Thermal Displacement by Marine Heatwaves

Michael G. Jacox[1,2,3*], Michael A. Alexander[2], Steven J. Bograd[1,3], James D. Scott[2,4]

[1]NOAA Southwest Fisheries Science Center, Monterey, CA, USA

[2]NOAA Earth System Research Laboratory, Boulder, CO, USA

[3]University of California Santa Cruz, Santa Cruz, CA, USA

[4]University of Colorado, Boulder, CO, USA

Abstract

Marine heatwaves (MHWs) can dramatically alter ocean ecosystems, with profound ecological and socioeconomic impacts[1,2,3,4,5,6,7,8]. Consequently, significant effort has been directed at understanding MHW patterns, drivers, and trends globally[9,10,11]. These studies typically characterize MHWs based on their intensity and persistence in a given location – an approach that is particularly relevant for corals and other sessile organisms that must endure elevated temperatures. However, many ecologically and commercially important marine species respond to environmental disruptions by relocating to favorable habitat, and dramatic range shifts of mobile marine species are included among the conspicuous impacts of MHWs[1,4,12,13]. While spatial temperature shifts have been studied extensively in the context of long-term warming trends[14,15,16,17,18], they are unaccounted for in existing global MHW analyses. Here, we introduce thermal displacement as a MHW metric that characterizes spatial shifts in temperature contours rather than local temperature anomalies. We show that thermal displacements during MHWs vary from tens to thousands of kilometers across the world's oceans and do not correlate spatially with MHW intensity. Furthermore, short-term thermal displacements during MHWs are of comparable magnitude to century-scale shifts inferred from warming trends[18], though their global spatial patterns are very different. These results expand our understanding of MHWs and their potential impacts on marine species, revealing which regions are most susceptible to thermal displacement and how those shifts may change under projected ocean warming. They also highlight the need for marine resource management to account for MHW-driven spatial shifts, which are of comparable scale to those associated with long-term climate change and are already happening now.

Main

The marine research community has been galvanized over the past decade by a series of high-profile MHWs – discrete but prolonged periods of anomalously warm ocean temperatures – with extensive impacts on marine ecosystems as well as the communities and economies they support[1,2,5,7,8,19,20]. In assessing such events, MHWs have been defined and characterized based on the local amplitude and persistence of SST anomalies[21], an approach that draws on similar definitions for atmospheric heatwaves[22]. However, while temporary relocation is generally not a feasible solution to heatwave impacts over land (e.g., on infrastructure, agriculture, and human health), mobile marine species (e.g., many fishes and marine mammals) can shift their distributions to find preferred habitat, and in some cases track ocean temperature with little to no lag[16,17]. Despite the fact that marine species respond in different ways to a wide variety of physical, chemical, and biological drivers and cues, relatively simple SST-based habitat metrics have proven informative for understanding species redistributions under environmental change[14,16,17,23]. To account for this critical dimension of MHW impacts, which is not captured by local temperature anomaly metrics, we introduce and quantify the "thermal displacement" associated with MHWs across the globe. Thermal displacement is the minimum distance that must be traveled away from a MHW to track constant sea surface temperature. It is related to climate velocity (the rate at which isotherms move across the earth's surface under climate change[18]) but is applied on an event-scale where the magnitude of the displacement, not the rate of change, is of greatest interest. Here, we use monthly sea surface temperature (SST) anomalies from version 2 of the NOAA 0.25˚ Optimum Interpolation SST product to explore historical (1982-2019) spatial and temporal patterns of thermal displacement throughout the world's oceans, and then quantify the future change in these displacements associated with projected warming from an ensemble of climate models.

On a global scale, MHW intensity is spatially heterogeneous[9,11], with typical SST anomalies ranging from under 1˚C (e.g., in the tropical Indian and Atlantic Oceans) to ~4˚C in the Eastern Tropical Pacific and in the vicinity of energetic midlatitude currents and their associated fronts (Fig. 1a,b). Thermal displacement also varies considerably in space, exhibiting two orders of magnitude difference (from tens to thousands of kilometers) across the world's oceans (Fig. 1c, Extended Data Fig. 1). The global median thermal displacement associated with MHWs, calculated over the ice-free regions of the ocean, is 183 km. For reference, the global median decadal shift associated with historical ocean warming trends has been estimated at 21.7 kilometers per decade[18]. Peaks in MHW intensity are evident near the equator and in the midlatitudes (centered on ~40˚N and ~40˚S) and thermal displacement is greatest near the equator. For both MHW intensity and thermal displacement, higher magnitude is also associated with higher variance (Fig. 1; Extended Data Fig. 2). While MHW intensity and thermal displacement are aligned in some regions (the Eastern Tropical Pacific stands out for its high values of both metrics due to El Niño events), they have little spatial correlation globally (Spearman rank correlation r = -0.27; Extended Data Fig. 3). In fact, some of the regions that are most susceptible to intense MHWs, particularly in western boundary current extensions and the Antarctic Circumpolar Current, are also characterized by very small thermal displacements (Fig. 1). However, temporal variability in thermal displacement does correlate with MHW intensity over much of the global ocean, though the Northwestern Atlantic and Northwestern Pacific are notable exceptions (Extended Data Fig. 4).

Spatial patterns in thermal displacement are strongly influenced by the spatial structure of the mean SST field. The SST gradient determines how much distance must be covered to compensate for a given SST anomaly, with weaker gradients translating to longer distances (r = -0.81; Fig. 1; Extended Data Fig. 3; ref 18). The most dramatic thermal displacements generally occur in regions of very weak SST gradients, particularly tropical oceans, where displacements reach upwards of 500 km per degree of SST anomaly (Fig. 2). In areas where MHWs are intense and also occur on a backdrop of very weak SST gradients (particularly the Eastern Tropical Pacific), thermal displacements can exceed 2000 km. Conversely, in regions of strong SST gradients colder water is generally not far away; while shifts in strong ocean currents and associated gradients can quickly generate large SST anomalies, those anomalies do not translate to large thermal displacements (e.g., in the Gulf Stream and Antarctic Circumpolar Current; Fig. 2). A special case arises for cold refugia – while these regions may be characterized by strong SST gradients, they are surrounded by warmer water. As a result, MHWs occurring in cold refugia can be particularly impactful in terms of thermal displacement (e.g., in the California and Humboldt Current Systems; Fig. 2). In some cases, MHWs can alter the surface temperature field such that thermal habitat is not accessible at all, particularly in inland seas as well as regions bounded by land in the poleward direction.

Several MHWs have received extensive scientific and public attention in the past decade, and can be viewed through the lens of thermal displacement. In the Northeast Pacific, 2014-16 brought an unprecedented MHW initially situated offshore (“The Blob”)[20] that later evolved into an arc warming pattern spanning the North American west coast[24]. During this event, thermal displacements exceeded 700 km in the Gulf of Alaska and along the U.S. west coast. Similar displacements were generated in 2005 by the delayed upwelling season and consequent warming[25,26] (Fig. 3a). The 2012 Northwest Atlantic MHW[1,27] was the most intense the region had seen in 30 years, and drove commercially valuable species to rapidly shift poleward by hundreds of kilometers[1]. While species shifts are not driven purely by surface temperature, they were consistent with calculated thermal displacements for that event (Fig. 3b). Given the complex political geography of the United States' eastern seaboard, this event highlighted tricky management questions introduced by MHW-driven shifts across state and national lines[1]. Along Australian coasts, the 2010s brought repeated MHWs, including in 2010-11 off Western Australia[2,19], in 2015-16 in the Tasman Sea[8], and in 2016 off the northern coast[5]. However, mean SST gradients are generally quite strong and meridionally oriented in Australian seas (Fig. 2), with resultant thermal displacements that are relatively small (Fig. 3c). Lastly, El Niño events have caused some of the largest thermal displacements globally; during the 2015-16 event they exceeded 2000 km in the Eastern Tropical Pacific, an impact matched by that of the 1997-98 El Niño (Fig. 3d), during which large poleward shifts of marine fishes were observed along both the North and South American west coasts[12,28,29].

Spatial shifts in climate driven by warming trends, and resultant changes in species distributions, have been studied extensively in terrestrial and marine systems[14,16,17,18,30]. However, changes in the variability around those long-term shifts (e.g., due to MHWs) have received little attention. Future ocean warming is projected to be spatially heterogeneous (Fig. 4), which will intensify SST gradients in some regions and weaken them in others. Consequently, thermal displacements during MHWs will be altered even if interannual SST variability is unchanged. Given the mean projected warming by the late 21st century (2070-2099) under the RCP 8.5 scenario, these changes reach ~30% of the historical thermal displacements (as much as several hundred kilometers depending on the region affected) and can be of either sign, meaning that discrete regions may become more or less vulnerable to short-term thermal displacements. In lower emissions scenarios (RCP 2.6 and RCP 4.5), thermal displacement changes are smaller but show the same spatial patterns (Fig. 4). In general, thermal displacement by MHWs will tend to increase under future warming in regions with decreased horizontal gradients; such is the case for much of the North Pacific where intensified warming in the subarctic region is projected. The opposite is true for much of the Northeast Atlantic and Southern Oceans, where warming is projected to be relatively weak at higher latitudes (Fig. 4b). The changes illustrated here for MHW displacements will occur on top of long-term temperature trends, and understanding both is crucial[31] as their regional signatures will be different. For example, relatively strong projected warming along the equatorial Pacific would drive large long-term thermal shifts, but would also intensify meridional SST gradients and thereby reduce thermal displacement during future MHWs (though it should be noted that the accuracy of climate models' tropical Pacific SST response to global warming has been called into question[31]). Similarly, species shifting to new areas in response to long-term temperature trends will likely experience different MHW-driven thermal displacements than they experience in their current locations.

Shifting species distributions must be accounted for in fisheries management[33], as species' range shifts take them across management boundaries, alter their proximity to fishing ports, and drive the need for adaptive measures by fishing communities[34]. Fisheries follow shifting species distributions, though the response is lagged, at least in part due to economic and regulatory constraints[35]. While these management issues are often discussed in the context of climate change[23], they are upon us now. Modern day MHWs can induce thermal displacements comparable to those from century-scale warming trends, and while these temperature shifts do not solely dictate species distributions, they do convey the scale of potential habitat disruption. Furthermore, while MHWs themselves are transient events with many species likely to return following a temporary displacement, in some cases the habitat shifts imparted by MHWs may trigger lasting ecological change as species gain access to previously unavailable habitat or lose access to previously available habitat (i.e., through ecological bridges and barriers[36]). Thus, it is crucial that resource management considers shifts in oceanographic habitat not only in the context of secular change but also relative to extreme events now and under future climatic conditions.

The utility of mapping thermal shifts to inform our understanding of ecological responses has been thoroughly demonstrated[14,16,17,23]. However, thermal displacement remains a simplistic proxy for potential changes in the distributions of marine species. We anticipate that our analysis will be expanded upon for individual (or groups of) species by incorporating additional considerations including vertical movements, physiology, additional essential habitat properties such as prey and oxygen, and other restrictions on species distributions (e.g., the need to be near shore or specific breeding or nursing grounds). Such analyses can further constrain whether areas of suitable temperature are actually viable habitat and if not, where suitable habitat may be available. Thermal displacement should also be considered in conjunction with more common MHW metrics including intensity and duration, as the amplitude and persistence of temperature anomalies relative to species' tolerances will dictate whether they can remain in place or need to relocate to find favorable conditions[37]. Characterizing MHWs by their thermal displacement in addition to these other metrics offers a new perspective on the spatial imprint of MHWs across the globe and their potential impacts on mobile marine species and the communities that depend on them.

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Figures

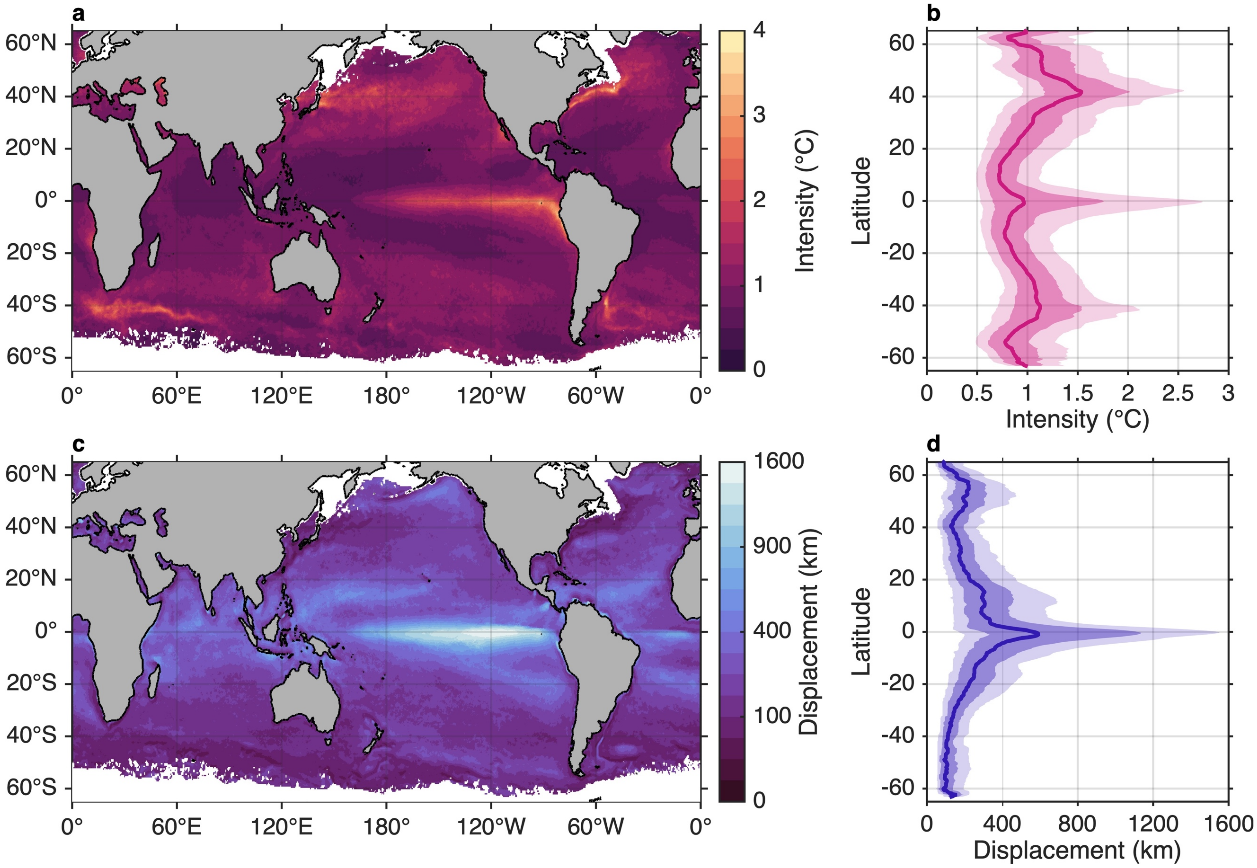

Figure 1: Marine heatwaves and their influence on thermal habitat redistribution globally. (**a)** Median MHW intensity (the SST anomaly associated with a MHW) from 1982 to 2019, calculated at each grid cell from all months with an active MHW. (**c)** Median thermal displacement associated with MHWs. Thermal displacements can be in any direction (see Methods). White regions have seasonal or permanent sea ice cover. **(b,d)** Zonal median values of MHW intensity and thermal displacement, with bands indicating the 25th-75th and 10th-90th percentile ranges. Medians and percentiles are used in place of means and variance as MHW metric distributions are skewed right (Extended Data Fig. 1).

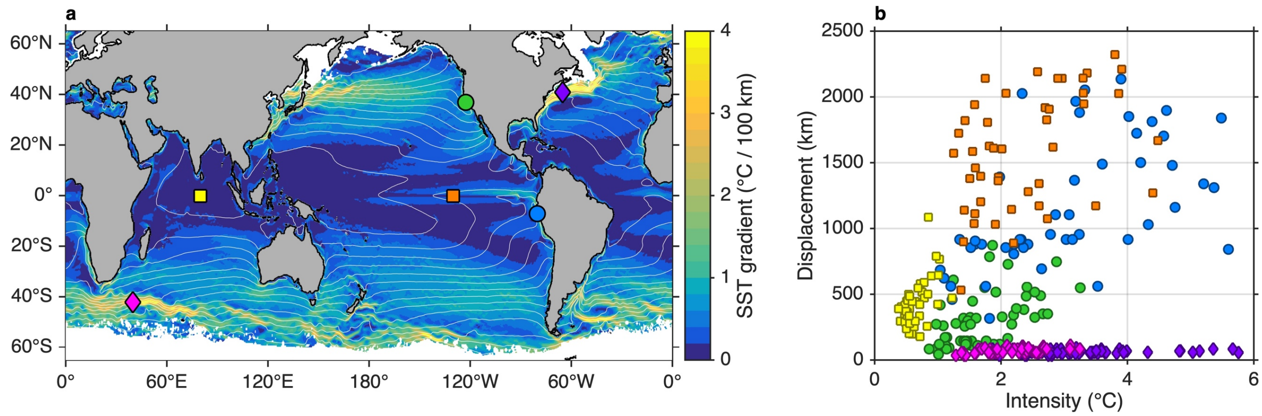

Figure 2: Dependence of thermal displacement on MHW intensity and background SST gradients. (a) Horizontal SST gradients (color) and mean SST (contours ranging 2-28˚C at 2˚C intervals), with sample locations indicated by colored markers. **(b)** Thermal displacement as a function of monthly MHW intensity for all 1982-2019 MHWs in six sample regions, characterized by strong SST gradients [diamonds; Gulf Stream (purple), Antarctic Circumpolar Current (pink)], weak SST gradients [squares; Tropical Indian Ocean (yellow), Eastern Tropical Pacific (orange)], and coastal upwelling that provides cold refugia [circles; California Current System (green), Humboldt Current System (blue)].

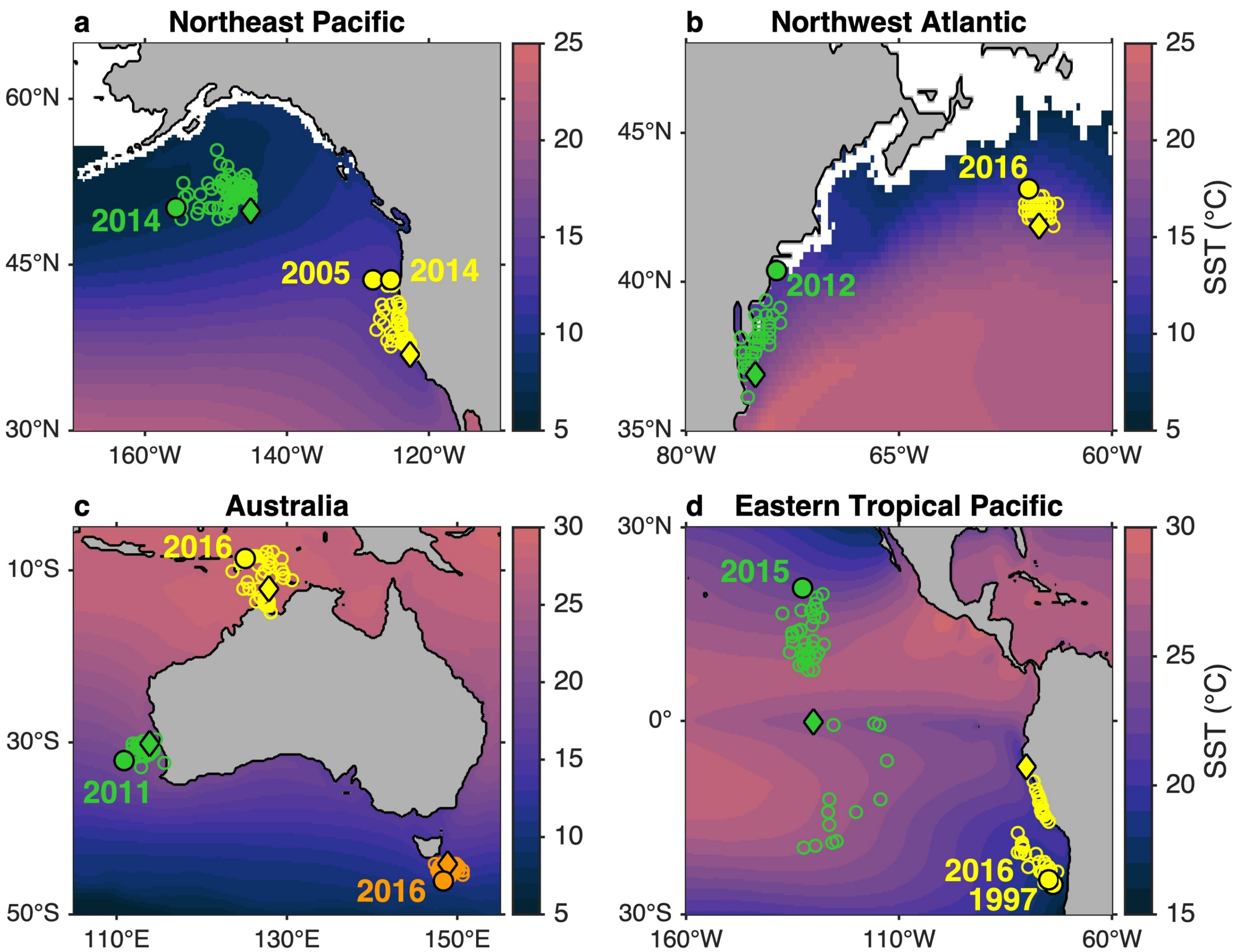

Figure 3: Thermal displacements for select locations subject to notable MHWs. For each region, displacements from select locations (diamonds) are shown for all months with an active MHW from 1982 to 2019 (open circles). Displacements and years of the most intense MHWs are also shown for each location (filled circles). For the South American west coast (d), displacements for the 1997 and 2016 MHWs are almost entirely overlapping. Spatial scales differ between panels; for reference, displacement distances for labeled events are (a) 750 km (Gulf of Alaska 2014), 872 km and 786 km (U.S. West Coast 2005 and 2014, respectively), (b) 410 km (2012) and 152 km (2016), (c) 362 km (Western Australia 2011), 492 km (Northern Australia 2016), and 226 km (Tasman Sea 2016), and (d) 2323 km (2015), 2135 km (1997) and 2025 km (2016). Background color indicates 1982-2019 mean SST.

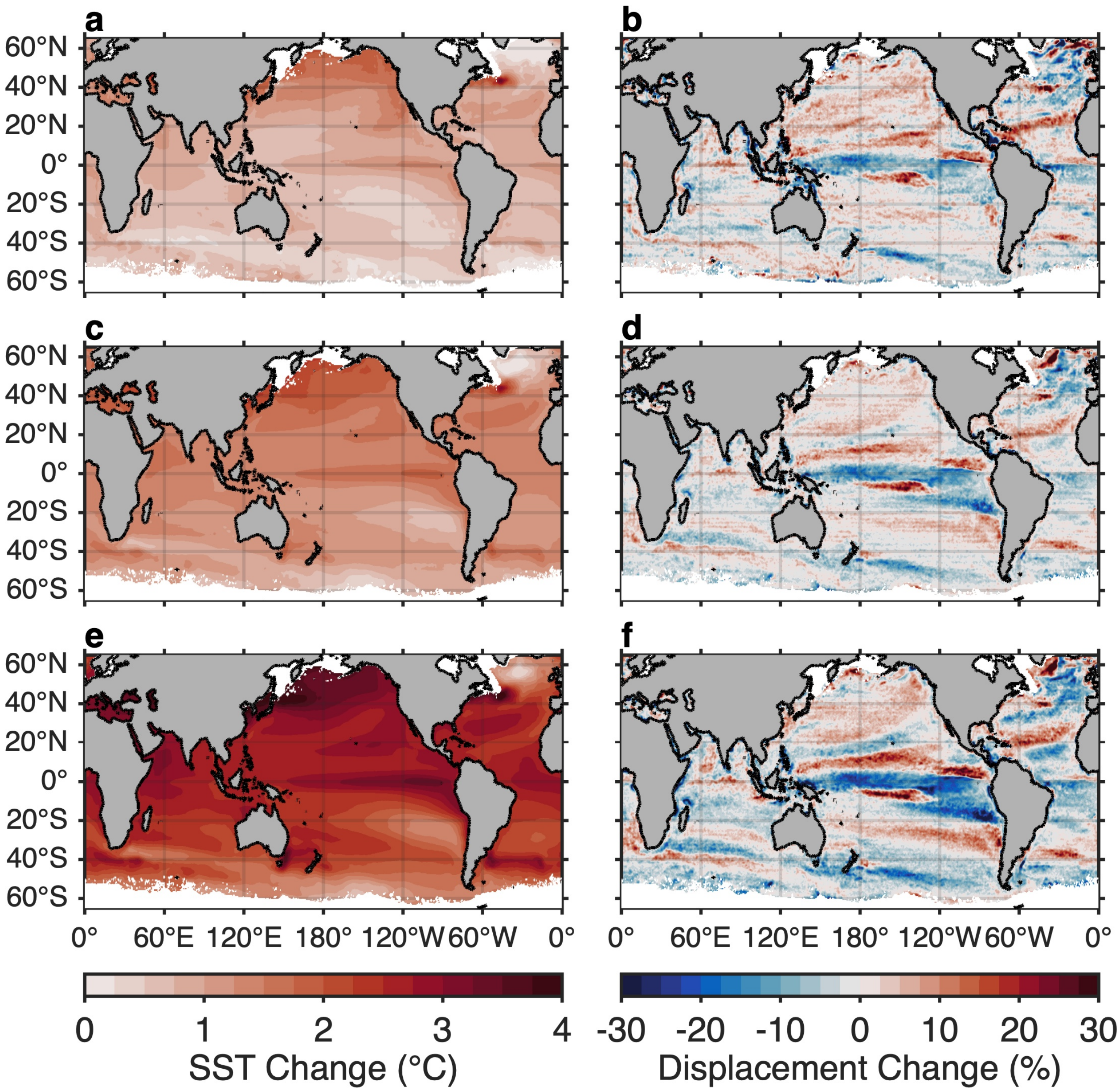

Figure 4: SST and thermal displacement changes under projected 21st century warming. CMIP5 ensemble mean SST change from the historical reference period (1982-2011) to end of century (2070-2099) are shown for (a) RCP2.6, (c) RCP4.5, and (e) RCP8.5. Changes in median MHW thermal displacement between the same two periods, with each calculated relative to its contemporaneous climatology, are shown for (b) RCP2.6, (d) RCP4.5, and (f) RCP8.5.

Methods

Defining Marine Heatwaves

Historical SST observations for the 1982-2019 period were obtained from the NOAA 0.25° Optimum Interpolation SST, version 2 (OISSTv2; refs 38 and 39), which has been used previously for MHW detection[9]. We masked out regions where OISSTv2 ice concentrations were greater than zero for more than 15 days in a month. MHWs were identified based on methodology adapted from Hobday et al.[21]. For each grid cell we calculated time series of SST anomalies relative to the 1982-2011 climatology and classified MHWs as periods with SST anomalies above a seasonally varying 90th percentile threshold (Extended Data Fig. 5). Our analysis differs from some others in that we used monthly averaged SST rather than daily data, and we detrended the SST anomalies to distinguish discrete, transient MHWs from the long-term warming signal[31]. While we believe the choices to use monthly data and to detrend anomalies are most appropriate for this analysis, we are aware of the lack of consensus on these aspects of MHW definition and detection. Therefore, we include a section below, *Justification for MHW Definition and Implications for this Study*, to outline the motivations for our choices and to compare our results to those based on daily data and those calculated without removing the warming trend. Neither the monthly data frequency nor the detrending qualitatively impact our results.

Calculating Thermal Displacement

For each MHW (i.e., every month characterized as a MHW in each grid cell), the climatological SST (SST_{CLIM}) for that location and time was first determined by subtracting the detrended SST anomaly from the observed SST. Thermal displacement was then calculated as the great circle distance to the nearest grid cell whose SST was equal to or less than SST_{CLIM} (Extended Data Fig. 5). Thermal displacements were constrained so that unrealistic paths through land barriers (e.g., entering or exiting inland seas, crossing continents between ocean basins) did not alter the large-scale patterns presented here. However, paths that interacted with land were allowed if they represented realistic displacements (e.g., along the California coast in Fig. 3a); in such cases reported thermal displacements underestimate the true distance traveled by an oceanic pathway. Regions for which displaced thermal habitat is sometimes unreachable include inland seas as well as gulfs, bays, and seas that are bounded by land masses on the poleward side. Note that an alternate approach drawing on the climate velocity literature would be to calculate thermal displacement as MHW intensity divided by the local SST gradient. This approach is appropriate for climate velocity, a local rate of change, but fails for MHW-driven thermal displacements that depend not only on the local SST gradient but also on the broader spatial structure of SST and locations of land masses.

Future Change

Projected global SST changes were calculated using historical and multiple future scenarios from coupled atmosphere-ocean models participating in the fifth Coupled Model Intercomparison Project (CMIP5). For the highest emissions scenario, RCP 8.5, model output was obtained for 28 models: ACCESS1-0, ACCESS1-3, CANESM2, CCSM4, CESM1-BGC, CESM1-CAM5, CMCC-CESM, CMCC-CM, CNRM-CM5, CSIRO-MK3-6-0, GFDL-CM3, GFDL-ESM2G, GFDL-ESM2M, GISS-E2-H, GISS-E2-R, HADGEM2-AO, HADGEM2-CC, HADGEM2-ES, INMCM4, IPSL-CM5A-LR, IPSL-CM5A-MR, IPSL-CM5B-LR, MIROC5, MIROC-ESM, MPI-ESM-LR, MPI-ESM-MR, NORESM1-ME, and NORESM1-M (for more information see https://www.esrl.noaa.gov/psd/ipcc/cmip5/models.html). For the moderate RCP 4.5 scenario, output was obtained for the same models, except for CMCC-CESM. For the lowest emissions scenario, RCP 2.6, output was available from just seven of these models: CANESM2, HADGEM2-AO, MIROC-ESM, MIROC-ESM-CHEM, MIROC5, MPI-ESM-LR, and MPI-ESM-MR. SST output from each model was bilinearly interpolated to a common 1° by 1° grid before creating an ensemble average SST. The future change was defined as the difference between monthly mean climates of historical (1982-2011) and future (2070-2099) periods. Month-dependent changes from the CMIP5 ensemble were interpolated to the OISST grid with a cubic interpolation and added to the observed 1982-2019 OISSTv2 data to produce future SST fields at the 0.25˚ OISST resolution. We then repeated the steps described in the previous section and Extended Data Fig. 5 to identify MHWs and thermal displacements for the future period as we did for the historical period. Our analysis retains interannual SST variability from historical observations, and thus considers only the impacts of the mean SST change, not changes in the interannual variability, on thermal displacements. Our aim is to illustrate that the mean SST change can impact the interannual variability in thermal displacement, which is not the case for MHW metrics such as intensity, frequency, and duration. Future changes in SST variance could also influence thermal displacement, though past analysis of CMIP5 output indicates that significant projected changes in SST variance are mostly limited to high-latitude regions with reduced ice cover under future warming[40], and these ice-covered regions are excluded from our analysis. Nonetheless, a more in-depth sensitivity analysis could explore thermal displacement changes forced by time-varying output from individual model projections, considering the strengths and weaknesses of each.

Note that for the future period we calculated SST anomalies relative to the future climatology, not the historical climatology. This approach defines MHWs and their associated thermal displacements as disturbances relative to the contemporaneous climate[31], which differs from studies that define future MHWs relative to a fixed historical baseline[9,10]. In the context of thermal displacement, the two approaches (i.e., using historical versus contemporaneous baselines) provide different information. If one defines displacements relative to a historical baseline, the analysis includes long term shifts due to the mean warming trend as well as short-term displacements due to higher frequency (interannual) variability. The long-term shift is certainly important and has been the focus of the well-established literature on climate velocity and its relation to marine species distributions[13,14,15,16,17]. The higher frequency variability is where we make a novel contribution, focusing on changes in thermal displacement relative to long-term shifts, which are also important from physical and ecological perspectives (see *Justification for MHW Definition and Implications for this Study* section below).

Statistics

As is often the case for data sets with lower boundaries, MHW metrics including intensity and thermal displacement are skewed right (Extended Data Fig. 1), with a long right tail made up of events that are especially intense or generate especially large displacements. Given the skewness of the distributions we characterize them using medians, percentiles, and interquartile ranges rather than means and standard deviations. Where spatial correlations are reported, they represent the Spearman rank correlation coefficient (r) calculated across all ocean areas without ice cover. In total, ~ 500,000 grid points are used for these correlations, but the number of effective degrees of freedom is much less due to spatial autocorrelation in the SST and MHW fields (e.g., in Figs.

1a,c and 2a). The spatial decorrelation scales of these fields are highly variable in space (e.g., they are lower in coastal regions and dynamic current systems), which complicates accurate determination of the effective degrees of freedom. As a result, we refrain from reporting the significance of spatial correlations; however, we can safely say that the stronger correlation coefficient we report (r = -0.81) is significant, as it would require only ~15 effective degrees of freedom, while the weaker correlation (r = -0.27), even if significant, indicates negligible correspondence between the two variables (~7% shared variance). For temporal correlations in a given location (Extended Data Fig. 4), each MHW is assumed to be statistically independent.

Justification for MHW Definition and Implications for this Study

Here we discuss the justifications for using monthly data and detrending SST anomalies, and the implications of those choices for the results of the present study. We note at the outset that they do not qualitatively impact our findings; using monthly data rather than daily alters the frequency and duration of identified MHWs (Extended Data Table 1, Extended Data Fig. 6), but MHW intensities are only slightly reduced and impacts on thermal displacements are negligible (Extended Data Table 1, Extended Data Fig. 7). Similarly, using a fixed 1982-2011 baseline climatology rather than detrending the historical SST data generally increases MHW intensities and thermal displacements, most notably in the high northern latitudes, but produces no consequential changes in our conclusions (Extended Data Figs. 8-10).

The recommended MHW definition of Hobday et al.[21] has been adopted by many in general terms, though details of the methodology have been altered depending on the particular aims and constrains of different studies. For example, Holbrook et al.[11] used the 98^{th} percentile as a threshold (rather than the 90th percentile), as "a 90th percentile threshold resulted in too many small events that made it unclear when the main event was taking place". Using monthly rather than daily data similarly limits identified MHWs to the "main events". Data with monthly resolution and/or coarse spatial resolution have been used for historical analyses and future projections[9,10,41], and monthly data is used in forecasts for MHWs and other SST anomalies[42,43,44]. With respect to the reference period for defining MHWs, several analyses of long-term MHW trends have used fixed baselines[9,10], though other studies have employed detrended anomalies[11,41] (note that these studies using fixed baselines and detrended anomalies share many of the same authors). Thus, modifying the Hobday et al.[21] definition is not without precedent; it is a proposal rather than a consensus and indeed they say "these metrics can, of course, be modified to suit the specific application". Below we outline justifications for our choices in the context of the present study, addressing first the use of the monthly data and then the removal of long-term warming trends.

We chose to use monthly SST data for our analysis for several reasons: (i) The atmospheric heatwave definition requires a minimum three-day event duration[21] and while Hobday et al.[21] note that for MHWs "minor differences to the atmospheric definition (minimum duration and minimum time between events) were implemented because of the naturally longer time scales of ocean variability compared with atmospheric variability", the adjustment from three days for the atmosphere to five days for the ocean is not representative of their different scales of variability. The atmosphere has very little memory and is often treated as stochastic, while decorrelation time scales in the ocean can range from days to over a year (ref 45 and references therein). Thus, we argue that a minimum MHW duration of a month represents a more appropriate scaling relative to the atmospheric heatwave definition. (ii) MHW definitions based on monthly data are more consistent with reported impacts. The MHWs identified as being the most impactful historically have with few exceptions lasted at least a month[46,47], and while MHWs are generally thought of as rare events, according to daily definitions they happen multiple times per year in most locations. For example, in the Eastern Tropical Pacific we find MHWs once every 3-4 years using monthly data, which is consistent with the frequency of El Niño events. In contrast, using daily data with a 5-day minimum duration there are on average 1.2 MHWs per year identified in that region (Extended Data Table 1). (iii) To the extent that thermal displacement can serve as a proxy for distributional shifts of marine species, MHWs must last long enough for those distributional shifts to occur. Such ecological impacts (e.g., marine fishes swimming hundreds or thousands of kilometers) will not be realized in a matter of days. (iv) Thermal displacement calculations are much more computationally expensive than calculations of other MHW metrics (e.g., intensity, duration, frequency). In addition to being more appropriate for this analysis for the reasons listed above, the use of monthly data also lowers the computational burden dramatically. Nonetheless, the same methodology can be applied to daily MHW definitions if desired.

There are physical and ecological arguments for detrending SST anomalies when defining and characterizing MHWs in the presence of a long-term warming trend[31]. From a physical perspective, we start from the premise that a MHW is, in fact, a wave (or more precisely the warmest part of a temperature anomaly wave). Using a fixed baseline leads to clear violations of wave property definitions (amplitude/intensity, frequency), which are objectively determined relative to a contemporaneous equilibrium position. Furthermore, the proposed qualitative MHW definition of "a discrete prolonged anomalously warm water event"[21] is violated when using a fixed baseline in a warming ocean; eventually historical MHW thresholds are permanently exceeded and MHWs are neither discrete (i.e., "with well-defined start and end times") nor anomalous (as something that occurs every day is not anomalous).

Arguments in favor of a fixed baseline for MHWs generally invoke impacts on marine species, specifically that (i) they respond to the total temperature change, not just the variability around the mean, and/or (ii) they have evolved in response to historical, not future, conditions. To the argument that the total warming is important for species responses, we agree, but that doesn't mean all warming is associated with MHWs. When changes in temperature due to the combination of MHWs and long-term warming are of interest, metrics like cumulative stress, degree days, or threshold exceedance are appropriate[48]. To the argument that species have evolved based on past conditions, again we agree. But different species respond in different ways, at different thresholds, and on different timescales, and their adaptive and evolutionary capacities are similarly disparate in nature and timescale. Thus, while MHW metrics are useful for characterizing marine ecosystem change, no MHW definition will pass the test of being broadly appropriate for marine species responses. As is done for other ecologically-important physical ocean phenomena (upwelling for example), MHW metrics should be defined based on the physics, and their impacts can then be explored for the organism or application of interest.

Finally, from the perspective of species that have evolved over perhaps millions of years, a 1980-2010 (or similar) baseline holds no more significance than an 1880-1910 or a 2080-2110 baseline. Rather, recent decades offer a useful baseline for us to evaluate the ecosystem as they represent our “normal”. Even though the oceans have warmed over the past century we evaluate MHWs relative to a recent baseline; in the future people will be similarly interested in variability relative to their “normal”. For example, taking the simplifying assumption that a commercial fish species follows surface isotherms, they will exhibit a relatively slow shift in their mean position due to mean warming as well as relatively fast shifts around their mean position due to MHWs. The two timescales of shifts have different implications for fisheries – the slow shift would dictate changes in where fishing operations should be based, while the fast shifts would dictate year-to-year disruptions in the fishery. One could think of an analogy using sea level – if a beach has waves that are one meter high and sea level rises two meters due to warming and ice melt, would we say that the waves are now three meters high? We argue that would be technically incorrect and misleading; characterizations of waves and mean sea level rise should be kept separate so that as appropriate waves can be assessed separately (e.g., by a surfer who cares only about the wave height) or in combination with the mean change (e.g., by a beachfront property owner who cares about the total sea level change).

Data and Code Availability

NOAA High Resolution OISSTv2 data were obtained from the NOAA/OAR/ESRL PSD, Boulder, Colorado, USA, at their website (https://www.esrl.noaa.gov/psd/). CMIP5 outputs were obtained from Earth System Grid Federation (https://esgf-node.llnl.gov/projects/cmip5/). For CMIP5 ensemble mean SST fields used in this analysis, contact Jamie Scott (james.d.scott@noaa.gov). All analyses were performed using MATLAB. Codes can be accessed at https://github.com/mjacox/Thermal_Displacement.

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Author Contributions

M.G.J conceived the study, performed the heatwave analysis, and drafted the manuscript. M.A.A. and S.J.B. contributed to interpretation and presentation of the results. J.D.S processed the CMIP5 output. All authors revised the manuscript.

Competing Interests

The authors declare no competing interests.

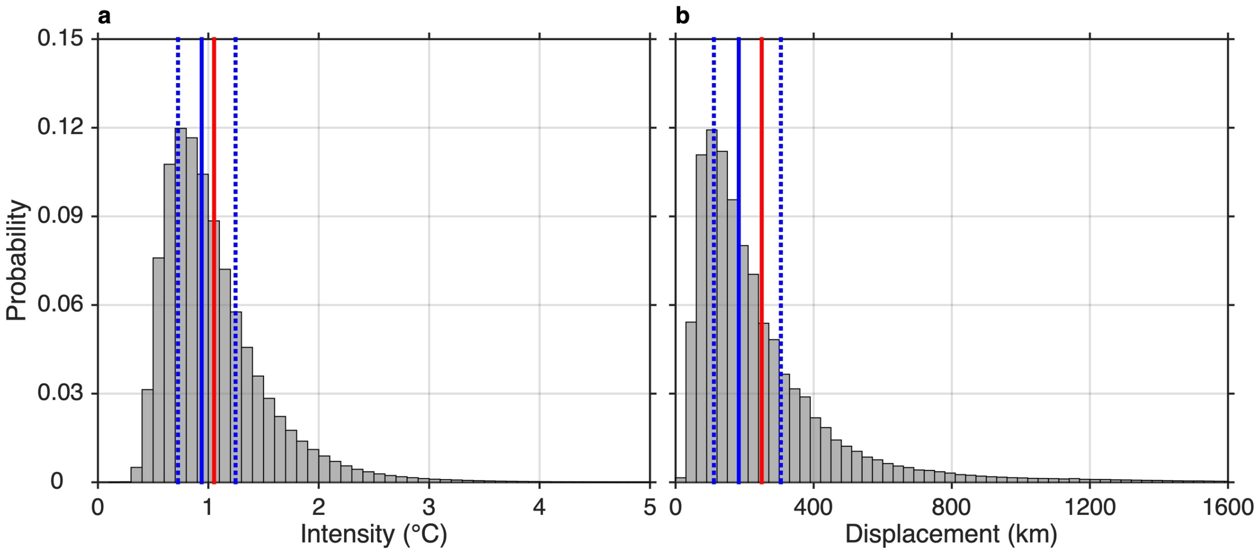
Materials and Correspondence

Correspondence and request for materials should be addressed to M.G.J. (michael.jacox@noaa.gov).

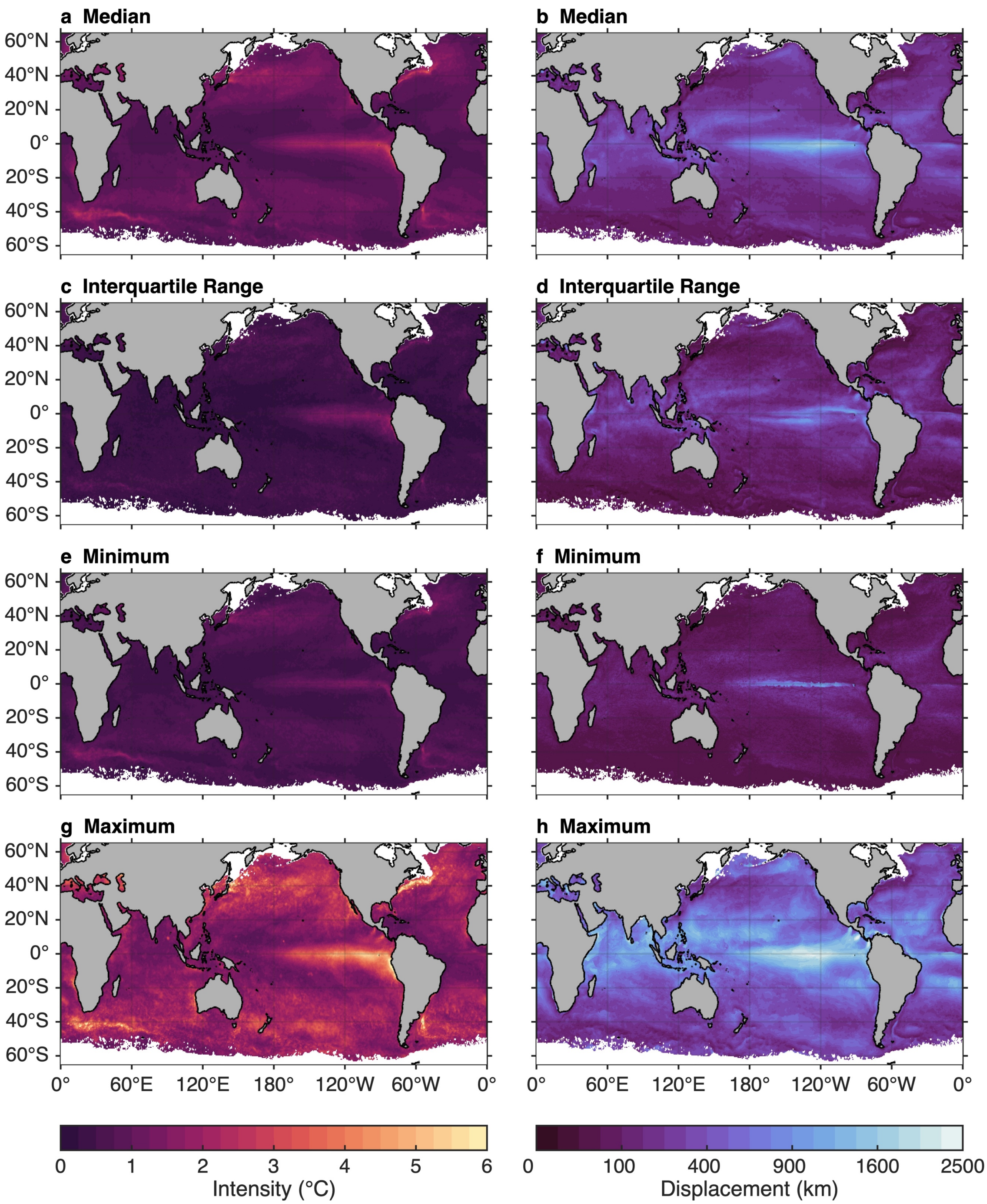
Extended Data

	Frequency (yr^{-1})		Duration (day)		Intensity (˚C)		Displacement (km)	
Location	Daily	Monthly	Daily	Monthly	Daily	Monthly	Daily	Monthly
Gulf of Alaska [145˚W, 50˚N]	2.0	0.7	12 (6-22)	61 (30-91)	1.6 (1.2-1.9)	1.3 (1.1-1.7)	279 (195-390)	287 (221-413)
Central California [122.5˚W, 37˚N]	1.8	0.8	9 (7-20)	30 (30-30)	2.0 (1.6-2.4)	1.5 (1.2-2.1)	273 (146-452)	273 (120-392)
Mid Atlantic Bight [75˚W, 37˚N]	2.7	0.8	8 (6-12)	30 (30-61)	2.4 (2.0-3.2)	1.9 (1.3-2.3)	139 (83-222)	111 (67-165)
Gulf Stream [55˚W, 42˚N]	2.8	0.9	8 (6-14)	61 (30-61)	2.8 (2.3-3.3)	2.1 (1.7-2.8)	83 (59-104)	83 (56-93)
Western Australia [114˚E, 30˚S]	2.0	0.7	7 (5-14)	30 (30-61)	1.7 (1.4-2.0)	1.3 (1.1-1.5)	114 (87-177)	114 (83-156)
Northern Australia [128˚E, 12˚S]	2.1	0.8	7 (5-12)	30 (30-61)	1.3 (1.0-1.6)	0.9 (0.8-1.1)	238 (169-389)	245 (178-424)
Tasman Sea [149˚E, 44˚S]	2.4	0.9	8 (6-16)	30 (30-61)	1.7 (1.4-2.1)	1.3 (1.1-1.7)	92 (68-118)	85 (74-113)
Eastern Tropical Pacific [130˚W, 0˚]	1.1	0.3	9 (6-17)	46 (30-213)	2.4 (1.9-3.2)	2.1 (1.6-2.9)	1390 (1133-1866)	1608 (1203-1948)
Peru [80˚W, 7˚S]	1.0	0.4	8 (6-15)	30 (30-76)	3.3 (2.3-4.6)	3.1 (2.1-4.3)	1105 (858-1538)	954 (861-1634)

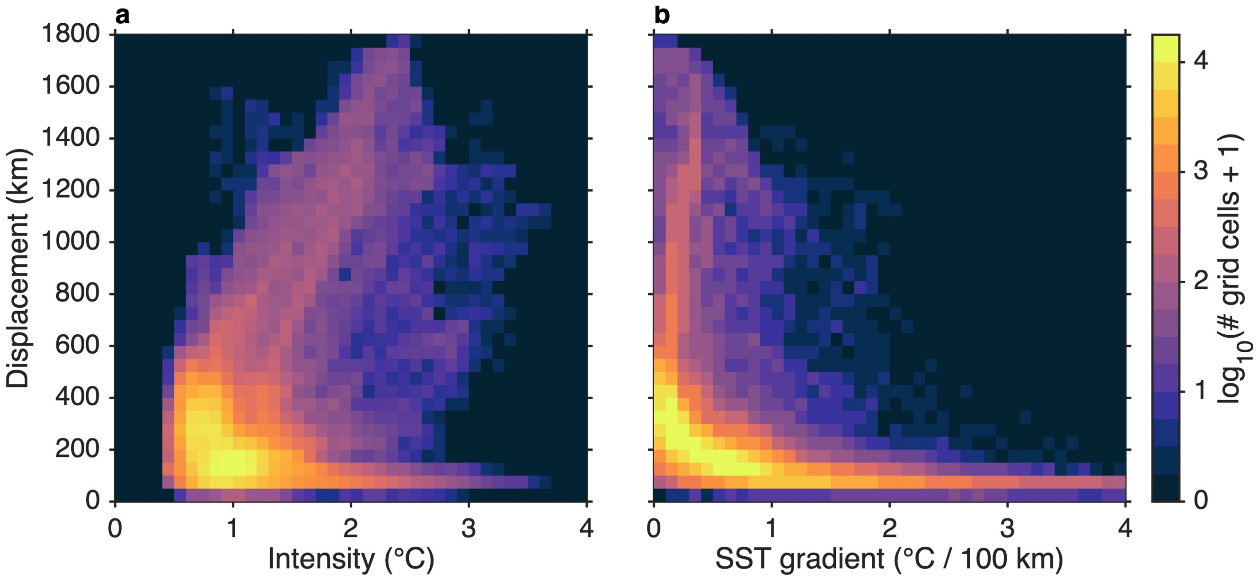
Extended Data Table 1. Influence of monthly averaging on MHW metrics. For each of the locations in Fig. 3, MHW metrics are shown based on (i) daily SST anomalies used to define MHW with a 90th percentile threshold and five-day minimum duration[21], and (ii) monthly SST data used to define MHW with a 90th percentile threshold and one-month minimum duration. For duration, intensity, and thermal displacement, median values are shown with 25th-75th percentile range in parentheses.



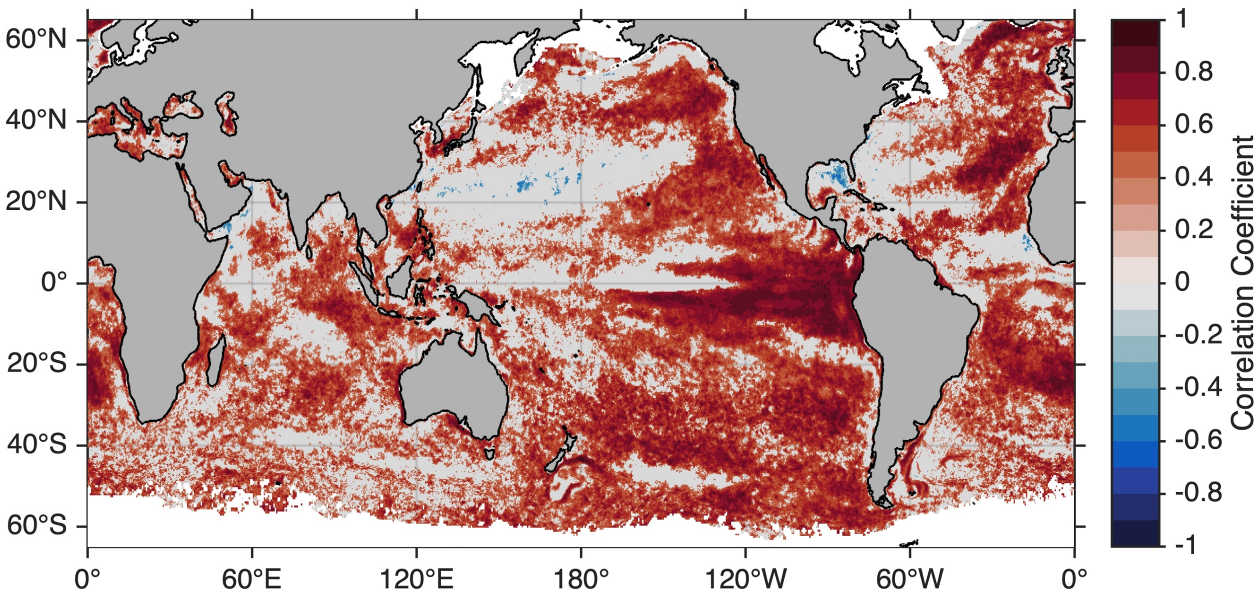
Extended Data Figure 1: Distributions of MHW intensity and thermal displacement. Histograms of **(a)** MHW intensity and **(b)** thermal displacement are shown for months with active MHWs from 1982 to 2019, aggregated across all OISST grid cells without ice cover. Vertical lines indicate medians (solid blue), 25th and 75th percentiles (dashed blue), and means (solid red) of each distribution.



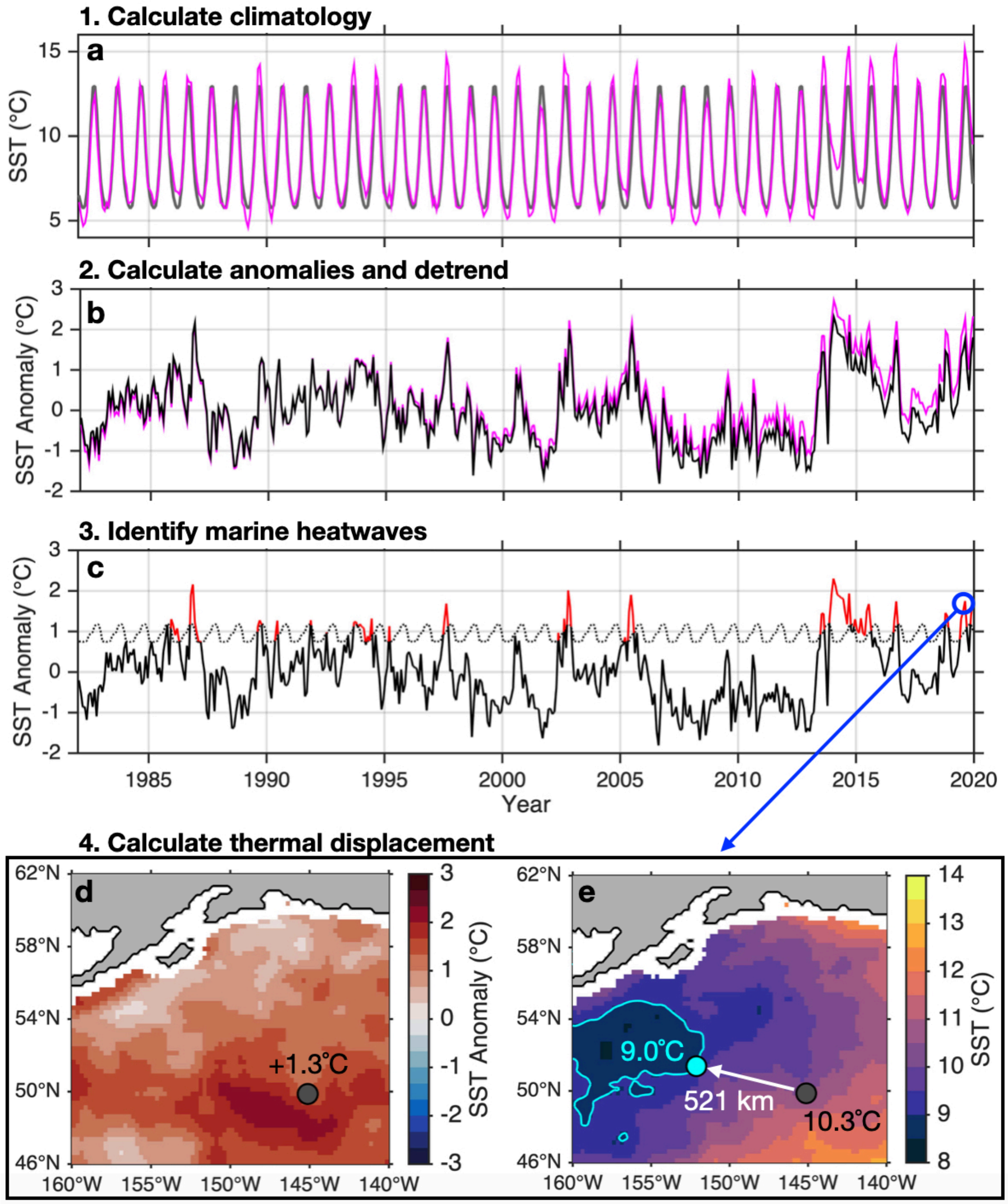
Extended Data Figure 2: Statistics of MHW intensity and thermal displacement. (a,b) median, **(c,d)** 25th-75th percentile range, **(e,f)** minimum, and **(g,h)** maximum values of **(a,c,e,g)** MHW intensity and **(b,d,f,h)** thermal displacement calculated across all MHW events from 1982 to 2019.



Extended Data Figure 3: Spatial variability in thermal displacement is dependent more on spatial SST gradients than on MHW intensity. Colors represent the number of 0.25 degree OISST grid cells that fall into each bin of thermal displacement and **(a)** MHW intensity or **(b)** SST gradient. The sum of grid cells in all bins is the total number of ice-free OISST grid cells (n ≅ 500,000). Spearman rank correlations are **(a)** r = -0.27 and **(b)** r = -0.81.

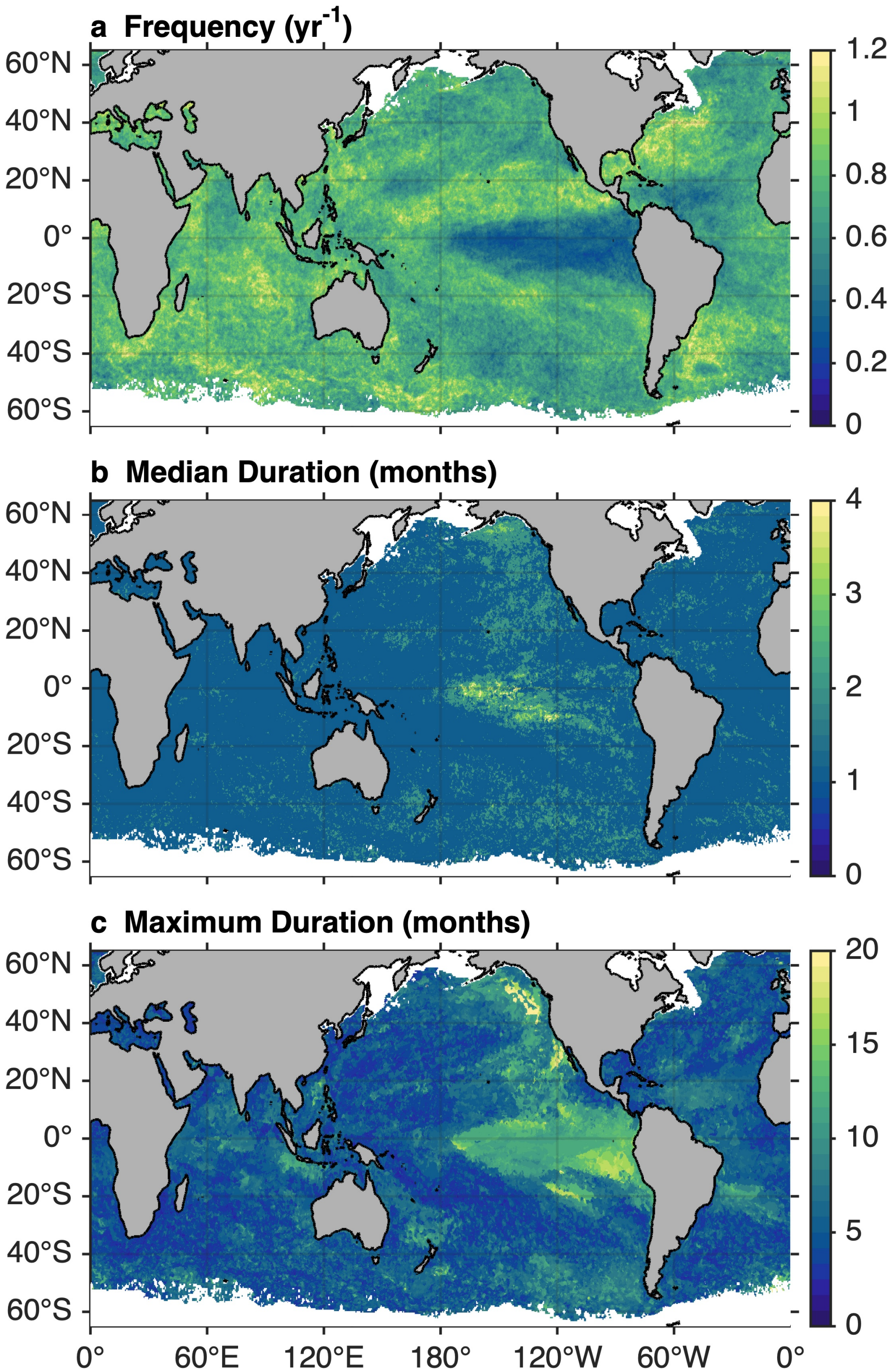


Extended Data Figure 4: Temporal variability in thermal displacement is dependent on MHW intensity for much of the global ocean. Spearman rank correlation coefficients between MHW intensity and thermal displacement are shown for each grid cell. Locations where correlations are insignificant at the 95% significance level are grayed out. Significance calculations assume each MHW event in a given location is statistically independent.

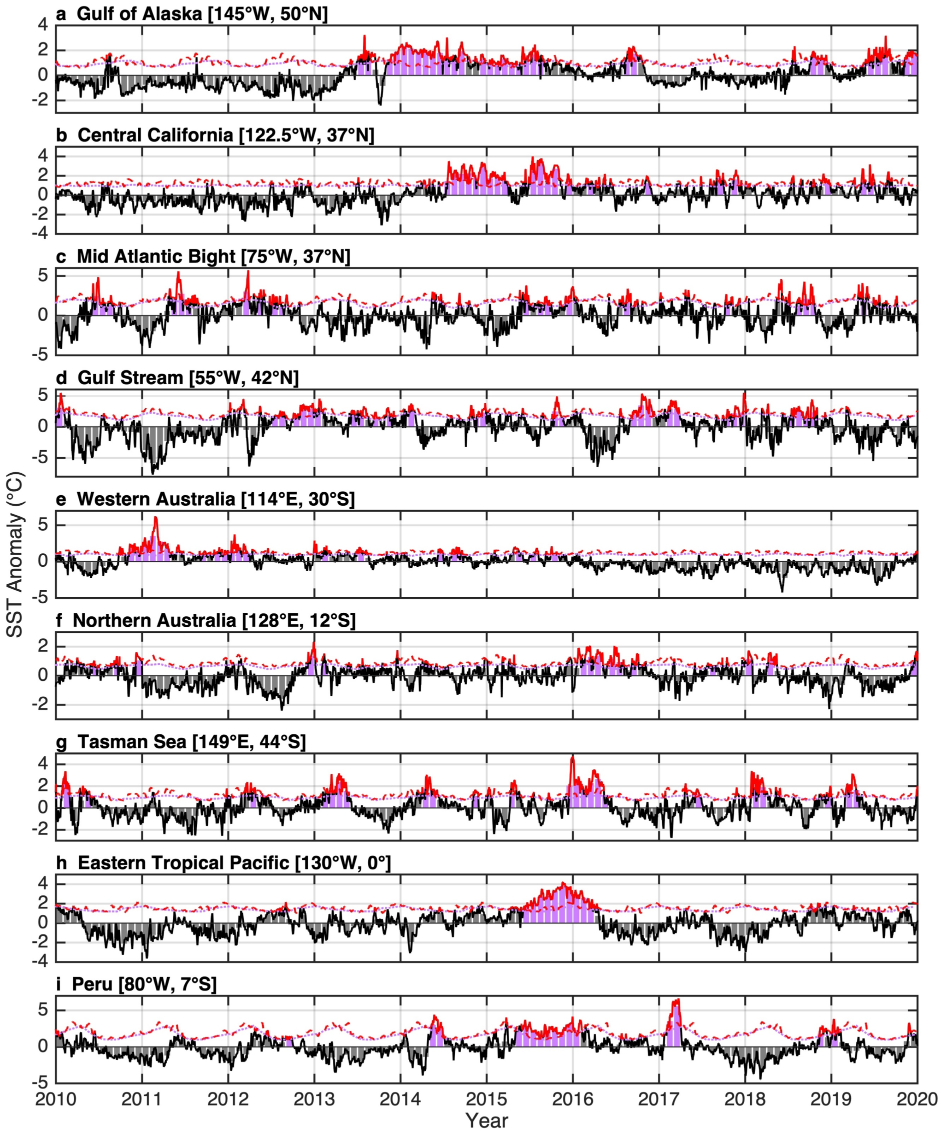


Extended Data Figure 5: Thermal displacement methodology. Steps for calculating thermal displacement are illustrated for a sample location in the Gulf of Alaska (145˚W, 50˚N). For each ice-free grid cell in the global ocean (n ≅ 500,000), the following steps are taken: **(a)** The 1982-2011 monthly climatological temperature (gray) is calculated from the OISSTv2 data (magenta). **(b)** The monthly climatology is subtracted to obtain monthly anomalies (magenta), which are then linearly detrended (black). **(c)** MHWs (red) are identified as months when the detrended

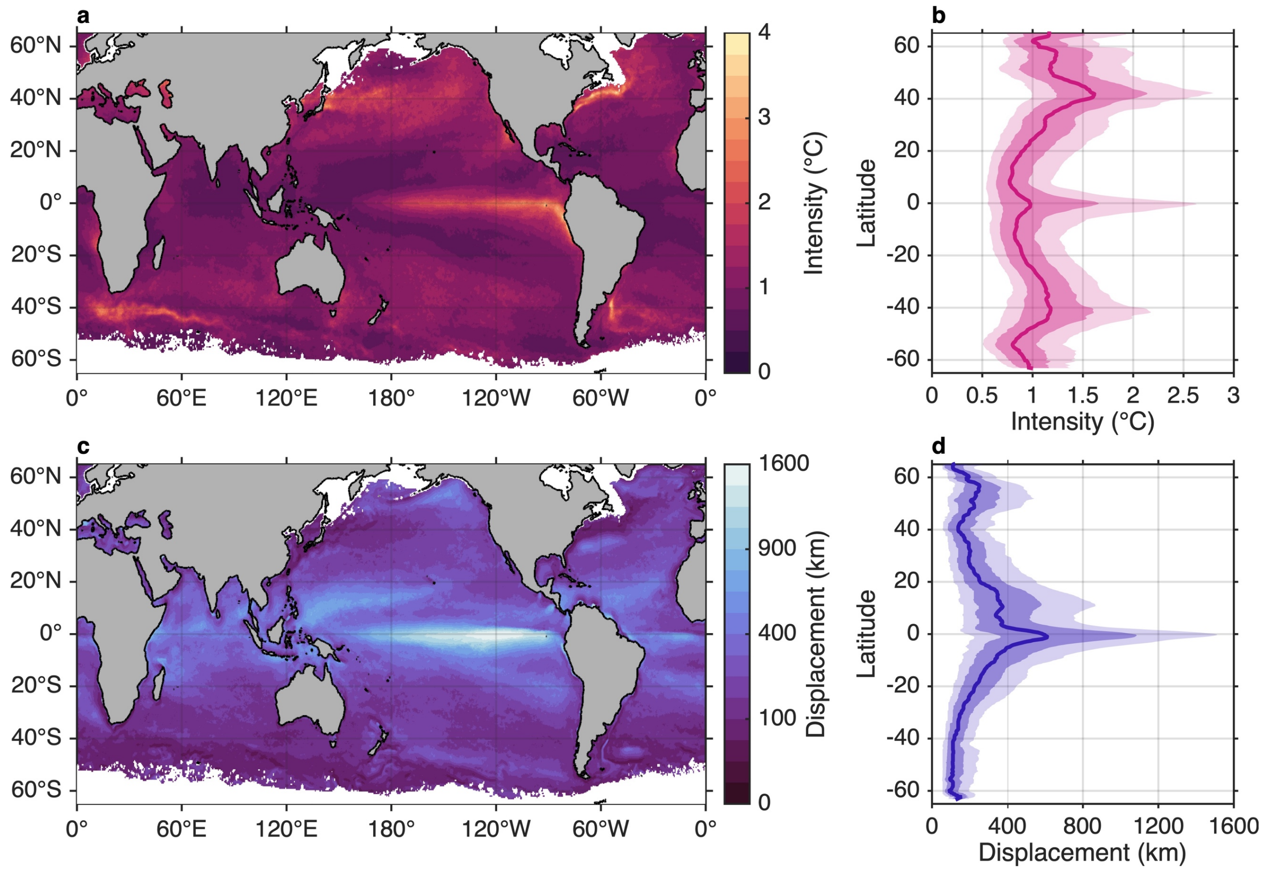
SST anomaly (black) exceeds a seasonally-varying 90^{th} percentile threshold (dotted black line). For each month with a MHW occurring (August 2019 is highlighted here for example), the detrended SST anomaly (1.3˚C in this case; panel **d**) is subtracted from the observed SST (10.3˚C; panel **e**) to obtain the “normal” temperature (9.0˚C) for that month of the year. **(e)** Thermal displacement is the shortest distance (521 km; white arrow) to SST at or below the “normal” temperature (cyan contour). For the future projections, the same methodology is used after adding the mean projected SST change to the time series in **(a)**.



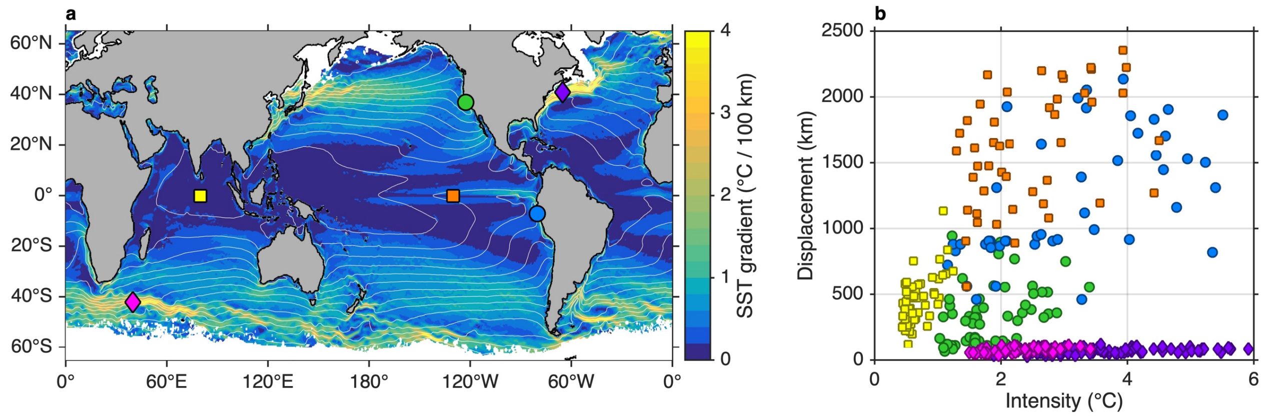
Extended Data Figure 6: Frequency and duration of MHW events. For each grid cell, MHW **(a)** frequency, **(b)** median duration, and **(c)** maximum duration, calculated from monthly mean SST anomalies, are shown for 1982-2019.



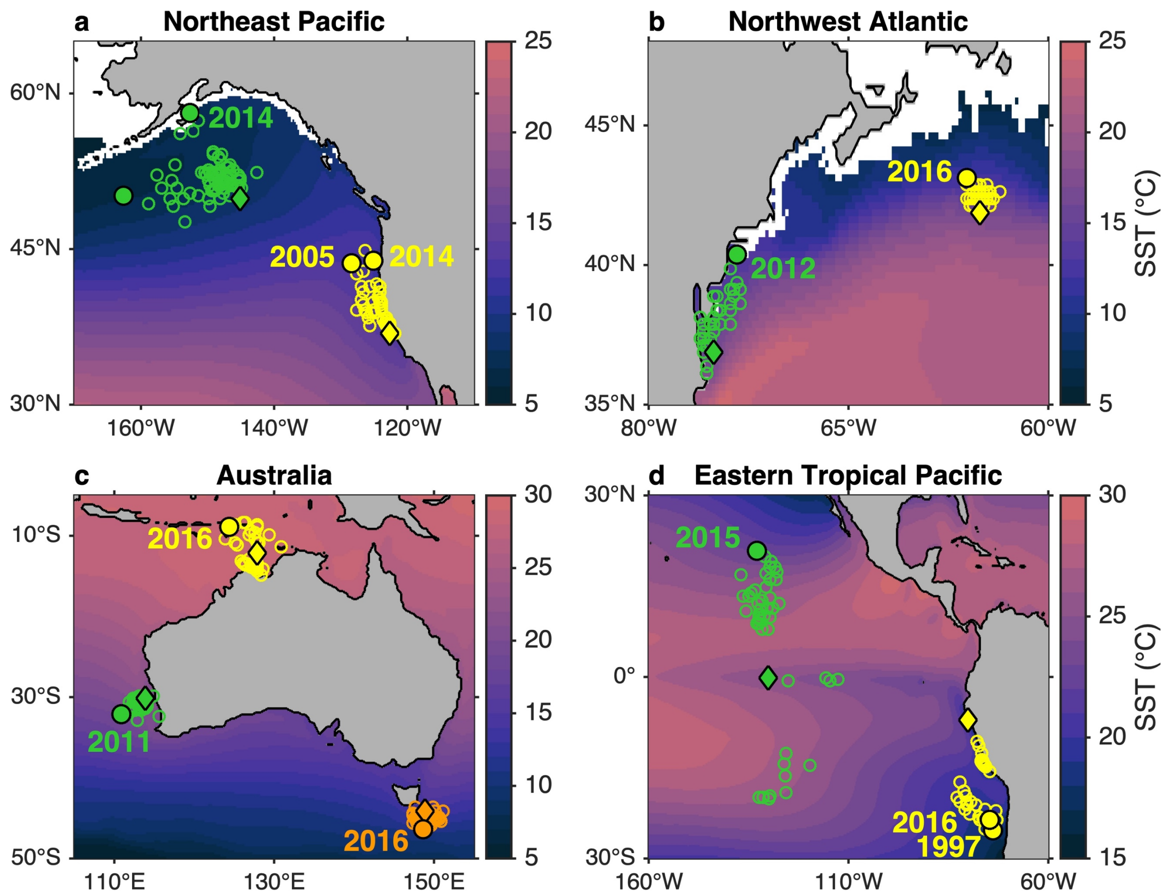
Extended Data Figure 7: MHW definitions based on daily vs. monthly SST data are consistent. (a-i) SST anomaly time series are shown for each of the locations in Fig. 3 Daily data are shown as lines while vertical bars depict monthly data. MHWs defined from the daily data (using 90th percentile threshold, five-day minimum duration, at least two days separating distinct events) are shown as red lines while MHWs defined from the monthly data (using 90th percentile threshold, one-month minimum duration) are shown as purple bars. The SST anomaly thresholds used to define MHWs in each location are shown as red dashed (daily) and purple dotted (monthly) lines, which are often overlapping.



Extended Data Figure 8: Marine heatwaves and their influence on thermal habitat redistribution globally, calculated with a fixed historical baseline. **(a)** Median MHW intensity (the SST anomaly associated with a MHW) from 1982 to 2019, calculated at each grid cell from all months with an active MHW. (**c**) Median thermal displacement associated with MHWs. Thermal displacements can be in any direction (see Methods). White regions have seasonal or permanent sea ice cover. **(b,d)** Zonal median values of MHW intensity and thermal displacement, with bands indicating the 25th-75th and 10th-90th percentile ranges. In contrast to Figure 1, MHWs here were calculated without detrending SST anomalies relative to the 1982-2011 climatology.



Extended Data Figure 9: Dependence of thermal displacement on MHW intensity and background SST gradients, calculated with a fixed historical baseline. (a) Horizontal SST gradients (color) and mean SST (contours ranging 2-28˚C at 2˚C intervals), with sample locations indicated by colored markers. **(b)** Thermal displacement as a function of monthly MHW intensity for all 1982-2019 MHWs in six sample regions, characterized by strong SST gradients [diamonds; Gulf Stream (purple), Antarctic Circumpolar Current (pink)], weak SST gradients [squares; Tropical Indian Ocean (yellow), Eastern Tropical Pacific (orange)], and coastal upwelling that provides cold refugia [circles; California Current System (green), Humboldt Current System (blue)]. In contrast to Figure 2, MHWs here were calculated without detrending SST anomalies relative to the 1982-2011 climatology.



Extended Data Figure 10: Thermal displacements for select locations subject to notable MHWs, calculated with a fixed historical baseline. For each region, displacements from select locations (diamonds) are shown for all months with an active MHW from 1982 to 2019 (open circles). Displacements and years of the most intense MHWs are also shown for each location (filled circles). Spatial scales differ between panels; for reference, displacement distances for labeled events are **(a)** 1039 km (Gulf of Alaska 2014), 895 km and 807 km (U.S. West Coast 2005 and 2014, respectively), **(b)** 418 km (2012) and 161 km (2016), **(c)** 362 km (Western Australia 2011), 526 km (Northern Australia 2016), and 251 km (Tasman Sea 2016), and **(d)** 2354 km (2015), 2135 km (1997) and 1926 km (2016). In contrast to Figure 3, MHWs here were calculated without detrending SST anomalies relative to the 1982-2011 climatology. Background color indicates 1982-2019 mean SST.