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# Global analysis of fish growth rates shows weaker responses to temperature than metabolic predictions

Daniël van Denderen<sup>1</sup>  | Henrik Gislason<sup>1</sup>  | Joost van den Heuvel<sup>2</sup> | Ken H. Andersen<sup>1</sup>

<sup>1</sup>Centre for Ocean Life, National Institute of Aquatic Resources, Technical University of Denmark, Kongens Lyngby, Denmark

<sup>2</sup>Laboratory of Genetics, Wageningen University, Wageningen, the Netherlands

## Correspondence

Daniël van Denderen, Centre for Ocean Life, National Institute of Aquatic Resources, Technical University of Denmark, Kemitorvet B-202, 2800 Kongens Lyngby, Denmark.  
Email: pdvd.science@gmail.com

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## Abstract

**Aim:** Higher temperatures increase the metabolic rate of ectothermic organisms up to a certain level and make them grow faster. This temperature-sensitivity of growth is frequently used to predict the long-term effects of climate warming on ectotherms. Yet, realized growth also depends on ecological factors and evolutionary adaptation. Here we study whether faster growth is observed along temperature clines within and between marine fish species from polar to tropical regions.

**Location:** Global.

**Time period:** The sampling or publication year is for 718 observations before 1980, 1,073 observations between 1980 and 2000, and 390 observations after 2000 (for 336 observations no year was recorded).

**Major taxa studied:** Marine teleost fish and elasmobranchs.

**Methods:** The effects of temperature on fish growth are studied using 2,517 growth observations, representing 771 species in 165 marine ecoregions. The effects of temperature are presented with a  $Q_{10}$ , describing relative increase in the rate of growth for each 10 °C increase.

**Results:** We find weak within- and between-species effects of temperature on growth. The typical within-species effect of temperature has a  $Q_{10}$  of 1.1. The between-species effect is a little higher ( $Q_{10} = 1.4$ , or  $Q_{10} = 1.2$  when corrected for phylogenetic relationships). When analysed per fish guild, growth responses vary from nearly independent of temperature in large demersals ( $Q_{10} = 1.1$ ) to positive in small pelagics ( $Q_{10} = 1.6$ ) and elasmobranchs ( $Q_{10} = 2.3$ ). Average growth is higher in ecoregions with high primary production.

**Main conclusion:** The change in average growth along temperature clines is weaker than predicted by metabolic theory, suggesting that the metabolic predictions are not sustainable in an ecosystem context. The long-term response of fish to the increase in temperature associated with climate change may hence be shaped more by local environmental and ecological dynamics than by the physiological temperature response of the species currently present.

## KEYWORDS

climate change, ectotherms, marine fish, metabolic theory, temperature response, von Bertalanffy growth

## 1 | INTRODUCTION

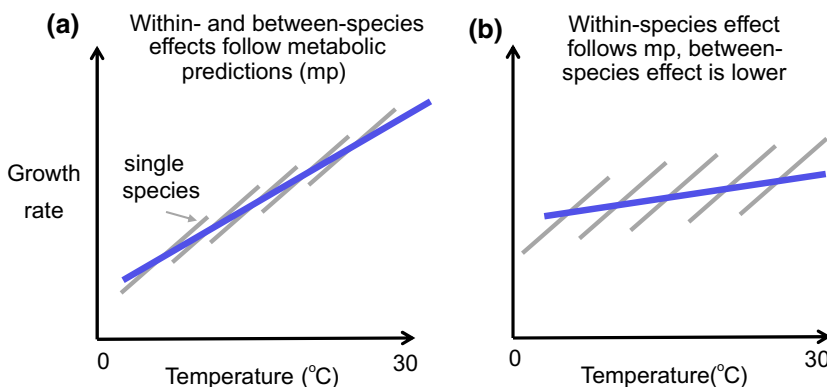
Making credible predictions of the response of individuals, populations and communities to changing temperatures with climate change is a pressing challenge in current ecology. Most organisms are ectotherms and temperature directly influences their physiology, thereby changing somatic growth. Somatic growth (hereafter growth) is typically observed to increase with temperature to a certain optimum after which it decelerates (Kingsolver, 2009). The increase in growth is predicted to scale with temperature in the same way as the metabolic rate, hence with a c. 2.5-fold increase for each 10 °C increase in temperature (Brown, Gillooly, Allen, Savage & West, 2004; Grady, Enquist, Dettweiler-Robinson, Wright & Smith, 2014). This metabolic temperature-sensitivity of growth is included in most modelling studies that predict the long-term effects of changing temperatures due to climate change on ectothermic organisms, from individuals to communities and from local environments to the global ocean, for example, for fish see Cheung, Bruggeman and Butenschön (2018) and Carozza, Bianchi and Galbraith (2019), see for an alternative approach O'Gorman et al. (2019).

The effects of temperature on growth have been studied extensively in the laboratory where food and predators can be manipulated (Atkinson, 1994; Jobling, 1997; Kremer, Thomas & Litchman, 2017). The effects are more difficult to study in natural environments where resource availability, predation risk and the length of the growing season are not easily manipulated (Arendt, 1997; Clarke, 2003). So far, the length of the growing season has gained most attention as it is inversely correlated to temperature at large spatial scales and has been found to reverse the effect of temperature on growth among populations within species, in some cases even resulting in counter-gradient variation in growth within species, that is, faster growth among populations that live in colder waters (Conover & Present, 1990). Between species, the effect of temperature on growth is further confounded by differences in phylogeny and ecology, for example, by prey types, habitats, and lifestyles, that may vary systematically with temperature. Despite the confounding factors that affect the within- and between-species effects of temperature on growth, models describing ectotherm growth in natural environments are typically inspired by the framework proposed by metabolic theory and parameterize the temperature sensitivity of

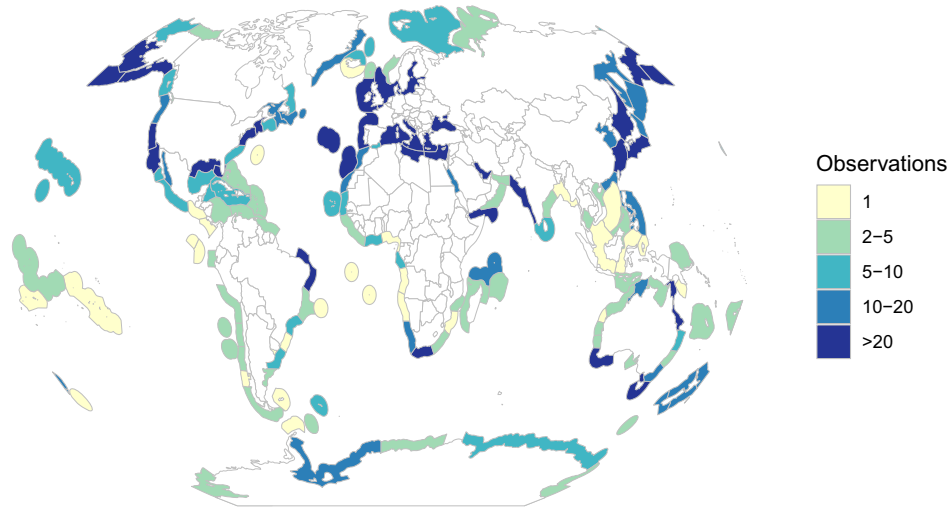
growth assuming it follows metabolic predictions (e.g., Blanchard et al., 2012; Cheung et al., 2013). Empirical support for these growth patterns with temperature is limited in natural systems.

Here we investigate how temperature influences the realized growth rates of marine fish in nature from polar to tropical environments considering both within and between fish species changes in growth. The effect of temperature on growth is in this study presented with a  $Q_{10}$ , describing the relative increase in the rate of growth for each 10 °C increase in temperature. Metabolic theory predicts that growth is fuelled by metabolism and that both scale with temperature following the Arrhenius equation and with a  $Q_{10}$  of approximately 2.5 (Brown et al., 2004). Previous work on the between-species effect of temperature on marine fish growth in natural environments suggests that the rate of increase with temperature is likely to be lower than the metabolic predictions, with  $Q_{10}$ s ranging between 1.5 and 2 (Clarke, 2017; Edgar & Shaw, 1995; Sibly et al., 2015). We extend this body of work using a larger dataset to explore if there are systematic differences between the within- and between-species effects of temperature on growth. We hypothesize that the typical within-species effect is stronger, and hence closer to the metabolic predictions, than the between-species effect, which is likely to be lower due to the evolutionary adaptation of species to their habitats and selection of life histories through community assembly (Figure 1). We furthermore test whether the between-species relationship between temperature and growth depends on phylogeny and fish guild, where guild is defined as a group of species that exploit the same resource and have a similar ecological niche. Lastly, we examine if growth varies consistently with regional changes in feeding conditions, as growth ultimately depends on the rate of energy acquisition throughout ontogeny.

We find weaker within- and between-species effects of temperature on growth than derived from metabolic predictions. These results do not invalidate temperature effects as predicted by metabolic theory at the individual level, but show that such predicted growth trajectories with temperature are not sustainable in an ecosystem context, potentially resulting from evolutionary adaptation of species to their habitats and selection of life histories through community assembly. Consequently, modelling studies based on metabolic theory are likely to predict much stronger long-term effects of temperature change with climate change than might occur.



**FIGURE 1** Potential growth response of different species with temperature where the within- and between-species effects follow the metabolic predictions (a) or where the between-species response (blue line) is lower (b). The grey lines show the increasing part of the thermal performance curve



**FIGURE 2** Number of von Bertalanffy parameter observations specified per marine ecoregion (total observations is 2,517 for 771 species). The observations were linked to a marine ecoregion, or to two neighbouring ecoregions based on sampling locality (if two ecoregions, we only coupled the observation to one of these regions to produce the figure)

Our results provide improved empirical constraints of temperature on fish growth and highlight that understanding natural variation in growth with temperature not only requires a correct description of the physiological response to temperature, but also of the ecological dynamics.

## 2 | METHODS

In the marine fish literature, growth is generally described with the von Bertalanffy growth model. This model contains the von Bertalanffy parameters  $L_{\infty}$  and  $K$ , where  $L_{\infty}$  is the asymptotic length and  $K$  the von Bertalanffy growth constant. We used von Bertalanffy parameters from FishBase (Froese & Pauly, 2018) to derive an estimate of growth, termed growth coefficient  $A$ , and examined the effects of temperature, fish guild, phylogeny and food availability on  $A$ .

### 2.1 | Growth coefficient $A$

The von Bertalanffy growth model describes the rate of growth in body weight,  $dw/dt$ , as the difference between acquisition of energy,  $Aw^n$ , and losses,  $fw$  (Von Bertalanffy, 1957):

$$\frac{dw}{dt} = Aw^n - fw^1. \quad (1)$$

where coefficients  $A$  and  $f$  describe the overall magnitude of the processes, while the exponents  $n$  and 1 describe how they scale with body weight,  $w$ . Von Bertalanffy argued that acquisition of energy is limited by processes that involve absorbing oxygen or food across a surface (gills or the digestive system), and therefore scales with size raised to a power 2/3, whereas losses can be assumed to scale linearly with weight. Modern interpretations of Equation 1 use an exponent 3/4

(West, Brown & Enquist, 2001), but we use 2/3 because it conforms with available data (see later), and because the exact value of the exponent is of limited importance in this context.

The above formulation (Equation 1) implies that the specific growth rate of fish,  $(dw/dt)/w$  is initially high and mainly dependent on growth coefficient  $A$  (Supporting Information Appendix S1: Figure S1.1). The higher the value of  $A$ , the faster individuals grow, and we therefore refer to  $A$  as the growth coefficient, see further Charnov, Gislason and Pope (2013) and Andersen (2019).

Empirical estimates of growth are made with the length-based version of the von Bertalanffy equation:

$$\frac{dl}{dt} = K(L_{\infty} - l), \quad (2)$$

where  $L_{\infty}$  is the asymptotic length in cm and  $K$  is the von Bertalanffy growth constant with units per year. Using the standard relation between length and weight  $w = cl^3$  (Froese, 2006), Equation 1 and Equation 2 are identical if  $K = f/3 = 1/3Ac^{-1/3}/L_{\infty}$ , which provides a way to calculate  $A$  from reports of  $K$  and  $L_{\infty}$ . With the condition factor  $c$  ( $g/cm^3$ ) assumed to be constant across fish species ( $c = 0.01$ ; Froese, 2006), the growth coefficient is  $A = c^{1/3}3KL_{\infty} = 0.65KL_{\infty}$ . We verify in Supporting Information Appendix S2: Table S2.1 that a species-specific length-weight relationship gives consistent results.

To obtain growth coefficient  $A$  estimates, we extracted von Bertalanffy  $L_{\infty}$  and  $K$  parameters from FishBase (Froese & Pauly, 2018) on 27 April 2018 for all marine fish species using the R package 'rfishbase' (Boettiger, Lang & Wainwright, 2012). We selected fish species where the von Bertalanffy parameters ( $L_{\infty}$  and  $K$ ) were reported and where  $t_0$ , describing the point in time or age (in years) where the growth curve intersects the abscissa (the theoretical age at which the model predicts the fish species to have zero length), was in the range  $[-2, 2]$  for teleosts and  $[-5, 2]$  for elasmobranchs because the latter often are born at a larger size.

A  $t_0$  outside this range indicates insufficient or biased data, a poor model fit and/or a systematic error in the procedure to estimate fish age. By selecting growth data from fish with a reported  $t_0$ , we made sure that our growth analysis only included estimates of fish based on length-at-age data and age readings, avoiding estimates based on subjective interpretation of peaks in length-frequency data from which absolute age and hence  $t_0$  cannot be estimated. The length-at-age is typically collected from catch or trawl survey data.

We manually linked each growth observation from FishBase to a particular marine ecoregion or to two neighbouring ecoregions (Spalding et al., 2007) when the sampling locality was provided. All data with indistinct, missing or unwanted (e.g., laboratory, rivers) localities or duplicated observations were removed. We also removed all species from the genera *Huso*, *Acipenser*, *Anguilla*, *Salmo* and *Oncorhynchus* that were classified as marine but mainly grow in fresh water and all oceanic elasmobranchs [16 species, following the classification of Compagno (2008)] that live in a different habitat than their shallow-water counterparts. This resulted in 2,517 observations of growth coefficient  $A$  representing 771 species in 165 ecoregions (Figure 2). The sampling year and/or publication year was before 1980 for 718 observations, between 1980 and 2000 for 1,073 observations, and after 2000 for 390 observations (for 336 observations no year was recorded in the database).

## 2.2 | Fish guild classification

We classified fish species into one of four guilds: pelagic, demersal, deep-living and elasmobranchs, following the functional group classification from the SeaAroundUs project (seararoundus.org; Supporting Information Appendix S1: Table S1.1). When fish were not classified in the SeaAroundUs project, we used the classification and feeding type/habitat description from FishBase to list the fish into one of the guilds.

## 2.3 | Environmental temperature and food conditions

For each ecoregion, we derived estimates of temperature, zooplankton fish prey biomass and production, and net primary production. Temperature and zooplankton estimates representative of the early 1990s were derived from a global earth system model (Geophysical Fluid Dynamics Laboratory - Earth System Model 2.6) coupled to a carbon, ocean biogeochemistry and lower trophic levels (COBALT) planktonic ecosystem model (Stock, Dunne & John, 2014; Stock et al., 2017); net primary production was derived from the vertically generalized production model using moderate resolution imaging spectroradiometer data between 2003 and 2014 (Behrenfeld & Falkowski, 1997). Because fish differ in their position in the water column, we calculated the most likely ambient temperature

(hereafter termed temperature) for each fish guild in the water column. Temperature for pelagic fish was defined as the average temperature in the upper 100 m, temperature for demersal fish and elasmobranchs as the average near the bottom at depths < 500 m, and temperature for deep-living fish as the average near the bottom at depths  $\geq 500$  m. Further details on the environmental conditions are provided in Supporting Information Appendix S3. Note that we did not include the length of the growing season as an environmental parameter as it is strongly correlated with temperature (but see Discussion).

## 2.4 | Data analysis

The effects of temperature on growth coefficient  $A$  were examined using within- and between-subject centring (van de Pol & Wright, 2009) in a stepwise process where we gradually increased the complexity of the statistical model. All models were mixed effects models with species and ecoregion as two separate random factors; for information on mixed effects models see, for example, Zuur et al. (2009). In each analysis, growth coefficient  $A$  was  $\log_{10}$  transformed. Our main analysis ignores nonlinearities in the shape of the growth curve with temperature, as we did not find indications that such nonlinearities are generic (see further Discussion and Supporting Information Appendix S4).

### 2.4.1 | Within- and between-species effects of temperature on growth

First, we examined a mixed model where we separated the effect of temperature on growth for the within- and between-species components:

$$\log_{10}(A_{ijr}) = (\beta_0 + v_{0j} + v_{0r}) + \beta_W (T_{ijr} - \bar{T}_j) + \beta_B \bar{T}_j + e_{0ijr} \quad (M1)$$

In this formulation,  $i$  refers to an individual observation of species  $j$  in ecoregion  $r$ . The intercept was determined by the fixed effect  $\beta_0$  and the random effect of species  $v_{0j}$  and ecoregion  $v_{0r}$ . The random intercepts and the residual error  $e_{0ijr}$  were assumed to be normally distributed. The within-species effect  $\beta_W$  was determined by subtracting the mean temperature  $\bar{T}_j$  of species  $j$  from the temperature  $T_{ijr}$  of each individual observation of species  $j$  in ecoregion  $r$ . The between-species effect  $\beta_B$  was determined from the mean temperature  $\bar{T}_j$  of each species.

Next, we determined whether there was a significant difference in the slopes of the within- and between-species effects of temperature on growth coefficient  $A$ . The difference between the within- and between-species effects is the difference between  $\beta_W$  and  $\beta_B$ . The statistical significance of this difference was obtained by contrasting the estimated slope parameters (van de Pol & Wright, 2009).

In the second model, we investigated whether there was between-species variation in the slopes of the within-species effect of temperature on growth by adding a random slope  $v_{Wj}$  to the random species intercept:

$$\log_{10}(A_{ijr}) = (\beta_0 + v_{0j} + v_{0r}) + (\beta_W + v_{Wj}) (T_{ijr} - \bar{T}_j) + \beta_B \bar{T}_j + e_{0ijr}. \quad (M2)$$

Models M1–M2 were fitted using the R package 'lme4' (Bates, Mächler, Bolker & Walker, 2015) and  $p$ -values were estimated using Satterthwaite's method from the 'lmerTest' R package (Kuznetsova, Brockhoff & Christensen, 2017). In all calculations, we calculated  $Q_{10}$  as  $A_{T2}/A_{T1}^{10/(T_2-T_1)}$  with  $T$  in °C, where the values of  $A$  are the predicted growth coefficients from the statistical model. The terms  $\beta_B$  and  $\beta_W$  in Model M1 were used to estimate a within- and between-species  $Q_{10}$  and 95% confidence intervals (CI) were calculated for  $\beta_B$  and  $\beta_W$  (and the  $Q_{10}$  associated with the 95% CI of these coefficients) using the 'confint' function, which computes a likelihood profile. In Model M2, a  $Q_{10}$  was estimated for each individual species based on the fixed and random effects  $\beta_W + v_{Wj}$ . All estimated coefficients are shown in Supporting Information Appendix S1: Table S1.2. Visual inspections of model fit are shown in Supporting Information Appendix S5. We did not include fish asymptotic length in Models M1–M2. Yet, note that fish asymptotic length does not systematically vary over the temperature gradient (Supporting Information Appendix S1: Figure S1.2).

## 2.4.2 | Role of phylogeny on the between-species effect of temperature on growth

Phylogenetic relatedness may affect the between-species effect of temperature on growth coefficient  $A$  when a phylogenetic group is dominant at low and/or high temperatures and driving the slope of the overall relationship. We used the Fish Tree of Life from the R package 'fishtree' (Chang, Rabosky, Smith & Alfa, 2019; Rabosky et al., 2018) to construct a phylogenetic covariance matrix that describes the phylogenetic relatedness between species. In this analysis, we assumed that species are likely to share similar growth rate values when their phylogenetic relatedness is high. The expected variance of the growth rate values is assumed to follow the Brownian motion model of trait evolution and is, as such, proportional to the phylogenetic distance (Felsenstein, 1985). The phylogenetic analysis was only done for a subset of 613 fish species for which data were available and this excluded all elasmobranchs. The effect of phylogeny was tested for the data subset with (and without) a phylogenetic covariance matrix (M) and a similar model structure as Model M2 using the R package 'MCMCglmm' (Hadfield, 2010):

$$\log_{10}(A_{ijr}) = (\beta_0 + v_{0j} + v_{0r}) + (\beta_W + v_{Wj}) (T_{ijr} - \bar{T}_j) + \beta_B \bar{T}_j + e_{0ijr} + M. \quad (M3)$$

## 2.4.3 | Role of fish guilds in the between-species effect of temperature

We determined the importance of fish guild and asymptotic length to explaining variation in the between-species effect of temperature on growth coefficient  $A$ . We tested different mixed models that varied from a three-way interaction (mean temperature  $\bar{T}_j$  of each species · the  $\log_{10}$  of mean asymptotic length  $\bar{L}_j$  of each species · fish guild  $G_j$ ) to no interaction. Models were fitted in a similar way as Models M1–M2. Model selection was based on evaluating Akaike's information criterion (AIC). Model selection is described in Supporting Information Appendix S1: Table S1.3. The model that best fit the data is presented here:

$$\log_{10}(A_{ijr}) = (\beta_0 + v_{0j} + v_{0r}) + (\beta_W + v_{Wj}) (T_{ijr} - \bar{T}_j) + \beta_{B1} \bar{T}_j + \beta_{B2} \bar{L}_j + \beta_{B3} G_j + \beta_{B4} \bar{T}_j \bar{L}_j + \beta_{B5} \bar{T}_j G_j + e_{0ijr}. \quad (M4)$$

To test the robustness of the predictions in Model M4, we also examined the effects of temperature, guild and asymptotic length on growth coefficient  $A$  in four additional analyses while selecting (a) all teleost data with a  $t_0$  between  $-1$  and  $1$  and elasmobranch data with a  $t_0$  between  $-5$  and  $1$ , (b) the maximum growth coefficient  $A$  for each species, (c) all data while including a phylogenetic covariance matrix, and (d) all data while using the mean temperature of the coldest and warmest calendar quarter per ecoregion instead of a yearly average.

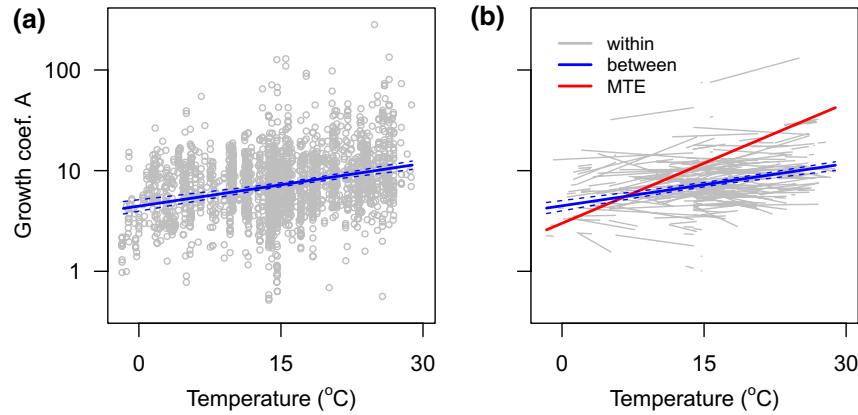
## 2.4.4 | Variation in growth across marine regions

We did not incorporate regional variation in food conditions into our statistical analysis, since our study is focused on the effect of temperature. Yet, we explored whether zooplankton production, zooplankton biomass or net primary production can explain variation in the estimated random ecoregion intercept  $v_{0r}$  taken from the results of Model M4. This was done for all regions where we have data for more than 10 different fish species.

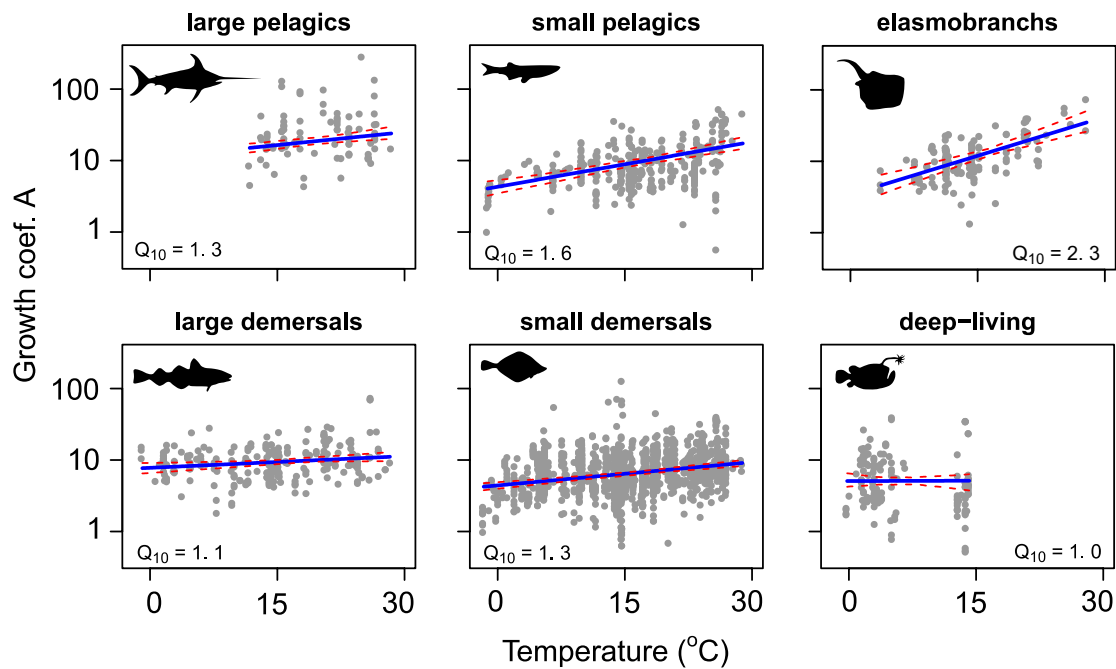
# 3 | RESULTS

## 3.1 | Within- and between-species effects of temperature on growth

Our results show that the average growth coefficient  $A$  between fish species is positively related to temperature when all fish data are pooled ( $Q_{10} = 1.38$ , 95% CI 1.29–1.49, Model M1, Figure 3a). The within-species effect of temperature is weaker ( $Q_{10} = 1.14$ , 95% CI 1.05–1.26, Model M1) than the between-species effect and the difference between the within- and between-species effects is significant ( $p$ -value < .001).



**FIGURE 3** Relationships between growth coefficient  $A$  and temperature. The between-species effect is shown with a blue solid line in (a, b); blue dashed lines show the bootstrapped 95% confidence interval (CI) using the function 'bootMer' in R package 'lme4'. The positive between-species effect of temperature on growth corresponds to a  $Q_{10} = 1.38$ , 95% CI 1.29–1.49 (Model M1), with  $Q_{10}$  describing the relative increase in the rate of growth for each 10 °C increase. The within-species effect of temperature on growth coefficient  $A$  is shown with grey solid lines in (b) based on Model M2 for the temperature range where data are available. The within-species effect corresponds to an average  $Q_{10}$  of 1.08. The red line in (b) illustrates a  $Q_{10}$  of 2.5 that corresponds to a temperature scaling as predicted from metabolic theory (MTE) with  $A$  is 3 at 0 °C



**FIGURE 4** The between-species effect of temperature on growth coefficient  $A$  differs with fish guild and asymptotic length (Model M4). Small pelagic fish and elasmobranchs have the strongest increase with temperature, whereas large demersal and deep-living fish (but note the restricted temperature range for deep-living fish) are weakly affected by temperature. The blue lines show the temperature effect on growth coefficient  $A$  given an average asymptotic length ( $L_{\infty}$ ). The 95% confidence intervals (red dashed lines) are estimated using the function 'bootMer' in R package 'lme4'. The breakpoint between small and large species is, for plotting purposes, set at  $L_{\infty} = 80$  cm.  $Q_{10}$  describes the relative increase in the rate of growth for each 10 °C increase

By allowing between-species variation in the slopes of the within-species effect (Model M2), we find that species differ in how strongly growth coefficient  $A$  depends on temperature (Model M2 provides a better fit to the data than Model M1, see Supporting Information Appendix S1: Table S1.4). The results show that growth

coefficient  $A$  declines for some species with increasing temperature ( $Q_{10} \approx 0.5$ ) and increases strongly for others ( $Q_{10} > 2.0$ ) (Figure 3b and Supporting Information Appendix S1: Figure S1.3). The average within-species relationship between temperature and growth coefficient  $A$  is weak (average  $Q_{10} = 1.08$ , Model M2).



### 3.2 | Role of phylogeny in the between-species effect of temperature on growth

For a subset of 613 fish species for which phylogenetic data were available, we find a similar between-species effect of temperature on growth coefficient  $A$  as in Model M1 without phylogeny ( $Q_{10} = 1.36$ , 95% CI 1.27–1.46). Including phylogenetic signal lowers the between-species effect of temperature on growth coefficient  $A$  ( $Q_{10} = 1.21$ , 95% CI 1.11–1.33, Model M3).

### 3.3 | Role of fish guilds in the between-species effect of temperature

Our results show that the between-species effect of temperature varies as a result of fish feeding guild and fish asymptotic length. We find most support for a model with a two-way interaction between temperature and fish guild and between temperature and asymptotic length (see Supporting Information Appendix S1: Table S1.2). The model predicts that average growth among demersal and deep-living fish (but note the restricted temperature range for deep-living fish) is weakly affected by temperature, whereas average growth among pelagic fish and elasmobranchs increases more strongly (Figure 4). Temperature effects on average growth decline with increasing asymptotic length. Model M4 also estimates between-species variation in the slopes of the within-species effect of temperature on growth coefficient  $A$ . These estimates follow the findings of Model M2 (average within-species  $Q_{10} = 1.08$  for Model M2 and 1.12 for Model M4), despite some variation in individual species (not shown).

Using the outcome of Model M4, we compare average growth for each fish guild across a temperature gradient for two asymptotic lengths (30 and 100 cm; Figure 5). In waters  $< 5^{\circ}\text{C}$ , the average growth of fish with  $L_{\infty} = 100$  cm is equally fast for demersals and deep-living fish (large pelagics are not included as there are no data available on large pelagics in this temperature range), whereas large

elasmobranchs and species with  $L_{\infty} = 30$  cm grow slower. In waters  $> 20^{\circ}\text{C}$ , average growth is highest in large elasmobranchs and pelagic fish, whereas demersal fish grow slower due to a weaker temperature effect on growth.

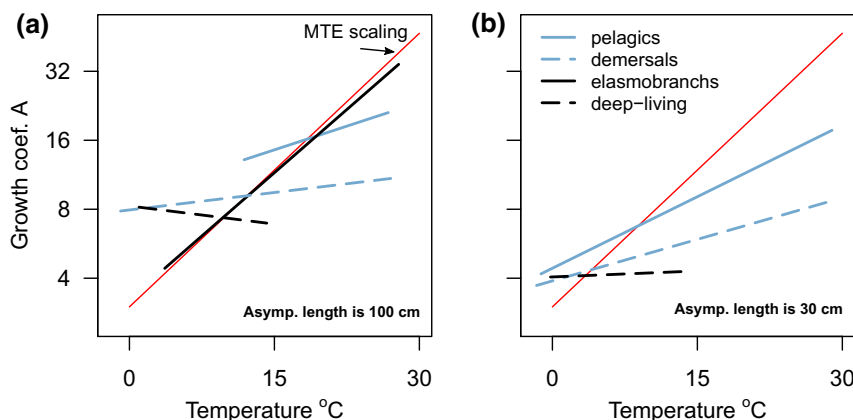
The effect of temperature on the different guilds is robust when compared with other methods of data selection, when corrected for phylogenetic signal or when the coldest or warmest calendar quarter is used instead of a yearly average temperature (Supporting Information Appendix S1: Table S1.5). The  $Q_{10}$  maximally varies  $\pm 0.2$  with the results in the main analysis.

### 3.4 | Growth variability across marine regions

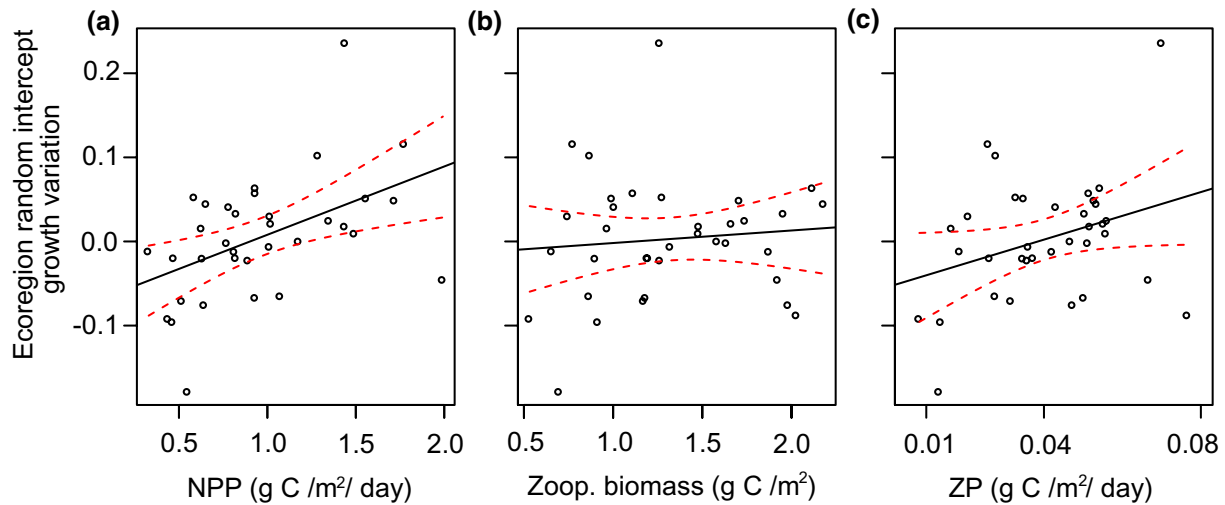
For all regions with data on more than 10 fish species, we find a positive relationship between the estimated random ecoregion intercept ( $v_{0r}$ ) and net primary production (NPP), suggesting that fish, on average, grow faster in regions with high NPP. The results show that the random intercept growth values vary  $\pm 0.1$  over the NPP gradient [ $v_{0r} = -0.07 + 0.08 \text{ NPP}$ ,  $p\text{-value} = .005$ , adjusted  $R^2 = .20$ ; Figure 6a]. This variation in the random intercept corresponds to a 1.3-fold increase in growth coefficient  $A$  over a 4-fold increase in NPP (the 1.3-fold increase is calculated by  $10^{0.09} / 10^{-0.03}$ , since growth coefficient  $A$  is  $\log_{10}$  transformed). There is a weak positive, but non-significant, relationship between the random intercept growth values and zooplankton prey production (ZP) [ $v_{0r} = -0.06 + 1.39 \text{ ZP}$ ,  $p\text{-value} = .07$ , adjusted  $R^2 = .07$ ] and no relationship with zooplankton biomass (Figure 6b,c).

## 4 | DISCUSSION

Our results show weaker within- and between-species effects of temperature on growth of fish than predicted from metabolic theory. The within-species effect of temperature varies between species. The between-species effect of temperature is smaller when corrected for phylogenetic signal and varies with fish guild and



**FIGURE 5** Predicted relationships between fish growth coefficient  $A$  and temperature across guilds for fish with asymptotic length ( $L_{\infty}$ ) = 100 cm (a) or 30 cm (b) based on Model M4. The temperature effect is only shown in the temperature range where data are available. The thin red lines illustrate a  $Q_{10}$  of 2.5 that corresponds to a temperature scaling as predicted from metabolic theory (MTE) with  $A$  is 3 at  $0^{\circ}\text{C}$ .  $Q_{10}$  describes the relative increase in the rate of growth for each  $10^{\circ}\text{C}$  increase



**FIGURE 6** Relationships between the ecoregion random intercept growth values from Model M4 and net primary production (NPP) (a), zooplankton biomass (b) and zooplankton production (ZP) (c). The relationship between the random intercept growth values and NPP is statistically significant [ $v_{0r} = -0.07 + 0.08 \text{ NPP}$ ,  $p$ -value = .005, adjusted  $R^2 = .20$ ] and remains positive and statistically significant when the lowest and highest random intercept values are removed (not shown). The relationships between the random intercept values and zooplankton biomass and production are not significant. Red dashed lines show the 95% confidence interval

asymptotic length. Net primary production has a positive effect on the average growth of fish. Below we first discuss the consequences of our findings for models predicting the responses of fish to climate warming. This section is followed by a more general discussion.

#### 4.1 | Consequences for models predicting the responses of fish to climate warming

The effects of changing temperatures with climate change on ectotherms are often predicted with a high temperature sensitivity of all physiological rates, including growth. Yet, based on our results, it is likely that there is a strong limit to the increase in growth with temperature as we find weak within- and between-species effects of temperature in natural environments. Our results hence suggest that the effect of temperature on growth is exaggerated in most climate change projections.

We suggest that our results can be used as an upper boundary, that is, reflecting the situation where community re-assembly and temperature adaptations have run their course, for predictions of the long-term effect of climate warming on fish growth. Most likely, average growth will initially decrease with warming due to higher metabolic demands (Dillon, Wang & Huey, 2010; Huey & Kingsolver, 2019). We can expect that the higher metabolic demands drive adjustments in fish life histories to counteract the effects of the new temperature regime. At the within-species level, these adjustments may occur through acclimatization and adaptations (Seebacher, White & Franklin, 2014). At the between-species level, adjustments may occur through community re-assembly generated by emigration, immigration and extirpation of species (Zhang, Takahashi, Hartvig &

Andersen, 2017). Some of these processes, such as fish migrations to new environments, thermal plasticity or a restructuring of ecological interactions, seem to occur fast (Frainer et al., 2017; Pinsky, Worm, Fogarty, Sarmiento & Levin, 2013; Seebacher et al., 2014), suggesting that average fish growth in ecosystems is probably not much (positively or negatively) affected in the long term by temperature change with climate change. Yet, other climate change impacts, such as changes in primary and secondary production (Stock et al., 2017), may affect growth rates and fish life histories with climate change. Additionally, for invading fish to establish a viable population in the new area they must be able to complete their life cycle. Life cycle completion will depend on several conditions, including the availability of suitable spawning locations that enable the larvae to encounter sufficient food and adequate transport to suitable nursery areas.

Despite the weak effects of warming on growth, fish still need to cope with a higher metabolism. Basal metabolism is predicted to increase with temperature with a  $Q_{10} \approx 2.5$  (Brown et al., 2004), whereas resting metabolism across teleost fish species has been found to increase with a  $Q_{10} \approx 1.8$  (Clarke & Johnston, 1999). Individual fish hence need to consume more food per unit time in warmer waters. Increased consumption in warmer waters may be achieved by increased enzymatic activities and hence digestive capacity, or enhanced activity levels [e.g., higher velocity (Dell, Pawar & Savage, 2014) or lower water viscosity] and hence higher clearance rates. Higher activity and metabolic levels will decrease trophic efficiency (Barneche & Allen, 2018). Therefore, despite limited change in average growth for some fish guilds, their ecological performance changes towards faster but less efficient transfer of energy in warmer systems. This will likely decline the biomass of populations and communities and potential fisheries production, *sensu* Lotze et al. (2019).



## 4.2 | The temperature response is weaker than the metabolic predictions

We hypothesized that the typical within-species effect of temperature on growth is stronger, and hence closer to the metabolic predictions, than the between-species effect, which is lower due to evolutionary adaptation. We find no support for our hypothesis as the within-species effect is generally weaker than the between-species effect, despite substantial variation between species in the within-species effect of temperature on growth. From our analysis, we are unable to determine if the within-species response is weak simply as a result of constraints on food availability (or other ecological factors) or due to counter gradient variation in growth. The latter would imply genetic variation within species that counteracts the effects of temperature (Conover & Present, 1990).

The between-species effect of temperature on growth is also weaker than the metabolic predictions and varies between fish guilds. Growth in elasmobranchs and, to a lesser extent, small pelagics largely follows the metabolic predictions, whereas growth in large demersal fish is weakly dependent on temperature ( $Q_{10}$  of 1.1, with data spanning a 30 °C temperature range). If the weak temperature effect on large demersal fish is just a constraint on food availability (or any other ecological factor), it would imply that large demersal fish species in warm water have a metabolic capacity to grow that is approximately 15 times higher ( $Q_{10} = 2.5$  over a 30 °C temperature gradient) than their observed growth. This overcapacity is unlikely without costs (Clarke, 2003) and we expect natural selection to have operated; warmer habitats select for life histories with a lower temperature-corrected growth capacity.

The between-species effect of temperature is lower when corrected for phylogenetic signal, suggesting that at low and/or high temperatures a phylogenetic group is dominant and driving the slope of the overall relationship. We expect that this is because fast-growing large pelagic fish, which are phylogenetically related (Rabosky et al., 2018), mainly occur in warm waters. Potentially, slow-growing deep-living fish may be important for the phylogenetic predictions in cold waters, but their phylogenetic relatedness is less strong.

The weak within- and between-species effects of temperature on growth do not invalidate temperature effects as predicted by metabolic theory at the individual level. It may be expected that any fish under laboratory conditions, or with climate warming, may initially increase its growth rate with temperature in a manner consistent with metabolic theory. Such increases of fish growth have been observed in temperature-size rule experiments (Atkinson, 1994). Our work rather suggests that the growth trajectories with temperature as predicted by metabolic theory are not sustainable in an ecosystem context, potentially the result of evolutionary adaptation of species to their habitats and selection of life histories through community assembly. The weak between-species effects of temperature on growth, relative to the metabolic predictions, confirm some earlier studies [Sibly et al. (2015) with a  $Q_{10}$  of 1.5 and Edgar & Shaw (1995) with a  $Q_{10}$  of 1.7 through the range 15–25 °C], whereas Clarke (2017) found a stronger temperature-sensitivity of growth ( $Q_{10}$  of 2).

Our results provide a potential explanation for these variable results as we observe that growth-temperature relationships vary with asymptotic size, fish guild and phylogeny and hence depend on the fish species and predictor variables examined.

## 4.3 | The effect of food availability on growth

We find a positive effect of net primary production on average fish growth (a 4-fold increase in NPP leads to a 1.3-fold increase in growth) and no relationship between growth and zooplankton production or biomass. The weak positive correlation between net primary production and fish growth is supported by a recent global analysis of reef fish growth, where growth variation of reef fish species weakly increased with regional variation in net primary production (Morais & Bellwood, 2018). The absence of a relationship between zooplankton biomass and growth is surprising. The absence of such a relationship may be related to uncertainty in the prey biomass estimates and to uncertainty regarding the extent to which our modelled data reflect the actual food availability. Alternatively, growth rates may be partly decoupled from prey availability as fish do not optimize growth but fitness (Giacomini, Shuter & Lester, 2013). Because feeding often is associated with a higher predation risk, fish may tend to prioritize a reduction in predation mortality over increased growth rate when resources are abundant (Biro, Post & Abrahams, 2005).

## 4.4 | Data uncertainty

Previous work that evaluated the precision and accuracy of FishBase has suggested that the database entries of life history parameters in FishBase often are unbiased even though they are imprecise (Thorson, Cope & Patrick, 2014). Ideally, we should have included parameter imprecision in our analysis by adding error estimates of the von Bertalanffy parameters to our models. Yet, these error estimates are not recorded in FishBase, and, they are often not reported in the more historical 'source' publications either. Without these error estimates, our analyses have likely reduced power and increased unexplained variance, but we expect that the slopes of the temperature-growth relationships are unbiased. The use of average ambient temperatures is another source of uncertainty as temperature varies within a region and fish may migrate between regions. Fish are further not uniformly distributed within an ecoregion, but rather occupy a particular habitat subset that may differ in its temperature characteristics (Guzzo, Blanchfield, & Rennie, 2017). Nevertheless, our results are robust against some temperature variation, which is exemplified by little difference in  $Q_{10}$  when using the coldest or warmest calendar quarter per ecoregion instead of a yearly average (Supporting Information Appendix S1: Table S1.5). Many of the fish species in our analysis are exploited and fishing is another source of uncertainty as it can influence growth rates by removing conspecifics, thus decreasing density-dependent growth. The impact of fishing could result in biased growth-temperature

estimates, if, in our database, fish in warmer systems are consistently less exploited than fish in colder waters. We are not aware of studies that suggest such a pattern.

Our statistical analyses did not consider potential nonlinearities in the shape of the growth curve with temperature. Temperatures experienced in the field may exceed the performance peak of a species, which can make the linear growth–temperature curve flat. There were no indications that such nonlinear within-species relationships between growth and temperature were generic. A separate species-specific analysis shows support for a decline at the warmer edge in 6 out of 46 fish species with highest quality data (Supporting Information Appendix S4: Figure S4.1). There was no support for a nonlinear between-species relationship between temperature and growth (Supporting Information Appendix S4).

## 4.5 | Conclusion

Our results show weak within- and between-species effects of temperature on growth that do not match metabolic predictions. These findings indicate that metabolic models of the effects of temperature on growth will overestimate the effect of temperature when the models are used to examine the effect of temperature on growth in space (across ecosystems) or in time (temperature change with climate change). Our results suggest that a proper understanding of how fish growth changes globally in response to climate change not only requires a correct description of the physiological response to temperature (Lefevre, McKenzie & Nilsson, 2017), but also of the ecological dynamics and phylogenetic constraints. It is crucial to understand the processes of environmental and ecological filtering that select the set of viable combinations of life history characteristics in a given environment and temperature.

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## DATA AVAILABILITY STATEMENT

All data used for the analyses, including the von Bertalanffy fish growth parameters (as downloaded on 27 April 2018 from 'rfishbase'), and code for all data analyses are available on github with <https://doi.org/10.5281/zenodo.1455234>.

## ORCID

Daniël van Denderen  <https://orcid.org/0000-0001-6351-0241>

Henrik Gislason  <https://orcid.org/0000-0003-0242-3333>

## REFERENCES

- Andersen, K. H. (2019). *Fish ecology, evolution, and exploitation*. Princeton, NJ; Oxford, UK: Princeton University Press.
- Arendt, J. D. (1997). Adaptive intrinsic growth rates: An integration across taxa. *The Quarterly Review of Biology*, 72(2), 149–177.
- Atkinson, D. (1994). Temperature and organism size: A biological law for ectotherms? *Advances in Ecological Research*, 25, 1–58.
- Barneche, D. R., & Allen, A. P. (2018). The energetics of fish growth and how it constrains food-web trophic structure. *Ecology Letters*, 21(6), 836–844.
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67(1), 1–48.
- Behrenfeld, M. J., & Falkowski, P. G. (1997). Photosynthetic rates derived from satellite-based chlorophyll concentration. *Limnology and Oceanography*, 42(1), 1–20.
- Biro, P. A., Post, J. R., & Abrahams, M. V. (2005). Ontogeny of energy allocation reveals selective pressure promoting risk-taking behaviour in young fish cohorts. *Proceedings of the Royal Society B: Biological Sciences*, 272(1571), 1443–1448.
- Blanchard, J. L., Jennings, S., Holmes, R., Harle, J., Merino, G., Allen, J. I., ... Barange, M. (2012). Potential consequences of climate change for primary production and fish production in large marine ecosystems. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367(1605), 2979–2989.
- Boettiger, C., Lang, D. T., & Wainwright, P. C. (2012). rfishbase: Exploring, manipulating and visualizing FishBase data from R. *Journal of Fish Biology*, 81(6), 2030–2039.
- Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., & West, G. B. (2004). Toward a metabolic theory of ecology. *Ecology*, 85(7), 1771–1789.
- Carozza, D. A., Bianchi, D., & Galbraith, E. D. (2019). Metabolic impacts of climate change on marine ecosystems: Implications for fish communities and fisheries. *Global Ecology and Biogeography*, 28(2), 158–169.
- Chang, J., Rabosky, D. L., Smith, S. A., & Alfaro, M. E. (2019). An R package and online resource for macroevolutionary studies using the ray-finned fish tree of life. *Methods in Ecology and Evolution*, 10(7), 1118–1124.
- Charnov, E. L., Gislason, H., & Pope, J. G. (2013). Evolutionary assembly rules for fish life histories. *Fish and Fisheries*, 14(2), 213–224.
- Cheung, W. W. L., Bruggeman, J., & Butenschön, M. (2018). Projected changes in global and national potential marine fisheries catch under climate change scenarios in the twenty-first century. In M. Barange, T. Bahri, M. C. Beveridge, K. L. Cochrane, S. Funge-Smith, & F. Poulain (Eds.) *Impacts of climate change on fisheries and aquaculture: synthesis of current knowledge, adaptation and mitigation options* (pp. 63–86). Rome, Italy: FAO.
- Cheung, W. W. L., Sarmiento, J. L., Dunne, J., Frölicher, T. L., Lam, V. W. Y., Deng Palomares, M. L., ... Pauly, D. (2013). Shrinking of fishes exacerbates impacts of global ocean changes on marine ecosystems. *Nature Climate Change*, 3, 254–258.
- Clarke, A. (2003). Costs and consequences of evolutionary temperature adaptation. *Trends in Ecology and Evolution*, 18(11), 573–581.
- Clarke, A. (2017). *Principles of thermal ecology - Temperature, energy and life*. Oxford, UK: Oxford University Press.
- Clarke, A., & Johnston, N. M. (1999). Scaling of metabolic rate with body mass and temperature in teleost fish. *Journal of Animal Ecology*, 68(5), 893–905.
- Compagno, L. J. V. (2008). Pelagic elasmobranch diversity. In M. D. Camhi, E. K. Pikitch, & E. A. Babcock (Eds.) *Sharks of the open ocean: Biology, fisheries and conservation* (pp. 14–23). Oxford, UK; Ames, IA; Carlton, Australia: Blackwell Publishing.
- Conover, D. O., & Present, T. M. C. (1990). Countergradient variation in growth rate: compensation for length of the growing season among Atlantic silversides from different latitudes. *Oecologia*, 83(3), 316–324.

- Dell, A. I., Pawar, S., & Savage, V. M. (2014). Temperature dependence of trophic interactions are driven by asymmetry of species responses and foraging strategy. *Journal of Animal Ecology*, 83(1), 70–84.
- Dillon, M. E., Wang, G., & Huey, R. B. (2010). Global metabolic impacts of recent climate warming. *Nature*, 467(7316), 704–706.
- Edgar, G. J., & Shaw, C. (1995). The production and trophic ecology of shallow-water fish assemblages in southern Australia I. Species richness, size-structure and production of fishes in Western Port, Victoria. *Journal of Experimental Marine Biology and Ecology*, 194(1), 53–81.
- Felsenstein, J. (1985). Phylogenies and the comparative method. *The American Naturalist*, 125(1), 1–15.
- Frainer, A., Primicerio, R., Kortsch, S., Aune, M., Dolgov, A. V., Fossheim, M., & Aschan, M. M. (2017). Climate-driven changes in functional biogeography of Arctic marine fish communities. *Proceedings of the National Academy of Sciences USA*, 114(46), 12202–12207.
- Froese, R. (2006). Cube law, condition factor and weight-length relationships: history, meta-analysis and recommendations. *Journal of Applied Ichthyology*, 22(4), 241–253.
- Froese, R., & Pauly, D. (2018). *FishBase world wide web electronic publication*. www.fishbase.org, version (10/2018).
- Giacomini, H. C., Shuter, B. J., & Lester, N. P. (2013). Predator bioenergetics and the prey size spectrum: Do foraging costs determine fish production? *Journal of Theoretical Biology*, 332, 249–260.
- Grady, J. M., Enquist, B. J., Dettweiler-Robinson, E., Wright, N. A., & Smith, F. A. (2014). Evidence for mesothermy in dinosaurs. *Science*, 344(6189), 1268–1272.
- Guzzo, M. M., Blanchfield, P. J., & Rennie, M. D. (2017). Behavioral responses to annual temperature variation alter the dominant energy pathway, growth, and condition of a cold-water predator. *Proceedings of the National Academy of Sciences USA*, 114(37), 9912–9917.
- Hadfield, J. D. (2010). MCMC methods for multi-response generalized linear mixed models: The MCMCglmm R package. *Journal of Statistical Software*, 33(2), 1–22.
- Huey, R. B., & Kingsolver, J. G. (2019). Climate warming, resource availability, and the metabolic meltdown of ectotherms. *The American Naturalist*, 194(6), E140–E150.
- Jobling, M. (1997). Temperature and growth: Modulation of growth rate via temperature change. *Seminar Series-Society for Experimental Biology*, 61, 225–254.
- Kingsolver, J. G. (2009). The well-temperated biologist. *The American Naturalist*, 174(6), 755–768.
- Kremer, C. T., Thomas, M. K., & Litchman, E. (2017). Temperature- and size-scaling of phytoplankton population growth rates: Reconciling the Eppley curve and the metabolic theory of ecology. *Limnology and Oceanography*, 62(4), 1658–1670.
- Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). lmerTest package: Tests in linear mixed effects models. *Journal of Statistical Software*, 82(13), 1–26.
- Lefevre, S., McKenzie, D. J., & Nilsson, G. E. (2017). Models projecting the fate of fish populations under climate change need to be based on valid physiological mechanisms. *Global Change Biology*, 23(9), 3449–3459.
- Lotze, H. K., Tittensor, D. P., Bryndum-Buchholz, A., Eddy, T. D., Cheung, W. W. L., Galbraith, E. D., ... Worm, B. (2019). Global ensemble projections reveal trophic amplification of ocean biomass declines with climate change. *Proceedings of the National Academy of Sciences USA*, 116(26), 12907–12912.
- Morais, R. A., & Bellwood, D. R. (2018). Global drivers of reef fish growth. *Fish and Fisheries*, 19(5), 874–889.
- O'Gorman, E. J., Petchey, O. L., Faulkner, K. J., Gallo, B., Gordon, T. A. C., Neto-Cerejeira, J., ... Woodward, G. (2019). A simple model predicts how warming simplifies wild food webs. *Nature Climate Change*, 9(8), 611–616.
- Pinsky, M. L., Worm, B., Fogarty, M. J., Sarmiento, J. L., & Levin, S. A. (2013). Marine taxa track local climate velocities. *Science*, 341(6151), 1239–1242.
- Rabosky, D. L., Chang, J., Title, P. O., Cowman, P. F., Sallan, L., Friedman, M., ... Alfaro, M. E. (2018). An inverse latitudinal gradient in speciation rate for marine fishes. *Nature*, 559(7714), 392–395.
- Seebacher, F., White, C. R., & Franklin, C. E. (2014). Physiological plasticity increases resilience of ectothermic animals to climate change. *Nature Climate Change*, 5, 61–66.
- Sibly, R. M., Baker, J., Grady, J. M., Luna, S. M., Kodric-Brown, A., Venditti, C., & Brown, J. H. (2015). Fundamental insights into ontogenetic growth from theory and fish. *Proceedings of the National Academy of Sciences USA*, 112(45), 13934–13939.
- Spalding, M. D., Fox, H. E., Allen, G. R., Davidson, N., Ferdeña, Z. A., Finlayson, M., ... Robertson, J. (2007). Marine ecoregions of the world: A bioregionalization of coastal and shelf areas. *BioScience*, 57(7), 573–583.
- Stock, C. A., Dunne, J. P., & John, J. G. (2014). Global-scale carbon and energy flows through the marine planktonic food web: An analysis with a coupled physical-biological model. *Progress in Oceanography*, 120, 1–28.
- Stock, C. A., John, J. G., Rykaczewski, R. R., Asch, R. G., Cheung, W. W. L., Dunne, J. P., ... Watson, R. A. (2017). Reconciling fisheries catch and ocean productivity. *Proceedings of the National Academy of Sciences USA*, 114(8), E1441–E1449.
- Thorson, J. T., Cope, J. M., & Patrick, W. S. (2014). Assessing the quality of life history information in publicly available databases. *Ecological Applications*, 24(1), 217–226.
- van de Pol, M., & Wright, J. (2009). A simple method for distinguishing within-versus between-subject effects using mixed models. *Animal Behaviour*, 77(3), 753–758.
- Von Bertalanffy, L. (1957). Quantitative laws in metabolism and growth. *The Quarterly Review of Biology*, 32(3), 217–231.
- West, G. B., Brown, J. H., & Enquist, B. J. (2001). A general model for ontogenetic growth. *Nature*, 413(6856), 628–631.
- Zhang, L., Takahashi, D., Hartvig, M., & Andersen, K. H. (2017). Food-web dynamics under climate change. *Proceedings of the Royal Society B: Biological Sciences*, 284(1867), 20171772.
- Zuur, A., Ieno, E. N., Walker, N., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. New York, NY: Springer Science & Business Media.

## BIOSKETCH

**Daniël van Denderen** is a postdoctoral researcher at the Centre for Ocean Life in Denmark. His research focuses on the importance of pelagic and benthic habitats for marine fish communities, food webs and fisheries production. The Centre for Ocean Life, where most of the authors are affiliated, aims to develop mechanistic trait-based approaches to study life in the ocean.

## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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