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Categorizing and naming marine heatwaves

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

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

The global ocean has warmed significantly over the past century, with far-reaching

implications for marine ecosystems[1]. Concurrent with long-term persistent warming,

discrete periods of extreme regional ocean warming (marine heatwaves, 'MHWs') have

increased in frequency[2]. Here we quantify trends and attributes of MHWs across all

ocean basins and examine their biological impacts from species to ecosystems. Multiple

regions within the Pacific, Atlantic and Indian Oceans are particularly vulnerable to

MHW intensification, due to the co-existence of high levels of biodiversity, a prevalence

of species found at their warm range edges, or concurrent non-climatic human impacts.

The physical attributes of prominent MHWs varied considerably, but all had

deleterious impacts across a range of biological processes and taxa, including critical

foundation species (corals, seagrasses and kelps). MHWs, which will likely intensify

with anthropogenic climate change[3], are rapidly emerging as forceful agents of

disturbance with the capacity to restructure entire ecosystems and disrupt the provision

of ecological goods and services in coming decades.

Anthropogenic climate change is driving the redistribution of species and reorganization of

natural systems and represents a major threat to global biodiversity[4,5]. The biosphere has

warmed significantly in recent decades with widespread implications for the integrity of

ecosystems and the sustainability of the goods and services they provide[6,7]. In addition to the

near ubiquitous long-term increases in temperature, the frequency of discrete extreme

warming events ('heatwaves') has increased[8,9] with projections indicating they will become

more frequent, more intense and longer lasting throughout the 21st Century[10]. While extremes

occur naturally within the climate system, there is growing confidence that the observed

intensification of heatwaves is due to human activities[11,12]. The 21st Century has already

experienced record-shattering atmospheric heatwaves[8,13], 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[8].

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[14]. 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[15-17]. By

84   impacting ecosystem goods and services, such as fisheries landings[18,19] and biogeochemical

85   processes[20,21], 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[22], the long-lasting 'Blob' (2013-2016) in the northeast Pacific[23]

88   and El Niño-related extreme warming in 2016 that affected most of the Indo-Pacific[24,25].

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[14] 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 90th percentile of climatological SST observations) for at

95   least 5 consecutive days[14], Oliver et al.[2] 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[14] 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 20th and early 21st 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)[2], 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[26]) 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; $p_{heterogeneity} < 0.001$, $I^2 = 97.13$). 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[16]. Corals were directly affected

150   by these MHWs, as extreme absolute temperatures resulted in widespread bleaching and

151   mortality[27,28], whereas birds were indirectly impacted through changes in prey availability[29].

152   Birds and corals are also particularly sensitive to longer term increases in sea temperature

153   associated with ocean warming[30]. 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[31] and highly mobile

156   species can quickly migrate in response to rapidly changing conditions[16]. 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[32].

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 10th and 90th 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[17,33,34].

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[35], 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[16,36].

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,
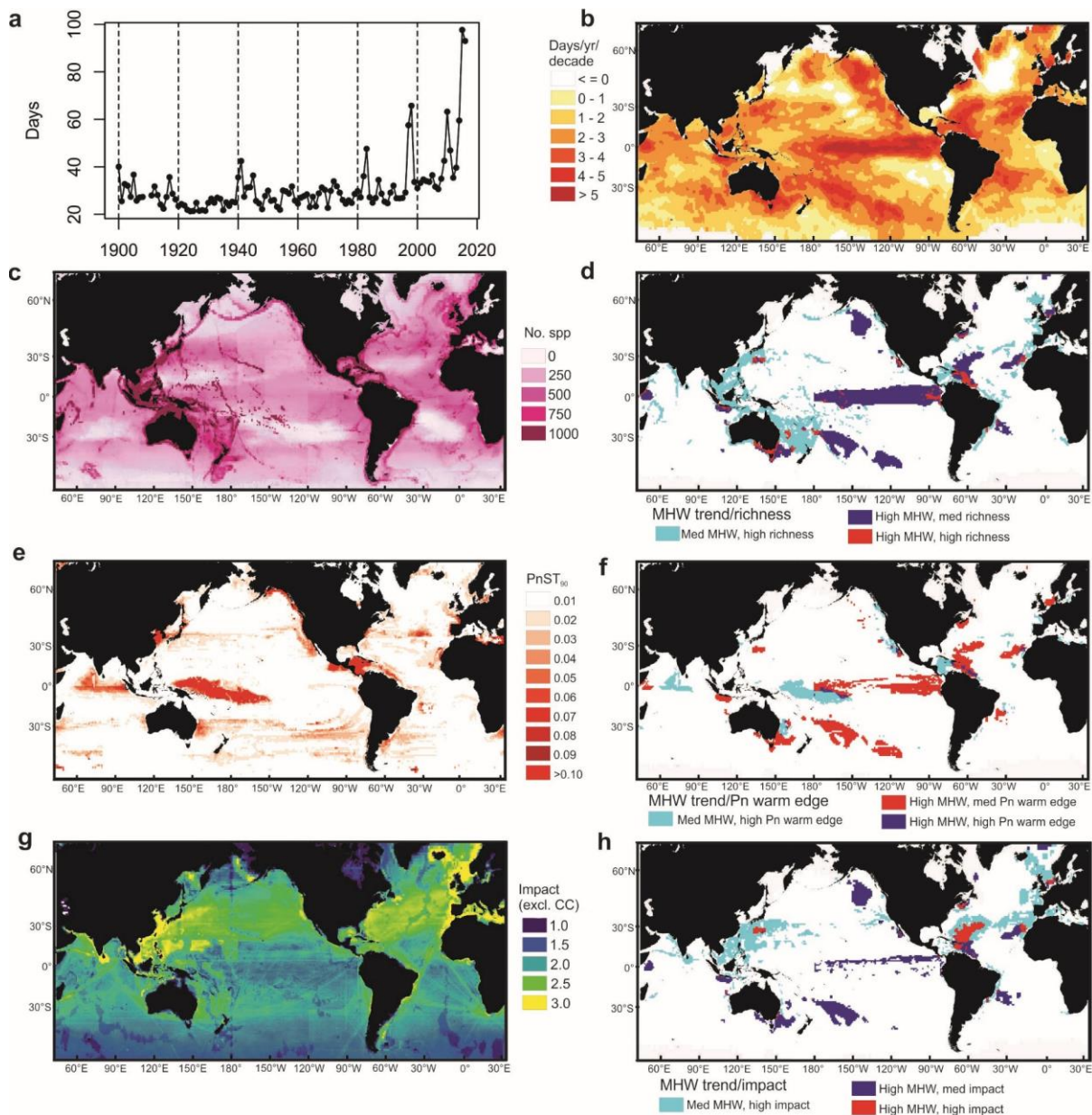
199 with hundreds of millions of people benefitting from coastal marine ecosystems[37,38]. As such,

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[2]. 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[8,39], 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**).
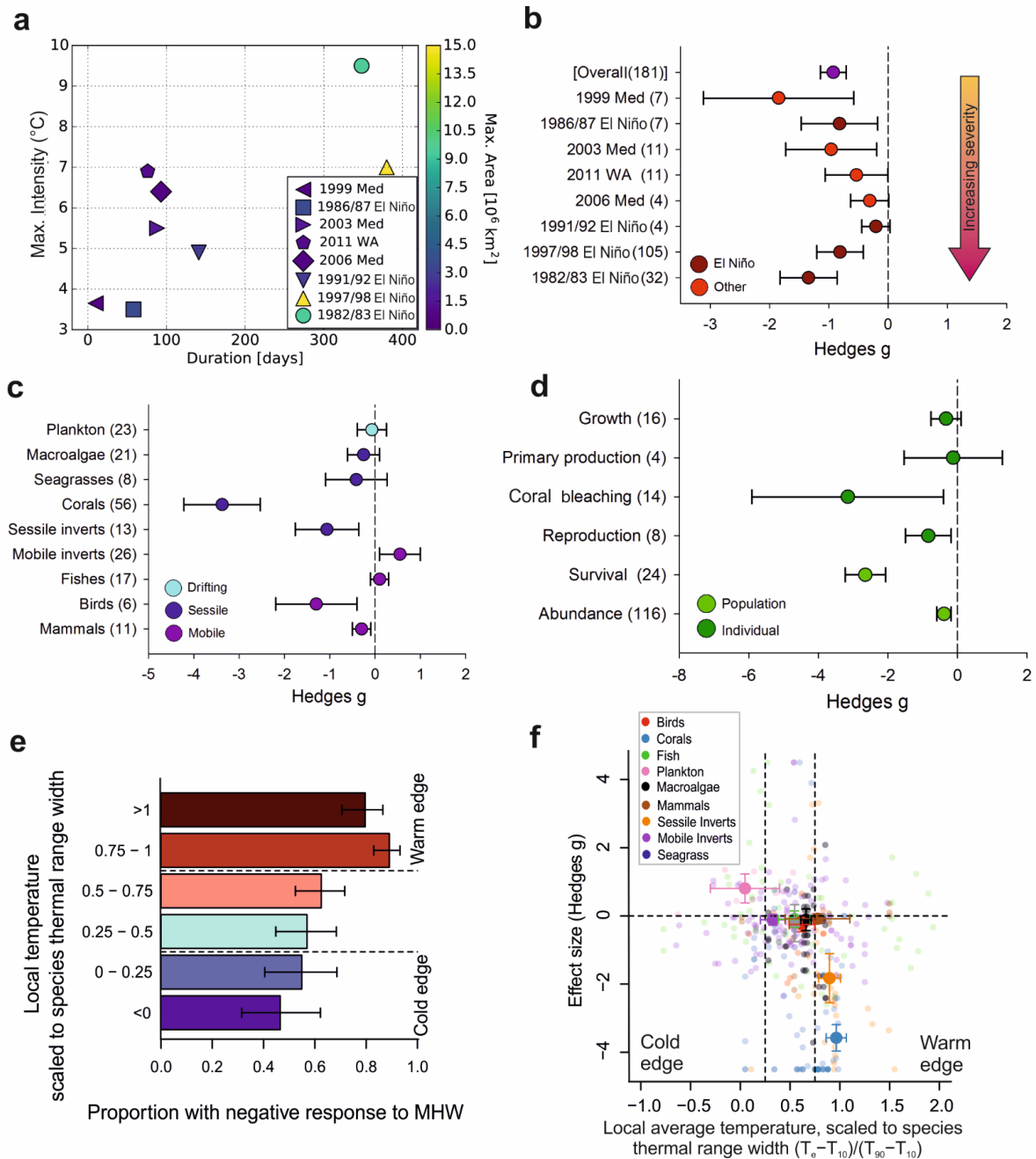
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Fig. 2. Ecological impacts of MHWs as determined by a meta-analysis of responses to eight prominent MHW events. **a,b,** The attributes of the eight MHW events used in the meta-analysis (**a**) and the overall effect of each MHW event across all ecological 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 (±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, ±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.
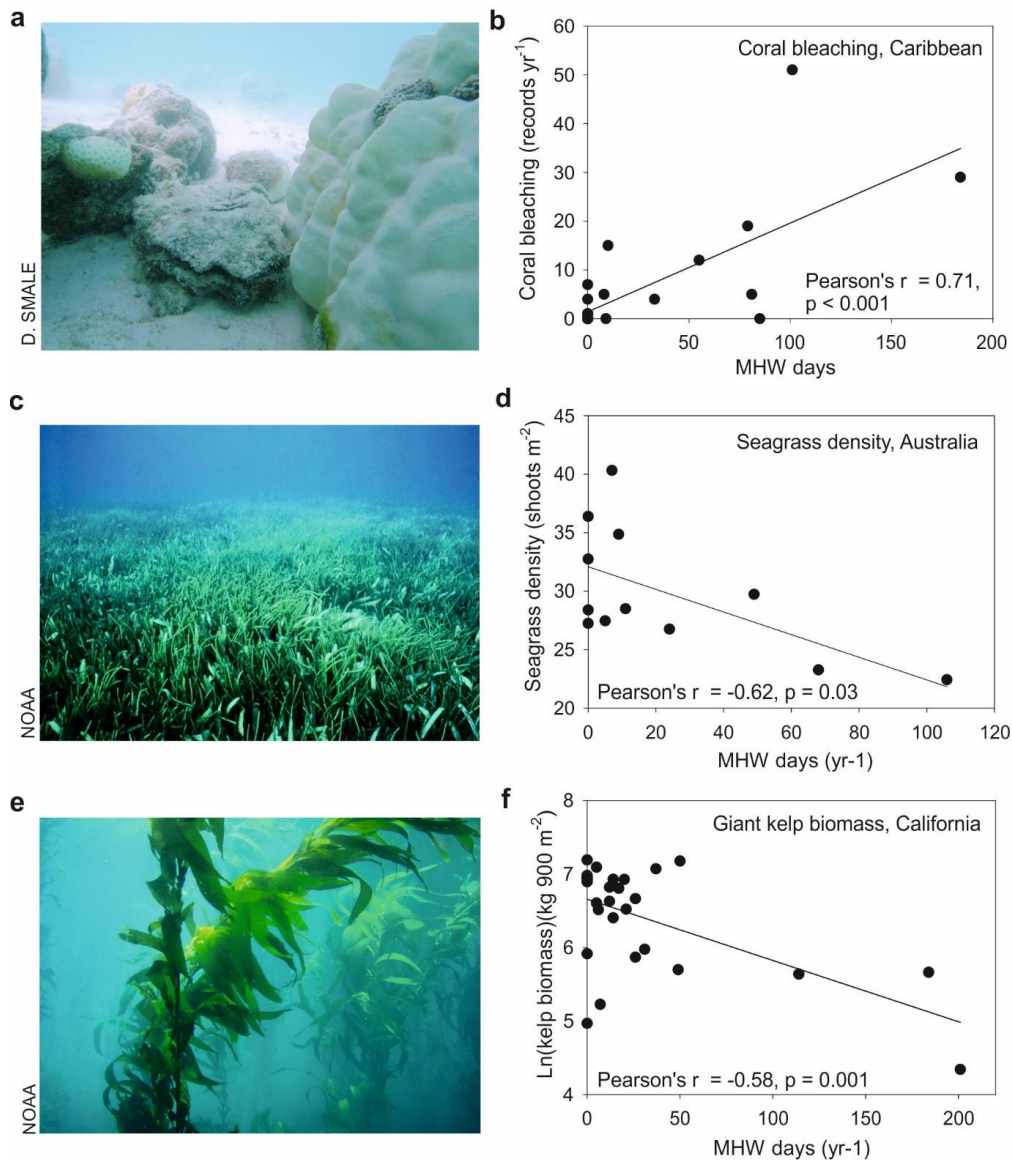
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254 Fig. 3. Impacts of MHWs on foundation species. **a,b**, Severe MHWs, such as those associated with the extreme
255 El Niño events of 1997/98 and 2015/16, have caused widespread bleaching and mortality of reef building corals
256 (**a**). Analysis of annual coral bleaching records from the Caribbean Sea/Gulf of Mexico region (1983-2010, data
257 from NOAA Coral Reef Watch) showed that the number of MHW days per year was positively correlated with
258 the frequency of coral bleaching observations (**b**). **c,d,** Seagrass meadows yield critical ecosystem services,
259 including carbon sequestration and biogenic habitat provision, yet recent MHWs have impacted seagrass
260 populations in several regions (**c**). Monitoring data from independent sites in Cockburn Sound, Western
261 Australia (2003-2014, data provided by Cockburn Sound Management Council) indicated that the number of
262 MHW days recorded in the previous year was negatively correlated with seagrass (*Posidonia sinuosa*) shoot
263 density (**d**). **e,f,** Kelp forests represent critical habitats along temperate coastlines but extreme temperatures
264 experienced during MHWs can cause widespread mortality and deforestation (**e**). Satellite-derived estimates of
265 giant kelp (*Macrocystis pyrifera*) biomass along the coastline of California/Baja California (1984-2011, data
266 from Santa Barbara Coastal Long-term Ecological Research program) showed that kelp biomass was negatively
267 correlated with the number of MHW days recorded during the previous year (**f**).
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273 Table 1. Impacts of MHWs on services provided by marine ecosystems (definitions of ecosystem services
274 adapted from The Economics of Ecosystems and Biodiversity, TEEB, developed by UNEP). Evidence of
275 impacts was collated from specific MHWs: (a) 1982/83 El Niño event, (b) 1997/98 El Niño event, (c) 1999
276 Mediterranean MHW, (d) 2003 Mediterranean MHW, (e) 2011 Western Australian MHW, (f) 2012 Northwest
277 Atlantic MHW, (g) the 2013-2016 Northeast Pacific 'Blob', and (h) the 2015/2016 El Niño event in northern
278 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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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-
296 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
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   Benthuysen, J. A., Oliver, E. C. J., Feng, M. & Marshall, A. G. Extreme marine warming across
338   tropical Australia during austral summer 2015–2016. *J. Geophy. 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 Liquete, 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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Methods

1. Definition of MHWs and analysis of multi-decadal trends

Marine heatwaves (MHWs) were identified from observational sea surface temperature (SST) time series using the definition proposed by Hobday et al.[14], whereby a MHW is defined as a "*discrete prolonged anomalously warm water event at a particular location*" with each of those terms (anomalously warm, prolonged, discrete) quantitatively defined and justified for the marine context. Specifically, "*discrete*" implies the MHW is an identifiable event with clear start and end dates, "*prolonged*" means it has a duration of at least five days, and "*anomalously warm*" means the temperature is above a climatological threshold (in this case the seasonally-varying 90th percentile). The climatological mean and threshold were calculated over a base period of 1983-2012. For each day-of-year, a pool of days across all years in the climatology period and within an 11-day window was taken as a sample, from which the mean and 90th percentile threshold were calculated. The climatological mean and threshold were then further smoothed using a 30-day running window. When two successive events occur with a break of two days or less, this was deemed to represent a single continuous event. The code used to identify MHWs and calculate key MHW metrics following this definition is freely available and has been implemented in Python (https://github.com/ecjoliver/marineHeatWaves) and R (https://robwschlegel.github.io/heatwaveR). MHWs detected using this definition were then characterized by a set of metrics, including duration and intensity (i.e. the maximum daily temperature above the seasonal climatology during the event). We then examined an annual time 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.[2]. 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[51], which were accumulated

464   from projected species distributions from the Aquamaps project[52]. 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[52], previously used to assess likely patterns of biodiversity change[51], 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 90th 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[53], 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.[54]. 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.[54,55]. 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[56], species richness and

504   distributions[57] and human stressors[54].

3. Meta-analysis of ecological responses to MHWs

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[26,58]. 'MHW$_{before}$' and 'MHW$_{after}$' 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$_{before}$'. 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[26,58]. 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 [59], may be suboptimal, compared to advanced modelling techniques[59]. 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[58]. 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[60-63]. 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[26,64,65]. 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[64,65]. 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[53] (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   10th and 90th 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 10th percentile of temperature, divided by the difference between the 10th and 90th

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 ($<=10^{th}$ percentile), while values of 1 or more

620   would be at the warm end of the range ($>=90^{th}$ 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.[66] 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*), 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.

672

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

710