

Large but uneven reduction in fish size across species in relation to changing sea temperatures

Itai van Rijn¹  | Yehezkel Buba¹ | John DeLong² | Moshe Kiflawi^{3,4} | Jonathan Belmaker^{1,5}

¹School of Zoology, George S. Wise Faculty of Life Sciences, Tel Aviv University, Tel Aviv, Israel

²School of Biological Sciences, University of Nebraska-Lincoln, Lincoln, NE, USA

³Department of Life Sciences, Ben-Gurion University, Be'er Sheva, Israel

⁴The Interuniversity Institute for Marine Sciences of Eilat, Eilat, Israel

⁵The Steinhardt Museum of Natural History, Tel Aviv University, Tel Aviv, Israel

Correspondence

Itai van Rijn, School of Zoology, George S. Wise Faculty of Life Sciences, Tel Aviv University, Tel Aviv, Israel.
Email: itaivanrijn@gmail.com

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Abstract

Ectotherms often attain smaller body sizes when they develop at higher temperatures. This phenomenon, known as the temperature–size rule, has important consequences for global fisheries, whereby ocean warming is predicted to result in smaller fish and reduced biomass. However, the generality of this phenomenon and the mechanisms that drive it in natural populations remain unresolved. In this study, we document the maximal size of 74 fish species along a steep temperature gradient in the Mediterranean Sea and find strong support for the temperature–size rule. Importantly, we additionally find that size reduction in active fish species is dramatically larger than for more sedentary species. As the temperature dependence of oxygen consumption depends on activity levels, these findings are consistent with the hypothesis that oxygen is a limiting factor shaping the temperature–size rule in fishes. These results suggest that ocean warming will result in a sharp, but uneven, reduction in fish size that will cause major shifts in size-dependent interactions. Moreover, warming will have major implications for fisheries as the main species targeted for harvesting will show the most substantial declines in biomass.

KEYWORDS

climate change, ectotherms, fish growth, fisheries, temperature–size rule

1 | INTRODUCTION

Ectotherms exposed to increasing temperatures often display smaller size at maturity and reduction in maximal body size. Known as the “temperature–size rule” (TSR), this phenomenon has been observed in a wide range of organisms including unicellular bacteria and protists, plants, and ectothermic animals (Atkinson, 1994). Due to the generality of TSR across many organisms, populations experiencing warming are expected to respond with a reduction in size (Gilbert et al., 2014; Yvon-Durocher, Montoya, Trimmer, & Woodward, 2011). The TSR is expected to have direct repercussions for humans by reducing the yield of consumed marine fishes. For example, Cheung et al. (2013) predicted a 14%–24% global reduction in fish size between 2000 and 2050 due to warming oceans. A comparable decline was observed when analyzing historical data on commercial

fish species in the North Sea (Baudron, Needle, Rijnsdorp, & Tara Marshall, 2014). To date, however, few studies have empirically measured the magnitude of the TSR in natural fish populations (Ohlberger, 2013). Moreover, the mechanisms underlying this phenomenon are still under considerable debate (Atkinson, Morley, & Hughes, 2006). Assessing the generality of how fish body size responds to warming, along with patterns of interspecific variation in this relationship, can lead to a better understanding of the processes that give rise to the TSR in nature.

Although the TSR is widely documented, the physiological mechanisms driving size reduction are not yet fully understood (Atkinson et al., 2006). In organisms that show indeterminate growth (e.g., fishes), maximal size may reflect the balance between the supply and demand of limiting resources. Hence, variation in the temperature dependence of supply or demand can influence maximal size

(DeLong, 2012). For example, oxygen supply has been shown to limit maximal body size of aquatic organisms (Forster, Hirst, & Atkinson, 2012; Hoefnagel & Verberk, 2015). For fishes, oxygen uptake rate (i.e., supply) depends on gill surface area whereas the demand is a function of body mass. As individuals grow, their gill surface area to body mass ratio decreases. Therefore, individuals may approach the size where they can no longer acquire the oxygen needed for maintaining their metabolic demands (Pauly, 1979). As warmer waters result in a higher metabolic rate and thus a higher demand for oxygen (Clarke & Johnston, 1999), oxygen limitation will occur at smaller body size and the asymptotic size will decrease. Although oxygen availability decreases with temperature, this change is small relative to the elevated demand for oxygen for a given temperature range (Verberk, Bilton, Calosi, & Spicer, 2011).

In nature, individuals can be expected to face oxygen limitation in the warmest season when metabolic rate is at its peak and oxygen saturation is lowest. This suggests that the maximum annual temperature, as opposed to the minimum or the mean, will be the best predictor of fish maximal size. This prediction contrasts with alternative explanations for the TSR, which are based on adaptive plasticity of body size (Angilletta, Steury, & Sears, 2004). According to these studies, maximal body size depends on size at maturation. Maturing at smaller sizes has a selective advantage in warmer water, where gonadal growth is faster and early maturation can prolong the breeding season and enable multiple reproductive events per season. If adaptive plasticity is behind the TSR, size will be determined by the entire annual temperature profile and hence the mean, rather than the maximal, temperature can be expected to be a better predictor of fish size.

The generality of TSR in aquatic organisms, coupled with physiological models of growth (Cheung et al., 2013), suggests that warming sea conditions will reduce the body size of many fish species. However, while it is unlikely that all species will react identically to the changing temperatures, it is unclear which factors will govern interspecific variation in this response. Under the oxygen limitation hypothesis, activity level and metabolic demand may influence species' responses to increasing temperature. As temperature increases, the difference between resting and active metabolism increases (Claireaux & Lagardère, 1999). Coupled with the fact that the field metabolic rate is generally higher in more active fish species (Dwyer, Stoffels, & Pridmore, 2014; Killen, Atkinson, & Glazier, 2010), we predict that for these species, the metabolic demand will increase more quickly than for less active fishes. Hence, under the oxygen limitation explanation of TSR, one would expect larger reduction in size with temperature in active species compared to those with lower activity levels.

Apart from temperature, additional factors which may affect fish size need to be considered when examining TSR in natural fish populations. First, food availability can potentially shape the growth of fish in their natural habitat. However, only a few studies have tested for food availability effects on fish in the wild (Barrett, 1999), often examining growth at early life stages but not maximal length (Jones, 1986). A second factor which may affect maximal size is fishing.

Fishing can directly alter size-specific mortality (Bianchi et al., 2000; Shin, Rochet, Jennings, Field, & Gislason, 2005). In addition, over the long term, fishing was found to affect life-history traits of the harvested populations, such as reduction in reproductive size (Sharpe & Hendry, 2009).

Finally, there are two species-specific factors that may affect the shape of size–temperature relationships: body size and climatic affinity. Evidence for size-related variation in the response to warming was found in aquatic Metazoans (Forster et al., 2012). This was attributed to increased challenges in meeting oxygen needs for larger organisms, which leads larger species to mature at relatively smaller sizes at higher temperatures (Forster et al., 2012). However, this effect was shown on small aquatic organisms, and this process may not operate in larger taxa such as fishes. Climatic affinity may result in evolutionary adaptations related to oxygen supply, such as gill structure or the degree of plasticity in the gills' response to local conditions (Nilsson, 2007). Thus, it is possible that species from colder regions will be more limited in their ability to cope with elevated temperatures compared to species from warmer conditions.

Here, we use the Mediterranean Sea as a model system to quantify the magnitude of the TSR across fish populations in their natural habitat, and to examine mechanisms driving variation in the TSR among species. The Mediterranean presents strong temperature gradients (Bricaud, Bosc, & Antoine, 2002; Marullo, Nardelli, Guarracino, & Santoleri, 2007), allowing us to explicitly examine the relationship between temperature and body size. Moreover, the Mediterranean has a diverse fish assemblage (Albouy et al., 2015) and environmental conditions (i.e., temperature and productivity) vary at a relatively small area, making local adaptations less likely. Together, these properties make the Mediterranean an ideal case study for testing variation in the TSR across populations in their natural habitats.

2 | METHODS

2.1 | Data collection

We extracted data on the size of Mediterranean fish species from publications found using the search term “Mediterranean fish size” on ISI Web of Knowledge (<http://apps.isiknowledge.com>) database in June 2015, resulting in over 6,000 publications. These publications were screened, and only publications that included information on the size of fish species from the Mediterranean, black sea and eastern Atlantic Ocean (including the coasts of Portugal, Spain and the Canary Islands) were retained. Relevant publications included studies of fish growth, allometry, reproduction, and diet. During the process of data extraction, additional publications were identified from the citation list of the scanned publication and added if appropriate. Additional data were added from fisheries-related reports on fish surveys and fish community structure.

We extracted the following data from each publication: geographic sampling coordinates, sample size (number of individuals from each species), and observed maximal length of each species. We used maximal length and not mean length because the latter is

strongly influenced by the population age structure and fishing pressure. In contrast, maximal size represents a trait of individuals within the local population, and in large samples, we expect to observe large individuals even when fishing is present.

We refined the data according to considerations of sample size and temperature range. We set the minimal number of data points for a single species (each representing a different location) to five. Additionally, we only considered species whose observations in the data set spanned over 3°C in average annual sea surface temperature. Also, we identified and removed six large pelagic species that show large-scale migration, as the yearly temperature profile at the capture site is unlikely to be representative of the temperature experienced by an individual (see Appendix S1). A total of 74 species were retained for the final analyses, and the number of data points per species ranged from 5 to 57 (mean of 16). A summary table of the data used in these analyses can be found in Appendix S3.

2.2 | Environmental variables

We extracted environmental data including maximum, minimum, mean, and range of monthly sea surface temperature (SST) and chlorophyll a concentrations from the Bio-ORACLE database (Tyberghein et al., 2012). Temperature measurements were expressed as inverse temperature $1/k_B T$ units where k_B is the Boltzmann constant (8.6×10^{-5} eV/K) and the temperature is given in Kelvin. This is due to the expected exponential effect of temperature on biological reactions, and is thus preferable to using temperature directly when modeling physiological responses to changing temperatures (Brown, Gillooly, Allen, Savage, & West, 2004).

2.3 | Species traits

We considered three species-level traits that may affect species' responses to temperature: body size, activity level, and climatic affinity. For determining the common size of the species, we used data from Albouy et al. (2015). Activity levels were estimated using the aspect ratio of the caudal fin, which is a good indicator of activity and swimming speed in fishes (Palomares & Pauly, 1998). Higher aspect ratios indicate higher activity levels. The aspect ratio was calculated from at least three photographs in which the caudal fin was adequately spread and in good condition. These were found in the FishBase (<http://www.fishbase.org>) database and other online resources. Measurements were made using IMAGEJ software (Rasband, W.S., IMAGEJ, U. S. National Institutes of Health, Bethesda, Maryland, USA, <http://imagej.nih.gov/ij/>, 1997–2015). Aspect ratios vary within families and are not strongly phylogenetically conserved (Figure S2).

To characterize the climatic affinity of a species, we used distribution data obtained from the Global Biodiversity Information Facility (GBIF <http://www.gbif.org/>). We considered observations from the Mediterranean and the Atlantic Ocean. We visually removed anomalous observations outside known species range. To characterize the climatic affinity, we recorded the minimal monthly temperature in which each species was found across its range. This measure

is expected to be a predictor of the affinity to cold environments. In contrast, maximal monthly temperature is bounded by the high temperature in the Levant, thus providing little variation among species, while the mean temperature is less indicative of thermal limits and heavily depends on the distribution of occurrence records.

We considered two additional factors that may potentially alter the observed size–temperature relationship. First, we considered species vulnerability to fishing, as more susceptible species may show greater variation in maximal size due to higher fishing mortality in some locales relative to others. We used the index of species vulnerability to fishery suggested by Cheung, Pitcher, and Pauly (2005) and obtained from FishBase (<http://www.fishbase.org>). In addition, to account for species location in the water column, with species which live deeper in the water column less likely to be affected by sea surface temperature and probably experiencing a shallower overall temperature gradient, we considered the minimal depth in which the species is observed (obtained from Albouy et al., 2015). Lastly, we considered the temperature range over which the species was observed in our data, as smaller ranges may statistically lead to smaller size responses.

2.4 | Statistical analysis

We first used linear mixed-effect models (LME) to find the best set of environmental conditions and species traits influencing maximal fish size. The response variable was the log-transformed ratio of a species maximal length in a given study divided by the maximal size for that species across its range. The process of finding the best LME consisted of two stages. First, we asked which environmental measure is the best predictor of maximal size. We compared models with minimum, mean, and maximal SST (expressed as $1/k_B T$) and productivity (measured as chlorophyll a concentration in mg/m^3). SST and productivity were mean-centered for each species (i.e., expressed as the deviation from the mean across all the sites at which a species was observed). Species were set as a random effect in all of these models, allowing for variation in the intercept and slope for each species.

After establishing the best environmental predictors, we then incorporated species traits. We started with a preliminary analysis aimed at establishing the best random-effect structure for the model. We constructed models that included all fixed effects including: aspect ratio (AR) of the caudal fin, minimal temperature in the distribution of each species, minimum depth, and common size of each species. We then compared two models with different random-effect structures: (i) species as random effect allowing for variation in the intercept only; (ii) species as random effect allowing for variation in the intercept and the slope in relation to temperature. Using the selected (lowest AIC) random-effect structure, we then compared models with different fixed effects. In all of these models, *maximal SST* was used as a fixed effect. We then compared models with an interaction of *maximal SST* with either aspect ratio, common length, minimal temperature, and all combination of these three (see Table 2). In order to confirm that species traits are affecting the size–temperature relationship regardless of phylogenetic

relationships, we examined models with species nested within families. Mixed models were performed using “lme” function in the “nlme” R package. Model comparison was made using the Akaike information criterion (AIC) and the Bayesian information criterion (BIC) that penalizes complex models more strongly. Model quality was evaluated by the marginal R^2 (R^2_m ; the proportion of the variation explained using fixed effects only), and conditional R^2 (R^2_c ; the variance explained by both fixed and random factors) (Nakagawa & Schielzeth, 2013).

Due to the complexity of visualizing and interpreting mixed-effect models containing multiple interactions term, we also took a meta-analytical approach. Here, the slope of the linear regression of size (relative to maximal size of each species) against temperature ($Max\ SST$, expressed as $1/k_B T$) for each species was used as the effect size. We used the standard error of the slope estimate as a weighting factor, indicative of both the quality of the fit and the sample size. We did not want to use the slope estimates obtained from the mixed-effect models because in these models estimated slopes are influenced by other species.

We compared meta-analytical models following a model selection approach using AIC scores. As with the mixed-effect models, we first examined models with the three variables: aspect ratio, common length, and minimal temperature within the geographic distribution of each species. These models included each variable alone and all the combinations of the three. After identifying the best model, we examined models with the additional independent variables vulnerability to fishing, minimal depth where the species is observed, and temperature range of species occurrences. We added these to the best model, each variable by itself and in combinations of all three. We used random-effect analyses (using the DerSimonian–Laird estimator) because of the expected difference between species in their reaction to temperature. Meta-analytical models were estimated using the “rma” function in the “metafor” R package.

3 | RESULTS

We collected data from over 341 publications on fish growth and size over multiple locations across the Mediterranean. These data include 74 fish species with considerable life-history variation, from 0.05-m-long bottom-associated Gobies to 3-m-long pelagic tunas. Sampling locations were evenly distributed geographically, with good representation of the entire Mediterranean basin and its associated temperature gradient (Figure 1). Most of the data are relatively recent, with the mean sampling year 2002 ($\pm 5.8\ SD$).

We found that the best model for predicting maximal length at a site included the maximal sea surface temperature (*maximal SST*) and *chlorophyll a* concentration (Table 1). Removing *chlorophyll a* from the model resulted in an almost equally favorable model ($\Delta AIC = 0.3$ $\Delta BIC = -4.7$). We therefore concluded that maximal SST is the best predictor of maximal size in our data.

After identifying maximal SST as the best environmental predictor, we incorporated species traits to explore mechanisms

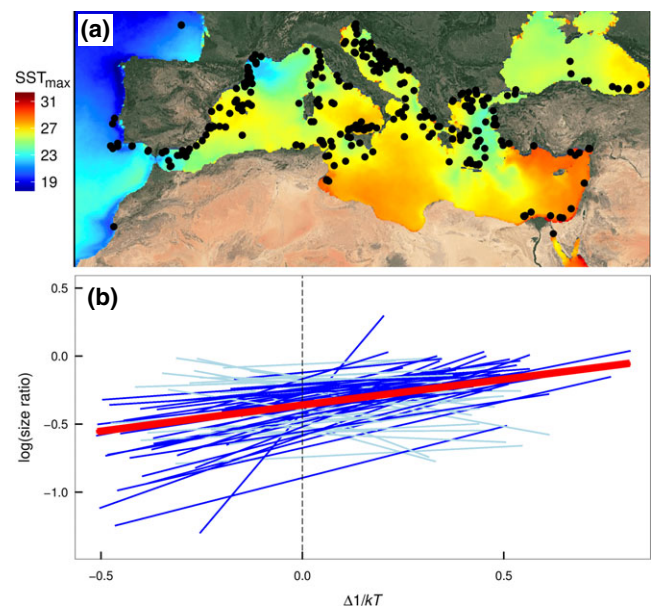


FIGURE 1 Reduction in maximal fish size with maximal sea surface temperature (SST) across the Mediterranean Sea. (a) Location of studies included in the data set overlaid on a maximal SST map of the Mediterranean Sea. (b) Slopes of the observed size (relative to maximal size for each species, log-transformed) plotted against maximal SST. Temperatures are given in $1/k_B T$ ($k_B = 8.6 \times 10^{-5}$ eV/K, T in Kelvin). Note that higher values indicate lower temperatures. Blue (thin) lines are individual species slopes and the red (bold) line is the overall slope estimated by the meta-analysis [Colour figure can be viewed at wileyonlinelibrary.com]

associated with interspecific variation in the response to maximal SST. We found that the best random-effect structure allowed interspecific variation in both the slopes and intercept ($\Delta AIC > 6$ compared to random intercept only). Comparing fixed effects resulted in two models having almost equal support ($\Delta AIC = 1$; Table 2). Both models included *maximum SST*, *fish activity level*, and *common length* of the species; the second best model additionally included the *minimum depth* at which the species is found. The results were very similar when phylogenetic relatedness was accounted for by nesting species within families (Table S1).

The meta-analysis confirmed an overall reduction in maximal size with *maximal SST* with a mean slope of 0.39 ($SE = 0.04$, $p < .0001$) (Figure S1), which corresponds to a reduction of $\sim 5\%$ in the length of individuals per 1°C warming over this temperature gradient (Figure S1).

Including species traits as moderators in the meta-analysis showed that the interspecific variation in species responses to temperature was best explained by a model including *activity level*, *common length*, and *minimal depth* in which the species is observed ($R^2 = .61$). *Activity level* had the strongest effect size (Table S2, Figure 2). This is in agreement with the results of the mixed-effect modeling. The four best models included *activity level*, and models without *activity level* had much less support ($\Delta AIC > 16$). Adding climatic affinity resulted in a less favorable model ($\Delta AIC = 2.3$). Lastly, we examined additional predictors that may bias the observed relationship. These included *vulnerability to fishing*, meant to rule out the

TABLE 1 Model comparison results for mixed-effect models with the log ratio of size to maximal size per species as the response variable and temperature (maximal, mean, and minimal SST [expressed $1/k_B T_{\text{Kelvin}}$]) and productivity (chlorophyll a as mg/m^3) as predictor variables

| Model | df | ΔAIC | AIC weight | ΔBIC | BIC weight | R^2_m | R^2_c |
|--------------------------------|----|--------------------|------------|--------------------|------------|---------|---------|
| Max SST \times chlorophyll a | 7 | 0.0 | 0.54 | 5.9 | 0.05 | 0.09 | 0.35 |
| Max SST | 6 | 0.3 | 0.46 | 0.0 | 0.95 | 0.09 | 0.35 |
| Mean SST | 6 | 26.3 | <0.001 | 54.1 | <0.001 | 0.06 | 0.32 |
| Chlorophyll a | 6 | 36.7 | <0.001 | 135.2 | <0.001 | 0.01 | 0.28 |
| Min SST | 6 | 40.6 | <0.001 | 142.7 | <0.001 | <0.01 | 0.26 |

The best models are those with the lowest ΔAIC and ΔBIC and the highest AIC and BIC weights. Model fit is evaluated using the variance explained without (R^2_m) and with (R^2_c) random effects.

TABLE 2 Model comparison results for mixed-effect models with the log ratio of size to maximal size per species as the response variable

| Model | df | ΔAIC | Weight | R^2_m | R^2_c |
|------------------------------------------------------------------------------------------------|----|--------------------|--------|---------|---------|
| Max SST + Max SST \times AR + Max SST \times Common length | 8 | 0 | 0.452 | 0.10 | 0.37 |
| Max SST + Max SST \times AR | 7 | 1 | 0.2804 | 0.09 | 0.37 |
| Max SST + Max SST \times AR + Max SST \times Common length + Max SST \times Minimum temp | 9 | 2 | 0.168 | 0.09 | 0.38 |
| Max SST + Max SST \times AR + Max SST \times Minimum temp | 8 | 3.3 | 0.09 | 0.09 | 0.38 |
| Max SST | 6 | 8.5 | <0.01 | 0.08 | 0.37 |
| Max SST + Max SST \times Minimum temp | 7 | 10.1 | <0.01 | 0.08 | 0.37 |
| Max SST + Max SST \times Common length | 7 | 10.5 | <0.01 | 0.08 | 0.37 |
| Max SST + Max SST \times Minimum temp + Max SST \times Common length | 8 | 12 | <0.01 | 0.08 | 0.37 |

Maximal temperature at the site (Max SST) was always used as a predictor along with different combinations of species traits: AR—aspect ratio of the caudal fin as a proxy for activity level, Common length—the common length of the species, Minimum temp—minimal temperature at the distribution range of the species, an estimate of climatic affinity. Species are modeled as a random effect allowing for variation in the slope and intercept of Max SST across species. Model fit is evaluated using the variance explained without (R^2_m) and with (R^2_c) random effects.

effect of fishing pressure on among-species changes in body size, and the observed temperature range for each species across the data set, included because species with larger ranges may display larger temperature responses. Adding these variables resulted in less favorable models ($\Delta\text{AIC} > 2$).

Based on the best meta-analysis model, we estimated that an active (aspect ratio of 5), average-size (TL = 0.36 m) shallow-water species will show a reduction of about 10% with an increase of 1°C in temperature (Figure 3). For comparison, a less active species (aspect ratio of 0.5) is predicted to decrease by less than 10% over the same temperature gradient.

We note that six large pelagic species, which migrate across the Mediterranean, were removed prior to the analysis. These species all have high aspect ratios (> 5). In contrast to the positive relationship

between aspect ratio and the magnitude of the temperature effect, these active species show little to no response to temperature (Figure 2).

4 | DISCUSSION

The effect of increased temperature on body size reduction (the TSR) is considered a widespread phenomenon with important consequences for future fishery yields (Baudron et al., 2014; Forster et al., 2012). Studying natural fish populations, we observed a reduction in maximal size with elevated temperatures. We found that species traits, in particular their activity level, are strongly related to the degree at which fish body size is affected by temperature. Our results indicate that active large species will show the strongest size reduction in response to warming temperature, with large implications for ecosystem structure and future fishery yields.

Annual maximum sea surface temperature was the best predictor of the observed variation in size (Table 1). This strong association is in agreement with the idea that oxygen limitation constrains maximal size (Atkinson et al., 2006) and undermines the adaptive plasticity hypothesis (Angilletta et al., 2004). In the heat of summer, fish metabolism is expected to be at its maximum and oxygen can restrict growth if gills surface area is not sufficiently large to meet metabolic demands (Pauly, 1979). An alternative hypothesis explaining the TSR relates to an adaptive response of individuals to environmental conditions. This will mainly affect the size at which maturation occurs. Long periods in which temperatures are suitable for growth and reproduction are expected to lead to maturation is smaller size and hence overall smaller maximal size (Angilletta et al., 2004). Our finding that mean temperature is unfavorable for predicting maximal size undermines this explanation as the length of the growing and reproduction period is expected to be more strongly associated with mean than maximum temperature. Additional support for oxygen limitation as a driver for TSR in fish is the finding that active species show greater reductions in body size with increasing temperature (Figure 2), which is consistent with stronger temperature dependence in oxygen demand for these species.

Our data are consistent with widespread reductions in fish body size at warmer temperatures across the Mediterranean. However, it is also possible that individual fish move toward colder regions at

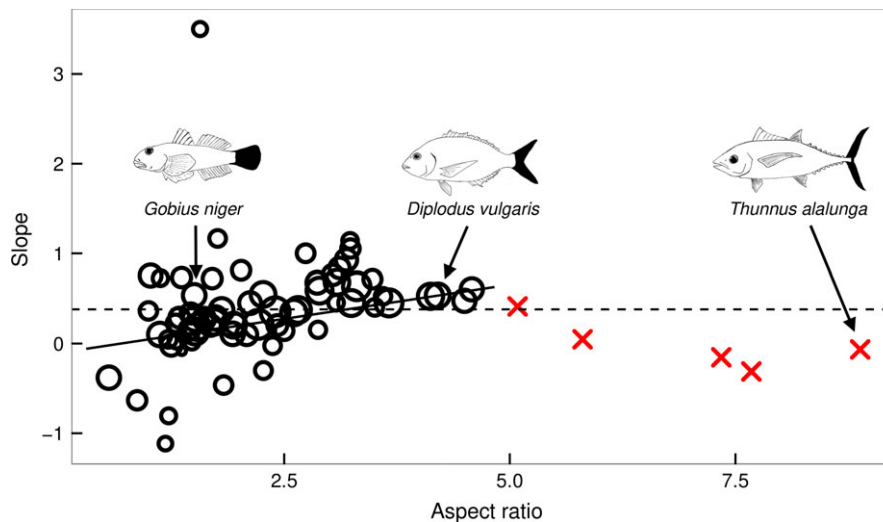


FIGURE 2 Interspecific variation in temperature dependence of body size as a function of aspect ratio. The slope of the linear regression of maximal body size in relation to temperature for each species is plotted against aspect ratio, a proxy for activity level. The sizes of dots are proportional to the inverse of the standard error in the slope estimation (i.e., larger dots have greater uncertainty). The mean overall reduction across species ($N = 74$) is plotted as a dashed line. Low aspect ratio values (<2.5) represent less active and/or bottom-associated species (e.g., gobies); higher aspect ratio values (~ 2.5 – 5) represent benthic-pelagic and more active species (e.g., sea breams); aspect ratio values >5 are pelagic species. Large pelagic species marked with crosses were not included in the meta-analysis (see Methods) and show weak response to temperature [Colour figure can be viewed at wileyonlinelibrary.com]

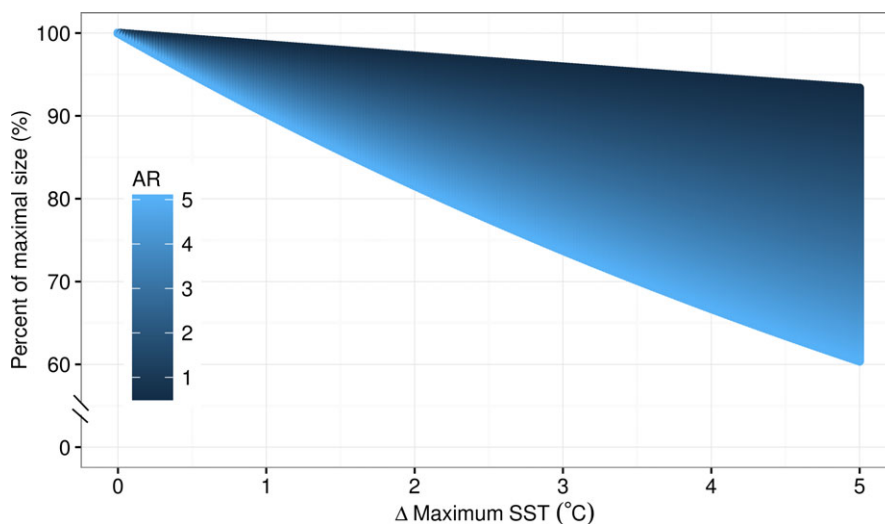


FIGURE 3 Predicted reduction in body size with increased temperature for species with different activity levels (estimated using the caudal fin aspect ratio, AR). Change in size is expressed as percentage of the maximal length observed for each species. Prediction is based on the best meta-analysis model including aspect ratio, common size, and minimum depth of each species as predictors. Predictions are shown for the mean values of size and minimum depth in our data ($\mu_{\text{size}} = 35$ cm, $\mu_{\text{minimum depth}} = 20$ m) [Colour figure can be viewed at wileyonlinelibrary.com]

larger sizes. This possibility may hold for pelagic species that are known to cover large distances in their migration routes. In these migratory species, larger individuals may avoid warmer areas in certain seasons or limit their distribution to overall cooler regions. Indeed, we found no evidence of size reduction in large pelagic species (Figure 2). However, for most benthic and other relatively sedentary fishes, it is less likely that individuals will migrate long distances to colder areas. In particular, migration is expected to be harder for benthic and demersal species in the Mediterranean, where the continental shelf is relatively narrow. We note, however, that direct temperature effect on body size and temperature avoidance is not mutually exclusive and depends on the scale of individual fish movement.

The results of this study demonstrate the effect of temperature on maximal fish size across a spatial gradient. One might also consider the temporal effect of future warming on fish size. The validity of using a space-for-time substitution to predict future body size would depend on having a mechanistic underpinning of the pattern. Our data suggest that physiological oxygen limitation is a driver of the TSR in fishes, so consideration of future oxygen levels may be important for predicting size changes. Additional processes may operate to shape the future body size distribution of species, including change in spatial distributions, community turnover (Cheung et al., 2009, 2013), and changes in other life history such as mortality (Djabali, Mechailia, Koudil, & Brahmi, 1994; Pauly, 1980). However, our finding regarding interspecific differences in the response

to temperature will be important to consider when attempting to forecast the effects of warming on fish body size.

The finding that active species show higher reduction in body size in relation to warmer temperatures (Figure 2) has important community-level implications. When active piscivores reduce their size faster than their prey, size-based predator–prey mismatches may occur (Scharf, Juanes, & Rountree, 2000; Woodward et al., 2005). Such mismatches may be especially strong for prey species that are less active than their predators. Additionally, active species may become compromised in size-based competition for common resources compared to sedentary species (Munday, Jones, & Caley, 2001). These processes may have complex and hard to forecast effects on community structure and energy flux under global warming scenarios (Brose et al., 2012; Ohlberger, 2013).

Despite these complexities, it is clear that fisheries will suffer from a general reduction in size of the catch (Figure 3). The most pronounced size reductions are expected for large, active, nonmigratory species that are often the major source of economic revenue (e.g., the family Sparidae in the Mediterranean Sea; Spedicato et al., 2002). On the other hand, elevated temperatures will have lower impacts on benthic, less active, and often less valuable, species. Thus, fisherman may have to adapt their strategy to optimize their catch (Salas, Sumaila, & Pitcher, 2004).

Besides activity level, other traits did not contribute much in explaining the interspecific variation in response to temperature. Previous work on small metazoans found body mass to be positively correlated to size reduction in response to temperature (Forster et al., 2012). However, for fish we found a small effect of common size over the size range examined. Under the oxygen limitation hypothesis, variation in the TSR across body sizes is only expected if larger species experience more severe oxygen limitation, which would be true if their gill growth rate is slower than the growth of their somatic tissue. However, among the species in this study, gill growth rates are similar to somatic tissue growth rates (Pauly, 1979). Hence, we would not expect strong size-based variation in response to temperature among these species. We also found no evidence that the magnitude of the TSR was correlated with species' climatic affinity. Thus, pre-adaptations to warm climates may not buffer the TSR and will not allow species to maintain the same body size when faced with elevated temperature. This suggests that the reduction in body size with climate warming will influence tropical and temperate species alike.

Patterns of fish size can be shaped by food availability and fishing pressure. Patterns of fish size can be shaped by food availability and fishing pressure. However, in our data, productivity did not add explanatory power for maximal size patterns. We further believe that the patterns we report do not result from gradients in fishing pressure for three main reasons. First, there is no clear gradient in fishing pressure across the Mediterranean (Tsikliras, Dinouli, & Tsalkou, 2013; Vasilakopoulos, Maravelias, & Tserpes, 2014). Second, we found that vulnerability to fishing was not a good predictor of the observed interspecific response to temperature (Table S3). Finally, even in the presence of substantial fishing pressure, some individuals

are expected to approach their maximal physiological size, especially for short-lived species. Hence, large samples are likely to include at least some large individuals. We therefore suggest that the observed reduction of maximal body with temperature is not likely to be a result of food availability or fishing, and is best explained by temperature.

To conclude, our results confirm that warming may lead to widespread reduction in the maximal size of natural fish populations. This decrease in size will not be uniform across species or regions. Within the fast warming Mediterranean (Nykjaer, 2009), active species, an important part of the local fisheries, are expected to show the largest decrease in size, creating a strong impact on fisheries. These shifts in size distributions across species may have cascading consequences for entire marine ecosystems.

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