thermal tolerances than less active or sessile taxa[31] and highly mobile species can quickly migrate in response to rapidly changing conditions[16]. All ecological response variables were negatively affected by MHWs, although growth and primary production were not significantly different from zero (Fig. 2d). Negative impacts were greatest for coral bleaching, survival and reproduction (Fig. 2d), a pattern consistent with effects of warming in manipulative experiments[32].

To examine links between MHWs and ecological responses, we conducted additional analysis at the species level to test the prediction that populations found towards the warm-water limit (that is, the equatorward range edge) of a species distribution would be more negatively affected by MHWs than other populations. From the database described above, we extracted all species-level observations (645 observations from 302 species) and for each population we classified their relative position in the species range by expressing the local average SST as a proportion of the difference between the 10th and 90th percentile temperatures experienced through the species geographical range. Critically, the most negative responses to MHWs were seen in populations found towards their warm range edge (Fig. 2e), suggesting that extreme temperatures exceeded thermal thresholds with adverse effects. Across all species-level observations, there was a negative relationship between any given population's location within the species range and the direction and magnitude of the MHW effect (Fig. 2f). This indicates that populations residing near the warm limit of a given species range are particularly vulnerable to warming events and range contractions are likely to occur in response to more frequent MHWs. Indeed, recent observations have shown that equatorward range edges of both plant and animal species have retracted poleward by >100 km following severe MHW events[17,33,34].

An examination of long-term time series on the health of three globally important foundation taxa showed that increased annual number of MHW days was correlated with (1) increased coral bleaching, (2) decreased seagrass density and (3) decreased kelp biomass (Fig. 3). Even though environmental variables such as storms, nutrients and light are known to strongly influence the health of these critical habitat-formers[35], the annual number of MHW days alone was strongly and significantly correlated with observed ecological performance and, crucially, had consistently stronger correlative relationships than more frequently used measures of ocean temperature (that is, mean and maximum SST, see Supplementary Table 1). An increased number of MHW days was significantly correlated to decreased ecological health of populations of all three foundation taxa, indicating the importance of discrete extreme ocean warming events in driving ecosystem structure[16,36].

A wide range of ecological goods and services derived from marine ecosystems have been severely affected by recent MHWs (Table 1). For example, the 2011 Ningaloo Niño caused widespread loss of biogenic habitat, depleted biodiversity, disruption to nutrient cycles and shifts in the abundance and distribution of commercial fisheries species off Western Australia (Table 1). Similarly, recent MHWs in the Mediterranean Sea have been linked to local extinctions, decreased rates of natural carbon sequestration, loss of critical habitat and diminished socioeconomic value (Table 1). These services have substantial societal benefit, with hundreds of millions of people benefitting from coastal marine ecosystems[37,38]. As such, managing and mitigating the deleterious effects of MHWs on the provision of ecosystem services is a major challenge for coastal societies.

Globally, MHWs are becoming more frequent and prolonged, and record-breaking events have been observed in most ocean basins in the past decade[2]. So far, the main focus of ecological research has been on trends in mean climate variables, yet discrete extreme events are emerging as pivotal in shaping ecosystems, by driving sudden and dramatic shifts in ecological structure and functioning. Given the confidence in projections of intensifying extreme warming events with anthropogenic climate change[8,39], marine conservation and management approaches must consider MHWs and other extreme climatic events if they are to maintain and conserve the integrity of highly valuable marine ecosystems over the coming decades.

Online content

Any methods, additional references, Nature Research reporting summaries, source data, statements of data availability and associated accession codes are available at https://doi.org/10.1038/s41558-019-0412-1.

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Author contributions

D.A.S. and T.W. conceived the initial idea. All authors contributed intellectually to its development. D.A.S., T.W., E.C.J.O. and N.J.H. co-convened the workshops. E.C.J.O. led the development of the M.H.W. analysis, which was supported by N.J.H., L.V.A., J.A.B., M.G.D., M.F., A.J.H., S.E.P.-K., H.A.S. and A.S.G. The meta-analysis of ecological impacts was conducted by M.T., B.P.H., S.C.S., M.T.B. and P.J.M. D.A.S. led manuscript preparation with input from all authors.

Competing interests

The authors declare no competing interests.

Additional information

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Methods

Definition of MHWs and analysis of multi-decadal trends. MHWs were identified from observational SST time series using the definition proposed by Hobday et al.[14], whereby a MHW is defined as a 'discrete prolonged anomalously warm-water event at a particular location' with each of those terms (anomalously warm, prolonged, discrete) quantitatively defined and justified for the marine context. Specifically, 'discrete' implies the MHW is an identifiable event with clear start and end dates, 'prolonged' means it has a duration of at least 5 days and 'anomalously warm' means the temperature is above a climatological threshold (in this case, the seasonally varying 90th percentile). The climatological mean and threshold were calculated over a base period of 1983–2012. For each day of the year, a pool of days across all years in the climatology period and within an 11-day window was taken as a sample, from which the mean and 90th percentile threshold were calculated. The climatological mean and threshold were then further smoothed using a 30-day running window. When two successive events occur with a break of 2 days or less, this was deemed to represent a single continuous event. The code used to identify MHWs and calculate key MHW metrics following this definition is freely available and has been implemented in Python (https://github.com/ecjoliver/marineHeatWaves) and R (https://robwschlegel.github.io/heatwaveR). MHWs detected using this definition were then characterized by a set of metrics, including duration and intensity (that is, the maximum daily temperature above the seasonal climatology during the event). We then examined an annual time series of 'total MHW days', which is the sum of days categorized as MHWs in any given year.

Global time series and regional trends in total MHW days were derived using a combination of satellite-based, remotely sensed SSTs and in situ-based seawater temperatures. First, total MHW days were calculated globally over 1982–2015 at 1/4° resolution from the National Oceanic and Atmospheric Administration (NOAA) Optimum Interpolation SST V2 high-resolution data. Then, proxies for total MHW days globally over 1900–2016 were developed on the basis of five monthly gridded SST datasets (HadISST v.1.1, ERSST v.5, COBE 2, CERA-20C and SODA si.3). A final proxy time series was calculated by averaging across the five datasets. The five monthly datasets were used since no global daily SST observations are available before 1982. From these proxy time series, we calculated (1) the difference in mean MHW days over the 1987–2016 and 1925–1954 periods and (2) a globally averaged time series of total MHW days. Further details on this method and resulting proxy data can be found in Oliver et al.[2]. Note that these calculations use the same climatology period as above, 1983–2012.

Global patterns of MHW intensification and overlaps with known hotspots of marine biodiversity, temperature-sensitive populations and non-climatic human stressors. We combined regional trends in MHW days with pre-existing data on marine biodiversity, the proportion of species found near their warm range edges and non-climatic human stressors to predict where MHW intensification may be a particular threat to biodiversity hotspots or temperature-sensitive communities, or be exacerbated by concurrent stressors. Biodiversity hotspots were determined using published marine taxon richness data[52], which were accumulated from projected species distributions from the Aquamaps project[53]. Patterns in taxon richness (Fig. 1c) showed characteristically high levels in coastal areas and in tropical regions. We also calculated the proportion of species in the local species pool that were near their warm range edge to determine locations where MHWs might be more likely to have a strong negative effect (as shown in Fig. 2f). We used 16,582 species global distribution maps from the Aquamaps project[53], previously used to assess probable patterns of biodiversity change[52], to represent global marine biodiversity. For each 1° latitude/longitude grid cell we counted the number of species present for which SST, derived as the 1960–2009 average annual temperature from the Hadley Centre HadISST v.1.1 dataset, exceeded the 90th percentile temperature of their geographical range, and divided this by the total number of species present. Aside from some artefacts where species geographical limits coincide with FAO (Food and Agriculture Organization of the United Nations) region boundaries, a feature prevalent in other studies using these datasets[54], the resulting map (Fig. 1e) showed areas with higher proportions of species at their warm range edges. Major concentrations (proportions >0.1 of all species) of warm-edge species were seen in the Eastern Mediterranean, the southern Red Sea, the Caribbean Sea, the Mexican part of the North Pacific and a large part of the tropical west Pacific. Locally, higher proportions of warm-edge species were also seen along coastlines of Europe, western USA and Canada, North Africa and in the Yellow Sea.

Information on stressors were obtained from supplementary online resources provided by Halpern et al.[55]. We additively combined multiple impact layers (demersal destructive fishing, demersal non-destructive high bycatch, demersal non-destructive low bycatch, ocean acidification, ocean pollution, pelagic high bycatch, pelagic low bycatch, shipping and ultraviolet) into a single cumulative impacts layer (Fig. 1e). Fishing intensity layers were obtained by apportioning reported catches in FAO areas by modelled productivity data for latitude/longitude cells. Shipping impacts were derived from a 12-month (2003–2004) global ship observing scheme, and the same data was used with ports data to give a measure of ocean pollution. Surface ultraviolet information was obtained from the GSFC TOMS EP/TOMS satellite programme at NASA. Ocean acidification data came from globally modelled aragonite saturation state. Details of the quantification of these layers are given in Halpern et al.[55,56]. Layers that included ocean warming variables were specifically excluded due to probable co-variance (to varying extents) with MHW metrics. The cumulative impacts layer was then re-projected and resampled onto the same 1° × 1° grid as for trends in total MHW days and biodiversity data. Maps of the combinations of medium to high trends in total MHW days and medium to high values of taxon richness (Fig. 1c) or cumulative impacts (Fig. 1e) were created by splitting the data into classes on the basis of the percentiles of the distribution of each variable (0–50% low, 50–90% medium, >90% high). Combined MHW trend/richness and MHW trend/impact layers were assigned to categories according to the classes of each contributing layer. While spatial bias due to variability in sampling effort may influence, to some degree, global-scale datasets on physical and biological variables, the datasets used in the current study have near-complete global coverage and represent the best approximations available for temperature[57], species richness and distributions[58] and human stressors[55].

Meta-analysis of ecological responses to MHWs. *Dependent and independent variables, literature searches and hypothesis.* The meta-analysis followed PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) guidelines, which provide an evidence-based minimum set of requirements for conducting and reporting meta-analyses (Supplementary Fig. 2). We searched for peer reviewed studies that compared six types of biological 'performance response' (survival, abundance, growth, reproduction, primary production or coral bleaching) that reported data variation, before and after any of eight well-described periods of extreme warming (El Niño-related events in 1982/83, 1986/87, 1991/92 and 1997/98, the Mediterranean MHWs of 1999, 2003 and 2006, and the 2011 MHW in Western Australia). Relevant studies were identified from two literature searches. First, we conducted a standardized Web of Science search, with search terms related to climate change, heatwaves, marine systems and the eight MHWs mentioned above. We used the following specific search string: ('TS = ((marine AND ('heatwave' OR heatwave)) OR El Niño OR La Niña OR ENSO OR (marine AND warming))'), identifying 29,395 potentially relevant papers. We read all abstracts from these papers and then obtained the full manuscripts of the papers that in their title, abstract or keywords indicated that relevant data could be collected (=517 papers). We read all these papers in detail to identify 116 papers that fulfilled our data criteria. For each of the identified publications we extracted all reported mean performance response, data dispersion and sample sizes, from text, tables and figures with Plot Digitizer (http://plotdigitizer.sourceforge.net/). Impact studies were widely distributed across the global ocean; impact studies relating to ENSO-associated MHWs were spread across the Pacific and Indian Oceans whereas impact studies relating to Mediterranean and Australian MHWs were conducted across a smaller area (Supplementary Fig. 3). Our fundamental hypothesis was that MHWs generally had negative effects on ecological performance across studies, bioregions, events, response types and organisms. We also tested (see the next section for the method) if the magnitude of effects varied between heatwave events (eight MHW events), performance responses (six types listed above) and impacted taxa (grouped into mammals, birds, fishes, mobile invertebrates, non-coral sessile invertebrates, corals, macroalgae, seagrasses and plankton, which included phytoplankton, zooplankton and open ocean microbes). For the MHW test, we hypothesized that the intensity of an event would correlate with the magnitude of effect size. For the biological response test, we hypothesized that coral bleaching and reproduction would be most affected by MHWs, the former because corals are known to be sensitive to elevated temperatures and the latter because reproduction is typically more sensitive to stress than growth, abundance and survival. Finally, for the test across taxa we hypothesized that mobile organisms and seagrasses/corals would exhibit the largest effect sizes because mobile organisms can respond rapidly (for example local heat-stressed species can emigrate and warm-tolerant species from adjacent region can immigrate) and seagrasses/corals are generally sensitive to elevated temperatures.

Effect sizes, data pooling, dealing with outliers and autocorrelation and statistical tests. We analysed impacts of MHWs on events, taxa and performance with Hedges *g* effect size, corrected for small sample sizes. Hedges *g* was calculated as $(\mathrm{MHW}_{\mathrm{After}} - \mathrm{MHW}_{\mathrm{Before}})/S) \times J$, where S is the pooled standard deviation and J is a factor that corrects for bias associated with small sample sizes[26,59]. $\mathrm{MHW}_{\mathrm{before}}$ and $\mathrm{MHW}_{\mathrm{after}}$ represent the mean performance response reported by the study before and after the period of extreme warming, respectively. These relied on the authors' designations of the timing of the MHW. When the mean performance response before the MHW event were reported for multiple time points, an average was taken to obtain $\mathrm{MHW}_{\mathrm{before}}$. In these cases, the associated variance of the time points was also pooled for use in S. In this analysis, negative and positive effects reflect inhibition and facilitation of organismal performance, respectively. Analyses were weighted by the sum of the inverse variance in each study and the variance pooled across studies and therefore give greater weight to those studies with higher replication and lower data dispersion. We used random-effect models, thereby assuming that summary statistics have both sampling error and a true random component of variation in effect sizes between studies[26,59]. Most publications reported multiple auto-correlated effects, for example when a study reported effects of a MHW on many different coral species. Within-study effects are typically not statistically independent from each other and will conflate analyses, for example by artificially increasing degrees of freedom. We reduced within-study autocorrelation by averaging 1,049 non-independent Hedges g values (extracted from 116 identified research papers) to 182 values, each being characterized by a unique combination of a MHW, affected taxa and performance response per research paper. Thus, before formal meta-analyses, within-study effects were averaged across multiple species and across nested designs (for example, across different sites within a study or different depth levels). We acknowledge that our approach to aggregate auto-correlated within-study effect sizes, albeit being the most common way to do this[60], may be suboptimal, compared to advanced modelling techniques[60]. However, many papers reported different types and nested layers of non-independent data in a single paper, requiring overly complex combinations and levels of aggregation models (compared to aggregating data with a mean), before the meta-analysis. Finally, we calculated mean effect sizes (E), 95% confidence intervals (CI), heterogeneity (Q), the probability that Q is significant (P-heterogeneity), and the proportion of real observed dispersion (I^2) on the basis of weighted random-effect models in OpenMEE[59]. Mean effect sizes were considered to be significantly different from zero or another effect if their 95% CIs did not overlap with zero or each other, respectively[61–64]. Effect sizes generated from a single study were excluded from plots (these were; a single mean effect size of −4.21 for the 1972 ENSO event and a single effect size of 1.183 for 'reptiles' in the taxon-specific analysis).

Publication bias. Our meta-analyses may be influenced by publication bias if we overlooked studies documenting strong positive effects, or if studies finding non-significant effects are not published[26,65,66]. We believe that the first type of publication bias is unlikely because we have worked intensively with MHW through primary research and by writing book chapters and reviews. We explored possible publication bias in different ways. We examined funnel plot asymmetry using the trimfill method and regression tests, and calculated the fail-safe number using the Rosenberg method that estimates the number of studies averaging null results that should be added to reduce the significance level (P value) of the average effect size (on the basis of a fixed-effects model) to $\alpha = 0.05$ (refs. [65,66]). These tests suggest that publication bias has limited effects and that our results are generally robust. Although the funnel plot was highly asymmetric (Supplementary Fig. 4), as shown by a significant regression test ($t = -3.598$, $P = 0.0004$), adjusting this possible bias using the trimfill method had no effects on our general conclusion, because the mean effect size remained significantly negative (−0.05, with 95% confidence intervals −0.08 to −0.02, $P < 0.01$). In addition, Rosenberg's fail-safe number was 11,318, that is, much larger than $5n + 10$, where n is the number of original studies included in our analyses. Thus, publication bias is unlikely to affect our results and did not change our main finding that MHWs generally had negative effects on marine organisms.

Effect of population location within the distributional range on responses to MHWs. We also tested the hypothesis that populations found towards the warm-water limit (that is, the equatorward range edge) of a species distribution will respond more negatively to MHWs. To do this, we first extracted all observations from the database that were recorded at the species-level (302 species and 645 observations). Global species distributions were produced using presence-only Maxent models for each species for which sufficient observations were available, and using default parameters for a random seed, convergence threshold, maximum number of iterations, maximum background points and the regularization parameter[54] (using Maxent v.3.3.3k). Observations of species presence from iOBIS were gridded such that 1° grid cells with observations were set as present. These observations were then modelled as a function of the following environmental predictors: (1) average annual temperatures from the HadISST v.1.1; (2) the logarithm of distance to the nearest coastline; (3) ocean depth from the GEBCO marine atlas and (4) FAO major fishing areas (http://www.fao.org/fishery/area/search/en). Global maps of predicted presence were produced using a threshold probability of 0.4. Presence maps were used to extract average annual SST values from Hadley Centre HadISST v.1.1 1° dataset long-term climatology average 1960–2009. Quantiles (0, 0.1, 0.25, 0.5, 0.75, 0.9 and 1.0) of the population of temperatures in occupied grid squares were used to define the thermal niche of the species (weighted by the relative area of grid cells given by the cosine of the latitude). The frequency distribution of these species-specific distributions were then described using percentiles and, for this analysis, the 10th and 90th percentiles were taken as measures of the warm and cold ends of the thermal range, respectively. Each location of a reported MHW effect was then used to extract the local average SST from the same SST climatology. Range location was then expressed as the local temperature less the 10th percentile of temperature, divided by the difference between the 10th and 90th percentiles of estimated species range temperatures. A range location value of zero or less was therefore at the cold end of the distribution range (≤ 10th percentile), while values of 1 or more would be at the warm end of the range (≥ 90th percentile). This process resulted in estimated range locations for 347 observations from 280 species within the ecological dataset.

The effect of range location on the size and direction of response to MHWs was assessed statistically using a linear model of Hedges g versus range location weighted by the inverse variance of each Hedges g value. Range location had a significant influence on responses, becoming more negative towards the warm edge of the species range (Fig. 2f; $F_{1,345} = 11.98$, $P < 0.001$). Differences among taxonomic groups followed the average range location in those groups. The average negative effect of MHWs on corals was associated with the average reported effect location being at the 90th percentile of the coral species temperature distribution. Those taxonomic groups reporting less negative effects were generally towards the middle of the distribution range, while those groups at the cold end of the species temperature range showed a positive effect (Fig. 2f; $F_{1,7} = 10.33$, $P = 0.015$).

Analysis of habitat-forming species responses to MHWs. High-resolution time series on coral bleaching, seagrass density and kelp biomass were obtained from the Caribbean Sea, Western Australia and California, respectively (Supplementary Fig. 5). Quality-controlled coral bleaching observations for the Caribbean Sea/Gulf of Mexico region (northernmost limit: 30.0° N, southernmost limit: 10.2° N, western limit: 97.5° W, eastern limit: 59.6° W) were obtained (at 11 km resolution) from NOAA's Coral Reef Watch programme (http://coralreefwatch.noaa.gov/satellite/index.php). Observations were first filtered by month (July–October inclusive) and then summed for each year (1983–2010). Links between MHWs and seagrass density were examined with long-term monitoring data from Cockburn Sound, Western Australia, which is collected and managed by the Cockburn Sound Management Council (Western Australian Government). The density of seagrass shoots was examined at two long-term sites (Garden Island and Warnbro Sound), where high-resolution data have been collected using SCUBA at depths of 2–7 m since 2003 (all surveys were conducted in late Austral summer of each year). Data were averaged across transects and depths before generating an annual mean value for the Cockburn Sound region (average of two sites). Annual estimates for giant kelp, *Macrocystis pyrifera*, biomass were generated from the satellite-derived dataset produced by Cavanaugh et al.[67] as part of the Santa Barbara Coastal Long-term Ecological Research (SBC-LTER) programme (http://sbc.lternet.edu//index.html). Estimates of the biomass of the kelp canopy (that is, floating fronds) were derived from LANDSAT 5 Thematic Mapper satellite imagery. Biomass data (wet weight per kg) were generated for individual $30 \times 30\,m^2$ pixels in the coastal areas adjacent to California and Baja California. Estimates of kelp canopy biomass were derived from the relationship between satellite surface reflectance and empirical measurements of kelp canopy biomass at long-term monitoring sites sampled using SCUBA. The extensive dataset was first filtered to remove uninformative values influenced by cloud cover and then by latitude (27.00–32.99°N) and time of year (only summer months, June–September inclusive). Average kelp biomass per year was then calculated from between 66,530 and 354,181 individual observations. The total number of MHW days observed for corresponding years and regions for each of the three separate datasets was then calculated, and correlations between MHWs and ecological response variables explored with Pearson's correlation coefficient.

Data availability

Daily 0.25° resolution NOAA OISST V2 data are provided by the NOAA/OAR/ESRLPSD, Boulder, Colorado, USA, at http://www.esrl.noaa.gov/psd/. Data on human impacts and marine biodiversity are available from NCEAS (https://www.nceas.ucsb.edu/globalmarine) and Aquamaps (www.aquamaps.org), respectively. Coral bleaching records were extracted from the NOAA Reef Watch programme (https://coralreefwatch.noaa.gov), giant kelp biomass data were sourced from the Santa Barbara Coastal Long-term Ecological Research (SBC-LTER) programme (http://sbc.lternet.edu//index.html). Additional data are available from the corresponding author upon request.

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