Title

Marine heatwaves are not a dominant driver of change in demersal fishes

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Summary

Marine heatwaves have been linked to negative ecological effects in recent decades.[1,2] If marine heatwaves regularly induce community reorganization and biomass collapses in fishes, the consequences could be catastrophic for ecosystems, fisheries, and human communities.[3,4] However, the extent to which marine heatwaves have negative impacts on fish biomass or community composition or even whether their effects can be distinguished from natural and sampling variability remains unclear. We investigated the effects of 248 sea bottom heatwaves from 1993 to 2019 on marine fishes by analyzing 82,322 hauls (samples) from long-term scientific surveys of continental shelf ecosystems in North America and Europe spanning the subtropics to the Arctic. We found that the effects of marine heatwaves on fish biomass were often minimal and could not be distinguished from natural and sampling variability. Further, marine heatwaves were not consistently associated with tropicalization (gain of warm-affiliated species) or deborealization (loss of cold-affiliated species) in these ecosystems. While steep declines in biomass occasionally occurred after marine heatwaves, these were the exception, not the rule. Against the highly variable backdrop of ocean ecosystems, marine heatwaves have not driven biomass change or community turnover in fish communities that support many of the world's largest and most productive fisheries.

Main text

Extreme climatic events exacerbated by global climate change are associated with many examples of ecological transformation[5]. Marine heatwaves (MHWs)[6]—prolonged periods of anomalously warm ocean temperatures—have been linked to widespread coral bleaching and die-offs of kelp forests and reef fishes in shallow coastal seas[1,2]. MHWs can rapidly displace some marine species by hundreds of kilometers and cause abrupt declines in phytoplankton and commercially important species[7–9]. These high-profile catastrophes and those emerging from regional and global model simulations predict that MHWs will likely wreak ecological devastation and negatively impact socio-economic systems[3,4,10]. However, accurate predictions must rely upon generalizable patterns and processes, not case-studies with limited spatial and taxonomic scope. The extent to which MHWs in general have negative ecological impacts or even whether they can be differentiated from other sources of natural and sampling variability in marine systems remains unclear. In the few studies that have compared responses to MHWs across multiple species within the same ecosystem, some species declined while others thrived[11–13], suggesting that single-species responses do not accurately reveal net ecological effects. These net effects are particularly important to understand in continental shelf ecosystems, where many of the world's largest ocean fisheries operate[14].

Here, we analyzed the cross-species and cross-ecosystem effects of MHWs in Northern-hemisphere shelf ecosystems from the subtropics to the Arctic. We analyzed 82,322 hauls (discrete samples) comprising 22,574,452 observations of 1,769 demersal fish taxa from 18 long-term scientific (i.e., fisheries-independent) bottom trawl surveys covering 45 degrees of latitude in the Northeast Pacific, Northwest Atlantic, and Northeast Atlantic (Fig. 1). Ninety percent of hauls occurred in waters 18-448 m deep. These surveys represent the most spatially, temporally, and taxonomically extensive observations available for testing MHW effects. We examined observations from 1993-2019 to quantify the effects of MHWs on regional fish biomass and community composition (Fig. 1).

We defined a MHW as a period of ≥ 5 days with sea bottom temperature (SBT) anomalies above the seasonally varying 95th percentile for that region[6] and used cumulative intensity as the primary metric characterizing MHWs (see Methods). Cumulative intensity is measured in °C-days and represents the sum of the time-varying anomalies above the 95th percentile threshold over the duration of the event. This approach—defining MHWs as physical phenomena based on relative temperature anomalies—is widely applied in oceanography.[15] A contrasting approach is to define absolute temperature thresholds above which deleterious ecological impacts consistently occur, as have been identified for coral reefs.[16] Such a biological threshold has not been described in most marine systems, including the ones we studied, so we explored a range of relative and absolute MHW metrics (see Methods). We hypothesized that MHWs altered fish biomass and community composition and that these effects would increase with the cumulative intensity of MHWs.

This dataset recorded some notable MHW impacts that mirror previous reports in the literature, including a 22% biomass loss in the Gulf of Alaska following the 2014-2016 Northeast Pacific MHW with a cumulative intensity of 57 °C-days[8,17] and a 70% biomass gain in the Northeast USA following the 2012 Northwest Atlantic MHW (67 °C-days; Fig. 2a, 3a)[11]. However, it is important to note that while these effects were substantial, they were neither large compared to natural variability in biomass nor repeated across other previously unreported MHWs. Other intense MHWs had little discernible effect on total biomass, such as the 42 °C-days MHW preceding the 2008 North Sea survey that recorded only a 6% biomass decline (Fig. 2a). Some of the largest biomass changes occurred in non-MHW years, such as the 97% increase in biomass in the North Sea in 2011, or the 77% biomass decline in the Southeast US in 1996.[18]

In addition, we observed that the most extreme biomass changes were often reversed in subsequent years. For example, the southern Gulf of St. Lawrence survey hauls caught an average of 4 metric tons of fish per km^2 in 2011, a non-MHW year; 13 metric tons per km^2 in

2012 following 36 °C-days MHW; and 4 metric tons per km^2 in 2013 following a MHW with 0.4 °C-days of cumulative intensity (Fig. 2a). The peak in biomass in 2012 was driven by Atlantic herring (*Clupea harengus*) and likely reflects a combination of survey variability and a true peak in population size of the fall Atlantic herring stock in the region[19].

Contrary to our expectations, both among surveys that were and were not preceded by a MHW, the median change in biomass was close to zero (0.023 ± 0.367 and 0.016 ± 0.323, respectively; medians and standard deviations of log ratios), indicating that regions were approximately as likely to exhibit net biomass gains as losses (Fig. 2a). Of the 369 survey-years we matched with sea bottom temperature data, 139 followed MHWs and 230 did not. There was no significant difference in mean biomass change between surveys that were and were not preceded by a MHW ($p = 0.40$, $t = 0.85$, $df = 249$; two-sided t-test; Fig. 2a). Further, the cumulative intensity of a MHW had no significant relationship with the change in biomass (linear regression; $R^2 = 0.00$; $p=0.88$; Fig. 2, Supp. Tab. 2).

The ecosystems we studied have distinct climates, species assemblages, and histories of anthropogenic pressures[20], and might respond at different rates and in different directions to environmental perturbation.[21] More broadly, pulse disturbances and other exogenous drivers (including heatwaves) are often expected to increase variance in the biomass of populations and communities[22]. However, we find no statistically significant relationship between the cumulative intensity of a MHW and biomass change of these demersal fish assemblages in any individual region (Extended Data Fig. 1, Supp. Tab. 3). Across all surveys, variability—measured as the absolute value of the year-over-year biomass log ratios—did not increase with MHW cumulative intensity (linear regression, $R^2 = 0.00$, $p = 0.24$; Fig. 2b, Supp. Tab. 4). Instead, we find that variability in biomass change from one year to the next is similarly high with or without MHWs

(0.22 ± 0.248 and 0.19 ± 0.214, respectively; medians and standard deviations of absolute log ratios) and that these absolute log ratios of biomass are not significantly different ($p = 0.24$, $t = 1.17$, $df = 245$; two-sided t-test; Fig. 2b).

Accounting for latitude, depth, temporal lags, autoregression in the biomass time-series, fisheries catch, and species traits (feeding mode, trophic level, and habitat) also did not reveal any meaningful effect sizes of MHWs on biomass (Supp. Tab. 6-10, Extended Data Fig. 6-7). Our results were also robust to the metric used (cumulative intensity, duration, intensity, or degree heating days) to characterize MHWs, how cumulative intensity was scaled, and to whether SBT data were detrended (Extended Data Fig. 2, Supp. Tab. 5). Because SBT data was only available from 1993 onward, we also analyzed a longer time-series of sea surface temperature (SST) that began in 1982 and thus could be paired additional fish surveys. The SST analysis included 100,877 hauls comprising 26,886,245 discrete taxon observations, and yielded results that were qualitatively similar to the SBT results described in the main text (Extended Data Fig. 2b). Because deleterious heatwave effects have often been recorded in summer[1], we also tested for an effect of summer-only MHWs on biomass (Extended Data Fig. 2g), finding a weak positive effect (i.e., greater biomass following more intense MHWs; linear regression, $R^2 = 0.02$, $p = 0.02$). While interpreting this result cautiously given the high leverage of a few data points, this result is consistent with the 2012 Northwest Atlantic MHW that occurred in summer and was associated with an increase in biomass in numerous fisheries[11].

Individual MHWs may lead to rapid ecological turnover by causing cold-affiliated species to decline or go extinct (“deborealization”) and/or by causing warm-affiliated species to spread or increase (“tropicalization”)[23–25]. We tested whether tropicalization or deborealization are general effects of MHWs by calculating the Community Temperature Index (CTI) for each survey in each year and comparing CTI change to MHW occurrence and cumulative intensity (Methods). CTI is an aggregate thermal niche index for the entire community calculated as the biomass-weighted mean of single-species' realized thermal niches[26].

Other studies show that CTI has increased in North American fish communities in recent decades, concomitant with ocean warming.[25] To explore whether MHWs induce CTI increases, we first focused on the 2014-2016 Northeast Pacific MHW, nicknamed "The Blob"—one of the largest MHWs in our dataset (Fig. 2, 3). Of the four regions in the Northeast Pacific for which we had data, the Gulf of Alaska exhibited the most pronounced CTI increase after the 2014-2016 MHW—from 7.25 °C in 2013 to 7.39 °C in 2015 and 7.50 °C in 2017. We also found a CTI increase in the West Coast USA in 2015 following an 8 °C-days SBT MHW (CTI change 0.11 °C), consistent with findings that warm-affiliated subtidal fishes increased in Southern California that year[27]. However, CTI in the Eastern Bering Sea decreased by 0.22 °C from 2015 to 2017. In British Columbia, we measured CTI values of 8.34 °C in 2013, 8.10 °C in 2015, and 8.31 °C in 2017 (Fig. 3b).

Our analysis found no evidence for systematic tropicalization or deborealization in marine fish communities across all 18 surveys and 369 survey-years in response to MHWs (Fig. 4). Year-over-year CTI change in communities that did not experience MHWs was not significantly different from those that did (0.024 ± 0.996 and 0.007 ± 0.983 °C, respectively; means and standard deviations; $p = 0.87$, $t = 0.16$, $df = 280$; two-sided t-test; Fig. 4b). Further, there was no relationship between MHW cumulative intensity and CTI change ($R^2 = 0.00$; $p = 0.33$; linear regression; Supp. Tab. 11).

Marine heatwaves may restructure ecological communities in other ways beyond tropicalization and deborealization[28]. Less predictable changes in species identity and underlying community structure could also emerge despite consistent biomass[29]. We tested for changes in community composition by calculating dissimilarity over the time-series using occurrence data (i.e., species presence-absence) as well as biomass data. Each of these dissimilarity indices is calculated from one year to the next using two components—one measure of how much species are substituted for one another and one measure of how much each community is a subset of the other[30] (see Methods). A high dissimilarity value between two years may be driven by a transition away from the baseline community structure as a result of disturbance, which has been observed in marine systems in response to climate change[29].

In some instances, fish communities exhibited high dissimilarity from the previous year following a MHW, such as in the Eastern Bering Sea and the West Coast US during the 2014-2016 MHW (Fig. 3c). However, this was not a general effect. We found that community dissimilarity measured between consecutive years was not, on average, significantly different whether or not a MHW occurred when measured with occurrence-based substitution ($p = 0.12$, $t = 1.57$), biomass-weighted substitution ($p = 0.99$, $t = -0.02$), or biomass-weighted subset ($p = 0.32$, $t = 1.00$; all two-sided t-tests; Extended Data Fig. 8). The one statistically significant relationship suggested that the subset component of occurrence-based dissimilarity was smaller after MHW years than after non-MHW years ($p = 0.01$, $t = -2.52$, two-sided t-test; Extended Data Fig. 8b), the opposite of the hypothesized effect. This observed community stability in the face of MHWs could indicate that climate refugia, such as depth refugia or other thermal refugia, provide safe havens for species during extreme events.[31] Further, changes in community structure at the local scale may not be reflected at the regional scale of our analysis.

This array of results suggests that the regional impacts of MHWs on fish communities are highly idiosyncratic, with dramatic effects in single cases but not in general. In particular, the effects of MHWs do not yet exceed natural variability in these ecosystems, or the variability due to the sampling process. These results also highlight the need to further explore context-dependent responses[32]. Species and spatial portfolio effects[33,34] as well as spatial and temporal storage effects[35] may explain individualistic responses to extreme events that could buffer many ecosystems from MHWs. Range shifts and mortality and fecundity rates may vary with latitude,[25] although we did not find a latitude effect in our analysis (Supp. Tab. 8). Interspecific variation in the timing, magnitude, and direction of MHW response may also be important[36]. For example, population dynamics of abundant species in response to the environment and fishing drive some of the biomass changes we observed (Extended Data Fig. 10). Ecological responses to warming may also be mediated by direct and indirect effects of other human impacts on the oceans, such as fishing, fisheries management, and changing primary productivity[3].

To verify that our dataset had sufficient statistical power, we developed a series of power analyses. First, we estimated that our dataset (n = 369 survey-years paired with SBT data) had the power to reveal a consistent MHW-induced regional fish biomass decline of 9% or greater (Extended Data Fig. 9c). Using the longer time-series of 441 survey-years that we paired with SST data had the power to detect a biomass decline of 8% or greater (Extended Data Fig. 9d). Such an effect did not emerge from the results of this study, suggesting that any MHW effects are smaller than this. We note that even decline in fish biomass of 8-9% or less, if permanent and sustained over time, would likely have substantial deleterious consequences for marine fisheries and social-ecological systems[3]. One model simulation of marine fishes experiencing MHWs under the high emission, no mitigation future climate scenario (RCP 8.5) projected that the negatively affected stocks (approximately ¾ of total stocks) would exhibit an average biomass decline of 6%[3]. Approximately 600 survey-years would be required to detect an average biomass decline of 6% (Extended Data Fig. 9a, b). Put another way, MHWs may have had effects on demersal fish communities in recent decades, but if so, those effects were small.

In addition, there are alternative explanations to consider. MHWs may affect survey methods themselves: a study on several coral trout species found that they were more catchable—i.e., encountered by fishing gear at higher rates—in warmer temperatures[37]. However, if this response was widespread among the species we studied, it would cause an increase in biomass following MHWs that we did not observe. The availability of fishes to surveys can also be influenced by range shifts, possibly induced by MHWs[38]. However, our analysis accounted for this by testing for tropicalization or deborealization within fixed spatial areas (the survey regions). Because biomass trends may be strongly structured by commercial fisheries catches, we fitted models predicting biomass change with fisheries catch as well as MHW cumulative intensity, with no significant results (Supp. Tab. 10). While the choice of metric to quantify MHWs[6,15,38,39] and fish community responses[11,37] may influence results, our results here were not sensitive to these decisions. The pattern in Fig. 2 emerged regardless of whether we analyzed fish biomass (i.e., weights) or fish abundance (i.e., counts) or whether taxon-level records were summarized as means or medians (Extended Data Fig. 5). The spatial scale of our study was determined by the surveys, which themselves are designed to capture distinct biogeographical and political regions and/or to follow fisheries management criteria[40] (see Methods). However, it is possible that fish community responses to MHWs vary with the spatial scale at which they are measured, as has been found with other metrics of biodiversity.[41]

Ecological effects of climate change result from the interaction of long-term climatic change combined with short-term extreme events such as heatwaves[5], which have been projected to cause widespread ecological devastation on land and in the sea (although see [36,42]). To date, this expectation has largely been based on case studies that select one or a few prominent species and ecosystems with remarkable MHW responses, rather than the comprehensive approach that we used. Analyses that focus on particular species that were historically prevalent in a region may be predisposed to find a biomass decline following a MHW, possibly due to unrelated time-series dynamics (e.g., mean reversion or density dependence) or because species that were dominant in historical climates might not be as successful after a MHW. In addition, case study approaches tend to select and emphasize extreme responses[43]—although several regional studies focused on a single MHW event have also found no net loss of abundance or biomass in coral- or kelp forest-associated fishes[27,44]. Further empirical research that builds on the present study and extends beyond individual case studies is needed to interpret, contextualize, and predict severe MHW effects.[2] Building partnerships to leverage existing non-public datasets from the southern hemisphere and other under-studied parts of the global ocean will also be helpful in understanding how ecological context influences MHW responses[40].

Our findings highlight the need to understand divergent responses to extreme events. Single-species responses may be mediated by thermal tolerances, but we did not find evidence that cold-affiliated species decline or that warm-affiliated species increase following MHWs (Fig. 4a). Other studies find that species' responses vary from one extreme event to another[42]. Portfolio and storage effects may explain why ecosystem-level MHW effects are rare, but they do not reveal what caused certain MHWs to have deleterious ecological effects. The community stability we observed in the face of MHWs could indicate that climate refugia, such as depth or other thermal refugia, provide safe havens for species during extreme events.[31] Cumulative impacts of MHWs and other stressors such as harmful algal blooms[13] or low-productivity events[9] could play a role. Perhaps very extreme MHWs in the future will cross a tipping point beyond which adverse ecological effects occur, but we did not see such a tipping point in the recent historical record. Other fields (e.g., coral reef ecology) have identified such thresholds, though the generality of thresholds across ecological systems remains unclear.[45] Gaining mechanistic insight into why only some MHWs have deleterious effects, and on only some species, is necessary for any future efforts to identify an effect threshold or forecast MHW impacts and should be a research priority for the field. Additionally, ecosystem responses to extreme "pulse" events such as MHWs can shape impacts of more gradual "press" trends; the complex interactions between these climate change effects warrant future research.[5]

Understanding MHW impacts on entire ocean ecosystems is particularly crucial in the context of accelerating global change and efforts to advance towards ecosystem-based management that considers the many links between species and with their environment[46]. MHW occurrences are projected to emerge above their natural variability within this century in many regions[47]. Future research will be needed to determine the extent to which fish community impacts of MHWs will grow as MHWs intensify, or whether portfolio and other ecological effects can buffer ecosystems from MHW impacts. Marine life is more vulnerable to warming than terrestrial life, because marine organisms tend to live close to their thermal limits and fewer thermal refugia exist in the seas[48]. Observed and predicted changes in marine ecosystems in response to global warming formed part of the rationale behind the Paris Climate Agreement to limit the global mean surface temperature increase above industrial levels to 1.5 °C by 2100[49]. As a future that is more than 1.5 °C warmer looks increasingly likely[50], it is more critical than ever to develop a deeper understanding of what drives ecological responses to extreme climate events.

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Figures

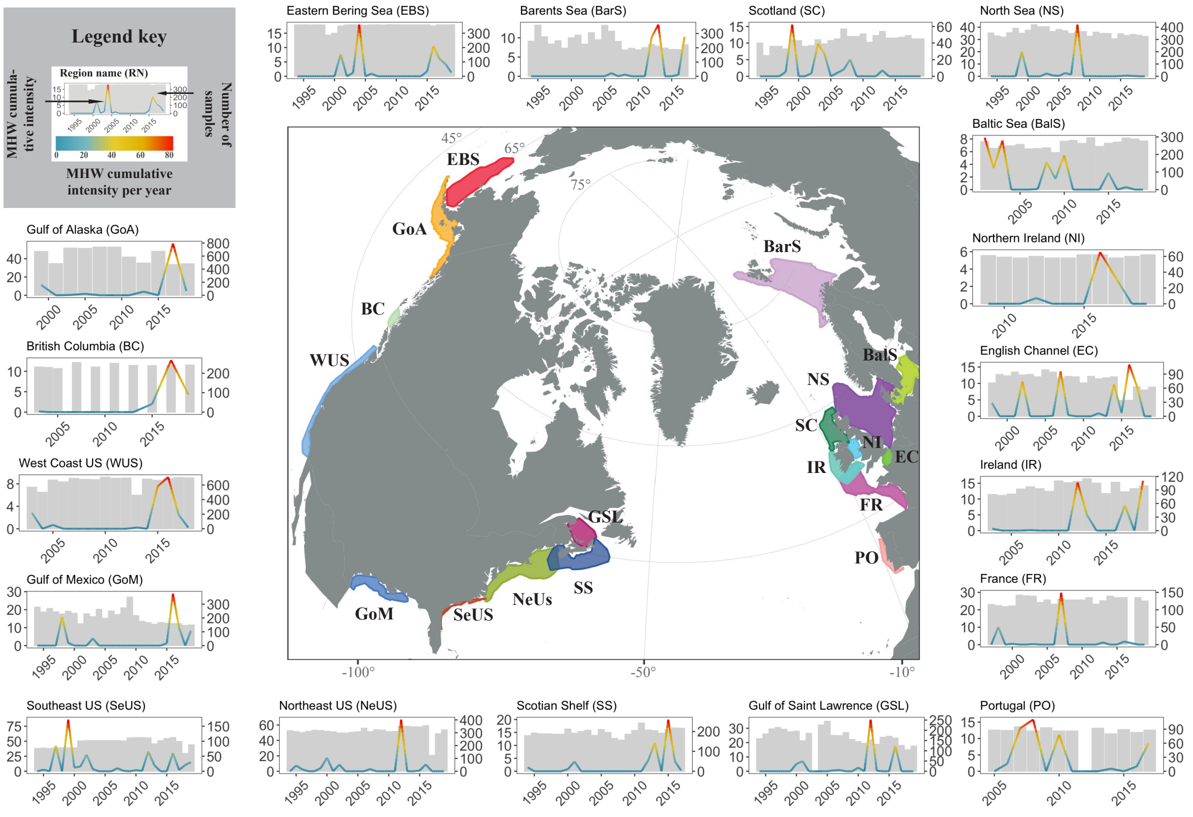

Fig. 1. Of 18 regions studied from the Atlantic and Pacific Oceans, all experienced marine heatwaves during the available scientific fish survey time-series. Highlighted areas on the map represent the spatial area surveyed by each trawl survey. Inset plots show the number of distinct sampling events (i.e., hauls of the trawl net) every year (grey bars, right y-axis) and the MHW cumulative intensity in °C-days calculated from sea bottom temperature data (lines, left y-axis; warmer colors represent greater cumulative intensity). Years correspond to “survey reference years”—the twelve months preceding the survey—rather than calendar years, and vary among regions (see Methods).

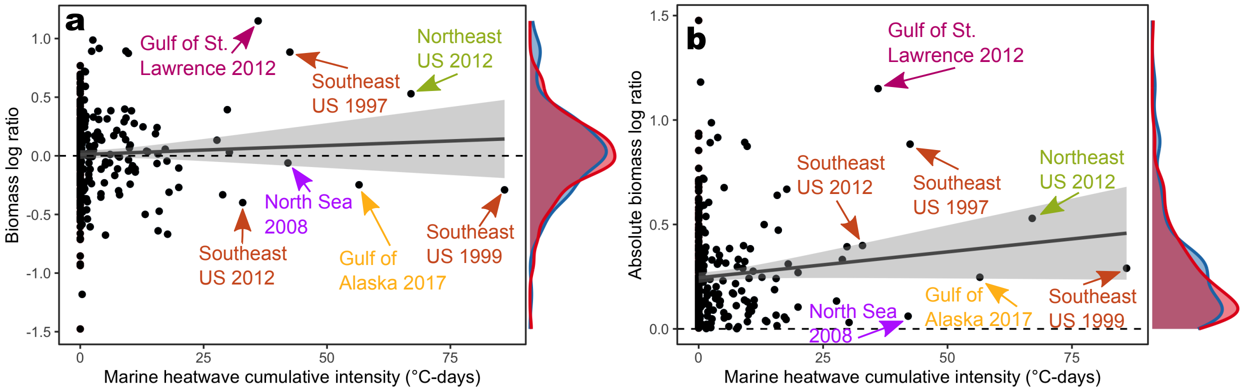

Fig. 2. More intense marine heatwaves were not associated with a decline in fish biomass or an increase in biomass variability, and biomass was approximately as likely to increase as it was to decrease from one year to the next, regardless of whether a marine heatwave occurred. MHW cumulative intensity (°C-days) had no relationship with (a) biomass change (measured as log ratio; linear regression, $R^2 = 0.00$, $p = 0.45$) or (b) absolute biomass change (measured as absolute log ratio; linear regression, $R^2 = 0.01$, $p = 0.07$). The grey shaded area is a 95% confidence interval. Density plots along the right-hand y-axes show that biomass changes from one year to the next were the same whether a MHW did (red, $n = 139$) or did not (blue, $n = 230$) occur. Points represent (a) log ratios or (b) absolute log ratios of mean biomass in a survey from one year to the next ($n = 369$). Surveys following the highest cumulative intensity MHWs are labeled (years correspond to when the survey was conducted). Colors correspond to regions in Fig. 1. Models exploring the relationships in (a) and (b) are reported in Supp. Tab. 2 and 4, respectively.

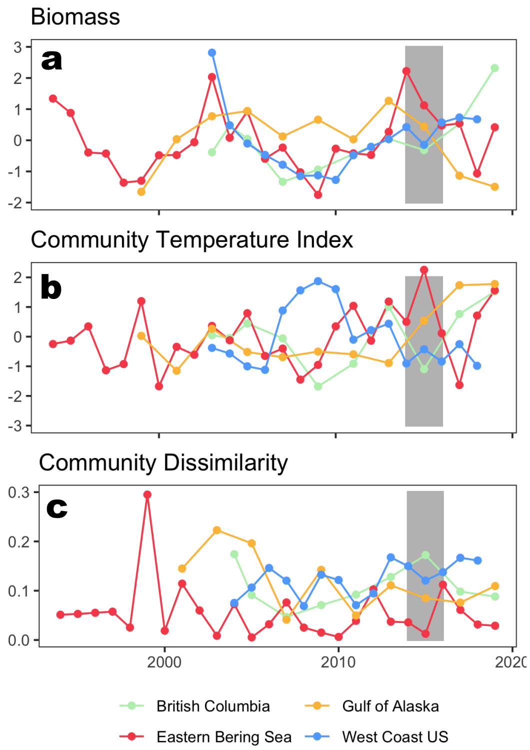

Fig. 3. Example of divergent responses to a large marine heatwave. Plots show (a) centered and scaled biomass and (b) Community Temperature Index (CTI), and (c) change in community composition over time (the substitution component of Bray-Curtis dissimilarity) between the previous and given year for four surveys in the Northeast Pacific. Colors correspond to survey footprints in Fig. 1. Higher values represent more biomass, tropicalization and/or deborealization, and greater community dissimilarity, respectively. The grey stripe denotes the 2014-2016 Northeast Pacific MHW ("The Blob").

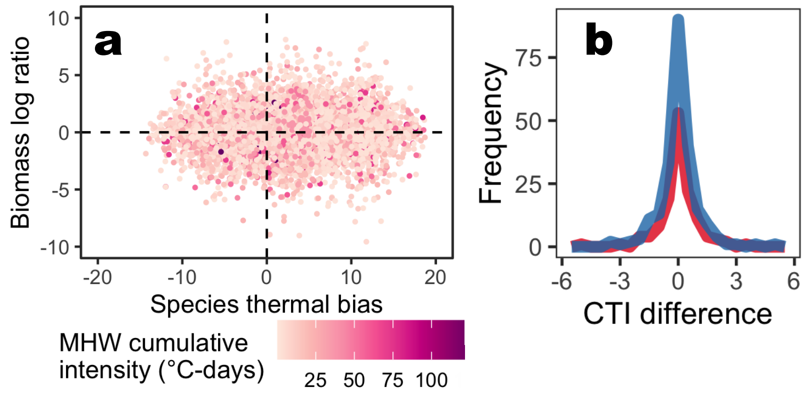

Fig. 4. Scientific bottom trawl surveys during the year following marine heatwaves were as likely to exhibit tropicalization and/or deborealization as those that did not follow marine heatwaves. (a) There was no relationship between a species' thermal bias (its cold or warm affinity relative to the assemblage mean, calculated as STI - CTI; see Methods) and its species-specific biomass change following a MHW (n = 13,438). (b) There was no difference in CTI change between surveys in the year following a MHW (red, n = 139) *versus* surveys that did not follow a MHW (blue, n = 230). Positive CTI values indicate tropicalization and/or deborealization. In (a), each point represents a single species that was present in a survey both before and after a MHW.

Methods

All analyses were conducted in R (R Core Team 2021). Software versions are listed on GitHub.

Fish biomass and abundance data. We collated publicly available datasets from fishery management agencies that use scientific (i.e., fisheries-independent) bottom trawl surveys to monitor marine fish communities[40]. These surveys monitor biogeographically and/or politically distinct areas that are relevant to fisheries management[40]. Their footprints often follow marine ecosystem boundaries (e.g., Large Marine Ecosystems[52]) and are similar in size to the spatial extents of MHWs[39]. Although these surveys are conducted by many nations, we used only surveys by agencies that make their raw data publicly available, which facilitates reproducibility of this study. Those agencies were the National Oceanic and Atmospheric Administration (NOAA), Fisheries and Oceans Canada (DFO), the International Council for the Exploration of the Sea (ICES), and the Institute of Marine Research (IMR). This limitation constrained our analysis to the Northeast Pacific, Northwest Atlantic, and the Northeast Atlantic (Supp. Tab. 1).

In these surveys, the sampling unit is a single haul, i.e., a sampling event in which a net is towed through the water. We filtered invalid hauls based on reported sample quality, sampling times, and availability of variables required to calculate taxon-level biomass data. Further detail on data cleaning and harmonization in addition to raw data and code can be found in Maureaud et al[53]. All primary analyses used biomass (weight) data; we conducted a supplementary analysis of the main results using abundance (count) data for the regions for which it was available (all but Northeast US; Extended Data Fig. 5).

Datasets were trimmed to standardize the spatial footprint of the survey over time, to match the available temperature datasets (GLORYS began in 1993 and OISST began in 1982; see **Marine heatwave data**), to remove years with very few samples, and to omit samples collected outside of the focal season (3-month interval) of each survey. We used the World Register of Marine Species[54] to standardize taxonomies, and the “dggridR” R package[55] to standardize the survey footprints. Across our 18 surveys, we paired 82,322 hauls with GLORYS and 101,376 hauls with OISST. Of the 94% of hauls with an associated depth value, 90% occurred between 18 m and 451 m depth. The depths sampled vary due to each region’s unique bathymetry and each survey’s protocols, but surveys tend to sample similar depths over time: for example, the Southeast US survey samples very shallow inshore areas of just 3 m depth, while the Scotian Shelf and West Coast surveys routinely trawl deeper than 1000 m. We used all taxa for biomass analyses but only the species-level observations for community analyses (see **Species and Community Temperature Indices**).

We imputed zeros representing an observed absence in every instance when a species (that was observed at some point in the region) was not recorded in a haul. These absences can be considered true non-detections due to the standardized spatiotemporal design of bottom trawl surveys. We then calculated a mean biomass for each species in every year, and calculated region-wide biomass as the sum of species-level biomass. To assess the sensitivity of our results to the metric used, we also calculated median biomass, mean abundance, and median abundance in the same way (although the Northeast US region did not have abundance data and was thus omitted from the abundance analysis). We did this across the entire survey domain (following the spatial standardization mentioned above), rather than within the "strata" used in some analyses[56], because not all of the surveys have stratified sampling designs and we wanted to be consistent across all regions.

Year-over-year mean biomass change was calculated as a natural log ratio, $\ln(\frac{biomass_t}{biomass_{t-1}})$. Log ratios for median biomass, mean abundance, and median abundance were calculated the same way. For straightforward interpretation, we also reported percentage biomass changes in the text, although biomass log ratios were used in all models. For example, a 67% biomass increase means that $biomass_t = 1.67 \times biomass_{t-1}$. A 67% decrease means that $biomass_t = (1 - 0.67) \times biomass_{t-1}$.

Because surveys began in different months, we paired each survey's biomass data with MHW data from the preceding 12 months. For example, for a survey that began in August, the

August 2010 data was paired with MHW data from August 2009 - July 2010. Because we have no *a priori* information on the season in which MHWs could have the greatest ecological impact—and this may vary by species and life stage—we analyzed MHW effects over a full year (i.e., 12-month interval). Some substantial MHW effects have been reported in summer,[57] and yet winter heatwaves strongly influence distribution and abundance for species limited by winter survival[58,59]. Warmer winters are hypothesized to have driven recent ecological changes in the Gulf of Alaska[12]. Winter MHWs may also reduce recruitment in habitat-forming seaweeds[6] and cause metabolic stress to coral reef fishes[60]. Spawners and embryos have narrower temperature tolerance ranges than non-spawning adults[61]; a spring heatwave could thus affect the survival or performance of spring-spawning fishes and their embryos. To test the sensitivity of our results to this choice, we also explored the effects of only summer anomalies on biomass change (Extended Data Fig. 2g).

Interannual biomass variability is significantly lower in surveys with more samples per year (linear regression; $R^2 = 0.08$; $p < 0.001$). To account for this, all models and statistical tests either included a survey effect or used biomass log ratios that were scaled and centered within surveys.

Marine heatwave data. We paired the demersal bottom trawl data with MHWs calculated with sea bottom temperature (SBT) data from the Copernicus 1/12° (about 8 km) global ocean reanalysis, the Global Ocean Reanalysis and Simulations (GLORYS12).[62] The reanalysis dataset is generated with the Nucleus for European Modelling of the Ocean (NEMO) ocean model forced by the ERA-Interim atmospheric reanalysis. The model assimilates satellite altimetry, satellite SST, sea ice concentrations, and in-situ profiles of salinity and temperature. We chose GLORYS12 for our analyses because it provided daily estimates of temperature anomalies at depth at a fine spatial resolution, and it reproduces nearshore bottom temperatures and recent MHWs with enhanced fidelity compared to other products.[63,64] Being highly dependent on ocean observations for data assimilation, GLORYS12 only began in 1993. We used the 1993-2019 period for our analysis.

Because many bottom trawl datasets began earlier than 1993, we also calculated SST MHWs to conduct supplementary analyses with a longer time-series. For SST, we used the NOAA daily Optimum Interpolation Sea Surface Temperature (OISST) Analysis version 2.1 dataset[65,66] with a horizontal grid resolution of 0.25°, which is available from 1982 onward, to characterize MHWs. This dataset provides a daily global record of surface ocean temperature observations obtained from satellites, ships, buoys, and Argo floats on a regular grid. Infrared satellite data from the Advanced Very High Resolution Radiometer is its main input and any large-scale satellite biases relative to in-situ data from ships and buoys are corrected. Gaps are filled in by interpolation. We used the 1982-2019 period for our analysis. OISST and GLORYS are plotted against one another in Extended Data Fig. 4.

Following standard MHW definition (e.g. [9,47]), both SBT and SST anomalies were calculated within (not across) spatial units—here, the survey regions. This approach defined anomalies relative to historical conditions in a region, which are likely reflective of the environments to which organisms are adapted. In other words, each MHW we identified represented a departure from whatever climate the marine organisms in that region typically experienced. Because our study regions varied substantially in seasonality, natural variability, and exposure to oceanographic phenomena, calculating anomalies from cross-region pooled SBT and SST values would identify only the most globally extreme events as MHWs and would omit the many events in which temperatures were anomalously high for species within a region but not necessarily high for the global oceans.

For both SBT and SST, we defined a MHW as a period of at least five continuous days during which the SBT (or SST) averaged for each survey area was larger than a seasonally varying threshold given by the 95th percentile of the survey-area averaged SBT (or SST) anomalies (relative to the mean seasonal cycle that is calculated for each calendar day individually). This is a common approach for defining MHWs, although some authors use the 90th percentile[6] or the 99th [39] instead of the 95th. Under our definition, MHWs may occur throughout the year and at all locations.

The temperature data was linearly detrended before any analysis to distinguish discrete MHWs from the long-term warming signal (see Jacox et al. [38,67] and Extended Data Fig. 3) although we also tested the sensitivity of our results to this decision by re-running the analysis with non-detrended data and reached equivalent conclusions (see Extended Data Fig. 2c). Using the five-day threshold and the detrended data, we identified 511 distinct surface MHWs in OISST and 248 bottom MHWs in GLORYS. Many years had multiple MHWs. GLORYS had fewer MHWs partly because the time-series is shorter and partly because the MHWs it recorded were longer in duration (leading to fewer discrete MHW events relative to OISST, which recorded many shorter MHWs).

We then calculated different MHW metrics: MHW cumulative intensity (the anomaly above the 95th percentile threshold summed over the duration of the event in °C-days, duration (number of days), and mean intensity (the average anomaly above the 95th percentile threshold over the course of the MHW in °C). We chose MHW cumulative intensity for the main analysis because it encompassed elements of both intensity and duration (i.e., cumulative intensity is higher for longer or for more intense MHWs)—but our biomass results did not change if we used different metrics (Extended Data Fig. 2d, e). Because under our definition all MHWs exceeded 95% of temperature anomalies in the region, even MHWs with relatively low cumulative intensities represented extreme events. Unless otherwise specified, models in the main text and Supplement used MHW cumulative intensity centered and scaled within regions, although our results were not sensitive to whether we scaled and centered within *vs* across regions (Supp. Tab. 5).

In coral reef ecology, a threshold for ecological damage (i.e., coral bleaching) has been identified using degree heating days—the number of days that exceed average temperatures for the hottest summer month by at least 1 °C.[16] We also processed the non-detrended GLORYS data using this method for each region (Extended Data Fig. 2f). One data product, Coral Reef Watch, calculates the average temperatures for the hottest summer month during a baseline period of 1985-1990 plus 1993.[16] Because GLORYS began in 1993, we used the four-year interval 1993-1996 as the baseline to calculate the average temperatures for the hottest summer month.

The five-day threshold for a MHW used in the main analysis was based on empirical analyses demonstrating that contemporary heatwaves last on average 4.6 days[68], and is widely used in the literature[6], although we note that alternate methods exist to define and measure MHWs[15,39,69]. We also assessed whether MHW responses would emerge from classifying any daily anomaly (without the five-day cutoff) as a MHW. We found no relationship (Extended Data Fig. 2a).

Species and Community Temperature Indices. The Species Temperature Index (STI) and Community Temperature Index (CTI) are measures of thermal affinity at the species and community level, respectively.[70] We quantified STI as the median sea surface temperatures found throughout a species' modeled range from the publicly available STI dataset in Burrows et al.[26]. STI values were available for 844 of our 1772 focal taxa, comprising 82% of total biomass in our survey dataset. CTI was calculated in each region and year as the biomass-weighted mean of all STIs, and we used the difference in CTI from one year to the next as our metric of CTI change. We also quantified the thermal bias of each species relative to the community (STI - CTI)[70].

Community beta-diversity metrics. Only observations identified at the species level were included in species composition change (beta diversity) analyses. To assess the impact of MHWs on community structure, we compared Bray-Curtis dissimilarity between surveys spanning a MHW to those between years that did not span a MHW. We partitioned Bray-Curtis dissimilarity into two components (biomass gradient and balanced variation) using the betapart package in R[30,71]. The biomass gradient component focuses on changes in biomass of species between years within the survey region, while the balanced variation component focuses on the substitution of the biomass of one species by the biomass of another species. For comparison, we also calculated occurrence-based dissimilarity metrics (i.e. species presence-absence data) using Jaccard dissimilarity partitioned into nestedness and turnover components. Balanced variation and turnover both measure substitution of species between communities while biomass gradient and nestedness both measure how species are subsetted between communities.

Additional predictors. We conducted supplementary analyses to explore the role of a number of additional predictors of fish biomass change. In addition to the geographical shifts that may lead to changes in biomass and community composition in a fixed area, marine fishes may shift deeper in response to warming[72,73]. We tested for this effect by calculating depth log ratios that described whether assemblages had shifted deeper or shallower from one survey to the next. Depth log ratio was quantified by: 1. Taking an average of depths at which a species was found in each survey and year, using the depth observations for each haul, and weighted by biomass in the haul; 2. Taking a biomass-weighted mean of all species-level depth values for the entire survey; 3. Calculating the log ratio of the survey-level, biomass-weighted depth values from one year to the next. We found no relationship between MHW cumulative intensity and depth log ratio and no difference between depth changes that did and did not follow a MHW (Extended Data Fig. 6, Supp. Tab. 9).

Marine communities across latitudes have responded differently to climate change, with some declines in species richness recorded in the tropics and at equatorward range edges[24,74] and some increases in species richness recorded in colder oceans and at poleward range edges[74,75]. We tested for latitudinal trends in biomass log ratios and found that the direction or magnitude of biomass change was not related to the median latitude of the region (Supp. Tab. 8).

We explored whether species traits helped to predict species-level biomass change in general, and specifically in the context of MHWs. All fish species traits were obtained from the database in Beukhof et al.[51]. Of the 1772 taxa used in the main analysis, 1620 had trophic level data, 1591 had feeding mode data, and 1612 had habitat data. The pattern of no relationship between MHW cumulative intensity and biomass log ratio persisted when data were grouped by trophic level, feeding mode, or habitat (Extended Data Fig. 7).

Some studies find that marine communities respond rapidly to environmental change[76]. Others suggest that ecological responses may lag disturbances by years[77]. We explored whether MHW data from further into the past—up to five years before each trawl survey—predicted biomass responses. Analogous to our findings for MHWs that occur up to 12 months before each survey reported in the main text, we found no evidence that biomass change is associated generally with MHW cumulative intensity from prior years (Supp. Tab. 6).

Because fishing, through increased mortality, can influence temporal biomass change, we also analyzed the effects of catch on biomass change. We extracted a historical time-series of reconstructed catch values from the *Sea Around Us* database[78] by Marine Ecoregions (MEs).[79] The *Sea Around Us* reconstructed catches are spatially allocated to half degree ocean cells,[80] which permits catch data to be assigned to spatial entities such as the 232 MEs identified by Spalding et al.[79] We then paired our survey footprints with the most-overlapping ME. In most cases, the MEs and survey footprints were similar. For two large surveys (the West Coast and the Northeast US) we summed catch data across two adjacent MEs. Two small surveys (France and the English Channel) did not correspond well to the MEs and were omitted from the fishing analysis. Because catch data are recorded by calendar year, and the surveys often occur midyear, we fitted models comparing biomass change in a given year to the mean catch level in the past three calendar years (Supp. Tab. 10).

Statistical methods. We tested for the effects of MHWs using linear models, generalized linear models, or generalized additive models for continuous variables. Models and transformation of variables are described in Supp. Tab. 2-11. Generalized linear models were fitted with the R package “glmmTMB”[81] and generalized additive models with the R package “mgcv”[82]. When comparing MHW *versus* non-MHW effects we used two-sided t-tests. While not all of the datasets were normally distributed, the t-test is insensitive to skewness for large sample sizes such as ours, whereas non-parametric alternatives are better suited to smaller sample sizes[83].

Power analysis. We simulated data to assess whether our study had sufficient power to detect MHW-driven biomass changes. We fitted an autoregressive linear model of log biomass over time (Gompertz model) to each region's biomass data, including MHW presence/absence as a predictor. We extracted the coefficient ρ, intercept α, and conditional standard deviation σ of this model, and used them to simulate data from the same Gompertz model

$$\ln(B_t) = \alpha + \rho \times \ln(B_{t-1}) + \gamma \times MHW_t + \sigma'$$

where *B* represents biomass in year *t*, *MHW* is a binary variable for MHW presence/absence, and γ represents the "true" MHW effect that we varied to explore power. This simulation also included an error term σ' calculated as a random draw from a normal distribution with mean 0 and standard deviation σ. We (1) varied the number of years the simulation was run (assuming that each of the 18 surveys was conducted for that number of years) from 10 to 40 in 1-year steps and 50-200 in 10-year steps with a fixed value of $\gamma = \ln(0.94)$, corresponding to the 6% loss of biomass predicted by Cheung et al.[3]; and (2) varied γ to represent biomass losses ranging from 1% to 30% (in 1% increments up to 10%, and then in 5% increments) given the actual number of years of data we have ($n = 369$ for GLORYS and $n = 441$ for OISST). Note that the mean survey duration in our analysis was 20-25 years depending on the paired temperature dataset used. For all these scenarios, simulations were run for each individual survey, converted into log ratio units (as used in the main text), scaled and centered within regions, and pooled across regions. Each set of simulations was run 1000 times for each condition (survey and either number of years or γ).

With these four simulated datasets—a true MHW effect on biomass of -6% and variable numbers of years, or a fixed number of years from the real dataset and a variable effect of MHW on biomass, each for OISST and GLORYS—we conducted the same statistical tests as we did in the main text to test for an effect. For every iteration of the simulation, we split the biomass log ratio data into MHW and non-MHW years and compared the two with a two-sided t-test. We then calculated what proportion of those tests were significant ($p = 0.05$). These results are shown in Extended Data Fig. 9.

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Author contributions

All authors contributed to writing and revising the manuscript. ALF, LP, WWLC, MLP, AAM, ZJK, MLDP, JTT, AA, BM, JPA, and NS contributed to the study conception and design. ALF, LP, MLP, AAM, ZJK, TLF, MLDP, JTT, BM, and JPA contributed to data acquisition and analysis. All authors approved the submitted manuscript and subsequent revisions.

Competing interest declaration

The authors declare no competing interests.

Additional information

Supplementary Information is available for this paper. Correspondence and requests for materials should be addressed to ALF. Reprints and permissions information is available at www.nature.com/reprints.

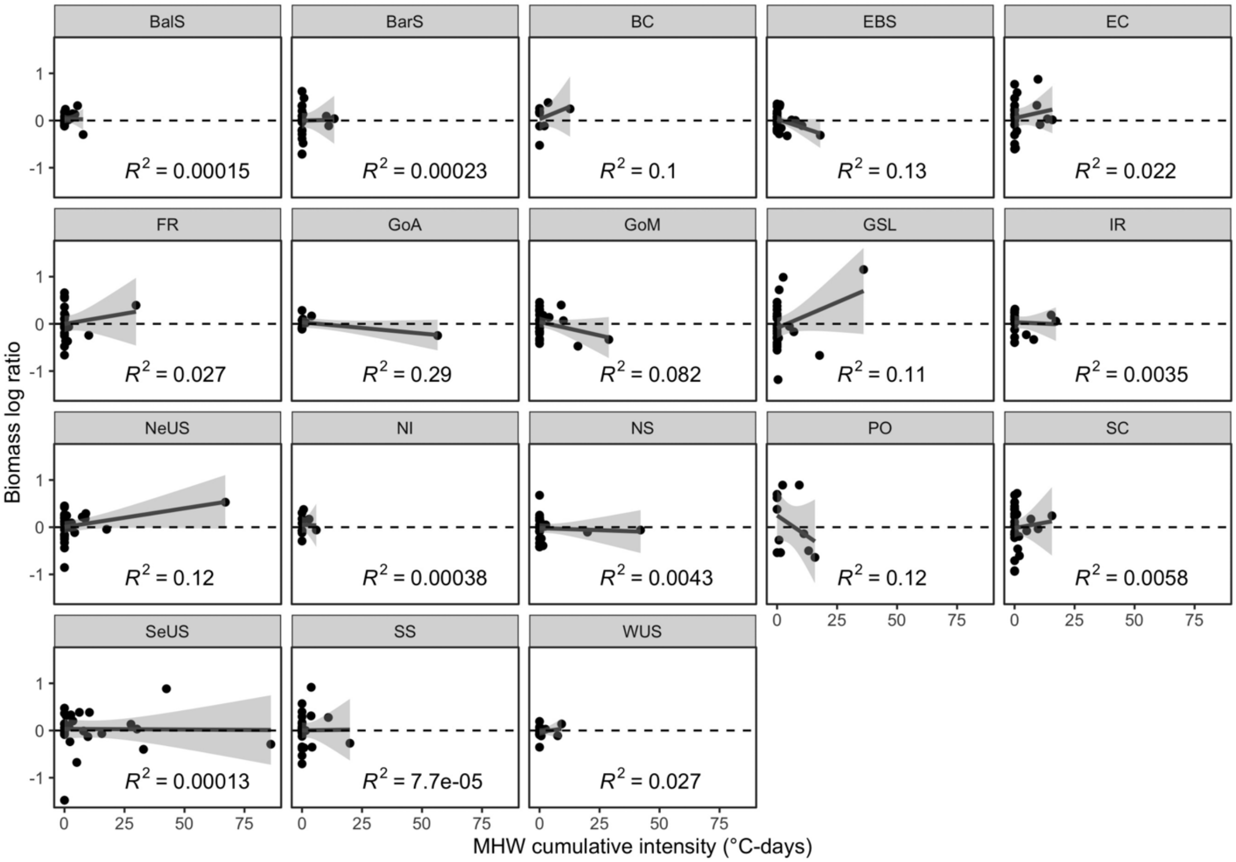
Code availability statement

The code for this study is publicly available on GitHub at https://github.com/afredston/marine_heatwaves_trawl and archived at https://doi.org/10.17605/OSF.IO/H6UKT.

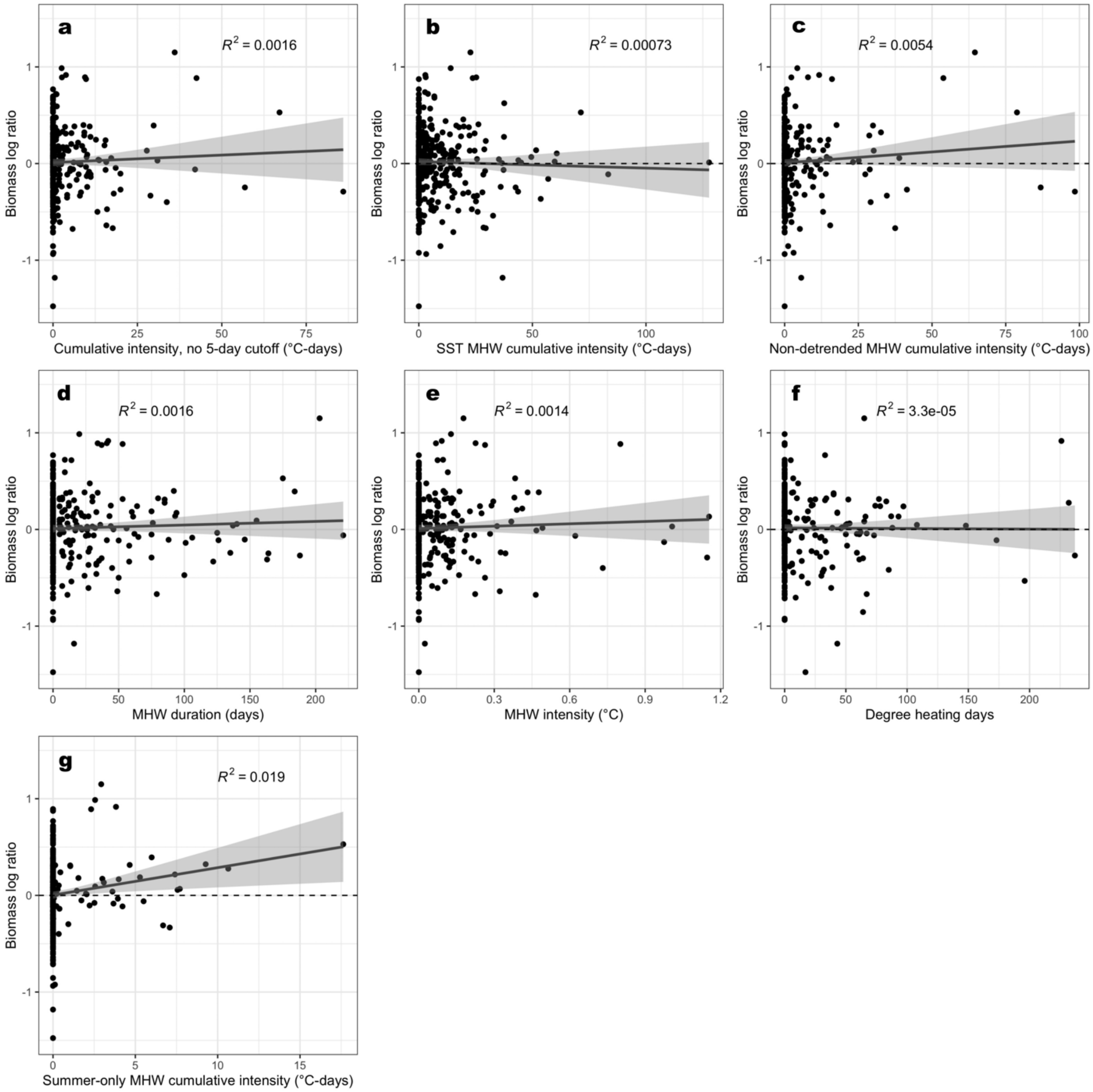
Data availability statement

The data used in this project are available on https://doi.org/10.17605/OSF.IO/H6UKT.

Extended data figures

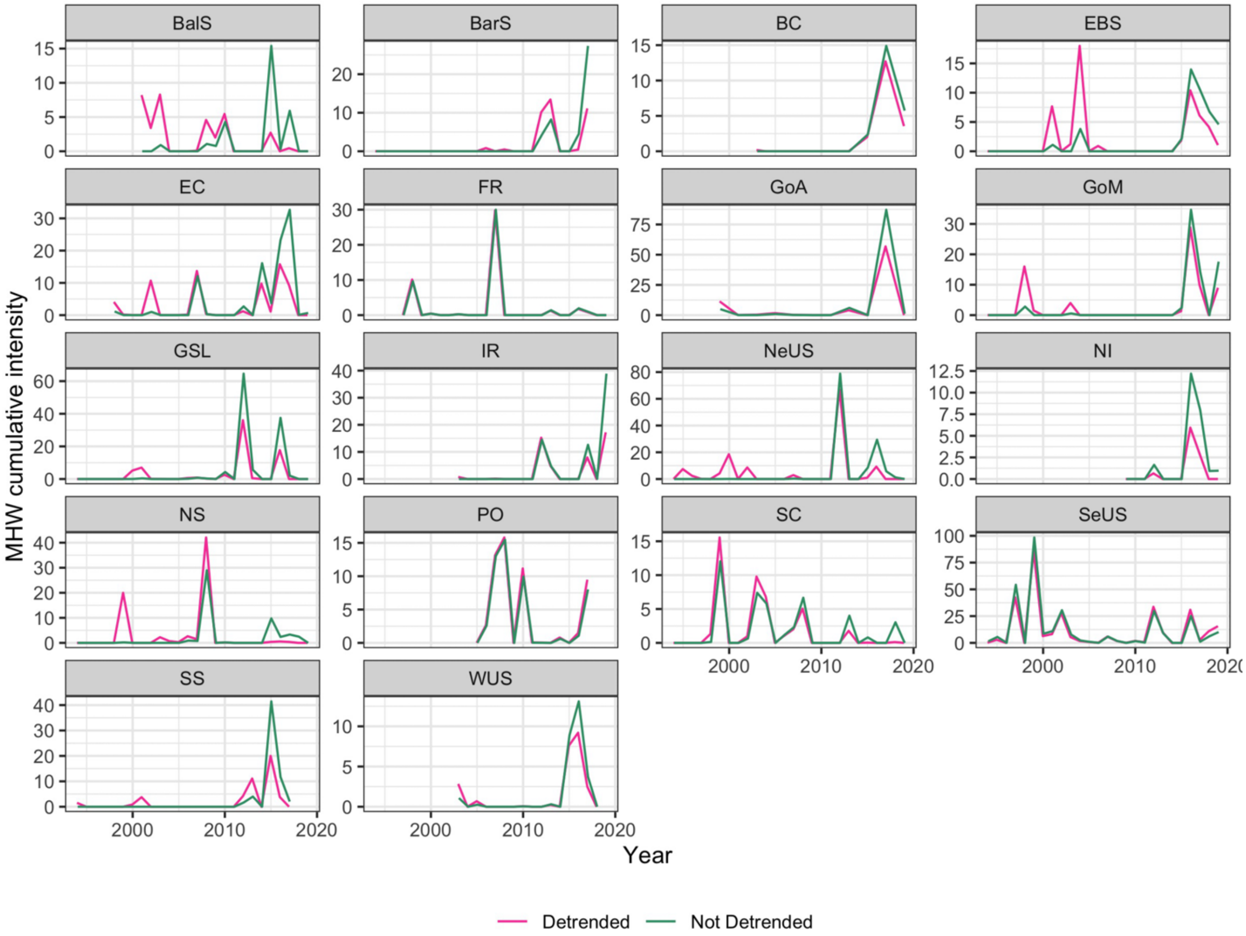


Extended Data Fig. 1. Alternate version of Fig. 2 from the main text, showing results by region. MHWs were calculated from the detrended GLORYS sea bottom temperature data with a five-day minimum duration threshold for MHWs, as used in the main text. Points represent log ratios of mean biomass in a survey from one year to the next. The fitted lines are linear regressions. The shaded areas are 95% confidence intervals. Survey names and sample sizes per survey are listed in Supp. Tab. 1.

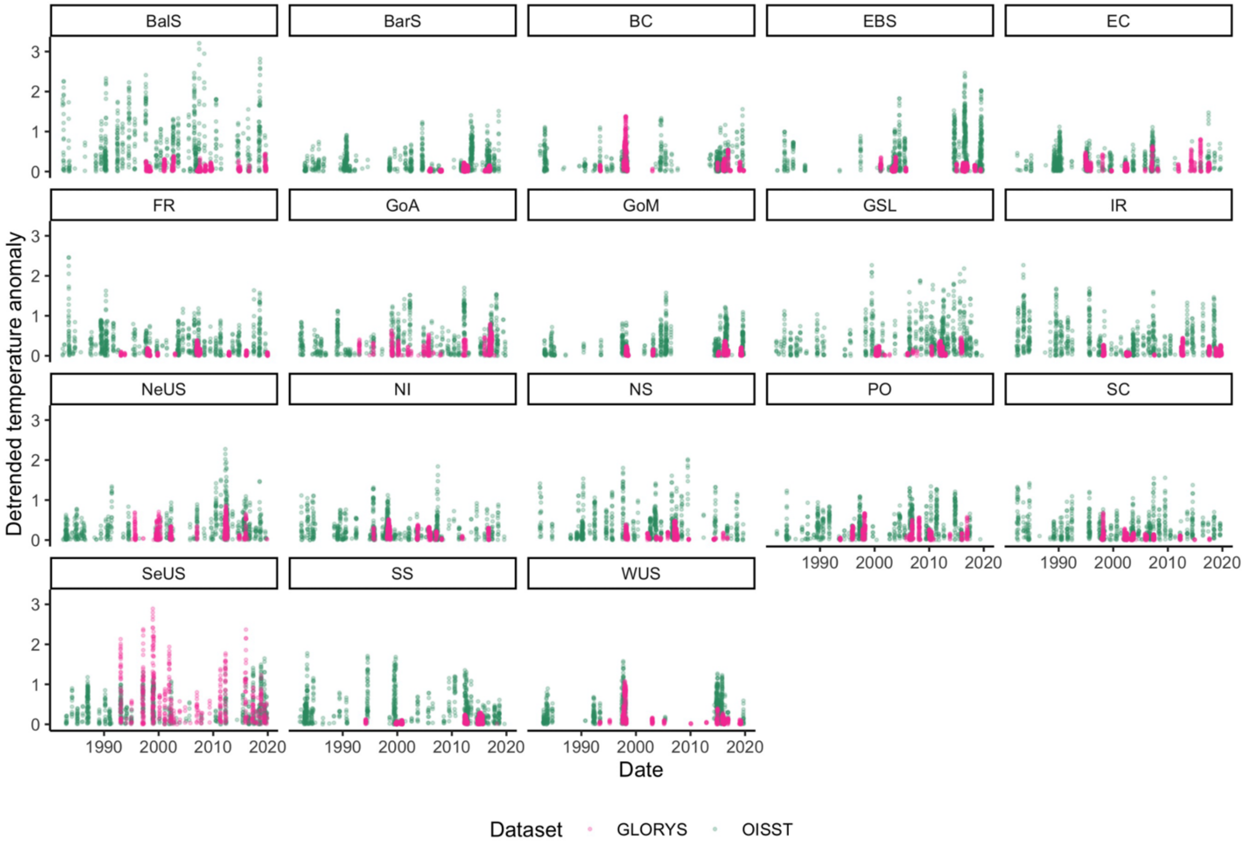


Extended Data Fig. 2. Results did not change when alternative methods were used to quantify marine heatwaves. Results were robust to (a) removing the five-day threshold for MHWs, (b) using SST from OISST instead of SBT from GLORYS (detrended), (c) using non-detrended data, (d) using a MHW metric of duration (days), (e) using a MHW metric of intensity (°C), (f) calculating degree heating days instead of MHW anomalies, and (g) using only summer

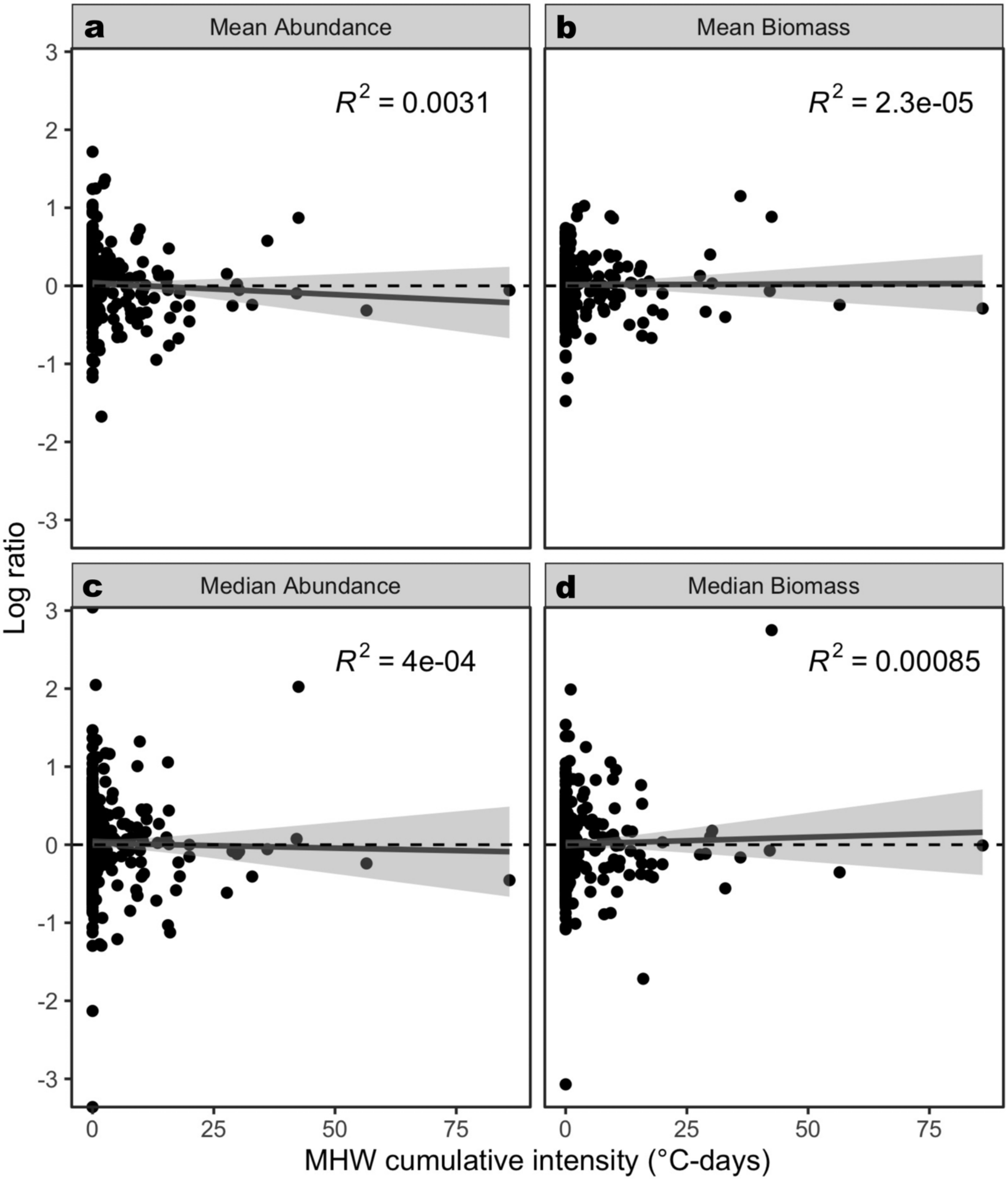
MHWs (see Methods). The fitted lines are linear regressions. The shaded areas are 95% confidence intervals. For all panels $n = 369$ except in (b) $n = 441$.



Extended Data Fig. 3. Marine heatwave cumulative intensity (total anomaly in °C-days) in each survey region with and without detrending the temperature data to remove the signal of secular warming. The main text results are detrended. Here, we plot MHW cumulative intensity based on all SBT anomalies from GLORYS, rather than applying the five-day threshold that was used the main text, to more clearly show the differences between the two methods.



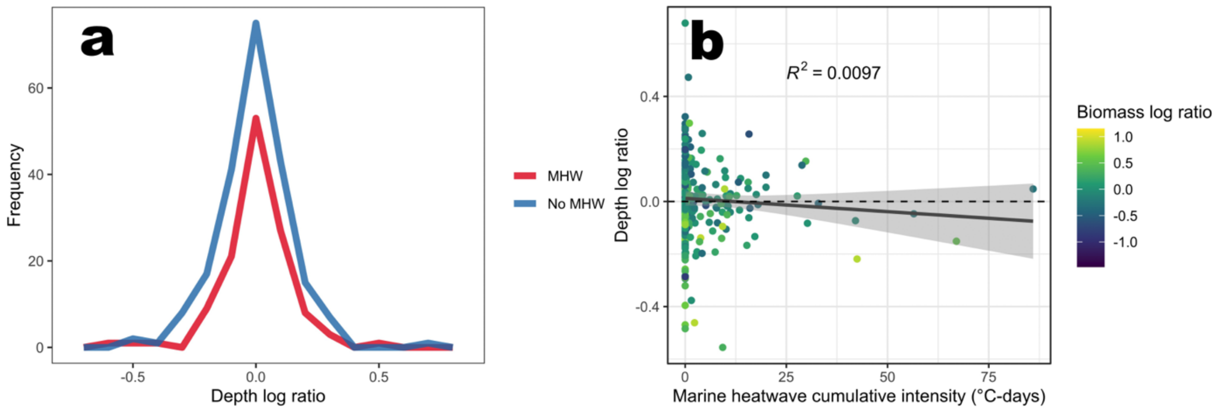
Extended Data Fig. 4. Daily 95th percentile anomalies in the two marine heatwave data sources: sea surface temperature from OISST and sea bottom temperature from GLORYS (both detrended). To simplify comparison we plot all anomalies, not just those MHWs that exceeded a five-day threshold. Note that the OISST time-series began in 1982 and GLORYS began in 1993. Region names are listed in Supp. Tab. 1.



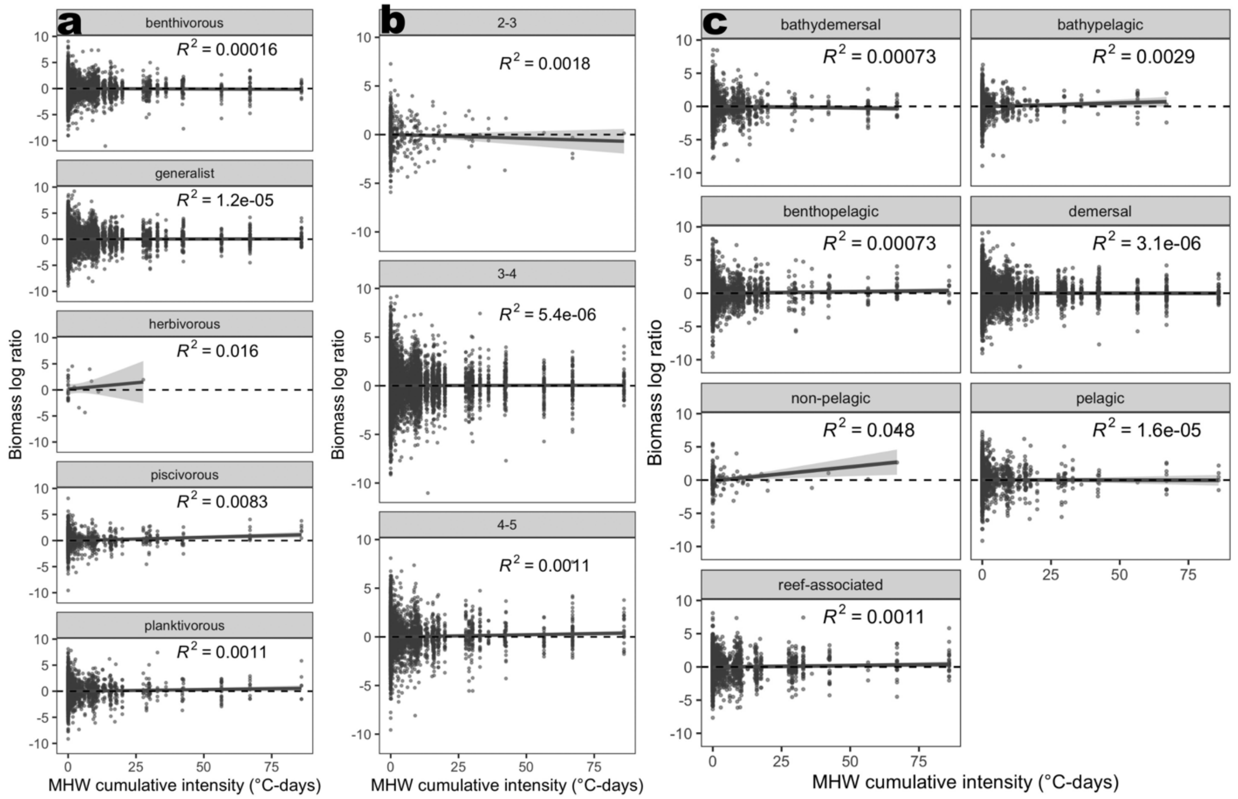
a
Mean Abundance
R^2 = 0.0031
b
Mean Biomass
R^2 = 2.3e-05
c
Median Abundance
R^2 = 4e-04
d
Median Biomass
R^2 = 0.00085
Log ratio
3
2
1
0
-1
-2
-3
0
25
50
75
MHW cumulative intensity (°C-days)

858

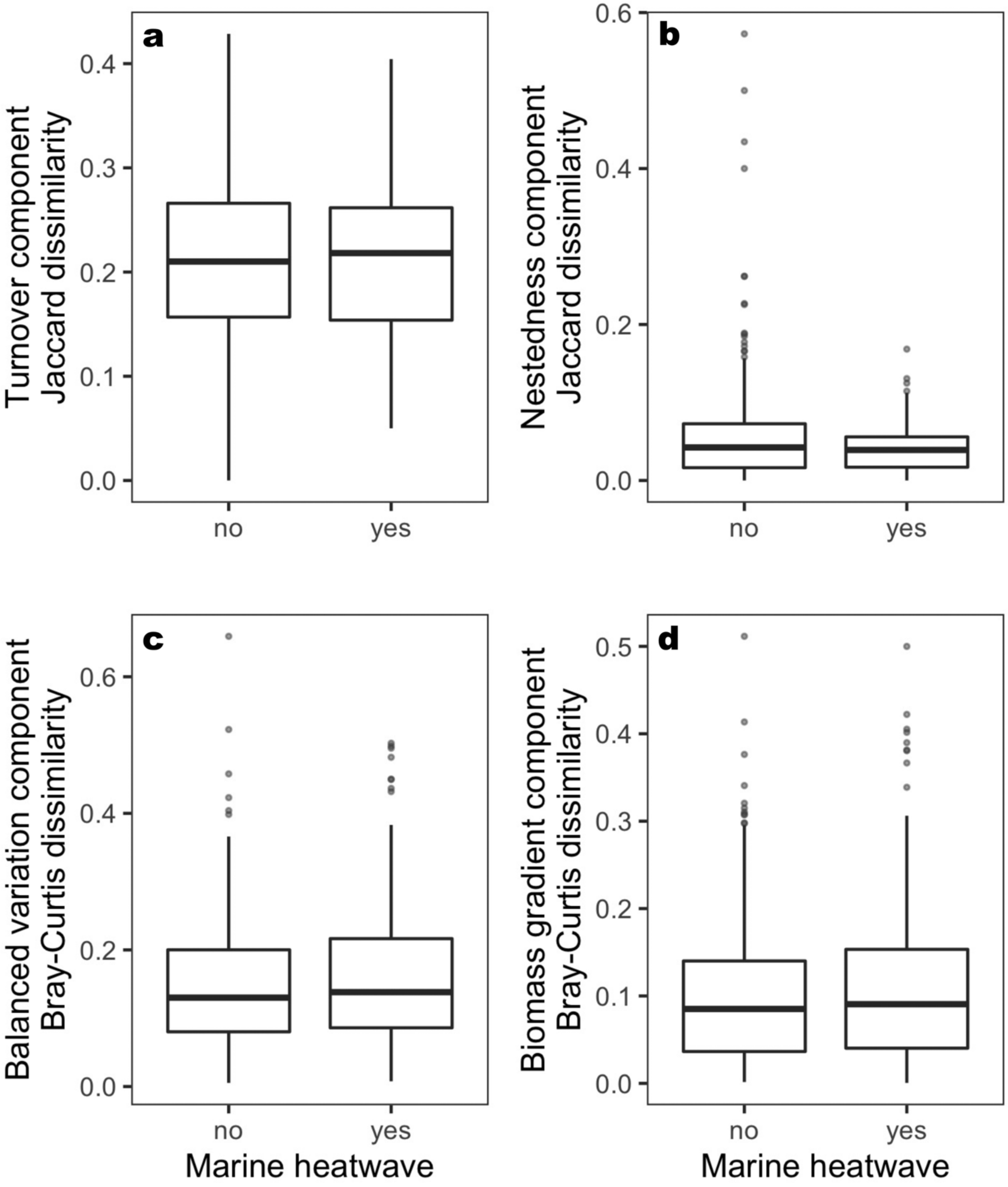
Extended Data Fig. 5. Results are consistent across different metrics of the fish community. We calculated mean abundance (a), mean biomass (b, used in the main text), median abundance (c), and median biomass (d). MHWs were calculated from the detrended GLORYS sea bottom temperature data with a five-day minimum duration threshold for MHWs, as used in the main text. Points represent log ratios of each metric in a survey from one year to the next (*n* = 343). The fitted lines are linear regressions. The shaded areas are 95% confidence intervals. The Northeast US survey was omitted because it did not have abundance data recorded.



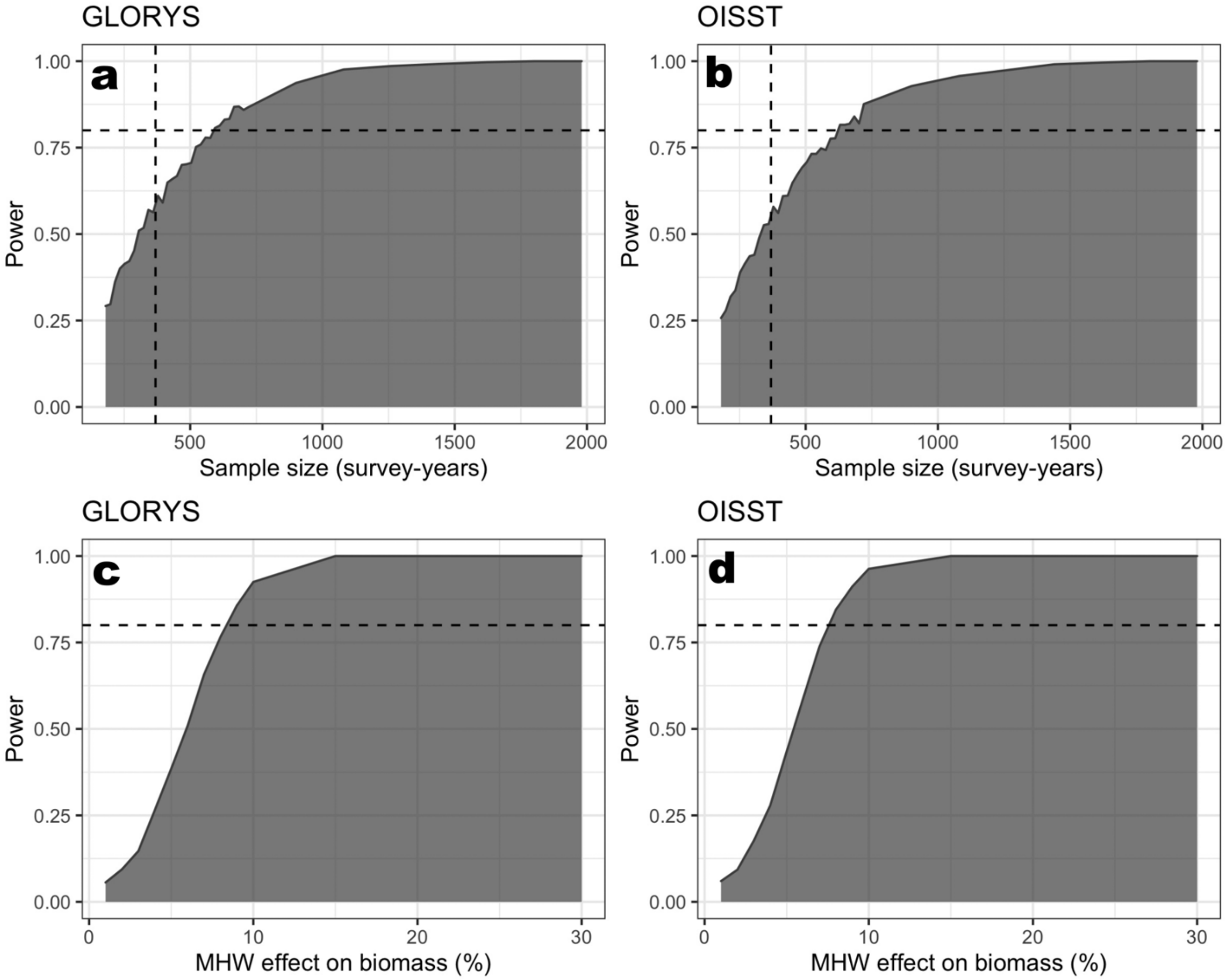
Extended Data Fig. 6. Depth changes in the fish assemblage in response to marine heatwaves. Fish assemblage depth change (log ratio) was not predicted by (a) the presence or absence of a MHW or (b) MHW cumulative intensity (total anomaly in °C-days; *n* = 369). MHWs were calculated from the detrended GLORYS sea bottom temperature data with a five-day minimum duration threshold for MHWs, as used in the main text. The fitted line in (b) is a linear regression and the shaded area is its 95% confidence interval.



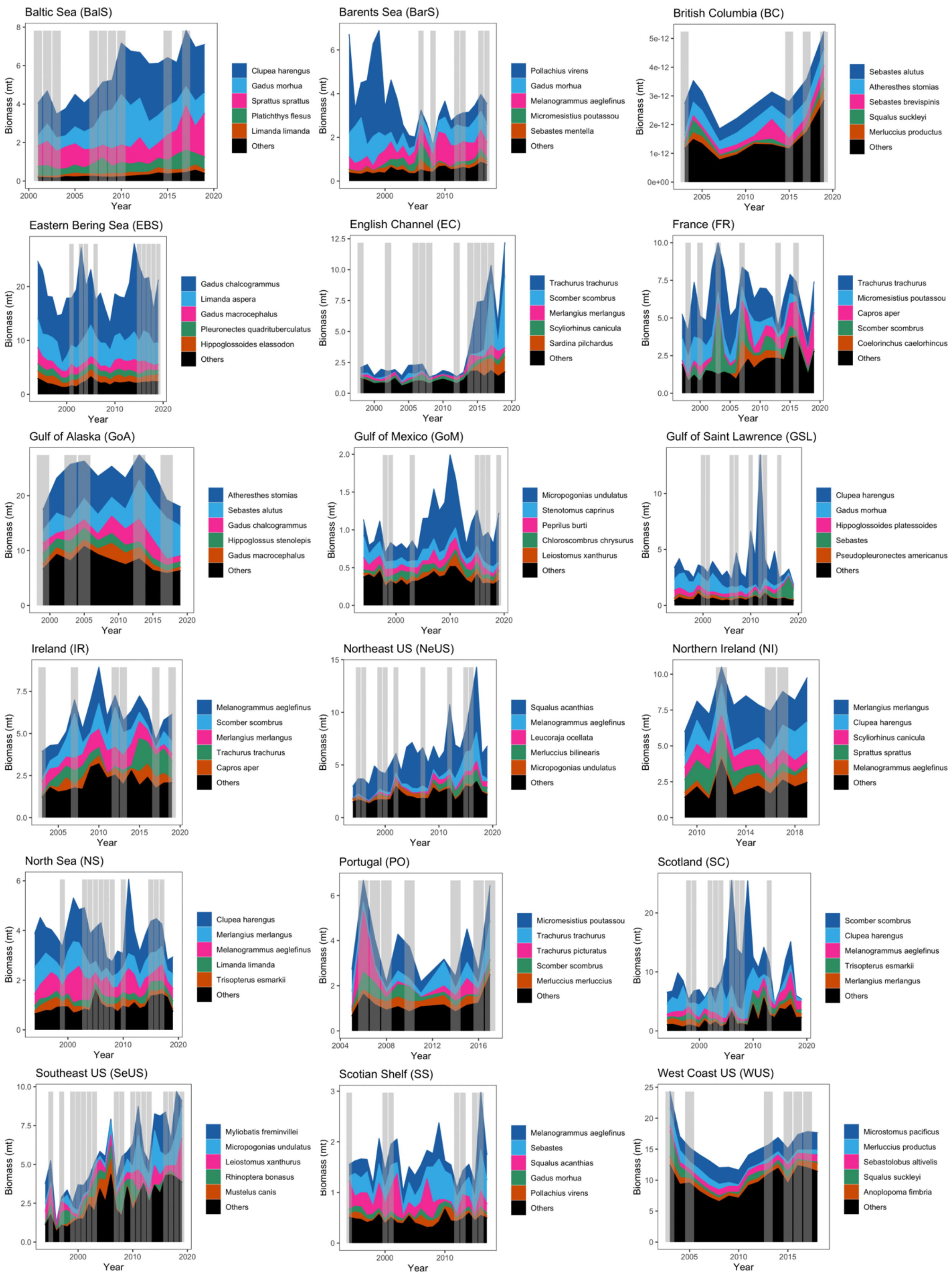
Extended Data Fig. 7. Marine heatwave effect on taxon-specific biomass log ratios grouped by traits. Biomass log ratio and MHW cumulative intensity (total anomaly in °C-days) grouped by (a) feeding mode (*n* = 29,628), (b) trophic level (*n* = 29,909), and (c) habitat preference (*n* = 29,681) of each taxon. Trait data were extracted from Beukhof et al.[51] (see Methods). MHWs were calculated from the detrended GLORYS sea bottom temperature data with a five-day minimum duration threshold for MHWs, as used in the main text. Fitted lines are linear regressions. Shaded areas are 95% confidence intervals.



Extended Data Fig. 8. The presence or absence of a MHW did not affect temporal community dissimilarity. We measured community dissimilarity as partitioned occurrence-based beta diversity metrics of substitution and subset (Jaccard turnover (a) and nestedness (b)) and partitioned biomass-based beta diversity metrics of substitution and subset (Bray-Curtis balanced variation (c) and biomass gradient (d)). Community dissimilarity metrics were calculated within each region from one year to the next (*n* = 369). MHWs were calculated from the detrended GLORYS sea bottom temperature data with a five-day minimum duration threshold for MHWs, as used in the main text.



Extended Data Fig. 9. Results from a power analysis simulating how much data would be required to detect a range of MHW-induced biomass losses. Approximately 600 survey-years in total (summed across all regions) would be required to find a significant effect if MHWs reduced biomass by 6% using either the GLORYS (a) or OISST (b) datasets; the dashed vertical line shows the sample size of our actual datasets. Given the true size of our datasets (*n* = 369 survey-years for GLORYS and 441 for OISST), our analysis had the power to detect a MHW-induced biomass decline of ~9% with GLORYS (c) and ~8% with OISST (d). The dashed horizontal line denotes one conventionally accepted threshold for power (0.8).


Baltic Sea (BalS)
Biomass (mt)
Year
0
2
4
6
8
2000
2005
2010
2015
2020
Clupea harengus
Gadus morhua
Sprattus sprattus
Platichthys flesus
Limanda limanda
Others
Barents Sea (BarS)
Biomass (mt)
Year
0
2
4
6
2000
2010
Pollachius virens
Gadus morhua
Melanogrammus aeglefinus
Micromesistius poutassou
Sebastes mentella
Others
British Columbia (BC)
Biomass (mt)
Year
0e+00
1e-12
2e-12
3e-12
4e-12
5e-12
2005
2010
2015
2020
Sebastes alutus
Atheresthes stomias
Sebastes brevispinis
Squalus suckleyi
Merluccius productus
Others
Eastern Bering Sea (EBS)
Biomass (mt)
Year
0
10
20
2000
2010
2020
Gadus chalcogrammus
Limanda aspera
Gadus macrocephalus
Pleuronectes quadrituberculatus
Hippoglossoides elassodon
Others
English Channel (EC)
Biomass (mt)
Year
0.0
2.5
5.0
7.5
10.0
12.5
2000
2005
2010
2015
2020
Trachurus trachurus
Scomber scombrus
Merlangius merlangus
Scyliorhinus canicula
Sardina pilchardus
Others
France (FR)
Biomass (mt)
Year
0.0
2.5
5.0
7.5
10.0
2000
2005
2010
2015
2020
Trachurus trachurus
Micromesistius poutassou
Capros aper
Scomber scombrus
Coelorinchus caelorhincus
Others
Gulf of Alaska (GoA)
Biomass (mt)
Year
0
10
20
2000
2005
2010
2015
2020
Atheresthes stomias
Sebastes alutus
Gadus chalcogrammus
Hippoglossus stenolepis
Gadus macrocephalus
Others
Gulf of Mexico (GoM)
Biomass (mt)
Year
0.0
0.5
1.0
1.5
2.0
2000
2010
2020
Micropogonias undulatus
Stenotomus caprinus
Peprilus burti
Chloroscombrus chrysurus
Leiostomus xanthurus
Others
Gulf of Saint Lawrence (GSL)
Biomass (mt)
Year
0
5
10
2000
2010
2020
Clupea harengus
Gadus morhua
Hippoglossoides platessoides
Sebastes
Pseudopleuronectes americanus
Others
Ireland (IR)
Biomass (mt)
Year
0.0
2.5
5.0
7.5
2005
2010
2015
2020
Melanogrammus aeglefinus
Scomber scombrus
Merlangius merlangus
Trachurus trachurus
Capros aper
Others
Northeast US (NeUS)
Biomass (mt)
Year
0
5
10
15
2000
2010
2020
Squalus acanthias
Melanogrammus aeglefinus
Leucoraja ocellata
Merluccius bilinearis
Micropogonias undulatus
Others
Northern Ireland (NI)
Biomass (mt)
Year
0.0
2.5
5.0
7.5
10.0
2010
2014
2018
Merlangius merlangus
Clupea harengus
Scyliorhinus canicula
Sprattus sprattus
Melanogrammus aeglefinus
Others
North Sea (NS)
Biomass (mt)
Year
0
2
4
6
2000
2010
2020
Clupea harengus
Merlangius merlangus
Melanogrammus aeglefinus
Limanda limanda
Trisopterus esmarkii
Others
Portugal (PO)
Biomass (mt)
Year
0
2
4
6
2004
2008
2012
2016
Micromesistius poutassou
Trachurus trachurus
Trachurus picturatus
Scomber scombrus
Merluccius merluccius
Others
Scotland (SC)
Biomass (mt)
Year
0
10
20
2000
2010
2020
Scomber scombrus
Clupea harengus
Melanogrammus aeglefinus
Trisopterus esmarkii
Merlangius merlangus
Others
Southeast US (SeUS)
Biomass (mt)
Year
0.0
2.5
5.0
7.5
10.0
2000
2010
2020
Myliobatis freminvillei
Micropogonias undulatus
Leiostomus xanthurus
Rhinoptera bonasus
Mustelus canis
Others
Scotian Shelf (SS)
Biomass (mt)
Year
0
1
2
3
2000
2010
Melanogrammus aeglefinus
Sebastes
Squalus acanthias
Gadus morhua
Pollachius virens
Others
West Coast US (WUS)
Biomass (mt)
Year
0
5
10
15
20
25
2005
2010
2015
Microstomus pacificus
Merluccius productus
Sebastolobus altivelis
Squalus suckleyi
Anoplopoma fimbria
Others

Extended Data Fig. 10. Biomass trends over time in each survey. The top five taxa by biomass are highlighted. Shaded grey rectangles denote when any MHWs occurred in the preceding survey-year. MHWs were calculated from the detrended GLORYS sea bottom temperature data with a five-day minimum duration threshold for MHWs, as used in the main text. Note that x- and y-axes vary depending on time-series length and overall survey catch.