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

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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 analysing 82,322 hauls (samples) from long-term scientific surveys of continental shelf ecosystems in North America and Europe spanning the subtropics to the Arctic. Here we show that the effects of marine heatwaves on fish biomass were often minimal and could not be distinguished from natural and sampling variability. Furthermore, marine heatwaves were not consistently associated with tropicalization (gain of warm-affiliated species) or deborealization (loss of cold-affiliated species) in these ecosystems. Although 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.

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 kilometres 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 are likely to wreak ecological devastation and negatively affect socio-economic systems[3,4,10]. However, accurate predictions must rely on 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 several species within the same ecosystem, some species declined whereas others thrived[11–13], suggesting that single-species responses do not accurately show 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 analysed the cross-species and cross-ecosystem effects of MHWs in Northern-Hemisphere shelf ecosystems from the subtropics to the Arctic. We analysed 82,322 hauls (discrete samples) comprising 22,574,452 observations of 1,769 demersal fish taxa from 18 long-term scientific (that is, fisheries-independent) bottom trawl surveys covering 45 degrees of latitude in the northeast Pacific, northwest Atlantic and northeast Atlantic (Fig. 1). Ninety per cent of hauls occurred in waters 18–451 m deep. These surveys represent the most spatially, temporally and taxonomically extensive observations available for testing MHW effects. We examined observations from 1993 to 2019 to quantify the effects of MHWs on regional fish biomass and community composition (Fig. 1).

We defined a MHW as a period of five days or more with sea-bottom temperature (SBT) anomalies above the seasonally varying 95th percentile for that region[6] and used cumulative intensity as the primary

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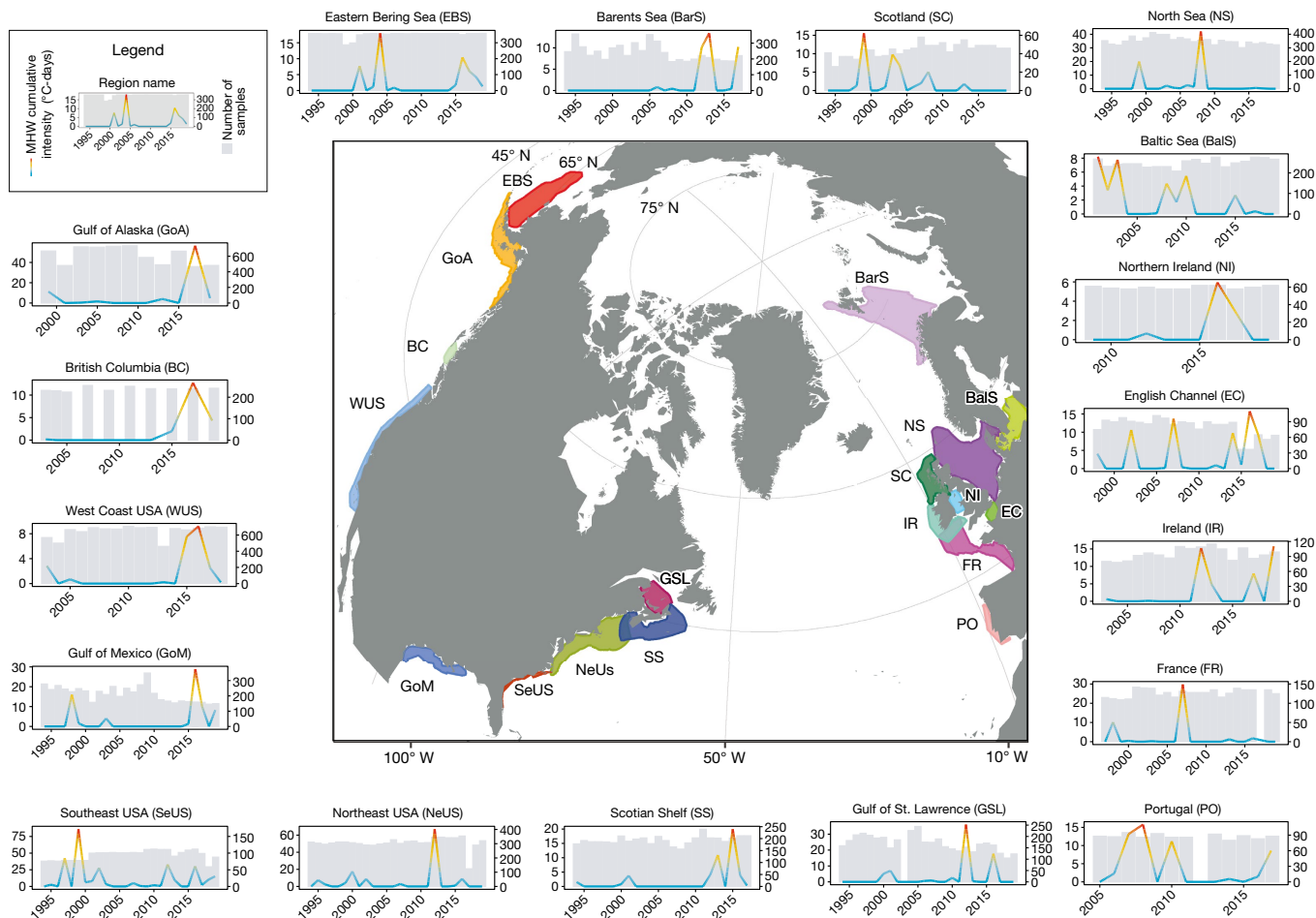
Fig. 1 | Of 18 regions studied from the Atlantic and Pacific Oceans, all experienced MHWs during the available scientific fish survey time series. Highlighted areas on the map represent the spatial area surveyed by each trawl survey. Inset plots show the number of distinct sampling events (that is, hauls of the trawl net) every year (grey bars, right y axis) and the MHW cumulative intensity in °C-days calculated from SBT data (lines, left y axis; warmer colours represent greater cumulative intensity). Years correspond to 'survey reference years'–the 12 months preceding the survey–rather than calendar years and vary among regions (Methods).

metric characterizing MHWs (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 on the basis of 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 (Methods). We proposed 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 (refs. 8,12) and a 70% biomass gain in northeast USA following the 2012 northwest Atlantic MHW (67 °C-days; Figs. 2a and 3a)[11]. However, it is important to note that, although these effects were substantial, they were neither large, compared with 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 a biomass decline of only 6% (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 USA in 1996[17].

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 km² in 2011, a non-MHW year; 13 metric tons per km² in 2012 following a 36-°C-days MHW; and 4 metric tons per km² 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 probably reflects a combination of survey variability and a true peak in population size of the autumn Atlantic herring stock in the region[18].

Contrary to our expectations, both among surveys that were and those that 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 SBT data, 139 followed MHWs and 230 did not. There was no significant difference in mean biomass change between surveys that were and those that were not preceded by a MHW ($P = 0.40$, $t = 0.85$, d.f. = 249; two-sided t-test; Fig. 2a). Furthermore, the cumulative intensity of a MHW had no significant relationship to the change in biomass (linear regression; $R^2 = 0.00$; $P = 0.88$; Fig. 2 and Supplementary Table 2).
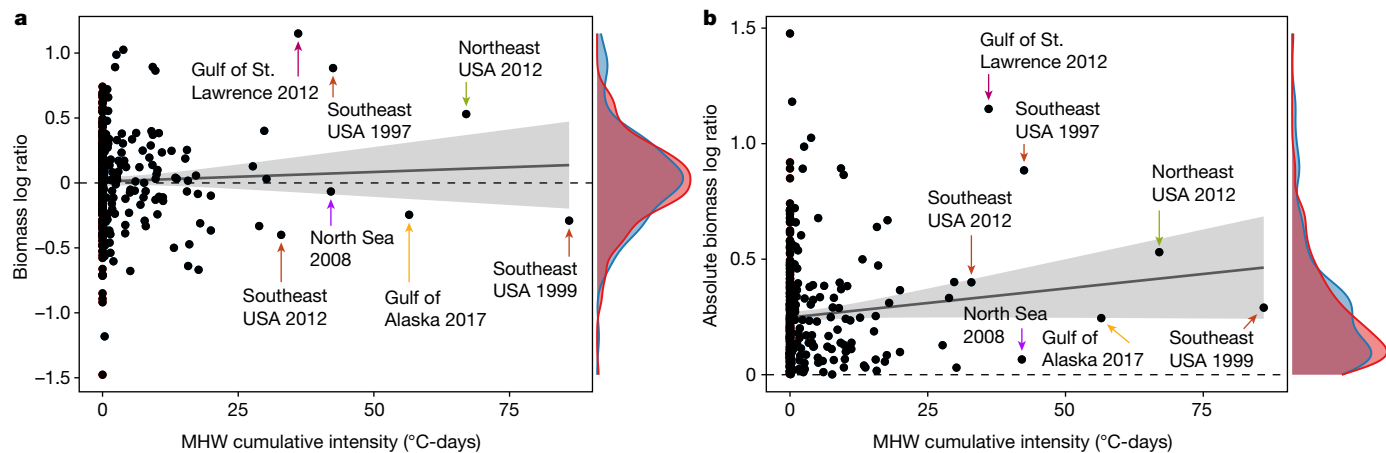
Fig. 2 | More intense MHWs were not associated with a decline in fish biomass or an increase in biomass variability, and biomass was approximately as likely to increase as it was to decrease from one year to the next, regardless of whether a MHW occurred. a,b, MHW cumulative intensity (°C-days) had no relationship with biomass change (**a**; measured as log ratio; linear regression, $R^2 = 0.00$, $P = 0.45$) or absolute biomass change (**b**; 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 ($n = 230$) occur. Points represent log ratios (**a**) or absolute log ratios (**b**) of mean biomass in a survey from one year to the next ($n = 369$). Surveys following the highest cumulative intensity MHWs are labelled (years correspond to when the survey was conducted). Arrow colours correspond to regions in Fig. 1. Models exploring the relationships in **a** and **b** are reported in Supplementary Tables 2 and 4, respectively.

The ecosystems we studied have distinct climates, species assemblages and histories of anthropogenic pressures[19], and might respond at different rates and in different directions to environmental perturbation[20]. More broadly, pulse disturbances and other exogenous drivers (including heatwaves) are often expected to increase variance in the biomass of populations and communities[21]. 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 and Supplementary Table 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 and Supplementary Table 4). Instead, we find that variability in biomass change from one year to the next is similarly high with MHWs as it is 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 ($P = 0.24$, $t = 1.17$, d.f. = 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 show any meaningful effect sizes of MHWs on biomass (Supplementary Tables 6–10 and Extended Data Figs. 6 and 7). Our results were also robust to the metric used (cumulative intensity, duration, intensity or heating degree-days) to characterize MHWs, to how cumulative intensity was scaled and to whether SBT data were detrended (Extended Data Fig. 2 and Supplementary Table 5). Because SBT data were available from only 1993 onward, we also analysed a longer time series of sea surface temperature (SST) that began in 1982, and thus could be paired with 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 (that is, greater biomass following more intense MHWs; linear regression, $R^2 = 0.02$, $P = 0.02$). Although we interpret this result cautiously given the high leverage of a few data points, it 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 locally extinct ('deborealization') and/or by causing warm-affiliated species to spread or increase ('tropicalization')[22-24]. 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[25].

Other studies show that CTI has increased in North Atlantic and Pacific fish communities in recent decades, concomitant with ocean warming[24]. 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. 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 of the 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[26]. 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; $P = 0.87$, $t = 0.16$, d.f. = 280; two-sided t-test; Fig. 4b). Furthermore, there was no relationship between MHW cumulative intensity and CTI change ($R^2 = 0.00$; $P = 0.33$; linear regression; Supplementary Table 11).

MHWs may restructure ecological communities in ways other than tropicalization and deborealization[27]. Less predictable changes in species identity and underlying community structure could also emerge despite consistent biomass[28]. We tested for changes in community composition by calculating dissimilarity over the time series using occurrence data (that is, species presence–absence) and biomass data. Each of these dissimilarity indices was calculated from one year to
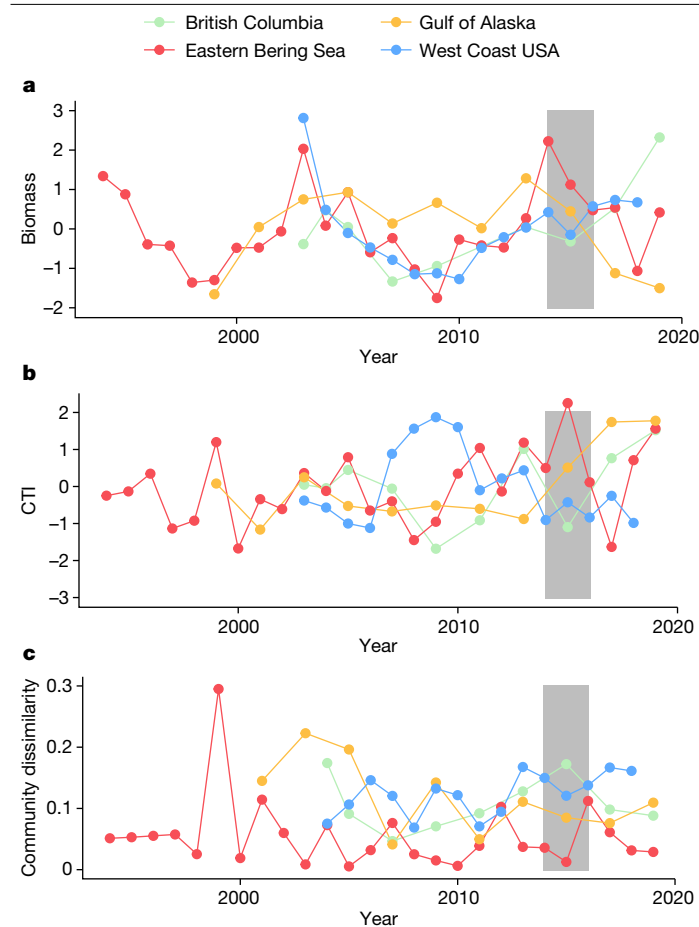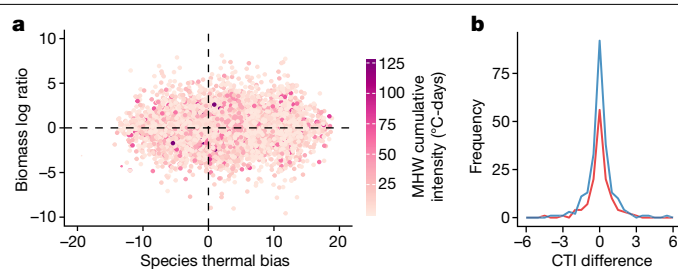
Fig. 4 | Scientific bottom trawl surveys during the year following MHWs were as likely to exhibit tropicalization and/or deborealization as those that did not follow MHWs. a, There was no relationship between a species' thermal bias (its cold or warm affinity relative to the assemblage mean, calculated as STI − CTI; 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.

Fig. 3 | Example of divergent responses to a large MHW. a–**c**, Plots show centred and scaled biomass (**a**), CTI (**b**) and change in community composition over time (the substitution component of the Bray–Curtis dissimilarity; **c**) between the previous and given year for four surveys in the northeast Pacific. Colours correspond to survey footprints in Fig. 1. Higher values represent more biomass, tropicalization and/or deborealization, and greater community dissimilarity. The grey stripe denotes the 2014–2016 northeast Pacific MHW ('The Blob').

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[29] (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[28].

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 of the USA 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 regardless of whether a MHW had 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 proposed 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[30]. Furthermore, changes in community structure at the local scale may not be reflected at the regional scale of our analysis.

This array of results indicates that the regional impacts of MHWs on fish communities are highly idiosyncratic, with pronounced 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[31]. Species and spatial portfolio effects[32,33], and spatial and temporal storage effects[34], 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[24], although we did not find a latitude effect in our analysis (Supplementary Table 8). Interspecific variation in the timing, magnitude and direction of MHW response may also be important[35]. 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 show 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 a decline in fish biomass of 8–9% or less, if permanent and sustained over time, would probably 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 (Representative Concentration Pathway 8.5) projected that the negatively affected stocks (roughly three-quarters 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—that is, encountered by fishing gear at higher rates—in warmer temperatures[36]. However, if this response was widespread among the species we studied, it would cause an increase in biomass following MHWs, which we did

not observe. The availability of fishes to surveys can also be influenced by range shifts, possibly induced by MHWs[37]. 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' catches as well as MHW cumulative intensity, with no significant results (Supplementary Table 10). Although the choice of metric to quantify MHWs[6,15,37,38] and fish community responses[11,36] may influence results, our results here were not sensitive to these decisions. The pattern in Fig. 2 emerged regardless of whether we analysed fish biomass (that is, weights) or fish abundance (that is, 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[39] (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[40].

Ecological effects of climate change result from the interaction of long-term climatic change 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 refs. 35,41). 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 (for example, 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[42]—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[26,43]. 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 understudied parts of the global ocean will also be helpful in understanding how ecological context influences MHW responses[39].

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[41]. 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. 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 (for example, coral reef ecology) have identified such thresholds, although the generality of thresholds across ecological systems remains unclear[44]. 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. In addition, 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 their environments[45]. MHW occurrences are projected to emerge above their natural variability within this century in many regions[46]. 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[47]. 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[48]. As a future that is more than 1.5 °C warmer looks increasingly likely[49], it is more critical than ever to develop a deeper understanding of what drives ecological responses to extreme climate events.

Online content

Any methods, additional references, Nature Portfolio reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at https://doi.org/10.1038/s41586-023-06449-y.

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Methods

All analyses were conducted in R[50]. Software versions are listed on GitHub.

Fish biomass and abundance data

We collated publicly available datasets from fishery management agencies that use scientific (that is, fisheries-independent) bottom trawl surveys to monitor marine fish communities[39]. These surveys monitor biogeographically and/or politically distinct areas that are relevant to fisheries management[39]. Their footprints often follow marine ecosystem boundaries (for example, large marine ecosystems[51]) and are similar in size to the spatial extents of MHWs[38]. 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, the northwest Atlantic and the northeast Atlantic (Fig. 1 and Supplementary Table 1).

In these surveys, the sampling unit is a single haul, that is, a sampling event in which a net is towed through the water. We filtered invalid hauls on the basis of 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.[52]. 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 USA; Extended Data Fig. 5).

Datasets were trimmed to standardize the spatial footprint of the survey over time, to match the available temperature datasets (SBT began in 1993 and SST began in 1982; MHW data), to remove years with very few samples and to omit samples collected outside the focal season (3-month interval) of each survey. We used the World Register of Marine Species[53] to standardize taxonomies, and the 'dggridR' R package[54] to standardize the survey footprints. Across our 18 surveys, we paired 82,322 hauls with SBT and 100,877 hauls with SST. Of the 94% of hauls with an associated depth value, 90% occurred at depths of between 18 m and 451 m. The depths sampled vary owing to each region's unique bathymetry and each survey's protocols, but surveys tend to sample similar depths over time; for example, the southeast USA survey samples very shallow inshore areas of just 3 m depth, whereas the Scotian Shelf and West Coast surveys routinely trawl deeper than 1,000 m. We used all taxa for biomass analyses, but only the species-level observations for community analyses (Species and CTIs).

We imputed zeros representing an observed absence in every instance when a taxon (that was observed at some point in the region) was not recorded in a haul. These absences can be considered true non-detections because of the standardized spatiotemporal design of bottom trawl surveys. We then calculated a mean biomass for each taxon in every year, and calculated region-wide biomass as the sum of taxon-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 USA 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[55], 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, $\ln\left(\frac{\text{biomass}_t}{\text{biomass}_{t-1}}\right)$, where t is year. 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 $\text{biomass}_t = 1.67 \times \text{biomass}_{t-1}$. A 67% decrease means that $\text{biomass}_t = (1 - 0.67) \times \text{biomass}_{t-1}$.

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 were paired with MHW data from August 2009 to 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 analysed MHW effects over a full year (that is, 12-month interval). Some substantial MHW effects have been reported in summer[56], and yet winter heatwaves strongly influence distribution and abundance for species limited by winter survival[57,58]. Warmer winters are considered 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[59]. Spawners and embryos have narrower temperature tolerance ranges than non-spawning adults[60]; 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 centred within surveys.

MHW data

We paired the demersal bottom trawl data with MHWs calculated with SBT data from the Copernicus 1/12° (about 8 km) global ocean reanalysis, the Global Ocean Reanalysis and Simulations (GLORYS)[61]. 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 GLORYS 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 with other products[62,63]. Being highly dependent on ocean observations for data assimilation, GLORYS began only 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 v.2.1 dataset[64,65] with a horizontal grid resolution of 0.25°, which is available from 1982 onwards, 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 are 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 the standard definition of a MHW (for example, refs. 9,46), both SBT and SST anomalies were calculated within (not across) spatial units—here, the survey regions. This approach defines anomalies relative to historical conditions in a region, which are probably 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

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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 percentile[38] instead of the 95th. Under our definition, MHWs may occur throughout the year and at all locations.

The temperature data were linearly detrended before any analysis to distinguish discrete MHWs from the long-term warming signal (refs. 37,66 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 (Extended Data Fig. 2c). Using the 5-day threshold and the detrended data, we identified 511 distinct surface MHWs in OISST and 248 bottom MHWs in GLORYS. Many years had several 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 (that is, 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 supplementary information used MHW cumulative intensity centred and scaled within regions, although our results were not sensitive to whether we scaled and centred within versus across regions (Supplementary Table 5).

In coral reef ecology, a threshold for ecological damage (that is, coral bleaching) has been identified using heating degree-days—the number of days that exceed average temperatures for the hottest summer month by at least 1 °C (ref. 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 5-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 (ref. 67), and is widely used in the literature[6], although we note that alternative methods exist to define and measure MHWs[15,38,68]. We also assessed whether MHW responses would emerge from classifying any daily anomaly (without the 5-day cutoff) as a MHW. We found no such relationship (Extended Data Fig. 2a).

Species and CTIs

The species temperature index (STI) and CTI are measures of thermal affinity at the species and community levels, respectively[69]. We quantified STI as the median SSTs found throughout a species' modelled range from the publicly available STI dataset in Burrows et al.[25]. STI values were available for 828 of our 1,769 focal taxa, comprising 82% of the 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)[69].

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 dissimilarities between surveys spanning a MHW with those between years that did not span a MHW. We partitioned the Bray–Curtis dissimilarity into two components (biomass gradient and balanced variation) using the betapart package in R[29,70]. The biomass gradient component focuses on changes in biomass of species between years within the survey region, whereas 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 (with species presence–absence data) using Jaccard dissimilarity partitioned into nestedness and turnover components. Balanced variation and turnover both measure substitution of species between communities whereas biomass gradient and nestedness both measure how species are subsetted between communities.

Further predictors

We conducted supplementary analyses to explore the role of several further 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[71,72]. We tested for this effect by calculating depth log ratios that described whether assemblages had shifted deeper or shallower from one survey-year to the next. Depth log ratio was quantified by the following three steps. (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 those that did not follow a MHW (Extended Data Fig. 6 and Supplementary Table 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[23,73] and some increases in species richness recorded in colder oceans and at poleward range edges[73,74]. 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 (Supplementary Table 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.[75]. Of the 1,769 taxa used in the main analysis, 1,588 had trophic-level data, 1,559 had feeding mode data and 1,580 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 5 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 (Supplementary Table 6).

Because fishing, through increased mortality, can influence temporal biomass change, we also analysed the effects of catch on biomass

change. We extracted a historical time series of reconstructed catch values from the Sea Around Us database[78] (http://www.seaaroundus.org/) by marine ecoregions[78]. The Sea Around Us reconstructed catches are spatially allocated to half degree ocean cells[79], which permits catch data to be assigned to spatial entities such as the 232 marine ecoregions identified by ref. 78. We then paired our survey footprints with the most overlapping marine ecoregions. In most cases, the marine ecoregions and survey footprints were similar. For two large surveys (the West Coast and the northeast USA), we summed catch data across two adjacent marine ecoregions. Two small surveys (France and the English Channel) did not correspond well to the marine ecoregions and were omitted from the fishing analysis. Because catch data are recorded by calendar year, and the surveys often occur mid-year, we fitted models comparing biomass change in a given year to the mean catch level in the previous 3 calendar years (Supplementary Table 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 Supplementary Tables 2–11. Generalized linear models were fitted with the R package 'glmmTMB'[80] and generalized additive models with the R package 'mgcv'[81]. When comparing MHW effects with non-MHW effects, we used two-sided t-tests. Although 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[82].

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:

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

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 had ($n = 369$ for SBT and $n = 441$ for SST). 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 centred within regions and pooled across regions. Each set of simulations was run 1,000 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 SST and SBT—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 ($P \le 0.05$). These results are shown in Extended Data Fig. 9.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

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

Code availability

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.

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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.
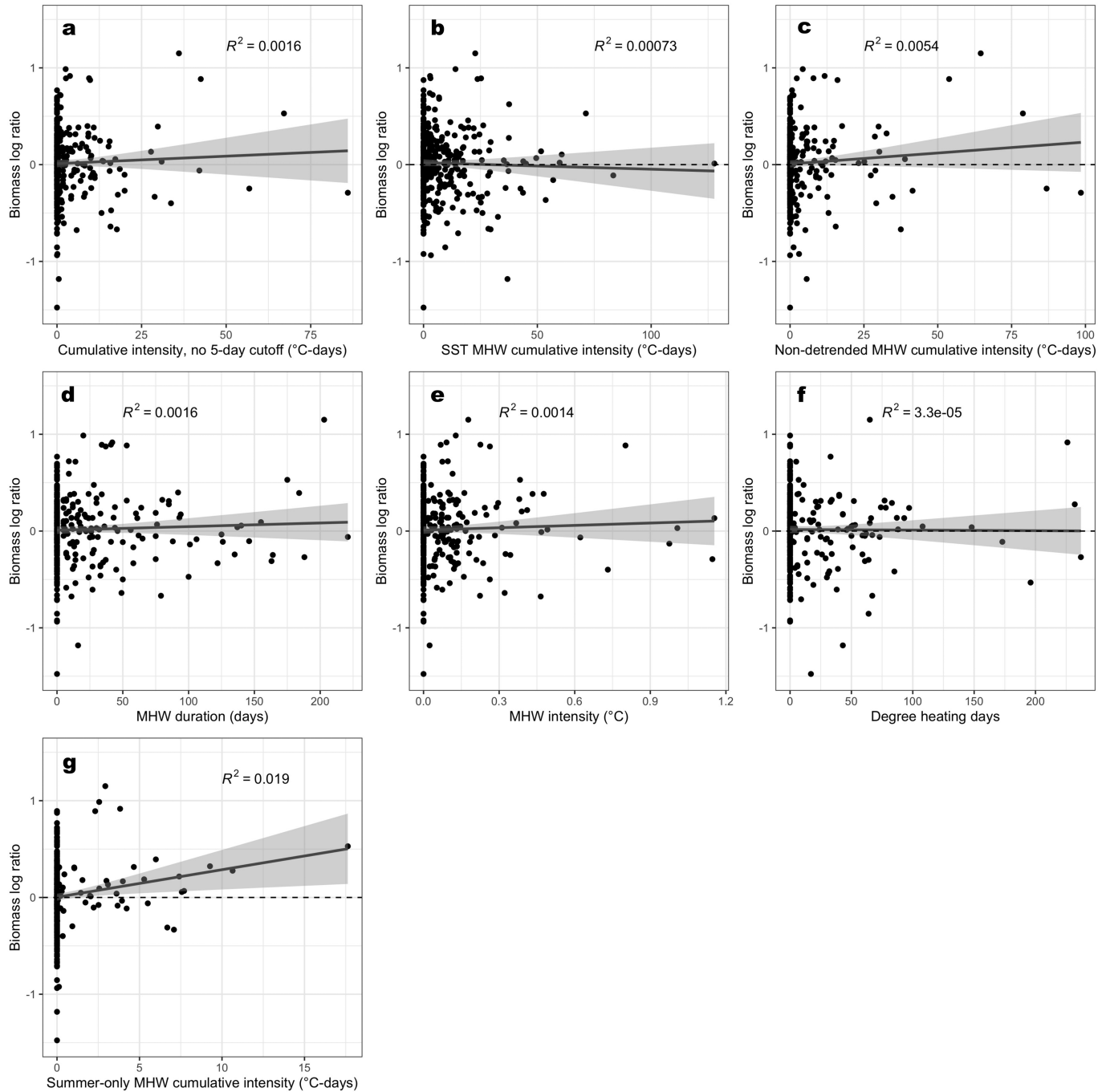
Extended Data Fig. 2 | Results did not change when alternative methods were used to quantify marine heatwaves. Results were robust to (a) removing the five-day threshold for MHWs, (b) using SST from OISST instead of SBT from GLORYS (detrended), (c) using non-detrended data, (d) using a MHW metric of 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) $n = 441$.
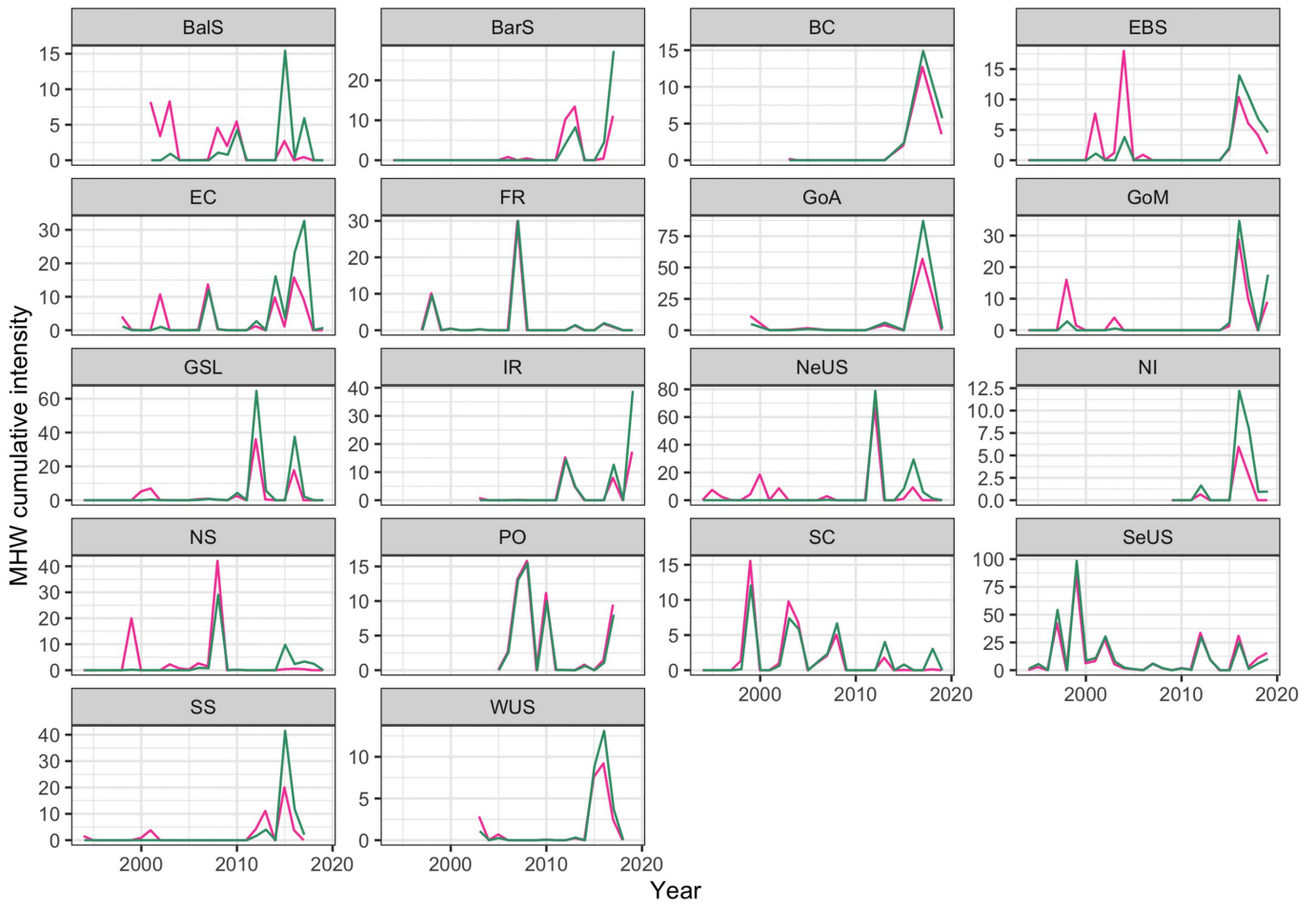
Extended Data Fig. 3 | Marine heatwave cumulative intensity (total anomaly in °C-days) in each survey region with and without detrending the temperature data to remove the signal of secular warming. The main text results are detrended. Here, we plot MHW cumulative intensity based on all SBT anomalies 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.
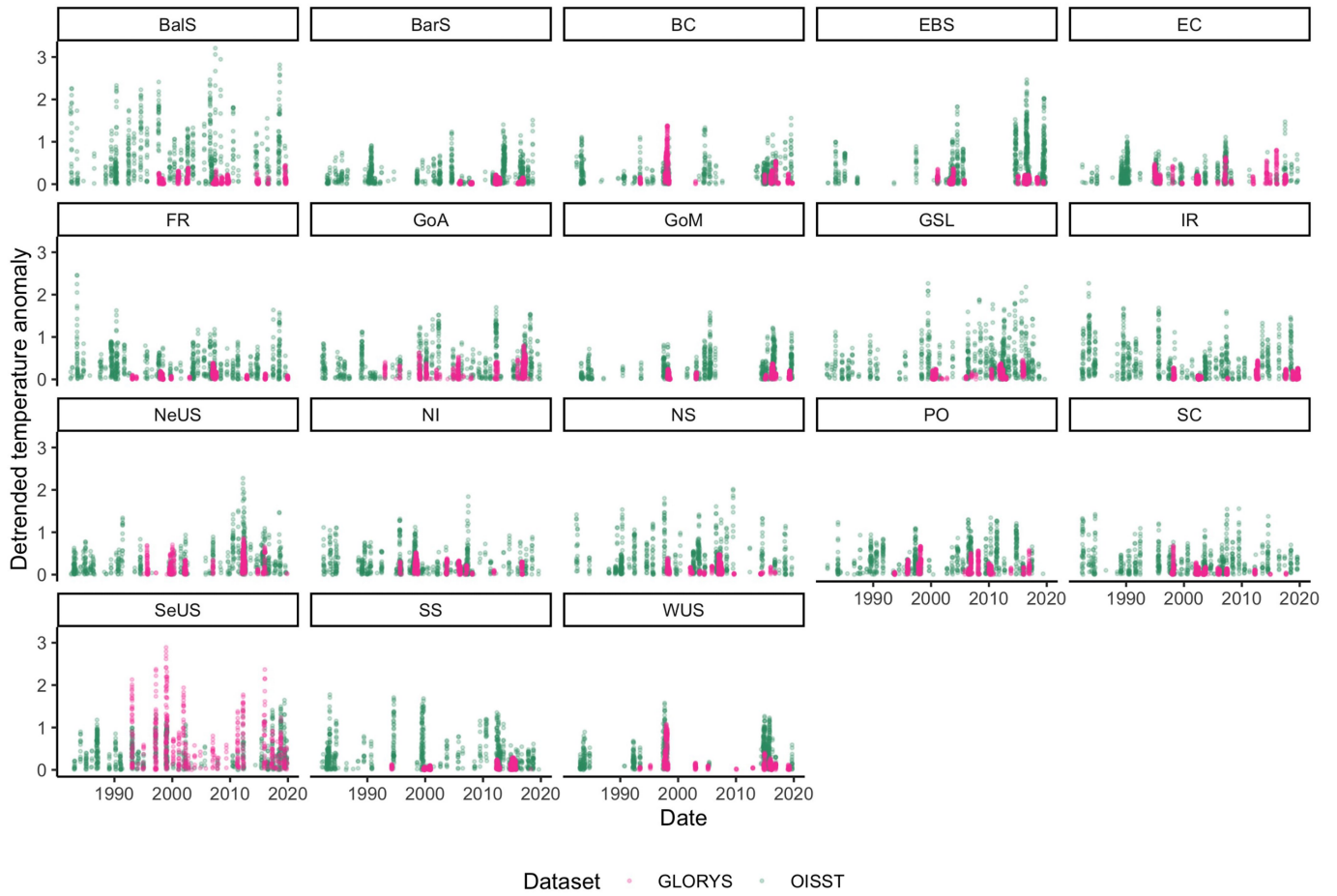
Extended Data Fig. 4 | Daily 95ᵗʰ percentile anomalies in the two marine heatwave data sources: sea surface temperature from OISST and sea bottom temperature from GLORYS (both detrended). To simplify comparison we plot all anomalies, not just those MHWs that exceeded a five-day threshold. Note that the OISST time-series began in 1982 and GLORYS began in 1993. Region names are listed in Supp. Tab. 1.
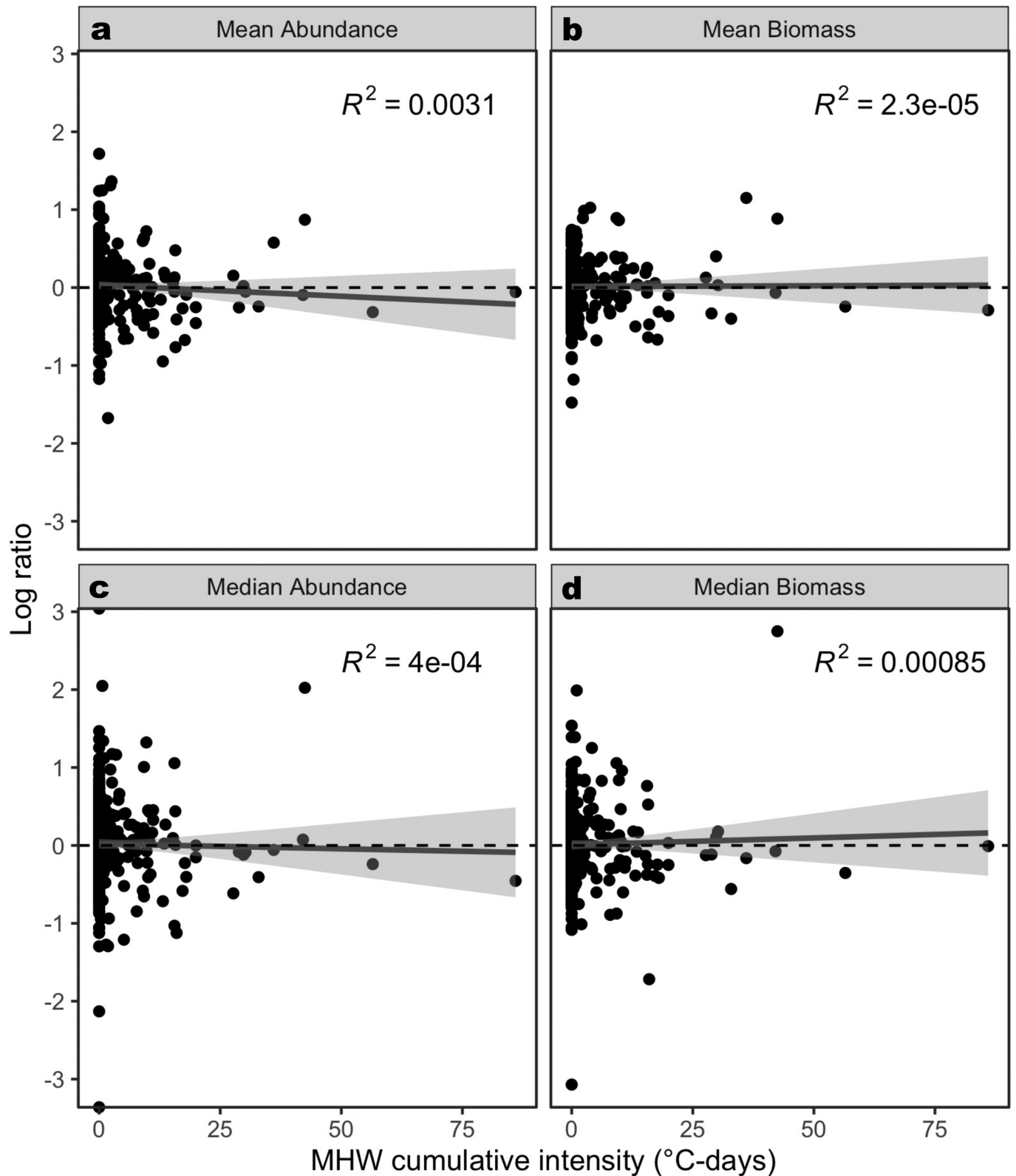
Extended Data Fig. 5 | Results are consistent across different metrics of the fish community. We calculated mean abundance (a), mean biomass (b, used in the main text), median abundance (c), and median biomass (d). MHWs were calculated from the detrended GLORYS sea bottom temperature data with a five-day 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.
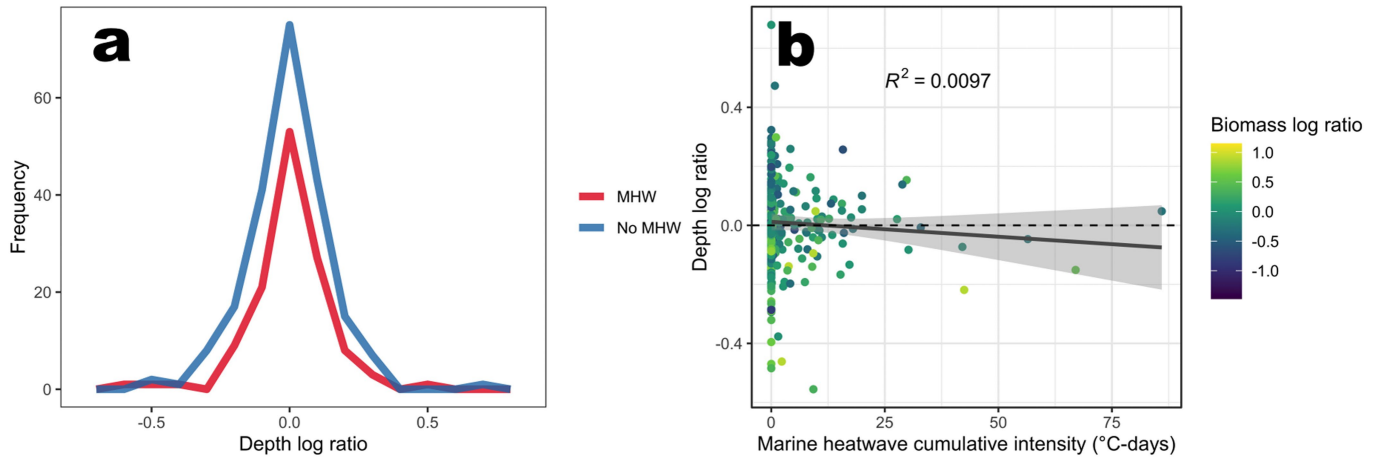
Extended Data Fig. 6 | Depth changes in the fish assemblage in response to marine heatwaves. Fish assemblage depth change (log ratio) was not predicted by (a) the presence or absence of a MHW or (b) MHW cumulative intensity (total anomaly in °C-days; n = 369). MHWs were calculated from the detrended 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.
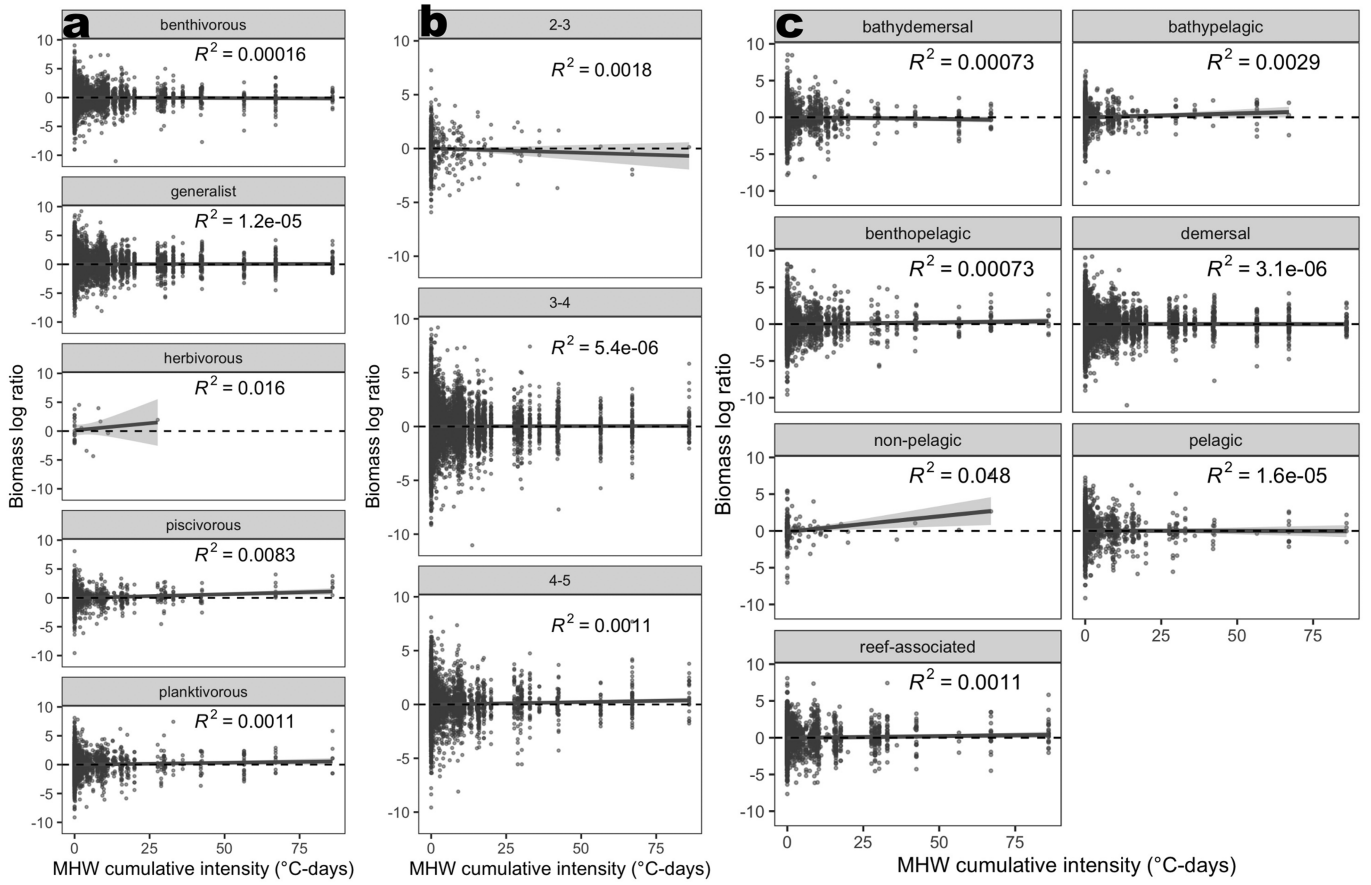
Extended Data Fig. 7 | Marine heatwave effect on taxon-specific biomass log ratios grouped by traits. Biomass log ratio and MHW cumulative intensity (total anomaly in °C-days) grouped by (a) feeding mode ($n = 29,628$), (b) trophic level ($n = 29,909$), and (c) habitat preference ($n = 29,681$) of each taxon. Trait data were extracted from Beukhof et al[75]. (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.
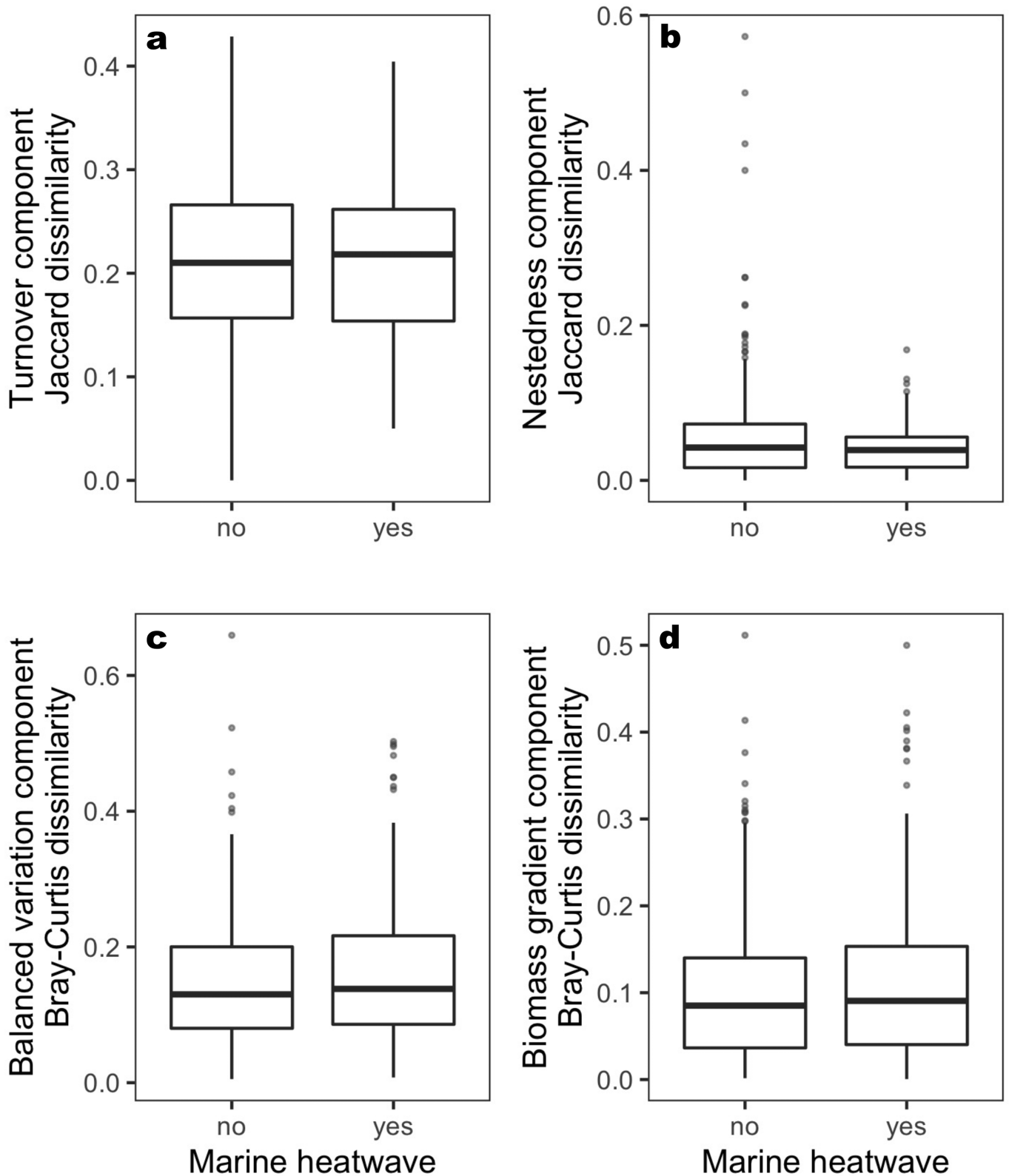
Extended Data Fig. 8 | The presence or absence of a MHW did not affect temporal community dissimilarity. We measured community dissimilarity as partitioned occurrence-based beta diversity metrics of substitution and subset (Jaccard turnover (a) and nestedness (b)) and partitioned biomass-based beta diversity 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.
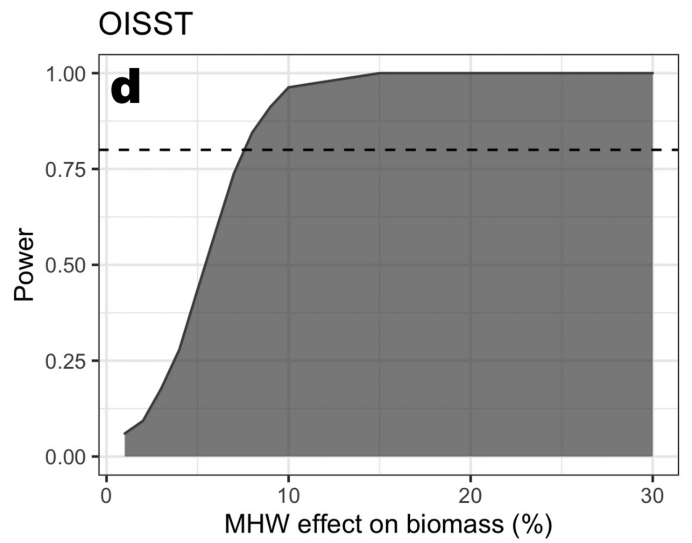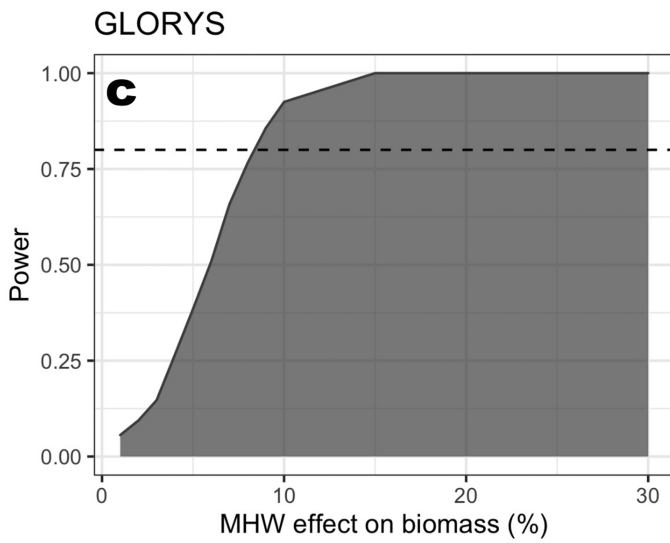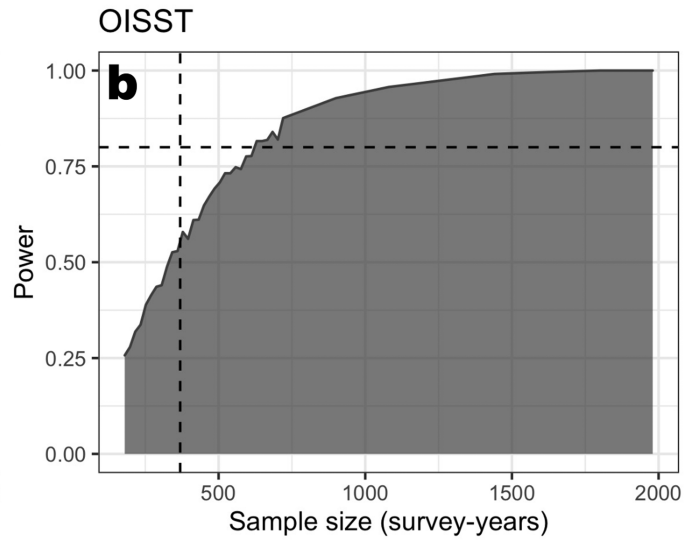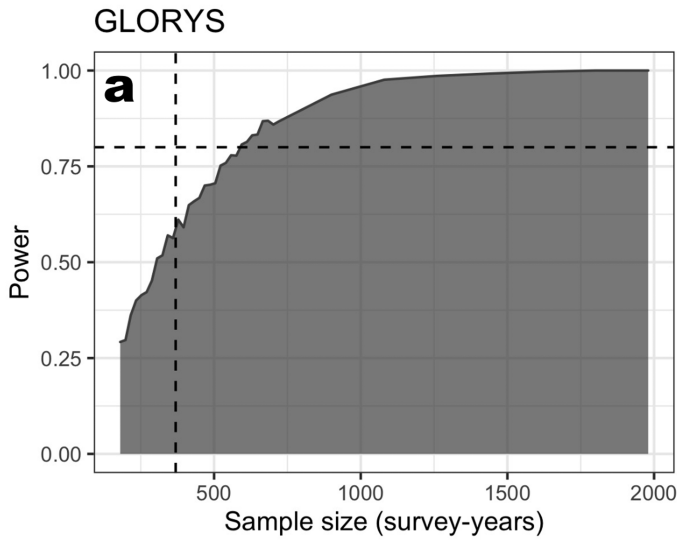
Extended Data Fig. 9 | Results from a power analysis simulating how much data would be required to detect a range of MHW-induced biomass losses. Approximately 600 survey-years in total (summed across all regions) would be required to find a significant effect if MHWs reduced biomass by 6% using either 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).

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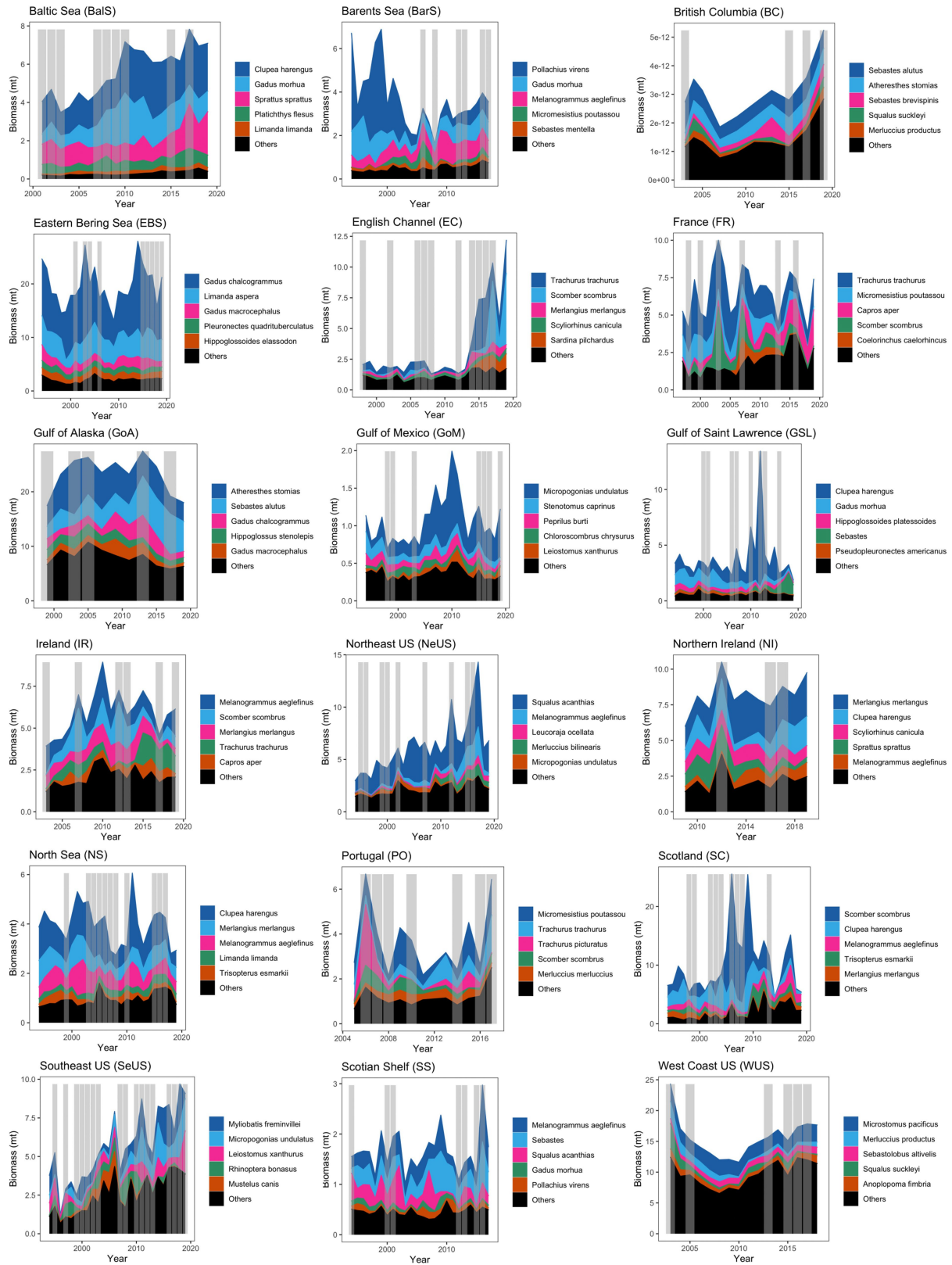
Extended Data Fig. 10 | Biomass trends over time in each survey. The top five taxa by biomass are highlighted. Shaded grey rectangles denote when any MHWs occurred in the preceding survey-year. MHWs were calculated from the detrended GLORYS sea bottom temperature data with a five-day minimum duration 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.

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Last updated by author(s): Jul 14, 2023

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Policy information about availability of computer code

Data collection	The code for this study is publicly available on GitHub at https://github.com/afredston/marine_heatwaves_trawl. The data and code are also available on OSF: https://osf.io/h6ukt
Data analysis	The code for this study is publicly available on GitHub at https://github.com/afredston/marine_heatwaves_trawl. The data and code are also available on OSF: https://osf.io/h6ukt

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The code for this study is publicly available on GitHub at https://github.com/afredston/marine_heatwaves_trawl. The data and code are also available on OSF: https://osf.io/h6ukt

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Ecological, evolutionary & environmental sciences study design

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Study description	We used scientific trawl survey datasets and historical ocean temperature data to assess the effect of marine heatwaves on fish communities. We defined a sample as a single "survey-year", i.e., all of the surveys conducted in a year that were retained after data standardization. Most survey-years included thousands of distinct biodiversity records. We had 369 distinct samples (i.e., survey-years) from 1993-2019. We related common metrics of community change (change in biomass and community composition, summarized with log ratios) in the biodiversity surveys to marine heatwave metrics calculated from satellite sea surface temperature and historical sea bottom and surface temperature data products. We also tested additional predictors of change in the survey dataset, such as survey depth, species traits, survey latitude, and lagged effects.
Research sample	We collated publicly available datasets from fishery management agencies that use scientific (i.e., fisheries-independent) bottom trawl surveys to monitor marine fish communities. Although these surveys are conducted by many nations, we used only surveys by agencies that make their raw data publicly available so as to facilitate reproducibility of this study (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)). These surveys sample all marine fishes that are large enough to be caught in the trawl net. We chose these data to provide the maximum taxonomic, temporal, and spatial extent possible in order to understand the overall effect of marine heatwaves on these communities.
Sampling strategy	Scientific trawl surveys survey fixed spatial areas in regular seasons at regular temporal intervals. All the surveys used here operate every year or every other year, and for those that are conducted in multiple seasons, we trimmed data to include one season only (the best-sampled season). Survey staff use the same vessels, gear, and protocols each year. Survey sites are chosen either as fixed stations (the same sites are re-surveyed every year) or with randomized stratified sampling (random coordinates are visited within pre-defined strata) depending on the survey. Fishing gear is towed through the water for a fixed length of time, and then researchers on board the vessel identify and weigh all of the catch. Each fishing event is recorded as a unique "haul". We used the full sample available and used a power analysis to assess what effect we had the power to detect given that sample size. Detailed methods are available for each survey (we used data from 18 distinct surveys) as manuals and can be provided upon request.
Data collection	The data used in this study are from fisheries-independent scientific trawl surveys conducted by federal agencies in a number of

Data collection	countries. Each of these agencies uses a standardized method that is well documented and was referenced in our code that harmonized metrics among surveys (see uploaded code). These data are publicly available and frequently used in scientific analysis.
Timing and spatial scale	We did not collect the data, so we did not have control over the timing and spatial scale of sampling. All the surveys used here operate every year or every other year, and for those that are conducted in multiple seasons, we trimmed data to include one season only (the best-sampled one). We used survey data starting in 1993 (because our earliest oceanographic records are from 1993) and ending in 2019. Not all individual surveys had data available for that entire interval (see Supplement). The spatial footprint of surveys is visualized in Figure 1.
Data exclusions	We omitted some invalid hauls that had very long or very short durations, were flagged by the data providers as being low quality, or did not report the data needed to standardize catch statistics. We also omitted some hauls that did not fall within a standardized spatial footprint over time that we calculated to ensure that samples were comparable between years. We also excluded data prior to 1993 because we did not have high-resolution oceanographic data to compare it to, and data from months beyond the season (continuous 3-month interval) that was best-sampled in each survey. These exclusion criteria were pre-established and intended to make the analysis more rigorous.
Reproducibility	This study did not involve experimental findings.
Randomization	We analyzed the survey data both against continuous variables (e.g., marine heatwave duration) and binned into groups (heatwave present/absent). We also tested for the influence of a number of potential covariates (see Supplement).
Blinding	Because we did not collect the data, blinding was not possible in this study.

Did the study involve field work? ☐ Yes ☒ No

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☒	☐ Animals and other organisms
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☒	☐ Plants

Methods

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