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### *Marine heatwaves threaten global biodiversity and the provision of ecosystem services*

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1 **Title: Marine heatwaves threaten global biodiversity and the provision of**  
2 **ecosystem services**

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41 **Article type:** Letter

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43 **One Sentence Summary:** Marine heatwaves alter ecosystem structure and functioning at  
44 global scales.

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49 **The global ocean has warmed significantly over the past century, with far-reaching**  
50 **implications for marine ecosystems<sup>1</sup>. Concurrent with long-term persistent warming,**  
51 **discrete periods of extreme regional ocean warming (marine heatwaves, ‘MHWs’) have**  
52 **increased in frequency<sup>2</sup>. Here we quantify trends and attributes of MHWs across all**  
53 **ocean basins and examine their biological impacts from species to ecosystems. Multiple**  
54 **regions within the Pacific, Atlantic and Indian Oceans are particularly vulnerable to**  
55 **MHW intensification, due to the co-existence of high levels of biodiversity, a prevalence**  
56 **of species found at their warm range edges, or concurrent non-climatic human impacts.**  
57 **The physical attributes of prominent MHWs varied considerably, but all had**  
58 **deleterious impacts across a range of biological processes and taxa, including critical**  
59 **foundation species (corals, seagrasses and kelps). MHWs, which will likely intensify**  
60 **with anthropogenic climate change<sup>3</sup>, are rapidly emerging as forceful agents of**  
61 **disturbance with the capacity to restructure entire ecosystems and disrupt the provision**  
62 **of ecological goods and services in coming decades.**

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64 Anthropogenic climate change is driving the redistribution of species and reorganization of  
65 natural systems and represents a major threat to global biodiversity<sup>4,5</sup>. The biosphere has  
66 warmed significantly in recent decades with widespread implications for the integrity of  
67 ecosystems and the sustainability of the goods and services they provide<sup>6,7</sup>. In addition to the  
68 near ubiquitous long-term increases in temperature, the frequency of discrete extreme  
69 warming events (‘heatwaves’) has increased<sup>8,9</sup> with projections indicating they will become  
70 more frequent, more intense and longer lasting throughout the 21<sup>st</sup> Century<sup>10</sup>. While extremes  
71 occur naturally within the climate system, there is growing confidence that the observed  
72 intensification of heatwaves is due to human activities<sup>11,12</sup>. The 21<sup>st</sup> Century has already  
73 experienced record-shattering atmospheric heatwaves<sup>8,13</sup>, such as the 2003 European

74 heatwave, the Australian ‘Angry Summer’ of 2012-2013, and the European ‘Lucifer’  
75 heatwave in 2017, with devastating consequences for human health, economies and the  
76 environment<sup>8</sup>.

77

78 Discrete and prolonged extreme warming events occur in the ocean as well as the  
79 atmosphere. ‘Marine heatwaves’ (MHWs) are caused by a range of processes operating  
80 across different spatial and temporal scales, from localised air-sea heat flux to large-scale  
81 climate drivers, such as the El Niño Southern Oscillation<sup>14</sup>. Regional case studies have  
82 documented how MHWs can alter the structure and functioning of entire ecosystems by  
83 causing widespread mortality, species range shifts and community reconfiguration<sup>15-17</sup>. By  
84 impacting ecosystem goods and services, such as fisheries landings<sup>18,19</sup> and biogeochemical  
85 processes<sup>20,21</sup>, MHWs can have major socioeconomic and political ramifications. Recent  
86 high-profile ocean warming events include the record-breaking 2011 ‘Ningaloo Niño’ (2010-  
87 2011) off Western Australia<sup>22</sup>, the long-lasting ‘Blob’ (2013-2016) in the northeast Pacific<sup>23</sup>  
88 and El Niño-related extreme warming in 2016 that affected most of the Indo-Pacific<sup>24,25</sup>.  
89 These events have increased awareness of MHWs as an important climatic phenomenon  
90 affecting both physical and biological processes. Until recently, the lack of a common  
91 framework to define MHWs<sup>14</sup> has hampered attempts to examine temporal trends or to  
92 compare physical attributes or biological impacts across different events, regions or taxa.  
93 However, by defining MHWs as periods when daily sea-surface temperatures (SSTs) exceed  
94 a local seasonal threshold (i.e. the 90<sup>th</sup> percentile of climatological SST observations) for at  
95 least 5 consecutive days<sup>14</sup>, Oliver et al.<sup>2</sup> showed that the frequency and duration of MHWs  
96 have increased significantly over the past century across most of the global ocean. Here, we  
97 used the same MHW framework<sup>14</sup> to examine observed trends in the annual number of MHW  
98 days and the implications for marine ecosystems globally. We incorporated existing data on

99 marine taxon richness, the proportion of species found at their warm range edges and non-  
100 climatic human impacts to identify regions of high vulnerability, where increased occurrences  
101 of MHWs overlap with areas of high biodiversity, temperature sensitivity or concurrent  
102 anthropogenic stressors. We also conducted a meta-analysis on the impacts of MHWs, by  
103 examining ecological responses to eight prominent MHW events that have been studied in  
104 sufficient detail for formal analysis. We examined 1049 ecological observations, recalculated  
105 to 182 independent effect sizes from 116 research papers that examined responses of  
106 organisms, populations and communities to MHWs. We also explored relationships between  
107 the occurrence of MHWs and the health of three globally-significant foundation species  
108 (coral, seagrass and kelp) from three independent time series that were collected at sufficient  
109 spatiotemporal resolutions to explicitly link ecological responses to MHWs. Finally, we  
110 reviewed the literature on MHWs for evidence of impacts of these events on goods and  
111 services to human society.

112

113 The total number of MHW days per year, based on five quasi-global SST datasets, has  
114 increased globally throughout the 20<sup>th</sup> and early 21<sup>st</sup> Century (Fig. 1A). As a global average,  
115 there are over 50% more MHW days per year in the latter part of the instrumental record  
116 (1987-2016) compared to the earlier part (1925-1954)<sup>2</sup>, with most regions experiencing  
117 increases in the number of MHW days (Fig 1B). Global patterns of marine taxon richness  
118 (Fig. 1C) overlaid with trends in annual MHW days reveal regions where increased MHW  
119 occurrences can influence biologically diverse regions, in particular, southern Australia, the  
120 Caribbean Sea, and the coastline bounding the mid-eastern Pacific (Fig 1D). Given that warm  
121 range edge populations are likely to be the most impacted by MHWs (as thermal tolerances  
122 are exceeded during anomalously high temperatures), regions which support a high  
123 proportion of species found near their warm range edge will be particularly vulnerable to

124 increased MHW activity (Fig 1E). Several regions were identified as having experienced  
125 marked increases in MHW days and also supporting a high proportion of species found near  
126 their warm range edges (Fig 1F), with marine ecosystems in the southwest Pacific and the  
127 mid-west Atlantic particularly at risk. Furthermore, regions where rapid increases in the  
128 annual number of MHW days overlap with existing high-intensity non-climate human  
129 stressors (Fig 1G) include the central west Atlantic, the northeast Atlantic and the northwest  
130 Pacific (Fig. 1H). Here, existing regional pressures, including overfishing and pollution, have  
131 the potential to exacerbate MHW impacts, and vice versa.

132

133 Examination of eight prominent (and sufficiently studied) MHWs showed they varied greatly  
134 with respect to spatial extent (by a factor of >15, Fig. 2A, Fig. S1), duration (10 to 380 days)  
135 and maximum intensity (3.5 to 9.5°C above climatological SST) (Fig. 2A). It should be noted  
136 that several MHWs were primarily driven by large-scale El Niño events which, by their  
137 nature, affected ocean climate at large spatial scales. Here, the largest contiguous MHW  
138 associated with each ENSO event was identified and characterised with MHW metrics. Our  
139 meta-analysis of ecological impacts (based on Hedges *g* effect sizes to account for bias  
140 associated with small sample sizes<sup>26</sup>) detected an overall negative effect of MHWs on biota  
141 across research papers, events, taxa, and response variables ( $E = -0.93$ ; 95 CI = 0.22;  $Q =$   
142 6303,  $df = 181$ ;  $p_{\text{heterogeneity}} < 0.001$ ,  $I^2 = 97.13$ ). All eight MHWs were associated with  
143 negative ecological impacts although the mean negative effect sizes were not significantly  
144 different from zero for the two events with lowest sample sizes (Fig. 2B). There was no clear  
145 relationship between the severity of the MHW (derived from normalized MHW intensity and  
146 duration) and their observed impacts (Fig. 2B). All taxonomic groups, with the exception of  
147 fishes and mobile invertebrates, responded negatively to MHWs with birds and corals being  
148 most adversely affected (Fig. 2C). The positive fish response was, in part, driven by new

149 incursions of tropical species into impacted temperate regions<sup>16</sup>. Corals were directly affected  
150 by these MHWs, as extreme absolute temperatures resulted in widespread bleaching and  
151 mortality<sup>27,28</sup>, whereas birds were indirectly impacted through changes in prey availability<sup>29</sup>.  
152 Birds and corals are also particularly sensitive to longer term increases in sea temperature  
153 associated with ocean warming<sup>30</sup>. Overall, our analyses suggest that sessile taxa were more  
154 impacted by MHWs than mobile and planktonic taxa (Fig. 2C), perhaps because mobile taxa  
155 generally have higher thermal tolerances than less active or sessile taxa<sup>31</sup> and highly mobile  
156 species can quickly migrate in response to rapidly changing conditions<sup>16</sup>. All ecological  
157 response variables were negatively affected by MHWs, although growth and primary  
158 production were not significantly different from zero (Fig. 2D). Negative impacts were  
159 greatest for coral bleaching, survival, and reproduction (Fig. 2D), a pattern consistent with  
160 effects of warming in manipulative experiments<sup>32</sup>.

161

162 To examine links between MHWs and ecological responses, we conducted additional  
163 analysis at the species level to test the prediction that populations found towards the warm-  
164 water limit (i.e. equatorward range edge) of a species' distribution would be more negatively  
165 impacted by MHWs than other populations. From the database described above, we extracted  
166 all species level observations (645 observations from 302 species) and for each population we  
167 classified their relative position within the species range by expressing the local average SST  
168 as a proportion of the difference between the 10<sup>th</sup> and 90<sup>th</sup> percentile temperatures  
169 experienced through the species geographical range. Critically, the most negative responses  
170 to MHWs were seen in populations found towards their warm range edge (Fig. 2E), implying  
171 that extreme temperatures exceeded thermal thresholds with adverse effects. Across all  
172 species-level observations, there was a negative relationship between any given population's  
173 location within the species' range and the direction and magnitude of the MHW effect (Fig.

174 2F). This indicates that populations residing near the warm limit of a given species range are  
175 particularly vulnerable to warming events and range contractions are likely to occur in  
176 response to more frequent MHWs. Indeed, recent observations have shown that equatorward  
177 range edges of both plant and animal species have retracted poleward by >100 km following  
178 severe MHW events<sup>17,33,34</sup>.

179

180 An examination of long-term time series on the health of three globally important foundation  
181 taxa showed that increased annual number of MHW days was correlated with (i) increased  
182 coral bleaching, (ii) decreased seagrass density and (iii) decreased kelp biomass (Fig. 3).

183 Even though environmental variables such as storms, nutrients and light are known to  
184 strongly influence the health of these critical habitat-formers<sup>35</sup>, the annual number of MHW  
185 days alone was strongly and significantly correlated with observed ecological performance  
186 and, crucially, had consistently stronger correlative relationships than more frequently used  
187 measures of ocean temperature (i.e. mean and maximum SST, see Table S1). An increased  
188 number of MHW days was significantly correlated to decreased ecological health of  
189 populations of all three foundation taxa, indicating the importance of discrete extreme ocean  
190 warming events in driving ecosystem structure<sup>16,36</sup>.

191

192 A wide range of ecological goods and services derived from marine ecosystems have been  
193 severely impacted by recent MHWs (Table 1). For example, the 2011 Ningaloo Niño caused  
194 widespread loss of biogenic habitat, depleted biodiversity, disruption to nutrient cycles and  
195 shifts in the abundance and distribution of commercial fisheries species off Western Australia  
196 (Table 1). Similarly, recent MHWs in the Mediterranean Sea have been linked to local  
197 extinctions, decreased rates of natural carbon sequestration, loss of critical habitat and  
198 diminished socioeconomic value (Table 1). These services have substantial societal benefit,

199 with hundreds of millions of people benefitting from coastal marine ecosystems<sup>37,38</sup>. As such,  
200 managing and mitigating the deleterious effects of MHWs on the provision of ecosystem  
201 services is a major challenge for coastal societies.

202

203 Globally, MHWs are becoming more frequent and prolonged, and record-breaking events  
204 have been observed in most ocean basins in the past decade<sup>2</sup>. To date, the main focus of  
205 ecological research has been on trends in mean climate variables, yet discrete extreme events  
206 are emerging as pivotal in shaping ecosystems, by driving sudden and dramatic shifts in  
207 ecological structure and functioning. Given the confidence in projections of intensifying  
208 extreme warming events with anthropogenic climate change<sup>8,39</sup>, marine conservation and  
209 management approaches must consider MHWs and other extreme climatic events if they are  
210 to maintain and conserve the integrity of highly valuable marine ecosystems over the coming  
211 decades.

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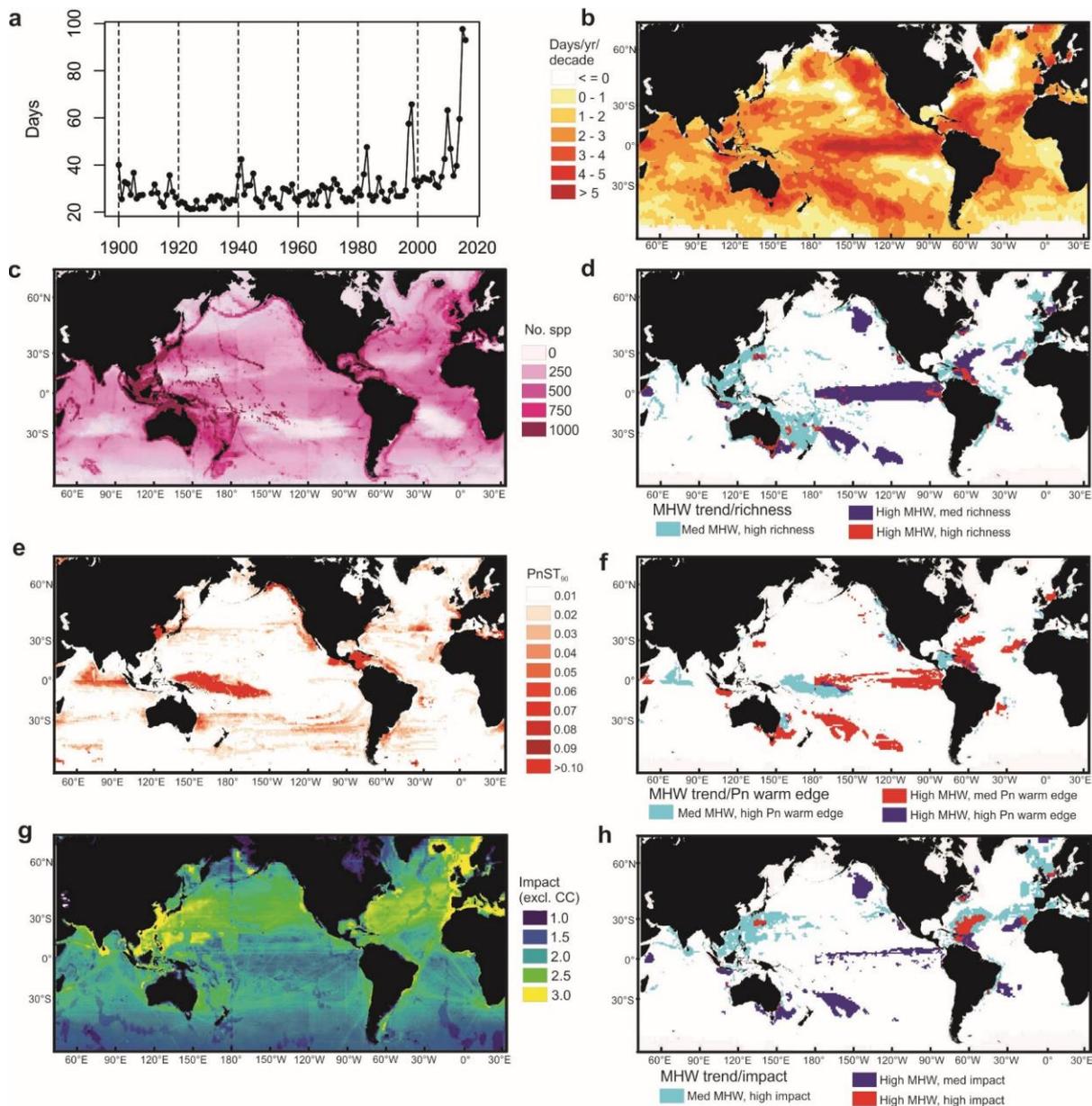


Fig. 1. Global patterns of MHW intensification, marine biodiversity, proportions of species found at their warm range edge and concurrent human impacts. **a,b**, Globally averaged time-series of the annual number of MHW days and trends in the annual number of MHW days (between 1925-1954 and 1987-2016) across the global ocean. **c,e,g**, Existing data on marine biodiversity (**c**), the proportion of species within the local species pool found near their warm range edge (**e**), and non-climatic human stressors (**g**) were combined with MHW intensification data. **d,f,h**, The resultant bivariate maps identify regions of high diversity value that may be impacted by MHWs (**d**), high thermal sensitivity of species which may have been particularly vulnerable to increased MHWs (**f**) and high levels of non-climatic human stressors where MHW intensification has impacted concurrently upon marine ecosystems (**h**).

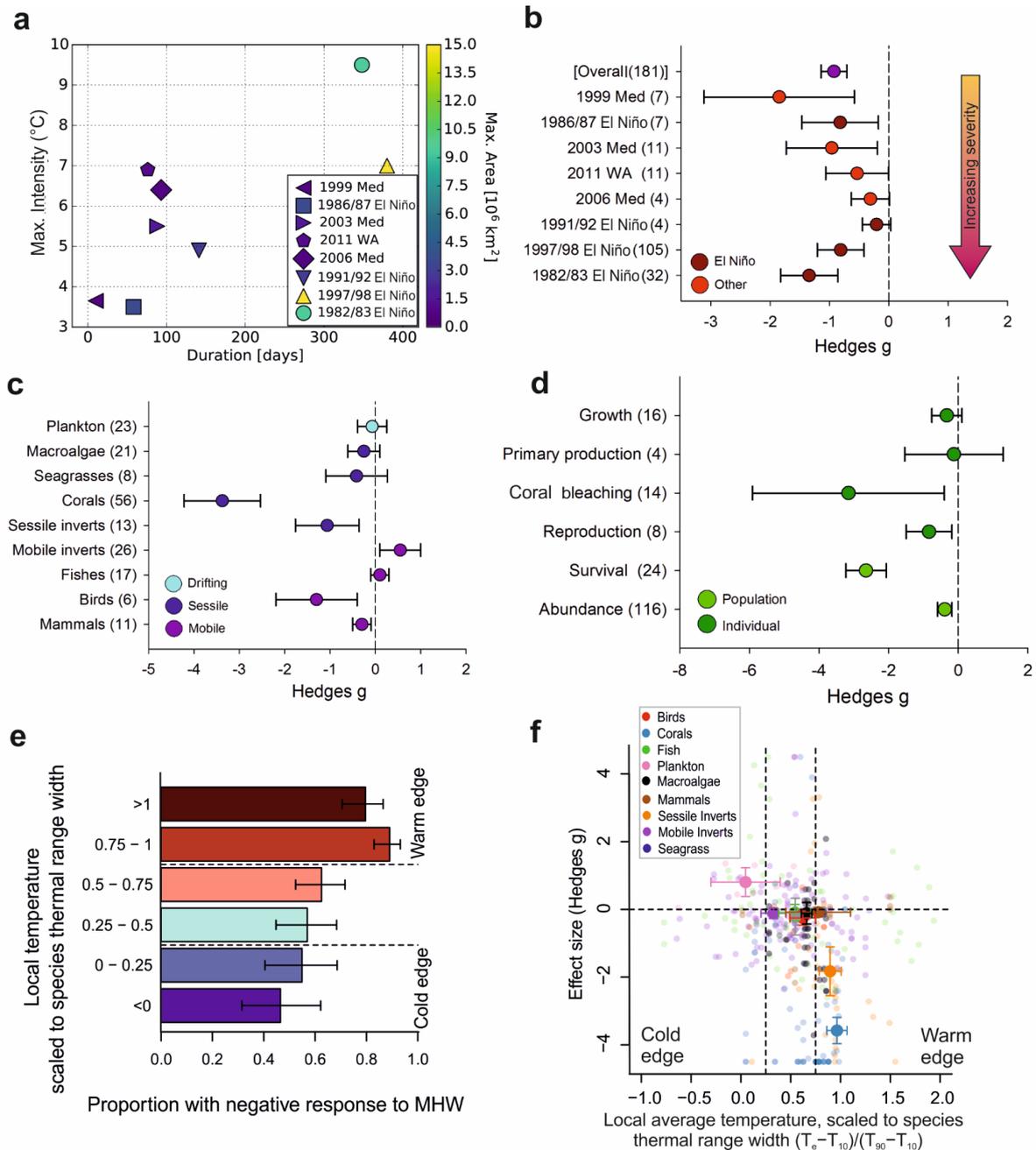
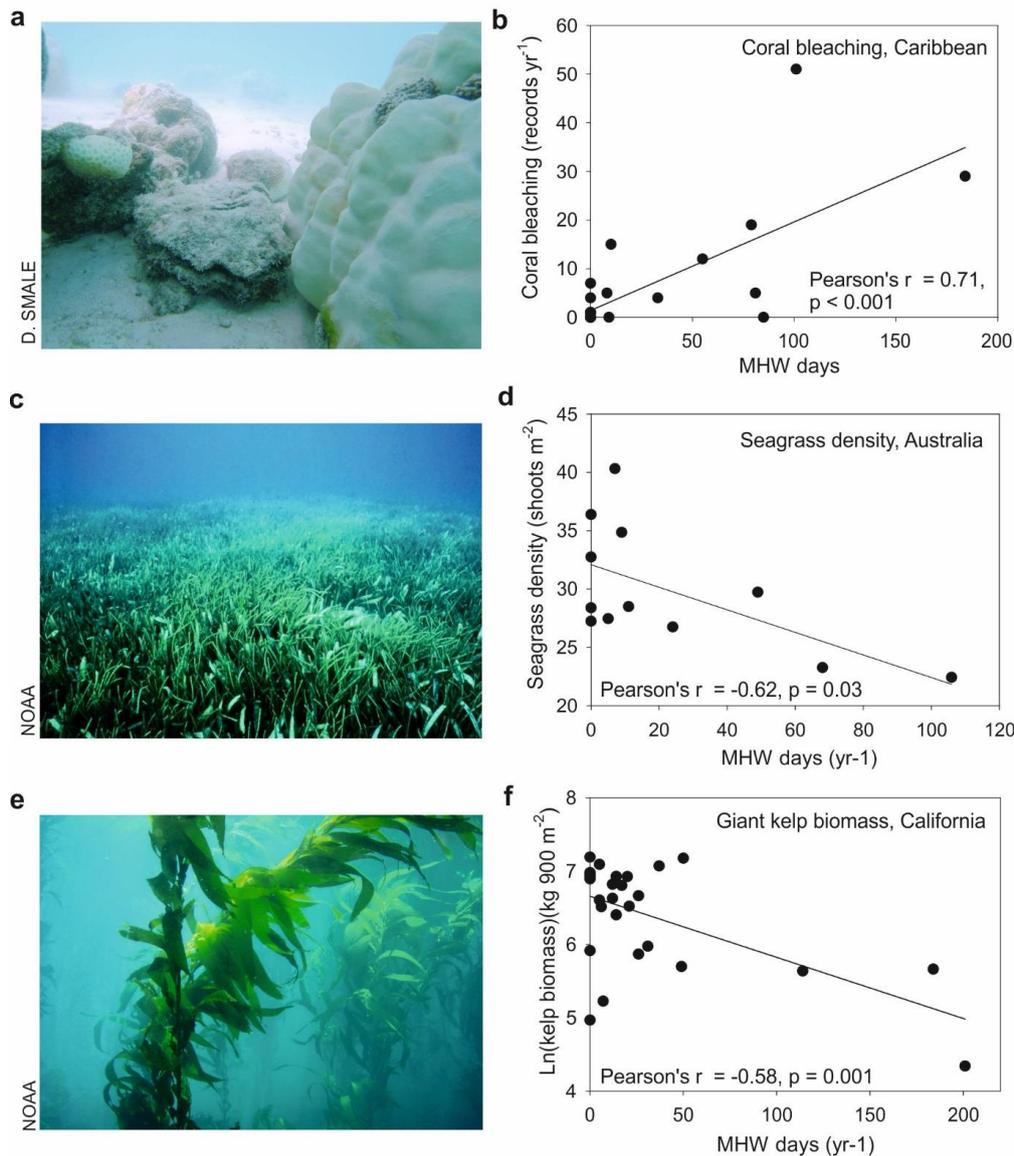


Fig. 2. Ecological impacts of MHWs as determined by a meta-analysis of responses to eight prominent MHW events. **a,b**, The attributes of the eight MHW events used in the meta-analysis (**a**) and the overall effect of each MHW event across all ecological responses (**b**). **c,d**, The effect of MHWs on major taxonomic groups (**c**) and types of ecological responses (**d**). The number of independent observations for each category are shown in parentheses and values represent mean ( $\pm 95\%$  CI) effect sizes (Hedges  $g$ , to account for bias associated with small sample sizes). **e,f**, Populations located towards the warm-water limit of species' distributions tended to respond more negatively to MHWs (**e**) with effect sizes (Hedges  $g$ ,  $\pm 95\%$  CI) generally becoming more negative for warmer equatorward range-edge populations (**f**). Plots are based on responses of 685 species-level observations; bold symbols in (**f**) indicate means for each major taxonomic group and faded symbols show individual studies ( $T_e$  temperature at effect location,  $T_{10}$ ,  $T_{90}$ , 10% and 90% species range temperatures). Horizontal (**e**) and vertical dashed lines (**f**) delineate the lower and upper quartiles of species' thermal ranges.

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Fig. 3. Impacts of MHWs on foundation species. **a,b**, Severe MHWs, such as those associated with the extreme El Niño events of 1997/98 and 2015/16, have caused widespread bleaching and mortality of reef building corals (**a**). Analysis of annual coral bleaching records from the Caribbean Sea/Gulf of Mexico region (1983-2010, data from NOAA Coral Reef Watch) showed that the number of MHW days per year was positively correlated with the frequency of coral bleaching observations (**b**). **c,d**, Seagrass meadows yield critical ecosystem services, including carbon sequestration and biogenic habitat provision, yet recent MHWs have impacted seagrass populations in several regions (**c**). Monitoring data from independent sites in Cockburn Sound, Western Australia (2003-2014, data provided by Cockburn Sound Management Council) indicated that the number of MHW days recorded in the previous year was negatively correlated with seagrass (*Posidonia sinuosa*) shoot density (**d**). **e,f**, Kelp forests represent critical habitats along temperate coastlines but extreme temperatures experienced during MHWs can cause widespread mortality and deforestation (**e**). Satellite-derived estimates of giant kelp (*Macrocystis pyrifera*) biomass along the coastline of California/Baja California (1984-2011, data from Santa Barbara Coastal Long-term Ecological Research program) showed that kelp biomass was negatively correlated with the number of MHW days recorded during the previous year (**f**).

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Table 1. Impacts of MHWs on services provided by marine ecosystems (definitions of ecosystem services adapted from The Economics of Ecosystems and Biodiversity, TEEB, developed by UNEP). Evidence of impacts was collated from specific MHWs: (a) 1982/83 El Niño event, (b) 1997/98 El Niño event, (c) 1999 Mediterranean MHW, (d) 2003 Mediterranean MHW, (e) 2011 Western Australian MHW, (f) 2012 Northwest Atlantic MHW, (g) the 2013-2016 Northeast Pacific ‘Blob’, and (h) the 2015/2016 El Niño event in northern Australia.

Service type	Ecosystem service	Impacts	Refs
Provisioning	Living resources (non-food)	- Extreme temperatures caused widespread mortality, local extinctions and range contractions of a diversity of taxa (c,d,e)	15,17,40
	Food	- Changes in the distributions and abundances of commercial fisheries species (b,e,f)	18,33,41
Regulating	Carbon sequestration and storage	- Reduced carbon burial and sequestration due to decreased growth and high mortality of seagrasses (d,e)	36,42
	Moderation of extreme events	- Complex, three-dimensional biogenic benthic habitat was replaced by simple poorly-structured habitat, altering hydrodynamics and sediment transport and reducing natural coastal defense (a,b)	43,44
	Nutrient cycling	- Increased stratification and extreme temperatures caused decreased phytoplankton production and nutrient turnover (b,g) - Widespread loss of productive benthic habitats (seagrass, kelp forests) disrupting carbon and nitrogen cycling (d,e)	16,20,36,45
	Biological control	- Anomalous warming events associated with influx of invasive non-native species (e)	33
Habitat or supporting services	Habitats for species	- Local extinctions, range contractions and high mortality rates of habitat-forming corals, seagrasses and macroalgae, resulting in simplified habitat structure and depleted local biodiversity (a,b,e,h)	34,42-44,46-48
Cultural	Tourism and recreation	- Locations affected by intense warming events are less attractive for recreational activities and have decreased socioeconomic value (d,g,h)	15,21,49,50

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## 282 References

- 283 1 IPCC. *Working group 1 contribution to the IPCC 5th assessment report (AR5), Climate Change 2013:*  
284 *The physical science basis.* (2013).
- 285 2 Oliver, E. *et al.* Longer and more frequent marine heatwaves over the past century. *Nat. Commun.* **9**,  
286 1324 (2018).
- 287 3 Frölicher, T. L., Fischer, E. M. & Gruber, N. Marine heatwaves under global warming. *Nature* **560**,  
288 360-364, doi:10.1038/s41586-018-0383-9 (2018).
- 289 4 Chen, I.-C., Hill, J. K., Ohlemüller, R., Roy, D. B. & Thomas, C. D. Rapid range shifts of species  
290 associated with high levels of climate warming. *Science* **333**, 1024-1026, doi:10.1126/science.1206432  
291 (2011).
- 292 5 Burrows, M. T. *et al.* Geographical limits to species-range shifts are suggested by climate velocity.  
293 *Nature* **507**, 492, doi:10.1038/nature12976 (2014).
- 294 6 Cardinale, B. J. *et al.* Biodiversity loss and its impact on humanity. *Nature* **486**, 59-67,  
295 doi:[http://www.nature.com/nature/journal/v486/n7401/abs/nature11148.html#supplementary-](http://www.nature.com/nature/journal/v486/n7401/abs/nature11148.html#supplementary-information)  
296 [information](http://www.nature.com/nature/journal/v486/n7401/abs/nature11148.html#supplementary-information) (2012).
- 297 7 Pecl, G. T. *et al.* Biodiversity redistribution under climate change: Impacts on ecosystems and human  
298 well-being. *Science* **355**, doi:10.1126/science.aai9214 (2017).
- 299 8 Coumou, D. & Rahmstorf, S. A decade of weather extremes. *Nature Clim. Change* **2**, 491-496 (2012).
- 300 9 Perkins, S. E., Alexander, L. V. & Nairn, J. R. Increasing frequency, intensity and duration of observed  
301 global heatwaves and warm spells. *Geophys. Res. Lett.* **39**, L20714, doi:10.1029/2012gl053361 (2012).

302 10 Meehl, G. & Tebaldi, C. More intense, more frequent, and longer lasting heat waves in the 21st  
303 Century. *Science* **305**, 994-997, doi:10.1126/science.1098704 (2004).

304 11 Trenberth, K. E., Fasullo, J. T. & Shepherd, T. G. Attribution of climate extreme events. *Nat. Clim.*  
305 *Change* **5**, 725-730, doi:10.1038/nclimate2657 (2015).

306 12 Oliver, E. C. J. *et al.* The unprecedented 2015/16 Tasman Sea marine heatwave. *Nature*  
307 *Communications* **8**, 16101, doi:10.1038/ncomms16101  
308 <https://www.nature.com/articles/ncomms16101#supplementary-information> (2017).

309 13 IPCC. *Managing the Risks of Extreme Events and Disasters to Advance Climate Change Adaptation. A*  
310 *Special Report of Working Groups I and II of the Intergovernmental Panel on Climate Change.* 582  
311 (Cambridge University Press, Cambridge, UK, and New York, NY, USA, 2012).

312 14 Hobday, A. J. *et al.* A hierarchical approach to defining marine heatwaves. *Prog. Oceanogr.* **141**, 227-  
313 238 (2016).

314 15 Garrabou, J. *et al.* Mass mortality in Northwestern Mediterranean rocky benthic communities: effects  
315 of the 2003 heat wave. *Glob. Change Biol.* **15**, 1090-1103, doi:10.1111/j.1365-2486.2008.01823.x  
316 (2009).

317 16 Wernberg, T. *et al.* An extreme climatic event alters marine ecosystem structure in a global  
318 biodiversity hotspot. *Nat. Clim. Change* **3**, 78-82, doi:10.1038/nclimate1627 (2013).

319 17 Smale, D. A. & Wernberg, T. Extreme climatic event drives range contraction of a habitat-forming  
320 species. *Proc. Roy. Soc. B Biol. Sci.* **280**, 20122829 doi:10.1098/rspb.2012.2829 (2013).

321 18 Mills, K. E. *et al.* Fisheries management in a changing climate lessons from the 2012 ocean heat wave  
322 in the Northwest Atlantic. *Oceanography* **26**, 191-195 (2013).

323 19 Cavole, L., M. *et al.* Biological impacts of the 2013-2015 warm-water anomaly in the Northeast  
324 Pacific: Winners, losers, and the future. *Oceanography* **29**, 273-285 (2016).

325 20 Chavez, F. P. *et al.* Biological and chemical consequences of the 1997-1998 El Niño in central  
326 California waters. *Prog. Oceanogr.* **54**, 205-232, doi:[http://dx.doi.org/10.1016/S0079-6611\(02\)00050-2](http://dx.doi.org/10.1016/S0079-6611(02)00050-2)  
327 (2002).

328 21 McCabe, R. M. *et al.* An unprecedented coastwide toxic algal bloom linked to anomalous ocean  
329 conditions. *Geophys. Res. Lett.* **43**, 10,366-310,376, doi:10.1002/2016GL070023 (2016).

330 22 Pearce, A. F. & Feng, M. The rise and fall of the “marine heat wave” off Western Australia during the  
331 summer of 2010/2011. *J. Mar. Syst.* **111-112**, 139-156,  
332 doi:<http://dx.doi.org/10.1016/j.jmarsys.2012.10.009> (2013).

333 23 Bond, N. A., Cronin, M. F., Freeland, H. & Mantua, N. Causes and impacts of the 2014 warm anomaly  
334 in the NE Pacific. *Geophys. Res. Lett.* **42**, 3414-3420, doi:10.1002/2015gl063306 (2015).

335 24 Hughes, T. P. *et al.* Spatial and temporal patterns of mass bleaching of corals in the Anthropocene.  
336 *Science* **359**, 80-83, doi:10.1126/science.aan8048 (2018).

337 25 Benthuisen, J. A., Oliver, E. C. J., Feng, M. & Marshall, A. G. Extreme marine warming across  
338 tropical Australia during austral summer 2015-2016. *J. Geophys. Res. Oceans* **online**, n/a-n/a,  
339 doi:10.1002/2017JC013326 (2018).

340 26 Borenstein, M., Hedges, L. V., Higgins, J. P. T. & Rothstein, H. R. *Introduction to Meta-Analysis.*  
341 (John Wiley & Sons, Ltd. West Sussex, UK., 2009).

342 27 Moore, J. A. Y. *et al.* Unprecedented Mass Bleaching and Loss of Coral across 12° of Latitude in  
343 Western Australia in 2010-11. *PLoS ONE* **7**, e51807, doi:10.1371/journal.pone.0051807 (2012).

344 28 Smith, T. B., Glynn, P. W., Maté, J. L., Toth, L. T. & Gyory, J. A depth refugium from catastrophic  
345 coral bleaching prevents regional extinction. *Ecology* **95**, 1663-1673, doi:10.1890/13-0468.1 (2014).

346 29 Vargas, F. H., Harrison, S., Rea, S. & Macdonald, D. W. Biological effects of El Niño on the  
347 Galápagos penguin. *Biol. Conserv.* **127**, 107-114, doi:<http://dx.doi.org/10.1016/j.biocon.2005.08.001>  
348 (2006).

349 30 Poloczanska, E. S. *et al.* Global imprint of climate change on marine life. *Nat. Clim. Change* **3**, 919-  
350 925, doi:10.1038/nclimate1958 (2013).

351 31 Somero, G. N. The physiology of climate change: how potentials for acclimatization and genetic  
352 adaptation will determine ‘winners’ and ‘losers’. *J. Exp. Biol.* **213**, 912-920, doi:10.1242/jeb.037473  
353 (2010).

354 32 Harvey, B. P., Gwynn-Jones, D. & Moore, P. J. Meta-analysis reveals complex marine biological  
355 responses to the interactive effects of ocean acidification and warming. *Ecol. Evol.* **3**, 1016-1030,  
356 doi:10.1002/ece3.516 (2013).

357 33 Pearce, A. *et al.* *The “marine heat wave” off Western Australia during the summer of 2010/11.*  
358 *Fisheries Research Report No. 222.* (Department of Fisheries, 2011).

359 34 Wernberg, T. *et al.* Climate driven regime shift of a temperate marine ecosystem. *Science* **353**, 169-172  
360 (2016).

- 361 35 Halpern, B. S., Selkoe, K. A., Micheli, F. & Kappel, C. V. Evaluating and ranking the vulnerability of  
362 global marine ecosystems to anthropogenic threats. *Conserv. Biol.* **21**, 1301-1315, doi:10.1111/j.1523-  
363 1739.2007.00752.x (2007).
- 364 36 Marba, N. & Duarte, C. M. Mediterranean warming triggers seagrass (*Posidonia oceanica*) shoot  
365 mortality. *Glob. Change Biol.* **16**, 2366-2375 (2010).
- 366 37 Liqueste, C. *et al.* Current status and future prospects for the assessment of marine and coastal  
367 ecosystem services: A systematic review. *PLOS ONE* **8**, e67737, doi:10.1371/journal.pone.0067737  
368 (2013).
- 369 38 Cavanagh, R. D. *et al.* Valuing biodiversity and ecosystem services: a useful way to manage and  
370 conserve marine resources? *Proc. Roy. Soc. B Biol. Sci.* **283**, doi:10.1098/rspb.2016.1635 (2016).
- 371 39 Cai, W. *et al.* Increased frequency of extreme La Nina events under greenhouse warming. *Nat. Clim.*  
372 *Change* **5**, 132-137, doi:10.1038/nclimate2492  
373 <http://www.nature.com/nclimate/journal/v5/n2/abs/nclimate2492.html#supplementary-information> (2015).
- 374 40 Cerrano, C. *et al.* A catastrophic mass-mortality episode of gorgonians and other organisms in the  
375 Ligurian Sea (North-western Mediterranean), summer 1999. *Ecol. Lett.* **3**, 284-293,  
376 doi:10.1046/j.1461-0248.2000.00152.x (2000).
- 377 41 Ñiquen, M. & Bouchon, M. Impact of El Niño events on pelagic fisheries in Peruvian waters. *Deep Sea*  
378 *Res Pt 2* **51**, 563-574, doi:<http://dx.doi.org/10.1016/j.dsr2.2004.03.001> (2004).
- 379 42 Thomson, J. A. *et al.* Extreme temperatures, foundation species, and abrupt ecosystem change: an  
380 example from an iconic seagrass ecosystem. *Glob. Change Biol.* **21**, 1463-1474,  
381 doi:10.1111/gcb.12694 (2015).
- 382 43 Brown, B. E. & Suharsono. Damage and recovery of coral reefs affected by El Niño related seawater  
383 warming in the Thousand Islands, Indonesia. *Coral Reefs* **8**, 163-170, doi:10.1007/bf00265007 (1990).
- 384 44 Edwards, M. S. Estimating scale-dependency in disturbance impacts: El Niños and giant kelp forests in  
385 the northeast Pacific. *Oecologia* **138**, 436-447, doi:10.1007/s00442-003-1452-8 (2004).
- 386 45 Whitney, F. A. Anomalous winter winds decrease 2014 transition zone productivity in the NE Pacific.  
387 *Geophys. Res. Lett.* **42**, 428-431, doi:10.1002/2014gl062634 (2015).
- 388 46 Glynn, P. W. El Niño-associated disturbance to coral reefs and post disturbance mortality by  
389 *Acanthaster planci* *Mar. Ecol. Prog. Ser.* **26**, 395-300 (1985).
- 390 47 Le Nohaïc, M. *et al.* Marine heatwave causes unprecedented regional mass bleaching of thermally  
391 resistant corals in northwestern Australia. *Sci. Rep.* **7**, 14999, doi:10.1038/s41598-017-14794-y (2017).
- 392 48 Hughes, T. P. *et al.* Global warming and recurrent mass bleaching of corals. *Nature* **543**, 373,  
393 doi:10.1038/nature21707 (2017).
- 394 49 Rodrigues, L. C., van den Bergh, J. C. J. M., Loureiro, M. L., Nunes, P. A. L. D. & Rossi, S. The cost  
395 of Mediterranean sea warming and acidification: a choice experiment among scuba divers at Medes  
396 Islands, Spain. *Environ Resource Econ.* 1-23, doi:10.1007/s10640-015-9935-8 (2015).
- 397 50 Prideaux, B., Thompson, M., Pabel, A. & Anderson, A. C. in *CAUTHE 2017: Time For Big Ideas? Re-*  
398 *thinking The Field For Tomorrow* (eds C. Lee, S. Filep, J. N. Albrecht, & W. J. L. Coetzee) (Dunedin,  
399 New Zealand: Department of Tourism, University of Otago, 2017).
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416

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423

## 424 **Methods**

### 425 **1. Definition of MHWs and analysis of multi-decadal trends**

426 Marine heatwaves (MHWs) were identified from observational sea surface temperature (SST)  
427 time series using the definition proposed by Hobday et al.<sup>14</sup>, whereby a MHW is defined as a  
428 “*discrete prolonged anomalously warm water event at a particular location*” with each of those  
429 terms (anomalously warm, prolonged, discrete) quantitatively defined and justified for the  
430 marine context. Specifically, “*discrete*” implies the MHW is an identifiable event with clear start  
431 and end dates, “*prolonged*” means it has a duration of at least five days, and “*anomalously*  
432 *warm*” means the temperature is above a climatological threshold (in this case the seasonally-  
433 varying 90<sup>th</sup> percentile). The climatological mean and threshold were calculated over a base  
434 period of 1983-2012. For each day-of-year, a pool of days across all years in the climatology  
435 period and within an 11-day window was taken as a sample, from which the mean and 90<sup>th</sup>  
436 percentile threshold were calculated. The climatological mean and threshold were then further  
437 smoothed using a 30-day running window. When two successive events occur with a break of  
438 two days or less, this was deemed to represent a single continuous event. The code used to  
439 identify MHWs and calculate key MHW metrics following this definition is freely available and  
440 has been implemented in Python (<https://github.com/ecjoliver/marineHeatWaves>) and R  
441 (<https://robwschlegel.github.io/heatwaveR>). MHWs detected using this definition were then  
442 characterized by a set of metrics, including duration and intensity (i.e. the maximum daily  
443 temperature above the seasonal climatology during the event). We then examined an annual time  
444 series of “total MHW days”, which is the sum of days categorized as MHWs in any given year.

445 Global time series and regional trends in total MHW days were derived using a combination of  
446 satellite-based, remotely-sensed SSTs and *in situ*-based seawater temperatures. First, total MHW  
447 days were calculated globally over 1982-2015 at 1/4° resolution from the National Oceanic and  
448 Atmospheric Administration (NOAA) Optimum Interpolation (OI) SST V2 high resolution data.  
449 Then, proxies for total MHW days globally over 1900-2016 were developed based on five  
450 monthly gridded SST datasets (HadISST v1.1, ERSST v5, COBE 2, CERA-20C and SODA  
451 si.3). A final proxy time series was calculated by averaging across the five datasets. The five  
452 monthly data sets were used since no global daily SST observations are available prior to 1982.  
453 From these proxy time-series we calculated (i) the difference in mean MHW days over the 1987-  
454 2016 and 1925-1954 periods and (ii) a globally-averaged times series of total MHW days.  
455 Further details on this method and resulting proxy data can be found in Oliver et al.<sup>2</sup>. Note that  
456 these calculations use the same climatology period as above, 1983-2012.

## 457 **2. Global patterns of MHW intensification and overlaps with known hotspots of marine** 458 **biodiversity, temperature-sensitive populations and non-climatic human stressors**

459 We combined regional trends in MHW days with pre-existing data on marine biodiversity, the  
460 proportion of species found near their warm range edges, and non-climatic human stressors to  
461 predict where MHW intensification may be a particular threat to biodiversity hotspots or  
462 temperature-sensitive communities, or be exacerbated by concurrent stressors. Biodiversity  
463 hotspots were determined using published marine taxon richness data<sup>51</sup>, which were accumulated  
464 from projected species distributions from the Aquamaps project<sup>52</sup>. Patterns in taxon richness  
465 (Fig. 1C) showed characteristically high levels in coastal areas and in tropical regions. We also  
466 calculated the proportion of species in the local species pool that were near their warm range  
467 edge to determine locations where MHWs might be more likely to have a strong negative effect

468 (as shown in Fig. 2F). We used 16,582 species global distribution maps from the Aquamaps  
469 project<sup>52</sup>, previously used to assess likely patterns of biodiversity change<sup>51</sup>, to represent global  
470 marine biodiversity. For each 1° latitude/longitude grid cell we counted the number of species  
471 present for which sea surface temperature, derived as the 1960-2009 average annual temperature  
472 from the Hadley Centre HadISST v1.1 dataset, exceeded the 90<sup>th</sup> percentile temperature of their  
473 geographical range, and divided this by the total number of species present. Aside from some  
474 artifacts where species geographical limits coincide with FAO (Food and Agriculture  
475 Organization of the United Nations) region boundaries, a feature prevalent in other studies using  
476 these datasets<sup>53</sup>, the resulting map (Fig. 1E) showed areas with higher proportions of species at  
477 their warm range edges. Major concentrations (proportions >0.1 of all species) of warm-edge  
478 species were seen in the Eastern Mediterranean, the southern Red Sea, the Caribbean Sea, the  
479 Mexican part of the North Pacific and a large part of the tropical west Pacific. Locally higher  
480 proportions of warm-edge species were also seen along coastlines of Europe, western USA and  
481 Canada, North Africa and in the Yellow Sea.

482 Information on stressors were obtained from supplementary online resources provided by  
483 Halpern et al.<sup>54</sup>. We additively combined multiple impact layers (demersal destructive fishing,  
484 demersal non-destructive high bycatch, demersal non-destructive low bycatch, ocean  
485 acidification, ocean pollution, pelagic high bycatch, pelagic low bycatch, shipping and UV) into  
486 a single cumulative impacts layer (Fig. 1E). Fishing intensity layers were obtained by  
487 apportioning reported catches in FAO areas by modelled productivity data for latitude/longitude  
488 cells. Shipping impacts were derived from a 12-month (2003-2004) global ship observing  
489 scheme, and the same data was used with ports data to give a measure of ocean pollution.  
490 Surface UV information was obtained from the GSFC TOMS EP/TOMS satellite program at

491 NASA. Ocean acidification data came from globally modelled aragonite saturation state. Details  
492 of the quantification of these layers are given in Halpern et al.<sup>54,55</sup>. Layers that included ocean  
493 warming variables were specifically excluded due to likely co-variance (to varying extents) with  
494 MHW metrics. The cumulative impacts layer was then re-projected and resampled onto the  
495 same 1°×1° grid as for trends in total MHW days and biodiversity data. Maps of the  
496 combinations of medium to high trends in total MHW days and medium to high values of taxon  
497 richness (Fig. 1C) or cumulative impacts (Fig. 1E) were created by splitting the data into classes  
498 based on the percentiles of the distribution of each variable (0-50% low, 50-90% medium, >90%  
499 high). Combined MHW trend/richness and MHW trend/impact layers were assigned to  
500 categories according to the classes of each contributing layer. While spatial bias due to  
501 variability in sampling effort may influence, to some degree, global-scale datasets on physical  
502 and biological variables, the datasets used in the current study have near-complete global  
503 coverage and represent the best approximations available for temperature<sup>56</sup>, species richness and  
504 distributions<sup>57</sup> and human stressors<sup>54</sup>.

### 505 **3. Meta-analysis of ecological responses to MHWs**

#### 506 **Dependent and independent variables, literature searches and hypothesis**

507 The meta-analysis followed PRISMA (Preferred Reporting Items for Systematic Reviews and  
508 Meta-Analyses) guidelines, which provide an evidence-based minimum set of requirements for  
509 conducting and reporting meta-analyses (Fig. S2). We searched for peer reviewed studies that  
510 compared six types of biological ‘performance response’ (survival, abundance, growth,  
511 reproduction, primary production or coral bleaching) that reported data variation, before and  
512 after any of eight well-described periods of extreme warming (El Niño related events in 1982/83,  
513 1986/87, 1991/92 and 1997/98, the Mediterranean MHWs of 1999, 2003 and 2006, and the 2011

514 MHW in Western Australia). Relevant studies were identified from two literature searches. First,  
515 we conducted a standardized Web of Science search, with search terms related to climate change,  
516 heat waves, marine systems, and the eight MHWs mentioned above. We used the following  
517 specific search string: ('TS=((marine AND ("heat wave" OR heatwave)) OR El Niño OR La  
518 Niña OR ENSO OR (marine AND warming)'), identifying 29,395 potentially relevant papers.  
519 We read all abstracts from these papers and then obtained the full manuscripts of the papers that  
520 in their title, abstract, or keywords, indicated that relevant data could be collected (= 517 papers).  
521 We read all these papers in detail to identify 116 papers that fulfilled our data criteria. For each  
522 of the identified publications we extracted all reported mean performance response, data  
523 dispersion and sample sizes, from text, tables and figures with Plot Digitizer™  
524 (<http://plotdigitizer.sourceforge.net/>). Impact studies were widely distributed across the global  
525 ocean; impact studies relating to ENSO-associated MHWs were spread across the Pacific and  
526 Indian Oceans whereas impact studies relating to Mediterranean and Australian MHWs were  
527 conducted across a smaller area (Fig. S3). Our fundamental hypothesis was that MHWs  
528 generally had negative effects on ecological performance across studies, bioregions, events,  
529 response types and organisms. We also tested (see next section for method) if the magnitude of  
530 effects varied between heatwave events (eight MHW events), performance responses (6 types  
531 listed above) and impacted taxa (grouped into mammals, birds, fishes, mobile invertebrates, non-  
532 coral sessile invertebrates, corals, macroalgae, seagrasses and plankton, which included  
533 phytoplankton, zooplankton and open ocean microbes). For the MHW test, we hypothesized that  
534 the intensity of an event would correlate with the magnitude of effect size. For the biological  
535 response test, we hypothesized that coral bleaching and reproduction would be most affected by  
536 MHWs, the former because corals are known to be sensitive to elevated temperatures and the

537 latter because reproduction is typically more sensitive to stress than growth, abundance and  
538 survival. Finally, for the test across taxa we hypothesized that mobile organisms and  
539 seagrasses/corals would exhibit the largest effect sizes because mobile organisms can respond  
540 rapidly (e.g. local heat-stressed species can emigrate and warm-tolerant species from adjacent  
541 region can immigrate) and seagrasses/corals are generally sensitive to elevated temperatures.

#### 542 **Effect sizes, data pooling, dealing with outliers and autocorrelation and statistical tests**

543 We analyzed impacts of MHWs on events, taxa and performance with Hedges  $g$  effect size,  
544 corrected for small sample sizes. Hedges'  $g$  was calculated as  $(MHW_{After} - MHW_{Before})/S \times J$ ,  
545 where  $S$  is the pooled standard deviation and  $J$  is a factor that corrects for bias associated with  
546 small sample sizes<sup>26,58</sup>. 'MHW<sub>before</sub>' and 'MHW<sub>after</sub>' represent the mean performance response  
547 reported by the study before and after the period of extreme warming, respectively. These relied  
548 on the authors' designations of the timing of the MHW. When the mean performance response  
549 before the MHW event were reported for multiple time points, an average was taken to obtain  
550 'MHW<sub>before</sub>'. In these cases, the associated variance of the time points was also pooled for use in  
551  $S$ . In this analysis, negative and positive effects reflect inhibition and facilitation of organismal  
552 performance, respectively. Analyses were weighted by the sum of the inverse variance in each  
553 study and the variance pooled across studies and therefore give greater weight to those studies  
554 with higher replication and lower data dispersion. We used random-effect models, thereby  
555 assuming that summary statistics have both sampling error and a true random component of  
556 variation in effect sizes between studies<sup>26,58</sup>. Most publications reported multiple auto-correlated  
557 effects, for example when a study reported effects of a MHW on many different coral species.  
558 Within-study effects are typically not statistically independent from each other and will conflate  
559 analyses, for example by artificially increasing degrees of freedom. We reduced within-study

560 autocorrelation by averaging 1049 non-independent Hedges  $g$  values (extracted from 116  
561 identified research papers) to 182 values, each being characterized by a unique combination of a  
562 MHW, impacted taxa and performance response per research paper. Thus, prior to formal meta-  
563 analyses, within-study effects were averaged across multiple species and across nested designs  
564 (e.g., across different sites within a study or different depth levels). We acknowledge that our  
565 approach to aggregate auto-correlated within-study effect sizes, albeit being the most common  
566 way to do this<sup>59</sup>, may be suboptimal, compared to advanced modelling techniques<sup>59</sup>. However,  
567 many papers reported different types and nested layers of non-independent data within a single  
568 paper, requiring overly complex combinations and levels of aggregation models (compared to  
569 aggregating data with a mean), prior to the meta-analysis. Finally, we calculated mean effect  
570 sizes ( $E$ ), 95% confidence intervals (CI), heterogeneity ( $Q$ ), and the proportion of real observed  
571 dispersion ( $I^2$ ) based on weighted random effect models in OpenMEE<sup>58</sup>. Mean effect sizes were  
572 considered to be significantly different from zero or another effect if their 95% CIs did not  
573 overlap with zero or each other, respectively<sup>60-63</sup>. Effect sizes generated from a single study were  
574 excluded from plots (these were: a single mean effect size of -4.21 for the 1972 ENSO event, and  
575 a single effect size of 1.183 for ‘reptiles’ in the taxon-specific analysis).

## 576 **Publication bias**

577 Our meta-analyses may be influenced by publication bias if we overlooked studies documenting  
578 strong positive effects, or if studies finding non-significant effects are not published<sup>26,64,65</sup>. We  
579 believe that the first type of publication bias is unlikely because we have worked intensively with  
580 MHW through primary research and by writing book chapters and reviews. We explored  
581 possible publication bias in different ways. We examined funnel plot asymmetry using the  
582 trimfill method and regression tests, and calculated the fail-safe number using the Rosenberg

583 method that estimates the number of studies averaging null results that should be added to reduce  
584 the significance level ( $p$ -value) of the average effect size (based on a fixed-effects model) to  
585  $\alpha = 0.05$ <sup>64,65</sup>. These tests suggest that publication bias has limited effects and that our results  
586 are generally robust. Although the funnel plot was highly asymmetric (Fig. S4), as shown by a  
587 significant regression test ( $t = -3.598$ ,  $p = 0.0004$ ), adjusting this possible bias using the trimfill  
588 method had no effects on our general conclusion, because the mean effect size remained  
589 significantly negative ( $-0.05$ , with 95% confidence intervals  $-0.08$  to  $-0.02$ ,  $p < 0.01$ ). In addition,  
590 Rosenberg's fail safe number was 11,318, i.e., much larger than  $5n + 10$ , where  $n$  is the number  
591 of original studies included in our analyses. Thus, publication bias is unlikely to affect our results  
592 and did not change our main finding that MHWs generally had negative effects on marine  
593 organisms.

#### 594 **Effect of population location within the distributional range on responses to MHWs**

595 We also tested the hypothesis that populations found towards the warm-water limit (i.e.  
596 equatorward range edge) of a species' distribution will respond more negatively to MHWs. To  
597 do this, we first extracted all observations from the database that were recorded at the species-  
598 level (302 species and 645 observations). Global species distributions were produced using  
599 presence-only Maxent models for each species for which sufficient observations were available,  
600 and using default parameters for a random seed, convergence threshold, maximum number of  
601 iterations, maximum background points and the regularization parameter<sup>53</sup> (using Maxent  
602 version 3.3.3k). Observations of species presence from iOBIS were gridded such that 1-degree  
603 grid cells with observations were set as present. These observations were then modelled as a  
604 function of the following environmental predictors: (1) average annual temperatures from the  
605 HadISST v1.1; (2) the logarithm of distance to the nearest coastline; (3) ocean depth from the

606 GEBCO marine atlas; and (4) FAO major fishing areas  
607 (<http://www.fao.org/fishery/area/search/en>). Global maps of predicted presence were produced  
608 using a threshold probability of 0.4. Presence maps were used to extract average annual SST  
609 values from Hadley Centre HadISST v1.1 1-degree dataset long-term climatology average 1960-  
610 2009. Quantiles (0, 0.1, 0.25, 0.5, 0.75, 0.9 and 1.0) of the population of temperatures in  
611 occupied grid squares were used to define the thermal niche of the species (weighted by the  
612 relative area of grid cells given by the cosine of the latitude). The frequency distribution of these  
613 species-specific distributions were then described using percentiles, and, for this analysis, the  
614 10<sup>th</sup> and 90<sup>th</sup> percentiles were taken as measures of the warm and cold ends of the thermal range,  
615 respectively. Each location of a reported MHW effect was then used to extract the local average  
616 SST from the same SST climatology. Range location was then expressed as the local temperature  
617 less the 10<sup>th</sup> percentile of temperature, divided by the difference between the 10<sup>th</sup> and 90<sup>th</sup>  
618 percentiles of estimated species range temperatures. A range location value of zero or less was  
619 therefore at the cold end of the distribution range ( $\leq 10^{\text{th}}$  percentile), while values of 1 or more  
620 would be at the warm end of the range ( $\geq 90^{\text{th}}$  percentile). This process resulted in estimated  
621 range locations for 347 observations from 280 species within the ecological dataset.

622

623 The effect of range location on the size and direction of response to MHWs was assessed  
624 statistically using a linear model of Hedges'  $g$  versus range location weighted by the inverse  
625 variance of each Hedges'  $g$  value. Range location had a significant influence on responses,  
626 becoming more negative toward the warm edge of the species range (Fig. 2F;  $F_{1,345} = 11.98$ ,  
627  $P < 0.001$ ). Differences among taxonomic groups followed the average range location within  
628 those groups. The average negative effect of MHWs on corals was associated with the average

629 reported effect location being at the 90th percentile of the coral species' temperature distribution.  
630 Those taxonomic groups reporting less negative effects were generally toward the middle of the  
631 distribution range, while those groups at the cold end of the species temperature range showed a  
632 positive effect (Fig 2F;  $F_{1,7} = 10.33$ ,  $P = 0.015$ ).

#### 633 **4. Analysis of habitat-forming species responses to MHWs**

634 High-resolution time series on coral bleaching, seagrass density and kelp biomass were obtained  
635 from the Caribbean Sea, Western Australia and California, respectively (Fig. S5). Quality-  
636 controlled coral bleaching observations for the Caribbean Sea/Gulf of Mexico region  
637 (northernmost limit: 30.0°N, southernmost limit: 10.2°N, western limit: 97.5°W, eastern limit:  
638 59.6°W) were obtained (at 11 km resolution) from NOAA's Coral Reef Watch program  
639 (<http://coralreefwatch.noaa.gov/satellite/index.php>). Observations were first filtered by month  
640 (July-October inclusive) and then summed for each year (1983-2010). Links between MHWs  
641 and seagrass density were examined with long-term monitoring data from Cockburn Sound,  
642 Western Australia, which is collected and managed by the Cockburn Sound Management  
643 Council (Western Australian Government). The density of seagrass shoots was examined at 2  
644 long-term sites (Garden Island and Warnbro Sound), where high-resolution data have been  
645 collected using SCUBA at depths of 2-7 m since 2003 (all surveys were conducted in late  
646 Austral summer of each year). Data were averaged across transects and depths before generating  
647 an annual mean value for the Cockburn Sound region (average of 2 sites). Annual estimates for  
648 giant kelp, *Macrocystis pyrifera*, biomass were generated from the satellite-derived dataset  
649 produced by Cavanaugh et al.<sup>66</sup> as part of the Santa Barbara Coastal Long-term Ecological  
650 Research (SBC-LTER) program (<http://sbc.lternet.edu/index.html>). Estimates of the biomass of  
651 the kelp canopy (i.e. floating fronds) were derived from LANDSAT 5 Thematic Mapper satellite

652 imagery. Biomass data (wet weight, kg) were generated for individual 30 x 30 m pixels in the  
653 coastal areas adjacent to California and Baja California. Estimates of kelp canopy biomass were  
654 derived from the relationship between satellite surface reflectance and empirical measurements  
655 of kelp canopy biomass at long-term monitoring sites sampled using SCUBA. The extensive  
656 dataset was first filtered to remove uninformative values influenced by cloud cover and then by  
657 latitude (27.00-32.99°N) and time of year (only summer months, June-September inclusive).  
658 Average kelp biomass per year was then calculated from between 66,530 and 354,181 individual  
659 observations. The total number of MHW days observed for corresponding years and regions for  
660 each of the three separate datasets was then calculated, and correlations between MHWs and  
661 ecological response variables explored with Pearson's correlation coefficient.

662

663 **Data availability:** *Daily 0.25° resolution NOAA OISST V2 data are provided by the*  
664 *NOAA/OAR/ESRLPSD, Boulder, Colorado, USA, at <http://www.esrl.noaa.gov/psd/>. Data on*  
665 *human impacts and marine biodiversity are available from NCEAS*  
666 *(<https://www.nceas.ucsb.edu/globalmarine>) and Aquamaps ([www.aquamaps.org](http://www.aquamaps.org)), respectively.*  
667 *Coral bleaching records were extracted from the NOAA Reef Watch program*  
668 *(<https://coralreefwatch.noaa.gov>), giant kelp biomass data were sourced from the Santa Barbara*  
669 *Coastal Long-term Ecological Research (SBC-LTER) program*  
670 *(<http://sbc.lternet.edu/index.html>). Additional data are available from the corresponding author*  
671 *upon request.*

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### 673 **Additional references**

674 51      García Molinos, J. *et al.* Climate velocity and the future global redistribution of marine biodiversity. *Nature*  
675 *Climate Change* **6**, 83, doi:10.1038/nclimate2769 (2016).

676 52 Kaschner, K. *et al.* *AquaMaps: Predicted range maps for aquatic species*. *World wide web electronic*  
677 *publication*, <<http://www.aquamaps.org/>> (2015).

678 53 Jones, M. C. & Cheung, W. W. L. Multi-model ensemble projections of climate change effects on global  
679 marine biodiversity. *ICES Journal of Marine Science* **72**, 741-752, doi:10.1093/icesjms/fsu172 (2015).

680 54 Halpern, B. S. *et al.* Spatial and temporal changes in cumulative human impacts on the world's ocean.  
681 *Nature Communications* **6**, 7615, doi:10.1038/ncomms8615  
682 <https://www.nature.com/articles/ncomms8615#supplementary-information> (2015).

683 55 Halpern, B. S. *et al.* A global map of human impact on marine ecosystems. *Science* **319**, 948-952,  
684 doi:10.1126/science.1149345 (2008).

685 56 Deser, C., Alexander, M. A., Xie, S.-P. & Phillips, A. S. Sea Surface Temperature Variability: Patterns and  
686 Mechanisms. *Annual Review of Marine Science* **2**, 115-143, doi:10.1146/annurev-marine-120408-151453  
687 (2009).

688 57 Ready, J. *et al.* Predicting the distributions of marine organisms at the global scale. *Ecological Modelling*  
689 **221**, 467-478, doi:<https://doi.org/10.1016/j.ecolmodel.2009.10.025> (2010).

690 58 Wallace, B. C. *et al.* OpenMEE: Intuitive, open-source software for meta-analysis in ecology and  
691 evolutionary biology. *Methods Ecol. Evol.* **8**, 941-947, doi:10.1111/2041-210X.12708 (2017).

692 59 Del Re, A. A practical tutorial on conducting meta-analysis in R. *The Quantitative Methods for Psychology*  
693 **11**, 37-50 (2015).

694 60 Kaplan, I., Halitschke, R., Kessler, A., Sardanelli, S. & Denno, R. F. Constitutive and induced defenses to  
695 herbivory in above-and-below ground plant tissues. *Ecology* **89**, 392-406, doi:10.1890/07-0471.1 (2008).

696 61 Gurevitch, J., Morrison, J. A. & Hedges, L. V. The interaction between competition and predation: A meta-  
697 analysis of field experiments. *Am. Nat.* **155**, 435-453, doi:10.1086/303337 (2000).

698 62 Gurevitch, J., Morrow, L. L., Wallace, A. & Walsh, J. S. A meta-analysis of competition in field  
699 experiments. *Am. Nat.* **140**, 539-572, doi:10.1086/285428 (1992).

700 63 Guo, L. B. & Gifford, R. M. Soil carbon stocks and land use change: a meta analysis. *Glob. Change Biol.* **8**,  
701 345-360, doi:10.1046/j.1354-1013.2002.00486.x (2002).

702 64 Rosenberg, M. S. & Goodnight, C. The file-drawer problem revisited: a general weighted method for  
703 calculating fail-safe numbers in meta-analysis. *Evolution* **59**, 464-468, doi:10.1554/04-602 (2005).

704 65 Rosenberg, M. S., Adams, D. C. & Gurevitch, J. *Metawin: Statistical software for meta-analysis, Version*  
705 *2. Sinauer Associates, Massachusetts.* (2000).

706 66 Cavanaugh, K. C., Siegel, D. A., Reed, D. C. & Bell, T. W. SBC LTER: Time series of kelp biomass in the  
707 canopy from Landsat 5, 1984 -2011. Santa Barbara Coastal LTER.  
708 doi:10.6073/pasta/329658f19d5e61dda0be5ee883cd1c41. (2014).

709