

1 Marine biodiversity exposed to prolonged and intense subsurface heatwaves

2
3 Eliza Fragkopoulou^{1*}, Alex Sen Gupta^{2,3}, Mark John Costello⁴, Thomas Wernberg^{5,6}, Miguel
4 B. Araújo^{7,8}, Ester A. Serrão¹, Olivier De Clerck⁹, Jorge Assis^{1,4*}

5
6 ¹ CCMAR – Center of Marine Sciences, University of Algarve, 8005-139, Faro, Portugal

7 ² Climate Change Research Centre, University of New South Wales, Sydney, Australia.

8 ³ Australian Research Council Centre of Excellence for Climate Extremes, University of New South Wales, Sydney,
9 Australia.

10 ⁴ Faculty of Biosciences and Aquaculture, Nord Universitet, Postboks 1490, Bodø 8049, Norway

11 ⁵ UWA Oceans Institute & School of Biological Sciences, University of Western Australia, 6009 Crawley WA,
12 Australia

13 ⁶ Norwegian Institute of Marine Research, Flødevigen Research Station, NO-4817 His, Norway

14 ⁷ Department of Biogeography and Global Change, National Museum of Natural Sciences, CSIC, Calle José
15 Gutiérrez Abascal, 2, 28806 Madrid, Spain

16 ⁸ Rui Nabeiro Biodiversity Chair, MED - Mediterranean Institute for Agriculture, Environment and Development,
17 University of Évora, Largo dos Colegiais, 7000 Évora, Portugal

18 ⁹ Phycology Research Group, Biology Department, Ghent University, Krijgslaan 281 (S8), 9000 Ghent, Belgium

19
20 * **Corresponding authors** (Eliza Fragkopoulou, eli_frag@hotmail.com; Jorge Assis,
21 jorgemfa@gmail.com)

23 Abstract

24 Marine heatwaves (MHWs) are becoming increasingly common, with devastating ecosystem
25 impacts. However, MHW understanding has almost exclusively relied on sea-surface
26 temperature with limited knowledge about their subsurface characteristics. Here, we
27 estimate global MHWs from the surface to 2000 m depth, covering the period 1993-2019,
28 and explore biodiversity exposure to their effects. We find that MHWs are typically more
29 intense in the subsurface at 50-200 m and their duration increases up to two-fold with depth,
30 although with large spatial variability linked to different oceanographic conditions. Cumulative
31 intensity (a thermal stress proxy) was highest in the upper 250 m, exposing subsurface
32 biodiversity to MHW effects. This can be particularly concerning for up to 22% of the ocean,
33 where high cumulative intensity overlapped the warm range edge of species distributions,

34 thus being more sensitive to thermal stress. Subsurface MHWs can hence drive biodiversity
35 patterns, with consequent effects on ecological interactions and ecosystem processes.

36

37 **Main**

38 The frequency and duration of marine heatwaves (MHWs) have been increasing over
39 the past century¹⁻³ and are anticipated to further increase in the decades to come⁴, driven by
40 anthropogenic climate change and ocean warming^{1,2,5}. MHWs have caused substantial
41 biological^{6,7} and socio-ecological⁸ impacts globally, ranging from rapid shifts in species
42 distributions to mass mortality of marine organisms⁸⁻¹⁰. To date, MHWs have been studied
43 primarily at the ocean surface due to the availability of high-quality sea surface temperature
44 datasets⁹ and only a few studies, all based on individual locations or events, have examined
45 MHWs throughout the water column¹⁰⁻¹⁸. These studies focused on sites with long-term
46 mooring data^{16,17}, or individual strong long-lasting MHWs partially resolved using ARGO
47 data^{11,13,14}, or ocean models^{12,15,18}. A global assessment of MHW spatial and temporal depth
48 structure is still missing, hindering the examination of commonalities and differences across
49 regions.

50 Localised observations have shown greater MHW intensity in the subsurface^{11,13,16,17},
51 with warming persisting for up to 2 years after the end of surface events¹⁹. Several processes
52 can affect the depth structure of MHWs. In the north-eastern Pacific, salinity differences
53 impacting the water column stratification determined the depth extent of warming during two
54 distinct MHW events¹³. The enhanced stratification in 2019-2020 restricted the warming from
55 extending as deep as in the 2013-2016 event¹³. In the tropical western Pacific, subsurface
56 MHWs were related to Ekman convergence and downwelling of warm surface waters¹⁷. In
57 south-eastern Australia, local downwelling also caused subsurface warming, at times without
58 a surface signal^{11,16}. In the north-western Atlantic, subsurface MHWs were driven by warm
59 core rings spinning off the Gulf Stream boundary current over the slope and shelf region and
60 were decoupled from surface events¹⁸.

61 Given that MHW intensity may be stronger below the surface^{11,13,16,17}, a global
62 characterization of subsurface MHWs could improve understanding of their potential impacts
63 on marine biodiversity^{9,20}. Here, we advance this understanding by using global high-
64 resolution (1/12°) reanalysis temperature data²¹ from 1993-2019 at eleven depths (0, 25, 50,
65 75, 100, 150, 200, 250, 500, 1000 and 2000 m), validated against *in-situ* observations (S1),
66 to estimate MHW metrics per depth and over time. Further, we provide novel insights into
67 the potential biodiversity exposure to MHWs globally by overlaying the spatial distribution of
68 cumulative MHW intensity with species richness estimates²² derived from the modelled
69 ranges of 25,078 species distributed from the surface to 2000 m²³.

70

71 **Global MHW metrics with depth**

72 Temperature reanalysis data from 1993 to 2019 showed multi-decadal warming of the
73 global ocean, with a stronger signal above 500 m (Fig. 1a). In the upper 100 m, warming was
74 modulated by strong interannual variability, such as the extreme 1997/98 and 2016/17 El
75 Niño events²⁴, whose impacts become lagged with depth. The progressive warming of the
76 global ocean expanded in depth, reaching 1000 m over recent years, with a lack of cold
77 temperature anomalies after 2015 (Fig.1a). The reanalysis and *in-situ* data showed a good
78 agreement (S1 Table 2), yet temperature estimates from the deep ocean, polar latitudes, ice-
79 covered regions and prior to 2004, when subsurface ARGO float data measurements were
80 less widespread, should be interpreted with caution because they are highly uncertain (see
81 methods).

82 The global average MHW maximum intensity, that is the average of the maximum
83 temperature anomaly from the climatology of each MHW event, remained greater than 1.3°C
84 in the upper 200 m of the ocean (Fig. 1). Remarkably, the highest intensity was found at 100
85 m depth with a mean \pm SD of $1.6 \pm 1.0^\circ\text{C}$. This was 19% higher than surface events ($1.3 \pm$
86 0.5°C ; Fig. 1; S2 Table 1). Even at 200 m depth, the intensity was still as high as at the surface
87 ($1.3 \pm 0.8^\circ\text{C}$). Deeper than 200 m, global MHW intensity typically reduced with depth,

88 decreasing to $0.37 \pm 0.28^\circ\text{C}$ at 1000 m and $0.15 \pm 0.09^\circ\text{C}$ at 2000 m depth (Fig. 1; S2 Table
89 1). This global pattern of subsurface MHW intensification could be related to vertical
90 displacements of the thermocline, the upper ocean layer characterized by a steep
91 temperature gradient with depth (Fig. 1f), resulting in warmer temperatures at fixed
92 depths^{11,13,16,17}.

93 The globally averaged occurrence of MHWs (i.e., the number of individual events from
94 1993 to 2019) decreased with depth, from an average of 44 ± 10 events at the surface to 28
95 ± 11 events at 2000 m depth (Fig. 1; S2 Table 1). Conversely, the average duration of MHW
96 increased two-fold, from 20 ± 6 days at the surface to 40 ± 19 days at 2000 m depth (Fig. 1;
97 S2 Table 1). Notably, both metrics showed little variation between 50 and 250 m depth.

98 The sum of cumulative intensity, i.e., the integral of MHW intensity over the duration
99 of each event²⁵ (in degree days; Fig. 1e), was estimated as a proxy of thermal stress. This
100 ranged from an average of 1007 ± 435 degree-days at the surface to 141 ± 92 degree-days
101 at 2000 m (S2 Table 1). Like the intensity pattern, the highest average cumulative intensity
102 was at 100 m depth with a mean of 1439 ± 849 degree-days. At 500 m, MHW cumulative
103 intensity decreased to almost half than at the surface and continued to decrease in deeper
104 waters, despite the increase in MHW duration (Fig. 1; S2 Table 1).

105 Timeseries analyses of temperature anomalies revealed strong synchrony between
106 surface and subsurface layers down to 50 m depth (corr. 0.75 ± 0.24 ; S2 Table 1), decreasing
107 rapidly from the surface to 100 m and more slowly subsequently, yet with large variability
108 (Fig. 1g). The increased synchrony in the upper 100 m is to be expected, as this represents
109 the typical mixed layer depth within which water mass homogenization occurs²⁶. Below the
110 mixed layer, reduced synchrony in warming indicates disassociated processes of surface
111 and subsurface temperature variability and therefore potentially disassociated MHW drivers.

112

113 **Spatial patterns of MHWs**

114 Spatial variations in MHW metrics prevailed across depths (Fig. 2). The strongest and
115 most frequent MHWs were primarily observed in regions of sharp temperature gradients,
116 such as those associated with boundary currents and fronts. However, these events tended
117 to have a short duration (Fig. 2). For example, in the Gulf Stream (north-western Atlantic
118 Ocean) and Agulhas Current (south Indian Ocean) extensions, frequent and strong MHWs
119 were detected as deep as 1000 m (Fig. 2), matching the depth extension of the boundary
120 currents²⁷. Strong MHWs also occurred in regions along the equator but in the subsurface
121 (e.g., 100 m depth; Fig. 2). The longest MHW durations were often estimated in polar regions
122 (e.g., Weddell Sea in the Antarctic), a pattern that was replicated down to the maximum depth
123 (Fig. 2). At 2000 m, prolonged MHWs were common in every ocean basin (Fig. 2).

124

125 **Biodiversity exposure to MHWs**

126 We used MHW cumulative intensity (degree-days) and species distributions to
127 estimate biodiversity exposure to MHWs. In this context, we defined richness exposure as
128 the overlap of cumulative intensity and species richness²² (i.e., the number of species in each
129 cell; Fig. 3). Because thermal tolerances are more easily exceeded at the warm range edge
130 of species distributions⁶, we used warm-edge exposure as a proxy of thermal sensitivity and
131 define it as the overlap of cumulative intensity and warm-edge richness (i.e., the number of
132 species at the warm range edge of their distributions in each cell; Fig. 3, S1 Fig. 8). Regions
133 of highest/least exposure were defined where high richness overlaid high/low cumulative
134 intensity.

135 Overall, regions of highest richness exposure varied across depths (Fig. 3), depending on
136 MHW cumulative intensity and species richness estimates, with both being greater in the
137 upper 250 m of the ocean (S2 Table 2). Averaged across depths, 14% of the ocean was
138 classified as high richness exposure, ranging between 11% at the surface and 250 m depth
139 and 16% at 75 and 100 m depth (Fig. 3; S2 Table 2). Despite spatial variability, some regions
140 were recurrently classified as high richness exposed across depths, such as in the Philippine

141 and Tasman Seas (West Pacific), the Gulf of Mexico (North Atlantic) and off South Africa in
142 the South Indian Ocean. In contrast, regions of least richness exposure represented a smaller
143 portion of the ocean (8% on average), ranging between 6% (e.g., equatorial Pacific at 500 m
144 depth) and 11% (e.g., surface tropical Atlantic). Highest warm-edge exposure comprised an
145 average of 15% of the global ocean across depths, ranging from only 6% at the surface to
146 up to 22% at 1000-2000 m depth, comprising large portions of the Indian and North Atlantic
147 Oceans (Fig. 3; S2 Table 3). Regions such as the Gulf of Mexico, the Gulf of Aden and the
148 Tasman Sea were consistently classified as highly exposed across depths, both for richness
149 and warm-edge exposure, being of particular concern for potential biological effects. In
150 contrast, regions classified as least warm-edge exposed represented on average 8% of the
151 ocean, ranging from 3% at 500 m (e.g., North Indian Ocean) to 17% at the surface (e.g.,
152 tropical Atlantic and Indian oceans; Fig. 3; S2 Table 3).

153

154 **Local MHW and biodiversity patterns**

155 Local time-depth analyses of maximum MHW intensity and biodiversity metrics were
156 produced for selected locations with distinct oceanographic or climatic conditions. Different
157 patterns in the intensity, frequency, duration and depth extent of MHW events emerged,
158 depending on the prevailing conditions (Fig. 4; Extended Data Fig. 1; Extended Data Fig. 2).
159 In regions of boundary currents and fronts (Fig. 4a,b; Extended Data Fig. 1a,b), MHWs
160 typically extended at depths well below the thermocline, reaching down to 1000 m (S1 Fig.
161 9ab). Under these conditions, MHWs had a short duration, and the highest (cumulative)
162 intensity was typically found from the surface to 500 m depth. In regions of subtropical gyres
163 (Fig. 4c; Extended Data Fig. 2c), MHWs tended to last longer, and higher MHW (cumulative)
164 intensities were found from the surface to the thermocline depth (S1 Fig. 9c), where they
165 often peaked. Weaker intensity MHWs also occurred below the thermocline, at times
166 unconnected to surface events. In regions of tropical gyres (Fig. 4d; Extended Data Fig 2d),
167 subsurface MHWs were predominantly unconnected to the surface and had shorter

168 durations. The highest intensities were estimated in the subsurface at the thermocline depth
169 (S1 Fig. 9d). In the Arctic (Fig. 4e; Extended Data Fig. 2e), subsurface MHWs were particularly
170 prolonged (up to 3 years) and appeared to be mostly unconnected to the surface. They
171 primarily occurred below the thermocline depth (S1 Fig. 9e), where cumulative intensity
172 peaked despite the higher intensities found at the surface. Regional biodiversity patterns of
173 species and warm-edge richness varied greatly among regions and depths, ranging from
174 over 400 species richness in the subtropical South Atlantic to less than 10 in the Arctic, with
175 a richness increase in deeper demersal communities (Fig. 4; Extended Data Fig. 2). The
176 highest exposure to MHW effects, estimated in depths where richness and cumulative
177 intensity were the greatest, was between 50-100 m depth across all regions except for
178 boundary currents, where exposure peaked deeper, at 250-500 m.

179

180 **Discussion**

181 Using state-of-the-art reanalysis data, we show that globally subsurface MHWs are,
182 on average, longer and more intense than surface events, with up to 22% of the subsurface
183 ocean being in the highest biodiversity exposure category. Biodiversity impacts could be
184 greater in the upper 250 m of the ocean, where MHW (cumulative) intensity was the highest.
185 This can be particularly concerning at the warm range edge of species' distribution, where
186 thermal tolerances are easily exceeded and more impacts have been recorded^{6,7}. Thus,
187 potential depth and distribution range shifts are likely in the upper 250 m as a response to
188 acute warming, driving changes in global biodiversity patterns with consequent effects on
189 marine communities and ecological interactions^{28,29}. However, the large variability found in
190 the regional patterns of MHWs highlights a complex picture of biodiversity exposure across
191 depths and regions.

192 Our results are consistent with previous regional findings¹⁰⁻¹⁸ and show that strong
193 subsurface MHWs are conspicuous across the global ocean, with varying characteristics that
194 depend on the prevailing oceanographic conditions. Surface events often extended to a

195 considerable depth, particularly in regions of boundary currents and oceanographic fronts
196 (Fig. 4a,b), but subsurface MHWs still occurred without a surface signal, driven by distinct
197 mechanisms (Fig. 4c,d,e). MHW duration increased with depth across the ocean, yet the
198 most prolonged events were often estimated in the subsurface of polar regions (Fig. 2).
199 Despite the acknowledged uncertainties of polar estimates (see methods), additional studies
200 corroborate the trends in our findings. The long-lasting subsurface MHWs in the Arctic Ocean
201 are in line with its borealization by Atlantic³⁰ and Pacific³¹ warm subsurface water flows at
202 ~150-900 m depth. Similar trends of subsurface warming have been reported across the
203 Antarctic³², including the Weddell Sea³³, where we estimated long-lasting subsurface MHWs.

204 The spatial variation in MHW characteristics is suggestive of distinct driving
205 mechanisms for different MHW types: the surface-confined, those that are intensified in the
206 subsurface, or that do not have a surface expression and those extending below the surface
207 mixed layer (Fig. 4). Events confined to the mixed layer (e.g., Fig. 4c; S1 Fig. 9c) are likely
208 generated by surface drivers, such as surface currents^{9,34,35} or anomalies in air-sea heat
209 fluxes^{34,35}. Yet, their depth extension may depend on the stratification of the water column
210 (S1 Fig. 9c), with weak stratification linked to deeper warming^{11,13,14,16,17}. Changes in seasonal
211 timing (e.g., the beginning of monsoon season) can influence the background variability of
212 the ocean (e.g., salinity and thermocline depth), thereby affecting the probability of
213 subsurface MHW emergence, without a surface signal (e.g., Fig. 4d)¹⁰⁻¹⁷. Specifically,
214 changes in wind patterns can prevent MHW emergence through upwelling³⁶ or promote it
215 through Ekman downwelling, driving subsurface MHWs below the mixed layer (S1 Fig. 9c,d),
216 where warming is insulated from surface processes and therefore can last longer^{10-12,14-17}.

217 Rossby and equatorial Kelvin waves can also drive changes in the climate and circulation
218 conditions, influencing the emergence of subsurface MHWs around the thermocline^{17,37}. At
219 boundary currents and fronts (Fig. 4a,b), MHWs can extend hundreds of meters into the water
220 column, well below the thermocline depth (S1 Fig. 9a,b), driven by anomalous current
221 circulation^{11,12,14,15,17,18}, related to variations in their location, strength and heat content.

222 Distinguishing the mechanisms driving each MHW event is challenging due to limited large-
223 scale, long-term oceanographic and atmospheric data, as multiple, complex drivers can
224 interact favouring or preventing MHW emergence. Therefore, systematic monitoring of the
225 global ocean across depths is necessary to enable a better understanding of subsurface
226 MHW drivers and potential changes related to future climate change.

227 MHWs have caused abrupt ecosystem changes across the globe, triggering diverse
228 ecophysiological responses of marine organisms^{38–40}. Most responses have been reported
229 from shallow coastal regions (< 40 m⁴¹), however, we show high MHW (cumulative) intensities
230 in the upper 250 m, translated into increased biodiversity exposure at depths depending on
231 the oceanographic conditions (e.g., at 50–100 m in tropical gyres and 250–500 m in boundary
232 currents). Coastal ecosystems, being readily accessible, are more frequently monitored and
233 biodiversity responses of deeper ecosystems could be overlooked. Indeed, deep surveys
234 have reported MHWs impacts extending to mesopelagic reefs, down to 100 m depth^{42–44}.
235 MHW impacts can be particularly detrimental on warm range edge populations of sessile
236 species^{6,7}, whose individuals cannot move to cooler waters. Characteristic examples include
237 the coral bleaching in the Great Barrier Reef⁴⁵ and the extensive kelp forest losses in southern
238 Australia and the north-eastern Pacific^{46,47}. In regions where multiple species have their warm
239 range edges (i.e., high warm-edge exposure), such as southwestern Australia and the coast
240 of Alaska (Fig. 3), MHW effects can be magnified into entire community shifts, lasting for
241 years after the events^{38,39}. As MHWs become more frequent/intense under long-term
242 warming⁴, species depth ranges are expected to deepen⁴⁸ and may become vertically
243 compressed⁴⁹, as already reported for cold-water species in the Mediterranean Sea²⁸.
244 However, where strong internal temperature variability prevails, such as in current fronts like
245 the Gulf Stream or at thermoclines like those of tropical gyres (Fig. 4a,d), populations may
246 have adapted their physiological responses to local temperature conditions^{50–53}. But despite
247 species' plasticity, ecosystems can still suffer abrupt changes, especially when MHWs are
248 frequent^{54,55}, prolonged³⁸ and coupled with additional disturbances^{56,57}.

249 Deeper than 250 m, MHWs are on average half as intense as at the surface (<1°C).
250 Empirical evidence of ecophysiological responses to thermal stress is limited for these
251 ecosystems, but available reports show temperature changes of only 0.1-0.4°C affecting
252 species richness and community structure of nematodes at 1500 m depth⁵⁸ and peracarid
253 crustaceans at depths of 600-2300 m⁵⁹. This suggests that deep-sea biodiversity could be
254 sensitive to small temperature changes. Despite the low intensities, MHWs in the deep ocean
255 may still have implications for biodiversity, especially if coupled with declines in oxygen
256 concentration, pH and organic material fluxes^{60,61}. For example, despite the decrease in MHW
257 cumulative intensity below 500 m depth, this depth coincides with oxygen minimum zones
258 for vast regions of the ocean⁶¹, therefore even a weak MHW could act synergistically on the
259 response of the ecosystems. However, empirical evidence is needed to verify this hypothesis.

260 While most studies reporting the impact of extreme ocean temperatures on
261 biodiversity are based on surface events, the high exposure found down to 250 m depth
262 suggests that subsurface biodiversity is also at considerable risk. Previous work has shown
263 that the main driver behind the increase in intensity and frequency of MHWs is ocean
264 warming⁵. While ocean warming could be more near the surface, warming does persist in the
265 deep ocean and is projected to increase in the future⁶². As such, future MHWs will likely
266 become more frequent and intense across all depths further exposing biodiversity to their
267 effects. This might shift species' depth distributions, particularly in the upper to 250 m of the
268 ocean, potentially changing global biodiversity patterns with consequent effects on
269 ecological interactions and ecosystem processes. However, these shifts may be hindered by
270 low oxygen zones or the lack of species' physiological adaptations to the conditions of the
271 deeper ocean⁶³. Baseline empirical evidence and time-series analyses of deep-sea
272 communities under MHWs are needed to acknowledge their response to warming and
273 increased MHWs, as those may be going unnoticed.

274

275 **Acknowledgements**

276 This study received Portuguese national funds from FCT - Foundation for Science and
277 Technology through the projects UIDB/04326/2020, UIDP/04326/2020, PTDC/BIA-
278 CBI/6515/2020, LA/P/0101/2020 and DivRestore/013/2020 to EF, ES and JA, the Individual
279 Call to Scientific Employment Stimulus 2022.00861 to JA and the fellowship
280 SFRH/BD/144878/2019 to EF. A Pew Marine Fellowship to ES, funding from the Australian
281 Research Council (DP200100201) to TW, an Australian Research Council Future Fellowship
282 (FT220100475) to ASG and funding from BNP-PARIBAS Foundation, through the
283 CORESCAM project (“Coastal Biodiversity Resilience to Increasing Extreme Events in Central
284 America”) to MBA. Lastly, the authors acknowledge the Copernicus Marine Environment
285 Monitoring Service for providing the reanalysis data
286 (<https://data.marine.copernicus.eu/products>).

287

288 **Authors contributions**

289 EF, JA and ODC conceived the study. EF and JA conducted the analyses. EF led the writing
290 with the support of all authors. All authors revised the final draft and approved the submitted
291 manuscript.

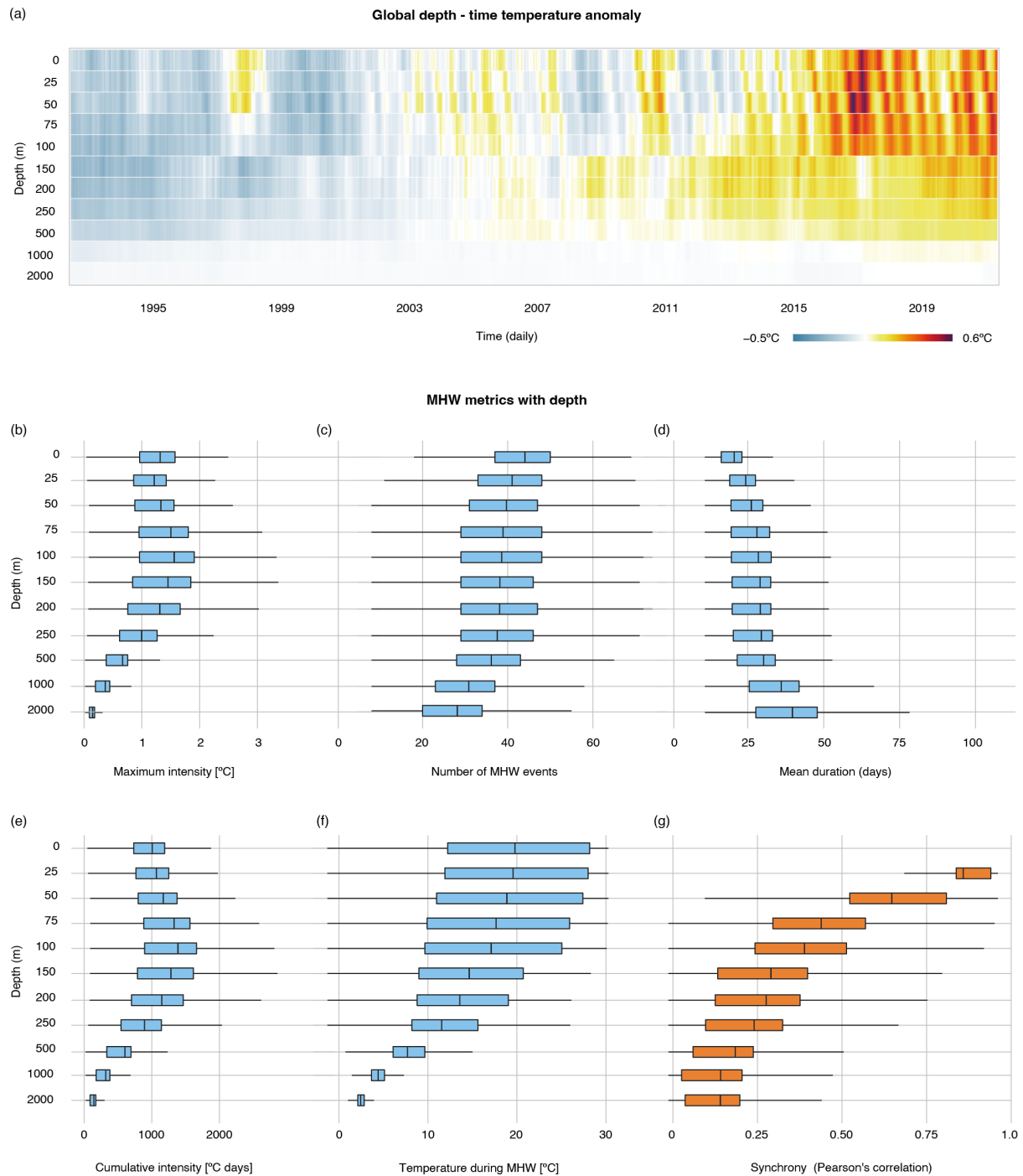
292

293 **Competing interests**

294 The authors declare no competing interests.

295

296 **Figures**



297

298

299

300

301

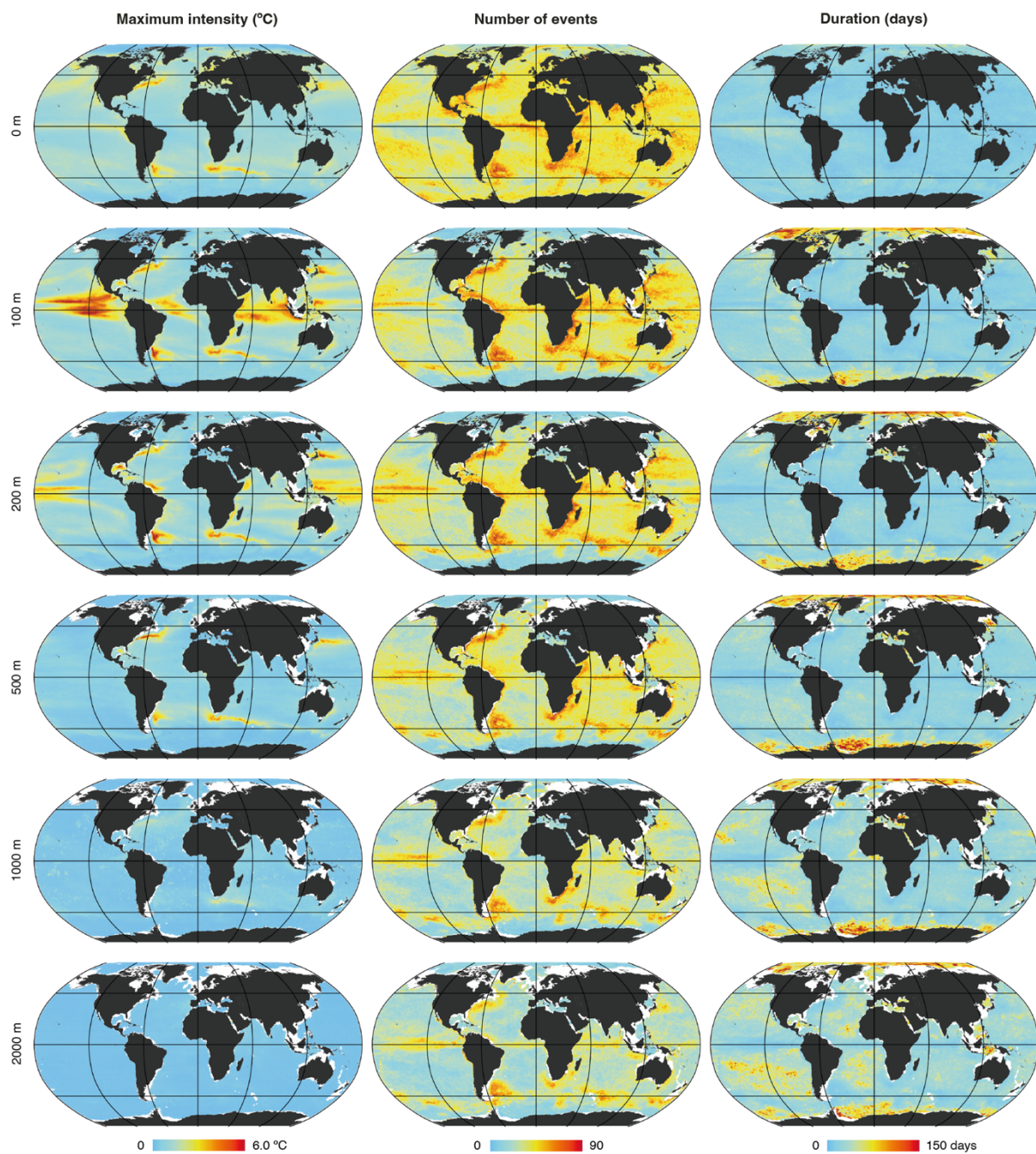
302

303

304

305

Fig. 1: Global marine heatwave (MHW) metrics from the surface to 2000 m for the period 1993-2019. **(a)** Time-depth global average temperature anomalies at each depth (levels not to scale). Global average estimates of MHW **(b)** maximum intensity, **(c)** occurrence, **(d)** duration, **(e)** cumulative intensity, and **(f)** ocean temperature during maximum MHW intensity, for each depth. **(g)** Temporal correlation of temperature anomalies between the surface and subsurface levels (95% confidence level). The boxplot central line represents the mean, edges the 25th and 75th percentile and whiskers the 5th and 95th percentile of values (n=31,073 cells). Outliers are not shown but full range values are presented in S2 Table 1.



307

308 Fig. 2. Spatial distribution of marine heatwave (MHW) metrics with depth for the period 1993-

309 2019. Global maps depicting MHW maximum intensity, occurrence (number of events from

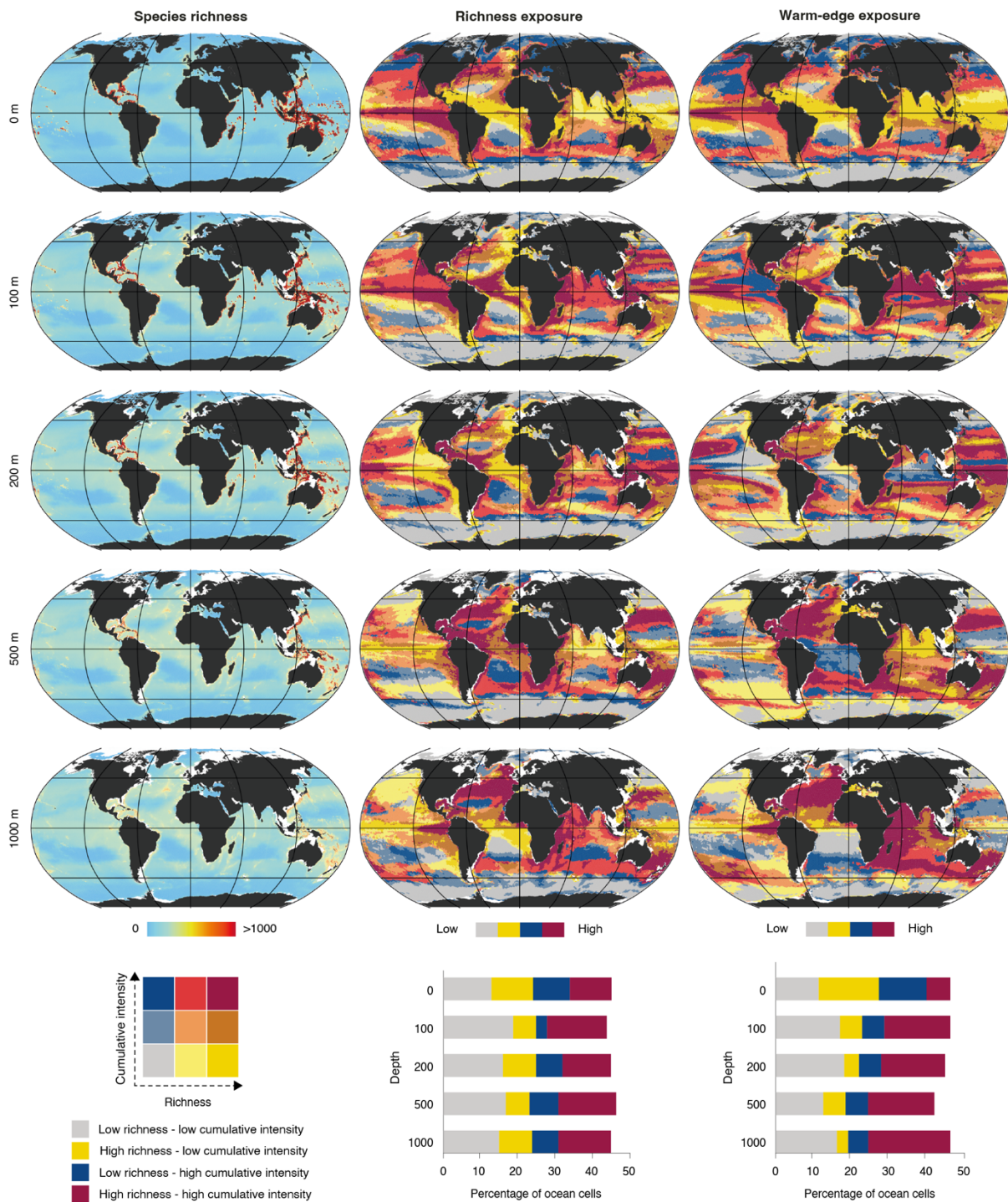
310 1993 to 2019) and average duration. White map areas have no corresponding data because

311 the ocean floor does not reach these depths. Maps are presented in Robinson projection

312 with the main graticules depicted. Scales have been adapted to improve visibility; full ranges

313 can be found in S2 Table 1.

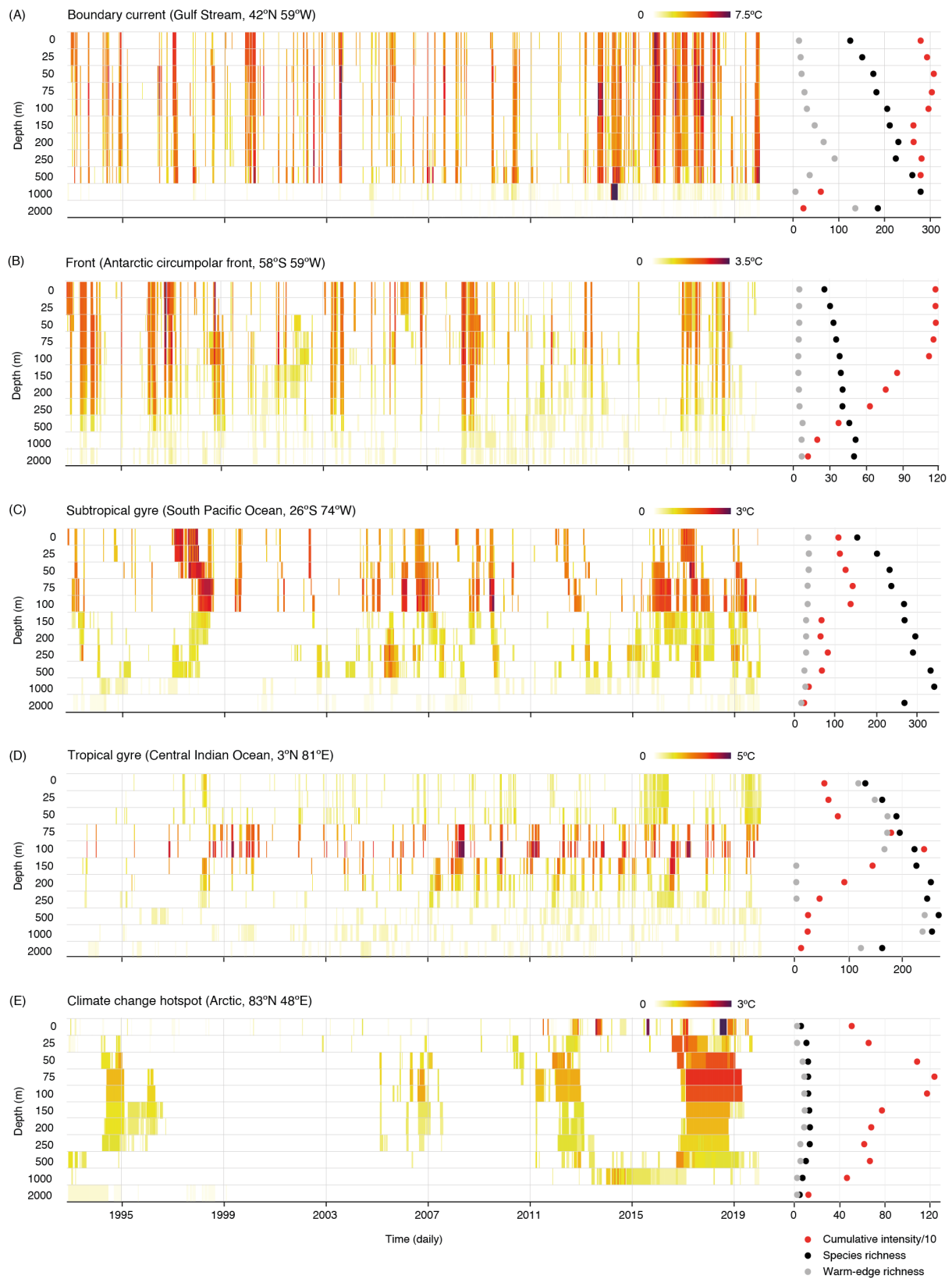
314



316

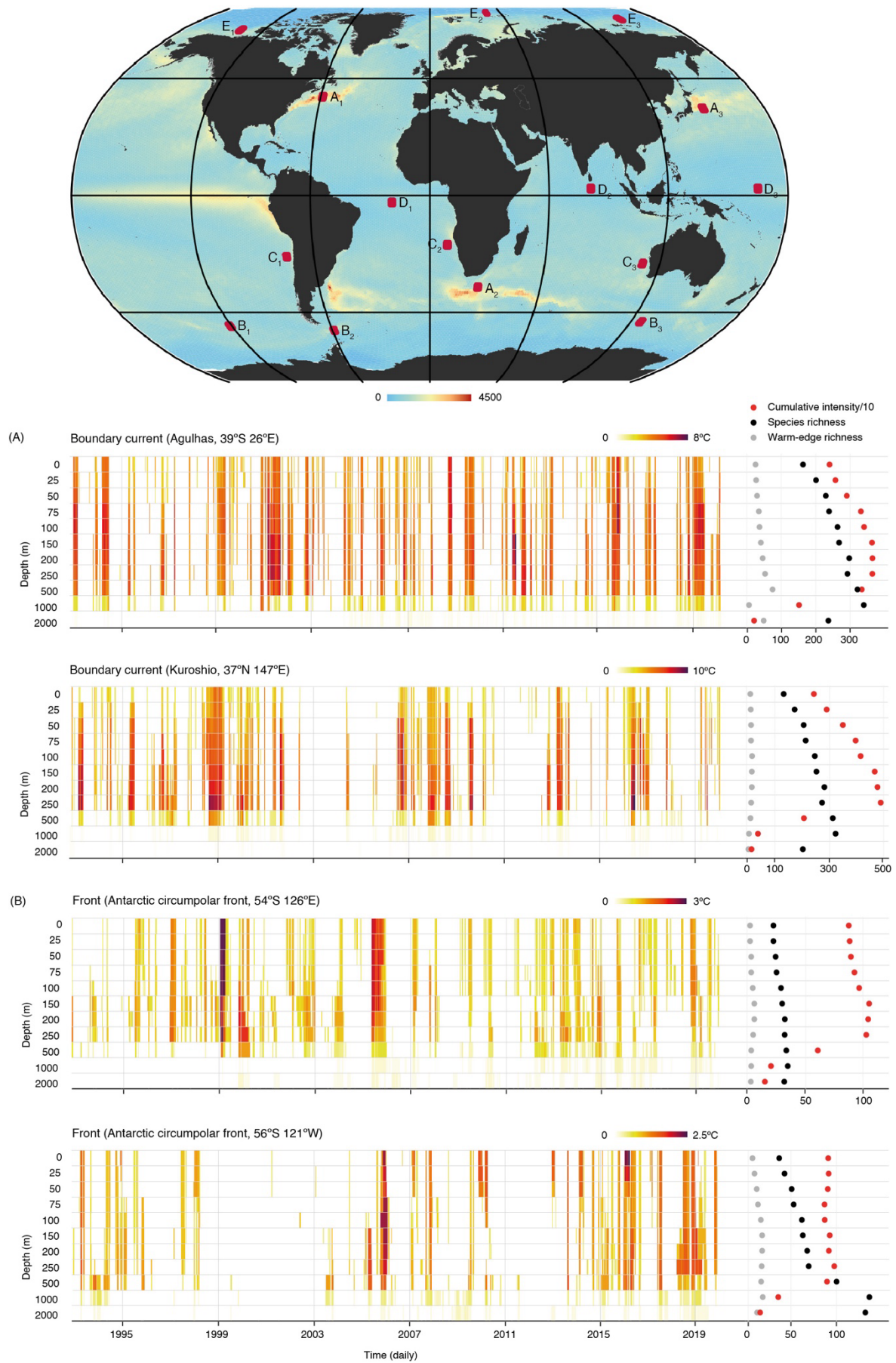
317 Fig. 3: Spatial distribution of biodiversity exposure to marine heatwaves (MHWs) with depth
 318 for the period 1993-2019. Global maps depicting species richness, richness exposure and
 319 warm-edge exposure to MHWs. Cumulative intensity, species richness and warm-edge
 320 richness were divided into terciles. Exposure was defined as the overlap of tercile
 321 combinations between cumulative intensity and biodiversity metrics, forming nine exposure
 322 categories. The percentage of ocean cells for the four most extreme overlapping terciles is

323 shown. White map areas have no corresponding data because the ocean floor does not reach
 324 these depths. Maps are presented in Robinson projection with the main graticules depicted.
 325



326

327 Fig. 4: Local marine heatwave (MHW) and biodiversity patterns in selected regions of distinct
328 oceanographic or climatic conditions. Time-depth maximum MHW intensity, cumulative
329 intensity, species and warm-edge richness for **(A)** boundary current, **(B)** oceanographic front,
330 **(C)** subtropical and **(D)** tropical gyre, and **(E)** Arctic Ocean. Depth levels and temperature
331 scales are not to scale. Regional characteristics were estimated from a 2 by 2-degree
332 resolution cell. The geographic location of each offshore region and additional analyses of
333 replicate regions are shown in Extended Data Fig. 1 and Extended Data Fig. 2.
334



335

336

Extended Data Fig. 1: Local marine heatwave (MHW) and biodiversity patterns in selected

337 regions of distinct oceanographic or climatic conditions. Global map depicting the
338 geographic location of **(A)** boundary current, **(B)** oceanographic front, **(C)** subtropical and **(D)**
339 tropical gyre, and **(E)** Arctic Ocean. Time-depth maximum MHW intensity, cumulative
340 intensity, species and warm-edge richness are shown for regions of boundary current and
341 oceanographic front (remaining regions are shown in Extended Data Fig. 2). Depth levels and
342 temperature scales are not to scale. Regional characteristics were estimated from a 2 by 2-
343 degree resolution cell. The global map features MHW cumulative intensity at the surface.
344



345

346 Extended Data Fig. 2: Local marine heatwave (MHW) and biodiversity patterns in selected

347 regions of distinct oceanographic or climatic conditions. (Continuous from Extended Data
348 Fig. 1) Time-depth maximum MHW intensity, cumulative intensity, species and warm-edge
349 richness for regions of **(C)** subtropical and **(D)** tropical gyre, and **(E)** Arctic Ocean. Depth
350 levels and temperature scales are not to scale. Regional characteristics were estimated from
351 a 2 by 2-degree resolution cell. The geographic location of each region is depicted in the
352 global map of Extended Data Fig. 1.

353

354 **References**

- 355 1. Frölicher, T. L., Fischer, E. M. & Gruber, N. Marine heatwaves under global
356 warming. *Nature* **560**, 360–364 (2018).
- 357 2. Oliver, E. C. J. *et al.* Longer and more frequent marine heatwaves over the past
358 century. *Nat Commun* **9**, 1324 (2018).
- 359 3. Tanaka, K. R. & van Houtan, K. S. The recent normalization of historical marine heat
360 extremes. *PLOS Climate* **1**, e0000007 (2022).
- 361 4. Oliver, E. C. J. *et al.* Projected Marine Heatwaves in the 21st Century and the
362 Potential for Ecological Impact. *Front Mar Sci* **6**:734, (2019).
- 363 5. Oliver, E. C. J. Mean warming not variability drives marine heatwave trends. *Clim*
364 *Dyn* **53**, 1653–1659 (2019).
- 365 6. Smale, D. A. *et al.* Marine heatwaves threaten global biodiversity and the provision of
366 ecosystem services. *Nat Clim Chang* **9**, 306–312 (2019).
- 367 7. Smith, K. E. *et al.* Biological Impacts of Marine Heatwaves. *Ann Rev Mar Sci* **15**,
368 (2023).
- 369 8. Smith, K. E. *et al.* Socioeconomic impacts of marine heatwaves: Global issues and
370 opportunities. *Science (1979)* **374**, 6566 (2021).
- 371 9. Oliver, E. C. J. *et al.* Marine Heatwaves. *Ann Rev Mar Sci* **13**, 313–342 (2021).
- 372 10. Benthuisen, J. A., Oliver, E. C. J., Feng, M. & Marshall, A. G. Extreme Marine
373 Warming Across Tropical Australia During Austral Summer 2015–2016. *J Geophys*
374 *Res Oceans* **123**, 1301–1326 (2018).
- 375 11. Elzahaby, Y. & Schaeffer, A. Observational Insight Into the Subsurface Anomalies of
376 Marine Heatwaves. *Front Mar Sci* **6**, 745 (2019).
- 377 12. Elzahaby, Y., Schaeffer, A., Roughan, M. & Delaux, S. Oceanic Circulation Drives
378 the Deepest and Longest Marine Heatwaves in the East Australian Current System.
379 *Geophys Res Lett* **48**, e2021GL094785 (2021).
- 380 13. Scannell, H. A., Johnson, G. C., Thompson, L., Lyman, J. M. & Riser, S. C.
381 Subsurface Evolution and Persistence of Marine Heatwaves in the Northeast Pacific.
382 *Geophys Res Lett* **47**, e2020GL090548 (2020).
- 383 14. Ryan, S. *et al.* Depth Structure of Ningaloo Niño/Niña Events and Associated
384 Drivers. *J Clim* **34**, 1767–1788 (2021).
- 385 15. Oliver, E. C. J. *et al.* Marine heatwaves off eastern Tasmania: Trends, interannual
386 variability, and predictability. *Prog Oceanogr* **161**, 116–130 (2018).
- 387 16. Schaeffer, A. & Roughan, M. Subsurface intensification of marine heatwaves off
388 southeastern Australia: The role of stratification and local winds. *Geophys Res Lett*
389 **44**, 5025–5033 (2017).
- 390 17. Hu, S. *et al.* Observed strong subsurface marine heatwaves in the tropical western
391 Pacific Ocean. *Environmental Research Letters* **16**, 104024 (2021).

- 392 18. Großelindemann, H., Ryan, S., Ummenhofer, C. C., Martin, T. & Biastoch, A. Marine
393 Heatwaves and Their Depth Structures on the Northeast U.S. Continental Shelf.
394 *Frontiers in Climate* **4**, 857937 (2022).
- 395 19. Jackson, J. M., Johnson, G. C., Dosser, H. v. & Ross, T. Warming From Recent
396 Marine Heatwave Lingers in Deep British Columbia Fjord. *Geophys Res Lett* **45**,
397 9757–9764 (2018).
- 398 20. Holbrook, N. J. *et al.* Keeping pace with marine heatwaves. *Nat Rev Earth Environ* **1**,
399 482–493 (2020).
- 400 21. Global Monitoring and Forecasting Center. GLORYS12V1-Global Ocean Physical
401 Reanalysis Product. *E.U. Copernicus Marine Service Information [Data set]*.
402 Available at:
403 [https://resources.marine.copernicus.eu/?option=com_csw&view=details&product_id](https://resources.marine.copernicus.eu/?option=com_csw&view=details&product_id=GLOBAL_REANALYSIS_PHY_001_030)
404 [=GLOBAL_REANALYSIS_PHY_001_030](https://resources.marine.copernicus.eu/?option=com_csw&view=details&product_id=GLOBAL_REANALYSIS_PHY_001_030) (Accessed: 13th May 2021) (2018)
405 doi:<https://doi.org/10.48670/moi-00021>.
- 406 22. Brito-Morales, I. *et al.* Climate velocity reveals increasing exposure of deep-ocean
407 biodiversity to future warming. *Nat Clim Chang* **10**, 576–581 (2020).
- 408 23. Kaschner, K. *et al.* AquaMaps: Predicted range maps for aquatic species. Retrieved
409 from <https://www.aquamaps.org>. <http://www.marine.csiro.au/csquares/> (2019).
- 410 24. Jacox, M. G. *et al.* Impacts of the 2015–2016 El Niño on the California Current
411 System: Early assessment and comparison to past events. *Geophys Res Lett* **43**, 7072–
412 7080 (2016).
- 413 25. Hobday, A. J. *et al.* A hierarchical approach to defining marine heatwaves. *Prog*
414 *Oceanogr* **141**, 227–238 (2016).
- 415 26. Holte, J., Talley, L. D., Gilson, J. & Roemmich, D. An Argo mixed layer climatology
416 and database. *Geophys Res Lett* **44**, 5618–5626 (2017).
- 417 27. Imawaki, S., Zenk, W., Wijffels, S., Roemmich, D. & Masaki, K. Oceanic Boundary
418 Currents. in *Observing the Oceans in the 21st Century* (eds. Koblinksky, C. & Smith,
419 N.) (Godae Project Office, Bureau of Meteorology, 2001).
- 420 28. Chaikin, S., Dubiner, S. & Belmaker, J. Cold-water species deepen to escape warm
421 water temperatures. *Global Ecology and Biogeography* **31**, 75–88 (2022).
- 422 29. Cartes, J. E., Maynou, F., Fanelli, E., López-Pérez, C. & Papiol, V. Changes in deep-
423 sea fish and crustacean communities at 1000–2200m in the Western Mediterranean
424 after 25years: Relation to hydro-climatic conditions. *Journal of Marine Systems* **143**,
425 138–153 (2015).
- 426 30. Polyakov, I. V. *et al.* Greater role for Atlantic inflows on sea-ice loss in the Eurasian
427 Basin of the Arctic Ocean. *Science (1979)* **356**, 285–291 (2017).
- 428 31. Woodgate, R. A. Increases in the Pacific inflow to the Arctic from 1990 to 2015, and
429 insights into seasonal trends and driving mechanisms from year-round Bering Strait
430 mooring data. *Prog Oceanogr* **160**, 124–154 (2018).
- 431 32. Schmidtko, S., Heywood, K. J., Thompson, A. F. & Aoki, S. Multidecadal warming
432 of Antarctic waters. *Science (1979)* **346**, 1227–1231 (2014).
- 433 33. Strass, V. H., Rohardt, G., Kanzow, T., Hoppema, M. & Boebel, O. Multidecadal
434 warming and density loss in the Deep Weddell Sea, Antarctica. *J Clim* **33**, 9863–9881
435 (2020).
- 436 34. Holbrook, N. J. *et al.* A global assessment of marine heatwaves and their drivers. *Nat*
437 *Commun* **10**, 2624 (2019).
- 438 35. sen Gupta, A. *et al.* Drivers and impacts of the most extreme marine heatwaves
439 events. *Sci Rep* **10**, 19359 (2020).

- 440 36. Varela, R., Rodríguez-Díaz, L., de Castro, M. & Gómez-Gesteira, M. Influence of
441 Eastern Upwelling systems on marine heatwaves occurrence. *Glob Planet Change*
442 **196**, 103379 (2021).
- 443 37. Pinault, J. L. A Review of the Role of the Oceanic Rossby Waves in Climate
444 Variability. *J Mar Sci Eng* **10**, 493 (2022).
- 445 38. Suryan, R. M. *et al.* Ecosystem response persists after a prolonged marine heatwave.
446 *Sci Rep* **11**, 6235 (2021).
- 447 39. Wernberg, T. *et al.* Climate-driven regime shift of a temperate marine ecosystem.
448 *Science (1979)* **353**, 169–172 (2016).
- 449 40. Straub, S. C. *et al.* Resistance, Extinction, and Everything in Between – The Diverse
450 Responses of Seaweeds to Marine Heatwaves. *Front Mar Sci* **6**, 763 (2019).
- 451 41. Garrabou, J. *et al.* Collaborative Database to Track Mass Mortality Events in the
452 Mediterranean Sea. *Front Mar Sci* **6**, 707 (2019).
- 453 42. Haguenaer, A. *et al.* Deep heat: A comparison of water temperature, anemone
454 bleaching, anemonefish density and reproduction between shallow and mesophotic
455 reefs. *Fishes* **6**, 37 (2021).
- 456 43. Bavestrello, G., Bo, M., Canese, S., Sandulli, R. & Cattaneo-Vietti, R. The red coral
457 populations of the gulfs of Naples and Salerno: human impact and deep mass
458 mortalities. *Italian Journal of Zoology* **81**, 552–563 (2014).
- 459 44. Perkins, N. R., Monk, J., Soler, G., Gallagher, P. & Barrett, N. S. Bleaching in
460 sponges on temperate mesophotic reefs observed following marine heatwave events.
461 *Climate Change Ecology* **3**, 100046 (2022).
- 462 45. Hughes, T. P. *et al.* Global warming and recurrent mass bleaching of corals. *Nature*
463 **543**, 373–377 (2017).
- 464 46. Arafeh-Dalmau, N. *et al.* Extreme Marine Heatwaves alter kelp forest community
465 near its equatorward distribution limit. *Front Mar Sci* **6**, 499 (2019).
- 466 47. Wernberg, T. Marine Heatwave Drives Collapse of Kelp Forests in Western
467 Australia. in *Ecosystem Collapse and Climate Change* (eds. Canadell, J. G. &
468 Jackson, R. B.) 325–343 (Springer Nature, 2021).
- 469 48. Santana-Falcón, Y. & Séférian, R. Climate change impacts the vertical structure of
470 marine ecosystem thermal ranges. *Nat Clim Chang* **12**, 935–942 (2022).
- 471 49. Jorda, G. *et al.* Ocean warming compresses the three-dimensional habitat of marine
472 life. *Nat Ecol Evol* **4**, 109–114 (2020).
- 473 50. Gouvêa, L. P. *et al.* Phenotypic Plasticity in Sargassum Forests May Not Counteract
474 Projected Biomass Losses Along a Broad Latitudinal Gradient. *Ecosystems* **26**, 29-
475 41(2022).
- 476 51. Schubert, N., Santos, R. & Silva, J. Living in a Fluctuating Environment Increases
477 Tolerance to Marine Heatwaves in the Free-Living Coralline Alga *Phymatolithon*
478 *lusitanicum*. *Front Mar Sci* **8**, 791422 (2021).
- 479 52. Coleman, M. A. & Wernberg, T. The Silver Lining of Extreme Events. *Trends Ecol*
480 *Evol* **35**, 1065–1067 (2020).
- 481 53. Pershing, A. J., Mills, K. E., Dayton, A. M., Franklin, B. S. & Kennedy, B. T.
482 Evidence for adaptation from the 2016 marine heatwave in the Northwest Atlantic
483 Ocean. *Oceanography* **31**, 152–161 (2018).
- 484 54. Seuront, L., Nicastro, K. R., Zardi, G. I. & Goberville, E. Decreased thermal tolerance
485 under recurrent heat stress conditions explains summer mass mortality of the blue
486 mussel *Mytilus edulis*. *Sci Rep* **9**, 17498 (2019).
- 487 55. Dalton, S. J. *et al.* Successive marine heatwaves cause disproportionate coral
488 bleaching during a fast phase transition from El Niño to La Niña. *Sci Total Environ*
489 **715**, 136951(2020).

- 490 56. Rogers-Bennett, L. & Catton, C. A. Marine heat wave and multiple stressors tip bull
491 kelp forest to sea urchin barrens. *Sci Rep* **9**, 15050 (2019).
- 492 57. Donovan, M. K. *et al.* Local conditions magnify coral loss after marine heatwaves.
493 *Science (1979)* **372**, 977–980 (2021).
- 494 58. Danovaro, R., Dell’Anno, A. & Pusceddu, A. Biodiversity response to climate change
495 in a warm deep sea. *Ecol Lett* **7**, 821–828 (2004).
- 496 59. Ashford, O. S. *et al.* Phylogenetic and functional evidence suggests that deep-ocean
497 ecosystems are highly sensitive to environmental change and direct human
498 disturbance. *Proc R Soc B: Biol Sci* **285**, 20180923 (2018).
- 499 60. Sweetman, A. K. *et al.* Major impacts of climate change on deep-sea benthic
500 ecosystems. *Elementa: Sci Anthropol* **5**, 4 (2017).
- 501 61. Shi, Z., Assis, J. & Costello, M. J. Vulnerability of Marine Species to Low Oxygen
502 Under Climate Change. in *Imperiled: The Encyclopedia of Conservation* (Elsevier,
503 2022).
- 504 62. IPCC 2021. *Climate Change 2021: The Physical Science Basis. Climate Change*
505 *2021: The Physical Science Basis. Contribution of Working Group I to the Sixth*
506 *Assessment Report of the Intergovernmental Panel on Climate Change [Masson-*
507 *Delmotte, V., P. Zhai, A. Pirani, S.L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen,*
508 *(2021).*
- 509 63. Gerringer, M. E. *et al.* Habitat influences skeletal morphology and density in the
510 snailfishes (family Liparidae). *Front Zool* **18**, 16 (2021).
- 511

512 **Methods**

513 **Daily global temperature data with depth covering 1993-2019**

514 MHW characteristics were estimated using daily temperature timeseries derived from
515 the Global Ocean Physics Reanalysis (GLORYS12V1)²¹ provided by the E.U. Copernicus
516 Marine Service (CMEMS). This is an eddy-permitting (1/12°) ocean reanalysis based on the
517 NEMO ocean model. The model is forced by ERA-interim (between 1993 and 2018) and ERA5
518 surface fluxes subsequently and assimilates satellite altimetry, sea surface temperature and
519 sea ice data as well as *in-situ* temperature and salinity profiles from the CORA⁶⁴ database,
520 which has global coverage and includes ARGO program data (S1 Fig. 1). Temperature data
521 are available at 50 depth levels covering the period 1993-2019.

522 The ability of the GLORYS12V1 reanalysis to capture ocean processes has been
523 previously verified against *in-situ* observations and alternative models at local⁶⁵⁻⁶⁷ and global⁶⁸
524 scales. However, some regional limitations exist. Specifically, the GLORYS12V1 shows a
525 higher than observed warming trend⁶⁸ and temperature biases (up to 1.2°C) occurring in the

526 50-100 m depth in the Atlantic and 50-200 m depth in the Indian Ocean⁶⁹. Because MHW
527 estimates depend on temperature variability and not on mean temperature²⁵, we assessed
528 the temporal variation of GLORYS12V1 against daily *in-situ* temperature datasets. Cross-
529 validation was performed between daily *in-situ* records, at the available locations
530 (geographical position, depth and date), and the nearest cell from the GLORYS12V1
531 reanalysis (as in^{69,70}). The paired relationships were statistically compared based on the mean
532 absolute error (MAE) of temperature, the mean absolute error of temperature variance from
533 the mean (MAEvar), and Pearson's correlation. The cross-validation scheme was based on
534 three different *in-situ* datasets (S1 Fig. 2): (1) the "polar moorings" timeseries dataset
535 (independent data that have not been assimilated in the reanalysis model) consisted of 47
536 moorings from 13 sources (S1 Table 1), resulting in 1.09 million daily temperature records at
537 different depths; (2) the "NOAA" timeseries dataset (assimilated in the reanalysis model)
538 consisted of 70 TAO/TRITON moorings in the tropical Pacific and 20 PIRATA moorings in the
539 Atlantic from the NOAA Pacific Marine Environmental Laboratory⁷¹, covering the period from
540 1993 to 2019, and resulting in 7.6 million daily temperature records at different depths; (3)
541 the Global Ocean Data Analysis Project (GLODAPv2.1) dataset⁷² (independent data that have
542 not been assimilated in the reanalysis model), derived by quality-controlled temperature
543 observations from cruises across the global ocean, resulting in 680,777 records at different
544 depths. Because the GLODAPv2.1 dataset does not provide temperature in timeseries, only
545 spatial differences in temperature were assessed and not temporal variability.

546 Cross-correlations of the GLORYS12V1 against the polar moorings resulted in a MAE
547 of 0.075°C, MAEvar of $1.4e^{-15}$ °C and a mean correlation across depths of 0.842 (S1 Table 2).
548 The lowest correlations were estimated at 150-500 m depth, ranging from 0.459 to 0.601 and
549 the largest MAE of 0.426°C between 0-25 m depth (S1 Table 2). Cross-correlations against
550 the NOAA moorings resulted in a MAE of 0.101°C, MAEvar of $1.8e^{-15}$ °C and a mean
551 correlation for all depths of 0.991 (S1 Table 2). The lowest correlation (0.858) was estimated
552 at 500-1000 m depth and the larger MAE of 1.2°C between 200-250 m depth. Cross-

553 correlations against the GLODAPv2.1 dataset resulted in a MAE of 0.049°C and a mean
554 correlation of 0.996 (S1 Table 2). The lowest correlation (0.983) was estimated at 500-1000
555 m depth and the larger MAE of 0.23°C between 200-250 m depth. Examples of correlation
556 plots of temperature variability between the GLORYS12V1 and the *in-situ* timeseries are
557 presented in S1 Fig. 3 and S1 Fig. 4 and all plots are available in Figshare
558 (<https://doi.org/10.6084/m9.figshare.19174985>). Also, scatterplots of the temperature
559 correlation between the GLORYS12V1 and each of the three *in-situ* datasets are presented
560 in S1 Fig. 5, S1 Fig. 6 and S1 Fig. 7. Lastly, the spatial distribution of temperature errors (S1
561 Fig. 8) for each depth was mapped onto a 2.5° grid by determining the average difference
562 between the GLORYS12V1 and all three *in-situ* datasets⁷⁰. Analyses revealed a spatial
563 distribution of errors being larger between 50-250 m depth, reaching regionally up to 6°C (S1
564 Fig. 8). However, temperature differences were mostly restricted to regions of the
565 northwestern (in the extension of the Gulf Stream) and central Atlantic Ocean (S1 Fig. 8).
566 Despite the regional temperature errors, correlations in temperature variability between the
567 reanalysis and *in-situ* datasets were still high, therefore, not affecting the MHW estimates
568 that depend on temperature variability and not on mean temperature.

569 Overall, we show that the GLORYS12V1 captures well temperature variability and can
570 be used to estimate MHWs across the global ocean, despite the existing regional differences
571 against the *in-situ* datasets. Yet, it is important to acknowledge that the reanalysis may still
572 carry biases that influence the prediction of extreme events, especially in regions/depths
573 where lower correlations were found. Specifically in polar regions, where the lowest
574 correlations between the reanalysis and *in-situ* datasets were found, MHW estimates have
575 higher uncertainty, due to the reduced number of *in-situ* data feeding the model.

576

577 **Spatial and depth resolution of global MHW estimates**

578 The GLORYS12V1 dataset was re-gridded onto an equal-area 60 km-resolution
579 hexagon grid (approx. 0.5° resolution) using Uber’s standardized hexagonal hierarchical
580 spatial data gridding system⁷³. Mean daily temperatures were retrieved for each hexagon to
581 produce distinct baseline climatologies for the identification of MHW events at eleven depths:
582 0, 25, 50, 75, 100, 150, 200, 250, 500, 1000 and 2000 m. Uber’s hexagonal framework was
583 chosen due to its equal-area projection and optimal indexing algorithm, which allows fast
584 data aggregation over its hierarchical resolutions⁷³.

585

586 **MHW analyses and characteristics with depth**

587 Marine heatwave events were identified following the definition of Hobday²⁵, which
588 defines a MHW as a discrete prolonged anomalously warm water event of at least 5-day
589 duration, during which daily temperatures exceeded the 90th percentile threshold of the
590 historical baseline climatology (in our case 27 years, from 1993 to 2019). Events less than 3
591 days apart were considered a single event. The historical baseline climatology for a given day
592 was calculated using an 11-day window centred on that date across all years of the
593 climatology period, and an additional 31-day moving average was applied to smooth the
594 climatology²⁵. A daily varying threshold was preferred to an absolute fixed value, as it allowed
595 the identification of MHW events throughout the year, rather than during the warmest
596 seasons only. Each MHW event was characterized by a set of metrics²⁵, namely the duration
597 (days), maximum intensity (°C), cumulative intensity (°C days) and the absolute temperature
598 (°C) of the ocean at the peak of maximum intensity. Metrics were estimated independently
599 for each depth. Regional (hexagon) estimates were calculated as the average of each metric
600 for the years 1993-2019.

601 Regional MHW occurrence was calculated as the total number of events from 1993-
602 2019 in each hexagon. Global estimates per depth were calculated as the average of all
603 hexagons for each depth. Regional time-depth MHW and biodiversity (see below) metrics
604 (i.e., MHW maximum intensity, cumulative intensity, temperature profiles, species richness

605 and warm-edge richness) were calculated as the daily average of hexagons at a 2 by 2-
606 degree resolution for each depth.

607 To explore potential temporal synchrony between the warming of the surface and
608 subsurface layers, Pearson's correlation coefficients for temperature anomalies were
609 determined and p-values were estimated as a measure of statistical significance ($p < 0.05$)
610 using the package "synchrony"⁷⁴ which accounts for temporal autocorrelation.

611

612 **Biodiversity data**

613 We used species richness as an indicator of biodiversity. Richness was estimated
614 from 25,078 modelled marine species ranges available in AquaMaps²³, including fishes,
615 invertebrates, mammals, algae and seagrasses. AquaMaps produces standardized species
616 distribution maps using a probability of occurrence threshold (0-1) resulting from
617 environmental niche models at 0.5° resolution. Here, we used a minimum threshold of 0.5
618 probability of occurrence to define species ranges^{22,75}. Considering the depth preferences of
619 each species provided by the AquaMaps database, we categorized their distributions on the
620 depth layers for which MHWs were estimated. Species richness was estimated as the
621 number of species with distribution ranges within each hexagon grid (approx. 0.5° resolution.
622 Because populations at the warm range edge of their distribution are more likely to exceed
623 their thermal tolerance when exposed to MHWs⁶, we inferred temperature-sensitive
624 populations for each species by dividing their distribution into terciles, corresponding to the
625 cold, central and warm distribution range edge⁶, based on the average temperature from
626 1993-2019 (derived from the same daily data used to estimate MHWs). Warm-edge richness
627 was determined as the number of species at their warm range edge within each hexagon.
628 Estimates of species richness, warm-edge richness and cumulative intensity at a given depth
629 were divided into terciles, corresponding to low, medium and high values²², and hexagons
630 were reclassified accordingly. We estimated potential richness/warm-edge exposure as the
631 overlap of MHW cumulative intensity (as a measure of cumulative heat stress on

632 biodiversity^{76,77}) and species richness/warm-edge richness per hexagon. Nine exposure
633 categories were defined as the overlap of tercile combinations between cumulative intensity
634 and biodiversity metrics. The highest exposure was considered in cells where high cumulative
635 intensity overlapped high species richness/warm-edge richness. In contrast, the lowest
636 exposure was considered in cells where low cumulative intensity overlapped high species
637 richness/ warm-edge richness.

638

639 All analyses were conducted in R⁷⁸ and the code is openly available in Figshare⁷⁹. MHWs
640 were estimated using the package “RmarineHeatWaves” and thermocline depth was
641 estimated using the function “thermo.depth” of the “rLAkeAnalyser”. Individual global maps
642 depicting MHW and biodiversity metrics can be found in Figshare
643 (<https://doi.org/10.6084/m9.figshare.19174985>).

644

645 **Data availability**

646 Daily temperature reanalysis data (GLORYS12V1) are openly provided by the E.U.
647 Copernicus Marine Service (<https://doi.org/10.48670/moi-00021>). The biodiversity dataset is
648 openly available from Aquamaps at <https://www.aquamaps.org>. The datasets used for the
649 validation of the GLORYS12V1 reanalysis are: (1) the NOAA dataset
650 (<https://doi.org/10.5270/OceanObs09.cwp.61>), available for download at:
651 <https://www.pmel.noaa.gov/tao/drupal/disdell/>, and (2) the GLODAPv2 dataset
652 (<https://doi.org/10.5194/essd-13-5565-2021>) available for download at:
653 <https://www.glodap.info/index.php/merged-and-adjusted-data-product-v22021/>. Sources
654 and detailed information on the (3) “polar moorings” dataset can be found in Supplementary
655 Material 1 Table 1.

656

657 **Code availability**

658 R code for data collection and MHW analyses is openly available on Figshare
659 (<https://doi.org/10.6084/m9.figshare.19174985>).

661 **Methods references**

- 662 64. Szekely, T., Gourrion, J., Pouliquen, S. & Reverdin, G. CORA, Coriolis Ocean Dataset
663 for Reanalysis. *SEANOE* (2023) <https://doi.org/10.17882/46219>.
- 664 65. Verezemskaya, P. *et al.* Assessing Eddying (1/12°) Ocean Reanalysis GLORYS12
665 Using the 14-yr Instrumental Record From 59.5°N Section in the Atlantic. *J Geophys*
666 *Res Oceans* **126**, e2020JC016317 (2021).
- 667 66. Artana, C. *et al.* The Malvinas Current at the Confluence With the Brazil Current:
668 Inferences From 25 Years of Mercator Ocean Reanalysis. *J Geophys Res Oceans* **124**,
669 7178–7200 (2019).
- 670 67. Poli, L. *et al.* Anatomy of Subinertial Waves Along the Patagonian Shelf Break in a
671 1/12° Global Operational Model. *J Geophys Res Oceans* **125**, e2020JC016549 (2020).
- 672 68. Lellouche, J.-M. *et al.* The Copernicus Global 1/12° Oceanic and Sea Ice GLORYS12
673 Reanalysis. *Front Earth Sci* **9**, 698876 (2021).
- 674 69. Drévillon, M. *et al.* *Quality information document for Global Ocean Reanalysis*
675 *Products GLOBAL REANALYSIS_PHY_001_030*.
676 [https://catalogue.marine.copernicus.eu/documents/QUID/CMEMS-GLO-QUID-001-](https://catalogue.marine.copernicus.eu/documents/QUID/CMEMS-GLO-QUID-001-030.pdf)
677 [030.pdf](https://catalogue.marine.copernicus.eu/documents/QUID/CMEMS-GLO-QUID-001-030.pdf) (2021) <https://doi.org/10.48670/moi-00021>.
- 678 70. Assis, J. *et al.* Bio-ORACLE v2.0: Extending marine data layers for bioclimatic
679 modelling. *Global Ecology and Biogeography* **27**, 277–284 (2018).
- 680 71. McPhaden, M. J. *et al.* The Global Tropical Moored Buoy Array. in *Proceedings of*
681 *OceanObs'09: Sustained Ocean Observations and Information for Society* 668–682
682 (European Space Agency, 2010). doi:10.5270/OceanObs09.cwp.61.
- 683 72. Olsen, A. *et al.* The global ocean data analysis project version 2 (GLODAPv2) - An
684 internally consistent data product for the world ocean. *Earth Syst Sci Data* **8**, 297–323
685 (2016).
- 686 73. Bondaruk, B., Roberts, S. A. & Robertson, C. Assessing the state of the art in Discrete
687 Global Grid Systems: OGC criteria and present functionality. *Geomatica* **74**, 9–30
688 (2020).
- 689 74. Gouhier, T. C. & Guichard, F. Synchrony: Quantifying variability in space and time.
690 *Methods Ecol Evol* **5**, 524–533 (2014).
- 691 75. Klein, C. J. *et al.* Shortfalls in the global protected area network at representing marine
692 biodiversity. *Sci Rep* **5**, 17539 (2015).
- 693 76. Laufkötter, C., Zscheischler, J. & Frölicher, T. L. High-impact marine heatwaves
694 attributable to human-induced global warming. *Science (1979)* **369**, 1621–1625 (2020).
- 695 77. Wyatt, A. S. J. *et al.* Hidden heatwaves and severe coral bleaching linked to mesoscale
696 eddies and thermocline dynamics. *Nat Commun* **14**, 25 (2023).
- 697 78. R Core Team. (2021) R: A language and environment for statistical computing. R
698 Foundation for Statistical Computing, Vienna, Austria. URL [https://www.R-](https://www.R-project.org)
699 [project.org](https://www.R-project.org).
- 700 79. Fragkopoulou *et al.*, Marine biodiversity exposed to prolonged and intense subsurface
701 heatwaves. figshare. Journal Contribution. (2023)
702 <https://doi.org/10.6084/m9.figshare.19174985>
703