1   **<u>Title</u>**

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

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5   **<u>Authors</u>**

6   Alexa L. Fredston, William W. L. Cheung, Thomas L. Frölicher, Zoë J. Kitchel, Aurore A.

7   Maureaud, James T. Thorson, Arnaud Auber, Bastien Mérigot, Juliano Palacios-Abrantes, Maria

8   Lourdes D. Palomares, Laurène Pecuchet, Nancy Shackell, Malin L. Pinsky

9

10   1. Alexa L. Fredston *corresponding author

11   fredston@ucsc.edu

12   Department of Ocean Sciences, University of California, Santa Cruz, Santa Cruz,

13   California, USA

14   2. William W. L. Cheung

15   w.cheung@fisheries.ubc.ca

16   Institute for the Oceans and Fisheries, University of British Columbia, Vancouver, British

17   Columbia, Canada

18   3. Thomas L. Frölicher

19   thomas.froelicher@unibe.ch

20   Climate and Environmental Physics, Physics Institute, University of Bern, Bern,

21   Switzerland

22   Oeschger Centre for Climate Change Research, University of Bern, Bern, Switzerland

23 4. Zoë J. Kitchel

24   zoe.kitchel@rutgers.edu

25   Department of Ecology, Evolution, and Natural Resources, Rutgers University, New

26   Brunswick, New Jersey, USA

27 5. Aurore A. Maureaud

28   aurore.aqua@gmail.com

29   Department of Ecology and Evolutionary Biology, Yale University, New Haven,

30   Connecticut, USA

31   Department of Ecology, Evolution, and Natural Resources, Rutgers University, New

32   Brunswick, New Jersey, USA

33 6. James T. Thorson

34   james.thorson@noaa.gov

35   Alaska Fisheries Science Center, National Marine Fisheries Service, National Oceanic

36   and Atmospheric Administration, Seattle, Washington, USA

37 7. Arnaud Auber

38   Arnaud.Auber@ifremer.fr

39   Institut Français de Recherche pour l'Exploitation de la MER (IFREMER), Unité

40   Halieutique Manche Mer du Nord, Laboratoire Ressources Halieutiques, Boulogne-sur-

41   Mer, France

42 8. Bastien Mérigot

43   bastien.merigot@umontpellier.fr

44   MARBEC, University of Montpellier, CNRS, Ifremer, IRD, Sète, France

45   9. Juliano Palacios-Abrantes

46   j.palacios@oceans.ubc.ca

47   Institute for the Oceans and Fisheries, University of British Columbia, Vancouver, British

48   Columbia, Canada

49   10. Maria Lourdes D. Palomares

50   m.palomares@oceans.ubc.ca

51   Sea Around Us, Institute for the Oceans and Fisheries, University of British Columbia,

52   Vancouver, British Columbia, Canada

53   11. Laurène Pecuchet

54   laurene.pecuchet@uit.no

55   The Arctic University of Norway, Tromsø, Norway

56   12. Nancy Shackell

57   Nancy.Shackell@dfo-mpo.gc.ca

58   Bedford Institute of Oceanography, Fisheries and Oceans Canada, Dartmouth, Canada

59   13. Malin L. Pinsky

60   malin.pinsky@rutgers.edu

61   Department of Ecology, Evolution, and Natural Resources, Rutgers University, New

62   Brunswick, New Jersey, USA

63   Department of Ecology and Evolutionary Biology, University of California, Santa Cruz,

64   Santa Cruz, California, USA

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66   **<u>Summary</u>**

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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 transformation[5]. 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 species[7–9]. 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 thrived[11–

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 operate[14].

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 $\geq$ 5 days with sea bottom temperature (SBT)

113   anomalies above the seasonally varying 95th percentile for that region[6] 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 km^2 in 2011, a non-MHW year; 13 metric tons per km^2 in

137 2012 following 36 °C-days MHW; and 4 metric tons per km^2 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 region[19].

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 pressures[20], 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 communities[22]. 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 summer[1], 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 fisheries[11].

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 niches[26].

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 year[27]. 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 deborealization[28]. Less predictable changes in species identity and underlying

206   community structure could also emerge despite consistent biomass[29]. 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   other[30] (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 change[29].

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 responses[32]. Species and spatial portfolio effects[33,34] as well as spatial and temporal

232   storage effects[35] 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 important[36]. 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 productivity[3].

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 systems[3]. 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 ¾ 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 temperatures[37].

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 MHWs[38]. 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 criteria[40]

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 heatwaves[5], 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 responses[43]—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 responses[40].

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 another[42].

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 blooms[13] or low-productivity events[9]

297   could play a role. Perhaps very extreme MHWs in the future will cross a tipping point beyond

298 which adverse ecological effects occur, but we did not see such a tipping point in the recent

299 historical record. Other fields (e.g., coral reef ecology) have identified such thresholds, though

300 the generality of thresholds across ecological systems remains unclear.[45] Gaining mechanistic

301 insight into why only some MHWs have deleterious effects, and on only some species, is

302 necessary for any future efforts to identify an effect threshold or forecast MHW impacts and

303 should be a research priority for the field. Additionally, ecosystem responses to extreme "pulse"

304 events such as MHWs can shape impacts of more gradual "press" trends; the complex

305 interactions between these climate change effects warrant future research.[5]

306   Understanding MHW impacts on entire ocean ecosystems is particularly crucial in the

307 context of accelerating global change and efforts to advance towards ecosystem-based

308 management that considers the many links between species and with their environment[46]. MHW

309 occurrences are projected to emerge above their natural variability within this century in many

310 regions[47]. Future research will be needed to determine the extent to which fish community

311 impacts of MHWs will grow as MHWs intensify, or whether portfolio and other ecological

312 effects can buffer ecosystems from MHW impacts. Marine life is more vulnerable to warming

313 than terrestrial life, because marine organisms tend to live close to their thermal limits and fewer

314 thermal refugia exist in the seas[48]. Observed and predicted changes in marine ecosystems in

315 response to global warming formed part of the rationale behind the Paris Climate Agreement to

316 limit the global mean surface temperature increase above industrial levels to 1.5 °C by 2100[49].

317 As a future that is more than 1.5 °C warmer looks increasingly likely[50], it is more critical than

318 ever to develop a deeper understanding of what drives ecological responses to extreme climate

319 events.

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431

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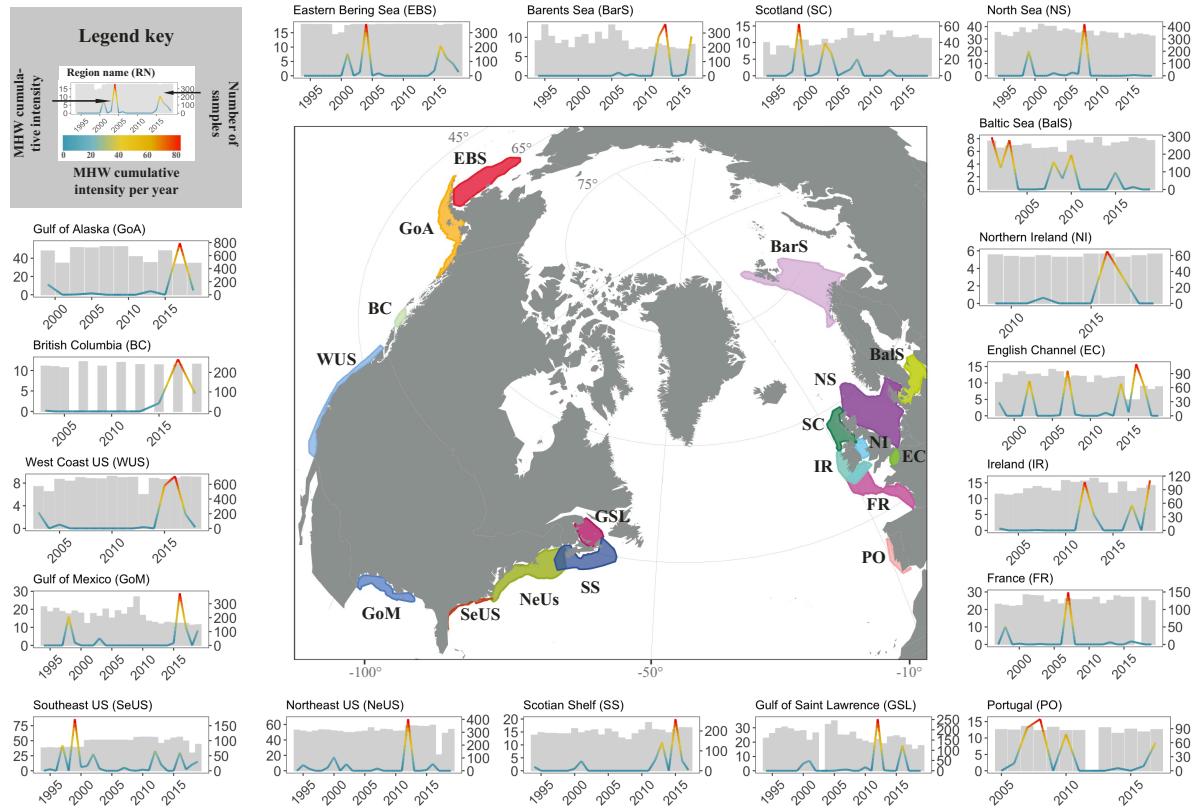
Fig. 1. Of 18 regions studied from the Atlantic and Pacific Oceans, all experienced marine heatwaves during the available scientific fish survey time-series. Highlighted areas on the map represent the spatial area surveyed by each trawl survey. Inset plots show the number of distinct sampling events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

443
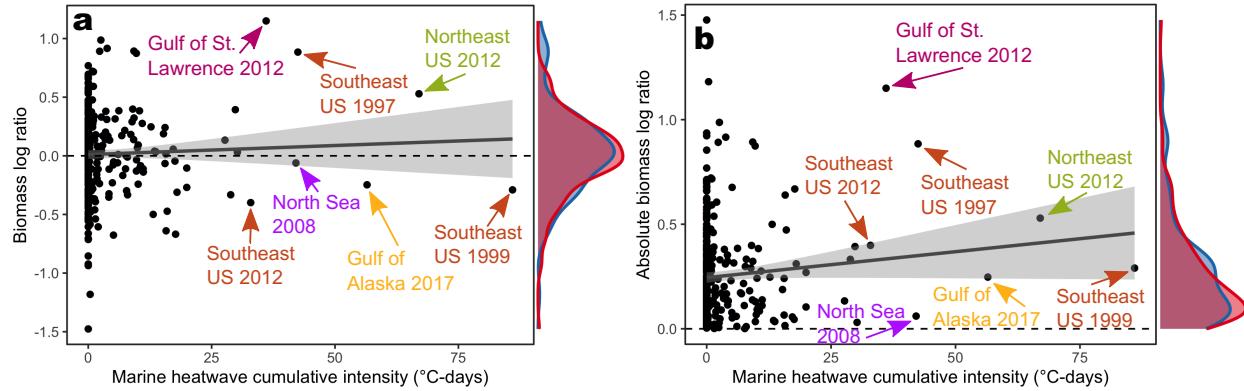
Fig. 2. More intense marine heatwaves were not associated with a decline in fish biomass or an increase in biomass variability, and biomass was approximately as likely to increase as it was to decrease from one year to the next, regardless of whether a marine heatwave occurred. MHW cumulative intensity (°C-days) had no relationship with (a) biomass change (measured as log ratio; linear regression, $R^2 = 0.00$, $p = 0.45$) or (b) absolute biomass change (measured as absolute log ratio; linear regression, $R^2 = 0.01$, $p = 0.07$). The grey shaded area is a 95% confidence interval. Density plots along the right-hand y-axes show that biomass changes from one year to the next were the same whether a MHW did (red, $n = 139$) or did not (blue, $n = 230$) occur. Points represent (a) log ratios or (b) absolute log ratios of mean biomass in a survey from one year to the next ($n = 369$). Surveys following the highest cumulative intensity MHWs are labeled (years correspond to when the survey was conducted). Colors correspond to regions in Fig. 1. Models exploring the relationships in (a) and (b) are reported in Supp. Tab. 2 and 4, respectively.

Biomass

Community Temperature Index

Community Dissimilarity

British Columbia   Gulf of Alaska
Eastern Bering Sea   West Coast US
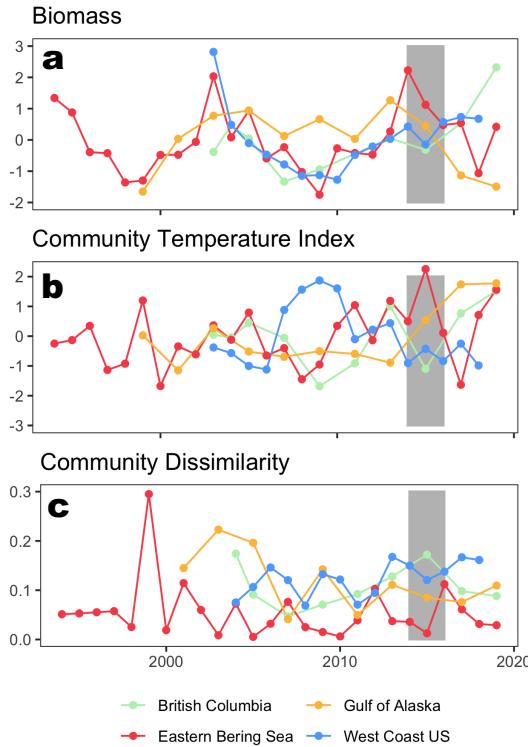
458

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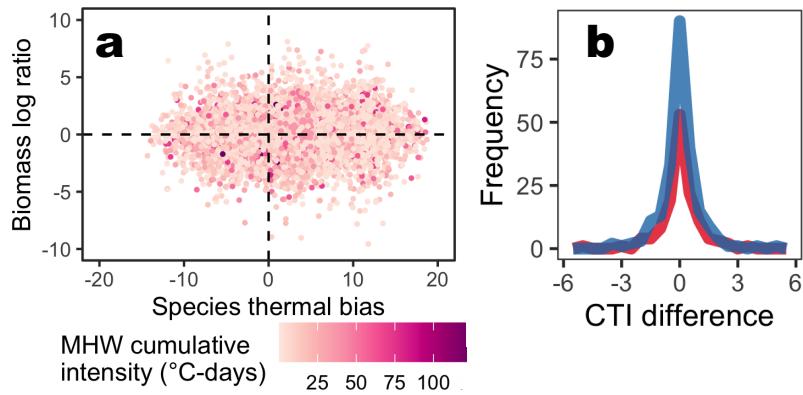
Fig. 4. Scientific bottom trawl surveys during the year following marine heatwaves were as likely to exhibit tropicalization and/or deborealization as those that did not follow marine heatwaves. (a) There was no relationship between a species' thermal bias (its cold or warm affinity relative to the assemblage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

Methods

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

Fish biomass and abundance data. We collated publicly available datasets from fishery management agencies that use scientific (i.e., fisheries-independent) bottom trawl surveys to monitor marine fish communities[40]. These surveys monitor biogeographically and/or politically distinct areas that are relevant to fisheries management[40]. Their footprints often follow marine

485   ecosystem boundaries (e.g., Large Marine Ecosystems[52]) and are similar in size to the spatial

486   extents of MHWs[39]. 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 al[53]. 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 Species[54] to standardize taxonomies, and the "dggridR" R package[55] 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   analyses[56], 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    $\ln(\frac{biomass_t}{biomass_{t-1}})$. 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 Alaska[12]. Winter MHWs may also reduce recruitment in habitat-forming seaweeds[6] and

538   cause metabolic stress to coral reef fishes[60]. Spawners and embryos have narrower temperature

539   tolerance ranges than non-spawning adults[61]; 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 percentile[6] or the 99th [39] 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 days[68], and is widely

616   used in the literature[6], 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 change[76].

665   Others suggest that ecological responses may lag disturbances by years[77]. 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* database[78] 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 sizes[83].

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

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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803   **<u>Author contributions</u>**

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   **<u>Competing interest declaration</u>**

810   The authors declare no competing interests.

811

812   **<u>Additional information</u>**

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   **<u>Code availability statement</u>**

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   **<u>Data availability statement</u>**

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

824

825   **<u>Extended data figures</u>**

826

Panel labels (rows): BalS, BarS, BC, EBS, EC; FR, GoA, GoM, GSL, IR; NeUS, NI, NS, PO, SC; SeUS, SS, WUS

Y-axis: Biomass log ratio
X-axis: MHW cumulative intensity (°C-days)

$R^2 = 0.00015$ (BalS); $R^2 = 0.00023$ (BarS); $R^2 = 0.1$ (BC); $R^2 = 0.13$ (EBS); $R^2 = 0.022$ (EC)
$R^2 = 0.027$ (FR); $R^2 = 0.29$ (GoA); $R^2 = 0.082$ (GoM); $R^2 = 0.11$ (GSL); $R^2 = 0.0035$ (IR)
$R^2 = 0.12$ (NeUS); $R^2 = 0.00038$ (NI); $R^2 = 0.0043$ (NS); $R^2 = 0.12$ (PO); $R^2 = 0.0058$ (SC)
$R^2 = 0.00013$ (SeUS); $R^2 = 7.7e\text{-}05$ (SS); $R^2 = 0.027$ (WUS)

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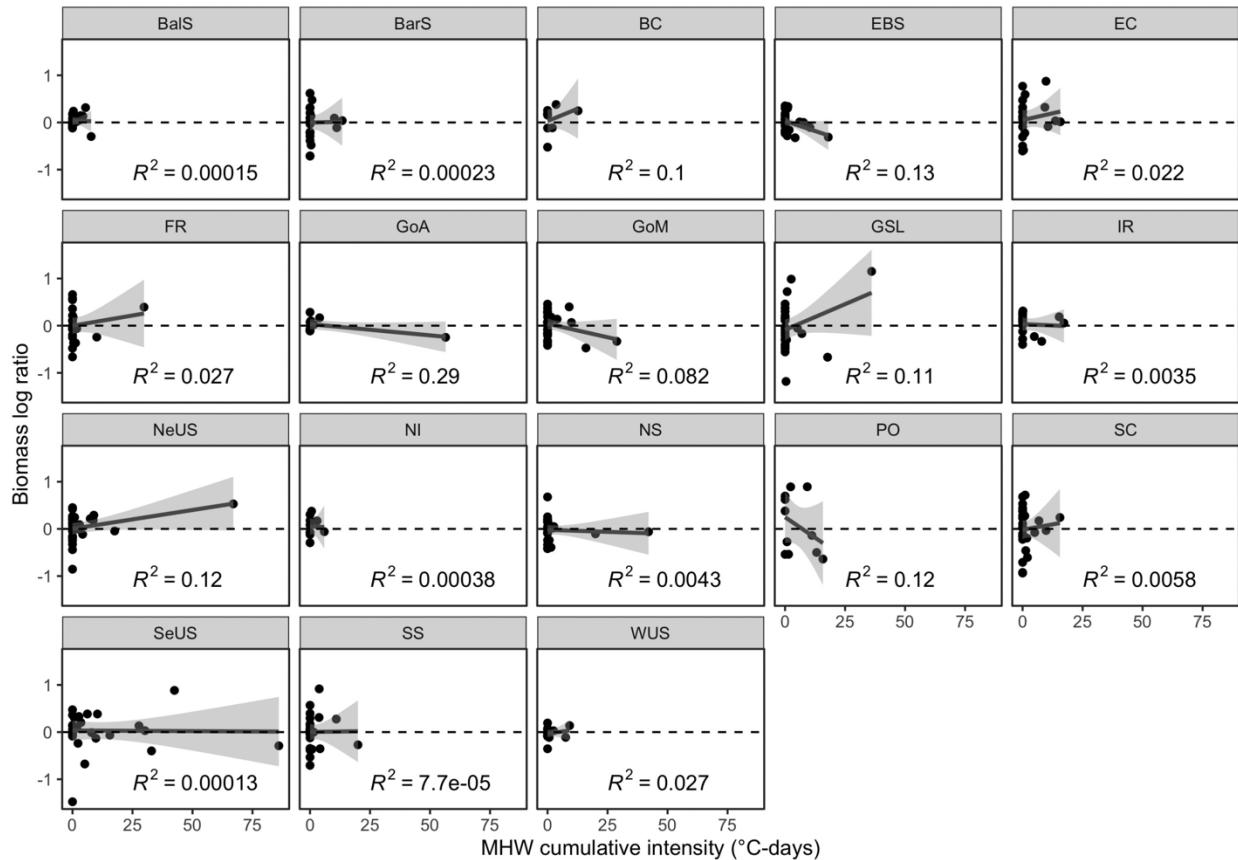
Extended Data Fig. 1. Alternate version of Fig. 2 from the main text, showing results by region. MHWs were calculated from the detrended GLORYS sea bottom temperature data with a five-day minimum duration threshold for MHWs, as used in the main text. Points represent log ratios of mean biomass in a survey 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.

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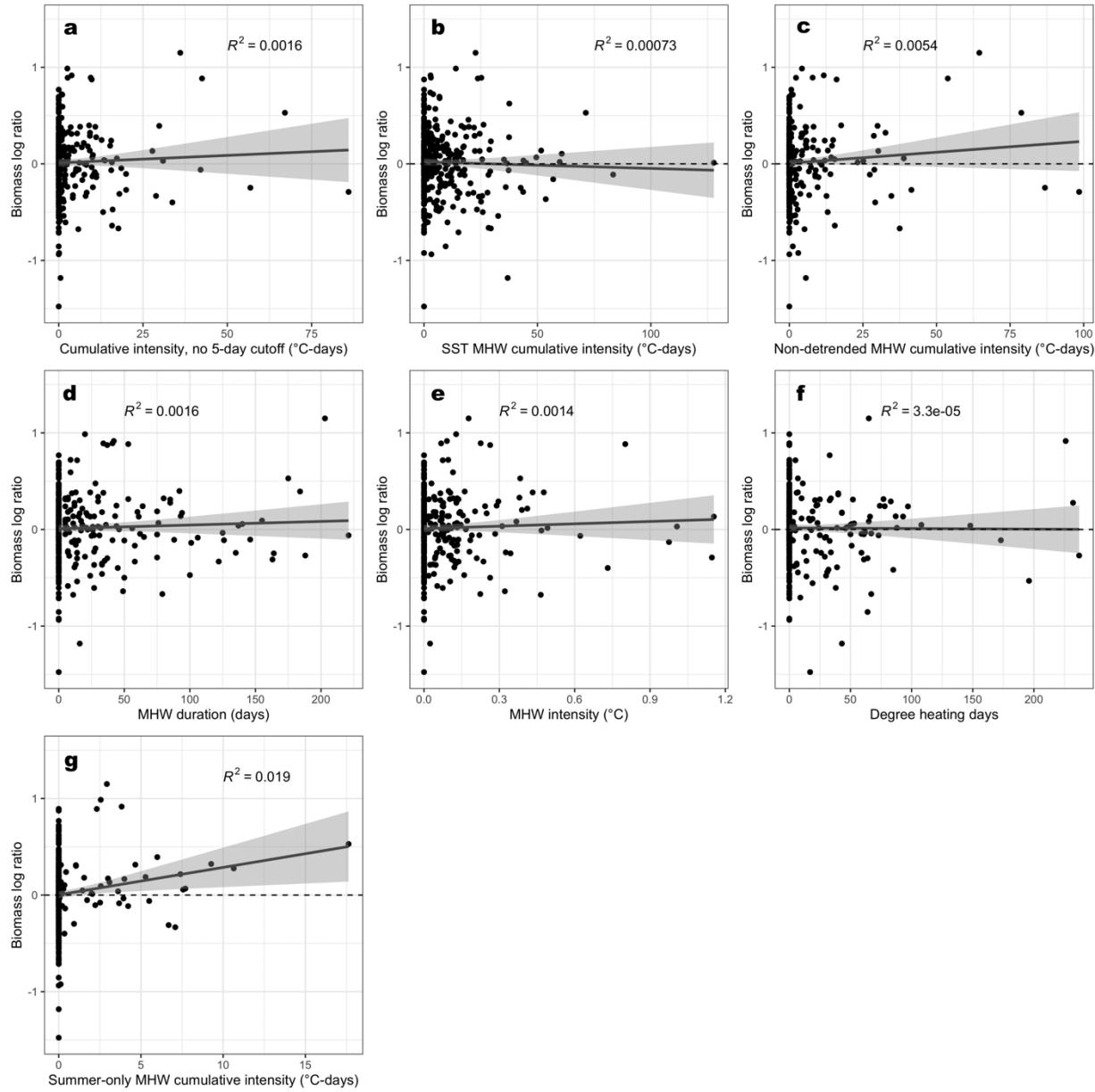
Extended Data Fig. 2. Results did not change when alternative methods were used to

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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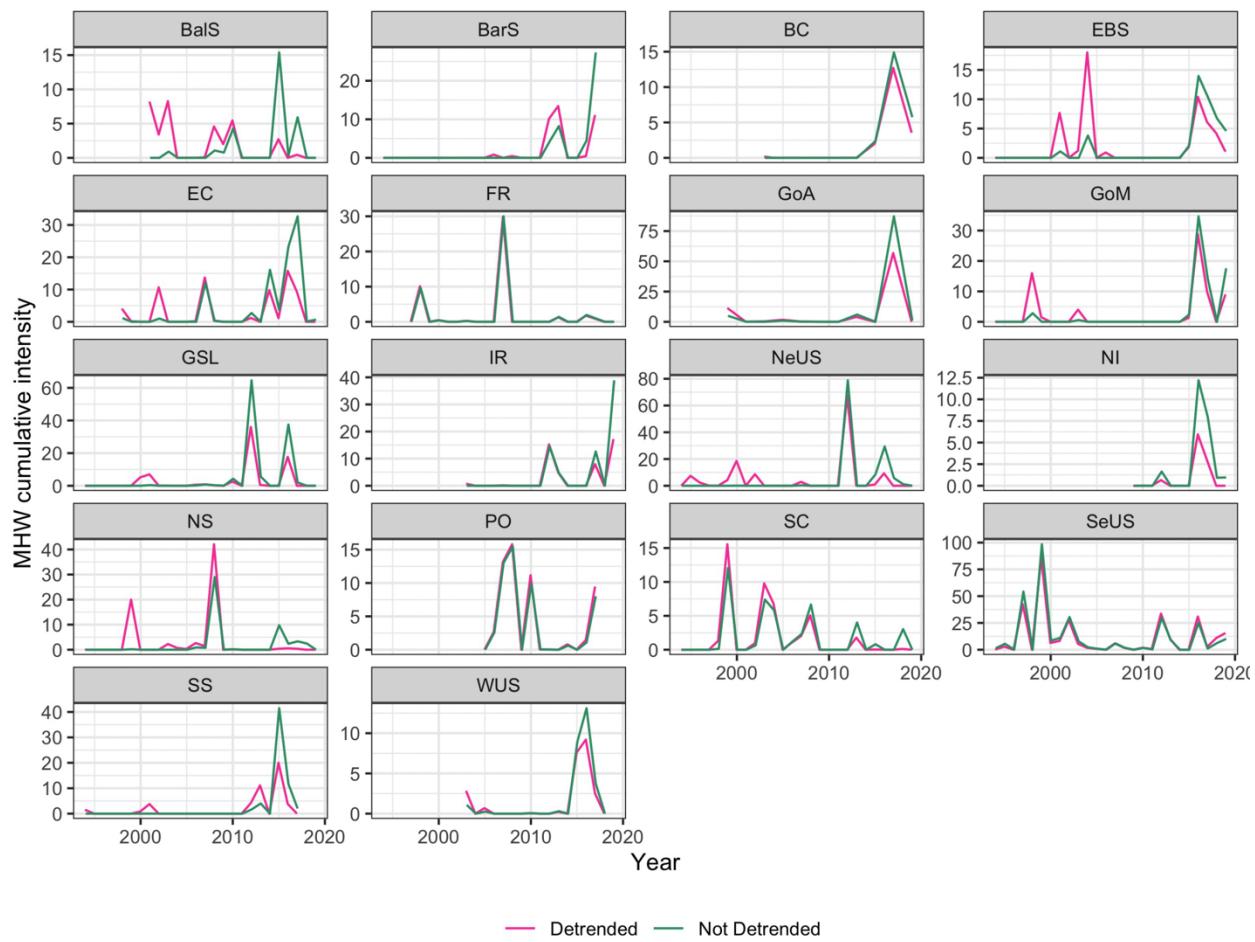
844

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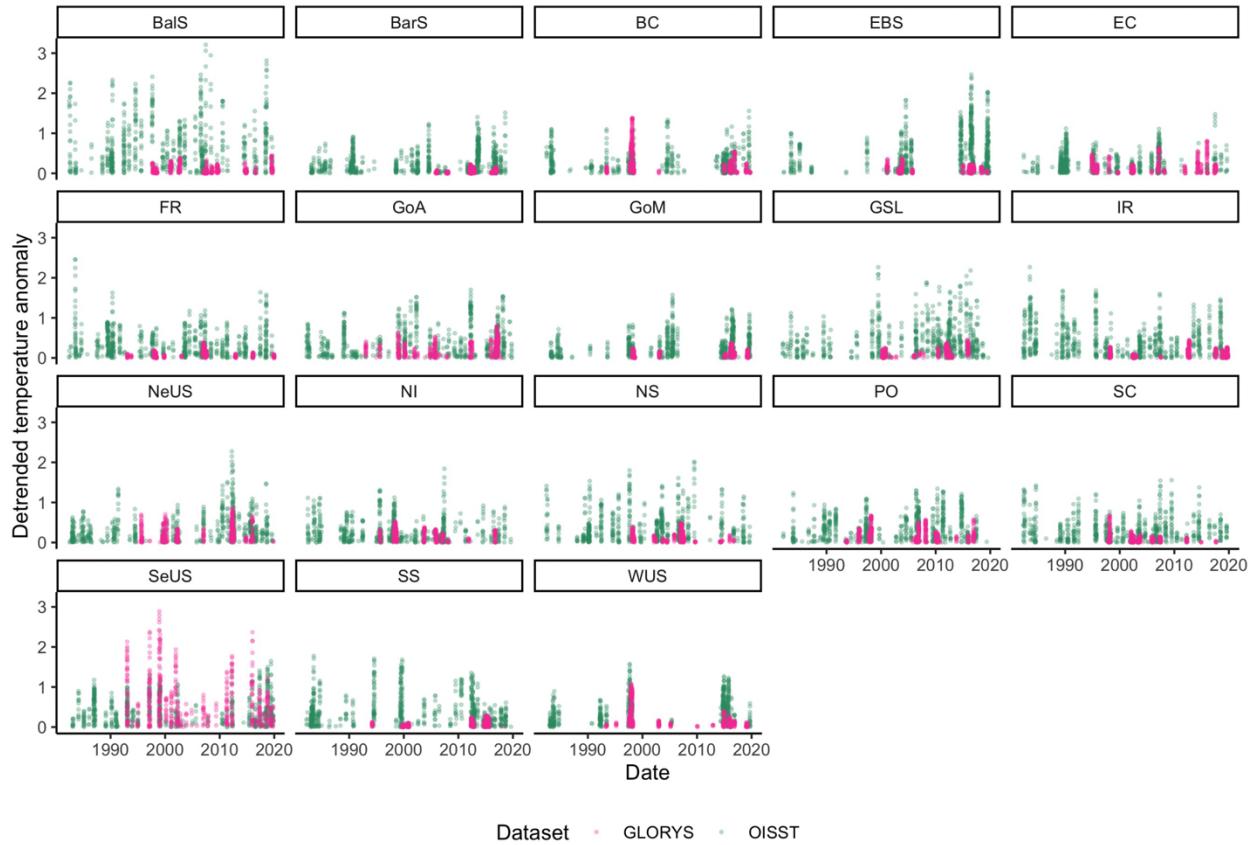
Extended Data Fig. 4. Daily 95th percentile anomalies in the two marine heatwave data sources: sea surface temperature from OISST and sea bottom temperature from GLORYS (both detrended). To simplify comparison we plot all anomalies, not just those MHWs that exceeded a five-day threshold. Note that the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

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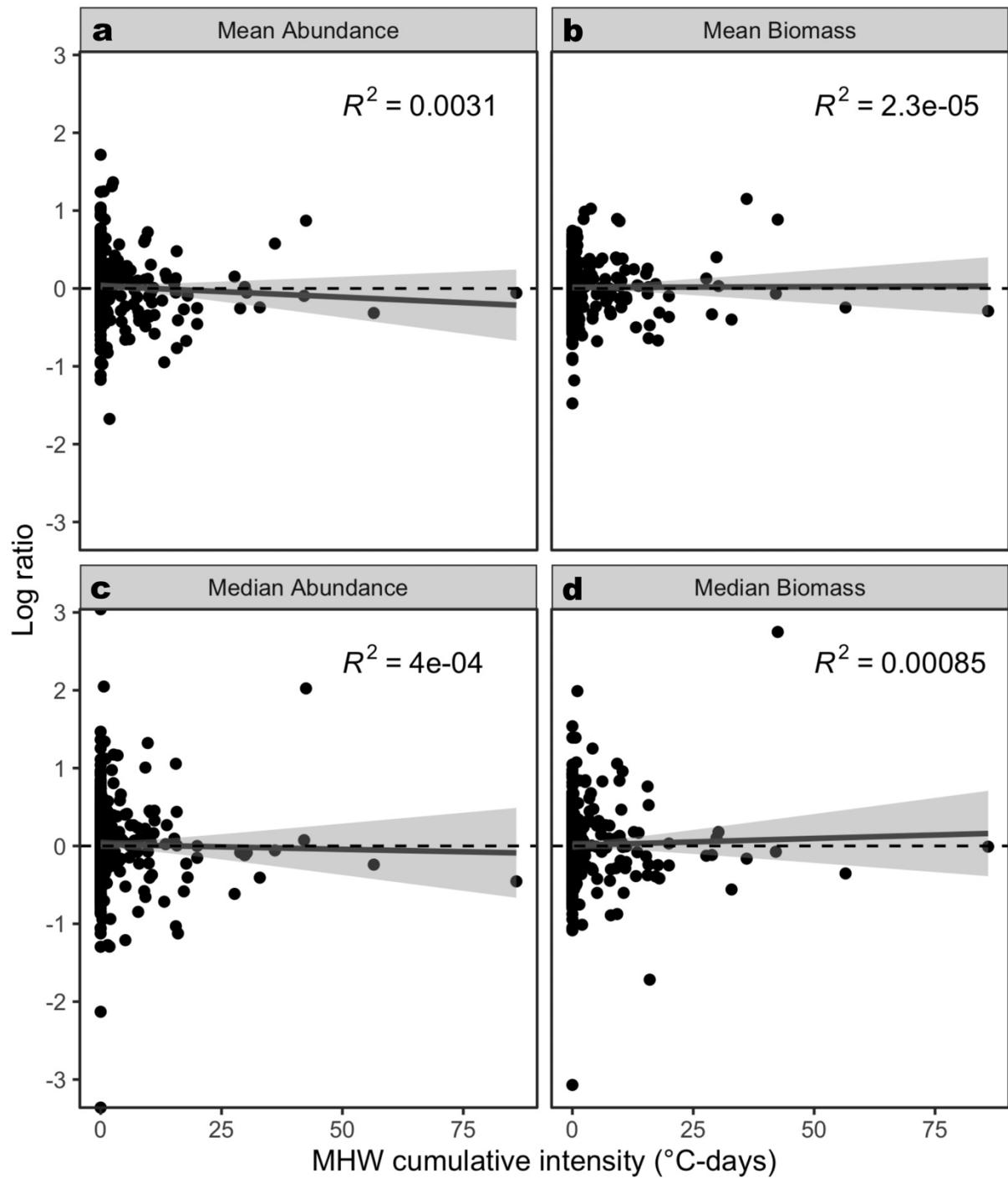
859   **Extended Data Fig. 5. Results are consistent across different metrics of the fish**

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.

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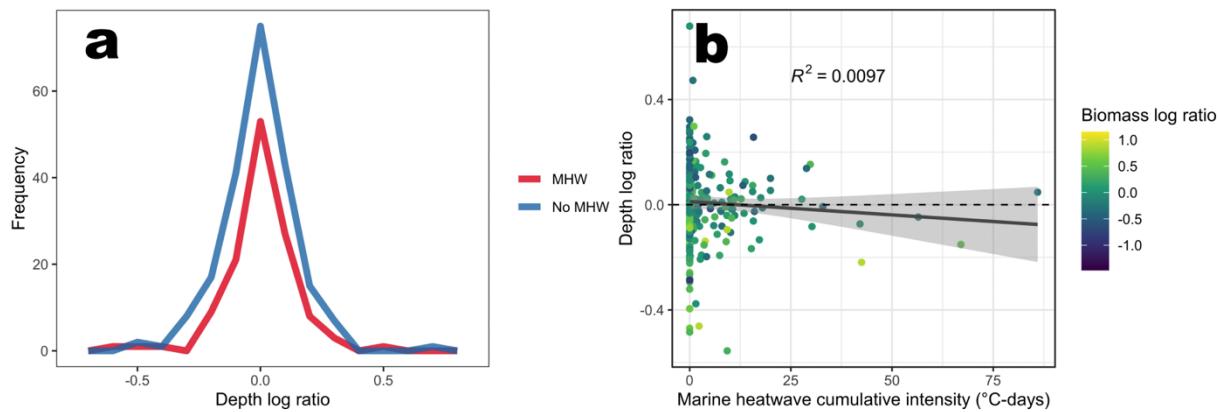
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869   **Extended Data Fig. 6. Depth changes in the fish assemblage in response to marine**

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.

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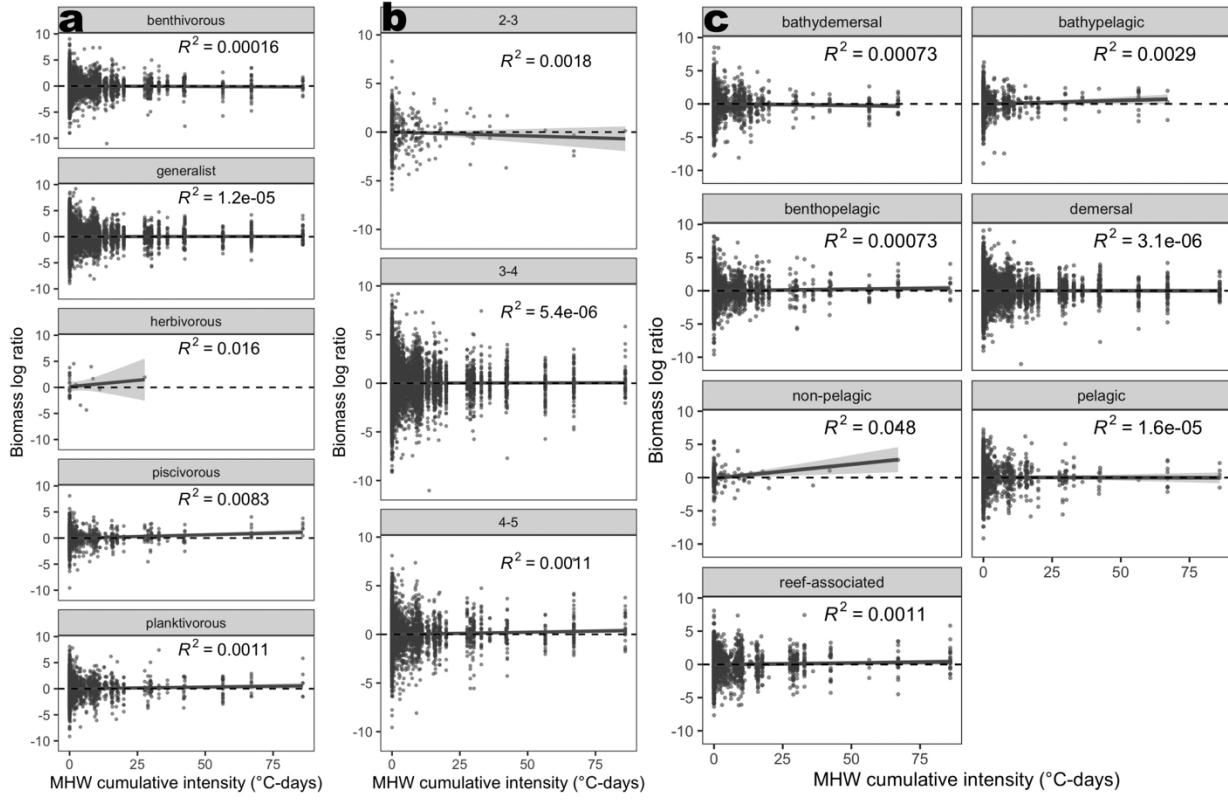
Extended Data Fig. 7. Marine heatwave effect on taxon-specific biomass log ratios grouped by traits. Biomass log ratio and MHW cumulative intensity (total anomaly in °C-days) grouped by (a) feeding mode ($n = 29,628$), (b) trophic level ($n = 29,909$), and (c) habitat preference ($n = 29,681$) of each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

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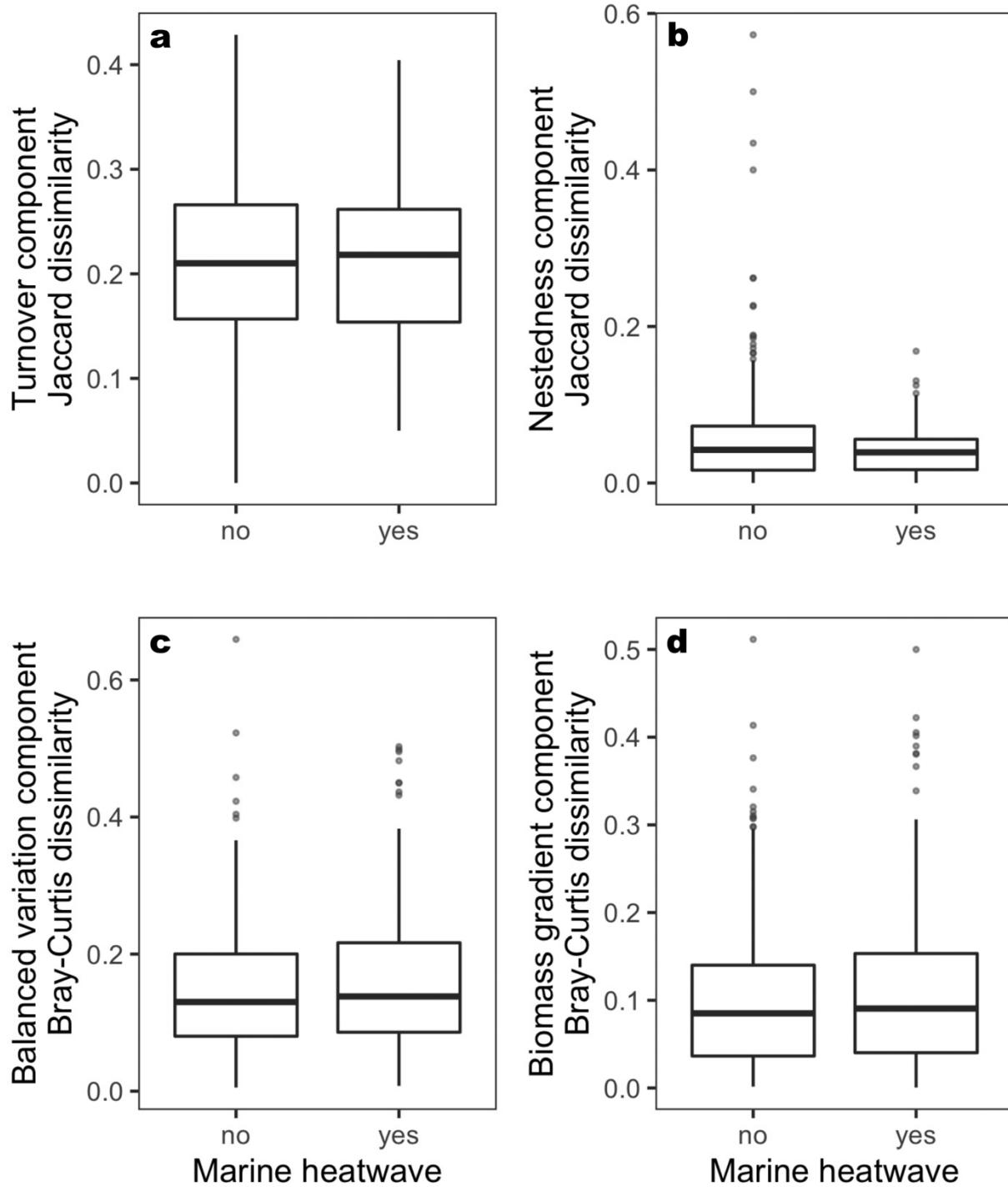
Extended Data Fig. 8. The presence or absence of a MHW did not affect temporal community dissimilarity. We measured community dissimilarity as partitioned occurrence-based beta diversity metrics of substitution and subset (Jaccard turnover (a) and nestedness (b))

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.

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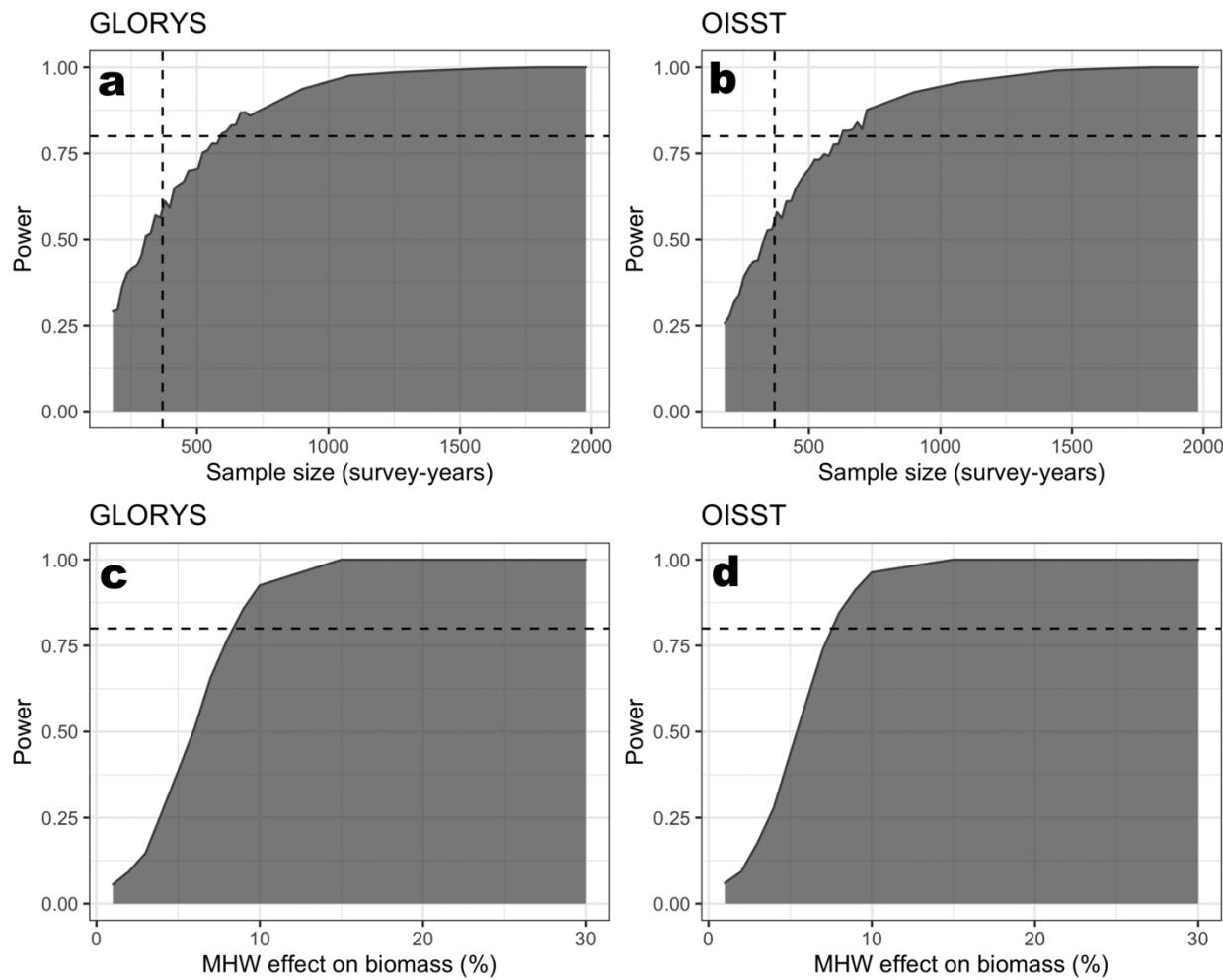
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896   **Extended Data Fig. 9. Results from a power analysis simulating how much data would be**

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).

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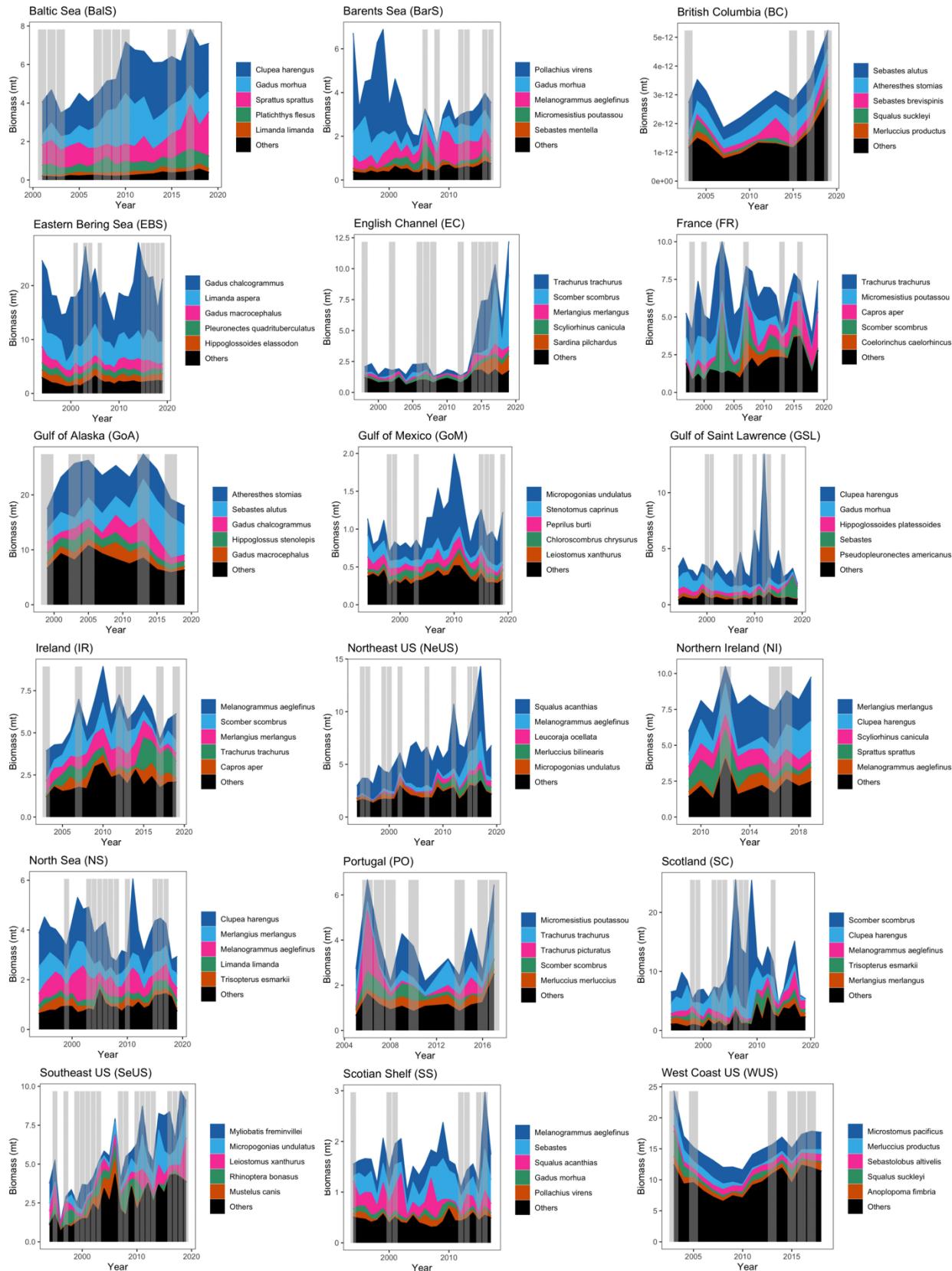
906 **Extended Data Fig. 10. Biomass trends over time in each survey.** The top five taxa by

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