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LETTER

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Mean reef fish body size decreases towards warmer waters

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Abstract

Aquatic ectotherms often attain smaller body sizes at higher temperatures. By analysing ~15,000 coastal-reef fish surveys across a 15°C spatial sea surface temperature (SST) gradient, we found that the mean length of fish in communities decreased by ~5% for each 1°C temperature increase across space, or 50% decrease in mean length from 14 to 29°C mean annual SST. Community mean body size change was driven by differential temperature responses within trophic groups and temperature-driven change in their relative abundance. Herbivores, invertivores and planktivores became smaller on average in warmer temperatures, but no trend was found in piscivores. Nearly 25% of the temperature-related community mean size trend was attributable to trophic composition at the warmest sites, but at colder temperatures, this was <1% due to trophic groups being similarly sized. Our findings suggest that small changes in temperature are associated with large changes in fish community composition and body sizes, with important ecological implications.

KEYWORDS

Bergmann's rule, biogeography, ecogeography, herbivore, latitudinal gradient, length, macroecology, predator, temperature size rule

INTRODUCTION

The effect of temperature on organism body size is well recognised at individual, population, species and community levels (Bergmann, 1847; Brown et al., 2004; Cheung et al., 2013; James, 1970). As climate change accelerates, local reductions in animal body sizes are predicted to be a widespread response to warmer temperatures (Daufresne et al., 2009; Forster et al., 2012; Ohlberger, 2013). Temperature impacts on body sizes are especially strong in ectotherms living in aquatic ecosystems, possibly owing to fewer options for local temperature refugia and limitations on oxygen availability (Forster et al., 2012; Lenoir et al., 2020). Temperature-driven changes in ectotherm physiology and energy allocation affect body sizes at population and community levels, and thus are likely to have profound ecological consequences (Brose, 2010; Brown et al., 2004). For example, temperature-dependent changes in diet, growth, mortality, dispersal and reproduction schedules can alter predator–prey interactions, community composition and emergent body size distributions (Audzijonyte et al., 2013; Lindmark et al., 2023). Given this complexity, it is not surprising that the causal processes of body size changes remain relatively poorly known, and despite decades of research, only limited empirical evidence exists of broad-scale temperature-driven body size changes in aquatic organisms.

Most studies investigating aquatic ectotherm body sizes and temperature suggest an overall negative relationship, a trend that matches broader biogeographic 'rules' operating at inter- or intra-specific scales (Bergman's rule, James' rule, temperature-size rule; Atkinson, 1994; Bergmann, 1847; James, 1970). While the underlying mechanisms are debated (Audzijonyte et al., 2019; Lefevre et al., 2017; Pauly, 2021; Verberk et al., 2021; Wootton et al., 2022), this evidence collectively suggests that fishes living in warmer conditions grow to smaller adult or maximum body sizes (see review in Verberk et al., 2021). However, at the intraspecific level mean body sizes of fishes do not always decrease with temperature (Audzijonyte et al., 2020), and it is not clear how these intra-specific responses collectively translate into community-level trends.

In addition to temperature directly driving changes in fish body sizes in communities, another potential driver of the relationship between community-level mean size and temperature is variation in diet. Food selection amongst fishes is potentially influenced by both temperature and body size (Rimmer, 1986; Scharf et al., 2000), with feeding modes and associated physiological adaptations in turn influencing trophic composition and community size structure. Morais and Bellwood (2018) found that both temperature and trophic guild classification were important variables determining growth rates in coral reef fishes, which suggests that the emergent body size structure of different trophic guilds may respond to temperature differently. This means that community mean body size responses to temperature may depend on responses within trophic groups and on the relative composition of these trophic groups in the community. This relative composition of trophic guilds may in some cases be related to body size, but the relationship is not always clear cut. It is typically suggested that marine ecosystems are strongly size-structured, with higher trophic levels in the food chain generally occupied by larger-bodied animals (Andersen, 2019; Brose et al., 2019; Potapov et al., 2019), as found in offshore or shelf ecosystems, such as the North Sea (Barnes et al., 2010; Jennings et al., 2001). However, in coastal or reef ecosystems, low trophic-level fishes such as herbivores or invertivores often reach body sizes larger than piscivores (see Trebilco et al., 2013), which means that in coastal systems body size is not a good indicator of the trophic level or trophic composition. Importantly, the trophic composition of fish communities varies with latitude and thus likely temperature (Ferreira et al., 2004; Holland et al., 2020), meaning that changes in the overall community mean length with temperature may be influenced not only by potentially different temperature-size responses within trophic guilds but also by the changes in trophic composition. Generally, as water temperature decreases omnivorous and carnivorous (e.g. planktivore, invertivore and piscivore) foraging strategies appear to become relatively more common (Longo et al., 2019; Madin et al., 2020), whereas a higher diversity and abundance of herbivorous fish species is found in tropical waters (e.g. >15°C annual SST; Floeter et al., 2005; Vejříková et al., 2016). The composition of trophic guilds within communities, and the temperature-size relationships within those guilds, are likely to be key pieces of the puzzle for understanding the nature of widespread temperature effects on body sizes in fish communities (Figure 1).

Investigating trends in body sizes or trophic structures across spatial-temperature gradients may provide insights into potential future states in a progressively warming ocean, through the form of a space-for-time substitution (Blois et al., 2013; Damgaard, 2019; Elmendorf et al., 2015). In this study, we investigate geographic relationships in fish community body size and temperature using underwater visual survey data surrounding the Australian continent. The dataset consists of over ~15,000 underwater visual fish surveys covering a range of ~15°C in mean sea surface temperature (SST) (14–29°C) and comprising ~9.5 million individual fish observations from 1582 species. This study builds on our knowledge of intraspecific variation in body size trends with temperature (Audzijonyte et al., 2020) by investigating if and how the mean individual fish body length at community—and trophic guild—levels scale with temperature. We also explore how the relative abundance of trophic guilds changes across the temperature gradient to produce an overall community body length response.

METHODS

Reef fish data

Fish community size and abundance data for shallow reefs were provided by the Reef Life Survey (RLS) and Australian Temperate Reef Collaboration (ATRC) programs (Edgar et al., 2020; Edgar & Barrett, 2012; Edgar & Stuart-Smith, 2014), accessed through the Integrated Marine Observing System's National Reef Monitoring Network facility (https://portal.aodn.org.au/search, 20/09/2020). We included Australian 'Method 1' transects sampled opportunistically (mostly in the austral spring/summer/autumn or dry season for temperate and tropical sites, respectively) between 2007 and 2018, for which size estimates were available for all species (Figure 2). This resulted in 14,941 transects (9,456,403 individual fish). RLS and ATRC both utilise the same methodology for fish surveys, which is described in full in Edgar and Barrett (2012), Edgar and Stuart-Smith (2014), and Edgar et al. (2020), and available online through http://www.reeflifesurvey.com. In brief, divers lay out 50 m transect lines, and all fishes observed within 5 m either side of the transect (total area of 500 m^2) are identified and tallied into 28 size class bins as divers swim along the line. The bins start at 2.5 cm, increasing in 2.5 cm increments until 15 cm, from which point size-bin increments increase by 5 cm until 40 cm, with 12.5 cm size class bin increments for fish over 50 cm. ATRC data were only collected by professional scientists, whereas RLS data are collected by a combination of scientists and selected, individually trained citizens. Statistical evaluations have shown that the data collected by fully trained citizens in RLS are indistinguishable from those collected by professional scientists (Edgar & Stuart-Smith, 2009).

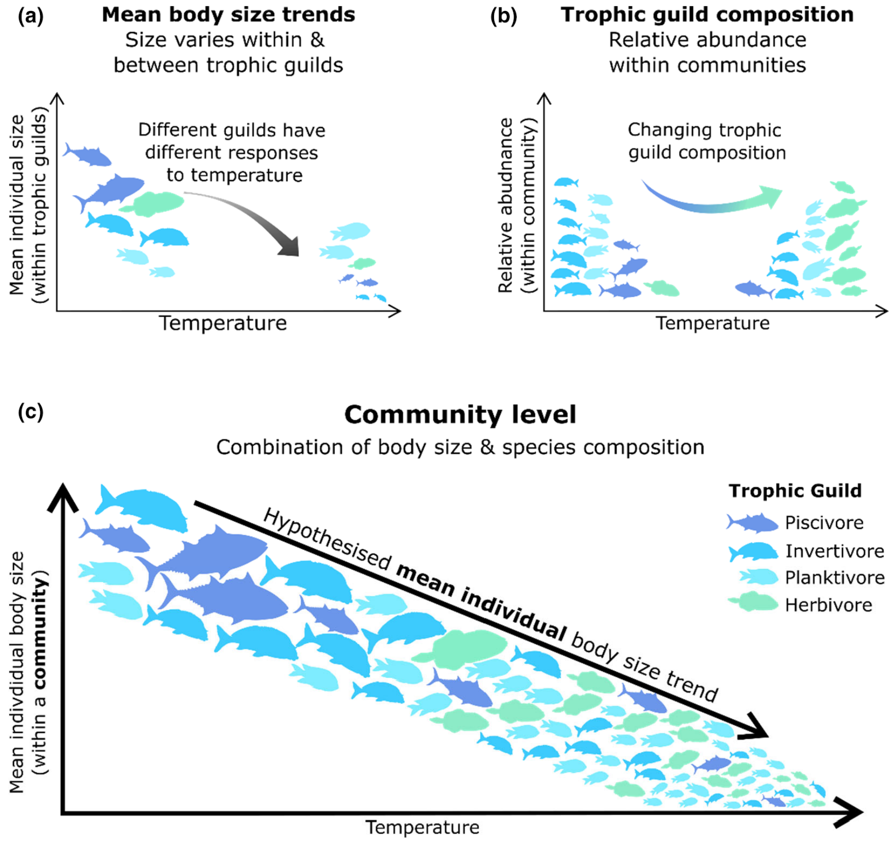

FIGURE 1 Hypothesis tested in the present study on how mean community-level individual body size is influenced by (a) within-guild body size trends (assuming that guilds may vary in their size and in their response to temperature) and (b) the trophic guild composition of that community (assuming that the composition of guilds may change with temperature). These two components may contribute to the predicted overall relationship of decreasing mean size of fish within communities with increasing mean sea surface temperature, although to what extent either component contributes is unknown (c). The scenarios presented in this figure are hypothetical, with the actual trends are unclear and likely complex.

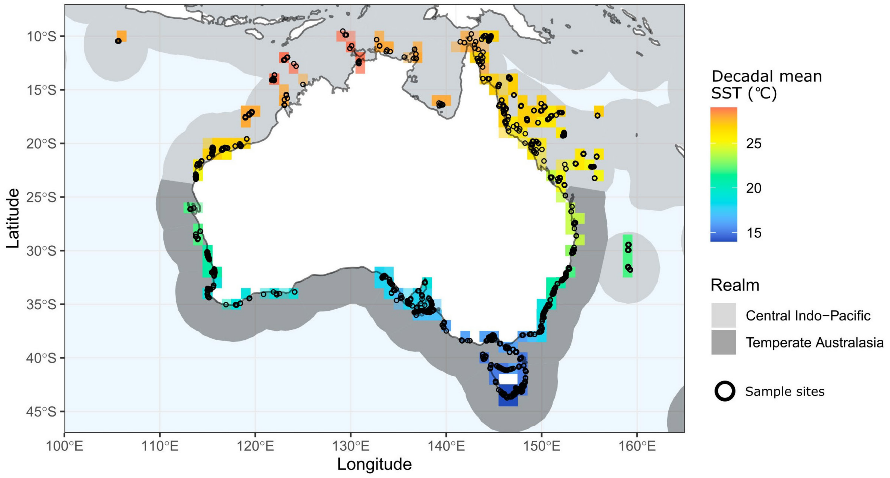

FIGURE 2 Location of sites sampled by Reef Life Survey and the Australian Temperate Reef Collaboration programs between 2007 and 2018 (open circles). Also shown is the mean annual Sea Surface Temperature (SST °C) for the 1° grid cells within which sites are found, averaged over the sampling timeframe (coloured tiles). Ecosystem 'realms' (Spalding et al., 2007) into which sites fall are provided, with northern (<24° S) sites within the tropical Central Indo-Pacific realm, and southern sites (>24° S) within the temperate realm.

We classified all observed fish species into four major trophic guilds (herbivore, planktivore, invertivore and piscivore) as per Coghlan et al. (2022), according to their trophic classification in the RLS database, expert elicitation, available literature or where no other sources are available, phylogenetic relatedness. Generally, the trophic guilds in this study were well represented on each underwater reef fish transect, with multiple individuals recorded.

Temperature data

The coordinates and year of each transect were used to extract the nearest available mean annual SST for that year, aggregated from the NOAA optimum interpolation ¼° daily SST model (Reynolds & Banzon, 2008). This model is widely used, including in another study of Australian coastal areas (e.g. Audzijonyte et al., 2020). While newer and higher resolution products may more accurately reflect local temperature conditions, this study looks at temperature-size patterns at broad spatial (1° or ~100 km size grid) and temporal (mean annual SST) scales, and for this purpose the NOAA model provides a suitable approximation. We used average annual SST rather than temperature at the time of sampling, because realised fish body sizes integrate temperature over their lifespans, which is most appropriately captured by the annual temperatures when fish ages are unknown. Nonetheless, we relate community mean body sizes to the cell SST values in each year sampled (rather than average over the whole sampling period) to account for the potential effect of heatwaves and climate warming in the dataset (see Edgar et al., 2023 for overall temperature trends across the studied area). For the purposes of this study, we classify sites as temperate (cool water) or tropical (warm water) according to the 'realm' category within the Marine Ecosystems of the World classification scheme, with tropical sites falling within the Central Indo-Pacific realm and temperate sites within the Temperate Australia realm (Figure 2). The boundary between these two realms is found at ~25° S and corresponds to mean decadal SSTs of >24°C for tropical sites, and <24°C for temperate sites.

Statistical analysis: Mean individual body size patterns

The association between SST and mean individual body lengths (size) across all the fishes observed in a community ('community-level mean'), for a given transect, was quantified using linear mixed effects (LME) models. Fish length data were first log-transformed to conform to the assumptions of linear models. In this analysis, the response variable was the mean size (length) of individuals in each transect and the explanatory variable was the mean annual SST of the transect in that year. Each transect was assigned a grid cell ID, as this was the resolution at which mean annual SST was applied (therefore multiple transects conducted in the same cell and in the same year were assigned the same mean annual SST value; Figure 2). To account for local variation that could influence mean body sizes across space (e.g. productivity, fishing), 'grid cell' was included as a random effect. To account for potential interannual variation that could influence mean individual body size in addition to temperature (such as *El Niño* events, higher wave or wind action), 'year' was included as a random effect. Therefore, the mean of the fish community or trophic guild size distribution in a transect was modelled as:

$$L_{ijkc} = \beta_0 + \beta_1 \mathrm{SST}_{j,k} + \gamma_j + \delta_k + \epsilon_{ijkc}$$

where L_{ijkc} is the log transformed mean community-level body length (in cm) of the whole community c on transect i contained in grid cell j in year k; $\mathrm{SST}_{j,k}$ is the mean SST for grid cell j in year k; γ_j and δ_k are the random effects for grid cell j and year k, respectively, ϵ_{ijkg} is the pure error term, and β_0 and β_1 are regression coefficients to be estimated. Models were built using the function 'lmer' in the package 'lme4' (Bates et al., 2012) using R (R Development Core Team, 2021).

Next, to test whether the association of SST and the mean individual body lengths differed among the four main trophic guilds, the model was refitted allowing the regression coefficients to vary across guilds. Here the response variable was the average individual body lengths for each trophic guild per transect and was modelled as

$$L_{ijkg} = \beta_{0,g} + \beta_{1,g} \mathrm{SST}_{j,k} + \gamma_j + \delta_k + \epsilon_{ijkg}$$

where the regression coefficients $\beta_{0,g}$ and $\beta_{1,g}$ were now specific to the guild.

All models were fitted by restricted maximum likelihood (REML) and residual and *Q–Q* plots were checked to ensure concordance with model assumptions. Post-hoc pairwise Tukey's tests were performed on the model term '*trophic guild*' using the R package 'emmeans' (Lenth, 2023).

We ran sensitivity tests to determine if our results were influenced by species or size bins included. As trends in mean body size and temperature may be affected by fishing, we re-ran the models on a dataset excluding fish species targeted by commercial or recreational fisheries (Bosch et al., 2021). Importantly, these fished species represent only a small proportion of the 1582 species recorded across the ~15,000 transects studied here, and so they are limited in their contribution to overall community mean body size and are mostly large-bodied and non-herbivorous. To account for potential under-sampling of highly mobile large-bodied species (see Rojo et al., 2021), we also re-ran the model on a dataset excluding chondrichthyans (Tables S2 and S3). Finally, the broader size bins into which large individuals are recorded (compared to smaller individuals, see Edgar & Barrett, 2012) could affect our estimates of mean size. We therefore repeated the same analyses excluding all individuals >50 cm to assess whether similar trends in community- and trophic group-level mean individual body sizes were observed (Table S3).

Community composition

To investigate whether trophic guild composition of communities changed with temperature, we applied a multinomial log-linear regression (MLR) model on the trophic guild abundance data for each transect for different SSTs. A multinomial approach was selected as it scales well for datasets with numerous categories and low count replication (Liu & Xie, 2014). A multinomial approach also enables us to incorporate different sample sizes by weighting the transects accordingly. To perform the multinomial regression, we first determined the total abundance of fish per trophic guild per transect, treating missing species/guilds as true absences (assigned 0). MLR model coefficients can be difficult to interpret directly. Instead, the probabilities of guild membership were predicted from the model for a typical range of temperatures, and trends deduced from these predictions (Figure 4b; but see also Table S5). Multinomial models were fitted using the function 'multinom' from the package 'nnet' (Ripley & Venables, 2016) using the R statistical language.

Finally, to assess the relationship between mean community size and temperature, for each temperature, the change in predicted mean community size was calculated for a ±1°C change. The resulting change in predicted mean community size was then further decomposed into (a) the contribution from community composition and (b) the contribution from change in guild mean sizes. The contribution from community composition (a) was calculated by predicting the mean community size for a ±1°C change while holding the guild mean sizes fixed. The contribution from the change in guild mean sizes (b) was calculated by predicting the mean community size for a ±1°C change while holding the community composition fixed. We then visualised the resulting change in size with temperature under these scenarios, for comparison.

RESULTS

Average individual body length of fishes in reef communities significantly decreased with increasing temperature-across-space, with a slope of −0.05 (Figure 3a; 95% confidence intervals of −0.04 to −0.06; Table 1; random effect results in Table S1). Since our size measurements refer to lengths, our model predicts a decrease in mean community-level fish body length of ~5% per 1°C increase in temperature-across-space. For a mean SST of 14°C this indicates a mean community-level fish body length of 15.7 cm, whereas at 29°C the mean length is 7 cm, or ~55% shorter. Using a general length (L) to weight (W) conversion of $W = 0.01 * L^3$ (based on a 'typical' fish body shape; Froese, 2006; Le Cren, 1951), this suggests an average weight of 39 g at 15°C and 3.5 g at 29°C – that is, a more than tenfold reduction in weight across the range of temperatures observed. Excluding fished-species, elasmobranchs or all fishes above 50 cm did not change the direction or magnitude of our results (Table S3).

Temperature-size relationships were negative in three of the four trophic guilds (herbivores, planktivores and invertivores), like those in the overall community (Figure 3b; Table S2). However, a significant interaction between SST and trophic group indicated different responses across trophic guilds, with piscivores showing an opposing trend of slightly increasing (1% per 1°C, $p < 0.001$) mean lengths with temperature-across-space (Figure 2b; Table S2). The steepest negative slope between mean length and SST was observed for planktivores (−6% per 1°C), followed by herbivores (−5%) and invertivores (−4%). A post hoc pairwise Tukey test on the trophic guild model term revealed that the temperature-size relationships were significantly different ($p < 0.01$) across all guild combinations. Sensitivity tests excluding fished species or chondrichthyans had only minor effects on these results (Table S4), resulting in slightly more negative slopes in herbivores and planktivores when fished species were excluded. Planktivores, on average, had the smallest mean size in warm water (tropical) communities, followed by invertivores, herbivores and piscivores (Figure 4a). However, in cool water (temperate) communities planktivores and invertivores became more similar in mean size, and the notable size gap between herbivores and piscivores in warmer waters was also considerably decreased.

The community composition of trophic guilds varied with temperature-across-space, with warm water tropical communities dominated by planktivorous fishes and temperate communities by invertivorous fishes (Figure 4b). Given that the change in community-level mean fish length could be driven both by a change in the composition of guilds in the community as well as changes to mean lengths within guilds, we quantified the contributions from these two components towards the overall community mean size. Across all temperatures, within-guild body size trends accounted for most of the overall community temperature-size trend (Figure 4b). However, in tropical waters ~25% of the variation in total community mean-size could be attributed to changes in community composition because of larger differences in mean body sizes across trophic guilds in tropical compared to temperate communities. For temperate areas community composition had little role in explaining the mean-size-temperature variation.

DISCUSSION

The community and ecosystem consequences of warming associated with climate change are already apparent

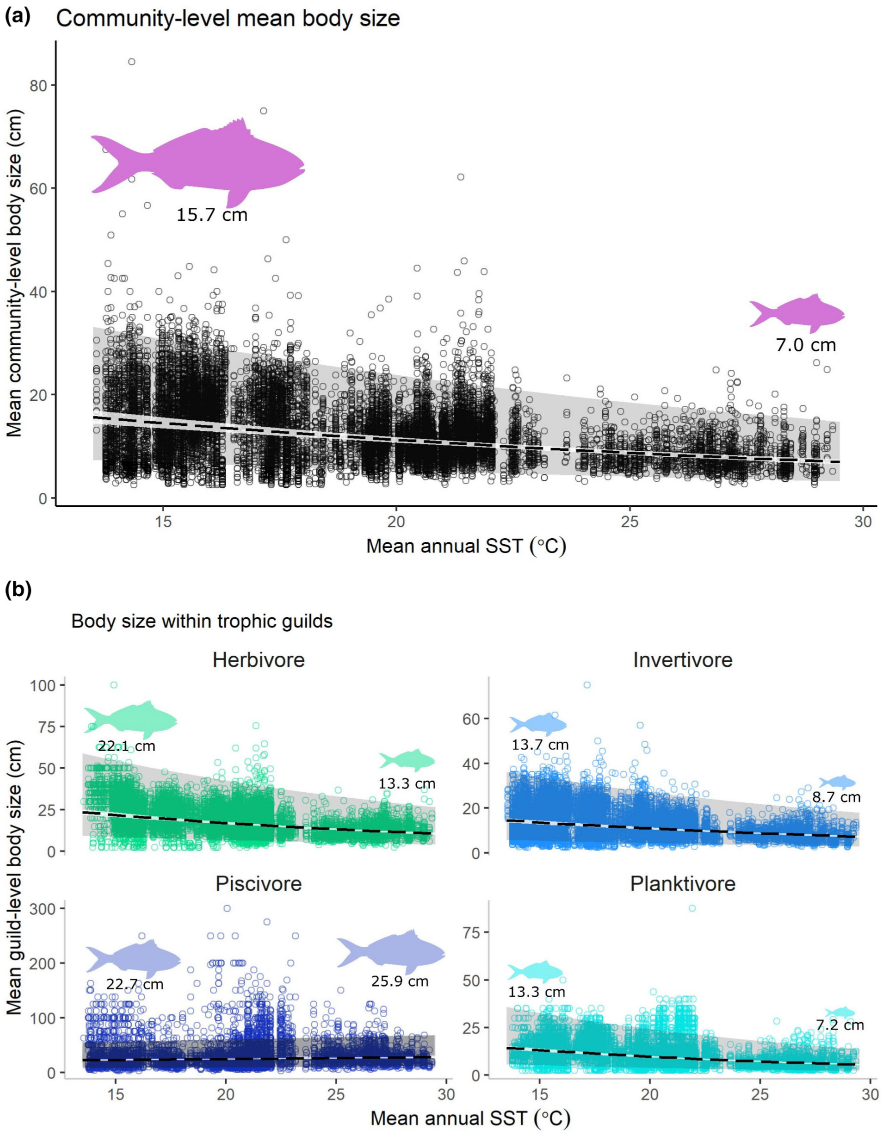

FIGURE 3 Temperature gradients in the length-structure of Australian reef fish communities. (a) Mean individual length (cm) of all fishes (bony and cartilaginous) per transect, with mean annual sea surface temperature (SST; °C) across space. (b) As for a, but with mean length calculated for each trophic guild, per transect, separately (note different scales on *y*-axes). Dashed line shows the average prediction lines. Grey bands show full confidence intervals from both fixed and random effects. Fish icons illustrate the approximate relative mean length of fishes at 15°C and 30°C.

and rapidly accelerating. Given the importance of body size for ecosystem function, establishing whether widely accepted temperature-size relationships hold at the community level across macroecological scales is needed to help inform potential future impacts. Our study provides four important findings: (1) a strong trend exists in community mean individual body size of coastal reef fishes with temperature, equating to a 50% decrease in mean individual fish length over a 15°C increase in SST-across-space; (2) different temperature-size relationships exist between the four major reef fish trophic guilds, with body size within guilds generally decreasing as temperature increased, except for piscivores, where mean size increased slightly as temperature increased; (3) trophic guild composition within communities also changed with temperature-across-space, with tropical communities dominated by planktivores and temperate communities dominated by invertivores; and (4) within-guild temperature relationships drive the majority of the temperature-size patterns at the community-level, but the importance of trophic composition in determining the community mean body size increases in warmer waters. Importantly, these findings were based on empirical observations of individual fish confirmed to have been present together at a scale at which ecological processes—such as competition, predation and population dynamics—occur (i.e. on a survey transect).

Our findings suggest that when aggregated at the community level, the average fish becomes smaller with increasing temperature-across-space. This finding is consistent with broad ecological expectations and arises at the community level despite variable mean size

TABLE 1 Linear model predicting mean community-level fish body length according to annual mean sea surface temperature (SST °C) across space, with random effects of year and grid cell.

	Log mean size		
Predictors	**Estimates**	**CI**	***p***
(Intercept)	3.43[a]	3.25 to 3.61	<0.001
SST (°C)	−0.05	−0.06 to −0.04	<0.001
Observations	14,908		
Marginal R^2/Conditional R^2	0.154/0.377		

Note: Observations are individual transects from which fish body length and abundance were collected.

[a] Back-transformation to original units indicates that predicted fish length at 0°C (intercept) is exp(3.43) = 30.9 cm. The slope of −0.05 indicates 5% decrease in length per subsequent 1°C. Random effect results in Table S1.

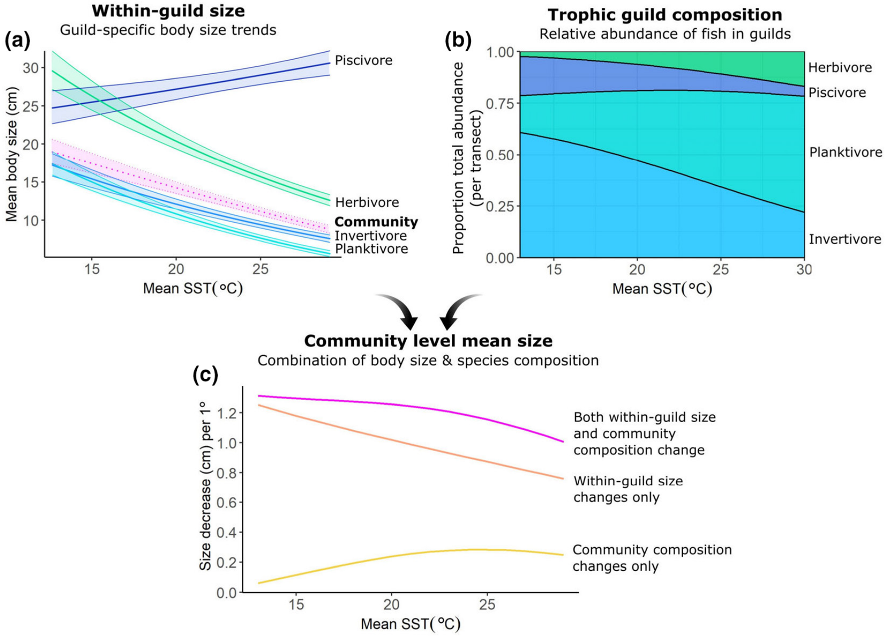

FIGURE 4 (a) Model outputs of temperature-related trends in the mean lengths of four common reef fish trophic guilds and the overall community (dashed line) mean length observed in transects across the temperature gradient, with 95% confidence intervals. (b) Model output of relative proportion of total fish abundance per transect accounted for by each trophic guild across the range of mean annual sea surface temperature (SST), as predicted by the multinomial model. CIs for this plot are not visible owing to being very small (~±0.005). (c) Model output of the relative contributions of community composition and within-guild mean sizes to the overall community mean size across temperatures. The y-axis shows the predicted *decrease* in mean body length, estimated as length change for ±1°C from any point along the x-axis (see Methods). The three lines show the overall community mean size decrease, where the overall community-level decrease (top, pink line) consists of decrease because of within guild size changes only (orange line) and owing to community composition only (yellow line).

changes within species (Audzijonyte et al., 2020) and different temperature-size trends across fish trophic guilds. Our results suggest that the emergent mean temperature–body size trends observed in natural communities arise through interactions of both physiological and ecological processes, happening at the individual, species, trophic guild and community levels. Our finding of a 5% reduction in mean fish body length per 1°C across space at the community-level is similar in magnitude to the 4% increase or decrease in mean length per 1°C across space observed at the species-level by Audzijonyte et al. (2020); however, the community-level temperature-size trend we found was always a decrease. Only two other empirical studies, to our knowledge, have investigated changes in community-level mean size with temporal (Daufresne et al., 2009) or spatial (Emmrich et al., 2014) temperature gradients in fishes. These two studies, both from freshwater systems, also observed decreases in mean community-level body size with increasing temperature.

Other studies exploring fish body size changes with temperature (across space or time) have used maximum rather than mean body sizes (Baudron et al., 2014; Cheung et al., 2013; van Rijn et al., 2017). This difference in methodology is important because shifts in maximum or maturation body sizes are driven only by changes in growth, whereas changes in mean body size depend upon the combination of both growth and mortality. Nonetheless, the magnitude of observed body size changes is broadly consistent across temperature-size studies. For example, spatial-temperature trends in the maximum species-level lengths for 74 Mediterranean fish species were also ~5% per 1°C (van Rijn et al., 2017). Likewise, using location-independent, species-specific maximum lengths Fernández-torres et al. (2018) found that coastal bony fish species decrease in maximum species length on average by 3.26% per 1°C temperature-across-space. Finally, Cheung et al. (2013) modelled that under the high emission scenario changes in the growth and species composition of demersal fish assemblages will lead to 14%–24% decrease in maximum weight of this group by 2050, with coastal areas most highly affected. About half of this predicted change was because of changes in species composition and half from intra-specific decrease in the maximum body size.

Despite the complexity of disentangling processes operating at physiological and ecological levels, the emergence of the general and strong decrease in mean community body size with temperature-across-space reported here attests to the general principles of temperature impacts on fish community size structure. However, while general trends are clear in our data, large variation of datapoints around the predicted means (Figure 3) indicates that on local or even regional scales, temperature may be a weaker predictor of fish body sizes compared to other influences, such as primary production or human impacts. O'Gorman et al. (2017) found that when primary production increases with temperature, the expected 'steepening' of size spectrum slopes was negated or obscured. Likewise, primary production explained positive maximum species-specific fish length trends with increasing latitude better than SST (although SST was still significant) across global shallow-water marine fish (Fernández-torres et al., 2018). In the present study, we have not explicitly accounted for other ecological drivers that affect growth and size, such as primary productivity or food nutritional quality changes (Ho et al., 2010). These factors certainly contribute to size changes, although in many cases are linked directly or indirectly to temperature. While some of these factors were captured by the spatial random effect of grid cell included in our models, further investigations on possible temperature and primary production interactions are needed.

Intensive fishing is also likely to have large effects on community sizes (Blanchard et al., 2005), potentially even reversing broad scale ecological temperature-size rules (Fisher et al., 2010). Excluding commonly fished species from our dataset did not change the direction or overall magnitude of our results (Table S3), suggesting that impacts of fishing in our analyses are likely to be small compared to that of the large temperature gradient investigated. Moreover, human population density, and hence expected fishing pressure, is very low across much of northern Australia where fish body sizes were smallest. The footprint of exploitation on the body size gradient around the Australian coast would be expected to show reductions in body size in the south-eastern portion of the country, rather than the northern. This suggests that the gradient we observed (i.e. increases in mean body size towards the southern latitudes where communities were sampled at lower temperatures) is more likely conservative when not accounting for fishing impacts.

One of the unexpected findings of this study was that piscivores, classified here as fishes consuming fish or cephalopod prey, were the only guild to increase in mean size with increasing temperature (albeit slightly, by 1%). This trend held even when fished species or chondrichthyans were excluded (Table S4). The absence of a negative temperature-size trend for fish piscivores over this large spatial-temperature gradient might be explained, at least in part, by the metabolic theory of ecology. At lower temperatures, active ectothermic predators are expected to have decreased foraging efficiencies compared to endothermic competitors (Grady et al., 2019), which may limit the body sizes ectothermic predators can reach in cold waters. The diversity of top predators in marine ecosystems shifts from being dominated by ectotherms (fish and sharks) at warm temperatures to endotherms (marine mammals and birds) at cold temperatures (Cairns et al., 2008; Grady et al., 2019). As piscivorous seabirds and marine mammals also increase in body size along spatial thermal gradients (Olson et al., 2009; Torres-Romero et al., 2016) it is possible that including these taxa would lead to an increase in the mean body size for the piscivore guild as a whole as temperature decreases, making piscivores more consistent with the other three trophic guilds. An alternative explanation, which may warrant future study, is the potential role of intraguild predation. Lower relative abundance may imply reduced competition, and thus increased feeding rates (and sizes) for piscivores (Uiterwaal et al., 2023). For the remaining three trophic groups (invertivores, herbivores and planktivores) the rates of decrease in body size with increasing temperature were similar, ranging 4%–6% per 1°C, suggesting that temperature-driven changes in foraging efficiencies may not vary between these guilds as greatly as for piscivores, or that other compensatory energetic mechanisms are at play.

In addition to exploring community body size changes across spatial-temperature gradients, we also investigated changes in community trophic composition (relative abundance) with temperature. We found a strong, positive trend in planktivore abundance with temperature, increasing from ~20% of the total abundance in temperate waters to ~50% in the tropics. In contrast, invertivore abundance decreased from nearly 60% in the coolest waters to ~20% in the tropics. Our findings are consistent with other studies showing an increase in herbivory and a decrease in invertebrate consumption with increasing temperature or decreasing latitude (see Edgar et al., 2017; Knight et al., 2021; Vejříková et al., 2016; Zhang et al., 2020 for potential explanations and hypotheses for why this is the case).

By exploring trends in trophic guild abundances across space, we were able to quantify how much of the trend in mean community body size was due to temperature-size trends within the trophic guilds versus changes in the community trophic guild composition. Overall, most of the change in community-level mean body size was driven by temperature-size relationships within guilds rather than changes in guild composition. This supports the idea that general physiology plays a major role in determining biogeographic patterns in fish body sizes, and therefore on local ecology. Nonetheless, the contribution of guild composition to the overall community body-size trend was not negligible, especially in tropical waters (Figure 4c). The differences in mean sizes between trophic guilds are greater in the tropics than temperate ecosystems (Figure 4a). Thus, switching the abundance of one trophic guild for another will have a bigger impact on community mean size in tropical rather than temperate ecosystems.

One important caveat is that although we explored the contribution of trophic guild to the mean community body size, we did not decompose the contribution from changing species composition within the trophic guilds. Cheung et al. (2013) suggested that half of the predicted 'shrinking' in maximum demersal fish body sizes could be driven by species redistributions, which are likely to be substantial. Since mean size relationships with temperature may be either positive or negative at the species-level (Audzijonyte et al., 2020; Solokas et al., 2023), decreasing mean body sizes within trophic guilds are likely to be largely influenced by changing species composition within trophic guilds. Another consideration is that we investigated temperature-body size relationships across space, and not in a fixed location over time. This was because we lacked sufficient time-series data to undertake detailed analyses across all parts of the temperature gradient (our dataset contained lower temporal replication in warmer water tropical locations). While space-for-time substitution can provide insights into possible future ecosystem states (Blois et al., 2013; Elmendorf et al., 2015), we suggest caution when inferring future trajectories from our results, as local-scale temporal processes that may exacerbate or obscure spatial trends (Damgaard, 2019) were not captured by our analyses. For example, although spatial and temporal intra-specific changes in mean sizes of temperate reef fish species were qualitatively similar in Audzijonyte et al. (2020), temporal size changes occurred 10 times more rapidly than those over an equivalent temperature-across-space gradient. Even if temporal changes in the future were not as rapid as that, our results still imply that a 1°C increase in temperature (well within the range predicted under the CMIP6 RCP8.5 scenario; McBride et al., 2021) could result in a 5% or larger decrease in mean individual length, and a much greater decrease in the mean individual weight of a fish community at any given location.

Using extensive field observational data, we have shown that community-level mean reef fish body size decreases with increasing temperature. While the physiological mechanisms underpinning temperature-size relationships remain debated (Audzijonyte et al., 2019; Pauly, 2021; Verberk et al., 2016) we suggest that ecological processes also contribute to realised mean-size temperature trends in fish communities. Given the dependence of most physiological rates and ecological interactions on individual body size and temperature (Ohlberger, 2013) understanding the strength and direction of feedback loops between temperature, size and ecology is a high priority. Overall, these mean body size trends and temperature-driven shifts in the community trophic composition suggest that widespread changes throughout this century in reef fish community size structure and composition are likely, with potentially important effects on ecosystem functioning and human society. For example, body size shifts can impact persistence of species (Hilbers et al., 2017; Olden et al., 2007; Reynolds et al., 2005) and ecosystem stability (Blanchard et al., 2009; Emmerson & Raffaellit, 2004; Plank & Law, 2012). Temperature-driven changes in community composition can alter ecosystem states, as is observed through the redistribution of herbivorous fishes with warmer waters (Holland et al., 2020; Pecl et al., 2017; Vergés et al., 2019). Likewise, ongoing and potentially similar temperature-size and temperature-composition shifts in plankton communities (Sommer et al., 2017; Zohary et al., 2021) may propagate from the base of marine food-webs to consumer size and trophic compositions (Carozza et al., 2019), with considerable effects on fish habitat and prey suitability (Heneghan et al., 2023; Santana-Falcón et al., 2023). Changes in fish sizes ultimately affect human populations through the impact on fisheries catch composition and biomass (Audzijonyte et al., 2013; To & de Mitcheson, 2009), which is critical considering the importance of fish in feeding world's population. Moreover, given the direct links of fish body sizes to other ecosystem services such carbon cycling, understanding how size-temperature patterns emerge from interacting physiological, ecological and evolutionary processes is essential to predict and help mitigate climate change impacts that are and will continue to impact marine ecosystems.

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AUTHOR CONTRIBUTIONS

ARC, AA, JLB and RDS wrote the first draft of the manuscript. RDS, GJE and NB designed and performed the surveys. ARC, AA, SW and JLB performed the statistical analysis. All authors contributed substantially to manuscript revisions.

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PEER REVIEW

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DATA AVAILABILITY STATEMENT

Original Reef Life Survey underwater visual survey datasets are available from the Integrated Marine Observing System through the Australian Open Data Network portal (https://portal.aodn.org.au/search). The final datasets and code used in this analysis are available through the code depository at https://github.com/amroco/Coghlan-et-al.-2023_reef-fish-mean-size, with the final datasets further archived at Zenodo: https://doi.org/10.5281/zenodo.10476705.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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