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

3 **Authors:** Dan A. Smale<sup>1,2\*</sup>, Thomas Wernberg<sup>2\*</sup>, Eric C. J. Oliver<sup>3,4,5</sup>, Mads Thomsen<sup>6</sup>, Ben P.  
4 Harvey<sup>7,8</sup>, Sandra C. Straub<sup>2</sup>, Michael T. Burrows<sup>9</sup>, Lisa V. Alexander<sup>10,11,12</sup>, Jessica A.  
5 Benthuyesen<sup>13</sup>, Markus G. Donat<sup>10,11</sup>, Ming Feng<sup>14</sup>, Alistair J. Hobday<sup>15</sup>, Neil J. Holbrook<sup>4,16</sup>,  
6 Sarah E. Perkins-Kirkpatrick<sup>10,11</sup>, Hillary Scannell<sup>17</sup>, Alex Sen Gupta<sup>10,11</sup>, Ben Payne<sup>9</sup>, Pippa J.  
7 Moore<sup>7,18</sup>

8 **Affiliations:**

- 9 1. Marine Biological Association of the United Kingdom, The Laboratory, Citadel Hill, Plymouth PL1 2PB,  
10 UK
- 11 2. UWA Oceans Institute and School of Biological Sciences, The University of Western Australia, Crawley  
12 6009 Western Australia, Australia
- 13 3. Department of Oceanography, Dalhousie University, Halifax, Nova Scotia, B3H 4R2, Canada
- 14 4. Institute for Marine and Antarctic Studies, University of Tasmania, Hobart, Australia
- 15 5. Australian Research Council Centre of Excellence for Climate System Science, University of Tasmania,  
16 Hobart, Tasmania, Australia
- 17 6. School of Biological Sciences, University of Canterbury, Private Bag 4800, Christchurch, New Zealand
- 18 7. Institute of Biological, Environmental and Rural Sciences, Aberystwyth University, Aberystwyth SY23  
19 3DA, UK
- 20 8. Shimoda Marine Research Center, University of Tsukuba, 5-10-1 Shimoda, Shizuoka, 415-0025, Japan
- 21 9. Department of Ecology, Scottish Association for Marine Science, Scottish Marine Institute, Oban, Argyll,  
22 PA37 1QA, Scotland, UK.
- 23 10. Climate Change Research Centre, The University of New South Wales, Sydney, New South Wales,  
24 Australia

- 25 11. Australian Research Council Centre of Excellence for Climate Extremes, The University of New South  
26 Wales, Sydney, New South Wales, Australia
- 27 12. Australian Research Council Centre of Excellence for Climate System Science, The University of New  
28 South Wales, Sydney, New South Wales, Australia
- 29 13. Australian Institute of Marine Science, Crawley, Western Australia, Australia
- 30 14. CSIRO Oceans and Atmosphere, Crawley, Western Australia, Australia
- 31 15. CSIRO Oceans and Atmosphere, Hobart, Tasmania, Australia
- 32 16. Australian Research Council Centre of Excellence for Climate Extremes, University of Tasmania, Hobart,  
33 Tasmania, Australia
- 34 17. School of Oceanography, University of Washington, Seattle, WA, USA
- 35 18. Centre for Marine Ecosystems Research, School of Natural Sciences, Edith Cowan University, Joondalup  
36 6027 Western Australia, Australia

37

38 \*Joint first-authors. Correspondence: [dansma@mba.ac.uk](mailto:dansma@mba.ac.uk), +441752426489

39 **Article type:** Letter

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

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

61  
62 Anthropogenic climate change is driving the redistribution of species and reorganization of  
63 natural systems and represents a major threat to global biodiversity<sup>3,4</sup>. The biosphere has warmed  
64 significantly in recent decades with widespread implications for the integrity of ecosystems and  
65 the sustainability of the goods and services they provide<sup>5,6</sup>. In addition to the near ubiquitous  
66 long-term increases in temperature, the frequency of discrete extreme warming events  
67 (‘heatwaves’) has increased<sup>7,8</sup> with projections indicating they will become more frequent, more  
68 intense and longer lasting throughout the 21<sup>st</sup> Century<sup>9</sup>. While extremes occur naturally within  
69 the climate system, there is growing confidence that the observed intensification of heatwaves is

70 due to human activities<sup>10,11</sup>. The 21<sup>st</sup> Century has already experienced record-shattering  
71 atmospheric heatwaves<sup>7,12</sup>, such as the 2003 European heatwave, the Australian ‘Angry Summer’  
72 of 2012-2013, and the European ‘Lucifer’ heatwave in 2017, with devastating consequences for  
73 human health, the economy and the environment<sup>7</sup>.

74  
75 Discrete and prolonged extreme warming events occur in the ocean as well as the atmosphere.  
76 ‘Marine heatwaves’ (MHWs) are caused by a range of processes operating across different  
77 spatial and temporal scales, from localised air-sea heat flux to large-scale climate drivers, such as  
78 the El Niño Southern Oscillation<sup>13</sup>. Regional case studies have documented how MHWs can alter  
79 the structure and functioning of entire ecosystems by causing widespread mortality, species  
80 range shifts and community reconfiguration<sup>14-16</sup>. By impacting ecosystem goods and services,  
81 such as fisheries landings<sup>17,18</sup> and biogeochemical processes<sup>19,20</sup>, MHWs can have major  
82 socioeconomic and political ramifications. Recent high-profile ocean warming events include the  
83 record-breaking 2011 ‘Ningaloo Niño’ (2010-2011) off Western Australia<sup>21</sup>, the long-lasting  
84 ‘Blob’ (2013-2016) in the northeast Pacific<sup>22</sup> and El Niño-related extreme warming in 2016 that  
85 affected most of the Indo-Pacific<sup>23,24</sup>. These events have increased awareness of MHWs as an  
86 important climatic phenomenon affecting both physical and biological processes. Until recently,  
87 the lack of a common framework to define MHWs<sup>13</sup> has hampered attempts to examine temporal  
88 trends or to compare physical attributes or biological impacts across different events, regions or  
89 taxa. However, by defining MHWs as periods when daily sea-surface temperatures (SSTs)  
90 exceed a local seasonal threshold (i.e. the 90<sup>th</sup> percentile of climatological SST observations) for  
91 at least 5 consecutive days<sup>13</sup>, Oliver et al.<sup>2</sup> showed that the frequency and duration of MHWs  
92 have increased significantly over the past century across most of the global ocean. Here, we used

93 the same MHW framework<sup>13</sup> to examine observed trends in the annual number of MHW days  
94 and the implications for marine ecosystems globally. We incorporated existing data on marine  
95 taxon richness, the proportion of species found at their warm range edges and non-climatic  
96 human impacts to identify regions of high vulnerability, where increased occurrences of MHWs  
97 overlap with areas of high biodiversity, temperature sensitivity or concurrent anthropogenic  
98 stressors. We also conducted a meta-analysis on the impacts of MHWs, by examining ecological  
99 responses to eight prominent MHW events that have been studied in sufficient detail for formal  
100 analysis. We examined 1049 ecological observations, recalculated to 182 independent effect  
101 sizes from 116 research papers that examined responses of organisms, populations and  
102 communities to MHWs. We also explored relationships between the occurrence of MHWs and  
103 the health of three globally-significant foundation species (coral, seagrass and kelp) from three  
104 independent time series that were collected at sufficient spatiotemporal resolutions to explicitly  
105 link ecological responses to MHWs. Finally, we reviewed the literature on MHWs for evidence  
106 of impacts of these events on goods and services to human society.

107

108 The total number of MHW days per year, based on five quasi-global SST datasets, has increased  
109 globally throughout the 20<sup>th</sup> and early 21<sup>st</sup> Century (Fig. 1A). As a global average, there are over  
110 50% more MHW days per year in the latter part of the instrumental record (1987-2016)  
111 compared to the earlier part (1925-1954)<sup>2</sup>, with most regions experiencing increases in the  
112 number of MHW days (Fig 1B). Global patterns of marine taxon richness (Fig. 1C) overlaid with  
113 trends in annual MHW days reveal regions where increased MHW occurrences can influence  
114 biologically diverse regions, in particular, southern Australia, the Caribbean Sea, and the  
115 coastline bounding the mid-eastern Pacific (Fig 1D). Given that warm range edge populations are

116 likely to be the most impacted by MHWs (as thermal tolerances are exceeded during  
117 anomalously high temperatures), regions which support a high proportion of species found near  
118 their warm range edge will be particularly vulnerable to increased MHW activity (Fig 1E).  
119 Several regions were identified as having experienced marked increases in MHW days and also  
120 supporting a high proportion of species found near their warm range edges (Fig 1F), with marine  
121 ecosystems in the southwest Pacific and the mid-west Atlantic particularly at risk. Furthermore,  
122 regions where rapid increases in the annual number of MHW days overlap with existing high-  
123 intensity non-climate human stressors (Fig 1G) include the central west Atlantic, the northeast  
124 Atlantic and the northwest Pacific (Fig. 1H). Here, existing regional pressures, including  
125 overfishing and pollution, have the potential to exacerbate MHW impacts.

126  
127 Examination of eight prominent (and sufficiently studied) MHWs showed they varied greatly  
128 with respect to spatial extent (by a factor of  $>15$ , Fig. 2A, Fig. S1), duration (10 to 380 days) and  
129 maximum intensity (3.5 to 9.5°C above climatological SST) (Fig. 2A). It should be noted several  
130 MHWs were primarily driven by large-scale El Niño events which, by their nature, affected  
131 ocean climate at large spatial scales. Here, the largest contiguous MHW associated with each  
132 ENSO event was identified and characterised with MHW metrics. Our meta-analysis of  
133 ecological impacts (based on Hedges  $g$  effect sizes to account for bias associated with small  
134 sample sizes<sup>25</sup>) detected an overall negative effect of MHWs on biota across research papers,  
135 events, taxa, and response variables ( $E = -0.93$ ; 95 CI = 0.22;  $Q = 6303$ ,  $df = 181$ ;  $p_{\text{heterogeneity}} <$   
136  $0.001$ ,  $I^2 = 97.13$ ). All eight MHWs were associated with negative ecological impacts although  
137 the mean negative effect sizes were not significantly different from zero for the two events with  
138 lowest sample sizes (Fig. 2B). There was no clear relationship between the severity of the MHW

139 (derived from normalized MHW intensity and duration) and their observed impacts (Fig. 2B).  
140 All taxonomic groups, with the exception of fishes and mobile invertebrates, responded  
141 negatively to MHWs with birds and corals being most adversely affected (Fig. 2C). The positive  
142 fish response was, in part, driven by new incursions of tropical species into impacted temperate  
143 regions<sup>15</sup>. Corals were directly affected by these MHWs, as extreme absolute temperatures  
144 resulted in widespread bleaching and mortality<sup>26,27</sup>, whereas birds were indirectly impacted  
145 through changes in prey availability<sup>28</sup>. Birds and corals are also particularly sensitive to longer  
146 term increases in sea temperature associated with ocean warming<sup>29</sup>. Overall, our analyses suggest  
147 that sessile taxa were more impacted by MHWs than mobile and planktonic taxa (Fig. 2C),  
148 perhaps because mobile taxa generally have higher thermal tolerances than less active or sessile  
149 taxa<sup>30</sup> and highly mobile species can quickly migrate in response to rapidly changing  
150 conditions<sup>15</sup>. All ecological response variables were negatively affected by MHWs, although  
151 growth and primary production were not significantly different from zero (Fig. 2D). Negative  
152 impacts were greatest for coral bleaching, survival, and reproduction (Fig. 2D), a pattern  
153 consistent with effects of warming in manipulative experiments<sup>31</sup>.  
154  
155 To examine links between MHWs and ecological responses, we conducted additional analysis at  
156 the species level to test the prediction that populations found towards the warm-water limit (i.e.  
157 equatorward range edge) of a species' distribution would be more negatively impacted by  
158 MHWs. From the database described above, we extracted all species level observations (645  
159 observations from 302 species) and for each population we classified their relative position  
160 within the species range by expressing the local average SST as a proportion of the difference  
161 between the 10<sup>th</sup> and 90<sup>th</sup> percentile temperatures experienced through the species geographical



162 range. Critically, the most negative responses to MHWs were seen in populations found towards  
163 their warm range edge (Fig. 2E), implying that extreme temperatures exceeded thermal  
164 thresholds with adverse effects. Across all species-level observations, there was a negative  
165 relationship between any given population's location within the species' range and the direction  
166 and magnitude of the MHW effect (Fig. 2F). This indicates that populations residing near the  
167 warm limit of a given species range are particularly vulnerable to warming events and range  
168 contractions are likely to occur in response to more frequent MHWs. Indeed, recent observations  
169 have shown that equatorward range edges of both plant and animal species have retracted  
170 poleward by >100 km following severe MHW events<sup>16,32,33</sup>.

171

172 An examination of long-term time series on the health of three globally important foundation  
173 taxa showed that increased annual number of MHW days was correlated with (i) increased coral  
174 bleaching, (ii) decreased seagrass density and (iii) decreased kelp biomass (Fig. 3). Even though  
175 environmental variables such as storms, nutrients and light are known to strongly influence the  
176 health of these critical habitat-formers<sup>34</sup>, the annual number of MHW days alone was strongly  
177 and significantly correlated with observed ecological performance and, crucially, had  
178 consistently stronger correlative relationships than more frequently used measures of ocean  
179 temperature (i.e. mean and maximum SST, see Table S1). An increased number of MHW days  
180 was significantly correlated to decreased ecological health of populations of all three foundation  
181 taxa, indicating the importance of discrete extreme ocean warming events in driving ecosystem  
182 structure<sup>15,35</sup>.

183

184 A wide range of ecological goods and services derived from marine ecosystems have been  
185 severely impacted by recent MHWs (Table 1). For example, the 2011 Ningaloo Niño caused  
186 widespread loss of biogenic habitat, depleted biodiversity, disruption to nutrient cycles and shifts  
187 in the abundance and distribution of commercial fisheries species off Western Australia (Table  
188 1). Similarly, recent MHWs in the Mediterranean Sea have been linked to local extinctions,  
189 decreased rates of natural carbon sequestration, loss of critical habitat and diminished  
190 socioeconomic value (Table 1). These services have substantial societal benefit, with hundreds of  
191 millions of people benefitting from coastal marine ecosystems<sup>36,37</sup>. As such, managing and  
192 mitigating the deleterious effects of MHWs on the provision of ecosystem services is a major  
193 challenge for coastal societies.

194

195 Globally, MHWs are becoming more frequent and prolonged, and record-breaking events have  
196 been observed in most ocean basins in the past decade<sup>2</sup>. To date, the main focus of ecological  
197 research has been on trends in mean climate variables, yet discrete extreme events are emerging  
198 as pivotal in shaping ecosystems, by driving sudden and dramatic shifts in ecological structure  
199 and functioning. Given the confidence in projections of intensifying extreme warming events  
200 with anthropogenic climate change<sup>7,38</sup>, marine conservation and management approaches must  
201 consider MHWs and other extreme climatic events if they are to maintain and conserve the  
202 integrity of highly valuable marine ecosystems over the coming decades.

203

204

205 Fig. 1. Global patterns of MHW intensification, marine biodiversity, proportions of species found at their warm  
206 range edge and concurrent human impacts. **a,b**, Globally averaged time-series of the annual number of MHW days  
207 and trends in the annual number of MHW days (between 1925-1954 and 1987-2016) across the global ocean. **c,e,g**,  
208 Existing data on marine biodiversity (**c**), the proportion of species within the local species pool found near their  
209 warm range edge (**e**), and non-climatic human stressors (**g**) were combined with MHW intensification data. **d,f,h**,  
210 The resultant bivariate maps identify regions of high diversity value that may be impacted by MHWs (**d**), high  
211 thermal sensitivity of species which may have been particularly vulnerable to increased MHWs (**f**) and high levels of  
212 non-climatic human stressors where MHW intensification has impacted concurrently upon marine ecosystems (**h**).  
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219 Fig. 2. Ecological impacts of MHWs as determined by a meta-analysis of responses to eight prominent MHW  
220 events. **a,b**, The attributes of the eight MHW events used in the meta-analysis (**a**) and the overall effect of each  
221 MHW event across all ecological responses (**b**). **c,d**, The effect of MHWs on major taxonomic groups (**c**) and types  
222 of ecological responses (**d**). The number of independent observations for each category are shown in parentheses  
223 and values represent mean ( $\pm 95\%$  CI) effect sizes (Hedges  $g$ , to account for bias associated with small sample sizes).  
224 **e,f**, Populations located towards the warm-water limit of species' distributions tended to respond more negatively to  
225 MHWs (**e**) with effect sizes (Hedges  $g$ ,  $\pm 95\%$  CI) generally becoming more negative for warmer equatorward range-  
226 edge populations (**f**). Plots are based on responses of 685 species-level observations; bold symbols in (**f**) indicate  
227 means for each major taxonomic group and faded symbols show individual studies ( $T_e$  temperature at effect  
228 location,  $T_{10}$ ,  $T_{90}$ , 10% and 90% species range temperatures). Horizontal (**e**) and vertical dashed lines (**f**) delineate  
229 the lower and upper quartiles of species' thermal ranges.

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235 Fig. 3. Impacts of MHWs on foundation species. **a,b**, Severe MHWs, such as those associated with the extreme El  
236 Niño events of 1997/98 and 2015/16, have caused widespread bleaching and mortality of reef building corals (**a**).  
237 Analysis of annual coral bleaching records from the Caribbean Sea/Gulf of Mexico region (1983-2010, data from  
238 NOAA Coral Reef Watch) showed that the number of MHW days per year was positively correlated with the  
239 frequency of coral bleaching observations (**b**). **c,d**, Seagrass meadows yield critical ecosystem services, including  
240 carbon sequestration and biogenic habitat provision, yet recent MHWs have impacted seagrass populations in  
241 several regions (**c**). Monitoring data from independent sites in Cockburn Sound, Western Australia (2003-2014, data  
242 provided by Cockburn Sound Management Council) indicated that the number of MHW days recorded in the  
243 previous year was negatively correlated with seagrass (*Posidonia sinuosa*) shoot density (**d**). **e,f**, Kelp forests  
244 represent critical habitats along temperate coastlines but extreme temperatures experienced during MHWs can cause  
245 widespread mortality and deforestation (**e**). Satellite-derived estimates of giant kelp (*Macrocystis pyrifera*) biomass  
246 along the coastline of California/Baja California (1984-2011) showed that kelp biomass was negatively correlated  
247 with the number of MHW days recorded during the previous year (**f**).  
248  
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250  
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252  
 253 Table 1. Impacts of MHWs on services provided by marine ecosystems (definitions of ecosystem services adapted  
 254 from The Economics of Ecosystems and Biodiversity, TEEB, developed by UNEP). Evidence of impacts was  
 255 collated from specific MHWs: (a) 1982/83 El Niño event, (b) 1997/98 El Niño event, (c) 1999 Mediterranean  
 256 MHW, (d) 2003 Mediterranean MHW, (e) 2011 Western Australian MHW, (f) 2012 Northwest Atlantic MHW, (g)  
 257 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)	14,16,39
	Food	- Changes in the distributions and abundances of commercial fisheries species (b,e,f)	17,32,40
Regulating	Carbon sequestration and storage	- Reduced carbon burial and sequestration due to decreased growth and high mortality of seagrasses (d,e)	35,41
	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)	42,43
	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)	15,19,35,44
	Biological control	- Anomalous warming events associated with influx of invasive non-native species (e)	32
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)	33,41-43,45-47
Cultural	Tourism and recreation	- Locations affected by intense warming events are less attractive for recreational activities and have decreased socioeconomic value (d, h)	14,48,49

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384

385 **Corresponding author:** Correspondence to Dan Smale ([dansma@mba.ac.uk](mailto:dansma@mba.ac.uk))

386

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## 394 **Methods**

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

396 Marine heatwaves (MHWs) were identified from observational sea surface temperature time  
397 series using the definition proposed by Hobday et al.<sup>13</sup>, whereby a MHW is defined as a “discrete  
398 prolonged anomalously warm water event at a particular location” with each of those terms  
399 (anomalously warm, prolonged, discrete) quantitatively defined and justified for the marine  
400 context. Specifically, “discrete” implies the MHW is an identifiable event with clear start and  
401 end dates, “prolonged” means it has a duration of at least five days, and “anomalously warm”  
402 means the temperature is above a climatological threshold (in this case the seasonally-varying  
403 90<sup>th</sup> percentile). The climatological mean and threshold were calculated over a base period of  
404 1983-2012. For each day-of-year, a pool of days across all years in the climatology period and  
405 within an 11-day window was taken as a sample, from which the mean and 90<sup>th</sup> percentile  
406 threshold were calculated. The climatological mean and threshold were then further smoothed  
407 using a 30-day running window. When two successive events occur with a break of two days or  
408 less, this was deemed to represent a single continuous event. The code used to identify MHWs  
409 and calculate key MHW metrics following this definition is freely available and has been  
410 implemented in Python (<https://github.com/ecjoliver/marineHeatWaves>) and R  
411 (<https://robwschlegel.github.io/heatwaveR>). MHWs detected using this definition were then  
412 characterized by a set of metrics, including duration and intensity (i.e. the maximum daily  
413 temperature above the seasonal climatology during the event). We then examined an annual time  
414 series of “total MHW days”, which is the sum of days categorized as MHWs in any given year.

415 Global time series and regional trends in total MHW days were derived using a combination of  
416 satellite-based, remotely-sensed sea surface temperatures and *in situ*-based seawater  
417 temperatures. First, total MHW days were calculated globally over 1982-2015 at 1/4° resolution  
418 from the National Oceanic and Atmospheric Administration (NOAA) Optimum Interpolation  
419 (OI) SST V2 high resolution data. Then, proxies for total MHW days globally over 1900-2016  
420 were developed based on five monthly gridded SST datasets (HadISST v1.1, ERSST v5, COBE  
421 2, CERA-20C and SODA si.3). A final proxy time series was calculated by averaging across the  
422 five datasets. The five monthly data sets were used since no global daily SST observations are  
423 available prior to 1982. From these proxy time-series we calculated (i) the difference in mean  
424 MHW days over the 1987-2016 and 1925-1954 periods and (ii) a globally-averaged times series  
425 of total MHW days. Further details on this method and resulting proxy data can be found in  
426 Oliver et al.<sup>2</sup>. Note that these calculations use the same climatology period as above, 1983-2012.

## 427 **2. Global patterns of MHW intensification and overlaps with known hotspots of marine** 428 **biodiversity, temperature-sensitive populations and non-climatic human stressors**

429 We combined regional trends in MHW days with pre-existing data on marine biodiversity, the  
430 proportion of species found near their warm range edges, and non-climatic human stressors to  
431 predict where MHW intensification may be a particular threat to biodiversity hotspots or  
432 temperature-sensitive communities, or be exacerbated by concurrent stressors. Biodiversity  
433 hotspots were determined using published marine taxon richness data<sup>50</sup>, which were accumulated  
434 from projected species distributions from the Aquamaps project<sup>51</sup>. Patterns in taxon richness  
435 (Fig. 1C) showed characteristically high levels in coastal areas and in tropical regions. We also  
436 calculated the proportion of species in the local species pool that were near their warm range  
437 edge to determine locations where MHWs might be more likely to have a strong negative effect

438 (as shown in Fig. 2F). We used 16582 species global distribution maps from the Aquamaps  
439 project<sup>51</sup>, previously used to assess likely patterns of biodiversity change<sup>50</sup>, to represent global  
440 marine biodiversity. For each 1° latitude/longitude grid cell we counted the number of species  
441 present for which sea surface temperature, derived as the 1960-2009 average annual temperature  
442 from the Hadley Centre HadISST v1.1 dataset, exceeded the 90<sup>th</sup> percentile temperature of their  
443 geographical range, and divided this by the total number of species present. Aside from some  
444 artefacts where species limits coincide with FAO (Food and Agriculture Organization of the  
445 United Nations) region boundaries, a feature prevalent in other studies using these datasets<sup>52</sup>, the  
446 resulting map (Fig. 1E) showed areas with higher proportions of species at their warm range  
447 edges. Major concentrations (proportions >0.1 of all species) of warm-edge species were seen in  
448 the Eastern Mediterranean, the southern Red Sea, the Caribbean Sea, the Mexican part of the  
449 North Pacific and a large part of the tropical west Pacific. Locally higher proportions of warm-  
450 edge species were also seen along coastlines of Europe, western USA and Canada, North Africa  
451 and in the Yellow Sea.

452 Information on stressors were obtained from supplementary online resources provided by  
453 Halpern et al.<sup>53</sup>. We additively combined multiple impact layers (demersal destructive fishing,  
454 demersal non-destructive high bycatch, demersal non-destructive low bycatch, ocean  
455 acidification, ocean pollution, pelagic high bycatch, pelagic low bycatch, shipping and UV) into  
456 a single cumulative impacts layer (Fig. 1E). Fishing intensity layers were obtained by  
457 apportioning reported catches in FAO areas by modelled productivity data for latitude/longitude  
458 cells. Shipping impacts were derived from a 12-month (2003-2004) global ship observing  
459 scheme, and the same data was used with ports data to give a measure of ocean pollution.  
460 Surface UV information was obtained from the GSFC TOMS EP/TOMS satellite program at

461 NASA. Ocean acidification data came from globally modelled aragonite saturation state. Details  
462 of the quantification of these layers are given in Halpern et al.<sup>53,54</sup>. Layers that included ocean  
463 warming variables were specifically excluded due to likely co-variance (to varying extents) with  
464 MHW metrics. The cumulative impacts layer was then re-projected and resampled onto the  
465 same 1°×1° grid as for trends in total MHW days and biodiversity data. Maps of the  
466 combinations of medium to high trends in total MHW days and medium to high values of taxon  
467 richness (Fig. 1C) or cumulative impacts (Fig. 1E) were created by splitting the data into classes  
468 based on the percentiles of the distribution of each variable (0-50% low, 50-90% medium, >90%  
469 high). Combined MHW trend/richness and MHW trend/impact layers were assigned to  
470 categories according to the classes of each contributing layer. While spatial bias due to  
471 variability in sampling effort may influence, to some degree, global-scale datasets on physical  
472 and biological variables, the datasets used in the current study have near-complete global  
473 coverage and represent the best approximations available for temperature<sup>55</sup>, species richness<sup>56</sup>  
474 and human stressors<sup>53</sup>.

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

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

477 The meta-analysis followed PRISMA (Preferred Reporting Items for Systematic Reviews and  
478 Meta-Analyses) guidelines, which provide an evidence-based minimum set of requirements for  
479 conducting and reporting meta-analyses (Fig. S2). We searched for peer reviewed studies that  
480 compared six types of biological ‘performance response’ (survival, abundance, growth,  
481 reproduction, primary production or coral bleaching) that reported data variation, before and  
482 after any of eight well-described periods of extreme warming (El Niño related events in 1982/83,  
483 1986/87, 1991/92 and 1997/98, the Mediterranean MHWs of 1999, 2003 and 2006, and the 2011

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

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

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

513 We analyzed impacts of MHWs on events, taxa and performance with Hedges  $g$  effect size,  
514 corrected for small sample sizes. Hedges'  $g$  was calculated as  $(MHW_{After} - MHW_{Before})/S \times J$ ,  
515 where  $S$  is the pooled standard deviation and  $J$  is a factor that corrects for bias associated with  
516 small sample sizes<sup>25,57</sup>. 'MHW<sub>before</sub>' and 'MHW<sub>after</sub>' represent the mean performance response  
517 reported by the study before and after the period of extreme warming, respectively. These relied  
518 on the authors' designations of the timing of the MHW. When the mean performance response  
519 before the MHW event were reported for multiple time points, an average was taken to obtain  
520 'MHW<sub>before</sub>'. In these cases, the associated variance of the time points was also pooled for use in  
521  $S$ . In this analysis, negative and positive effects reflect inhibition and facilitation of organismal  
522 performance, respectively. Analyses were weighted by the sum of the inverse variance in each  
523 study and the variance pooled across studies and therefore give greater weight to those studies  
524 with higher replication and lower data dispersion. We used random-effect models, thereby  
525 assuming that summary statistics have both sampling error and a true random component of  
526 variation in effect sizes between studies<sup>25,57</sup>. Most publications reported multiple auto-correlated  
527 effects, for example when a study reported effects of a MHW on many different coral species.  
528 Within-study effects are typically not statistically independent from each other and will conflate  
529 analyses, for example by artificially increasing degrees of freedom. We reduced within-study

530 autocorrelation by averaging 1049 non-independent Hedges  $g$  values (extracted from 116  
531 identified research papers) to 182 values, each being characterized by a unique combination of a  
532 MHW, impacted taxa and performance response per research paper. Thus, prior to formal meta-  
533 analyses, within-study effects were averaged across multiple species and across nested designs  
534 (e.g., across different sites within a study or different depth levels). We acknowledge that our  
535 approach to aggregate auto-correlated within-study effect sizes, albeit being the most common  
536 way to do this<sup>58</sup>, may be suboptimal, compared to advanced modelling techniques<sup>58</sup>. However,  
537 many papers reported different types and nested layers of non-independent data within a single  
538 paper, requiring overly complex combinations and levels of aggregation models (compared to  
539 aggregating data with a mean), prior to the meta-analysis. Finally, we calculated mean effect  
540 sizes ( $E$ ), 95% confidence intervals (CI), heterogeneity ( $Q$ ), and the proportion of real observed  
541 dispersion ( $I^2$ ) based on weighted random effect models in OpenMEE<sup>57</sup>. Mean effect sizes were  
542 considered to be significantly different from zero or another effect if their 95% CIs did not  
543 overlap with zero or each other, respectively<sup>59-62</sup>. Effect sizes generated from a single study were  
544 excluded from plots (these were: a single mean effect size of -4.21 for the 1972 ENSO event, and  
545 a single effect size of 1.183 for ‘reptiles’ in the taxon-specific analysis).

#### 546 **Publication bias**

547 Our meta-analyses may be influenced by publication bias if we overlooked studies documenting  
548 strong positive effects, or if studies finding non-significant effects are not been published<sup>25,63,64</sup>.  
549 We believe that the first type of publication bias is unlikely because we have worked intensively  
550 with MHW through primary research and by writing book chapters and reviews. We explored  
551 possible publication bias in different ways. We examined funnel plot asymmetry using the  
552 trimfill method and regression tests, and calculated the fail-safe number using the Rosenberg



553 method that estimates the number of studies averaging null results that should be added to reduce  
554 the significance level ( $p$ -value) of the average effect size (based on a fixed-effects model) to  
555  $\alpha = 0.05$ <sup>63,64</sup>. These tests suggest that publication bias has limited effects and that our results  
556 generally are robust. Although the funnel plot was highly asymmetric (Fig. S4), as shown in a  
557 significant regression test ( $t = -3.598$ ,  $p = 0.0004$ ), adjusting this possible bias using the trimfill  
558 method had not effects on our general conclusion, because the mean effect size remained  
559 significantly negative ( $-0.05$ , with 95% confidence intervals  $-0.08$  to  $-0.02$ ,  $p < 0.01$ ). In addition,  
560 Rosenberg's fail safe number was 11,318, i.e., much larger than  $5n + 10$ , where  $n$  is the number  
561 of original studies included in our analyses. Thus, publication bias is unlikely to affect our results  
562 and did not change our main finding that MHW generally had negative effects on marine  
563 organisms.

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

565 We also tested the hypothesis that populations found towards the warm-water limit (i.e.  
566 equatorward range edge) of a species' distribution will respond more negatively to MHWs. To  
567 do this, we first extracted all observations from the database that were recorded at the species-  
568 level (302 species and 645 observations). Global species distributions were produced using  
569 presence-only Maxent models for each species in fish and plankton datasets for which sufficient  
570 observations were available, and using default parameters for a random seed, convergence  
571 threshold, maximum number of iterations, maximum background points and the regularization  
572 parameter<sup>52</sup> (using Maxent version 3.3.3k). Observations of species presence from iOBIS were  
573 gridded such that 1-degree grid cells with observations were set as present. These observations  
574 were then modelled as a function of the following environmental predictors: (1) average annual  
575 temperatures from the HadISST v1.1; (2) the logarithm of distance to the nearest coastline; (3)

576 ocean depth from the GEBCO marine atlas; and (4) FAO major fishing areas  
577 (<http://www.fao.org/fishery/area/search/en>). Global maps of predicted presence were produced  
578 using a threshold probability of 0.4. Presence maps were used to extract average annual sea  
579 surface temperature values from Hadley Centre HadISST v1.1 1-degree dataset long-term  
580 climatology average 1960-2009. Quantiles (0, 0.1, 0.25, 0.5, 0.75, 0.9 and 1.0) of the population  
581 of temperatures in occupied grid squares were used to define the thermal niche of the species  
582 (weighted by the relative area of grid cells given by the cosine of the latitude). The frequency  
583 distribution of these species-specific distributions were then described using percentiles, and, for  
584 this analysis, the 10<sup>th</sup> and 90<sup>th</sup> percentiles were taken as measures of the warm and cold ends of  
585 the thermal range, respectively. Each location of a reported MHW effect was then used to extract  
586 the local average SST from the same SST climatology. Range location was then expressed as the  
587 local temperature less the 10<sup>th</sup> percentile of temperature, divided by the difference between the  
588 10<sup>th</sup> and 90<sup>th</sup> percentiles of estimated species range temperatures. A range location value of zero  
589 or less was therefore at the cold end of the distribution range ( $\leq 10^{\text{th}}$  percentile), while values of  
590 1 or more would be at the warm end of the range ( $\geq 90^{\text{th}}$  percentile). This process resulted in  
591 estimated range locations for 347 observations from 280 species within the ecological dataset.  
592

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

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

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

604 High-resolution time series on coral bleaching, seagrass density and kelp biomass were obtained  
605 from the Caribbean Sea, Western Australia and California, respectively (Fig. S5). Quality-  
606 controlled coral bleaching observations for the Caribbean Sea/Gulf of Mexico region  
607 (northernmost limit: 30.0°N, southernmost limit: 10.2°N, western limit: 97.5°W, eastern limit:  
608 59.6°W) were obtained (at 11 km resolution) from NOAA's Coral Reef Watch program  
609 (<http://coralreefwatch.noaa.gov/satellite/index.php>). Observations were first filtered by month  
610 (July-October inclusive) and then summed for each year (1983-2010). Links between MHWs  
611 and seagrass density were examined with long-term monitoring data from Cockburn Sound,  
612 Western Australia, which is collected and managed by the Cockburn Sound Management  
613 Council (Western Australian Government). The density of seagrass shoots was examined at 2  
614 long-term sites (Garden Island and Warnbro Sound), where high-resolution data have been  
615 collected using SCUBA at depths of 2-7 m since 2003 (all surveys were conducted in late  
616 Austral summer of each year). Data were averaged across transects and depths before generating  
617 an annual mean value for the Cockburn Sound region (average of 2 sites). Annual estimates for  
618 giant kelp, *Macrocystis pyrifera*, biomass were generated from the satellite-derived dataset  
619 produced by Cavanaugh et al.<sup>65</sup> as part of the Santa Barbara Coastal Long-term Ecological  
620 Research (SBC-LTER) program (<http://sbc.lternet.edu/index.html>). Estimates of the biomass of  
621 the kelp canopy (i.e. floating fronds) were derived from LANDSAT 5 Thematic Mapper satellite

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

632

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

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