



Original Article

Decreases in length at maturation of Mediterranean fishes associated with higher sea temperatures

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Shapiro Goldberg, D., van Rijn, I., Kiflawi, M., and Belmaker, J. Decreases in length at maturation of Mediterranean fishes associated with higher sea temperatures. – ICES Journal of Marine Science, 76: 946–959.

Received 21 February 2018; revised 31 December 2018; accepted 15 January 2019; advance access publication 8 February 2019.

Fish size at maturation influences lifetime reproductive success and is an important parameter in managing stocks. Fish tend to reach maturity at a smaller size in warmer water; however, the generality of this pattern is a matter of controversy. The mechanisms by which temperature influences fish size at maturation are not well understood, particularly in natural populations, but may have broad implications if climate change continues to warm the seas. In this study, we use populations of 16 fish species across the Mediterranean Sea to evaluate the association between different temperature metrics and fish size at maturation, and to understand the variation among species. We found that both mean annual temperature and growing degree days (GDD) were the best supported environmental predictors of fish size at maturation. This suggests that the mechanisms affecting size at maturation may differ from those affecting maximum size, for which maximum temperature was the best predictor. Across species, we found that the effect of temperature is stronger for more active species, while other species-level predictors had limited influence. The correlation of fish size at maturation to specific temperature metrics should help fisheries and conservation programmes better predict the effects of climate change on fish populations.

Keywords: climate change, ectotherms, fish growth, fisheries, growing degree days, temperature-size rule.

Introduction

Age and size at maturation are key life-history traits (Stearns and Koella, 1986). Size at maturation influences lifetime reproductive success, especially in animals like fish who continue to grow throughout their lives and have fertility that increases with size (Stearns, 1992). Fish size at maturation is also an important parameter for stock management (Jennings *et al.*, 2001) and can be used to determine the optimal minimum capture size, to ensure that fish have the potential to spawn before being caught (Wolff *et al.*, 2015). As size at maturation influences both intrinsic population dynamics and the species' sensitivity to fishing, it is essential to understand the factors that affect it.

Ectotherms were suggested to reach maturity at a smaller size in warmer environments following a “temperature-size rule” (Atkinson, 1994); an observation that may have broad

implications if climate change continues to drive increasing sea temperatures. Yet, the generality of this rule remains a matter of some controversy (Berrigan and Charnov, 1994; Lefevre *et al.*, 2017; Pauly and Cheung, 2018). Some controlled studies support this relationship (Jonsson *et al.*, 2013), while others find that the reduction in size is limited to certain temperature ranges (Dhillon and Fox, 2004). Moreover, most studies are based on single-species experiments while the applicability of the pattern to the more complex natural environment is unclear. Importantly, where the pattern does hold, it stands to have wide-reaching implications if climate change continues to drive global (ocean) warming.

Several hypotheses have been proposed to explain how the size at maturation of fish changes with temperature. In addition to these hypotheses, phylogenetic constraints of each species may be

a significant source of variation in fish size at maturation, which would mean a large proportion of variation in size at maturation cannot be explained by environmental variables.

The first hypothesis we will consider is that fish growth is limited by oxygen supply (Portner, 2010; Pauly and Cheung, 2018). As temperatures rise, individuals require more oxygen to meet the demands of higher metabolic rates. Since gill surface area typically shows a negative allometry with body weight, oxygen demands will effectively limit maximum attainable size (Pauly, 1979). As the ratio of size at maturation (L_m) and maximum size (L_{max}) is similar across species (Froese and Binohlan, 2000), it would seem reasonable to expect that a decrease in the latter will also be manifested in the former (Pauly, 1984). Controlled experiments have shown that, within species, reduced levels of ambient oxygen lead to smaller sizes at maturation (Kolding *et al.*, 2008; Diaz Pauli *et al.*, 2017); although there is some debate as to the physiological mechanisms behind these changes (Lefevre *et al.*, 2017; Audzijonyte *et al.*, 2018). Based on the “oxygen limitation” hypothesis, we would expect maximum temperature to be the best predictor of both L_m and L_{max} , since the limit to L_{max} must be set by the upper bound of the temperatures experienced (van Rijn *et al.*, 2017).

A second alternate hypothesis is that the mechanism responsible for lowering L_m with increasing temperatures is elevated pre-reproductive growth, which is not necessarily associated with the asymptotic size. Berrigan and Charnov (1994) suggest that the explanation of the temperature-size rule in ectotherms differs for growth (size) and for development (maturity). This idea is supported by a model that assigns different energy allocation patterns for growth at various developmental stages in ectotherms (Zuo *et al.*, 2012). Under this scenario, size (and age) at maturation will be better predicted by a cumulative heat measurement that indicates the length of the development period, rather than the maximum temperature.

Finally, a third hypothesis is that food availability is the primary factor determining size at maturation (Gardner *et al.*, 2011). Assuming the time it takes the fish to reach the onset of maturation is fixed, reduced food availability would result in a lower growth rate during this period, and therefore a smaller size at maturation (Reznick, 1990). Warmer water elevates consumer metabolism, resulting in a larger demand for food (Edeline *et al.*,

2013), which may reduce food availability. In such a case, we would expect food availability and temperature to be the best predictors of fish size at maturation.

These mechanisms are not mutually exclusive; they may act individually, or combine, to affect the life-history traits of fish, including size at maturation. Each hypothesis, however, implies a different leading environmental predictor of size at maturation (Figure 1). In addition, species may differ in their responses to temperature changes based on a range of species-specific characteristics such as climatic origin, common length, trophic level, and other unique species-specific traits. Our goal is to test the possible mechanisms that underlie the temperature-size rule for L_m , both within and across multiple species in their natural habitats. We start by identifying the main environmental predictors of L_m across multiple populations of different species and then assess how these associations are influenced by species-specific traits. We use the Mediterranean as a case study since there are steep temperature and productivity gradients within a relatively small area (Bricaud *et al.*, 2002; Marullo *et al.*, 2006). By establishing how fish length at maturation varies along environmental gradients (e.g. Figure 2a) and across species, we can better predict the effects of climate change on fish stock size and quality.

Methods

Size at maturation estimates

Our main data source was the review of size at maturation of Mediterranean marine fishes (Tsikliras and Stergiou, 2014). The review contains data on the length at maturation (L_m) collected on 565 Mediterranean marine fish stocks. We extracted the following data: species name, location of sampling, sex, length at maturation (cm), and maximum length (cm). We treated each sex, within a species, as a separate unit for analysis. We removed cartilaginous fish from the data and selected only those species-sex units with data from a minimum of three different locations (populations). This left us with 16 species, comprised of 30 species-sex units, for the final analysis, with the number of distinct data locations per species sex ranging from 3 to 6 (average of 3.6). A list of species-sex units by location, including sampling year, is included in Appendix 3.

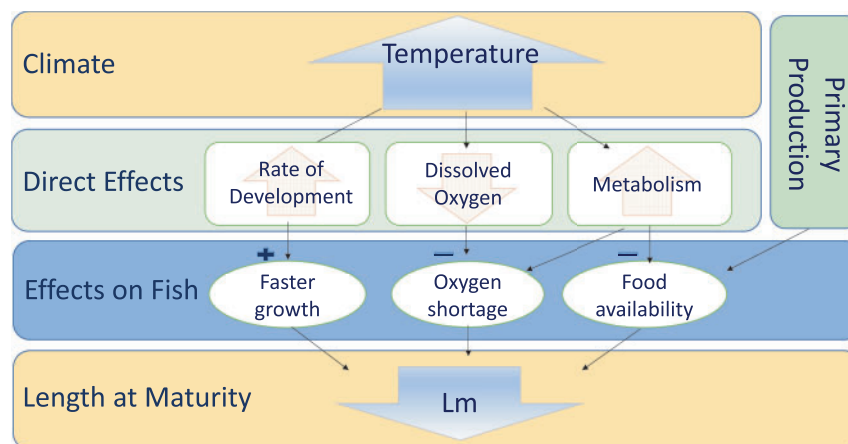


Figure 1. The major hypothesized processes linking elevated temperature to fish size at maturation. An increase in temperature directly effects the rate of development, dissolved oxygen in the water, and the fish metabolism. An additional driver is environmental food availability, e.g. quantified using primary productivity. These processes together and individually may act on fish length at maturation by stimulating faster growth, creating oxygen shortages and/or changing food availability.

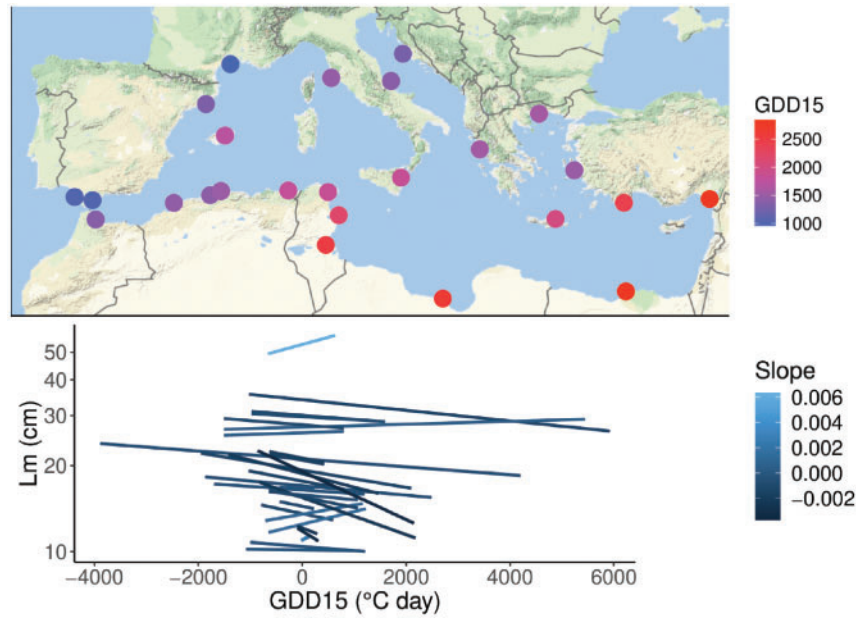


Figure 2. (a) Locations with samples used in our analysis and the associated average annual GDD15 (degree days with temperatures above a threshold of 15°C) at each location. (b) The slope of a regression of length at maturation (L_m , cm) against GDD15 (°C day) plotted separately for each species sex. The outlier positive slope belongs to *Epinephelus marginatus* (female).

Environmental predictors

We extracted environmental data for each population of each species based on the study's geographic coordinates. Where available, we used the exact coordinates of the original fish sampling. If exact coordinates were not provided, we estimated coordinates based on the description of the sampling site within the original publication.

We used FishBase (<http://www.fishbase.org>) to identify the range of depths in which each species is typically found. We then estimated species preferred depth as the 33% percentile of this range. Thus, a species observed between 30 and 90 m depth was assigned a preferred depth of 50 m. We did not use the median depth as we felt it may bias the results toward depths deeper than the typical depth for the species, as the maximum depth recorded may often represent an extreme observation. We then used that depth to extract historic temperature and productivity data, by day, in each location at each species' preferred depth from the Mediterranean Sea Physics Reanalysis (1987–2015) in 0.063° resolution (<http://marine.copernicus.eu>).

We used daily estimates of temperature at depth covering 10 years (2005–2014).

From this data, we calculated the average (across years), yearly minimum, mean, and maximum temperatures, as well as temperature range, for each location at each relevant depth. We expressed temperatures as $(1/k_B T)$, where T is temperature in Kelvin and k_B is the Boltzmann constant (8.6×10^{-5} eV/K). We used this transformation since it is commonly used for modelling physiological responses to changing temperature and some theories make a specific prediction for the slope of the relationship between size and temperature (Brown et al., 2004). Thus, using this transformation makes our results more comparable to similar studies.

We further created growing degree day (GDD) indices to sum the degree days (°C day) with (non-transformed) temperatures over a minimum threshold needed for growth. GDD has been

shown to be associated with fish length and may serve as a predictor for reproductive system development time (Neuheimer and Taggart, 2007; Venturelli et al., 2010; Neuheimer and Grønckjaer, 2012). For example, higher values of GDD may lead to earlier maturation, which may result in more resource allocation toward reproduction at the expense of somatic growth (Heibo and Magnhagen, 2005).

We calculated two sets of GDD indices, one annual GDD and one that accounts for each species' preferred depth and expected development time from spawning to first maturation ("species-specific GDD"). To create the annual GDD indices, we summed the degrees per day over a threshold of 10°C, 15°C, and 20°C across a year using sea surface temperature (extracted from Tyberghein et al., 2012). Although the threshold for growth is likely to vary between species, a minimum temperature between 10°C and 20°C is likely to be the most relevant in the temperate Mediterranean Sea.

However, as GDD measure days that allow growth, and species differ in their time to maturity, the cumulative days spent in temperatures over the minimum threshold would differ for species with different ages at maturity. Moreover, the temperature at a depth a species lives may be more relevant biologically than sea surface temperature. We therefore created a species-specific cumulative measure of GDD, for each species and its associated depth, for each location over their entire development time. To create this species-specific GDD, we summed the degrees per day over a threshold of 10°C, 15°C, and 20°C across a year using each species' preferred depth; then multiplied this annual measurement by the average number of years between spawning and first maturation for each species. We then averaged this value across all 10 years examined to establish a single GDD measurement. This more elaborate calculation of GDD may be more biologically meaningful and can thus help us understand effects of development time measured using GDD on a physiologically

relevant time scale. Nevertheless, the simplistic calculation of annual GDD (using sea surface temperature only and without accounting for age of first maturation) is highly correlated to the new GDD index (Pearson's $r = 0.91$ for GDD15, Appendix 5) and the results did not change according to the GDD index used. Thus, we show here only the results of the more biologically realistic and complex species-specific GDD. Unsurprisingly, GDD is also correlated with other temperature indices (Appendix 6). Specifically, the GDD indices were most strongly correlated to mean and maximal yearly temperature ($|r| > 0.85$) but less so to minimum yearly temperatures ($|r| > 0.4$).

Fishing pressure

Any explanation of the effect of temperature on size of exploited fish would be complicated by the effects of fishing pressure. Intense fishing contributes to decreasing size at maturation through high mortality rates and thus selection for smaller-sized individuals. The effect of fishing on size at maturation is expected to vary between species, with long-lived and large bodied species being more affected (Kuparinen and Merilä, 2007). On the population level, we developed two indices to reflect fishing pressure. The first approach is based on the total tonnage fished per commercial group, by country, along the Mediterranean coast (www.seaaroundus.org/data/#/topic/biodiversity). We categorized each species in the data into one of the following commercial groups available in the data: anchovies, cod-like, herring-like, perch-like, or scorpion fishes. We also compiled data on the Mediterranean coastline length by country based on the UN Food and Agriculture Organization data (www.fao.org), and the World Factbook (www.cia.gov/library/publications/the-world-factbook). We used Google Maps to estimate the percentage of total coastline that is on the Mediterranean Sea where that data were not specifically reported in the sources above. We divided the tonnage fished in each country by their Mediterranean coastline in kilometres to create the first fishing pressure index (fishing tonnes).

The second approach is based on the change in tonnage fished over a 30-year period. For this index we extracted 50 years of historic fishing data by commercial group and country as above. We averaged the tonnage fished between 1980 and 1984 and between 2010 and 2014. We then divided these measures to create an index showing the change in tonnes fished over a 30-year period. This index serves as another measure of fishing pressure by population (fishing change). However, these indices explained very little of the variance in L_m ($R^2 = 0.03$) and were not found to be significant in any of the models.

To complement these indices, we also examined a commonly used species-level index of intrinsic sensitivity to fishing (Cheung et al., 2005) downloaded from FishBase (<http://www.fishbase.org>)

Species traits

To test the influence of species traits on the relationship between size at maturation and temperature, we compiled trait information at the species level. These include traits such as activity level, common length, longevity, trophic level, and climate affinity (Appendix 1). For the correlations among predictors, see Appendix 7. We expect intraspecific variation in these traits to be small relative to the strong interspecific differences among all fishes examined. We explain why we chose these traits and how they were compiled below.

Activity level

If oxygen limitation is the main environmental determinant of size at maturation, we would expect to see interspecific variation by activity level (van Rijn et al., 2017). We estimated activity levels using the aspect ratio of the caudal fin, which is a good indicator of swimming speed and activity in fishes (Palomares and Pauly, 1998). Higher aspect ratios indicate higher activity levels which may affect oxygen demands and therefore may affect the species' responses to temperature changes (van Rijn et al., 2017). The aspect ratio was calculated using photographs gathered from FishBase (<http://www.fishbase.org>) and other online resources that clearly showed the caudal fin.

Common length, longevity, and trophic level

Across species, location along the slow-fast life-history continuum may also affect the influence of temperature on size at maturation, with the exact effect likely to differ between the long and short term (Rijnsdorp et al., 2009; Quetglas et al., 2016). We gathered information on trophic level, longevity, and common length, all associated with location along the slow-fast life-history continuum, from the original surveys (Tsikiras and Stergiou, 2014) where available, and used other sources to complete this data where it was not provided in the original surveys (Albouy et al., 2015, the Animal Aging and Longevity Database, <http://genomics.senescence.info>).

Climate affinity

Climatic affinity may potentially affect the influence of temperature on size at maturation, as cold adapted species may experience warming differently than warm water species. 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. We were specifically interested in understanding the cold tolerance of a species for two main reasons: First, it is more relevant when examining the influence of climate affinity on the early life of fish, since fish may have a minimal threshold that enables growth. Second, specifically within the Mediterranean, the minimum monthly temperature shows more variation across the regions than maximum monthly temperature.

Statistical analysis

Population-level analyses

We looked for the best environmental predictors of fish size at maturation using generalized linear mixed-effect models. The response variable was set as the log-transformed L_m (cm) of each species sex at each location. Log transformation was performed as we were interested in understanding proportional changes in L_m and not absolute changes (for which changes in L_m of large species will contribute much more to the analyses than changes in L_m for small species). We set species sex as a random effect on the intercept to reflect differences among species in L_m . We used gamma models as they were found to be superior to Gaussian models for our data. Linear models provided a good fit to the data and showed appropriate distribution of residuals. We did

not detect any substantial non-linear effects. Thus, the final general model for the population level analysis was:

$$L_m \sim \text{temperature} + (1|\text{species sex}),$$

where temperature represents any of the different temperature indices, and 1|species sex represents the random effect of species sex on the intercept.

To test for the best environmental predictor to explain variation in L_m , we compared models with the following temperature measurements: minimum, mean, and maximum temperature at species' preferred depth ($1/k_B T$ transformed); and species-specific GDD with each of three temperature thresholds (10°C, 15°C, and 20°C). We assessed each temperature metric on its own and then compared this with models that also included productivity and temperature range. We did not examine interactions among these predictors. We compared all the models using the small-sample corrected Akaike Information Criterion (AICc). The best supported model is that with the lowest AICc. We evaluated model quality by the proportion of the variation explained by the fixed effects (Jaeger *et al.*, 2017). We performed mixed-model analysis using the “glmer” function in the “lme4” R package (Bates *et al.*, 2015). All the models examined displayed adequate error distribution (as assessed by Q–Q plots) and we did not detect non-linear relationships between the response and the predictors. We were also interested in understanding how the association between L_m and L_{max} changes along environmental gradients. To examine this, we constructed mixed-effect models containing population-level observations of L_{max} (log transformed) reported by Tsikliras and Stergiou (2014). As before, we used L_m as the response, but use L_{max} as a covariate, and thus essentially examine which predictors best explain variation in L_m after controlling for variation in L_{max} . For example, if both L_m and L_{max} vary similarly with temperature, their ratio will be independent of temperature, and temperature will appear to be a poor predictor. Thus, the model structure was:

$$L_m \sim L_{max} + \text{temperature} + (1|\text{species.sex}),$$

where L_m and L_{max} are estimated for each species sex from similar populations.

Species-level analyses

After establishing the best supported environmental predictors as GDD15 and mean temperature (see results; Table 1), we checked the influence of species-level predictors including aspect ratio, longevity, common length, vulnerability to fishing, trophic level, and climate affinity. We did this using two approaches. First, we used the species-level predictors within the mixed-model analysis presented above (Appendix 4). Hence, we added species level predictors to our population level analyses. As GDD has a more direct biological meaning than mean temperature (and given they are correlated with $|r| = -0.93$) we focus on GDD15 as the main thermal predictors in the remainder of the analyses. Since we were interested in examining how the slope of L_m to GDD15 changes across species, we explicitly tested for GDD15 and species traits interactions. Hence, the general model structure was:

$$L_m \sim \text{GDD15} * \text{species trait} + (1|\text{species.sex}),$$

We also took a meta-analytical approach (Table 3), where the slope, for each species sex, of the linear regression of L_m against

Table 1. Model selection (AICc) results for mixed-effects models with different temperature predictors as fixed factors, species sex as a random effect on the intercept and the length at maturation (log transformed) as the response.

Model	DF	ΔAICc	Weight	R ²
Mean temp	4	0.0	0.367	0.05
GDD 15	4	1.4	0.18	0.043
GDD 10	4	2.0	0.137	0.041
Max temp	4	2.5	0.105	0.043
GDD 20	6	3.6	0.060	0.039
Mean temp + productivity + temp range	4	3.7	0.057	0.051
GDD 10 + productivity + temp range	6	5.2	0.028	0.045
GDD 15 + productivity + temp range	6	5.3	0.027	0.044
Min temp + productivity + temp range	6	6.5	0.014	0.043
Max temp + productivity + temp range	6	6.6	0.014	0.043
GDD 20 + productivity + temp range	6	7.0	0.011	0.041
Min temp	4	12.6	<0.001	0.01

Results include models for temperature (temp, $1/k_B T$ transformed) or GDD alone and models that include productivity and temperature range. The best supported model is that with the lowest AICc. We evaluated model quality by the proportion of the variation explained using fixed effects only (R^2).

GDD15 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.

For the meta-analysis, we tested all single traits alone and in combination (exhaustive search) using additive models and show the top 10 models. For the mixed-effect model, we compared models with an interaction between each species trait and GDD15 independently (two-way interactions) and all combinations of two predictors as interactions with GDD15 (three-way interactions). We also performed a separate but similar analysis in which the fishing indices were used as additional additive predictors. For both approaches, we ranked the models using AICc. The meta-analysis was done using the “rma” function in the “metafor” R package (Viechtbauer, 2010).

Finally, we compared the resulting species-sex slope of L_m against GDD15, with the slope of observed L_{max} against maximum temperature found in a previous study (van Rijn *et al.*, 2017).

Results

Population-level analyses

Our data included samples taken from 25 locations across the Mediterranean with yearly mean temperatures ranging from 12°C to 23°C and maximum temperatures ranging between 23°C and 30°C (Figure 2). We compared temperature (max, min, and mean; $1/k_B T_{\text{Kelvin}}$ transformed) and GDD (thresholds at 10°C, 15°C, and 20°C) as predictors of L_m . We found that GDD15 and mean temperature, which are closely correlated, were both good predictors of L_m ($\Delta\text{AICc} = 1.4$, Table 1). While the R^2 explained by the predictors is low, this is expected in these mixed-effect models in which much of the variability in L_m is associated with intrinsic differences among species and sex (the random effect). Maximal temperature received lower support than mean temperature ($\Delta\text{AICc} = 2.5$, Table 1). Models that included productivity and temperature range received lower support than models with GDD or other temperature indices alone ($\Delta\text{AICc} = 3.7$, Table 1).

When we examine how the association between L_m and L_{max} changes along environmental gradients, using L_{max} as a covariate

Table 2. Model selection (AICc) results using L_{max} (log transformed) as a covariate in the analyses.

Model	DF	$\Delta AICc$	AIC weight	R^2	R^2 excluding L_{max}
L_{max} + min temp	5	0.0	0.172	0.752	0.001
L_{max} + GDD 20	5	0.0	0.168	0.712	0.004
L_{max} + max temp	5	0.5	0.135	0.718	0.004
L_{max} + mean temp	5	0.8	0.114	0.724	0.005
L_{max} + GDD 10	5	1.2	0.095	0.734	0.004
L_{max} + GDD 15	5	1.2	0.095	0.734	0.004
L_{max} + max temp + productivity + temp range	7	2.5	0.041	0.748	0.003
L_{max} + min temp + productivity + temp range	7	2.5	0.040	0.747	0.004
L_{max} + GDD 15 + productivity + temp range	7	2.6	0.039	0.750	0.004
L_{max} + GDD 10 + productivity + temp range	7	2.8	0.035	0.745	0.004
L_{max} + GDD 20 + productivity + temp range	7	2.8	0.034	0.727	0.004
L_{max} + mean temp + productivity + temp range	7	3.0	0.031	0.738	0.005

Results shown for mixed-effects models with different temperature predictors as fixed factors, species as a random effect and the length at maturation (log transformed) as the response. Results include models for temperature (temp, $1/k_B T$ transformed) or GDD alone, and models that include productivity and temperature range. The best supported model is that with the lowest AICc. We evaluated model quality by the proportion of the variation explained using fixed effects only (R^2). In addition, we present the proportion of the variation explained by all covariates excluding L_{max} .

Table 3. Results of the meta-analysis relating species level slopes of the relationship between GDD15 and size at maturation (L_m) and species level attributes.

Model name	AICc	ΔAIC
Aspect ratio + climate affinity	-472.87	-
Aspect ratio + climate affinity + longevity + trophic level	-472.87	0
Aspect ratio + common length + climate affinity	-472.67	0.20
Aspect ratio + common length + trophic level + climate affinity	-472.46	0.41
Common length + climate affinity	-472.24	0.63
Aspect ratio + longevity	-471.62	1.25
Aspect ratio	-471.60	1.27
Aspect ratio + longevity + climate affinity	-471.40	1.47
Aspect ratio + fishing sensitivity + climate affinity	-471.39	1.48
Common length	-471.27	1.60

We show the top 10 results from an exhaustive search of each species level predictor, individually and in combination. Only additive models were considered. The best supported model is that with the lowest AICc.

in the analyses, we find that many additional environmental predictors receive similar high support, including mean temperature, GDD20, and maximum temperature (Table 2). Importantly, the environmental predictors' ability to explain the variation in L_m drops considerably when adding L_{max} as a covariate ($R^2 < 0.005$) suggesting that L_m and L_{max} tend to vary similarly across the environmental gradients examined (Table 2).

Species-level analyses

Although we found evidence of a trend toward reduction of L_m with increased temperature, there was variability in the pattern among species (Appendix 2). Using meta-analyses with species-level traits as predictors, we found that the slope of the relationship between L_m and GDD15 was best explained using aspect ratio of the caudal fin (AR) and climate affinity that were consistently found in the best supported models (Figure 3). Other species-level predictors such as common length, longevity, and trophic level were also found within the highest supported models (Table 3). Fishing sensitivity and sex receive lower support.

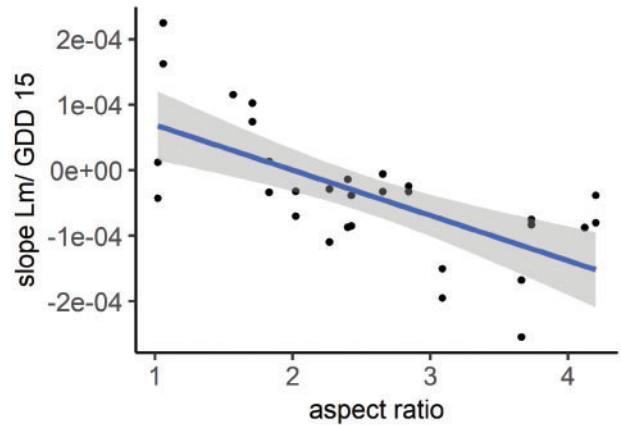


Figure 3. The slope of length at maturation (cm, log transformed) against GDD15 (°C days) in relation to aspect ratio (AR) of the caudal fin across species. Although variable, species with higher AR tend to show faster decrease in length at maturation in warmer water ($p < 0.001$). The line represents results of an ordinary linear regression and the shaded area 95% prediction intervals.

Similar patterns were found when we examined the interactions between GDD15 and species-level predictors within a mixed-effect modelling framework (Appendix 4). Here too, aspect ratio was found within most highly supported model, both when fishing was accounted for (Appendix 4a) and when it was not (Appendix 4b). Fishing sensitivity and longevity were also found within the highest supported models. Climatic affinity, which received high support in the meta-analyses, was not found within the best supported models.

Across species, we found a significant correlation ($r = -0.60$, $p < 0.001$) between the species-sex slope of L_m against GDD15, with the slope of L_{max} against maximum temperature (obtained from different data sources; van Rijn et al., 2017) (Figure 4). Thus, species with a strong reaction in L_{max} to maximal temperature may also exhibit changes in L_m with GDD15. We note that we used the $1/k_B T$ temperature transformation for maximal temperature and not for GDD and therefore the correlation is negative.

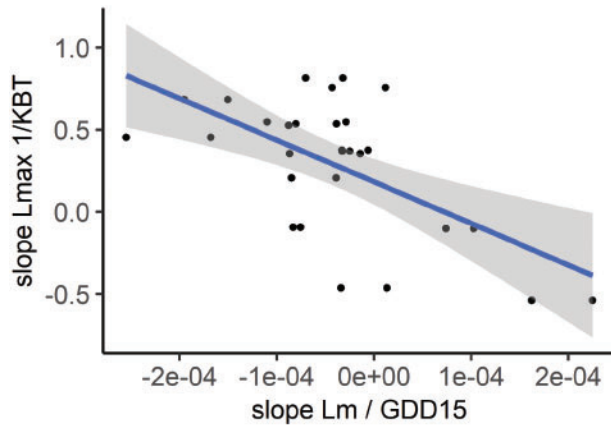


Figure 4. Comparison of species-level slopes for observed L_{\max} (cm, log transformed) against maximal yearly temperature (extracted from van Rijn et al., 2017) to slopes estimated in this study for species L_m (cm, log transformed) against GDD15 ($^{\circ}\text{C}$ days). Each dot represents a different species sex. The relationship is negative ($r = -0.60$) and significant ($p = <0.001$) meaning that species that strongly respond to temperature change in their L_{\max} also respond in L_m . Note that maximum temperature is transformed ($1/k_B T$; $k_B = 8.6 \times 10^{-5}$ eV/K, T in Kelvin), and thus higher values indicate species that decrease faster in size with higher temperature. Data used is without one outlier point from the slope of L_{\max} for *Epinephelus marginatus* with Y-axis value of 3.5 (regression becomes non-significant if the outlier is retained).

Discussion

Although it is well established that fish tend to grow smaller in warmer water (Atkinson, 1994), the mechanisms by which temperature influences fish length at maturation is less studied, particularly in natural populations. We found that fish length at maturation decreases with a rise in water temperature across the Mediterranean Sea. We further found that the best environmental predictors of this change are GDD and mean temperature, which are closely correlated (Appendix 6). We found mean temperature alone to be a statistically stronger predictor of fish length at maturation than maximum temperature alone (although the two are highly correlated at $r=0.92$). Moreover, models with GDD or mean temperature were better supported than models that include productivity. The correlation of fish size at maturation to specific temperature indices will help fisheries and conservation programmes make more accurate estimates of the effect of climate change on length at maturation, an important predictor of the risk of overexploitation (Reynolds et al., 2005).

These findings suggest that the reduction in fish size at maturation is not driven primarily by either oxygen limitation or food availability. If oxygen limitation was the driving mechanism, we would expect to see a strong correlation to maximal temperature (where the effects on oxygen limitation is strongest; van Rijn et al., 2017). If food availability was the driving mechanism, we would expect to see a strong correlation to temperature measures in combination with productivity. Hence, our findings suggest that the mechanism directing fish size at maturation could be associated with a faster development rate of the reproductive system in warmer waters.

Among the GDD indices, we found that the best predictor of changes in length at maturation was GDD with a threshold of

15°C . Although species differ in the minimal temperature which enables their growth, this threshold temperature (15°C) is consistent with the minimal temperature allowing growth for some Mediterranean species (Russell et al., 1996). A threshold of 15°C for GDD supports the explanation that the key mechanism explaining length at maturation is the amount of time an individual is found within the temperature range that allows development.

This finding that GDD and mean temperature are better predictors than maximal temperature of fish length at maturation directly contrasts with a previous study in Mediterranean fishes (van Rijn et al., 2017) that found maximal fish size to be best predicted by maximal yearly temperature. Nevertheless, we found that species who show a strong reaction in L_{\max} to maximal temperature also exhibit changes in L_m with GDD15 (Figure 4). The complexity of the association between L_m and L_{\max} is exemplified by the mixed-model analysis in which we examined L_m after controlling for L_{\max} (Table 2). Here, no single environmental predictor was clearly superior to the rest. Thus, it seems that, on one hand, L_m and L_{\max} vary similarly across environmental gradients, while at the same time separate mechanisms may link temperature to fish growth before maturation and at maximum size.

The oxygen limitation hypothesis (Pauly and Cheung, 2018) seems to better explain maximum size by presenting a physiological barrier above which fish cannot supply enough oxygen for their metabolic demands. However, oxygen is less likely to be a limiting factor for young, relatively small, immature individuals. We find here that for immature individuals, higher values of GDD and mean temperature lead to earlier maturation, which suggests sexual development rate, and not oxygen supply, is the primary factor controlling size at maturation. One implication of maximal size and size at maturation both responding to temperature, but through separate mechanisms, is that predicting the fate of fish under warming waters is unlikely to be achieved using models evoking a single mechanism.

Across species, we find that more active species (higher aspect ratio) are more affected by temperature (Table 3, Figure 3). The correlation to activity level can be easily explained if oxygen limitation is the primary factor determining growth, as active species will show faster elevation in oxygen demand with rising temperature (van Rijn et al., 2017). It is less clear, however, why activity level should affect development of the reproductive system. The relationship between AR and maturation size may indicate an indirect effect of anticipated individual maximal size on maturation size (Pauly, 1984).

Our finding that warmer waters in the Mediterranean Sea are associated with smaller fish length at maturation raises concerns about how climate change will alter the dynamics of natural fish populations. Smaller length at maturation is expected to reduce fecundity and lower egg quality of first breeding individuals (Mehault et al., 2010; Cooper et al., 2013). However, although a larger size at maturation allows for higher fecundity, this must be balanced with the ability to survive until maturity (Tsoukali et al., 2016). Thus, lower fecundity and egg quality could be offset by selective advantages to smaller length at maturation in warmer water. Several pathways may favour smaller length at maturation with increased temperature. For example, either higher mortality rates on older fish (Angilletta et al., 2004) or prolonged breeding periods that enable multiple reproductive events per season (Azevedo, 2010) may evolutionarily favour early maturation since additional opportunities to reproduce compensate for the

drawbacks of smaller size. Prolonged breeding may be particularly relevant in temperate areas, such as the Mediterranean Sea, where most species have seasonal spawning periods (Tsikiras *et al.*, 2010).

Faced with warming waters and smaller length at maturation, future fishery management strategies may need to reconsider the optimal harvest size of exploited species. Whereas smaller length at maturation may allow fisheries to target smaller individuals while still allowing fish to reach breeding size, smaller fishes may also result in a decrease in overall reproductive output. Since climate change is likely to unevenly influence different temperature measurements (Easterling, 1997), quantifying how GDD impacts length at maturation will help ecologists to more accurately understand the implications of climate change on natural fish populations.

Acknowledgements

We thank A.C. Tsikiras and K.I. Stergiou for compiling and making available the length at maturation data on which this analysis is based. IvR was supported by the Manna Center for Food Safety and Security, Tel Aviv University.

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Handling editor: Mikko Heino

Appendix 1

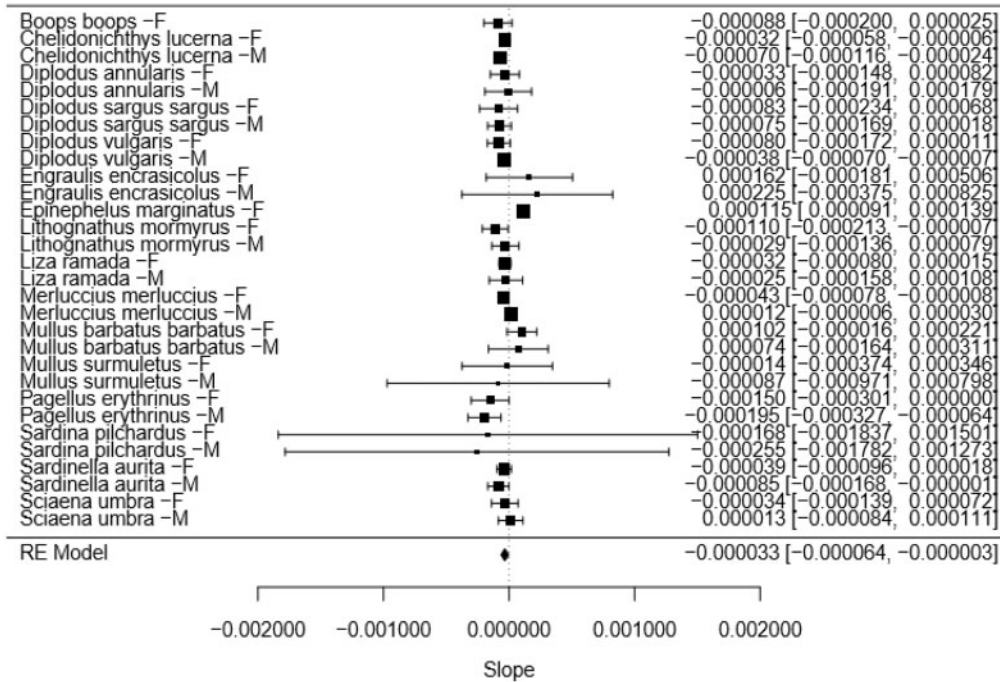
Summary of species-level traits.

Species	Sex	Aspect ratio	Fishing vulnerability	Common length	Age at maturation	Trophic level	Longevity	Climate affinity (min)
<i>Boops boops</i>	F	4.12	41.22	22.5	2	2.8	7	-0.110
<i>Chelidonichthys lucerna</i>	F	2.02	57.70	55	3	4	15	0.458
<i>Chelidonichthys lucerna</i>	M	2.02	57.70	55	1.5	4	15	0.458
<i>Diplodus annularis</i>	F	2.66	26.64	16.5	2	3.6	7	4.927
<i>Diplodus annularis</i>	M	2.66	26.64	16.5	2	3.6	7	4.927
<i>Diplodus sargus sargus</i>	F	3.74	63.39	25	2	3.4	21	8.880
<i>Diplodus sargus sargus</i>	M	3.74	63.39	25	2	3.4	21	8.880
<i>Diplodus vulgaris</i>	F	4.20	65.73	25	2	3.5	20	9.505
<i>Diplodus vulgaris</i>	M	4.20	65.73	25	2	3.5	20	9.505
<i>Engraulis encrasicolus</i>	F	1.06	23.87	14	1	3.1	3	-1.610
<i>Engraulis encrasicolus</i>	M	1.06	23.87	14	1	3.1	3	-1.610
<i>Epinephelus marginatus</i>	F	1.57	71.52	90	5	4.4	24	7.195
<i>Lithognathus mormyrus</i>	F	2.27	40.38	35	2	3.4	8	7.450
<i>Lithognathus mormyrus</i>	M	2.27	40.38	35	2	3.4	8	7.450
<i>Liza ramada</i>	F	2.84	53.41	50	3	2.3	10	-0.213
<i>Liza ramada</i>	M	2.84	53.41	50	3	2.3	10	-0.213
<i>Merluccius</i>	F	1.02	64.74	80	3.3	4.4	20	-0.938
<i>Merluccius</i>	M	1.02	64.74	80	3.3	4.4	20	-0.938
<i>Mullus barbatus</i>	F	1.71	29.30	20	1.3	3.1	8	4.927
<i>Mullus barbatus</i>	M	1.71	29.3	20	1.3	3.1	5	4.927
<i>Mullus surmuletus</i>	F	2.40	39.0	27.5	1.5	3.5	10	-1.365
<i>Mullus surmuletus</i>	M	2.40	39.0	27.5	1.5	3.5	10	-1.365
<i>Pagellus erythrinus</i>	F	3.09	39.81	35	2	3.5	10	6.058
<i>Pagellus erythrinus</i>	M	3.09	39.81	35	2	3.5	10	6.058
<i>Sardina pilchardus</i>	F	3.66	24.55	19	1	3.1	15	1.003
<i>Sardina pilchardus</i>	M	3.66	24.55	19	1	3.1	15	1.003
<i>Sardinella aurita</i>	F	2.42	35.95	25	1	3.4	7	1.822
<i>Sardinella aurita</i>	M	2.42	35.95	25	1	3.4	7	1.822
<i>Sciaena umbra</i>	F	1.83	63.57	37.5	3	3.8	18	6.058
<i>Sciaena umbra</i>	M	1.83	63.57	37.5	3	3.8	18	6.058

Common length is the length in centimetres at which most individuals of the population are likely to be sampled, measured from the tip of the snout to the tip of the longer lobe of the caudal fin (equivalent to total length).

Appendix 2

Forest plot of the slope of L_m (log transformed) against GDD15 by species sex. Each box shows the slope of the single species sex and the diamond at the bottom shows the overall effect. Confidence intervals are indicated by the horizontal lines through the boxes where longer lines indicate less reliable results. Although we found evidence of an overall trend toward reduction of L_m with increased GDD, there was considerable variability in the pattern among species sex.



Appendix 3

Summary of populations included in the analysis.

Species	Sex	Location	Sample Year
<i>Boops boops</i>	F	Oran Coast, Algeria	1986–1987
		Adriatic Sea, Croatia	1957–1958
		Cretan Sea, Greece	1988–1990
<i>Chelidonichthys lucerna</i>	F	Alexandria coast, Egypt	1996–1997
		Adriatic Sea, Italy	2005–2009
		Gulf of Gabes, Tunisia	2003–2004
		Aegean Sea, Turkey	1999–2000
		Iskenderun Bay, Turkey	1999–2000
		Marmara Sea, Turkey	1996–1997
<i>Chelidonichthys lucerna</i>	M	Alexandria coast, Egypt	1996–1997
		Adriatic Sea, Italy	2005–2009
		Gulf of Gabes, Tunisia	2003–2004
		Aegean Sea, Turkey	1999–2000
		Iskenderun Bay, Turkey	1999–2000
<i>Diplodus annularis</i>	F	Adriatic Sea, Croatia	2000–2002
		Gulf of Tunis, Tunisia	2004–2006
		Tunisian coast, Tunisia	1986–1987
		Aegean Sea, Turkey	1997–2001
<i>Diplodus annularis</i>	M	Adriatic Sea, Croatia	2000–2002
		Gulf of Tunis, Tunisia	2004–2006
		Tunisian coast, Tunisia	1986–1987
		Aegean Sea, Turkey	1997–1998
<i>Diplodus sargus sargus</i>	F	Algerian coast, Algeria	Unreported
		Adriatic Sea, Croatia	1986–1999
		Gulf of Tunis, Tunisia	2002–2006
<i>Diplodus sargus sargus</i>	M	Algerian coast, Algeria	Unreported
		Adriatic Sea, Croatia	1986–1999

Continued

Appendix 3. Continued

Species	Sex	Location	Sample Year
<i>Diplodus vulgaris</i>	F	Gulf of Tunis, Tunisia	2002–2006
		Adriatic Sea, Croatia	1986–1999
		Sicilian Channel, Italy	1997–1999
<i>Diplodus vulgaris</i>	M	Gulf of Tunis, Tunisia	2004–2006
		Adriatic Sea, Croatia	1986–1999
		Alexandria coast, Egypt	Unreported
<i>Engraulis encrasicolus</i>	F	Sicilian Channel, Italy	1997–1999
		Gulf of Tunis, Tunisia	2004–2006
		Alboran Sea, Spain	1990–1991
<i>Engraulis encrasicolus</i>	M	Bay of Cadiz, Spain	1989–1992
		Sicilian Channel, Italy	1997–2002
		Alboran Sea, Spain	1990–1991
<i>Epinephelus marginatus</i>	F	Bay of Cadiz, Spain	1989–1992
		Algerian coast, Algeria	1993–1994
		Sicilian Channel, Italy	1994–1997
<i>Lithognathus mormyrus</i>	F	Balearic Sea, Spain	1998–2004
		Adriatic Sea, Croatia	1986–1999
		Aegean Sea, Greece	1997–1999
<i>Lithognathus mormyrus</i>	M	Sicilian Channel, Italy	1997–1998
		Levantine Sea, Turkey	1998–2007
		Aegean Sea, Greece	1997–1999
<i>Liza ramada</i>	F	Sicilian Channel, Italy	1997–1998
		Levantine Sea, Turkey	1998–2007
		Aegean Sea, Greece	1989–1990
<i>Liza ramada</i>	M	Ionian Sea, Greece	1990–1995
		Levantine Sea, Turkey	1992–1994
		Aegean Sea, Greece	1989–1990
<i>Merluccius merluccius</i>	F	Ionian Sea, Greece	1990–1995
		Levantine Sea, Turkey	1992–1994
		Algerian coast, Algeria	Unreported
<i>Merluccius merluccius</i>	M	Gulf of Lions, France	1989–1991
		Tyrrhenian Sea, Italy	1992–1999
		Libyan coast, Libya	1972
<i>Merluccius merluccius</i>	F	Balearic Sea, Spain	1990–1993
		Catalan Sea, Spain	1997–1998
		Gulf of Lions, France	1989–1991
<i>Mullus barbatus barbatus</i>	M	Tyrrhenian Sea, Italy	1993
		Libyan coast, Libya	1972
		Balearic Sea, Spain	1990–1993
<i>Mullus barbatus barbatus</i>	F	Adriatic Sea, Croatia	1972–1975
		Aegean Sea, Greece	1990–1991
		Ionian Sea, Greece	1983–1985
<i>Mullus barbatus barbatus</i>	M	Alboran Sea, Spain	2001–2002
		Gulf of Tunis, Tunisia	2003–2004
		Aegean Sea, Greece	1990–1991
<i>Mullus surmuletus</i>	F	Ionian Sea, Greece	1983–1985
		Alboran Sea, Spain	2001–2002
		Gulf of Tunis, Tunisia	2003–2004
<i>Mullus surmuletus</i>	M	Aegean Sea, Greece	1991–1992
		Mediterranean coast, Morocco	2009
		Balearic Sea, Spain	1990–1992
<i>Pagellus erythrinus</i>	F	Aegean Sea, Greece	1991–1992
		Mediterranean coast, Morocco	2009
		Balearic Sea, Spain	1990–1992
<i>Pagellus erythrinus</i>	M	Aegean Sea, Greece	Unreported
		Cretan Sea, Greece	1988–1991
		Ionian Sea, Greece	1983–1985
<i>Pagellus erythrinus</i>	F	Tunisian coast, Tunisia	1978
		Aegean Sea, Turkey	1999–2007
		Aegean Sea, Greece	Unreported
<i>Pagellus erythrinus</i>	M	Ionian Sea, Greece	1983–1985

Continued

Appendix 3. Continued

Species	Sex	Location	Sample Year
<i>Sardina pilchardus</i>	F	Tunisian coast, Tunisia	1978
		Aegean Sea, Turkey	2002–2007
		Bou–Ismail, Algeria	Unreported
		Adriatic Sea, Croatia	2002–2005
<i>Sardina pilchardus</i>	M	Alboran Sea, Spain	1983–1991
		Bou–Ismail, Algeria	Unreported
		Adriatic Sea, Croatia	2002–2005
<i>Sardinella aurita</i>	F	Alboran Sea, Spain	1983–1991
		Adriatic Sea, Croatia	2007–2009
		Aegean Sea, Greece	2000–2002
<i>Sardinella aurita</i>	M	Tunisian coast, Tunisia	1994–1996
		Adriatic Sea, Croatia	2007–2009
		Aegean Sea, Greece	2000–2002
<i>Sciaena umbra</i>	F	Tunisian coast, Tunisia	1994–1997
		Gulf of Annaba, Algeria	2001–2002
		Balearic Sea, Spain	1998–2000
<i>Sciaena umbra</i>	M	Gulf of Tunis, Tunisia	1995–1996
		Gulf of Annaba, Algeria	2001–2002
		Balearic Sea, Spain	1998–2000
		Gulf of Tunis, Tunisia	1995–1996

Appendix 4

Model selection (AICc) results for mixed effects models with all single species-level predictors as interactions with GDD15, and all combinations of two predictors as interactions with GDD15.

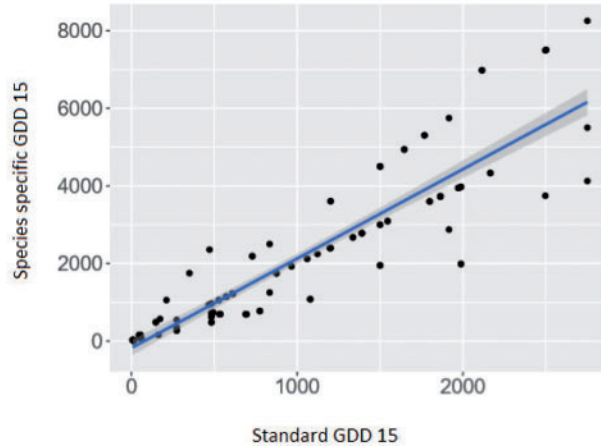
Model name	DF	ΔAICc	Weight	R ²
(a) Species level traits only (top 10 results)				
GDD15 * aspect ratio	5	–	0.15	0.07
GDD15 * aspect ratio * fishing sensitivity	6	1.2	0.13	0.08
GDD15 * aspect ratio * longevity	6	1.4	0.08	0.08
GDD15 * aspect ratio * sex	6	2.2	0.08	0.07
GDD15 * fishing sensitivity	5	2.2	0.06	0.07
GDD15 * aspect ratio * common length	6	2.3	0.05	0.07
GDD15 * aspect ratio * climate affinity	6	2.3	0.05	0.07
GDD15 * longevity	5	2.9	0.05	0.07
GDD15 * common length	5	3.0	0.04	0.07
GDD15 * fishing sensitivity * climate affinity	6	3.6	0.04	0.07

The best supported model is that with the lowest ΔAICc. We evaluated model quality by the proportion of the variation explained using fixed effects only (R²).

Model name	DF	ΔAICc	Weight	R ²
(b) Species level traits as in A, but also including the two fishing indices as additional additive predictors (top 10 results)				
GDD15 * aspect ratio	7	–	0.135	0.07
GDD15 * aspect ratio * fishing sensitivity	8	0.6	0.10	0.08
GDD15 * fishing sensitivity	7	0.9	0.09	0.08
GDD15 * aspect ratio * longevity	8	1.4	0.07	0.07
GDD15 * aspect ratio * sex	8	1.6	0.06	0.07
GDD15 * longevity	7	1.8	0.06	0.07
GDD15 * aspect ratio * common length	8	2.1	0.05	0.07
GDD15 * common length	7	2.2	0.05	0.07
GDD15 * aspect ratio * climate affinity	8	2.2	0.05	0.07
GDD15 * climate affinity	7	2.2	0.05	0.07

Appendix 5

Correlation of annual GDD15 to species-specific GDD15. The annual GDD (using sea surface temperature only and without accounting for age of first maturation) is highly correlated to the species-specific GDD index (Pearson's $r = 0.91$).



Appendix 6

Pearson correlations between pairs of population-level environmental predictors.

	GDD10	GDD15	GDD20	Min. temp	Mean temp	Max. temp	Productivity	Temp. range	Fishing tonnes	Fishing change
GDD10	1									
GDD15	0.99	1								
GDD20	0.89	0.92	1							
Min. temp	-0.66	-0.57	-0.4	1						
Mean temp	-0.94	-0.93	-0.86	0.69	1					
Max. temp	-0.87	-0.89	-0.87	0.41	0.93	1				
Productivity	-0.04	-0.03	-0.17	-0.02	0.07	0.05	1			
Temp. range	0.55	0.63	0.71	0.15	-0.59	-0.84	-0.07	1		
Fishing tonnes	0.48	0.49	0.51	-0.24	-0.5	-0.49	-0.06	0.39	1	
Fishing change	0.14	0.14	0.19	-0.26	-0.21	-0.08	0.14	-0.06	0.23	1

Appendix 7

Pearson correlations between pairs of species-level traits.

	Aspect ratio	Fishing sensitivity	Climate affinity	Common length	Trophic level	Longevity
Aspect ratio	1					
Fishing sensitivity	0.06	1				
Climate affinity	0.37	0.25	1			
Common length	-0.41	0.68	-0.21	1		
Trophic level	-0.39	0.46	0.12	0.56	1	
Longevity	0.2	0.83	0.27	0.55	0.54	1