Marine heatwaves threaten global biodiversity and the provision of ecosystem services

Smale, Dan A.; Wernberg, Thomas; Oliver, Eric C. J.; Thomsen, Mads; Harvey, Ben P.; Straub, Sandra C.; Burrows, Michael T.; Alexander, Lisa V.; Benthuysen, Jessica A.; Donat, Markus G.; Feng, Ming; Hobday, Alistair J.; Holbrook, Neil J.; Perkins-kirkpatrick, Sarah E.; Scannell, Hillary A.; Sen Gupta, Alex; Payne, Ben L.; Moore, Pippa J.

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39   **Article type:** Letter

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

42   scales.

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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]. We quantified trends and attributes of MHWs across all ocean basins and examined their biological impacts from species to ecosystems. Multiple regions within the Pacific, Atlantic and Indian Oceans are particularly vulnerable to MHW intensification, due to 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, 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[3,4]. 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[5,6]. In addition to the near ubiquitous long-term increases in temperature, the frequency of discrete extreme warming events ('heatwaves') has increased[7,8] with projections indicating they will become more frequent, more intense and longer lasting throughout the 21st Century[9]. While extremes occur naturally within the climate system, there is growing confidence that the observed intensification of heatwaves is

70 due to human activities[10,11]. The 21st Century has already experienced record-shattering

71 atmospheric heatwaves[7,12], such as the 2003 European heatwave, the Australian 'Angry Summer'

72 of 2012-2013, and the European 'Lucifer' heatwave in 2017, with devastating consequences for

73 human health, the economy and the environment[7].

74

75 Discrete and prolonged extreme warming events occur in the ocean as well as the atmosphere.

76 'Marine heatwaves' (MHWs) are caused by a range of processes operating across different

77 spatial and temporal scales, from localised air-sea heat flux to large-scale climate drivers, such as

78 the El Niño Southern Oscillation[13]. Regional case studies have documented how MHWs can alter

79 the structure and functioning of entire ecosystems by causing widespread mortality, species

80 range shifts and community reconfiguration[14-16]. By impacting ecosystem goods and services,

81 such as fisheries landings[17,18] and biogeochemical processes[19,20], MHWs can have major

82 socioeconomic and political ramifications. Recent high-profile ocean warming events include the

83 record-breaking 2011 'Ningaloo Niño' (2010-2011) off Western Australia[21], the long-lasting

84 'Blob' (2013-2016) in the northeast Pacific[22] and El Niño-related extreme warming in 2016 that

85 affected most of the Indo-Pacific[23,24]. These events have increased awareness of MHWs as an

86 important climatic phenomenon affecting both physical and biological processes. Until recently,

87 the lack of a common framework to define MHWs[13] has hampered attempts to examine temporal

88 trends or to compare physical attributes or biological impacts across different events, regions or

89 taxa. However, by defining MHWs as periods when daily sea-surface temperatures (SSTs)

90 exceed a local seasonal threshold (i.e. the 90th percentile of climatological SST observations) for

91 at least 5 consecutive days[13], Oliver et al.[2] showed that the frequency and duration of MHWs

92 have increased significantly over the past century across most of the global ocean. Here, we used

93   the same MHW framework[13] to examine observed trends in the annual number of MHW days

94   and the implications for marine ecosystems globally. We incorporated existing data on marine

95   taxon richness, the proportion of species found at their warm range edges and non-climatic

96   human impacts to identify regions of high vulnerability, where increased occurrences of MHWs

97   overlap with areas of high biodiversity, temperature sensitivity or concurrent anthropogenic

98   stressors. We also conducted a meta-analysis on the impacts of MHWs, by examining ecological

99   responses to eight prominent MHW events that have been studied in sufficient detail for formal

100   analysis. We examined 1049 ecological observations, recalculated to 182 independent effect

101   sizes from 116 research papers that examined responses of organisms, populations and

102   communities to MHWs. We also explored relationships between the occurrence of MHWs and

103   the health of three globally-significant foundation species (coral, seagrass and kelp) from three

104   independent time series that were collected at sufficient spatiotemporal resolutions to explicitly

105   link ecological responses to MHWs. Finally, we reviewed the literature on MHWs for evidence

106   of impacts of these events on goods and services to human society.

107

108   The total number of MHW days per year, based on five quasi-global SST datasets, has increased

109   globally throughout the 20th and early 21st Century (Fig. 1A). As a global average, there are over

110   50% more MHW days per year in the latter part of the instrumental record (1987-2016)

111   compared to the earlier part (1925-1954)[2], with most regions experiencing increases in the

112   number of MHW days (Fig 1B). Global patterns of marine taxon richness (Fig. 1C) overlaid with

113   trends in annual MHW days reveal regions where increased MHW occurrences can influence

114   biologically diverse regions, in particular, southern Australia, the Caribbean Sea, and the

115   coastline bounding the mid-eastern Pacific (Fig 1D). Given that warm range edge populations are

116   likely to be the most impacted by MHWs (as thermal tolerances are exceeded during

117   anomalously high temperatures), regions which support a high proportion of species found near

118   their warm range edge will be particularly vulnerable to increased MHW activity (Fig 1E).

119   Several regions were identified as having experienced marked increases in MHW days and also

120   supporting a high proportion of species found near their warm range edges (Fig 1F), with marine

121   ecosystems in the southwest Pacific and the mid-west Atlantic particularly at risk. Furthermore,

122   regions where rapid increases in the annual number of MHW days overlap with existing high-

123   intensity non-climate human stressors (Fig 1G) include the central west Atlantic, the northeast

124   Atlantic and the northwest Pacific (Fig. 1H). Here, existing regional pressures, including

125   overfishing and pollution, have the potential to exacerbate MHW impacts.

126

127   Examination of eight prominent (and sufficiently studied) MHWs showed they varied greatly

128   with respect to spatial extent (by a factor of >15, Fig. 2A, Fig. S1), duration (10 to 380 days) and

129   maximum intensity (3.5 to 9.5°C above climatological SST) (Fig. 2A). It should be noted several

130   MHWs were primarily driven by large-scale El Niño events which, by their nature, affected

131   ocean climate at large spatial scales. Here, the largest contiguous MHW associated with each

132   ENSO event was identified and characterised with MHW metrics. Our meta-analysis of

133   ecological impacts (based on Hedges g effect sizes to account for bias associated with small

134   sample sizes[25]) detected an overall negative effect of MHWs on biota across research papers,

135   events, taxa, and response variables (E = -0.93; 95 CI = 0.22; Q = 6303, df = 181; $p_{heterogeneity}$ <

136   0.001, I^2 = 97.13). All eight MHWs were associated with negative ecological impacts although

137   the mean negative effect sizes were not significantly different from zero for the two events with

138   lowest sample sizes (Fig. 2B). There was no clear relationship between the severity of the MHW

139 (derived from normalized MHW intensity and duration) and their observed impacts (Fig. 2B).

140 All taxonomic groups, with the exception of fishes and mobile invertebrates, responded

141 negatively to MHWs with birds and corals being most adversely affected (Fig. 2C). The positive

142 fish response was, in part, driven by new incursions of tropical species into impacted temperate

143 regions[15]. Corals were directly affected by these MHWs, as extreme absolute temperatures

144 resulted in widespread bleaching and mortality[26,27], whereas birds were indirectly impacted

145 through changes in prey availability[28]. Birds and corals are also particularly sensitive to longer

146 term increases in sea temperature associated with ocean warming[29]. Overall, our analyses suggest

147 that sessile taxa were more impacted by MHWs than mobile and planktonic taxa (Fig. 2C),

148 perhaps because mobile taxa generally have higher thermal tolerances than less active or sessile

149 taxa[30] and highly mobile species can quickly migrate in response to rapidly changing

150 conditions[15]. All ecological response variables were negatively affected by MHWs, although

151 growth and primary production were not significantly different from zero (Fig. 2D). Negative

152 impacts were greatest for coral bleaching, survival, and reproduction (Fig. 2D), a pattern

153 consistent with effects of warming in manipulative experiments[31].

154

155 To examine links between MHWs and ecological responses, we conducted additional analysis at

156 the species level to test the prediction that populations found towards the warm-water limit (i.e.

157 equatorward range edge) of a species' distribution would be more negatively impacted by

158 MHWs. From the database described above, we extracted all species level observations (645

159 observations from 302 species) and for each population we classified their relative position

160 within the species range by expressing the local average SST as a proportion of the difference

161 between the 10th and 90th percentile temperatures experienced through the species geographical

162   range. Critically, the most negative responses to MHWs were seen in populations found towards

163   their warm range edge (Fig. 2E), implying that extreme temperatures exceeded thermal

164   thresholds with adverse effects. Across all species-level observations, there was a negative

165   relationship between any given population's location within the species' range and the direction

166   and magnitude of the MHW effect (Fig. 2F). This indicates that populations residing near the

167   warm limit of a given species range are particularly vulnerable to warming events and range

168   contractions are likely to occur in response to more frequent MHWs. Indeed, recent observations

169   have shown that equatorward range edges of both plant and animal species have retracted

170   poleward by >100 km following severe MHW events[16,32,33].

171

172   An examination of long-term time series on the health of three globally important foundation

173   taxa showed that increased annual number of MHW days was correlated with (i) increased coral

174   bleaching, (ii) decreased seagrass density and (iii) decreased kelp biomass (Fig. 3). Even though

175   environmental variables such as storms, nutrients and light are known to strongly influence the

176   health of these critical habitat-formers[34], the annual number of MHW days alone was strongly

177   and significantly correlated with observed ecological performance and, crucially, had

178   consistently stronger correlative relationships than more frequently used measures of ocean

179   temperature (i.e. mean and maximum SST, see Table S1). An increased number of MHW days

180   was significantly correlated to decreased ecological health of populations of all three foundation

181   taxa, indicating the importance of discrete extreme ocean warming events in driving ecosystem

182   structure[15,35].

183

184   A wide range of ecological goods and services derived from marine ecosystems have been

185   severely impacted by recent MHWs (Table 1). For example, the 2011 Ningaloo Niño caused

186   widespread loss of biogenic habitat, depleted biodiversity, disruption to nutrient cycles and shifts

187   in the abundance and distribution of commercial fisheries species off Western Australia (Table

188   1). Similarly, recent MHWs in the Mediterranean Sea have been linked to local extinctions,

189   decreased rates of natural carbon sequestration, loss of critical habitat and diminished

190   socioeconomic value (Table 1). These services have substantial societal benefit, with hundreds of

191   millions of people benefitting from coastal marine ecosystems[36,37]. As such, managing and

192   mitigating the deleterious effects of MHWs on the provision of ecosystem services is a major

193   challenge for coastal societies.

194

195   Globally, MHWs are becoming more frequent and prolonged, and record-breaking events have

196   been observed in most ocean basins in the past decade[2]. To date, the main focus of ecological

197   research has been on trends in mean climate variables, yet discrete extreme events are emerging

198   as pivotal in shaping ecosystems, by driving sudden and dramatic shifts in ecological structure

199   and functioning. Given the confidence in projections of intensifying extreme warming events

200   with anthropogenic climate change[7,38], marine conservation and management approaches must

201   consider MHWs and other extreme climatic events if they are to maintain and conserve the

202   integrity of highly valuable marine ecosystems over the coming decades.

203

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

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

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) showed that kelp biomass was negatively correlated with the number of MHW days recorded during the previous year (**f**).

252

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

Service type	Ecosystem service	Impacts	Refs
Provisioning	Living resources (non-food)	- Extreme temperatures caused widespread mortality, local extinctions and range contractions of a diversity of taxa (c,d,e)	14,16,39
	Food	- Changes in the distributions and abundances of commercial fisheries species (b,e,f)	17,32,40
Regulating	Carbon sequestration and storage	- Reduced carbon burial and sequestration due to decreased growth and high mortality of seagrasses (d,e)	35,41
	Moderation of extreme events	- Complex, three-dimensional biogenic benthic habitat was replaced by simple poorly-structured habitat, altering hydrodynamics and sediment transport and reducing natural coastal defense (a,b)	42,43
	Nutrient cycling	- Increased stratification and extreme temperatures caused decreased phytoplankton production and nutrient turnover (b,g) - Widespread loss of productive benthic habitats (seagrass, kelp forests) disrupting carbon and nitrogen cycling (d,e)	15,19,35,44
	Biological control	- Anomalous warming events associated with influx of invasive non-native species (e)	32
Habitat or supporting services	Habitats for species	- Local extinctions, range contractions and high mortality rates of habitat-forming corals, seagrasses and macroalgae, resulting in simplified habitat structure and depleted local biodiversity (a,b,e, h)	33,41-43,45-47
Cultural	Tourism and recreation	- Locations affected by intense warming events are less attractive for recreational activities and have decreased socioeconomic value (d, h)	14,48,49

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370   New Zealand: Department of Tourism, University of Otago, 2017).
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386

387 **Author contributions:** DS and TW conceived the initial idea; all authors contributed intellectually to its

388 development. DS, TW, EO, NH co-convened the workshops. EO led the development of the MHW analysis, which

389 was supported by NH, LA, JB, MD, MF, AH, SP, HS and ASG. The meta-analysis of ecological impacts was

390 conducted by MT, BH, SS, MB and PM. DS led manuscript preparation with significant input from all authors.

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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 time series using the definition proposed by Hobday et al.[13], 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.

415   Global time series and regional trends in total MHW days were derived using a combination of

416   satellite-based, remotely-sensed sea surface temperatures and *in situ*-based seawater

417   temperatures. First, total MHW days were calculated globally over 1982-2015 at 1/4° resolution

418   from the National Oceanic and Atmospheric Administration (NOAA) Optimum Interpolation

419   (OI) SST V2 high resolution data. Then, proxies for total MHW days globally over 1900-2016

420   were developed based on five monthly gridded SST datasets (HadISST v1.1, ERSST v5, COBE

421   2, CERA-20C and SODA si.3). A final proxy time series was calculated by averaging across the

422   five datasets. The five monthly data sets were used since no global daily SST observations are

423   available prior to 1982. From these proxy time-series we calculated (i) the difference in mean

424   MHW days over the 1987-2016 and 1925-1954 periods and (ii) a globally-averaged times series

425   of total MHW days. Further details on this method and resulting proxy data can be found in

426   Oliver et al.[2]. Note that these calculations use the same climatology period as above, 1983-2012.

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

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

429   We combined regional trends in MHW days with pre-existing data on marine biodiversity, the

430   proportion of species found near their warm range edges, and non-climatic human stressors to

431   predict where MHW intensification may be a particular threat to biodiversity hotspots or

432   temperature-sensitive communities, or be exacerbated by concurrent stressors. Biodiversity

433   hotspots were determined using published marine taxon richness data[50], which were accumulated

434   from projected species distributions from the Aquamaps project[51]. Patterns in taxon richness

435   (Fig. 1C) showed characteristically high levels in coastal areas and in tropical regions. We also

436   calculated the proportion of species in the local species pool that were near their warm range

437   edge to determine locations where MHWs might be more likely to have a strong negative effect

438   (as shown in Fig. 2F). We used 16582 species global distribution maps from the Aquamaps

439   project[51], previously used to assess likely patterns of biodiversity change[50], to represent global

440   marine biodiversity. For each 1° latitude/longitude grid cell we counted the number of species

441   present for which sea surface temperature, derived as the 1960-2009 average annual temperature

442   from the Hadley Centre HadISST v1.1 dataset, exceeded the 90th percentile temperature of their

443   geographical range, and divided this by the total number of species present. Aside from some

444   artefacts where species limits coincide with FAO (Food and Agriculture Organization of the

445   United Nations) region boundaries, a feature prevalent in other studies using these datasets[52], the

446   resulting map (Fig. 1E) showed areas with higher proportions of species at their warm range

447   edges. Major concentrations (proportions >0.1 of all species) of warm-edge species were seen in

448   the Eastern Mediterranean, the southern Red Sea, the Caribbean Sea, the Mexican part of the

449   North Pacific and a large part of the tropical west Pacific. Locally higher proportions of warm-

450   edge species were also seen along coastlines of Europe, western USA and Canada, North Africa

451   and in the Yellow Sea.

452   Information on stressors were obtained from supplementary online resources provided by

453   Halpern et al.[53]. We additively combined multiple impact layers (demersal destructive fishing,

454   demersal non-destructive high bycatch, demersal non-destructive low bycatch, ocean

455   acidification, ocean pollution, pelagic high bycatch, pelagic low bycatch, shipping and UV) into

456   a single cumulative impacts layer (Fig. 1E). Fishing intensity layers were obtained by

457   apportioning reported catches in FAO areas by modelled productivity data for latitude/longitude

458   cells. Shipping impacts were derived from a 12-month (2003-2004) global ship observing

459   scheme, and the same data was used with ports data to give a measure of ocean pollution.

460   Surface UV information was obtained from the GSFC TOMS EP/TOMS satellite program at

461   NASA. Ocean acidification data came from globally modelled aragonite saturation state. Details

462   of the quantification of these layers are given in Halpern et al.[53,54]. Layers that included ocean

463   warming variables were specifically excluded due to likely co-variance (to varying extents) with

464   MHW metrics. The cumulative impacts layer was then re-projected and resampled onto the

465   same 1°×1° grid as for trends in total MHW days and biodiversity data. Maps of the

466   combinations of medium to high trends in total MHW days and medium to high values of taxon

467   richness (Fig. 1C) or cumulative impacts (Fig. 1E) were created by splitting the data into classes

468   based on the percentiles of the distribution of each variable (0-50% low, 50-90% medium, >90%

469   high). Combined MHW trend/richness and MHW trend/impact layers were assigned to

470   categories according to the classes of each contributing layer. While spatial bias due to

471   variability in sampling effort may influence, to some degree, global-scale datasets on physical

472   and biological variables, the datasets used in the current study have near-complete global

473   coverage and represent the best approximations available for temperature[55], species richness[56]

474   and human stressors[53].

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

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

477   The meta-analysis followed PRISMA (Preferred Reporting Items for Systematic Reviews and

478   Meta-Analyses) guidelines, which provide an evidence-based minimum set of requirements for

479   conducting and reporting meta-analyses (Fig. S2). We searched for peer reviewed studies that

480   compared six types of biological 'performance response' (survival, abundance, growth,

481   reproduction, primary production or coral bleaching) that reported data variation, before and

482   after any of eight well-described periods of extreme warming (El Niño related events in 1982/83,

483   1986/87, 1991/92 and 1997/98, the Mediterranean MHWs of 1999, 2003 and 2006, and the 2011

484 MHW in Western Australia). Relevant studies were identified from two literature searches. First,

485 we conducted a standardized Web of Science search, with search terms related to climate change,

486 heat waves, marine systems, and the eight MHWs mentioned above. We used the following

487 specific search string: ('TS=((marine AND ("heat wave" OR heatwave)) OR El Niño OR La

488 Niña OR ENSO OR (marine AND warming))'), identifying 29,395 potentially relevant papers.

489 We read all abstracts from these papers and then obtained the full manuscripts of the papers that

490 in their title, abstract, or keywords, indicated that relevant data could be collected (= 517 papers).

491 We read all these papers in detail to identify 116 papers that fulfilled our data criteria. For each

492 of the identified publications we extracted all reported mean performance response, data

493 dispersion and sample sizes, from text, tables and figures with Plot Digitizer™

494 (http://plotdigitizer.sourceforge.net/). Impact studies were widely distributed across the global

495 ocean; impact studies relating to ENSO-associated MHWs were spread across the Pacific and

496 Indian Oceans whereas impact studies relating to Mediterranean and Australian MHWs were

497 conducted across a smaller area (Fig. S3). Our fundamental hypothesis was that MHWs

498 generally had negative effects on ecological performance across studies, bioregions, events,

499 response types and organisms. We also tested (see next section for method) if the magnitude of

500 effects varied between heatwave events (eight MHW events), performance responses (6 types

501 listed above) and impacted taxa (grouped into mammals, birds, fishes, mobile invertebrates, non-

502 coral sessile invertebrates, corals, macroalgae, seagrasses and plankton, which included

503 phytoplankton, zooplankton and open ocean microbes). For the MHW test, we hypothesized that

504 the intensity of an event would correlate with the magnitude of effect size. For the biological

505 response test, we hypothesized that coral bleaching and reproduction would be most affected by

506 MHWs, the former because corals are known to be sensitive to elevated temperatures and the

507 latter because reproduction is typically more sensitive to stress than growth, abundance and

508 survival. Finally, for the test across taxa we hypothesized that mobile organisms and

509 seagrasses/corals would exhibit the largest effect sizes because mobile organisms can respond

510 rapidly (e.g. local heat-stressed species can emigrate and warm-tolerant species from adjacent

511 region can immigrate) and seagrasses/corals are generally sensitive to elevated temperatures.

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

513 We analyzed impacts of MHWs on events, taxa and performance with Hedges g effect size,

514 corrected for small sample sizes. Hedges' g was calculated as $(MHW_{After} - MHW_{Before})/S) \times J$,

515 where S is the pooled standard deviation and J is a factor that corrects for bias associated with

516 small sample sizes[25,57]. 'MHW_{before}' and 'MHW_{after}' represent the mean performance response

517 reported by the study before and after the period of extreme warming, respectively. These relied

518 on the authors' designations of the timing of the MHW. When the mean performance response

519 before the MHW event were reported for multiple time points, an average was taken to obtain

520 'MHW_{before}'. In these cases, the associated variance of the time points was also pooled for use in

521 S. In this analysis, negative and positive effects reflect inhibition and facilitation of organismal

522 performance, respectively. Analyses were weighted by the sum of the inverse variance in each

523 study and the variance pooled across studies and therefore give greater weight to those studies

524 with higher replication and lower data dispersion. We used random-effect models, thereby

525 assuming that summary statistics have both sampling error and a true random component of

526 variation in effect sizes between studies[25,57]. Most publications reported multiple auto-correlated

527 effects, for example when a study reported effects of a MHW on many different coral species.

528 Within-study effects are typically not statistically independent from each other and will conflate

529 analyses, for example by artificially increasing degrees of freedom. We reduced within-study

530   autocorrelation by averaging 1049 non-independent Hedges g values (extracted from 116

531   identified research papers) to 182 values, each being characterized by a unique combination of a

532   MHW, impacted taxa and performance response per research paper. Thus, prior to formal meta-

533   analyses, within-study effects were averaged across multiple species and across nested designs

534   (e.g., across different sites within a study or different depth levels). We acknowledge that our

535   approach to aggregate auto-correlated within-study effect sizes, albeit being the most common

536   way to do this [58], may be suboptimal, compared to advanced modelling techniques[58]. However,

537   many papers reported different types and nested layers of non-independent data within a single

538   paper, requiring overly complex combinations and levels of aggregation models (compared to

539   aggregating data with a mean), prior to the meta-analysis. Finally, we calculated mean effect

540   sizes (E), 95% confidence intervals (CI), heterogeneity (Q), and the proportion of real observed

541   dispersion (I^2) based on weighted random effect models in OpenMEE [57]. Mean effect sizes were

542   considered to be significantly different from zero or another effect if their 95% CIs did not

543   overlap with zero or each other, respectively[59-62]. Effect sizes generated from a single study were

544   excluded from plots (these were: a single mean effect size of -4.21 for the 1972 ENSO event, and

545   a single effect size of 1.183 for 'reptiles' in the taxon-specific analysis).

546   **Publication bias**

547   Our meta-analyses may be influenced by publication bias if we overlooked studies documenting

548   strong positive effects, or if studies finding non-significant effects are not been published[25,63,64].

549   We believe that the first type of publication bias is unlikely because we have worked intensively

550   with MHW through primary research and by writing book chapters and reviews. We explored

551   possible publication bias in different ways. We examined funnel plot asymmetry using the

552   trimfill method and regression tests, and calculated the fail-safe number using the Rosenberg

553   method that estimates the number of studies averaging null results that should be added to reduce

554   the significance level (*p*-value) of the average effect size (based on a fixed-effects model) to

555   alpha = 0.05[63,64]. These tests suggest that publication bias has limited effects and that our results

556   generally are robust. Although the funnel plot was highly asymmetric (Fig. S4), as shown in a

557   significant regression test (t = -3.598, p = 0.0004), adjusting this possible bias using the trimfill

558   method had not effects on our general conclusion, because the mean effect size remained

559   significantly negative (-0.05, with 95% confidence intervals -0.08 to -0.02, p < 0.01). In addition,

560   Rosenberg's fail safe number was 11,318, i.e., much larger than $5n$ +10, where n is the number

561   of original studies included in our analyses. Thus, publication bias is unlikely to affect our results

562   and did not change our main finding that MHW generally had negative effects on marine

563   organisms.

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

565   We also tested the hypothesis that populations found towards the warm-water limit (i.e.

566   equatorward range edge) of a species' distribution will respond more negatively to MHWs. To

567   do this, we first extracted all observations from the database that were recorded at the species-

568   level (302 species and 645 observations). Global species distributions were produced using

569   presence-only Maxent models for each species in fish and plankton datasets for which sufficient

570   observations were available, and using default parameters for a random seed, convergence

571   threshold, maximum number of iterations, maximum background points and the regularization

572   parameter[52] (using Maxent version 3.3.3k). Observations of species presence from iOBIS were

573   gridded such that 1-degree grid cells with observations were set as present. These observations

574   were then modelled as a function of the following environmental predictors: (1) average annual

575   temperatures from the HadISST v1.1; (2) the logarithm of distance to the nearest coastline; (3)

576   ocean depth from the GEBCO marine atlas; and (4) FAO major fishing areas

577   (http://www.fao.org/fishery/area/search/en). Global maps of predicted presence were produced

578   using a threshold probability of 0.4. Presence maps were used to extract average annual sea

579   surface temperature values from Hadley Centre HadISST v1.1 1-degree dataset long-term

580   climatology average 1960-2009. Quantiles (0, 0.1, 0.25, 0.5, 0.75, 0.9 and 1.0) of the population

581   of temperatures in occupied grid squares were used to define the thermal niche of the species

582   (weighted by the relative area of grid cells given by the cosine of the latitude). The frequency

583   distribution of these species-specific distributions were then described using percentiles, and, for

584   this analysis, the 10th and 90th percentiles were taken as measures of the warm and cold ends of

585   the thermal range, respectively. Each location of a reported MHW effect was then used to extract

586   the local average SST from the same SST climatology. Range location was then expressed as the

587   local temperature less the 10th percentile of temperature, divided by the difference between the

588   10th and 90th percentiles of estimated species range temperatures. A range location value of zero

589   or less was therefore at the cold end of the distribution range ($<=10^{th}$ percentile), while values of

590   1 or more would be at the warm end of the range ($>=90^{th}$ percentile). This process resulted in

591   estimated range locations for 347 observations from 280 species within the ecological dataset.

592

593   The effect of range location on the size and direction of response to MHWs was assessed

594   statistically using a linear model of Hedges' g versus range location weighted by the inverse

595   variance of each Hedges' g value. Range location had a significant influence on responses,

596   becoming more negative toward the warm edge of the species range (Fig. 2F; $F_{1,345} = 11.98$,

597   P<0.001). Differences among taxonomic groups followed the average range location within

598   those groups. The average negative effect of MHWs on corals was associated with the average

599   reported effect location being at the 90th percentile of the coral species' temperature distribution.

600   Those taxonomic groups reporting less negative effects were generally toward the middle of the

601   distribution range, while those groups at the cold end of the species temperature range showed a

602   positive effect (Fig 2F; $F_{1,7}$ = 10.33, P =0.015).

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

604   High-resolution time series on coral bleaching, seagrass density and kelp biomass were obtained

605   from the Caribbean Sea, Western Australia and California, respectively (Fig. S5). Quality-

606   controlled coral bleaching observations for the Caribbean Sea/Gulf of Mexico region

607   (northernmost limit: 30.0°N, southernmost limit: 10.2°N, western limit: 97.5°W, eastern limit:

608   59.6°W) were obtained (at 11 km resolution) from NOAA's Coral Reef Watch program

609   (http://coralreefwatch.noaa.gov/satellite/index.php). Observations were first filtered by month

610   (July-October inclusive) and then summed for each year (1983-2010). Links between MHWs

611   and seagrass density were examined with long-term monitoring data from Cockburn Sound,

612   Western Australia, which is collected and managed by the Cockburn Sound Management

613   Council (Western Australian Government). The density of seagrass shoots was examined at 2

614   long-term sites (Garden Island and Warnbro Sound), where high-resolution data have been

615   collected using SCUBA at depths of 2-7 m since 2003 (all surveys were conducted in late

616   Austral summer of each year). Data were averaged across transects and depths before generating

617   an annual mean value for the Cockburn Sound region (average of 2 sites). Annual estimates for

618   giant kelp, *Macrocystis pyrifera*, biomass were generated from the satellite-derived dataset

619   produced by Cavanaugh et al.[65] as part of the Santa Barbara Coastal Long-term Ecological

620   Research (SBC-LTER) program (http://sbc.lternet.edu//index.html). Estimates of the biomass of

621   the kelp canopy (i.e. floating fronds) were derived from LANDSAT 5 Thematic Mapper satellite

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 programme

(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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