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

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**The global ocean has warmed substantially 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 in 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 probably 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 considerably 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 twenty-first century[10]. While extremes occur naturally in the climate system, there is growing confidence that the

observed intensification of heatwaves is due to human activities[11,12]. The twenty-first century has already experienced record-shattering atmospheric heatwaves[8,13], such as the 2003 European heatwave, the Australian 'Angry Summer' of 2012–2013 and the European 'Lucifer' heatwave in 2017, with devastating consequences for human health, economies and the environment[8].

Discrete and prolonged extreme warming events occur in the ocean as well as the atmosphere. MHWs are caused by a range of processes operating across different spatial and temporal scales, from localized air–sea heat flux to large-scale climate drivers, such as the El Niño Southern Oscillation[14]. Regional case studies have documented how MHWs can alter the structure and functioning of entire ecosystems by causing widespread mortality, species range shifts and community reconfiguration[15–17]. By affecting ecosystem goods and services, such as fisheries landings[18,19] and biogeochemical processes[20,21], MHWs can have major socioeconomic and political ramifications. Recent high-profile ocean warming events include the record-breaking 2011 'Ningaloo Niño' (2010–2011) off Western Australia[22], the long-lasting 'Blob' (2013–2016) in the northeast Pacific[23] and El Niño-related extreme warming in 2016 that affected most of the Indo–Pacific[24,25]. These events have increased awareness of MHWs as an important climatic phenomenon affecting both physical and biological processes. Until recently, the lack of a common framework to define MHWs[14] has hampered attempts to examine temporal trends or to compare physical attributes or biological impacts across different events, regions or taxa. However, by defining MHWs as periods when daily sea-surface temperatures (SSTs) exceed a local seasonal threshold (that is, the 90th percentile of climatological SST observations) for at least 5 consecutive days[14], Oliver et al.[2] showed that the frequency and duration of MHWs have increased significantly over the past century across most of

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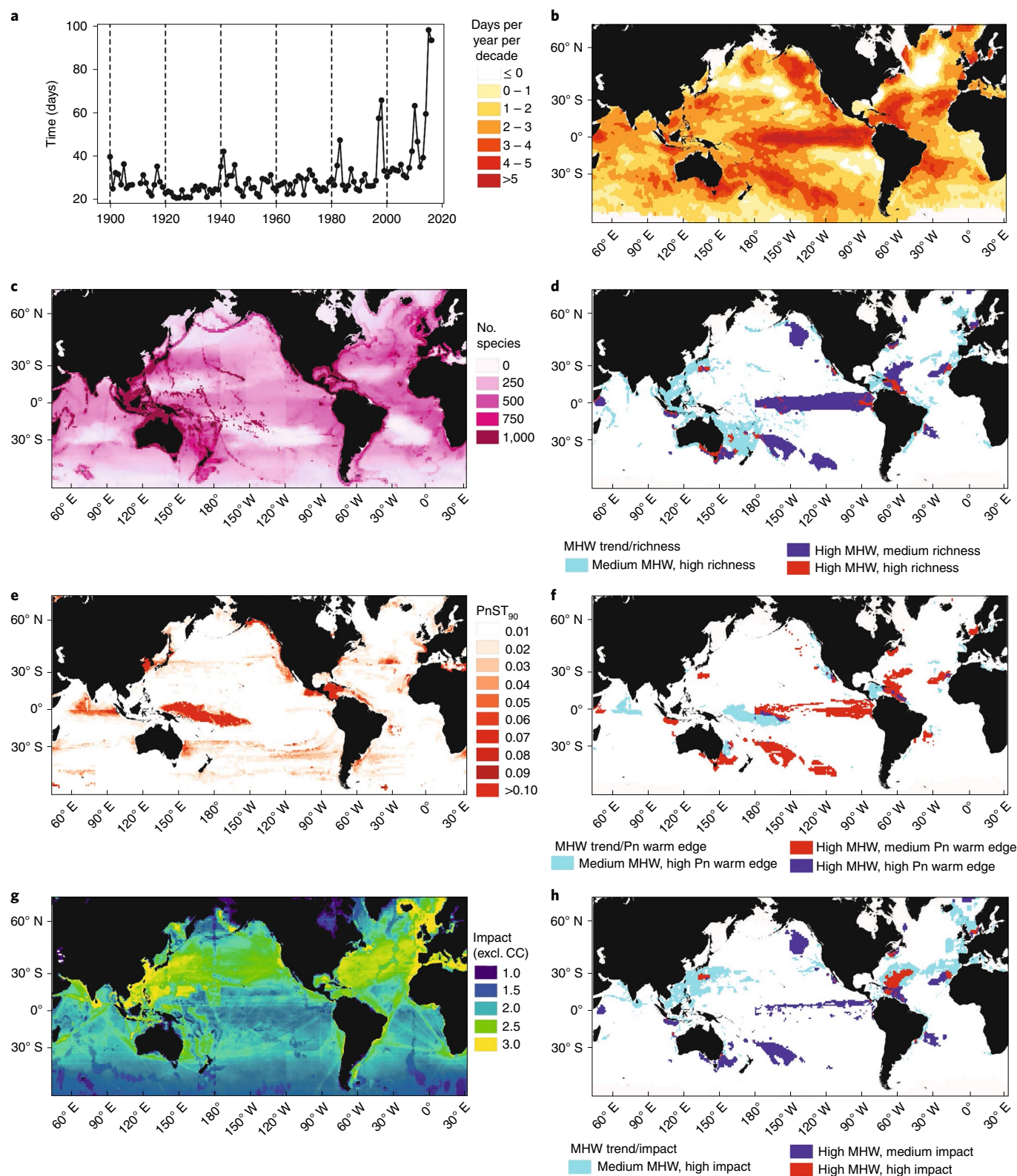
**Fig. 1 | Global patterns of MHW intensification, marine biodiversity, proportions of species found at their warm range-edge and concurrent human impacts. a,b**, Globally averaged time series of the annual number of MHW days and trends in the annual number of MHW days (in the periods 1925–1954 and 1987– 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 trends in the annual number of MHW days (**b**). **d,f,h**, The resultant bivariate maps identify regions of high diversity value that may be affected by MHWs (**d**), high thermal sensitivity of species that may have been particularly vulnerable to increased MHWs (**f**) and high levels of non-climatic human stressors where MHW intensification has affected concurrently on marine ecosystems (**h**). Pn, proportion; $PnST_{90}$, proportion of species beyond 90% species thermal range; excl. CC, excluding climate change.
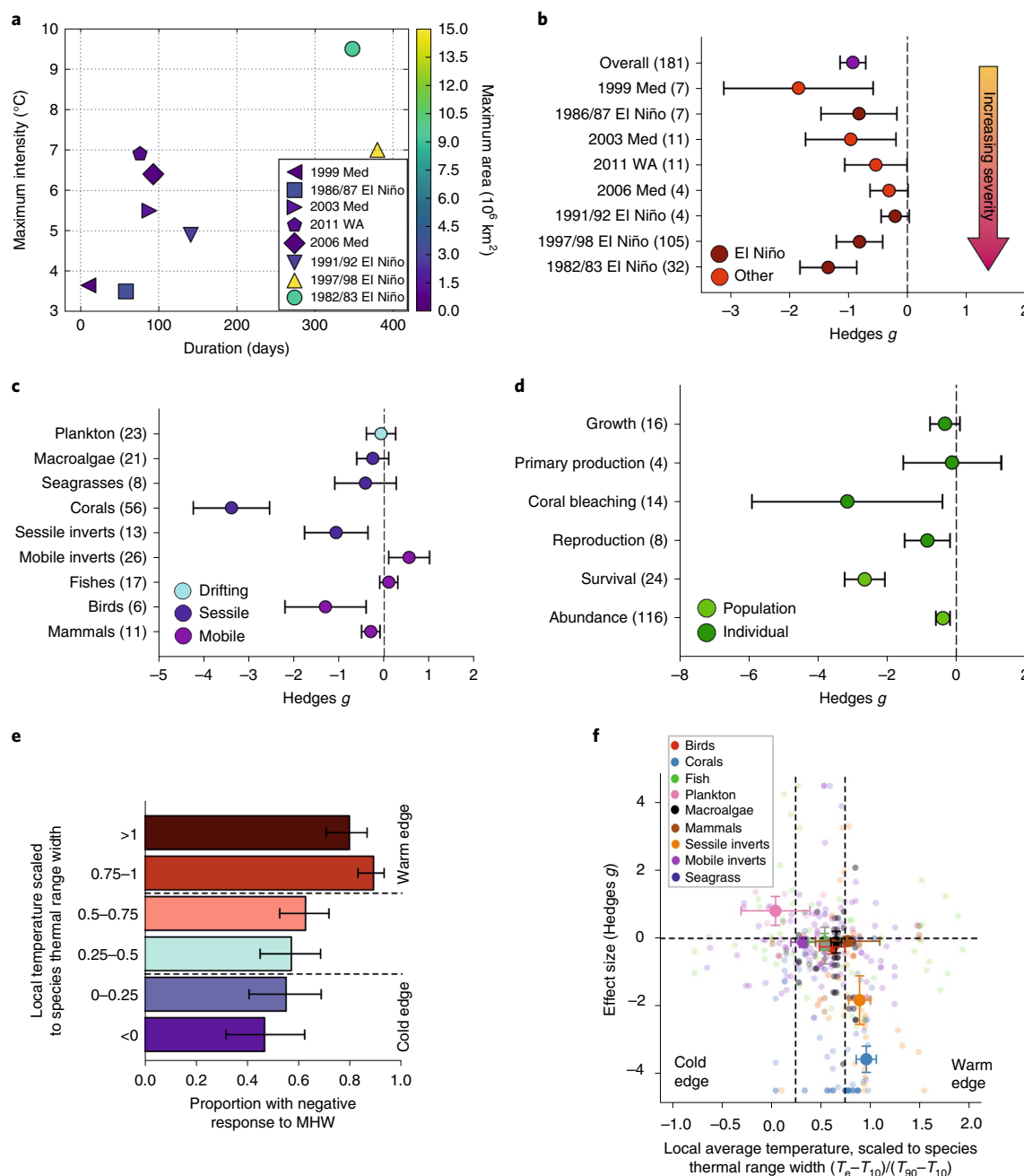
**Fig. 2 | Ecological impacts of MHWs as determined by a meta-analysis of responses to eight prominent MHW events. a,b,** The attributes of the eight MHW events used in the meta-analysis (**a**) and the overall effect of each MHW event across all ecological responses (**b**). **c,d,** The effect of MHWs on major taxonomic groups (**c**) and types of ecological response (**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 (**f**) lines delineate the lower and upper quartiles of species thermal ranges. Med, Mediterranean; WA, Western Australia.

the global ocean. Here, we used the same MHW framework[14] to examine observed trends in the annual number of MHW days and the implications for marine ecosystems globally. We incorporated existing data on marine taxon richness, the proportion of species found at their warm range edges and non-climatic human impacts to identify regions of high vulnerability, where increased occurrences of MHWs overlap with areas of high biodiversity, temperature

sensitivity or concurrent anthropogenic stressors. We also conducted a meta-analysis on the impacts of MHWs by examining ecological responses to eight prominent MHW events that have been studied in sufficient detail for formal analysis. We examined 1,049 ecological observations, recalculated to 182 independent effect sizes from 116 research papers that examined responses of organisms, populations and communities to MHWs. We also
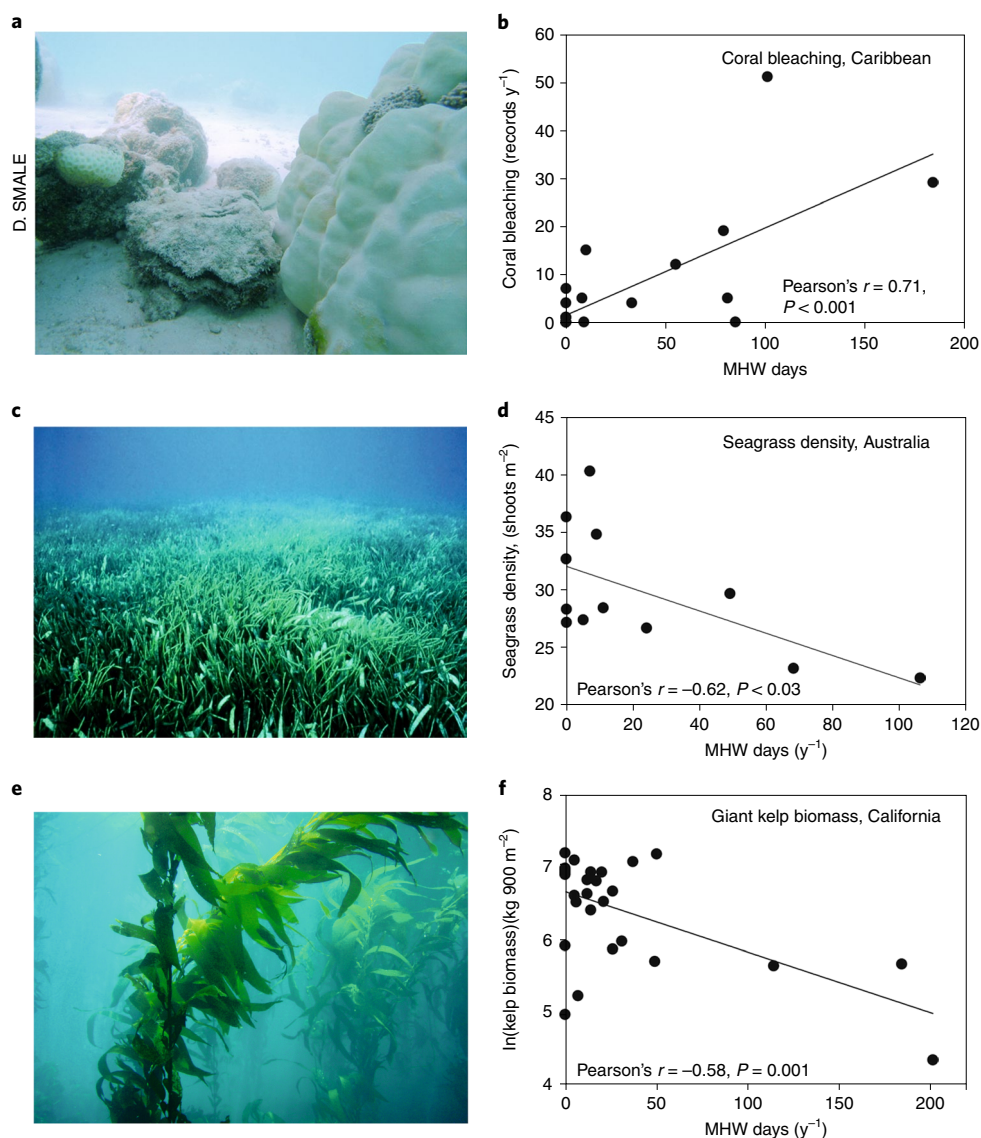
**Fig. 3 | Impacts of MHWs on foundation species. a**, Severe MHWs, such as those associated with the extreme El Niño events of 1997–1998 and 2015–2016, have caused widespread bleaching and mortality of reef building corals. **b**, Analysis of annual coral bleaching records from the Caribbean Sea/Gulf 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. **c**, Seagrass meadows yield critical ecosystem services, including carbon sequestration and biogenic habitat provision, yet recent MHWs have affected seagrass populations in several regions. **d**, 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. **e**, Kelp forests represent critical habitats along temperate coastlines but extreme temperatures experienced during MHWs can cause widespread mortality and deforestation. **f**, 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 programme) showed that kelp biomass was negatively correlated with the number of MHW days recorded during the previous year. Credit: National Oceanic and Atmospheric Administration, US Department of Commerce (panels **c** and **e**).

explored relationships between the occurrence of MHWs and the health of three globally important foundation species (coral, seagrass and kelp) from three independent time series that were collected at sufficient spatiotemporal resolutions to explicitly link ecological responses to MHWs. Finally, we reviewed the literature on MHWs for evidence of impacts of these events on goods and services to human society.

The total number of MHW days per year, based on five quasi-global SST datasets, has increased globally throughout the twentieth and early twenty-first centuries (Fig. 1a). As a global average, there were over 50% more MHW days per year in the last part of the instrumental record (1987–2016) compared to the earlier

part (1925–1954)[2], with most regions experiencing increases in the number of MHW days (Fig. 1b). Global patterns of marine taxon richness (Fig. 1c) overlaid with trends in annual MHW days reveal regions where increased MHW occurrences can influence biologically diverse regions; in particular, southern Australia, the Caribbean Sea and the coastline bounding the mid-eastern Pacific (Fig. 1d). Given that warm range-edge populations are likely to be the most affected by MHWs (as thermal tolerances are exceeded during anomalously high temperatures), regions that support a high proportion of species found near their warm range edge will be particularly vulnerable to increased MHW activity (Fig. 1e). Several regions were identified as having experienced marked

**Table 1 | Impacts of MHWs on services provided by marine ecosystems.**

| 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 defence[a,b] | 43,44 |
| | Nutrient cycling | Increased stratification and extreme temperatures caused decreased phytoplankton production and nutrient turnover[b,g]<br>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 |

Definitions of ecosystem services adapted from The Economics of Ecosystems and Biodiversity, TEEB, developed by UNEP[51]. Evidence of impacts was collated from specific MHWs: [a]1982/83 El Niño event; [b]1997/98 El Niño event; [c]1999 Mediterranean MHW; [d]2003 Mediterranean MHW; [e]2011 Western Australian MHW; [f]2012 Northwest Atlantic MHW; [g]the 2013–2016 Northeast Pacific 'Blob'; [h]the 2015/2016 El Niño event in northern Australia.

increases in MHW days and also supporting a high proportion of species found near their warm range edges (Fig. 1f), with marine ecosystems in the southwest Pacific and the mid-west Atlantic particularly at risk. Furthermore, regions where rapid increases in the annual number of MHW days overlap with existing high-intensity non-climate human stressors (Fig. 1g) include the central west Atlantic, the northeast Atlantic and the northwest Pacific (Fig. 1h). Here, existing regional pressures, including overfishing

and pollution, have the potential to exacerbate MHW impacts and vice versa.

Examination of eight prominent (and sufficiently studied) MHWs showed they varied greatly with respect to spatial extent (by a factor of >15, Fig. 2a and Supplementary Fig. 1), duration (10–380 days) and maximum intensity (3.5–9.5 °C above climatological SST) (Fig. 2a). It should be noted that several MHWs were primarily driven by large-scale El Niño events that, by their nature, affected ocean climate at large spatial scales. Here, the largest contiguous MHW associated with each ENSO (El Niño Southern Oscillation) event was identified and characterized with MHW metrics. Our meta-analysis of ecological impacts (on the basis of Hedges $g$ effect sizes to account for bias associated with small sample sizes[26]) detected an overall negative effect of MHWs on biota across research papers, events, taxa and response variables ($E = -0.93$; 95% CI = 0.22; $Q = 6303$, d.f. = 181; $p_{heterogeneity} < 0.001$, $I^2 = 97.13$; see Methods). All eight MHWs were associated with negative ecological impacts although the mean negative effect sizes were not significantly different from zero for the two events with lowest sample sizes (Fig. 2b). There was no clear relationship between the severity of the MHW (derived from normalized MHW intensity and duration) and their observed impacts (Fig. 2b). All taxonomic groups, with the exception of fishes and mobile invertebrates, responded negatively to MHWs with birds and corals being most adversely affected (Fig. 2c). The positive fish response was, in part, driven by new incursions of tropical species into affected temperate regions[16]. Corals were directly affected by these MHWs, as extreme absolute temperatures resulted in widespread bleaching and mortality[27,28], whereas birds were indirectly affected through changes in prey availability[29]. Birds and corals are also particularly sensitive to longer term increases in sea temperature associated with ocean warming[30]. Overall, our analyses suggest that sessile taxa were more affected by MHWs than mobile and planktonic taxa (Fig. 2c), perhaps because mobile taxa generally have higher thermal tolerances than less active or sessile taxa[31] and highly mobile species can quickly migrate in response to rapidly changing conditions[16]. All ecological response variables were negatively affected by MHWs, although growth and primary production were not significantly different from zero (Fig. 2d). Negative impacts were greatest for coral bleaching, survival and reproduction (Fig. 2d), a pattern consistent with effects of warming in manipulative experiments[32].

To examine links between MHWs and ecological responses, we conducted additional analysis at the species level to test the prediction that populations found towards the warm-water limit (that is, the equatorward range edge) of a species distribution would be more negatively affected by MHWs than other populations. From the database described above, we extracted all species-level observations (645 observations from 302 species) and for each population we classified their relative position in the species range by expressing the local average SST as a proportion of the difference between the 10th and 90th percentile temperatures experienced through the species geographical range. Critically, the most negative responses to MHWs were seen in populations found towards their warm range edge (Fig. 2e), suggesting that extreme temperatures exceeded thermal thresholds with adverse effects. Across all species-level observations, there was a negative relationship between any given population's location within the species range and the direction and magnitude of the MHW effect (Fig. 2f). This indicates that populations residing near the warm limit of a given species range are particularly vulnerable to warming events and range contractions are likely to occur in response to more frequent MHWs. Indeed, recent observations have shown that equatorward range edges of both plant and animal species have retracted poleward by >100 km following severe MHW events[17,33,34].

An examination of long-term time series on the health of three globally important foundation taxa showed that increased annual

number of MHW days was correlated with (1) increased coral bleaching, (2) decreased seagrass density and (3) decreased kelp biomass (Fig. 3). Even though environmental variables such as storms, nutrients and light are known to strongly influence the health of these critical habitat-formers[35], the annual number of MHW days alone was strongly and significantly correlated with observed ecological performance and, crucially, had consistently stronger correlative relationships than more frequently used measures of ocean temperature (that is, mean and maximum SST, see Supplementary Table 1). An increased number of MHW days was significantly correlated to decreased ecological health of populations of all three foundation taxa, indicating the importance of discrete extreme ocean warming events in driving ecosystem structure[16,36].

A wide range of ecological goods and services derived from marine ecosystems have been severely affected by recent MHWs (Table 1). For example, the 2011 Ningaloo Niño caused widespread loss of biogenic habitat, depleted biodiversity, disruption to nutrient cycles and shifts in the abundance and distribution of commercial fisheries species off Western Australia (Table 1). Similarly, recent MHWs in the Mediterranean Sea have been linked to local extinctions, decreased rates of natural carbon sequestration, loss of critical habitat and diminished socioeconomic value (Table 1). These services have substantial societal benefit, with hundreds of millions of people benefitting from coastal marine ecosystems[37,38]. As such, managing and mitigating the deleterious effects of MHWs on the provision of ecosystem services is a major challenge for coastal societies.

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

## Online content

Any methods, additional references, Nature Research reporting summaries, source data, statements of data availability and associated accession codes are available at https://doi.org/10.1038/s41558-019-0412-1.

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## Author contributions

D.A.S. and T.W. conceived the initial idea. All authors contributed intellectually to its development. D.A.S., T.W, E.C.J.O. and N.J.H. co-convened the workshops. E.C.J.O. led the development of the M.H.W. analysis, which was supported by N.J.H., L.V.A., J.A.B., M.G.D., M.F., A.J.H., S.E.P.-K., H.A.S. and A.S.G. The meta-analysis of ecological impacts was conducted by M.T., B.P.H., S.C.S., M.T.B. and P.J.M. D.A.S. led manuscript preparation with input from all authors.

## Competing interests

The authors declare no competing interests.

## Additional information

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## Methods

**Definition of MHWs and analysis of multi-decadal trends.** MHWs were identified from observational 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 5 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 the 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 2 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 (that is, 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.

Global time series and regional trends in total MHW days were derived using a combination of satellite-based, remotely sensed SSTs and in situ-based seawater temperatures. First, total MHW days were calculated globally over 1982–2015 at 1/4° resolution from the National Oceanic and Atmospheric Administration (NOAA) Optimum Interpolation SST V2 high-resolution data. Then, proxies for total MHW days globally over 1900–2016 were developed on the basis of five monthly gridded SST datasets (HadISST v.1.1, ERSST v.5, COBE 2, CERA-20C and SODA si.3). A final proxy time series was calculated by averaging across the five datasets. The five monthly datasets were used since no global daily SST observations are available before 1982. From these proxy time series, we calculated (1) the difference in mean MHW days over the 1987–2016 and 1925–1954 periods and (2) a globally averaged time series of total MHW days. Further details on this method and resulting proxy data can be found in Oliver et al.[2]. Note that these calculations use the same climatology period as above, 1983–2012.

**Global patterns of MHW intensification and overlaps with known hotspots of marine biodiversity, temperature-sensitive populations and non-climatic human stressors.** We combined regional trends in MHW days with pre-existing data on marine biodiversity, the proportion of species found near their warm range edges and non-climatic human stressors to predict where MHW intensification may be a particular threat to biodiversity hotspots or temperature-sensitive communities, or be exacerbated by concurrent stressors. Biodiversity hotspots were determined using published marine taxon richness data[52], which were accumulated from projected species distributions from the Aquamaps project[53]. Patterns in taxon richness (Fig. 1c) showed characteristically high levels in coastal areas and in tropical regions. We also calculated the proportion of species in the local species pool that were near their warm range edge to determine locations where MHWs might be more likely to have a strong negative effect (as shown in Fig. 2f). We used 16,582 species global distribution maps from the Aquamaps project[53], previously used to assess probable patterns of biodiversity change[52], to represent global marine biodiversity. For each 1° latitude/longitude grid cell we counted the number of species present for which SST, derived as the 1960–2009 average annual temperature from the Hadley Centre HadISST v.1.1 dataset, exceeded the 90th percentile temperature of their geographical range, and divided this by the total number of species present. Aside from some artefacts where species geographical limits coincide with FAO (Food and Agriculture Organization of the United Nations) region boundaries, a feature prevalent in other studies using these datasets[54], the resulting map (Fig. 1e) showed areas with higher proportions of species at their warm range edges. Major concentrations (proportions >0.1 of all species) of warm-edge species were seen in the Eastern Mediterranean, the southern Red Sea, the Caribbean Sea, the Mexican part of the North Pacific and a large part of the tropical west Pacific. Locally, higher proportions of warm-edge species were also seen along coastlines of Europe, western USA and Canada, North Africa and in the Yellow Sea.

Information on stressors were obtained from supplementary online resources provided by Halpern et al.[55]. We additively combined multiple impact layers (demersal destructive fishing, demersal non-destructive high bycatch, demersal non-destructive low bycatch, ocean acidification, ocean pollution, pelagic high bycatch, pelagic low bycatch, shipping and ultraviolet) into a single cumulative impacts layer (Fig. 1e). Fishing intensity layers were obtained by apportioning reported catches in FAO areas by modelled productivity data for latitude/longitude cells. Shipping impacts were derived from a 12-month (2003–2004) global ship observing scheme, and the same data was used with ports data to give a measure of ocean pollution. Surface ultraviolet information was obtained from the GSFC TOMS EP/TOMS satellite programme at NASA. Ocean acidification data came

from globally modelled aragonite saturation state. Details of the quantification of these layers are given in Halpern et al.[55,56]. Layers that included ocean warming variables were specifically excluded due to probable co-variance (to varying extents) with MHW metrics. The cumulative impacts layer was then re-projected and resampled onto the same 1° × 1° grid as for trends in total MHW days and biodiversity data. Maps of the combinations of medium to high trends in total MHW days and medium to high values of taxon richness (Fig. 1c) or cumulative impacts (Fig. 1e) were created by splitting the data into classes on the basis of the percentiles of the distribution of each variable (0–50% low, 50–90% medium, >90% high). Combined MHW trend/richness and MHW trend/impact layers were assigned to categories according to the classes of each contributing layer. While spatial bias due to variability in sampling effort may influence, to some degree, global-scale datasets on physical and biological variables, the datasets used in the current study have near-complete global coverage and represent the best approximations available for temperature[57], species richness and distributions[58] and human stressors[55].

**Meta-analysis of ecological responses to MHWs.** *Dependent and independent variables, literature searches and hypothesis.* The meta-analysis followed PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) guidelines, which provide an evidence-based minimum set of requirements for conducting and reporting meta-analyses (Supplementary Fig. 2). We searched for peer reviewed studies that compared six types of biological 'performance response' (survival, abundance, growth, reproduction, primary production or coral bleaching) that reported data variation, before and after any of eight well-described periods of extreme warming (El Niño-related events in 1982/83, 1986/87, 1991/92 and 1997/98, the Mediterranean MHWs of 1999, 2003 and 2006, and the 2011 MHW in Western Australia). Relevant studies were identified from two literature searches. First, we conducted a standardized Web of Science search, with search terms related to climate change, heatwaves, marine systems and the eight MHWs mentioned above. We used the following specific search string: ('TS = ((marine AND ('heatwave' OR heatwave)) OR El Niño OR La Niña OR ENSO OR (marine AND warming))'), identifying 29,385 potentially relevant papers. We read all abstracts from these papers and then obtained the full manuscripts of the papers that in their title, abstract or keywords indicated that relevant data could be collected (=517 papers). We read all these papers in detail to identify 116 papers that fulfilled our data criteria. For each of the identified publications we extracted all reported mean performance response, data dispersion and sample sizes, from text, tables and figures with Plot Digitizer (http://plotdigitizer.sourceforge.net/). Impact studies were widely distributed across the global ocean; impact studies relating to ENSO-associated MHWs were spread across the Pacific and Indian Oceans whereas impact studies relating to Mediterranean and Australian MHWs were conducted across a smaller area (Supplementary Fig. 3). Our fundamental hypothesis was that MHWs generally had negative effects on ecological performance across studies, bioregions, events, response types and organisms. We also tested (see the next section for the method) if the magnitude of effects varied between heatwave events (eight MHW events), performance responses (six types listed above) and impacted taxa (grouped into mammals, birds, fishes, mobile invertebrates, non-coral sessile invertebrates, corals, macroalgae, seagrasses and plankton, which included phytoplankton, zooplankton and open ocean microbes). For the MHW test, we hypothesized that the intensity of an event would correlate with the magnitude of effect size. For the biological response test, we hypothesized that coral bleaching and reproduction would be most affected by MHWs, the former because corals are known to be sensitive to elevated temperatures and the latter because reproduction is typically more sensitive to stress than growth, abundance and survival. Finally, for the test across taxa we hypothesized that mobile organisms and seagrasses/corals would exhibit the largest effect sizes because mobile organisms can respond rapidly (for example local heat-stressed species can emigrate and warm-tolerant species from adjacent region can immigrate) and seagrasses/corals are generally sensitive to elevated temperatures.

*Effect sizes, data pooling, dealing with outliers and autocorrelation and statistical tests.* We analysed impacts of MHWs on events, taxa and performance with Hedges g effect size, corrected for small sample sizes. Hedges g was calculated as $(MHW_{After} - MHW_{Before})/S) \times J$, where $S$ is the pooled standard deviation and $J$ is a factor that corrects for bias associated with small sample sizes[26,59]. $MHW_{before}$ and $MHW_{after}$ represent the mean performance response reported by the study before and after the period of extreme warming, respectively. These relied on the authors' designations of the timing of the MHW. When the mean performance response before the MHW event were reported for multiple time points, an average was taken to obtain $MHW_{before}$. In these cases, the associated variance of the time points was also pooled for use in $S$. In this analysis, negative and positive effects reflect inhibition and facilitation of organismal performance, respectively. Analyses were weighted by the sum of the inverse variance in each study and the variance pooled across studies and therefore give greater weight to those studies with higher replication and lower data dispersion. We used random-effect models, thereby assuming that summary statistics have both sampling error and a true random component of variation in effect sizes between studies[26,59]. Most publications

reported multiple auto-correlated effects, for example when a study reported effects of a MHW on many different coral species. Within-study effects are typically not statistically independent from each other and will conflate analyses, for example by artificially increasing degrees of freedom. We reduced within-study autocorrelation by averaging 1,049 non-independent Hedges *g* values (extracted from 116 identified research papers) to 182 values, each being characterized by a unique combination of a MHW, affected taxa and performance response per research paper. Thus, before formal meta-analyses, within-study effects were averaged across multiple species and across nested designs (for example, across different sites within a study or different depth levels). We acknowledge that our approach to aggregate auto-correlated within-study effect sizes, albeit being the most common way to do this[60], may be suboptimal, compared to advanced modelling techniques[60]. However, many papers reported different types and nested layers of non-independent data in a single paper, requiring overly complex combinations and levels of aggregation models (compared to aggregating data with a mean), before the meta-analysis. Finally, we calculated mean effect sizes (*E*), 95% confidence intervals (CI), heterogeneity (*Q*), the probability that Q is significant (P-heterogeneity), and the proportion of real observed dispersion ($I^2$) on the basis of weighted random-effect models in OpenMEE[59]. Mean effect sizes were considered to be significantly different from zero or another effect if their 95% CIs did not overlap with zero or each other, respectively[61–64]. Effect sizes generated from a single study were excluded from plots (these were; a single mean effect size of −4.21 for the 1972 ENSO event and a single effect size of 1.183 for 'reptiles' in the taxon-specific analysis).

*Publication bias.* Our meta-analyses may be influenced by publication bias if we overlooked studies documenting strong positive effects, or if studies finding non-significant effects are not published[26,65,66]. We believe that the first type of publication bias is unlikely because we have worked intensively with MHW through primary research and by writing book chapters and reviews. We explored possible publication bias in different ways. We examined funnel plot asymmetry using the trimfill method and regression tests, and calculated the fail-safe number using the Rosenberg method that estimates the number of studies averaging null results that should be added to reduce the significance level (*P* value) of the average effect size (on the basis of a fixed-effects model) to α = 0.05 (refs. [65,66]). These tests suggest that publication bias has limited effects and that our results are generally robust. Although the funnel plot was highly asymmetric (Supplementary Fig. 4), as shown by a significant regression test (*t* = −3.598, *P* = 0.0004), adjusting this possible bias using the trimfill method had no effects on our general conclusion, because the mean effect size remained significantly negative (−0.05, with 95% confidence intervals −0.08 to −0.02, *P* < 0.01). In addition, Rosenberg's fail-safe number was 11,318, that is, much larger than $5n + 10$, where *n* is the number of original studies included in our analyses. Thus, publication bias is unlikely to affect our results and did not change our main finding that MHWs generally had negative effects on marine organisms.

*Effect of population location within the distributional range on responses to MHWs.* We also tested the hypothesis that populations found towards the warm-water limit (that is, the equatorward range edge) of a species distribution will respond more negatively to MHWs. To do this, we first extracted all observations from the database that were recorded at the species-level (302 species and 645 observations). Global species distributions were produced using presence-only Maxent models for each species for which sufficient observations were available, and using default parameters for a random seed, convergence threshold, maximum number of iterations, maximum background points and the regularization parameter[54] (using Maxent v.3.3.3k). Observations of species presence from iOBIS were gridded such that 1° grid cells with observations were set as present. These observations were then modelled as a function of the following environmental predictors: (1) average annual temperatures from the HadISST v.1.1; (2) the logarithm of distance to the nearest coastline; (3) ocean depth from the GEBCO marine atlas and (4) FAO major fishing areas (http://www.fao.org/fishery/area/search/en). Global maps of predicted presence were produced using a threshold probability of 0.4. Presence maps were used to extract average annual SST values from Hadley Centre HadISST v.1.1 1° dataset long-term climatology average 1960–2009. Quantiles (0, 0.1, 0.25, 0.5, 0.75, 0.9 and 1.0) of the population of temperatures in occupied grid squares were used to define the thermal niche of the species (weighted by the relative area of grid cells given by the cosine of the latitude). The frequency distribution of these species-specific distributions were then described using percentiles and, for this analysis, the 10th and 90th percentiles were taken as measures of the warm and cold ends of the thermal range, respectively. Each location of a reported MHW effect was then used to extract the local average SST from the same SST climatology. Range location was then expressed as the local temperature less the 10th percentile of temperature, divided by the difference between the 10th and 90th percentiles of estimated species range temperatures. A range location value of zero or less was therefore at the cold end of the distribution range (≤ 10th percentile), while values of 1 or more would be at the warm end of the range (≥ 90th percentile). This process resulted in estimated range locations for 347 observations from 280 species within the ecological dataset.

The effect of range location on the size and direction of response to MHWs was assessed statistically using a linear model of Hedges *g* versus range location weighted by the inverse variance of each Hedges *g* value. Range location had a significant influence on responses, becoming more negative towards the warm edge of the species range (Fig. 2f; $F_{1,345} = 11.98$, $P < 0.001$). Differences among taxonomic groups followed the average range location in those groups. The average negative effect of MHWs on corals was associated with the average reported effect location being at the 90th percentile of the coral species temperature distribution. Those taxonomic groups reporting less negative effects were generally towards the middle of the distribution range, while those groups at the cold end of the species temperature range showed a positive effect (Fig. 2f; $F_{1,7} = 10.33$, $P = 0.015$).

**Analysis of habitat-forming species responses to MHWs.** High-resolution time series on coral bleaching, seagrass density and kelp biomass were obtained from the Caribbean Sea, Western Australia and California, respectively (Supplementary Fig. 5). Quality-controlled coral bleaching observations for the Caribbean Sea/Gulf of Mexico region (northernmost limit: 30.0° N, southernmost limit: 10.2° N, western limit: 97.5° W, eastern limit: 59.6° W) were obtained (at 11 km resolution) from NOAA's Coral Reef Watch programme (http://coralreefwatch.noaa.gov/satellite/index.php). Observations were first filtered by month (July–October inclusive) and then summed for each year (1983–2010). Links between MHWs and seagrass density were examined with long-term monitoring data from Cockburn Sound, Western Australia, which is collected and managed by the Cockburn Sound Management Council (Western Australian Government). The density of seagrass shoots was examined at two long-term sites (Garden Island and Warnbro Sound), where high-resolution data have been collected using SCUBA at depths of 2–7 m since 2003 (all surveys were conducted in late Austral summer of each year). Data were averaged across transects and depths before generating an annual mean value for the Cockburn Sound region (average of two sites). Annual estimates for giant kelp, *Macrocystis pyrifera*, biomass were generated from the satellite-derived dataset produced by Cavanaugh et al.[67] as part of the Santa Barbara Coastal Long-term Ecological Research (SBC-LTER) programme (http://sbc.lternet.edu//index.html). Estimates of the biomass of the kelp canopy (that is, floating fronds) were derived from LANDSAT 5 Thematic Mapper satellite imagery. Biomass data (wet weight per kg) were generated for individual 30 × 30 m² 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) programme (http://sbc.lternet.edu//index.html). Additional data are available from the corresponding author upon request.

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