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Marine heatwaves threaten global biodiversity and the provision of ecosystem services

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

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41   **Article type:** Letter

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43   **One Sentence Summary:** Marine heatwaves alter ecosystem structure and functioning at

44   global scales.

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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
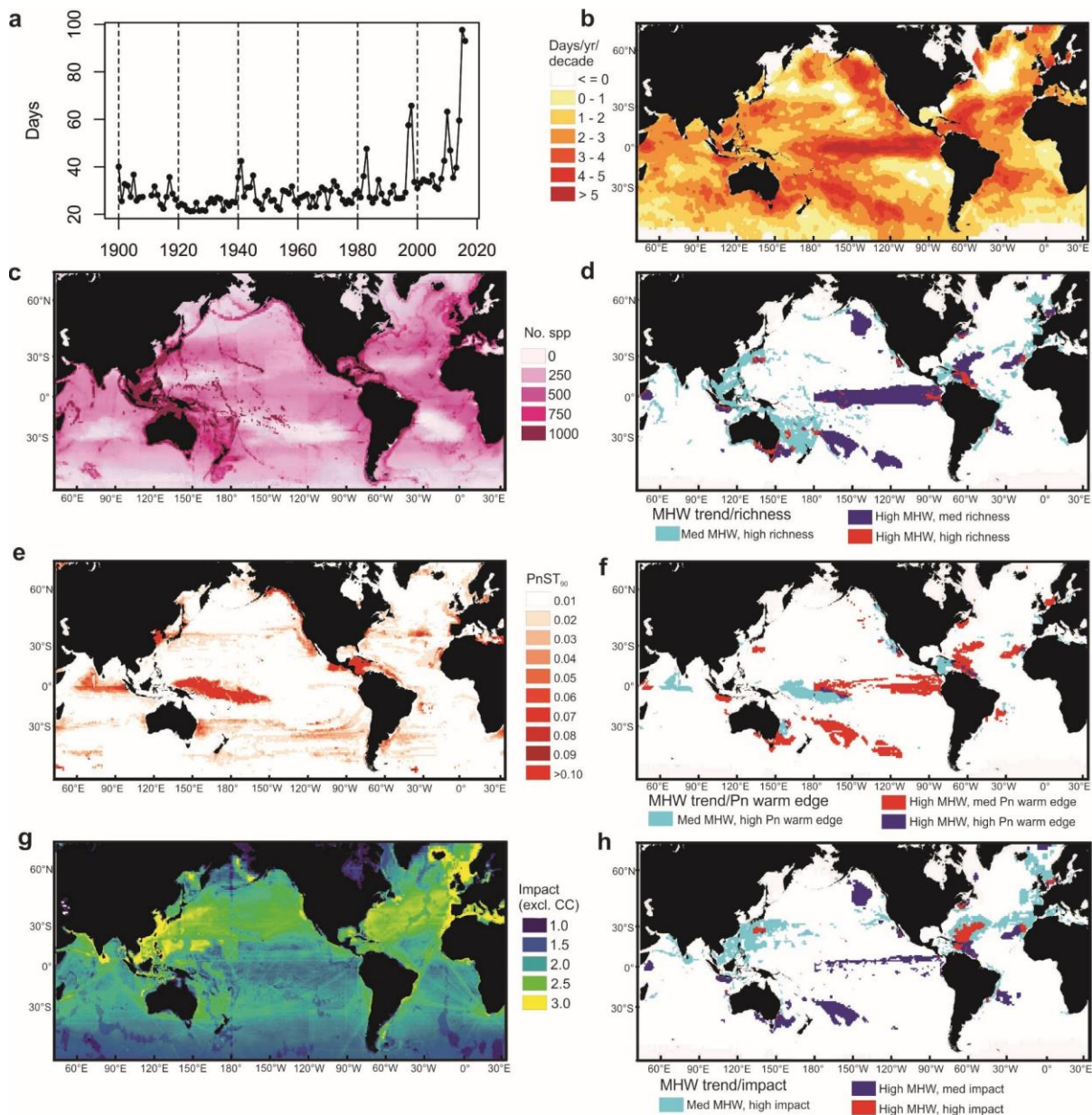
211   decades.

212

213

Fig. 1. Global patterns of MHW intensification, marine biodiversity, proportions of species found at their warm range edge and concurrent human impacts. **a,b,** Globally averaged time-series of the annual number of MHW days and trends in the annual number of MHW days (between 1925-1954 and 1987-2016) across the global ocean. **c,e,g,** Existing data on marine biodiversity (**c**), the proportion of species within the local species pool found near their warm range edge (**e**), and non-climatic human stressors (**g**) were combined with MHW intensification data. **d,f,h,** The resultant bivariate maps identify regions of high diversity value that may be impacted by MHWs (**d**), high thermal sensitivity of species which may have been particularly vulnerable to increased MHWs (**f**) and high levels of non-climatic human stressors where MHW intensification has impacted concurrently upon marine ecosystems (**h**).
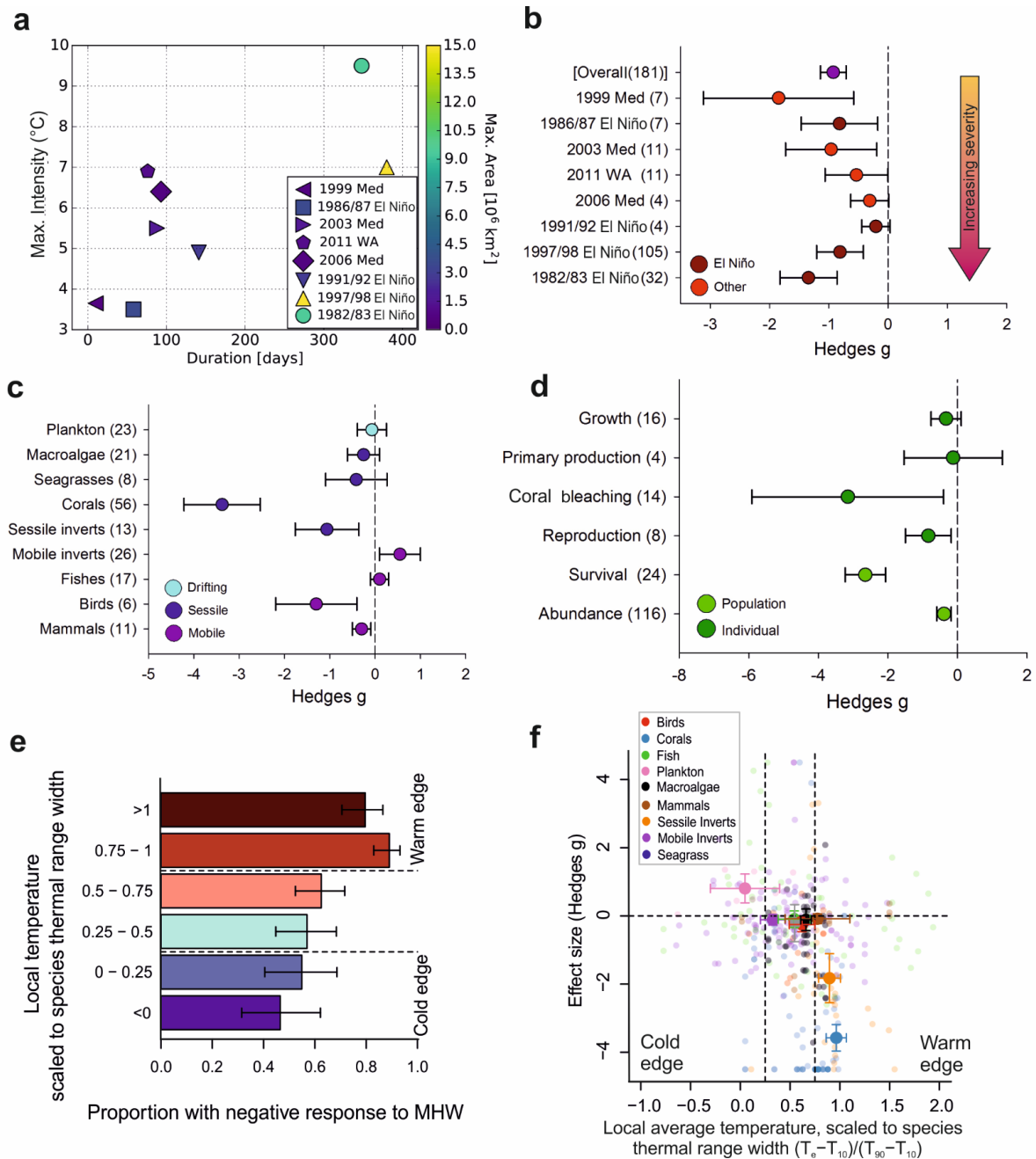
Fig. 2. Ecological impacts of MHWs as determined by a meta-analysis of responses to eight prominent MHW events. **a,b,** The attributes of the eight MHW events used in the meta-analysis (**a**) and the overall effect of each MHW event across all ecological responses (**b**). **c,d,** The effect of MHWs on major taxonomic groups (**c**) and types of ecological responses (**d**). The number of independent observations for each category are shown in parentheses and values represent mean ($\pm$95% CI) effect sizes (Hedges g, to account for bias associated with small sample sizes). **e,f,** Populations located towards the warm-water limit of species' distributions tended to respond more negatively to MHWs (**e**) with effect sizes (Hedges g, $\pm$95% CI) generally becoming more negative for warmer equatorward range-edge populations (**f**). Plots are based on responses of 685 species-level observations; bold symbols in (**f**) indicate means for each major taxonomic group and faded symbols show individual studies (T_e temperature at effect location, T_{10}, T_{90}, 10% and 90% species range temperatures). Horizontal (**e**) and vertical dashed lines (**f**) delineate the lower and upper quartiles of species' thermal ranges.
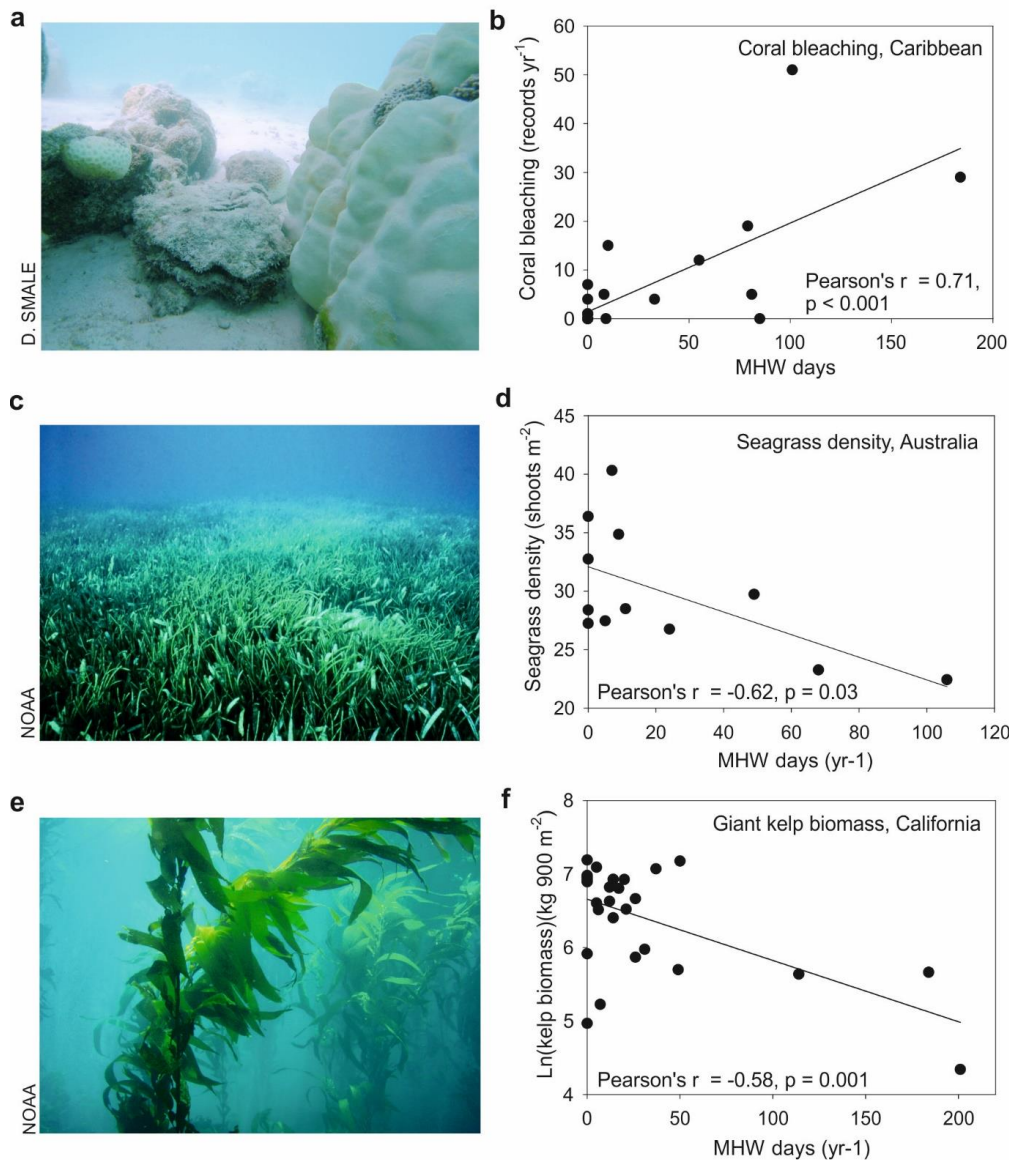
Fig. 3. Impacts of MHWs on foundation species. **a,b**, Severe MHWs, such as those associated with the extreme El Niño events of 1997/98 and 2015/16, have caused widespread bleaching and mortality of reef building corals (**a**). Analysis of annual coral bleaching records from the Caribbean Sea/Gulf of Mexico region (1983-2010, data from NOAA Coral Reef Watch) showed that the number of MHW days per year was positively correlated with the frequency of coral bleaching observations (**b**). **c,d,** Seagrass meadows yield critical ecosystem services, including carbon sequestration and biogenic habitat provision, yet recent MHWs have impacted seagrass populations in several regions (**c**). Monitoring data from independent sites in Cockburn Sound, Western Australia (2003-2014, data provided by Cockburn Sound Management Council) indicated that the number of MHW days recorded in the previous year was negatively correlated with seagrass (*Posidonia sinuosa*) shoot density (**d**). **e,f**, Kelp forests represent critical habitats along temperate coastlines but extreme temperatures experienced during MHWs can cause widespread mortality and deforestation (**e**). Satellite-derived estimates of giant kelp (*Macrocystis pyrifera*) biomass along the coastline of California/Baja California (1984-2011, data from Santa Barbara Coastal Long-term Ecological Research program) showed that kelp biomass was negatively correlated with the number of MHW days recorded during the previous year (**f**).

272
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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411   Challenge on Extremes, the NESP Earth Systems and Climate Change Hub Project 2.3 (Component 2) on the

412   predictability of ocean temperature extremes, and the interests and activities of the International Commission on

413   Climate of IAMAS/IUGG.

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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.

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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.

2. Global patterns of MHW intensification and overlaps with known hotspots of marine

457

biodiversity, temperature-sensitive populations and non-climatic human stressors

458

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 $1° \times 1°$ 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

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

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

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