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

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4

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65

66 **Summary**

67

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

84

85 **Main text**

86

87 Extreme climatic events exacerbated by global climate change are associated with many
88 examples of ecological transformation⁵. Marine heatwaves (MHWs)⁶—prolonged periods of
89 anomalously warm ocean temperatures—have been linked to widespread coral bleaching and
90 die-offs of kelp forests and reef fishes in shallow coastal seas^{1,2}. MHWs can rapidly displace

91 some marine species by hundreds of kilometers and cause abrupt declines in phytoplankton and
92 commercially important species⁷⁻⁹. These high-profile catastrophes and those emerging from
93 regional and global model simulations predict that MHWs will likely wreak ecological
94 devastation and negatively impact socio-economic systems^{3,4,10}. However, accurate predictions
95 must rely upon generalizable patterns and processes, not case-studies with limited spatial and
96 taxonomic scope. The extent to which MHWs in general have negative ecological impacts or
97 even whether they can be differentiated from other sources of natural and sampling variability in
98 marine systems remains unclear. In the few studies that have compared responses to MHWs
99 across multiple species within the same ecosystem, some species declined while others thrived¹¹⁻
100 ¹³, suggesting that single-species responses do not accurately reveal net ecological effects. These
101 net effects are particularly important to understand in continental shelf ecosystems, where many
102 of the world's largest ocean fisheries operate¹⁴.

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

112 We defined a MHW as a period of ≥ 5 days with sea bottom temperature (SBT)
113 anomalies above the seasonally varying 95th percentile for that region⁶ and used cumulative

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

124 This dataset recorded some notable MHW impacts that mirror previous reports in the
125 literature, including a 22% biomass loss in the Gulf of Alaska following the 2014-2016
126 Northeast Pacific MHW with a cumulative intensity of 57 °C-days^{8,17} and a 70% biomass gain in
127 the Northeast USA following the 2012 Northwest Atlantic MHW (67 °C-days; Fig. 2a, 3a)¹¹.
128 However, it is important to note that while these effects were substantial, they were neither large
129 compared to natural variability in biomass nor repeated across other previously unreported
130 MHWs. Other intense MHWs had little discernible effect on total biomass, such as the 42 °C-
131 days MHW preceding the 2008 North Sea survey that recorded only a 6% biomass decline (Fig.
132 2a). Some of the largest biomass changes occurred in non-MHW years, such as the 97% increase
133 in biomass in the North Sea in 2011, or the 77% biomass decline in the Southeast US in 1996.¹⁸

134 In addition, we observed that the most extreme biomass changes were often reversed in
135 subsequent years. For example, the southern Gulf of St. Lawrence survey hauls caught an
136 average of 4 metric tons of fish per km² in 2011, a non-MHW year; 13 metric tons per km² in

137 2012 following 36 °C-days MHW; and 4 metric tons per km² in 2013 following a MHW with 0.4
138 °C-days of cumulative intensity (Fig. 2a). The peak in biomass in 2012 was driven by Atlantic
139 herring (*Clupea harengus*) and likely reflects a combination of survey variability and a true peak
140 in population size of the fall Atlantic herring stock in the region¹⁹.

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

150 The ecosystems we studied have distinct climates, species assemblages, and histories of
151 anthropogenic pressures²⁰, and might respond at different rates and in different directions to
152 environmental perturbation.²¹ More broadly, pulse disturbances and other exogenous drivers
153 (including heatwaves) are often expected to increase variance in the biomass of populations and
154 communities²². However, we find no statistically significant relationship between the cumulative
155 intensity of a MHW and biomass change of these demersal fish assemblages in any individual
156 region (Extended Data Fig. 1, Supp. Tab. 3). Across all surveys, variability—measured as the
157 absolute value of the year-over-year biomass log ratios—did not increase with MHW cumulative
158 intensity (linear regression, $R^2 = 0.00$, $p = 0.24$; Fig. 2b, Supp. Tab. 4). Instead, we find that
159 variability in biomass change from one year to the next is similarly high with or without MHWs

160 (0.22 ± 0.248 and 0.19 ± 0.214, respectively; medians and standard deviations of absolute log
161 ratios) and that these absolute log ratios of biomass are not significantly different ($p = 0.24$, $t =$
162 1.17, $df = 245$; two-sided t-test; Fig. 2b).

163 Accounting for latitude, depth, temporal lags, autoregression in the biomass time-series,
164 fisheries catch, and species traits (feeding mode, trophic level, and habitat) also did not reveal
165 any meaningful effect sizes of MHWs on biomass (Supp. Tab. 6-10, Extended Data Fig. 6-7).
166 Our results were also robust to the metric used (cumulative intensity, duration, intensity, or
167 degree heating days) to characterize MHWs, how cumulative intensity was scaled, and to
168 whether SBT data were detrended (Extended Data Fig. 2, Supp. Tab. 5). Because SBT data was
169 only available from 1993 onward, we also analyzed a longer time-series of sea surface
170 temperature (SST) that began in 1982 and thus could be paired additional fish surveys. The SST
171 analysis included 100,877 hauls comprising 26,886,245 discrete taxon observations, and yielded
172 results that were qualitatively similar to the SBT results described in the main text (Extended
173 Data Fig. 2b). Because deleterious heatwave effects have often been recorded in summer¹, we
174 also tested for an effect of summer-only MHWs on biomass (Extended Data Fig. 2g), finding a
175 weak positive effect (i.e., greater biomass following more intense MHWs; linear regression, $R^2 =$
176 0.02, $p = 0.02$). While interpreting this result cautiously given the high leverage of a few data
177 points, this result is consistent with the 2012 Northwest Atlantic MHW that occurred in summer
178 and was associated with an increase in biomass in numerous fisheries¹¹.

179 Individual MHWs may lead to rapid ecological turnover by causing cold-affiliated
180 species to decline or go extinct (“deborealization”) and/or by causing warm-affiliated species to
181 spread or increase (“tropicalization”)^{23–25}. We tested whether tropicalization or deborealization
182 are general effects of MHWs by calculating the Community Temperature Index (CTI) for each

183 survey in each year and comparing CTI change to MHW occurrence and cumulative intensity
184 (Methods). CTI is an aggregate thermal niche index for the entire community calculated as the
185 biomass-weighted mean of single-species' realized thermal niches²⁶.

186 Other studies show that CTI has increased in North American fish communities in recent
187 decades, concomitant with ocean warming.²⁵ To explore whether MHWs induce CTI increases,
188 we first focused on the 2014-2016 Northeast Pacific MHW, nicknamed “The Blob”—one of the
189 largest MHWs in our dataset (Fig. 2, 3). Of the four regions in the Northeast Pacific for which
190 we had data, the Gulf of Alaska exhibited the most pronounced CTI increase after the 2014-2016
191 MHW—from 7.25 °C in 2013 to 7.39 °C in 2015 and 7.50 °C in 2017. We also found a CTI
192 increase in the West Coast USA in 2015 following an 8 °C-days SBT MHW (CTI change 0.11
193 °C), consistent with findings that warm-affiliated subtidal fishes increased in Southern California
194 that year²⁷. However, CTI in the Eastern Bering Sea decreased by 0.22 °C from 2015 to 2017. In
195 British Columbia, we measured CTI values of 8.34 °C in 2013, 8.10 °C in 2015, and 8.31 °C in
196 2017 (Fig. 3b).

197 Our analysis found no evidence for systematic tropicalization or deborealization in
198 marine fish communities across all 18 surveys and 369 survey-years in response to MHWs (Fig.
199 4). Year-over-year CTI change in communities that did not experience MHWs was not
200 significantly different from those that did (0.024 ± 0.996 and 0.007 ± 0.983 °C, respectively;
201 means and standard deviations; $p = 0.87$, $t = 0.16$, $df = 280$; two-sided t-test; Fig. 4b). Further,
202 there was no relationship between MHW cumulative intensity and CTI change ($R^2 = 0.00$; $p =$
203 0.33 ; linear regression; Supp. Tab. 11).

204 Marine heatwaves may restructure ecological communities in other ways beyond
205 tropicalization and deborealization²⁸. Less predictable changes in species identity and underlying

206 community structure could also emerge despite consistent biomass²⁹. We tested for changes in
207 community composition by calculating dissimilarity over the time-series using occurrence data
208 (i.e., species presence-absence) as well as biomass data. Each of these dissimilarity indices is
209 calculated from one year to the next using two components—one measure of how much species
210 are substituted for one another and one measure of how much each community is a subset of the
211 other³⁰ (see Methods). A high dissimilarity value between two years may be driven by a
212 transition away from the baseline community structure as a result of disturbance, which has been
213 observed in marine systems in response to climate change²⁹.

214 In some instances, fish communities exhibited high dissimilarity from the previous year
215 following a MHW, such as in the Eastern Bering Sea and the West Coast US during the 2014-
216 2016 MHW (Fig. 3c). However, this was not a general effect. We found that community
217 dissimilarity measured between consecutive years was not, on average, significantly different
218 whether or not a MHW occurred when measured with occurrence-based substitution ($p = 0.12$, t
219 $= 1.57$), biomass-weighted substitution ($p = 0.99$, $t = -0.02$), or biomass-weighted subset ($p =$
220 0.32 , $t = 1.00$; all two-sided t-tests; Extended Data Fig. 8). The one statistically significant
221 relationship suggested that the subset component of occurrence-based dissimilarity was smaller
222 after MHW years than after non-MHW years ($p = 0.01$, $t = -2.52$, two-sided t-test; Extended
223 Data Fig. 8b), the opposite of the hypothesized effect. This observed community stability in the
224 face of MHWs could indicate that climate refugia, such as depth refugia or other thermal refugia,
225 provide safe havens for species during extreme events.³¹ Further, changes in community
226 structure at the local scale may not be reflected at the regional scale of our analysis.

227 This array of results suggests that the regional impacts of MHWs on fish communities are
228 highly idiosyncratic, with dramatic effects in single cases but not in general. In particular, the

229 effects of MHWs do not yet exceed natural variability in these ecosystems, or the variability due
230 to the sampling process. These results also highlight the need to further explore context-
231 dependent responses³². Species and spatial portfolio effects^{33,34} as well as spatial and temporal
232 storage effects³⁵ may explain individualistic responses to extreme events that could buffer many
233 ecosystems from MHWs. Range shifts and mortality and fecundity rates may vary with
234 latitude,²⁵ although we did not find a latitude effect in our analysis (Supp. Tab. 8). Interspecific
235 variation in the timing, magnitude, and direction of MHW response may also be important³⁶. For
236 example, population dynamics of abundant species in response to the environment and fishing
237 drive some of the biomass changes we observed (Extended Data Fig. 10). Ecological responses
238 to warming may also be mediated by direct and indirect effects of other human impacts on the
239 oceans, such as fishing, fisheries management, and changing primary productivity³.

240 To verify that our dataset had sufficient statistical power, we developed a series of power
241 analyses. First, we estimated that our dataset (n = 369 survey-years paired with SBT data) had
242 the power to reveal a consistent MHW-induced regional fish biomass decline of 9% or greater
243 (Extended Data Fig. 9c). Using the longer time-series of 441 survey-years that we paired with
244 SST data had the power to detect a biomass decline of 8% or greater (Extended Data Fig. 9d).
245 Such an effect did not emerge from the results of this study, suggesting that any MHW effects
246 are smaller than this. We note that even decline in fish biomass of 8-9% or less, if permanent and
247 sustained over time, would likely have substantial deleterious consequences for marine fisheries
248 and social-ecological systems³. One model simulation of marine fishes experiencing MHWs
249 under the high emission, no mitigation future climate scenario (RCP 8.5) projected that the
250 negatively affected stocks (approximately $\frac{3}{4}$ of total stocks) would exhibit an average biomass
251 decline of 6%³. Approximately 600 survey-years would be required to detect an average biomass

252 decline of 6% (Extended Data Fig. 9a, b). Put another way, MHWs may have had effects on
253 demersal fish communities in recent decades, but if so, those effects were small.

254 In addition, there are alternative explanations to consider. MHWs may affect survey
255 methods themselves: a study on several coral trout species found that they were more
256 catchable—i.e., encountered by fishing gear at higher rates—in warmer temperatures³⁷.
257 However, if this response was widespread among the species we studied, it would cause an
258 increase in biomass following MHWs that we did not observe. The availability of fishes to
259 surveys can also be influenced by range shifts, possibly induced by MHWs³⁸. However, our
260 analysis accounted for this by testing for tropicalization or deborealization within fixed spatial
261 areas (the survey regions). Because biomass trends may be strongly structured by commercial
262 fisheries catches, we fitted models predicting biomass change with fisheries catch as well as
263 MHW cumulative intensity, with no significant results (Supp. Tab. 10). While the choice of
264 metric to quantify MHWs^{6,15,38,39} and fish community responses^{11,37} may influence results, our
265 results here were not sensitive to these decisions. The pattern in Fig. 2 emerged regardless of
266 whether we analyzed fish biomass (i.e., weights) or fish abundance (i.e., counts) or whether
267 taxon-level records were summarized as means or medians (Extended Data Fig. 5). The spatial
268 scale of our study was determined by the surveys, which themselves are designed to capture
269 distinct biogeographical and political regions and/or to follow fisheries management criteria⁴⁰
270 (see Methods). However, it is possible that fish community responses to MHWs vary with the
271 spatial scale at which they are measured, as has been found with other metrics of biodiversity.⁴¹

272 Ecological effects of climate change result from the interaction of long-term climatic
273 change combined with short-term extreme events such as heatwaves⁵, which have been projected
274 to cause widespread ecological devastation on land and in the sea (although see ^{36,42}). To date,

275 this expectation has largely been based on case studies that select one or a few prominent species
276 and ecosystems with remarkable MHW responses, rather than the comprehensive approach that
277 we used. Analyses that focus on particular species that were historically prevalent in a region
278 may be predisposed to find a biomass decline following a MHW, possibly due to unrelated time-
279 series dynamics (e.g., mean reversion or density dependence) or because species that were
280 dominant in historical climates might not be as successful after a MHW. In addition, case study
281 approaches tend to select and emphasize extreme responses⁴³—although several regional studies
282 focused on a single MHW event have also found no net loss of abundance or biomass in coral- or
283 kelp forest-associated fishes^{27,44}. Further empirical research that builds on the present study and
284 extends beyond individual case studies is needed to interpret, contextualize, and predict severe
285 MHW effects.² Building partnerships to leverage existing non-public datasets from the southern
286 hemisphere and other under-studied parts of the global ocean will also be helpful in
287 understanding how ecological context influences MHW responses⁴⁰.

288 Our findings highlight the need to understand divergent responses to extreme events.
289 Single-species responses may be mediated by thermal tolerances, but we did not find evidence
290 that cold-affiliated species decline or that warm-affiliated species increase following MHWs
291 (Fig. 4a). Other studies find that species' responses vary from one extreme event to another⁴².
292 Portfolio and storage effects may explain why ecosystem-level MHW effects are rare, but they
293 do not reveal what caused certain MHWs to have deleterious ecological effects. The community
294 stability we observed in the face of MHWs could indicate that climate refugia, such as depth or
295 other thermal refugia, provide safe havens for species during extreme events.³¹ Cumulative
296 impacts of MHWs and other stressors such as harmful algal blooms¹³ or low-productivity events⁹
297 could play a role. Perhaps very extreme MHWs in the future will cross a tipping point beyond

308 which adverse ecological effects occur, but we did not see such a tipping point in the recent
309 historical record. Other fields (e.g., coral reef ecology) have identified such thresholds, though
310 the generality of thresholds across ecological systems remains unclear.⁴⁵ Gaining mechanistic
311 insight into why only some MHWs have deleterious effects, and on only some species, is
312 necessary for any future efforts to identify an effect threshold or forecast MHW impacts and
313 should be a research priority for the field. Additionally, ecosystem responses to extreme “pulse”
314 events such as MHWs can shape impacts of more gradual “press” trends; the complex
315 interactions between these climate change effects warrant future research.⁵

316 Understanding MHW impacts on entire ocean ecosystems is particularly crucial in the
317 context of accelerating global change and efforts to advance towards ecosystem-based
318 management that considers the many links between species and with their environment⁴⁶. MHW
319 occurrences are projected to emerge above their natural variability within this century in many
320 regions⁴⁷. Future research will be needed to determine the extent to which fish community
321 impacts of MHWs will grow as MHWs intensify, or whether portfolio and other ecological
322 effects can buffer ecosystems from MHW impacts. Marine life is more vulnerable to warming
323 than terrestrial life, because marine organisms tend to live close to their thermal limits and fewer
324 thermal refugia exist in the seas⁴⁸. Observed and predicted changes in marine ecosystems in
325 response to global warming formed part of the rationale behind the Paris Climate Agreement to
326 limit the global mean surface temperature increase above industrial levels to 1.5 °C by 2100⁴⁹.
327 As a future that is more than 1.5 °C warmer looks increasingly likely⁵⁰, it is more critical than
328 ever to develop a deeper understanding of what drives ecological responses to extreme climate
329 events.

320

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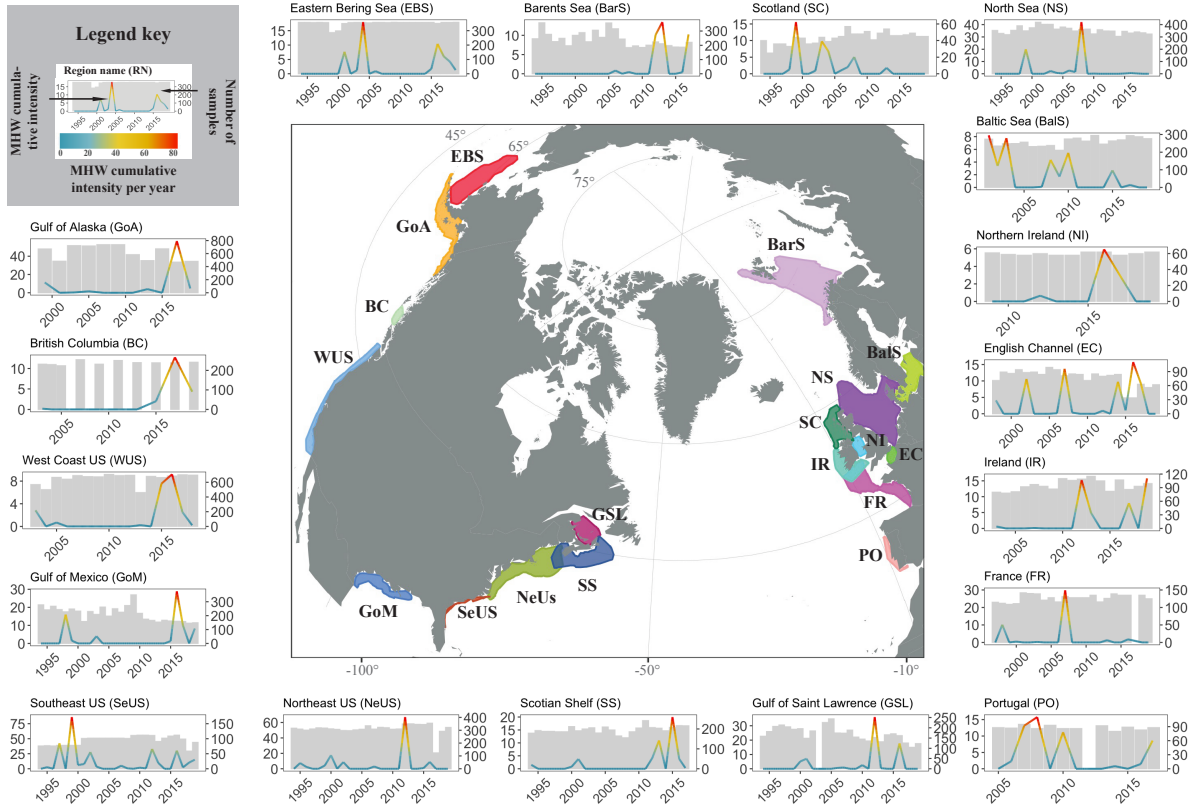
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431

432 **Figures**



433

434 **Fig. 1. Of 18 regions studied from the Atlantic and Pacific Oceans, all experienced marine**

435 **heatwaves during the available scientific fish survey time-series. Highlighted areas on the**

436 **map represent the spatial area surveyed by each trawl survey. Inset plots show the number of**

437 **distinct sampling events (i.e., hauls of the trawl net) every year (grey bars, right y-axis) and the**

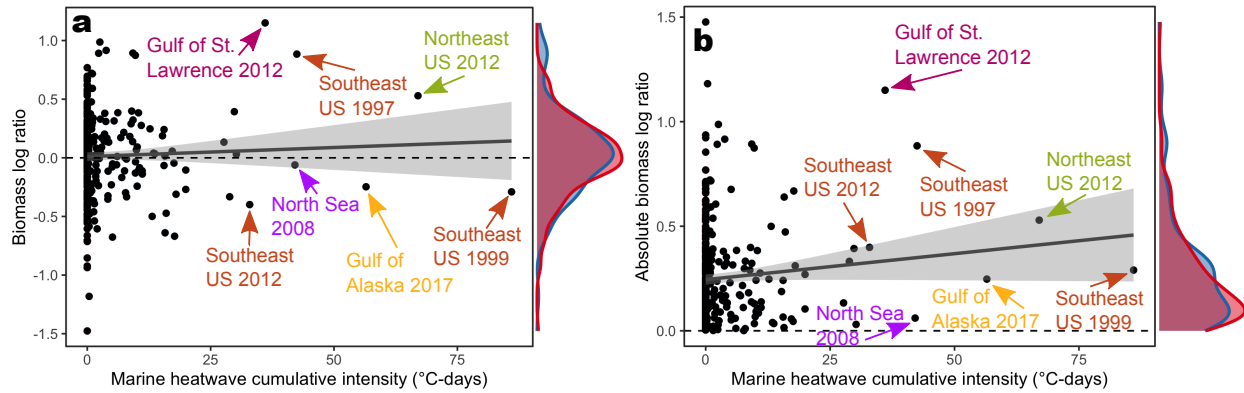
438 **MHW cumulative intensity in °C-days calculated from sea bottom temperature data (lines, left y-**

439 **axis; warmer colors represent greater cumulative intensity). Years correspond to “survey**

440 **reference years”—the twelve months preceding the survey—rather than calendar years, and vary**

441 **among regions (see Methods).**

442



443

444 **Fig. 2. More intense marine heatwaves were not associated with a decline in fish biomass or**

445 **an increase in biomass variability, and biomass was approximately as likely to increase as it**

446 **was to decrease from one year to the next, regardless of whether a marine heatwave**

447 **occurred.** MHW cumulative intensity (°C-days) had no relationship with (a) biomass change

448 (measured as log ratio; linear regression, $R^2 = 0.00$, $p = 0.45$) or (b) absolute biomass change

449 (measured as absolute log ratio; linear regression, $R^2 = 0.01$, $p = 0.07$). The grey shaded area is a

450 95% confidence interval. Density plots along the right-hand y-axes show that biomass changes

451 from one year to the next were the same whether a MHW did (red, $n = 139$) or did not (blue, $n =$

452 230) occur. Points represent (a) log ratios or (b) absolute log ratios of mean biomass in a survey

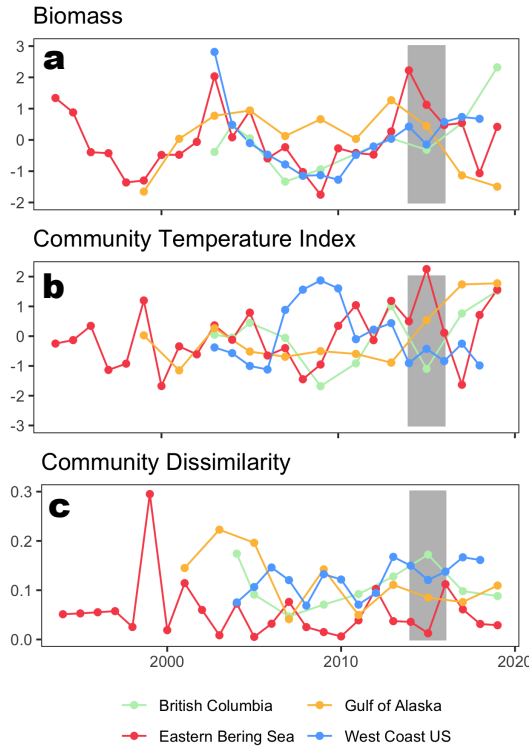
453 from one year to the next ($n = 369$). Surveys following the highest cumulative intensity MHWs

454 are labeled (years correspond to when the survey was conducted). Colors correspond to regions

455 in Fig. 1. Models exploring the relationships in (a) and (b) are reported in Supp. Tab. 2 and 4,

456 respectively.

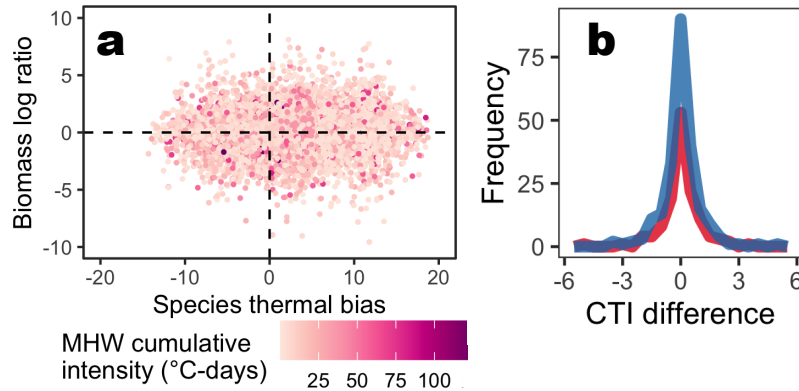
457



458

459 **Fig. 3. Example of divergent responses to a large marine heatwave.** Plots show (a) centered
 460 and scaled biomass and (b) Community Temperature Index (CTI), and (c) change in community
 461 composition over time (the substitution component of Bray-Curtis dissimilarity) between the
 462 previous and given year for four surveys in the Northeast Pacific. Colors correspond to survey
 463 footprints in Fig. 1. Higher values represent more biomass, tropicalization and/or
 464 deborealization, and greater community dissimilarity, respectively. The grey stripe denotes the
 465 2014-2016 Northeast Pacific MHW (“The Blob”).

466



467

468 **Fig. 4. Scientific bottom trawl surveys during the year following marine heatwaves were as**

469 **likely to exhibit tropicalization and/or deborealization as those that did not follow marine**

470 **heatwaves. (a) There was no relationship between a species' thermal bias (its cold or warm**

471 **affinity relative to the assemblage mean, calculated as STI - CTI; see Methods) and its species-**

472 **specific biomass change following a MHW ($n = 13,438$). (b) There was no difference in CTI**

473 **change between surveys in the year following a MHW (red, $n = 139$) versus surveys that did not**

474 **follow a MHW (blue, $n = 230$). Positive CTI values indicate tropicalization and/or**

475 **deborealization. In (a), each point represents a single species that was present in a survey both**

476 **before and after a MHW.**

477

478 **Methods**

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

480 GitHub.

481 **Fish biomass and abundance data.** We collated publicly available datasets from fishery

482 management agencies that use scientific (i.e., fisheries-independent) bottom trawl surveys to

483 monitor marine fish communities⁴⁰. These surveys monitor biogeographically and/or politically

484 distinct areas that are relevant to fisheries management⁴⁰. Their footprints often follow marine

485 ecosystem boundaries (e.g., Large Marine Ecosystems⁵²) and are similar in size to the spatial
486 extents of MHWs³⁹. Although these surveys are conducted by many nations, we used only
487 surveys by agencies that make their raw data publicly available, which facilitates reproducibility
488 of this study. Those agencies were the National Oceanic and Atmospheric Administration
489 (NOAA), Fisheries and Oceans Canada (DFO), the International Council for the Exploration of
490 the Sea (ICES), and the Institute of Marine Research (IMR). This limitation constrained our
491 analysis to the Northeast Pacific, Northwest Atlantic, and the Northeast Atlantic (Supp. Tab. 1).

492 In these surveys, the sampling unit is a single haul, i.e., a sampling event in which a net is
493 towed through the water. We filtered invalid hauls based on reported sample quality, sampling
494 times, and availability of variables required to calculate taxon-level biomass data. Further detail
495 on data cleaning and harmonization in addition to raw data and code can be found in Maureaud
496 et al⁵³. All primary analyses used biomass (weight) data; we conducted a supplementary analysis
497 of the main results using abundance (count) data for the regions for which it was available (all
498 but Northeast US; Extended Data Fig. 5).

499 Datasets were trimmed to standardize the spatial footprint of the survey over time, to
500 match the available temperature datasets (GLORYS began in 1993 and OISST began in 1982;
501 see **Marine heatwave data**), to remove years with very few samples, and to omit samples
502 collected outside of the focal season (3-month interval) of each survey. We used the World
503 Register of Marine Species⁵⁴ to standardize taxonomies, and the “dggridR” R package⁵⁵ to
504 standardize the survey footprints. Across our 18 surveys, we paired 82,322 hauls with GLORYS
505 and 101,376 hauls with OISST. Of the 94% of hauls with an associated depth value, 90%
506 occurred between 18 m and 451 m depth. The depths sampled vary due to each region’s unique
507 bathymetry and each survey’s protocols, but surveys tend to sample similar depths over time: for

508 example, the Southeast US survey samples very shallow inshore areas of just 3 m depth, while
509 the Scotian Shelf and West Coast surveys routinely trawl deeper than 1000 m. We used all taxa
510 for biomass analyses but only the species-level observations for community analyses (see
511 **Species and Community Temperature Indices**).

512 We imputed zeros representing an observed absence in every instance when a species
513 (that was observed at some point in the region) was not recorded in a haul. These absences can
514 be considered true non-detections due to the standardized spatiotemporal design of bottom trawl
515 surveys. We then calculated a mean biomass for each species in every year, and calculated
516 region-wide biomass as the sum of species-level biomass. To assess the sensitivity of our results
517 to the metric used, we also calculated median biomass, mean abundance, and median abundance
518 in the same way (although the Northeast US region did not have abundance data and was thus
519 omitted from the abundance analysis). We did this across the entire survey domain (following
520 the spatial standardization mentioned above), rather than within the “strata” used in some
521 analyses⁵⁶, because not all of the surveys have stratified sampling designs and we wanted to be
522 consistent across all regions.

523 Year-over-year mean biomass change was calculated as a natural log ratio,
524 $\ln\left(\frac{biomass_t}{biomass_{t-1}}\right)$. Log ratios for median biomass, mean abundance, and median abundance were
525 calculated the same way. For straightforward interpretation, we also reported percentage biomass
526 changes in the text, although biomass log ratios were used in all models. For example, a 67%
527 biomass increase means that $biomass_t = 1.67 \times biomass_{t-1}$. A 67% decrease means that $biomass_t$
528 $= (1 - 0.67) \times biomass_{t-1}$.

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

531 August 2010 data was paired with MHW data from August 2009 - July 2010. Because we have
532 no *a priori* information on the season in which MHWs could have the greatest ecological
533 impact—and this may vary by species and life stage—we analyzed MHW effects over a full year
534 (i.e., 12-month interval). Some substantial MHW effects have been reported in summer,⁵⁷ and
535 yet winter heatwaves strongly influence distribution and abundance for species limited by winter
536 survival^{58,59}. Warmer winters are hypothesized to have driven recent ecological changes in the
537 Gulf of Alaska¹². Winter MHWs may also reduce recruitment in habitat-forming seaweeds⁶ and
538 cause metabolic stress to coral reef fishes⁶⁰. Spawners and embryos have narrower temperature
539 tolerance ranges than non-spawning adults⁶¹; a spring heatwave could thus affect the survival or
540 performance of spring-spawning fishes and their embryos. To test the sensitivity of our results to
541 this choice, we also explored the effects of only summer anomalies on biomass change
542 (Extended Data Fig. 2g).

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

547 **Marine heatwave data.** We paired the demersal bottom trawl data with MHWs
548 calculated with sea bottom temperature (SBT) data from the Copernicus 1/12° (about 8 km)
549 global ocean reanalysis, the Global Ocean Reanalysis and Simulations (GLORYS12).⁶² The
550 reanalysis dataset is generated with the Nucleus for European Modelling of the Ocean (NEMO)
551 ocean model forced by the ERA-Interim atmospheric reanalysis. The model assimilates satellite
552 altimetry, satellite SST, sea ice concentrations, and in-situ profiles of salinity and temperature.
553 We chose GLORYS12 for our analyses because it provided daily estimates of temperature

554 anomalies at depth at a fine spatial resolution, and it reproduces nearshore bottom temperatures
555 and recent MHWs with enhanced fidelity compared to other products.^{63,64} Being highly
556 dependent on ocean observations for data assimilation, GLORYS12 only began in 1993. We
557 used the 1993-2019 period for our analysis.

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

568 Following standard MHW definition (e.g. ^{9,47}), both SBT and SST anomalies were
569 calculated within (not across) spatial units—here, the survey regions. This approach defined
570 anomalies relative to historical conditions in a region, which are likely reflective of the
571 environments to which organisms are adapted. In other words, each MHW we identified
572 represented a departure from whatever climate the marine organisms in that region typically
573 experienced. Because our study regions varied substantially in seasonality, natural variability,
574 and exposure to oceanographic phenomena, calculating anomalies from cross-region pooled SBT
575 and SST values would identify only the most globally extreme events as MHWs and would omit

576 the many events in which temperatures were anomalously high for species within a region but
577 not necessarily high for the global oceans.

578 For both SBT and SST, we defined a MHW as a period of at least five continuous days
579 during which the SBT (or SST) averaged for each survey area was larger than a seasonally
580 varying threshold given by the 95th percentile of the survey-area averaged SBT (or SST)
581 anomalies (relative to the mean seasonal cycle that is calculated for each calendar day
582 individually). This is a common approach for defining MHWs, although some authors use the
583 90th percentile⁶ or the 99th³⁹ instead of the 95th. Under our definition, MHWs may occur
584 throughout the year and at all locations.

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

594 We then calculated different MHW metrics: MHW cumulative intensity (the anomaly
595 above the 95th percentile threshold summed over the duration of the event in °C-days, duration
596 (number of days), and mean intensity (the average anomaly above the 95th percentile threshold
597 over the course of the MHW in °C). We chose MHW cumulative intensity for the main analysis
598 because it encompassed elements of both intensity and duration (i.e., cumulative intensity is

599 higher for longer or for more intense MHWs)—but our biomass results did not change if we used
600 different metrics (Extended Data Fig. 2d, e). Because under our definition all MHWs exceeded
601 95% of temperature anomalies in the region, even MHWs with relatively low cumulative
602 intensities represented extreme events. Unless otherwise specified, models in the main text and
603 Supplement used MHW cumulative intensity centered and scaled within regions, although our
604 results were not sensitive to whether we scaled and centered within *vs* across regions (Supp. Tab.
605 5).

606 In coral reef ecology, a threshold for ecological damage (i.e., coral bleaching) has been
607 identified using degree heating days—the number of days that exceed average temperatures for
608 the hottest summer month by at least 1 °C.¹⁶ We also processed the non-detrended GLORYS
609 data using this method for each region (Extended Data Fig. 2f). One data product, Coral Reef
610 Watch, calculates the average temperatures for the hottest summer month during a baseline
611 period of 1985-1990 plus 1993.¹⁶ Because GLORYS began in 1993, we used the four-year
612 interval 1993-1996 as the baseline to calculate the average temperatures for the hottest summer
613 month.

614 The five-day threshold for a MHW used in the main analysis was based on empirical
615 analyses demonstrating that contemporary heatwaves last on average 4.6 days⁶⁸, and is widely
616 used in the literature⁶, although we note that alternate methods exist to define and measure
617 MHWs^{15,39,69}. We also assessed whether MHW responses would emerge from classifying any
618 daily anomaly (without the five-day cutoff) as a MHW. We found no relationship (Extended
619 Data Fig. 2a).

620 **Species and Community Temperature Indices.** The Species Temperature Index (STI)
621 and Community Temperature Index (CTI) are measures of thermal affinity at the species and

622 community level, respectively.⁷⁰ We quantified STI as the median sea surface temperatures
623 found throughout a species' modeled range from the publicly available STI dataset in Burrows et
624 al.²⁶. STI values were available for 844 of our 1772 focal taxa, comprising 82% of total biomass
625 in our survey dataset. CTI was calculated in each region and year as the biomass-weighted mean
626 of all STIs, and we used the difference in CTI from one year to the next as our metric of CTI
627 change. We also quantified the thermal bias of each species relative to the community (STI -
628 CTI)⁷⁰.

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

641 **Additional predictors.** We conducted supplementary analyses to explore the role of a
642 number of additional predictors of fish biomass change. In addition to the geographical shifts
643 that may lead to changes in biomass and community composition in a fixed area, marine fishes
644 may shift deeper in response to warming^{72,73}. We tested for this effect by calculating depth log

645 ratios that described whether assemblages had shifted deeper or shallower from one survey to the
646 next. Depth log ratio was quantified by: 1. Taking an average of depths at which a species was
647 found in each survey and year, using the depth observations for each haul, and weighted by
648 biomass in the haul; 2. Taking a biomass-weighted mean of all species-level depth values for the
649 entire survey; 3. Calculating the log ratio of the survey-level, biomass-weighted depth values
650 from one year to the next. We found no relationship between MHW cumulative intensity and
651 depth log ratio and no difference between depth changes that did and did not follow a MHW
652 (Extended Data Fig. 6, Supp. Tab. 9).

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

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

664 Some studies find that marine communities respond rapidly to environmental change⁷⁶.
665 Others suggest that ecological responses may lag disturbances by years⁷⁷. We explored whether
666 MHW data from further into the past—up to five years before each trawl survey—predicted
667 biomass responses. Analogous to our findings for MHWs that occur up to 12 months before each

668 survey reported in the main text, we found no evidence that biomass change is associated
669 generally with MHW cumulative intensity from prior years (Supp. Tab. 6).

670 Because fishing, through increased mortality, can influence temporal biomass change, we
671 also analyzed the effects of catch on biomass change. We extracted a historical time-series of
672 reconstructed catch values from the *Sea Around Us* database⁷⁸ by Marine Ecoregions (MEs).⁷⁹
673 The *Sea Around Us* reconstructed catches are spatially allocated to half degree ocean cells,⁸⁰
674 which permits catch data to be assigned to spatial entities such as the 232 MEs identified by
675 Spalding et al.⁷⁹ We then paired our survey footprints with the most-overlapping ME. In most
676 cases, the MEs and survey footprints were similar. For two large surveys (the West Coast and the
677 Northeast US) we summed catch data across two adjacent MEs. Two small surveys (France and
678 the English Channel) did not correspond well to the MEs and were omitted from the fishing
679 analysis. Because catch data are recorded by calendar year, and the surveys often occur midyear,
680 we fitted models comparing biomass change in a given year to the mean catch level in the past
681 three calendar years (Supp. Tab. 10).

682 **Statistical methods.** We tested for the effects of MHWs using linear models, generalized
683 linear models, or generalized additive models for continuous variables. Models and
684 transformation of variables are described in Supp. Tab. 2-11. Generalized linear models were
685 fitted with the R package “glmmTMB”⁸¹ and generalized additive models with the R package
686 “mgcv”⁸². When comparing MHW *versus* non-MHW effects we used two-sided t-tests. While
687 not all of the datasets were normally distributed, the t-test is insensitive to skewness for large
688 sample sizes such as ours, whereas non-parametric alternatives are better suited to smaller
689 sample sizes⁸³.

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

$$695 \quad \ln(B_t) = \alpha + \rho \times \ln(B_{t-1}) + \gamma \times MHW_t + \sigma'$$

696 where B represents biomass in year t , MHW is a binary variable for MHW presence/absence, and
697 γ represents the "true" MHW effect that we varied to explore power. This simulation also
698 included an error term σ' calculated as a random draw from a normal distribution with mean 0
699 and standard deviation σ . We (1) varied the number of years the simulation was run (assuming
700 that each of the 18 surveys was conducted for that number of years) from 10 to 40 in 1-year steps
701 and 50-200 in 10-year steps with a fixed value of $\gamma = \ln(0.94)$, corresponding to the 6% loss of
702 biomass predicted by Cheung et al.³; and (2) varied γ to represent biomass losses ranging from
703 1% to 30% (in 1% increments up to 10%, and then in 5% increments) given the actual number of
704 years of data we have ($n = 369$ for GLORYS and $n = 441$ for OISST). Note that the mean survey
705 duration in our analysis was 20-25 years depending on the paired temperature dataset used. For
706 all these scenarios, simulations were run for each individual survey, converted into log ratio units
707 (as used in the main text), scaled and centered within regions, and pooled across regions. Each
708 set of simulations was run 1000 times for each condition (survey and either number of years or
709 γ).

710 With these four simulated datasets—a true MHW effect on biomass of -6% and variable
711 numbers of years, or a fixed number of years from the real dataset and a variable effect of MHW
712 on biomass, each for OISST and GLORYS—we conducted the same statistical tests as we did in

713 the main text to test for an effect. For every iteration of the simulation, we split the biomass log
714 ratio data into MHW and non-MHW years and compared the two with a two-sided t-test. We
715 then calculated what proportion of those tests were significant ($p = 0.05$). These results are
716 shown in Extended Data Fig. 9.

717

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787

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802

803 **Author contributions**

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

808

809 **Competing interest declaration**

810 The authors declare no competing interests.

811

812 **Additional information**

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

816

817 **Code availability statement**

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

821

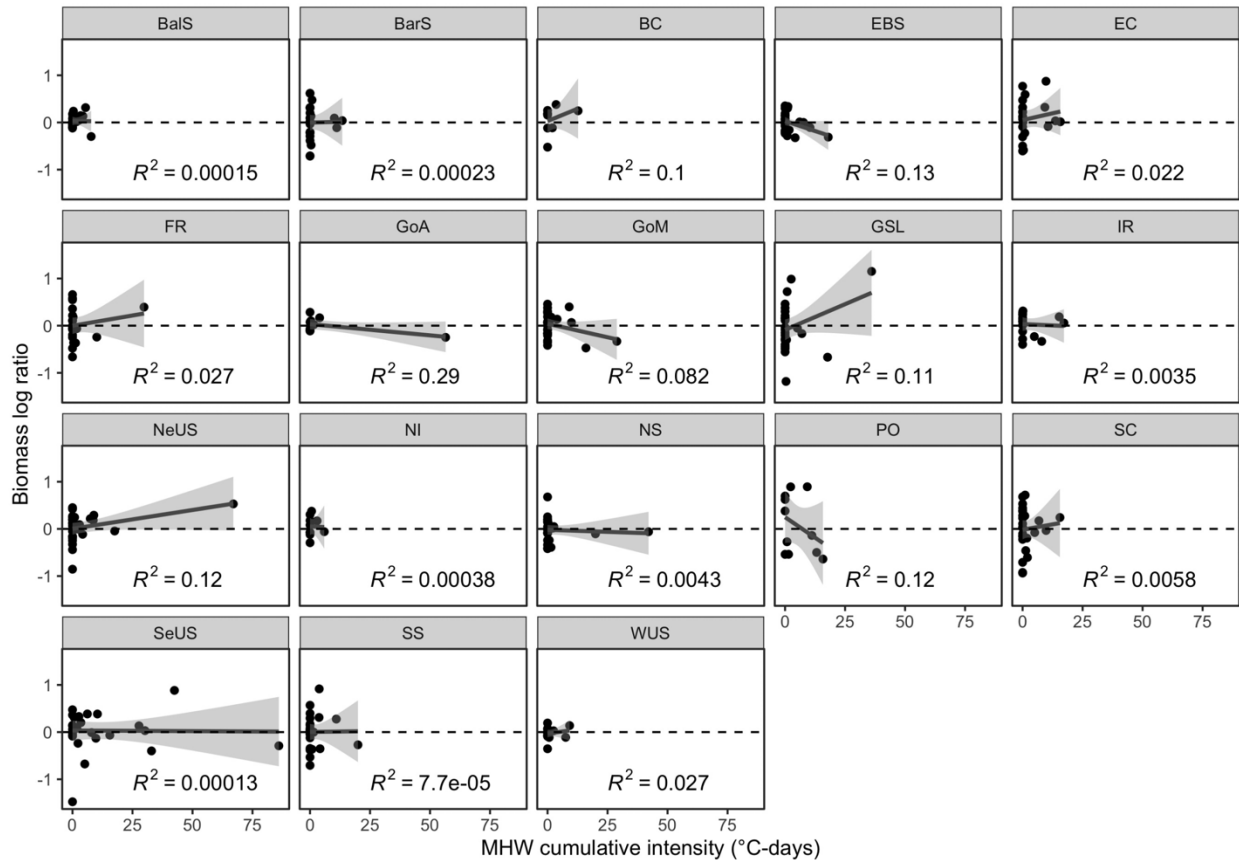
822 **Data availability statement**

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

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825 **Extended data figures**

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827

828 **Extended Data Fig. 1. Alternate version of Fig. 2 from the main text, showing results by**

829 **region.** MHWs were calculated from the detrended GLORYS sea bottom temperature data with

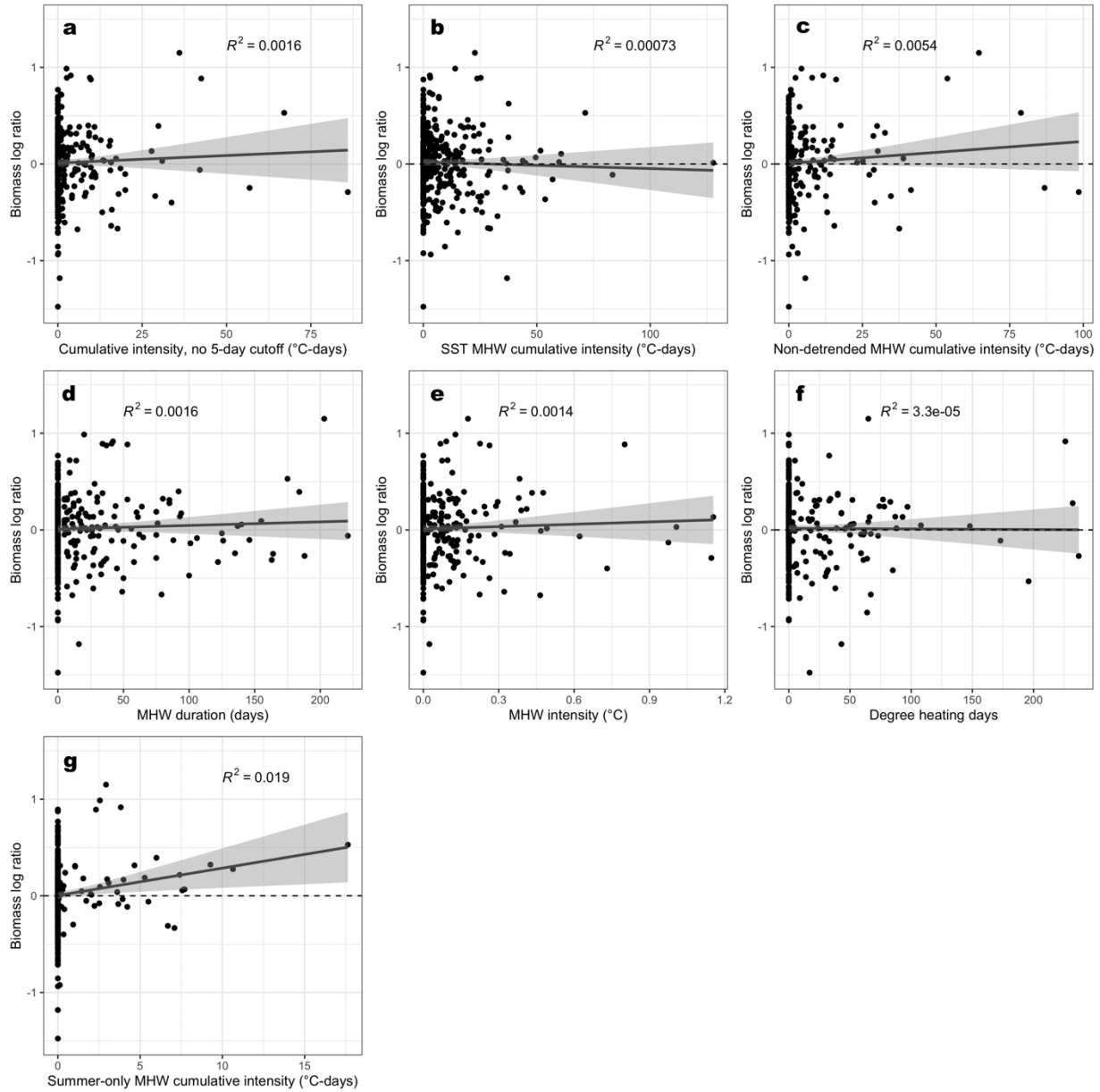
830 a five-day minimum duration threshold for MHWs, as used in the main text. Points represent log

831 ratios of mean biomass in a survey from one year to the next. The fitted lines are linear

832 regressions. The shaded areas are 95% confidence intervals. Survey names and sample sizes per

833 survey are listed in Supp. Tab. 1.

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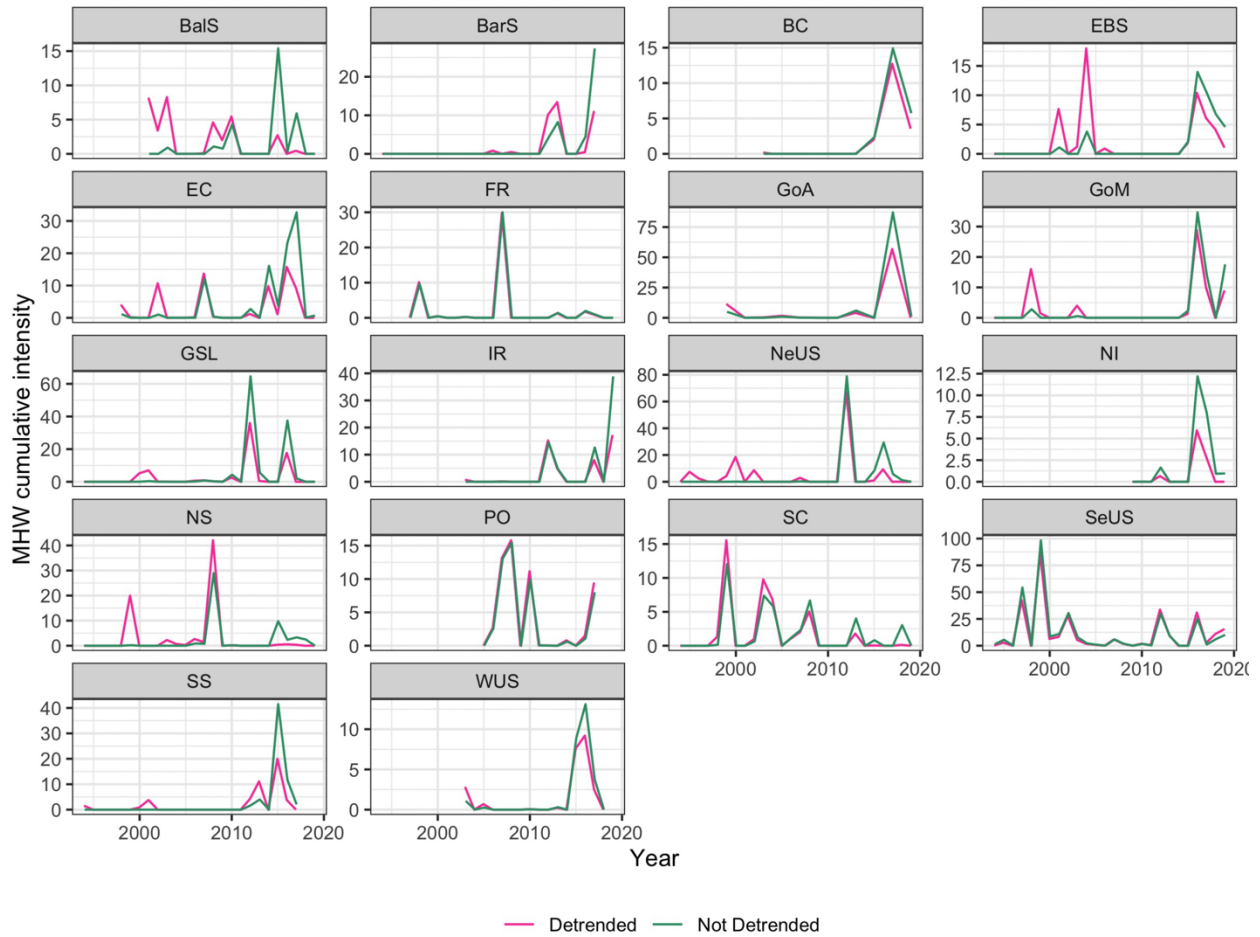
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840

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

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

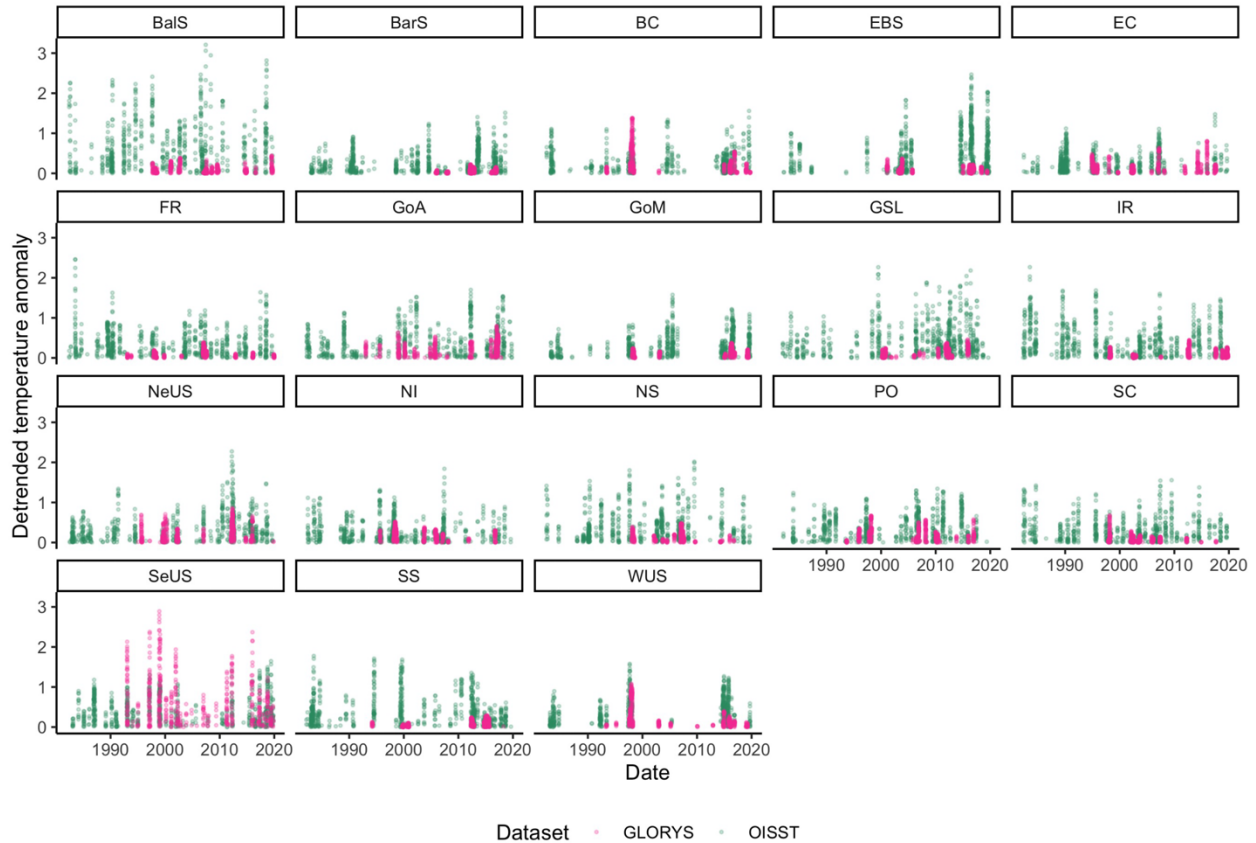
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845 **Extended Data Fig. 3. Marine heatwave cumulative intensity (total anomaly in °C-days) in**
846 **each survey region with and without detrending the temperature data to remove the signal**
847 **of secular warming.** The main text results are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

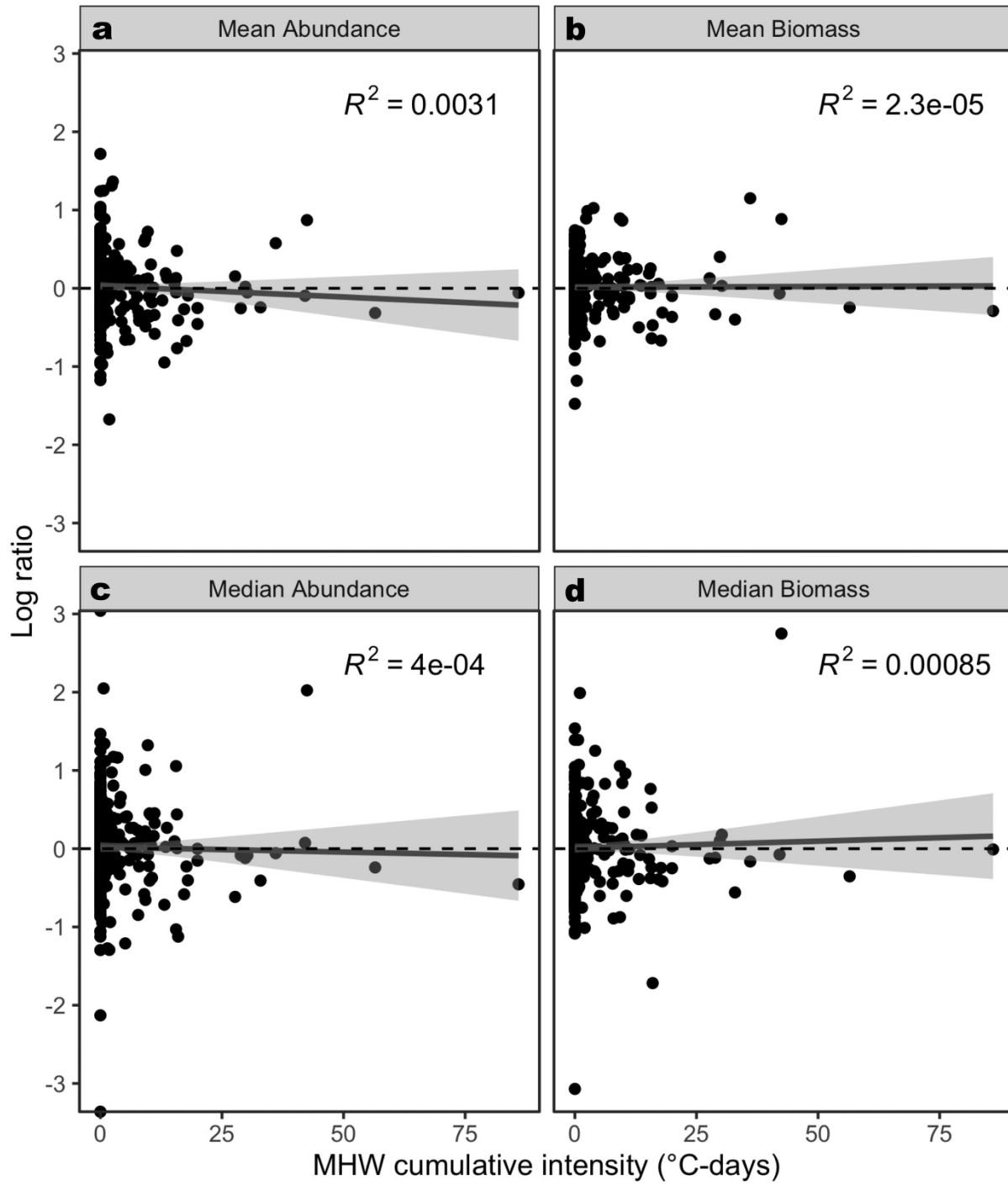
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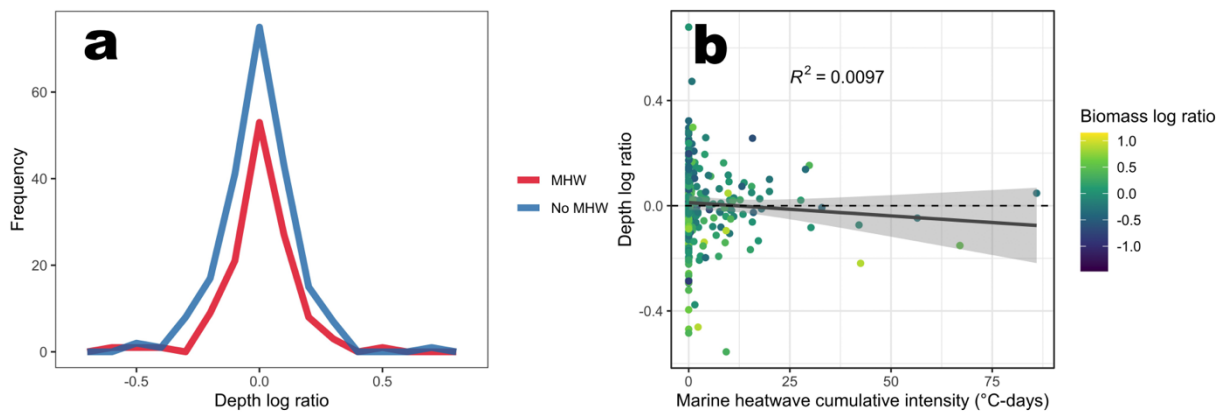
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852 **Extended Data Fig. 4. Daily 95th percentile anomalies in the two marine heatwave data**
 853 **sources: sea surface temperature from OISST and sea bottom temperature from GLORYS**
 854 **(both detrended).** To simplify comparison we plot all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

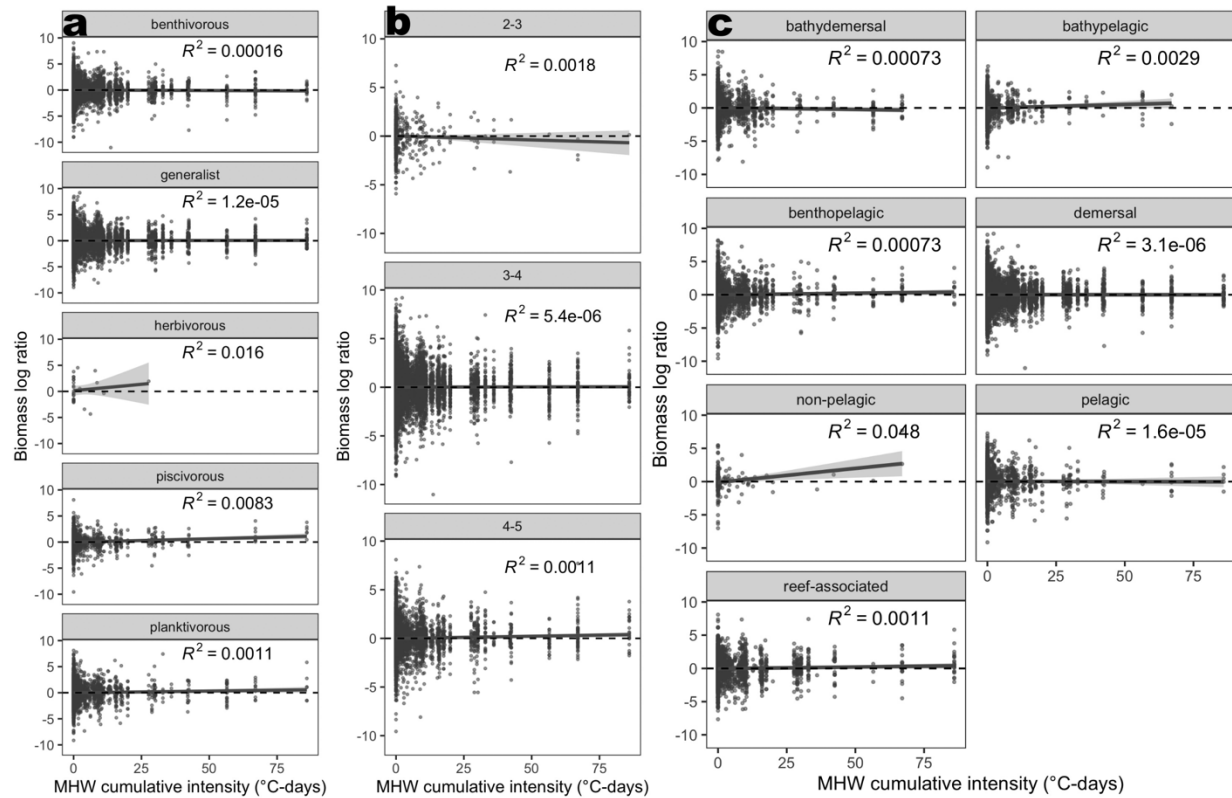
857



859 **Extended Data Fig. 5. Results are consistent across different metrics of the fish**
860 **community.** We calculated mean abundance (a), mean biomass (b, used in the main text),
861 median abundance (c), and median biomass (d). MHWs were calculated from the detrended
862 GLORYS sea bottom temperature data with a five-day minimum duration threshold for MHWs,
863 as used in the main text. Points represent log ratios of each metric in a survey from one year to
864 the next ($n = 343$). The fitted lines are linear regressions. The shaded areas are 95% confidence
865 intervals. The Northeast US survey was omitted because it did not have abundance data
866 recorded.
867



868
869 **Extended Data Fig. 6. Depth changes in the fish assemblage in response to marine**
870 **heatwaves.** Fish assemblage depth change (log ratio) was not predicted by (a) the presence or
871 absence of a MHW or (b) MHW cumulative intensity (total anomaly in °C-days; $n = 369$).
872 MHWs were calculated from the detrended GLORYS sea bottom temperature data with a five-
873 day minimum duration threshold for MHWs, as used in the main text. The fitted line in (b) is a
874 linear regression and the shaded area is its 95% confidence interval.
875



876

877 **Extended Data Fig. 7. Marine heatwave effect on taxon-specific biomass log ratios grouped**

878 **by traits.** Biomass log ratio and MHW cumulative intensity (total anomaly in °C-days) grouped

879 by (a) feeding mode ($n = 29,628$), (b) trophic level ($n = 29,909$), and (c) habitat preference ($n =$

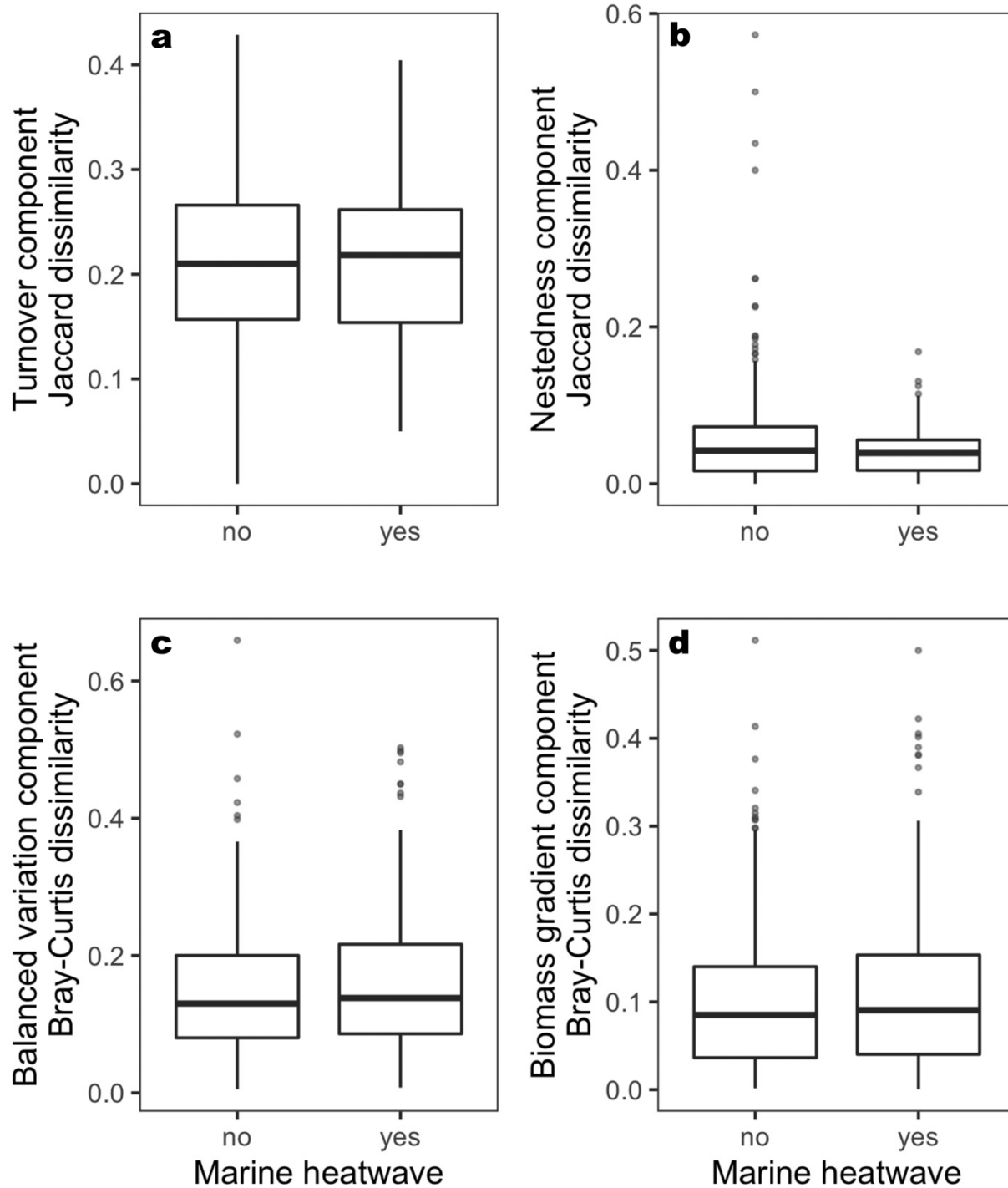
880 29,681) of each taxon. Trait data were extracted from Beukhof et al.⁵¹ (see Methods). MHWs

881 were calculated from the detrended GLORYS sea bottom temperature data with a five-day

882 minimum duration threshold for MHWs, as used in the main text. Fitted lines are linear

883 regressions. Shaded areas are 95% confidence intervals.

884



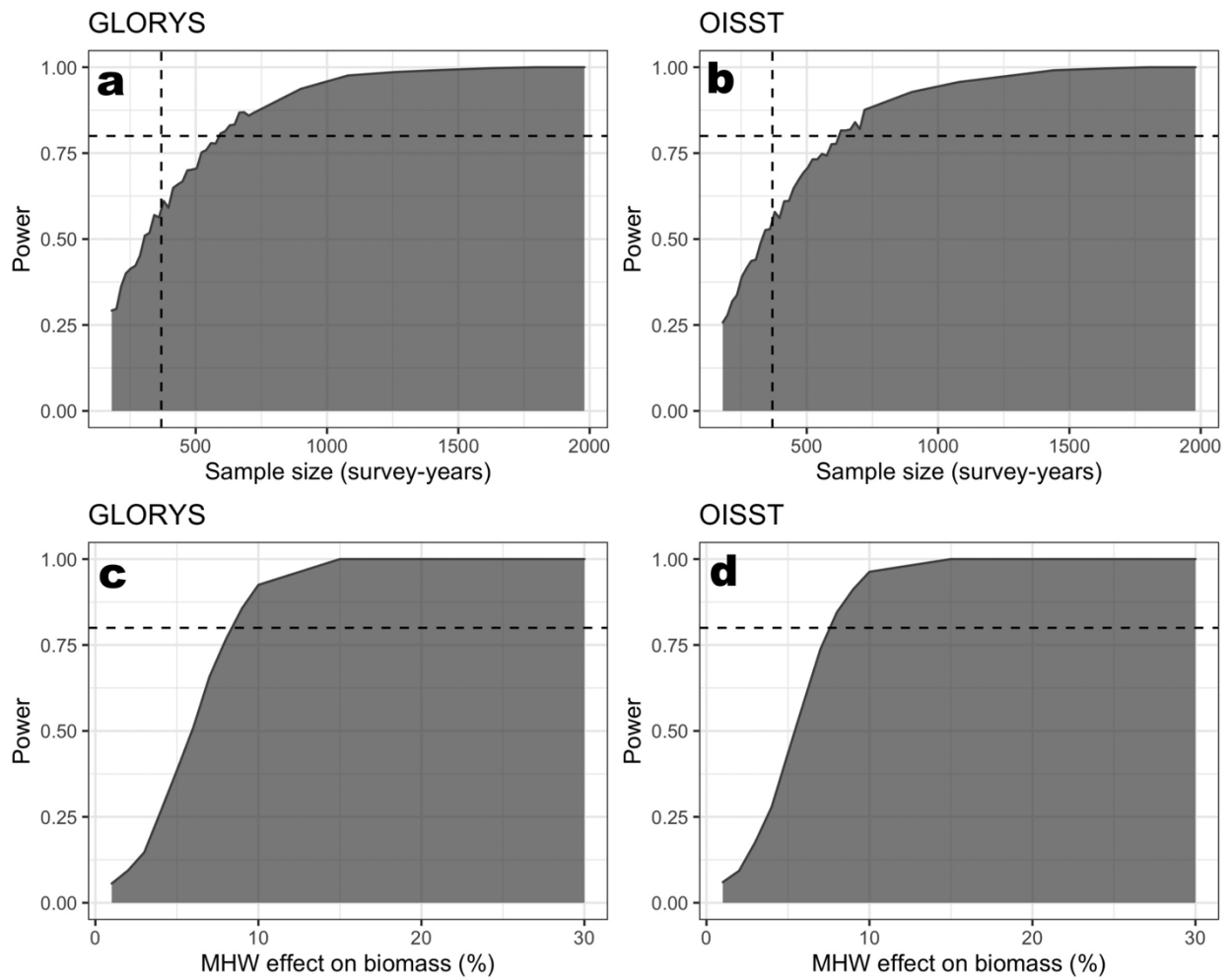
885

886 **Extended Data Fig. 8. The presence or absence of a MHW did not affect temporal**

887 **community dissimilarity.** We measured community dissimilarity as partitioned occurrence-

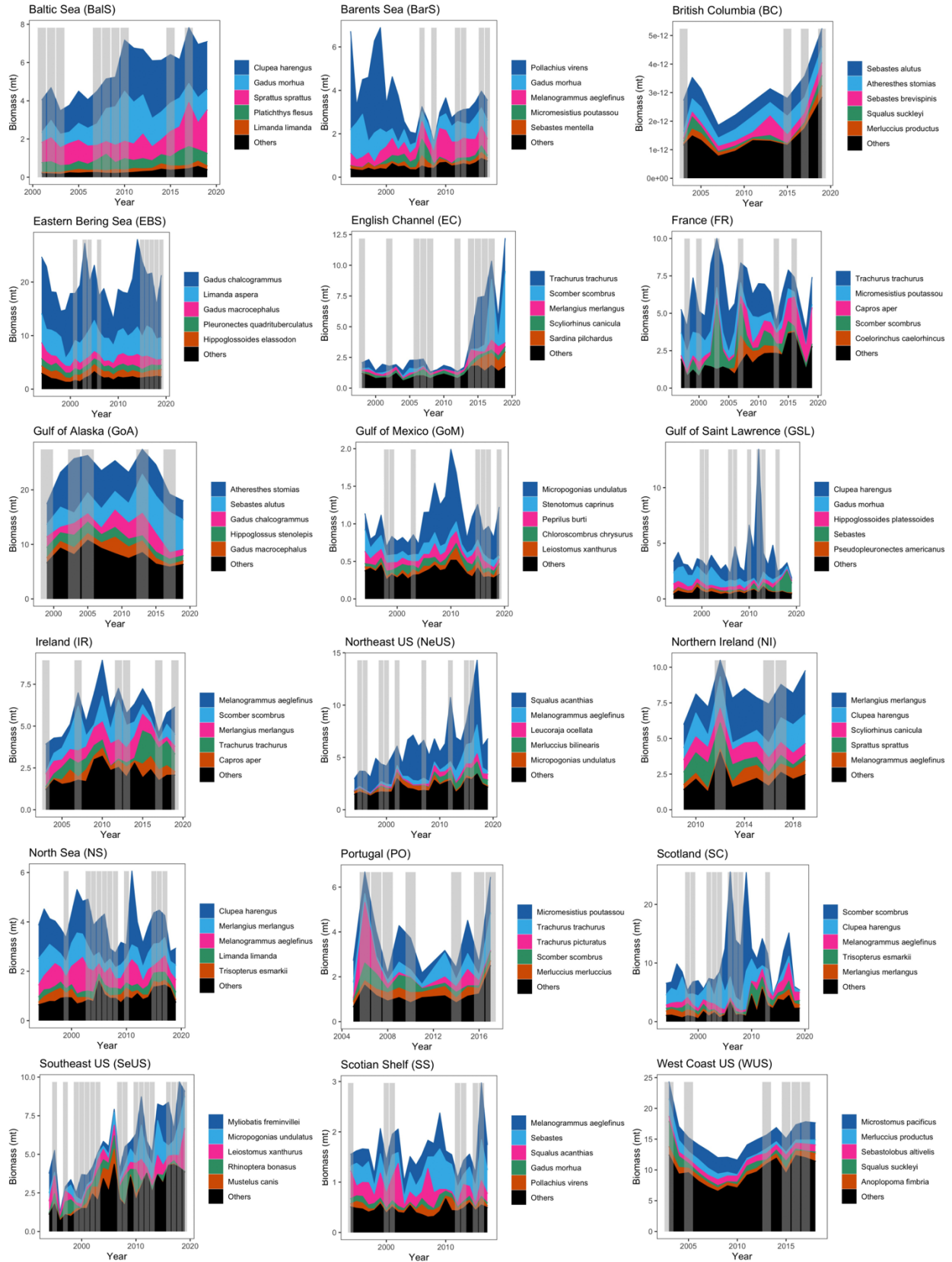
888 based beta diversity metrics of substitution and subset (Jaccard turnover (a) and nestedness (b))

889 and partitioned biomass-based beta diversity metrics of substitution and subset (Bray-Curtis
890 balanced variation (c) and biomass gradient (d)). Community dissimilarity metrics were
891 calculated within each region from one year to the next ($n = 369$). MHWs were calculated from
892 the detrended GLORYS sea bottom temperature data with a five-day minimum duration
893 threshold for MHWs, as used in the main text.
894



895
896 **Extended Data Fig. 9. Results from a power analysis simulating how much data would be**
897 **required to detect a range of MHW-induced biomass losses. Approximately 600 survey-years**
898 **in total (summed across all regions) would be required to find a significant effect if MHWs**

899 reduced biomass by 6% using either the GLORYS (a) or OISST (b) datasets; the dashed vertical
900 line shows the sample size of our actual datasets. Given the true size of our datasets ($n = 369$
901 survey-years for GLORYS and 441 for OISST), our analysis had the power to detect a MHW-
902 induced biomass decline of ~9% with GLORYS (c) and ~8% with OISST (d). The dashed
903 horizontal line denotes one conventionally accepted threshold for power (0.8).
904



906 **Extended Data Fig. 10. Biomass trends over time in each survey.** The top five taxa by
907 biomass are highlighted. Shaded grey rectangles denote when any MHWs occurred in the
908 preceding survey-year. MHWs were calculated from the detrended GLORYS sea bottom
909 temperature data with a five-day minimum duration threshold for MHWs, as used in the main
910 text. Note that x- and y-axes vary depending on time-series length and overall survey catch.
911