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Fish body sizes change with temperature but not all species shrink with warming

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Ectotherms generally shrink under experimental warming, but whether this pattern extends to wild populations is uncertain. We analysed ten million visual survey records, spanning the Australian continent and multiple decades and comprising the most common coastal reef fishes (335 species). We found that temperature indeed drives spatial and temporal changes in fish body size, but not consistently in the negative fashion expected. Around 55% of species were smaller in warmer waters (especially among small-bodied species), while 45% were bigger. The direction of a species' response to temperature through space was generally consistent with its response to temperature increase through time at any given location, suggesting that spatial trends could help forecast fish responses to long-term warming. However, temporal changes were about ten times faster than spatial trends (~4% versus ~40% body size change per 1 °C change through space and time, respectively). The rapid and variable responses of fish size to warming may herald unexpected impacts on ecosystem restructuring, with potentially greater consequences than if all species were shrinking.

Body size is a key biological and ecological trait[1,2], but many natural populations have undergone declines in average body sizes due to harvesting, with consequent reductions in ecosystem functional diversity and resilience[3–5]. More equivocal are declines in ectotherm body size caused by increased temperature, even though such declines are considered a third universal response to global warming[6] and, unlike harvesting, act on all species in an ecosystem. While some models forecast a 15–30% decrease in body sizes due to warming by 2050[7,8], the generality of these responses remains debated on a theoretical basis[9] and in the light of some empirical observations[10]. Within species, smaller adult body sizes at warmer temperatures are commonly found under experimental conditions, having been observed in animals as diverse as insects, worms, reptiles and fishes[11]. Nevertheless, the mechanisms and adaptive role of this phenomenon, often described as a temperature–size rule, remain elusive and controversial since Bergman's publication in 1847[11–13]. Experimental temperature–size responses are particularly apparent for aquatic species, a pattern that has spawned hotly debated hypotheses on the role of oxygen supply[14–16]. For example, an average adult body weight decrease of 5% per 1 °C of warming was observed across 169 aquatic species, versus just a 0.5% decrease in terrestrial taxa[14]. Yet the applicability of experimental studies to wild populations remains questionable, because few experiments have explored body size responses through multiple generations where intergenerational plasticity and rapid adaptations are likely to alter the observed responses[17]. Moreover, the realized size in wild populations integrates growth, recruitment, mortality, competition, predation risk and food availability simultaneously, and the interplay among these factors cannot be adequately addressed in experiments[10].

Climate change ecology has thus far largely focused on shifting geographic distributions, phenology and abundance of organisms, and the consequences of these[18], whereas warming-driven changes in body size across a broad range of species (both unexploited and exploited) have not been systematically assessed. This study takes advantage of large underwater visual survey datasets from the National Reef Monitoring Network in Australia (consisting of the Australian Temperate Reef Collaboration (https://atrc.org.au/) and Reef Life Survey (https://reeflifesurvey.com/))[19,20]. The datasets consist of >30,000 surveys of rocky and coral reefs around the Australian continent (Extended Data Fig. 1), where the abundance and size of all fish species along standardized transects are recorded by trained divers. Some locations have been monitored continuously for over 26 years. From these surveys we selected all fish species that satisfied minimum abundance and occurrence frequency criteria, resulting in 335 common coastal species spanning a range of maximum body size and life-history characteristics. The majority of these species (254 out of 335) are unlikely to be targeted by fishing in the study region, and only 42 species are known to be commonly caught by recreational or commercial fishers (the remaining 39 species could be occasionally caught, but fishing mortality is likely to be low; see Supplementary Table 1). We then use Bayesian methods to fit hierarchical, mixed-effects models that account for random errors in space and time to quantify spatial and temporal relations between mean individual body length and temperature or time.

Results

In the first set of analyses, species' mean annual body length was assessed against the annual mean sea surface temperature (SST) at locations spanning their distributions. Approximately half of the species showed clear trends in body size with temperature (for which the lower or upper 10% of the posterior probability density or PPD range of the size–SST slope was above or below zero, respectively), with 97 species declining in size towards the warmer edge of their distribution but 64 species increasing (Fig. 1a and Supplementary Table 2). Fish species included in our study grouped into two major thermal guilds[21], corresponding to temperate and tropical distribution types. In our analyses, temperate species constituted about a

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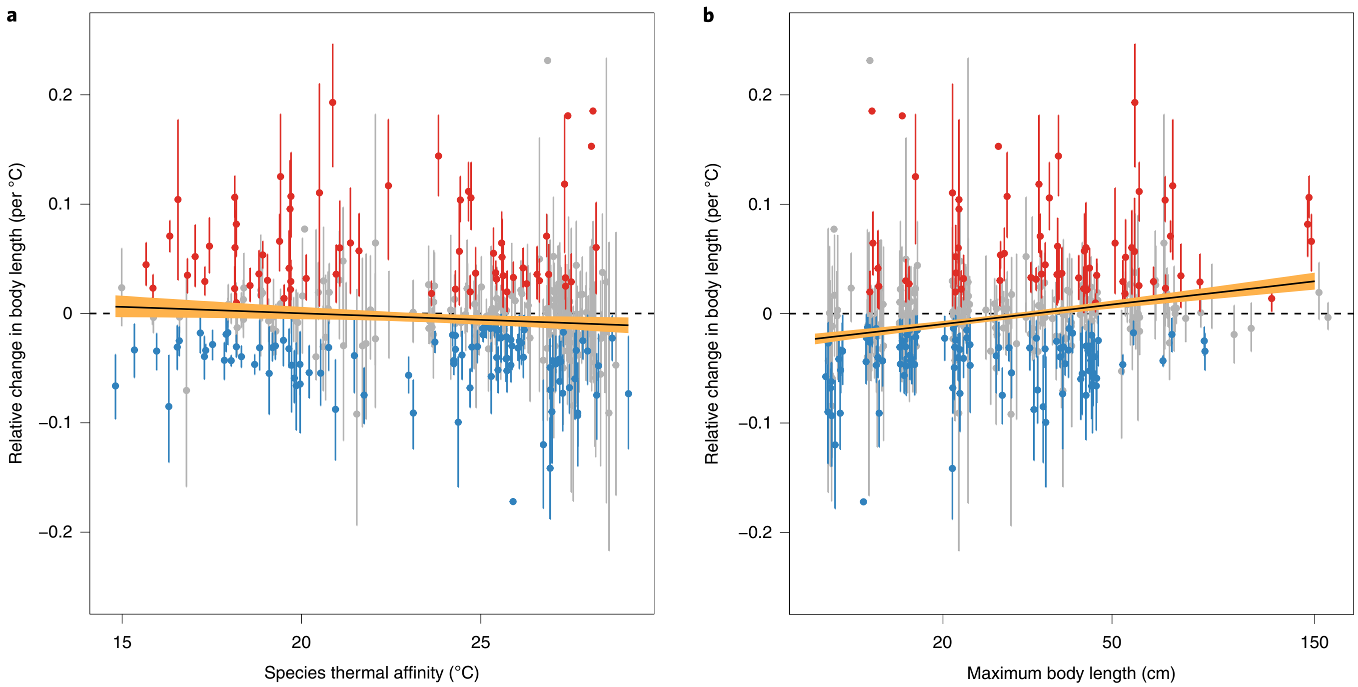

Fig. 1 | Relative change in mean body length of 335 coastal marine fish species per 1 °C change in SST observed across their geographic distributions. **a**,**b**, Change varies with species' thermal affinity[21] (**a**) and maximum observed body length (**b**). Dots and vertical bars represent the median and 80% PPD ranges of individual species responses, respectively (wide intervals that fall outside the picture limits are not shown). Species that show clear body size responses to SST (90% PPD range above or below zero) are shown in red and blue colour. Solid black line is the linear regression weighted according to the individual species' uncertainty level. Orange shading depicts the 95% credible interval for the regression.

third of the total species analysed and were equally likely to have negative or positive body size responses to temperature (Fig. 1a and Supplementary Table 2). In contrast, tropical species were twice as likely to be smaller than larger at their warm distribution edge (see Supplementary Table 1 showing the list of species and their individual body size responses to temperature). In addition, the relative change in species' mean body length was, on average, positively related to their maximum body length (Fig. 1b), meaning that small-bodied species tended to be smaller in warmer areas whereas larger species tended to be larger. This contradicts experimental temperature–size observations, where the strongest declines in adult body size occurred in the largest species[14] and where oxygen supply was suggested to play a critical role. Given that small individuals are more likely to be overestimated in size by divers undertaking surveys (due to inherent and consistent biases in divers' perceptions of size underwater[22]), our result is likely conservative. Notably, body size–temperature trends in space were most often linear, or at least not strongly curved, suggesting that for most species there was not an 'optimal' temperature in the central part of the distribution range at which body size was maximized (Supplementary Fig. 1). Density-dependent processes, such as skew of abundance statistics across species distribution ranges[23], did not appear to explain the observed size trends either (see Methods and Extended Data Fig. 2).

While the spatial analyses ascertained length–temperature relations across many species' distributions, we sought further evidence that these body size changes related specifically to temperature by quantifying intraspecific changes in mean body length over time for all common fish species at nine sites monitored for 15–26 years. Specifically, we estimated temporal trends in body sizes for 105 species; of these, 77 species were found at eight locations that have warmed substantially over the time of observations (average trend of 0.025 °C per year, Supplementary Table 3). Clear temporal changes in body size (90% PPD outside zero) were seen in more than half of the studied fish species (40 out of 77) at these warming locations (Supplementary Table 2), and among these, most (36 out of 40) were consistently decreasing or increasing in size across different, geographically distant locations. No notable linear long-term warming trend was observed at one of the monitored locations in Western Australia (Jurien Bay, Supplementary Table 3 and Extended Data Figs. 1 and 3), and this location also had the smallest proportion of species with temporal trends in body size (Supplementary Table 3). Some of the fastest rates of warming were observed in the southernmost locations in Tasmania, where 50–66% of species showed clear changes in body size through time. The correlation between the rate of warming and the number of species changing in size was weaker closer to the tropics (Jervis Bay site), where, despite the fast warming, only a third of species were clearly increasing or decreasing in size. Importantly, for species that were included in both spatial and temporal analyses (71 species), long-term rates of change in body length at the eight warming locations were positively correlated with the relative change in body length observed across the temperature gradient in space (Fig. 2). In other words, species that were smaller at the warmer edge of their geographical distribution were also more likely to become smaller at locations that are warming, and vice versa.

The two sets of analyses strongly suggest that temperature is a major determinant of reef fish body sizes in the wild, and that the magnitude of average body size changes across space and time can be surprisingly large (Fig. 2 and Extended Data Fig. 3). For example, for species that showed clear body size changes with temperature through space (90% PPD outside zero, Fig. 1, constituting about half of all species), mean body length changed by ~4% for each 1 °C of warming throughout their distribution (Supplementary Tables 1 and 2). For a median-length (15 cm) temperate fish with a typical body shape, this change in length corresponds to an approximately 12% change in body mass per 1 °C, and nearly a threefold difference

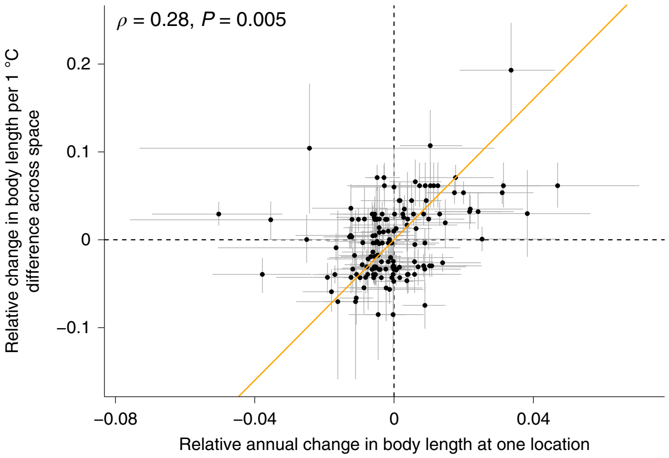

Fig. 2 | Long-term annual relative change in mean body length of 71 species at eight warming locations. Change through time is positively correlated with change in mean body length per 1 °C SST across their geographic distribution (see Fig. 1). The orange line shows the case where spatial and temporal trends are perfectly correlated but change in body length per 1 °C of warming through time is ten times faster than change per 1 °C of warming through space (see text for details). Correlation between spatial and temporal responses was calculated using bootstrapped weighted Spearman's correlation (ρ).

in mean mass between the equatorial and poleward range of an average species distribution (8 °C of annual SST range, giving 12 cm and 32 g versus 17 cm and 89 g at the extreme temperature ranges across the distribution, see Supplementary Table 2). Temporal changes in body size were even greater, averaging a roughly 1% change in length per year in the 40 clearly changing species (90% PPD outside zero). If the rate of body size change and warming observed over the last 20 years is maintained, then 1 °C of warming predicted over the next 40 years would result in a ~40% change (either increase or decrease) in fish body length. This means that body size responses to a 1 °C temperature change through time were about ten times faster than those seen through space (depicted with the orange line in Fig. 2). The result was similar if the space–time comparison was constrained to the 71 species for which both temporal and spatial data were available (for these species, the average change through space was ~3.5% for each 1 °C of warming).

Several alternative explanations exist for the different rates of response to temperature gradients in space and time. First, rapid warming in time also leads to species redistribution, and changing species interactions may accentuate emergent body size changes through time. Second, rapid warming is also likely to coincide with changes in productivity and changes in the growing season itself, which again are likely to magnify changes in body sizes observed in the field. Third, species are adapted to the local temperature range, more so than to temperatures experienced across their full distributional range, and are consequently sensitive to relatively slight temperature changes in the local environment[24]. Fourth, size patterns through space have emerged over many generations and probably involve adaptations that may reduce the temperature effects on growth. Counter-gradient variation, or opposite influences of genetic and environmental factors on phenotypes, has been detected in dozens of fish species and often involves changes in physiological rates that dampen the effects of temperature[25]. Presumably, rapid warming over the last two decades would not have allowed sufficient time for such adaptations to emerge. Nevertheless, even though the observed temporal rates of change are high, they are comparable to the rates of growth or maturation change reported in harvested fish species (ca. 0.5–4.0% per year) and smaller than evolutionary changes in size under strong selection experiments (2–17% per year)[26].

Discussion

Our study provides strong empirical support for the differential effects of warming on the body sizes of many common coastal marine fishes. Until now, the majority of size trend information for marine species was only available from commercially harvested or charismatic species, where effects of harvesting and warming are difficult to separate[27]. In our study, the effects of exploitation on body size are unlikely to affect overall conclusions because the number of commercially or recreationally fished species is small relative to the number of unexploited fish species inhabiting the shallow reefs surveyed, and because the temporal body size–temperature correlations inside and outside no-take marine protected areas were broadly similar (Supplementary Fig. 2). Species that showed the greatest responses of body size to temperature represent useful priorities for further study to understand the underlying drivers, such as growth, mortality, recruitment, food availability and other demographic changes. Future work is also needed to disentangle the multiple ecological mechanisms and environmental stressors at play, as well as potential feedbacks. For example, how do warming-driven species redistributions interact with changes in body sizes? And what are the main reasons for different rates of responses through space and time?

Differential responses of species' body size to warming have implications for the restructuring of food webs and ecosystems, with consequences for the stability and resilience of local communities to other external stressors, such as fishing, coastal pollution and the multifaceted effects of climate change. Many biological functions scale allometrically with body size, hence the mean, variance and shape of body size distributions within a community all influence aggregate ecosystem functioning[28]. Modelling studies show that even small changes in species body sizes, such as a 4% decrease over 50 years, could lead to increased mortality and up to a 30% decrease in biomass and productivity[29,30], yet the body size changes of common species in warming locations are often much greater (Extended Data Fig. 3). Of particular consequence is our finding that body size changes across the community are not proportionate across species—total biomass and production of larger predatory species are likely to increase with rising temperatures, whereas production of small-bodied prey species will decline. Complex changes to food web structure can thus be expected. Understanding how such body size trends might change the functional roles of dominant species in marine ecosystems should be one of the top priorities for management and protection of marine biodiversity in a rapidly changing ocean.

Methods

Reef fish data. The study is based on up to 26 years of underwater surveys from around the Australian continent and includes around 10 million observations of 335 fish species from around 30,000 surveys. Data were obtained from standardized quantitative censuses of fishes undertaken as part of the Australian Temperate Reef Collaboration (ATRC) monitoring programme conducted from 1992 to present, and the Reef Life Survey (RLS) programme from 2008 to present. The RLS programmme was developed based on the ATRC programme, and the two approaches use consistent methodology other than extent of replication. Full details of fish census methods are provided in refs. [19,20], and an online methods manual (http://www.reeflifesurvey.com) describes the different data collection methods. To maximize consistency in this study, we only used data from method 1 surveys. These surveys involve divers laying 50 m transect lines and recording all fish species present within duplicate 5-m-wide blocks (total area 500 m^2), tallying abundance in size classes as the divers move along the transect. Fish sizes are recorded in $K = 28$ size (length) bin categories, with bin widths ranging from 2.5 cm for fish lengths below 15 cm, to 5 cm for fish lengths between 15 and 40 cm, then 12.5 cm for fish lengths over 50 cm. Data quality and training of divers are detailed in refs. [20,31]. ATRC data are only collected by professional marine scientists with field experience, while the RLS data were collected by selected, trained and experienced recreational divers, who were each provided one-on-one training and calibration with experienced scientists before contributing data to the database. The data collected by these trained RLS volunteers have been formally evaluated and found to be indistinguishable from those of professional scientists at the same time and place[31].

Temperature data. For the spatial analyses, we grouped all fish survey sites into 0.5° grid cells, resulting in 280 cells spanning mean annual SST from 12 °C to 29 °C (Extended Data Fig. 1). For each of these cells, we then extracted mean yearly SST values using daily temperature records from the NOAA Optimum Interpolation 1/4 Degree Daily Sea Surface Temperature model data[32] from 1982 until the end of 2018. Alternative temperature metrics (such as growth degree days, that is, days with temperature above 12 °C, or mean annual SST in previous years) gave overall similar results. Long-term annual change in SST was also estimated for nine locations using monthly average SST values, and accounting for a sinusoidal component of seasonal temperature variation. For each location mean SST at time t was described by: $\mu(t) = \beta_0 + \beta_1 t + \beta_2 \cos(2\pi(t - \phi))$, where t is years since 1 January 1982. Variation in observed SST about this mean was assumed to be normally distributed with fixed standard deviation, σ. All parameters were estimated using Bayesian methods, and the resulting long-term rates of change, given by β_1, are presented in Supplementary Table 2 (analysis code available at https://github.com/astaaudzi/RLSfishSize).

Data filtering and selection. Reef fish size data were assessed for outliers and possible taxonomic errors by: (1) filtering out observations in cells above and below 97.5% and 2.5% of the species distribution temperature (~1% of records) and (2) removing records that were 1.5 times larger than maximum species size known in FishBase (a larger cut-off was used because the reported maximum size in FishBase is smaller than the true maximum size for many unexploited species with limited life-history data) (~1.5% of records). To ensure enough data and statistical power to infer body size responses and account for random annual and spatial variation, the dataset used in the spatial analyses was restricted to taxa identified to species level, and only species containing at least 1,000 individuals occurring in at least 10 geographic cells and over at least 5 years (for example a species with 1,000 individuals observed in a single geographic cell or only recorded in 3 years was not used). We also excluded the smallest species that had maximum body sizes below 10 cm, because their data spanned too few size bins to discriminate trends. This gave 335 fish and shark species, across a range of temperature preferences and life-history strategies. To reduce the effect of recruitment pulses and vagrant recruits occurring outside species' normal distribution limits on estimates of body size–temperature responses, we removed observations below the 10th percentile of the annual observed species body length (annual rather than one overall length was used to allow for the body size trends) (~3% of observations). While out-of-range observations may be important indicators of redistribution, we were interested in temperature–body size responses over the core ranges occupied consistently by species. The possible effects of this exclusion procedure on the conclusions from the hierarchical models (Fig. 1a) were tested by repeating spatial analyses using all data from ten small and ten large species; we found that data exclusion did not affect the main conclusion (Supplementary Fig. 3). Temporal analyses were restricted to locations where surveys spanned at least 15 years with at least 10 annual surveys conducted in total. This left 9 locations (Extended Data Fig. 1), each with an average of 44 sites repeatedly monitored (Supplementary Table 2). To improve estimates of temporal trends and associated random temporal errors, we restricted temporal analyses to species/location combinations where at least 20 individuals of a given species were observed per year at a location and at least 8 years of such observations were available (a species that was common for 5 years but for which fewer than 20 individuals were observed per year in later years was not used, and likewise a location that was only sampled in for example 1992, 2000 and 2015 was not used).

Statistical analyses. The association between SST and the distribution of observed body sizes across a species' range was quantified using a hierarchical, mixed-effect model. We assumed that observed log-transformed fish lengths were drawn from a normal distribution with standard deviation, σ_{lnlength}, which was constant across all surveys but differed among species. Size distributions within one species generally followed a lognormal distribution (Supplementary Fig. 4). For survey i the mean of this distribution is given by:

$$\mu_i = \beta_0 + \beta_1 x_i + \alpha_{\text{cell}(i)} + \alpha_{\text{year}(i)} + \alpha_i$$

where μ_i is the log-transformed body length, x_i is the normalized mean annual SST in the cell, and β_0 and β_1 are species-specific regression coefficients to be estimated. We normalized SST by subtracting the median SST observed across the species' range. This variable transformation improved convergence when fitting and reduced the potential correlation between β_0 and β_1, thereby removing the need to also estimate an additional correlation parameter. A positive estimate for β_1 would indicate a positive association between local SST and mean fish length. The α terms describe random effects due to spatial variation among surveyed cells ($\alpha_{\text{cell}(i)}$, due to, for example, different productivity, human pressure), temporal variation among survey years ($\alpha_{\text{year}(i)}$, due to random variation across years not associated with temperature) and random variation among the surveys themselves (α_i, for example, observer, site or weather differences). In this study a 'survey' is treated as a specific day in a given cell and may comprise several 50 m transect surveys. Each of the three α terms were assumed to be drawn from a normal distribution with zero mean and standard deviation to be estimated (denoted σ_{cell}, σ_{year}, σ_{survey}). To account for the observed fish lengths being necessarily binned, we integrated this normal distribution across each of the K bin ranges to calculate the probability of fish being observed in each bin. To account for potential outliers in estimated lengths, we also assumed that there was a small probability $\varepsilon = 0.01$ that a fish was observed in a randomly chosen bin. These probabilities form the basis of our likelihood function, and Bayesian methods were then used to estimate the six model parameters for each species and assess their uncertainty. Uniform priors were used for all parameters: [1.5–3.5] for β_0, [−0.5–0.5] for β_1, [0.001–1] for σ_{cell} and σ_{survey}, [0.001–1.5] for σ_{year}, and [0.1–0.3] for σ_{lnlength}. After the first set of analyses the posterior probability density plots were visually inspected for each species, and if the posterior densities were not fully included in the prior value range the priors were adjusted and analyses repeated. Yet, we found that priors had little influence on their posteriors due to large sample sizes. Markov chain Monte Carlo sampling was run with 3 chains of 1,000 iterations each, of which the first 500 were discarded as the burn-in and the last 500 were used to generate posterior probability density ranges. Some species did not converge at these settings, and analyses were repeated using 1,500 iterations and a burn-in period of 1,000. Further details and the code can be found at https://github.com/astaaudzi/RLSfishSize. Because μ_i is the log-transformed body length, the estimated values of β_1 are converted to the relative (or %) change in body length as $\exp(\beta_1)$, where a β_1 of, for example, −0.02 corresponds to $\exp(-0.02) = 0.98$ or a 2% decrease in body length. Thus β_1 values ranging from −0.2 to 0.2 can be interpreted as proportional changes in body length.

Given estimates of the slope of mean body size against SST (β_1) for all species, we then assessed whether these slopes were linearly associated with either the thermal affinity of a species or its maximum body size. Species thermal affinity is defined as the SST at the midpoint of its realized thermal distribution, as described in refs. [21,33] and also often referred to as the species temperature index. For the maximum body size we used the median value of the five largest observed body size records, which alleviated potential observation errors in the datasets. We accounted for variation in uncertainty associated with each estimate of β_1 as follows. For each species, we calculated the median and the standard deviation of the posterior for β_1. These standard deviations weighted the influence of each median in the linear regression, which we implemented using a hierarchical mixed-effects model. Again, Bayesian methods were used to estimate the regression coefficients and their associated uncertainty for both linear regressions (Fig. 1). Uniform priors were adopted for the y-intercept and slope ([−0.1–0.1] in both cases), and a uniform prior of [0.01,0.1] was also assumed for the standard deviation describing the variation in the β_1 estimates about the fitted regression line (Fig. 1).

Evidence of local, linear trends in mean body size were based on observations for 105 species at nine long-term monitoring locations[19]. We adopted a model very similar to the one used for the spatial analysis, except we assumed a linear relation of body length to year, rather than SST, and allowed both the y-intercept and the slope to vary across locations. For survey i at location j the mean of the ln-length distribution of a species is given by:

$$\mu_{i,j} = \beta_{0,j} + \beta_{1,j} y_i + \alpha_{\text{year}(i)} + \alpha_i$$

where y_i and year(i) are the year of the survey described as a covariate and a factor, respectively. The $\beta_{1,j}$ describe long-term temporal change in log-length across locations, which is of specific interest, and the $\alpha_{\text{year}(i)}$ describe stochastic year-to-year changes in length common across locations due to unknown environmental factors. The binning of observed fish lengths was treated in the same way as in the spatial analysis. Bayesian methods were again used to estimate the model parameters. Uniform priors were used for all parameters: [1–4] for $\beta_{0,j}$, [−0.1–0.1] for $\beta_{1,j}$, [0.001–0.5] for σ_{year} and σ_{survey}, and [0.1–0.5] for σ_{lnlength}. These priors had little influence on the posteriors.

Five of the long-term locations included observations both inside and outside of no-take marine protected areas (MPAs), and we also tested whether temporal trends in body size differed between sites inside and outside MPAs. This was done to assess whether harvesting could be driving temporal trends in observed body size. The MPAs are officially no-take areas, and even though a small amount of illegal harvesting is likely to occur, the fishing rates are more intense outside MPA areas. The two datasets had 84 and 74 species, respectively, with 69 species found with sufficient abundance both inside and outside MPAs. The overall average body size trends through time were similar inside and outside MPAs (Supplementary Fig. 2), suggesting that temporal body size trends were not driven by exploitation. This was not surprising, given that the majority of the species analysed (after the filtering described above) are not routinely targeted by commercial or recreational fishing. Final temporal analyses were therefore done on a combined dataset ignoring the MPA effects (105 species across 9 locations).

To compare rates of body size change across space and time, we explored the correlation between the body size responses in spatial analyses (β_1) and annual body size trends ($\beta_{1,j}$) at eight locations with substantial warming trends (Supplementary Table 3). Out of 105 species included in the temporal analyses, 28 species were found at only one non-warming location (Jurien Bay) and were not included in the space–time rate comparison. From the remaining 77 species, six species did not have sufficient spatial data, so the final dataset for the space–time rate comparison included 71 species. For these species, correlations between spatial and temporal slopes were assessed using bootstrapped weighted Spearman's correlation (10,000 bootstrap replicates), where each value was weighted by the inverse of its uncertainty range (code available at https://github.com/astaaudzi/RLSfishSize).

Species abundance and therefore potential density dependence effects were not included in the main model, because the relationships describing potential abundance effects on body size are unlikely to be linear, and because competition is likely to occur at both intra- and inter specific level. Accounting for all these effects would require a very complex, parameter-rich model and much larger datasets than were available for most species. However, to assess whether density dependence could still be the major driver of the observed body trends (if abundance was determined by SST), we compared the species-specific spatial body size slopes (β_1) with abundance–SST skew statistics assessed in ref. [23]. The skew statistics describe relative abundances of a species across its distribution range, where positive skew means that a species is more abundant at the warmer half of its distribution and vice versa. If abundance was a major driver of average body size, we could expect an overall negative correlation between size–temperature and abundance–temperature slopes, such as mean body size being smaller at sites with higher abundance. Alternatively, larger average body sizes might have positive effects on abundance through, for example, improved recruitment or interspecific effects. In this case, we could expect a positive correlation between size–temperature and abundance–temperature slopes. Estimates of both size–temperature slopes (this study) and abundance–temperature skew[23] were available for 300 species. The correlation between body size slopes and abundances was close to zero ($r=0.09$, $P=0.14$), suggesting that abundance is unlikely to be a major driver of body sizes and vice versa (Extended Data Fig. 2).

All statistical analyses were performed using R v.3.2. Bayesian analyses were done using the rstan package[34].

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

Underwater visual survey datasets are available through the Reef Life Survey site www.reeflifesurvey.com. The final datasets used in this analysis are available through the code depository at https://github.com/astaaudzi/RLSfishSize and as Supplementary datasets linked to this article.

Code availability

All codes used in this analysis are available at https://github.com/astaaudzi/RLSfishSize.

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Author contributions

A.A. designed the study and led the writing. A.A. and S.A.R. designed and conducted the statistical analyses. R.D.S.-S., G.J.E. and N.S.B. led field surveys and data collection. G.P., N.P. and J.L.B. contributed critically to the development of the study. All authors contributed to the manuscript writing and gave final approval for publication.

Competing interests

The authors declare no competing interests.

Additional information

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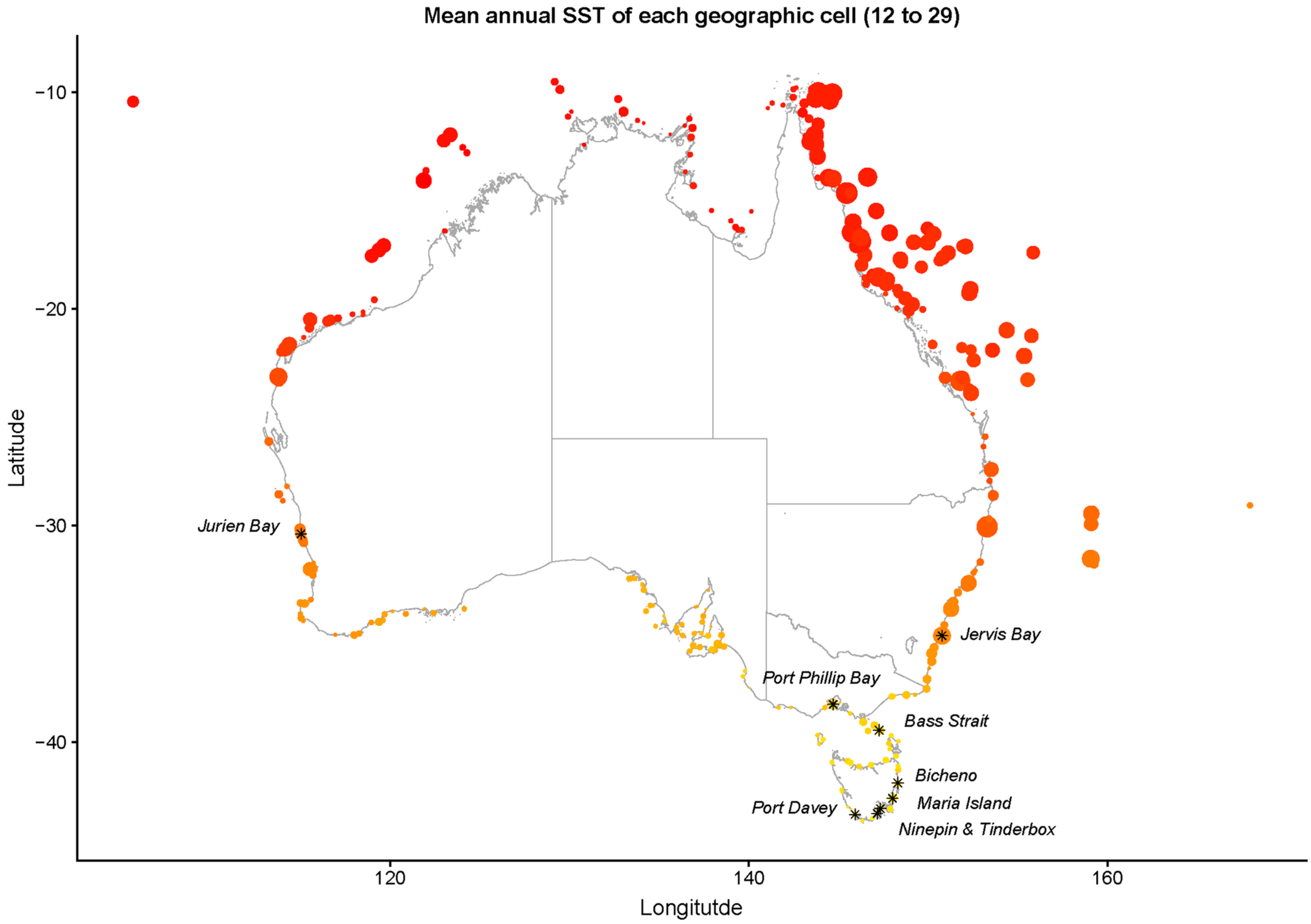
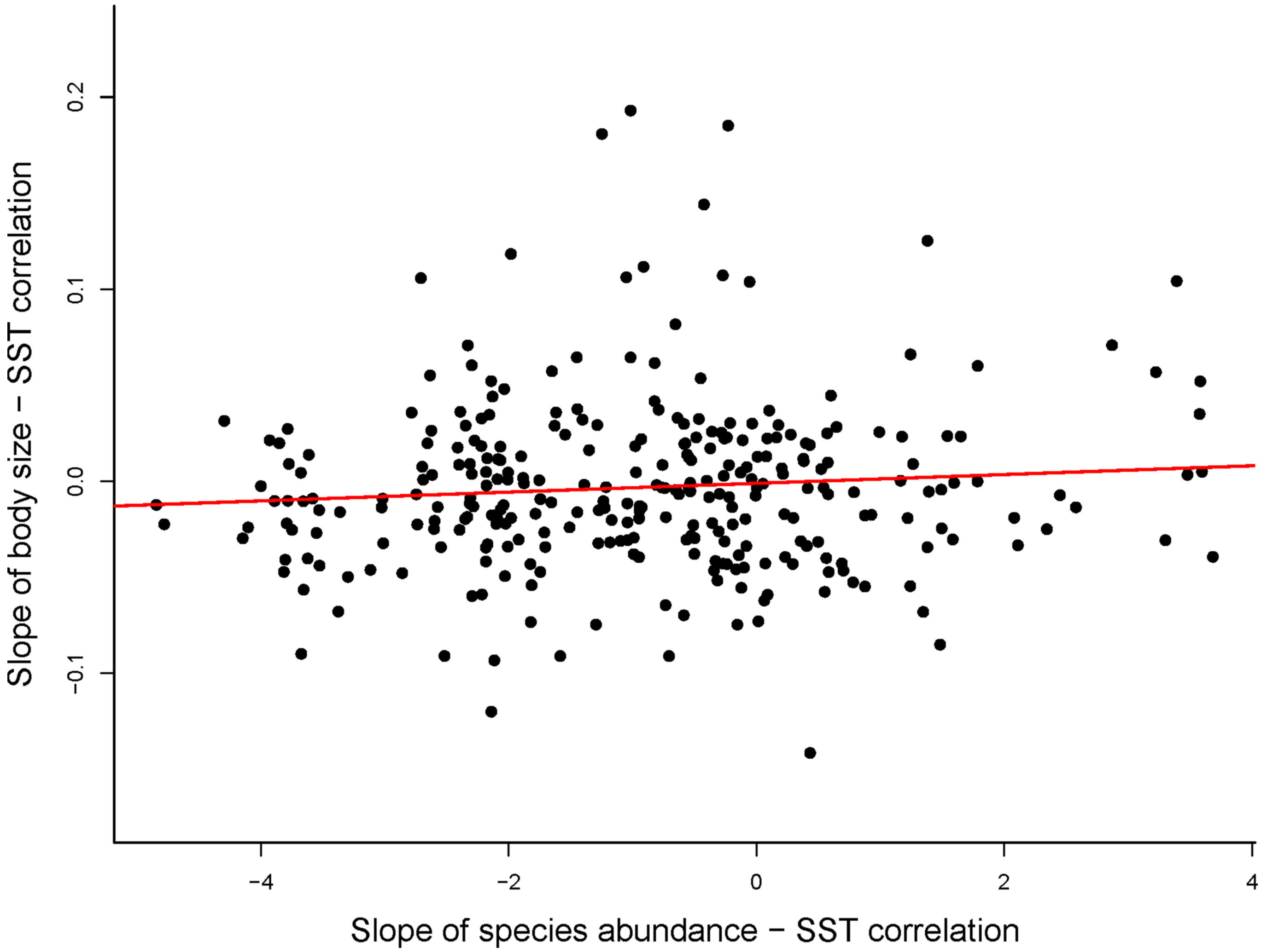
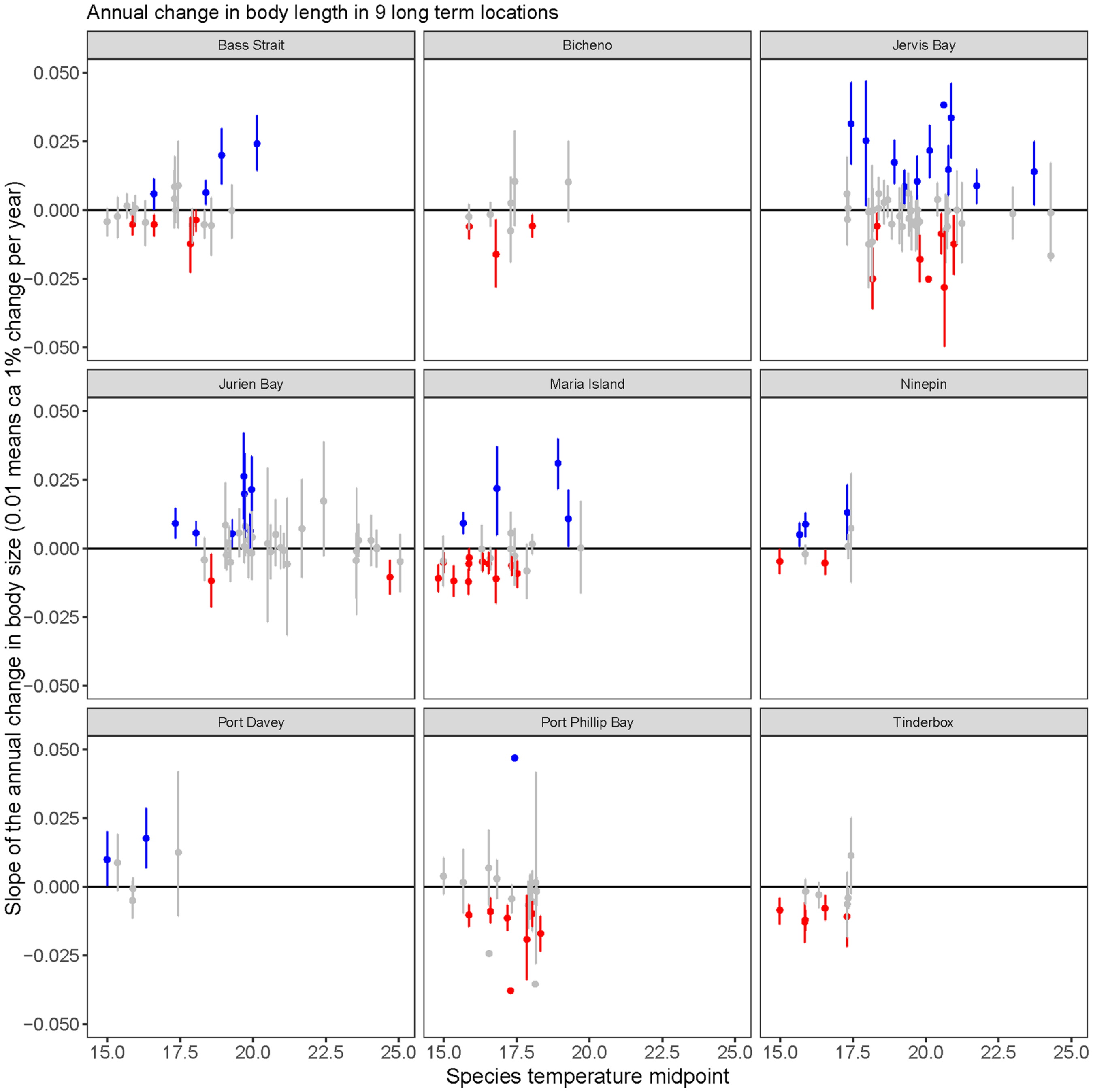


Extended Data Fig. 1 | Spatial distribution of Australian fish survey data used, coloured according to the mean annual sea surface temperature. All sites are grouped onto 0.5 degree grid cells. Colours represent mean annual SST over the entire sampling period in that cell (ranging from 12 °C for yellow to 29 °C for red) and circle size is proportional to the total number of species used for the analyses in the cell (determined by species richness and number of surveys in the cell). Black stars indicate the nine long-term monitoring locations. The Australian coastline shapefile was downloaded from the Australian Natural Resources Data Library website (Commonwealth of Australia).



Extended Data Fig. 2 | Correlation between species body size – SST slopes and abundance – SST slopes from literature. Species-specific slopes between body size and mean annual SST through space (β_1, on y axis) are compared with the species specific abundance and mean annual SST slopes estimated in Waldock et al. (2019). Data on both slopes was available for 300 species. If abundance was a major driver of average body size, we could expect an overall negative correlation between size-temperature and abundance-temperature slopes, such as mean body size is smaller at sites with higher abundances. Alternatively, larger average body sizes might have positive effects on abundance through e.g. improved recruitment or inter-specific effects. In this case we could expect a positive correlation between size-temperature and abundance-temperature slopes. The correlation between body size slopes and abundances was close to zero ($r = 0.09$, $P = 0.14$), suggesting that abundance is unlikely to be a major driver of body sizes and vice versa.



Extended Data Fig. 3 | Species-specific body length changes at nine long-term monitored and warming locations. Location and species specific temporal responses, represented by slopes of body length change in 105 coastal fish species in nine warming and long-term monitored locations. Each dot represents a species, arranged according to the temperature at the centre of their distribution area (temperature midpoint). Blue and red colours indicate species for which 90% of the posterior probability density range for the slope of the annual body length change (on y axis) was above or below zero, respectively. For the map of the nine locations see Extended Data Fig. 1.

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Our web collection on statistics for biologists contains articles on many of the points above.

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Policy information about availability of computer code

Data collection	No software was used to collect data
Data analysis	All statistical analyses were performed using R v.3.2, Bayesian analyses were done using the rstan package.

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Sample size	The study is based on up to 26 years of underwater surveys from around Australian continent and includes around 10 mln observations of 335 fish species from around 30000 surveys.
Data exclusions	Rare species were excluded from the main data sets based on predefined criteria (number of year found, number of individuals seen) that are explained in the methods. We also tested the effect of juvenile exclusion on the main findings (Extended Data Fig. 7) and found it to be negligible
Replication	This was not an experimental study, but analysis of field data. All codes and datasets used in the analyses are available through the Github site, making the analyses completely repeatable. The hypotheses were tested with different study designs (spatian and temporal) and potential effects of factors not included in the main statistical model (abundance and effects of recreational fishing) were also tested separately
Randomization	This study was not based on experimental data or pre-determined survey selection, so no randomisation was applied.
Blinding	Blinding of divers was not relevant and divers did not know that correlation of fish size with temperature will be eventually explored (surveys were done over 26 years by hundreds of divers). General (not related to hypotheses tested here) diver biases in scoring fish sizes have been explored in an earlier study and are likely to make our predictions conservative (discussed in the manuscript).

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Laboratory animals	No laboratory animals were used
Wild animals	No animals were captured or collected in the field. Field observations across regular transects were conducted by SCUBA divers on all coastal fish species (over 1000 species and over 10 mln individuals).
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