Little difference in average fish growth and maximum size across temperatures

P. Daniël van Denderen[1], Henrik Gislason[1] and Ken H. Andersen[1]

[1] Centre for Ocean Life, National Institute of Aquatic Resources, Technical University of Denmark, Kemitorvet B-202, 2800 Kongens Lyngby, Denmark

Corresponding author: P. Daniël van Denderen; E-mail: pdvd@aqua.dtu.dk; Address: Technical University of Denmark, Kemitorvet B-202, 2800 Kongens Lyngby, Denmark

Abstract

Ectotherms typically increase growth and reduce body size when temperature increases. This physiological response to temperature, termed the temperature-size rule (TSR), is often used to predict how rising temperatures with climate change will affect higher levels of organization, *i.e.* guilds, communities and ecosystems. However, such predictions disregard 1) possible systematic differences in the life histories (and thus growth rates) of species selected by colder and warmer environments and 2) variation in food availability that may offset the temperature response on growth. Here we examine whether faster growth and reduction in adult body size are observed with temperature across marine fish in natural communities from polar to tropical regions. We find no effect of increasing temperature on the average asymptotic body length of fish species present in ecosystems and only a limited increase in average growth of fish species in warmer systems ($Q_{10} = 1.4$). When analyzed per fish guild, average asymptotic lengths are largely constant across temperature, whereas growth responses vary from nearly independent of temperature in large demersals ($Q_{10} = 1.2$) to positive in small pelagics ($Q_{10} = 1.7$) and elasmobranchs ($Q_{10} = 1.9$). The limited change in average growth and asymptotic length across ecosystems in some fish guilds shows that the ultimate response of ectotherms to changing temperature cannot be predicted exclusively from the TSR. Since average growth is only weakly affected by regional variation in food availability, our results suggest that colder and warmer environments select for different life histories of coexisting species. This highlights that the long term response of fish communities to rising temperatures may be characterized more by acclimatization, evolutionary adaptation, local extinctions and invasions than by the immediate temperature response of the present species.

Keywords: Climate change, ectotherms, metabolic theory, teleost fish, temperature response

Introduction

Most organisms are ectotherms and their physiological response to temperature has often been used to infer how their growth would respond to changing temperatures with climate change. For ectotherms, ontogenetic growth (hereafter growth) within a species is typically increasing with temperature to a certain optimum after which growth decelerates (Kingsolver 2009). The increase in growth is predicted to scale with temperature in the same way as metabolic rates and with a ≈2.5-fold increase for each 10°C increase in temperature (Brown et al. 2004, Grady et al. 2014). Faster growth at higher temperature is normally associated with a reduction in adult body size and the combined response is referred to as the temperature-size rule (TSR) (Atkinson 1994). Used in a climate-change context, the TSR predicts that a net increase in temperature leads to faster growth and shrinking of adult body size. These changes are predicted to initiate loss of diversity and reductions in production (Sheridan and Bickford 2011, Cheung et al. 2013).

While changes in growth and adult body size with temperature are observed in many within-species studies (Atkinson 1994, Angilletta et al. 2004, Daufresne et al. 2009), it is unclear whether the TSR translates into a community response with faster average growth and smaller average adult body sizes at higher temperatures. At least three other processes could affect the community response: acclimatization, local extinctions and invasions, and evolutionary adaptation. These processes may affect average growth and adult body size of species in an ecosystem similar to the TSR, but they may also work in the opposite direction (Ohlberger 2013). Previous work has shown that it is possible for ectotherms to grow relatively fast in cold waters (Clarke 1983, 2003) and that evolutionary adaptation may offset the effect of temperature on body size and physiological rates (Clarke and Johnston 1999, Belk and Houston 2002, Kingsolver and Huey 2008). Such adaptations are likely to be driven by community assembly processes, where species are selected according to how well they are adapted to a given environment. Community assembly may therefore override the short-term physiological response to temperature change such that average growth and body size no longer follow the TSR predictions.

Here we examine whether faster average growth and reduction in average adult body size are consistently observed with increasing temperature across marine fish guilds (where guild is defined as a group of species that exploit the same resource and have a similar ecological niche). Previous studies on marine fish support to some extent that the interspecific response could be in line with the TSR predictions. Studies have found that average fish growth is faster in warmer waters (Sibly et al. 2015, Clarke 2017), even though the rate of increase with temperature is lower than predicted from metabolic theory. Furthermore, the average maximum body length of fish species has been found to increase with latitude in some oceanic regions (Fisher et al. 2010a). However, the variability around the average response is high in these studies. We hypothesize that much of this variability arises because large-scale comparisons ignore differences in guilds. Some fish guilds may be characterized by limited temperature ranges, e.g. deep sea fish mainly occur in cold waters, while other guilds may extend over a wide temperature range. Fish within a guild, may also have a guild-specific response to temperature, due to (guild-specific) life-history strategies (Killen et al. 2016). In addition to the possible effect of fish guilds, we hypothesize that changes in food availability across regions could offset the physiological temperature effect on growth rate, as growth ultimately depends on the rate of energy acquisition throughout ontogeny.

The aims of this paper are (1) to describe empirical relationships between temperature and average growth and asymptotic length across marine fish from polar to tropical environments;

(2) to test whether relationships between temperature and average growth and asymptotic length depend on fish guild; (3) to test whether relationships between temperature and average growth depend on food availability.

Methods

We use the von Bertalanffy growth model to describe fish growth and asymptotic body length. The model describes the rate of growth in body weight, d*w*/d*t*, as the difference between acquisition of energy, Aw^n, and losses, kw (Von Bertalanffy 1957):

$$\frac{\mathrm{d}w}{\mathrm{d}t} = Aw^n - kw^1. \qquad \text{eq. 1}$$

The coefficients *A* and *k* 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 $n = 2/3$, whereas losses can be assumed to scale linearly with weight. Modern interpretations of eq. 1 use $n = 3/4$ (West et al. 2001), but we use 2/3 because it conforms with available data (see later), and the exact value of *n* is of limited importance in this context. With a 2/3 exponent, asymptotic weight of a fish is:

$$W_\infty = \left(\frac{A}{k}\right)^{1/(1-n)} = \left(\frac{A}{k}\right)^3. \qquad \text{eq. 2}$$

The coefficients, *A* and *k*, can each be interpreted as characterizing different aspects of ecology and bioenergetics. *A* depends on the amount of encountered food and the digestive capacity of the fish: the more food is encountered, the more energy is available, up to the limit that can be processed. If the specific dynamic action associated with the intake of the food is also assumed to scale with exponent *n*, then *A* will be reduced accordingly. "*k*" may be interpreted as weight-specific reproductive output (West et al. 2001, Lester et al. 2004) and basal metabolism (Ursin 1967), possibly combined with activity metabolism (Andersen and Beyer 2015).

Depending upon the exact interpretation of *A* and *k* and upon the effects of temperature on food encounter, digestive capacity, and metabolism, three broad hypotheses about how temperature affects growth rates and asymptotic weight can be formulated: 1) *A* is not affected by temperature and *k* increases with temperature. This could happen if *A* is mainly determined by encounter with food and *k* represents metabolic processes. In that case, fish growth rates are weakly affected by temperature at body weights much smaller than asymptotic weight, whereas growth rates closer to asymptotic weight and asymptotic weight decrease with temperature. 2) If *A* and *k* are equally affected by temperature, e.g. if they are both governed by metabolic processes, then growth rates increase with temperature, whereas asymptotic weight is unaffected. 3) Finally, if *k* increases faster with temperature than *A*, warm-water fish will grow faster and have a smaller asymptotic weight (resembling the TSR response). The effect of temperature on *A* will also depend on the availability of food. We can expect that an increase in prey biomass will increase *A*, at least until *A* becomes limited by digestive capacity. Since fish from different guilds (may) have different clearance rates, prey types and metabolic rates, we further expect changes in *A* with temperature across individuals from different guilds. All the above expectations are based on an individual (physiological) response to temperature and food availability. This ignores community-level processes, such as predation and resource competition, that may select species according to whether they are well adapted to an environment. These community assembly processes may select for growth rates and asymptotic weights that differ from the physiological responses to temperature. Selection may result in average growth rates and asymptotic weights in ecosystems with different temperatures that may not reflect the immediate physiological responses to temperature.

To examine the effects of temperature on the average growth rate and adult body size of fish guilds across regions, we used data to calculate growth coefficient A and asymptotic body size and derived estimates of temperature, fish guilds and food availability.

Growth coefficient and asymptotic body size

Growth from length-at-age data in the marine fish literature has generally been estimated with von Bertalanffy L_∞ and K parameters. The von Bertalanffy L_∞ and K parameters can be used to derive the growth coefficient A, when assuming a 2/3 exponent and the standard relation between length and weight $w=cl^3$, as equation 1 can be rewritten in the length-based form:

$$\frac{\mathrm{d}l}{\mathrm{d}t} = K(L_\infty - l), \qquad \text{eq. 3}$$

where L_∞ is the asymptotic length and $K = 3k = 1/3Ac^{-1/3}/L_\infty$ is the von Bertalanffy growth constant with dimension time^{-1}. With the condition factor c assumed to be a constant across fish species (c = 0.01), the relation displays that growth coefficient $A = c^{1/3}3KL_\infty = 0.65KL_\infty$. The estimation of A avoids the use of von Bertalanffy growth constant K as a measure of growth and hence avoids interdependency of K and L_∞ (Appendix S1: Fig. S1). We use the asymptotic length L_∞ as a measure of asymptotic body size. We verified in Appendix S2 that a species-specific length-weight relationship gives consistent results.

We extracted von Bertalanffy L_∞ and K parameters from FishBase (Froese and Pauly 2018) on 27 April 2018 for all marine fish species using rfishbase (Boettiger et al. 2012). We selected fish species where the von Bertalanffy parameters (L_∞ and K) were reported and where t_0, describing the point in time where fish have zero length, was in the range [-2, 2] as a t_0 outside this range indicates a poor data fit and/or a systematic error in the procedure to estimate fish age. When

FishBase provided the sampling locality, we manually linked it to a particular marine ecoregion, or to two neighboring ecoregions (Spalding et al. 2007). 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 freshwater and *Rhincodon typus* (whale shark), which is much larger than any other species in the data. This resulted in 2502 observations of L_∞ and K representing 774 species in 165 ecoregions (Fig. 1).

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 (seaaroundus.org) (Appendix S1: Table S1). When fish were not classified in the SeaAroundUs project, we used the feeding type/habitat description from FishBase and checked for elasmobranchs. The classification of fish into one of these four main guilds ignores differences in asymptotic length that also determines a guild/ecological niche (prey versus predator species). Rather than dividing each fish guild into a few asymptotic length categories, we included the effect of asymptotic length as a continuous variable.

Environmental temperature

We derived temperature estimates for each ecoregion from a global earth system model (GFDL-ESM2.6), as described in (Stock et al. 2017). The model is based on a high-resolution physical climate simulation model, coupled to a Carbon, Ocean Biogeochemistry and Lower Trophics (COBALT) planktonic ecosystem model (Stock et al. 2014). The model-derived temperature estimates match with temperature data from the World Ocean Atlas (correlation coefficient for sea surface temperature = 0.997) (Stock et al. 2017). Modeled temperatures on a 1 degree grid were used to calculate for each ecoregion the average temperature in the upper 100 meter (ambient temperature for pelagic fish), the average at bottom depths < 500 meter (ambient temperature for demersal fish and elasmobranchs) and the average at bottom depths >= 500 meter (ambient temperature for deep-living fish). In ecoregions without grid cells < 500 meter of depth (the 1 degree grid is coarse for areas with a small shelf), we predicted the temperature at bottom depths < 500 meter based on the relationship between bottom temperature < 500 meter and temperature in the upper 100 meter found for the other ecoregions (regression analysis shows $y = 0.01 + 0.94x$; $r^2 = 0.97$).

Zooplankton and benthic food availability

We derived estimates of zooplankton and benthic biomass for each ecoregion. Zooplankton biomass was derived using COBALT output on a 1 degrees grid from the global earth system model (GFDL-ESM2.6). The zooplankton biomass conditions have been shown to match with zooplankton biomass observations (correlation coefficient = 0.65) (Stock et al. 2017). The model includes zooplankton prey biomass estimates for three different size groups: microzooplankton (< 200 µm), zooplankton representing small to medium sized copepods (0.2–2.0 mm) and zooplankton representing large copepods and krill (2.0–20 mm). Fish mainly feed on medium and large-sized zooplankton and these groups were combined to estimate zooplankton biomass density (gr C m^{-2}) in the upper 100 meter of the water column. The biomass estimates of zooplankton in the model do take into account mortality from fish predation (parameterized using a density dependent closure term). Hence, our zooplankton prey biomass estimates reflect, as much as possible, the zooplankton concentrations that fish perceive in a particular region.

Benthic biomass was taken from a global statistical model of macrofauna invertebrate biomass (gr C m^{-2}) on a 1 degrees grid (Wei et al. 2011) and only the shallow water (< 500 meter) benthic biomass estimates were included. In regions without information on benthic biomass < 500 meter (because of a small shelf in combination with a 1 degree grid), values were predicted based on the relationship between shallow biomass and biomass >= 500 meter found for the other ecoregions (regression analysis shows $\log_{10}(y) = 0.25 + 0.68\log_{10}(x)$; $r^2 = 0.62$).

Data analysis

The effects of temperature, fish guild and food availability on growth coefficient *A* and asymptotic length were examined in a stepwise process (Table 1). For each statistical analysis, we examined the across-species response. We did not examine the within-species response, as there were only 1 or 2 observations for ~70% of the species. The across-species response was examined with a resampling procedure to incorporate variation in the number of observations per species. The resampling was done by randomly picking one observation per species with replacement to estimate model parameters and by repeating the resampling 5000 times to evaluate variation in parameter estimates. In each analysis, growth coefficient *A* and asymptotic length were $\log_{10}$ transformed. The temperature effect was examined on a °C scale and Q_{10} was estimated (the use of inverse temperature following the Arrhenius equation gives similar outcomes in terms of model selection and almost similar parameter estimates; not shown).

We first analyzed the relationships between temperature and growth coefficient *A* (Table 1-M1) and asymptotic length (Table 1-M2) using a linear model. We compared the model to a null model without the temperature effect. Model selection was based on evaluating the Akaike's Information Criterion (AIC) within the resampling procedure, and the final model was selected as the model that fitted the data in the 5000 simulations best. From the final model, we derived the mean of the estimates from the resampling procedure. Afterwards, we examined the effect of temperature, fish guild and asymptotic length on fish growth (*A*) with different linear models that varied from a three-way interaction between predictor variables to no interaction (Table 1-M3). For each model, we also included t_0 as a predictor variable as part of the growth variation might be dependent on the estimated point in time where fish have zero length. We performed a similar analysis on asymptotic length, while incorporating temperature and fish guild as predictor variables (t_0 was not included as it is only affects growth and not asymptotic length) (Table 1-M4). Lastly, we tested for the effects of food availability. The effect of food availability on growth was only determined for a subset of the fish guilds as (modeled) data on prey availability are difficult to obtain. Since small pelagic fish ($L_\infty < 50$ cm) primarily feed on zooplankton prey throughout their life, zooplankton biomass was assumed to be a proxy for food availability for small pelagics (Table 1-M5). Similarly, benthic biomass was assumed to be a proxy for food availability for small demersals (Table 1-M6). Pelagic and demersal species with larger asymptotic lengths and the other fish guilds were not included in the food availability analysis.

To test the robustness of the patterns, we included different alternative analyses. We examined the effects of temperature on A and L_∞ while selecting *i)* all data with $t_0 \pm 1$, *ii)* the maximum growth coefficient A for each species, and *iii*) using a re-sampling procedure to evaluate model performance when randomly picking 80% of the species (Appendix S1: Table S2-3). We further tested how small pelagic and demersal growth varies with estimates of prey production, instead of prey biomass (Appendix S1: Table S4).

The classification of fish species into different guilds, the coupling of sampling localities to marine ecoregions, ecoregion environmental conditions, the von Bertalanffy parameters (as downloaded on 27 April 2018 from rfishbase) and code for all data analyses are available on github with DOI: http://doi.org/10.5281/zenodo.1455235.

Results

Effects of temperature on growth

Our results show that the average growth coefficient A among fish is positively related to temperature when all fish data is pooled ($Q_{10} = 1.4$) (Fig. 2, Table 2-M1). The temperature effects on growth become variable when we incorporate fish guild and asymptotic length in the model. We find most support for a model with a two-way interaction between temperature - fish guild and temperature - asymptotic length (Table 2-M3). The model predicts that average growth among demersal and deep-living fish is weakly affected by temperature, whereas average growth among pelagic fish and elasmobranchs increase more strongly (Fig. 2). Temperature effects on average growth decline with increasing asymptotic length. Using the model outcome, we compare average growth for each fish guild across a temperature gradient for two asymptotic lengths (30 and 100 cm) (Fig. 3). In waters < 5°C, the average growth of fish with $L_\infty = 100$ cm is equally fast for demersals, elasmobranchs and deep-living fish (pelagics are not included as there is no data available on large pelagics in this temperature range), whereas species with $L_\infty =$ 30 cm grow slower. In waters > 20°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 (Appendix S1: Table S2), despite some variation in large pelagics and deep-living fish (with $L_\infty = 100$ cm, Q_{10} is between 1.3 - 1.6 for pelagics and 1.1 - 1.5 for deep-living fish).

Effects of temperature on asymptotic length

We find no relationship between average asymptotic length and temperature when all fish data is pooled (Fig. 4, Table 2-M2). When including fish guilds, we find most support for a model with an interaction between temperature and fish guild. The model shows that the average asymptotic length of deep-living fish declines with temperature ($Q_{10} = 0.6$), whereas the average asymptotic length of the other guilds is largely constant with temperature (Fig. 4, Table 2-M4). Three additional analyses with other methods of data selection show either a similar weak effect of temperature on asymptotic length or no effect (Appendix S1: Table S3).

Effects of food availability on the relationship between temperature and growth coefficient *A*

There is no effect of zooplankton biomass on the average growth of small pelagic fish (a model without zooplankton biomass is best supported) (Table 2-M5, Appendix S1: Fig S2). There is also no effect on pelagic fish growth when estimates of zooplankton production are used instead of zooplankton biomass (Appendix S1: Table S4). For demersal fish, we find support for a model with a three-way interaction between temperature, asymptotic length and benthic biomass (Table 2-M6). The outcome shows that benthic biomass has a positive effect on growth coefficient *A* in warm waters (> 15°C) and for fish in cold waters with a small asymptotic length. There is a negative effect on the average growth coefficient *A* of fish with a larger asymptotic length (30-50 cm). As shown in Fig. 5, the rate of change over the benthic biomass gradient (given average temperature and asymptotic length conditions) is small. When estimates of benthic production are used instead of benthic biomass, we find a positive effect of production on demersal growth and no interaction (Appendix S1: Table S4).

Discussion

Our results show no effect of increasing temperature on the average asymptotic length of fish species present in ecosystems, and only a limited increase in average growth of fish species in warmer systems. The increase in average growth with temperature varies with fish guild and asymptotic length. Food availability has a limited effect on the average growth of fish species.

The TSR response is weaker than predicted and not consistently observed across fish guilds

Our results highlight that the TSR response poorly predicts growth rates and body lengths of extant fish guilds across ecosystems. In relation to growth, we find a weak positive effect of temperature on average growth of fish species (as previously shown by (Sibly et al. 2015, Clarke 2017)) that is smaller than predicted from metabolic theory. The temperature effect is varying with fish guild. In relation to asymptotic body length, there is no clear indication that temperature is affecting the average asymptotic body length of fish species across guilds (except for deep-living fish, but note the very restricted temperature range for which data are available). Yet, the effects of temperature on average asymptotic length may be compromised since many of the fish species in our dataset are being fished and since fisheries mortality may cause a decline in body size (Fisher et al. 2010b). Nevertheless, a meta-analysis on TSR has shown that for large aquatic species (≥ 100 mg dry mass) body mass declines of 5% per °C are to be expected (Forster et al. 2012) and such a reduction is not observed in our analysis. This finding begs the question of which effect is responsible for negating the TSR response on individual fish species.

The effect of food availability on growth is limited

Variations in food availability across regions could be partly responsible for offsetting the expected growth increase with temperature. This would happen if growth rates scale with food concentration, and if food availability declines with temperature. Our results contradict this hypothesis as fish growth is rather unresponsive to regional differences in prey biomass or production (despite a minor effect of benthic biomass on demersal fish). The absence of a relation between food and growth is surprising and may be related to uncertainty in the prey biomass estimates and to uncertainty regarding the extent to which our data reflect the actual food availability. Yet, our findings are supported by a recent global analysis of reef fish growth, where growth variation of reef fish species across regions was weakly linked to regional variation in primary production (Morais and Bellwood 2018). Growth rates are perhaps decoupled from overarching prey conditions as fish do not optimize growth but fitness. 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 et al. 2005). Whatever the reason, the average growth rate of fish is remarkably unrelated to food conditions, and changes in food conditions can therefore not explain the absence of a TSR response.

Selection by community assembly?

An alternative explanation for the weak effects of temperature on average growth rates of fish guilds is that ecosystems at different temperatures select for different life histories. The implication of the weak effect of temperature on average growth rates is that ecosystems at higher temperatures select life histories with slower growth, corrected for temperature, than ecosystems at lower temperatures. This hypothesis implies that average fish growth and asymptotic body size will not be much affected by temperature change, provided that the community can respond sufficiently fast through invasions of new species or extirpations (Zhang et al. 2017) or by adaptations of existing species. Most marine ecosystems are open and invasions from nearby areas seem easy. However, for an invader to establish a viable population it must be able to close its life cycle in the new area. Life cycle closure will depend on a number of conditions, including the availability of suitable spawning locations that enable the larvae to encounter sufficient food and adequate transport to suitable nursery areas.

Consequences for fish performance in warmer waters

The hypothesis that the average growth and body size of fish in an ecosystem is adjusted by community assembly processes does not necessarily invalidate temperature effects at the individual level. Our observations of a constant asymptotic size and somewhat faster growth with temperature is expected when temperature equally affects growth coefficient *A* and loss coefficient *k* (following eq. 1, hypothesis 2). If we assume that this response applies not just within, but also across species, it can be used to predict changes in the performance of fish in ecosystems at different temperatures. Therefore, we can expect that, on average *A* and *k* may increase with temperature, though our findings suggest less so than predicted by metabolic theory ($Q_{10} \approx 2.5$) (Brown et al. 2004) or found (for resting metabolism) across teleost fish species ($Q_{10} \approx 1.8$) (Clarke and Johnston 1999). It is difficult to disentangle the processes that control the temperature effects on *A* and *k* as each characterizes several aspects of ecology and bioenergetics. Overall, the increase in growth with temperature across fish guilds suggests that individual fish need to consume more food per unit time to cope with a higher basal metabolism and a faster growth. Increased consumption in warmer waters may occur due to increased enzymatic activities and hence digestive capacity, or enhanced activity levels (higher velocity (Dell et al. 2014), lower water viscosity) and hence higher clearance rates. Higher activity and metabolic levels will decrease trophic efficiency (Barneche and Allen 2018). Therefore, despite limited change in average growth and asymptotic length for some fish guilds, their ecological performance changes towards faster but less efficient transfer of energy in warmer systems.

Data uncertainty

Different processes may have caused uncertainty in our data analyses and in the estimated temperature effects on growth and asymptotic size. This may be related to 1) the aggregation of fish into different fish guilds, 2) the use of sampling locality to define average ambient temperatures (ignoring seasonal variation in temperature within a region and movement of fish species across regions) and 3) the estimation of von Bertalanffy parameters from length-at-age observations (Spence and Turtle 2017), using collated data from different sources (Thorson et al. 2014). One way to overcome most of the above uncertainty is to compile more detailed age and body size data, available for many commercially important fish, yet with the cost of a lower number of observations. Finally, our outcome also ignores that some species in a guild are more abundant than others. The growth and body size characteristics of the dominant species may scale differently with temperature than the average across species response.

Conclusion

Our results suggest that the physiological response to temperature in marine fish cannot be used to infer the temperature response at the level of guilds. This is because increased growth rates and reductions in adult body size with temperature are not (consistently) observed across species at the guild level. Our results highlight that a proper understanding of how fish communities change globally in response to climate change not only require a correct description of the physiological response to temperature (Lefevre et al. 2017), but also of the ecological dynamics. Crucial is to understand the processes of environmental and ecological filtering that select the set of viable combinations of life-history characters in a given environment and temperature.

Acknowledgements

We thank CA Stock and C Petrik for the GFDL-ESM2.6 model output, MK Thomas for advice on the statistical analyses and FishBase for collating data on fish parameters. We also thank two reviewers for their valuable comments on an earlier draft. PDvD received funding from the People Programme (Marie Curie Actions) under Research Executive Agency grant agreement number 609405 (COFUNDPostdocDTU). PDvD and KHA conducted the work within the Centre for Ocean Life, a VKR center of excellence supported by the Villum Foundation.

References

Andersen, K. H., and J. E. Beyer. 2015. Size structure, not metabolic scaling rules, determines fisheries reference points. Fish and Fisheries 16:1–22.

Angilletta, M. J. J., T. D. Steury, and M. W. Sears. 2004. Temperature, growth rate, and body size in ectotherms: fitting pieces of a life-history puzzle. Integrative and Comparative Biology 44:498–509.

Atkinson, D. 1994. Temperature and organism size: a biological law for ectotherms? Advances in ecological research 25:1–58.

Barneche, D. R., and A. P. Allen. 2018. The energetics of fish growth and how it constrains food-web trophic structure. Ecology Letters

Belk, M. C., and D. D. Houston. 2002. Bergmann's rule in ectotherms: a test using freshwater fishes. The American Naturalist 160:803–808.

Von Bertalanffy, L. 1957. Quantitative laws in metabolism and growth. The quarterly review of biology 32:217–231.

Biro, P. A., J. R. Post, and M. V Abrahams. 2005. Ontogeny of energy allocation reveals selective pressure promoting risk-taking behaviour in young fish cohorts. Proceedings of the Royal Society B: Biological Sciences 272:1443–1448.

Boettiger, C., D. T. Lang, and P. C. Wainwright. 2012. rfishbase: exploring, manipulating and visualizing FishBase data from R. Journal of Fish Biology 81:2030–2039.

Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. Toward a metabolic theory of ecology. Ecology 85:1771–1789.

Cheung, W. W. L., J. L. Sarmiento, J. Dunne, T. L. Frölicher, V. W. Y. Lam, M. L. Deng Palomares, R. Watson, and D. Pauly. 2013. Shrinking of fishes exacerbates impacts of global ocean changes on marine ecosystems. Nature Climate Change 3:254–258.

Clarke, A. 1983. Life in cold water: the physiological ecology of polar marine ectotherms. Oceanography and Marine Biology Annual Review 21:341–453.

Clarke, A. 2003. Costs and consequences of evolutionary temperature adaptation. Trends in Ecology & Evolution 18:573–581.

Clarke, A. 2017. Principles of thermal ecology - Temperature, energy and life. Oxford University Press.

Clarke, A., and N. M. Johnston. 1999. Scaling of metabolic rate with body mass and temperature in teleost fish. Journal of Animal Ecology 68:893–905.

Daufresne, M., K. Lengfellner, and U. Sommer. 2009. Global warming benefits the small in aquatic ecosystems. Proceedings of the National Academy of Sciences 106:12788–12793.

Dell, A. I., S. Pawar, and V. M. Savage. 2014. Temperature dependence of trophic interactions are driven by asymmetry of species responses and foraging strategy. Journal of Animal Ecology 83:70–84.

Fisher, J. A. D., K. T. Frank, and W. C. Leggett. 2010a. Global variation in marine fish body size and its role in biodiversity–ecosystem functioning. Marine Ecology Progress Series 405:1–13.

Fisher, J. A. D., K. T. Frank, and W. C. Leggett. 2010b. Breaking Bergmann’s rule: truncation of Northwest Atlantic marine fish body sizes. Ecology 91:2499–2505.

Forster, J., A. G. Hirst, and D. Atkinson. 2012. Warming-induced reductions in body size are greater in aquatic than terrestrial species. Proceedings of the National Academy of Sciences 109:19310-19314.

Froese, R., and D. Pauly. 2018. FishBase World Wide Web electronic publication.

www.fishbase.org, version (10/2018).

Grady, J. M., B. J. Enquist, E. Dettweiler-Robinson, N. A. Wright, and F. A. Smith. 2014. Evidence for mesothermy in dinosaurs. Science 344:1268–1272.

Killen, S. S., D. S. Glazier, E. L. Rezende, T. D. Clark, D. Atkinson, A. S. T. Willener, and L. G. Halsey. 2016. Ecological influences and morphological correlates of resting and maximal metabolic rates across teleost fish species. The American Naturalist 187:592–606.

Kingsolver, J. G. 2009. The well-temperatured biologist. The American Naturalist 174:755–768.

Kingsolver, J. G., and R. B. Huey. 2008. Size, temperature, and fitness: three rules. Evolutionary Ecology Research 10:251–268.

Lefevre, S., D. J. McKenzie, and G. E. Nilsson. 2017. Models projecting the fate of fish populations under climate change need to be based on valid physiological mechanisms. Global Change Biology 23:3449–3459.

Lester, N. P., B. J. Shuter, and P. A. Abrams. 2004. Interpreting the von Bertalanffy model of somatic growth in fishes: the cost of reproduction. Proceedings: Biological Sciences 271:1625–1631.

Morais, R. A., and D. R. Bellwood. 2018. Global drivers of reef fish growth. Fish and Fisheries 19:874–889.

Ohlberger, J. 2013. Climate warming and ectotherm body size – from individual physiology to community ecology. Functional Ecology 27:991–1001.

Sheridan, J. A., and D. Bickford. 2011. Shrinking body size as an ecological response to climate change. Nature Climate Change 1:401–406.

Sibly, R. M., J. Baker, J. M. Grady, S. M. Luna, A. Kodric-Brown, C. Venditti, and J. H. Brown. 2015. Fundamental insights into ontogenetic growth from theory and fish. Proceedings of the National Academy of Sciences 112:13934–13939.

Spalding, M. D., et al. 2007. Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. BioScience 57:573–583.

Spence, M. A., and A. J. Turtle. 2017. Making the most of survey data: Incorporating age uncertainty when fitting growth parameters. Ecology and Evolution 7:7058–7068.

Stock, C. A., J. P. Dunne, and J. G. John. 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., J. G. John, R. R. Rykaczewski, R. G. Asch, W. W. L. Cheung, J. P. Dunne, K. D. Friedland, V. W. Y. Lam, J. L. Sarmiento, and R. A. Watson. 2017. Reconciling fisheries catch and ocean productivity. Proceedings of the National Academy of Sciences 114:E1441–E1449.

Thorson, J. T., J. M. Cope, and W. S. Patrick. 2014. Assessing the quality of life history information in publicly available databases. Ecological Applications 24:217–226.

Ursin, E. 1967. A Mathematical Model of Some Aspects of Fish Growth, Respiration, and Mortality. Journal of the Fisheries Research Board of Canada 24:2355–2453.

Wei, C.-L. et al. 2011. Global patterns and predictions of seafloor biomass using random forests. PLOS ONE 5:e15323.

West, G. B., J. H. Brown, and B. J. Enquist. 2001. A general model for ontogenetic growth. Nature 413:628.

Zhang, L., D. Takahashi, M. Hartvig, and K. H. Andersen. 2017. Food-web dynamics under climate change. Proceedings of the Royal Society B: Biological Sciences 284:20171772.

Tables

Table 1. Overview of the different models used to examine growth coefficient A and asymptotic length L_∞. Obs. shows the number of unique species. The variables in brackets were tested for interactive effects. T is temperature in °C, growth coefficient A and asymptotic length are $\log_{10}$ transformed.

Model	**Obs.**	**Aim**	**Name**
$A \sim T$	774	Effect of temperature on growth across marine fish	M1
$L_\infty \sim T$	774	Effect of temperature on asymptotic length across marine fish	M2
$A \sim [T, L_\infty, Guild] + t_0$	774	Effect of temperature on growth across marine fish, while incorporating the effect of fish guild, L_∞ and t_0	M3
$L_\infty \sim [T, Guild]$	774	Effect of temperature on asymptotic length across marine fish, while incorporating the effect of fish guild	M4
$A_{spel} \sim [T, L_\infty, B_{zoop}] + t_0$	75	Effect of zooplankton biomass (B_{zoop}) on growth of small pelagics (L_∞ < 50 cm), while incorporating the effect of temperature, L_∞ and t_0	M5
$A_{sdem} \sim [T, L_\infty, B_{benth}] + t_0$	378	Effect of benthic biomass (B_{benth}) on growth for small demersals (L_∞ < 50 cm), while incorporating the effect of temperature, L_∞ and t_0	M6

Table 2. Overview of the models that fitted the data best. Model selection is based on the number of times a model had the lowest AIC in the 5000 simulations. R-square shows the amount of variance explained by the selected model and is based on the average adjusted R-square in the 5000 simulations. T is temperature in °C, growth coefficient A and asymptotic length are $\log_{10}$ transformed. Appendix S1: Table S5 presents all estimated parameters of the best models.

Model		**% lowest AIC**	**R-square**
M1:	$A \sim T$	100	0.12
	$A \sim 1$	0	
M2:	$L_\infty \sim 1$	99	-
	$L_\infty \sim T$	1	
M3:	$A \sim T \cdot L_\infty + T \cdot Guild + t_0$	63	0.46
	$A \sim T \cdot L_\infty \cdot Guild + t_0$	37	
M4:	$L_\infty \sim T \cdot Guild$	70	0.13
	$L_\infty \sim Guild$	30	
M5:	$A_{spel} \sim T \cdot L_\infty + t_0$	50	0.42
	$A_{spel} \sim T + L_\infty + t_0$	24	
M6:	$A_{sdem} \sim T \cdot L_\infty \cdot B_{benth} + t_0$	72	0.36
	$A_{sdem} \sim T + L_\infty + t_0$	17	

Figure legends

Figure 1. Number of von Bertalanffy parameter observations specified per marine ecoregion (total observations is 2502 within t_0 ± 2 for 774 species). The observations were linked to a particular marine ecoregion, or to two neighboring ecoregions based on sampling locality (if two ecoregions, we only coupled the observation to one of these regions to produce the figure).

Figure 2. Relationships between fish growth coefficient A and temperature for all fish species (774 species, 2502 observations) and for different fish guilds and asymptotic lengths. There is a positive relationship between temperature and growth coefficient A when fish data is pooled. Temperature effects on average growth become variable when a guild effect is included (Table 2-M3). The lines in each panel show the temperature effect on growth coefficient A given an average L_∞ and $t_0 = 0$ (since L_∞ and t_0 also affect A). The red dashed lines show the maximum variability around these predictions as determined from the 5000 simulations. The breakpoint between small and large species is at $L_\infty = 80$ cm.

Figure 3. Relationships between fish growth coefficient A and temperature across guilds for fish with $L_\infty = 100$ cm (solid lines) or 30 cm (dashed lines) (based on Table 2-M3). The temperature effect is only shown in the temperature range where data is available. $t_0 = 0$. The thin dashed line illustrates a temperature scaling as predicted from metabolic theory with A is 3 at 0 °C.

Figure 4. Relationships between fish asymptotic length and temperature for all fish species (774 species, 2502 observations) and for different fish guilds. There is no relationship between temperature and asymptotic length for all fish. There is a negative relationship between average asymptotic length and temperature for deep-living fish, whereas the other guilds are weakly affected (Table 2-M4). The lines in each panel show the temperature effect on asymptotic length.

The red dashed lines show the maximum variability around these predictions as determined from the 5000 simulations.

Figure 5. Relationships between growth coefficient A and benthic biomass for all small demersal fish ($L_\infty < 50$ cm) (Table 2-M6). To illustrate the interaction between L_∞, temperature and benthic biomass, the data is plotted in four sub-panels. Species with L_∞ less (a, c) or more (b, d) than 30 cm and with ambient temperatures less (a, b) or more (c, d) than 15°C. The lines in each panel show the effect of benthic biomass on growth coefficient A given an average L_∞ and temperature and $t_0 = 0$ (since L_∞, temperature and t_0 also affect A). The red dashed lines show the maximum variability around these predictions as determined from the 5000 simulations.

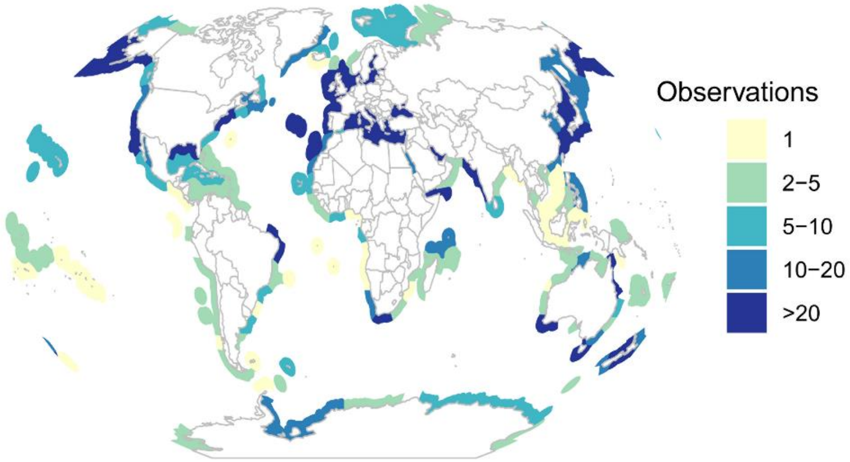

Figure 1.

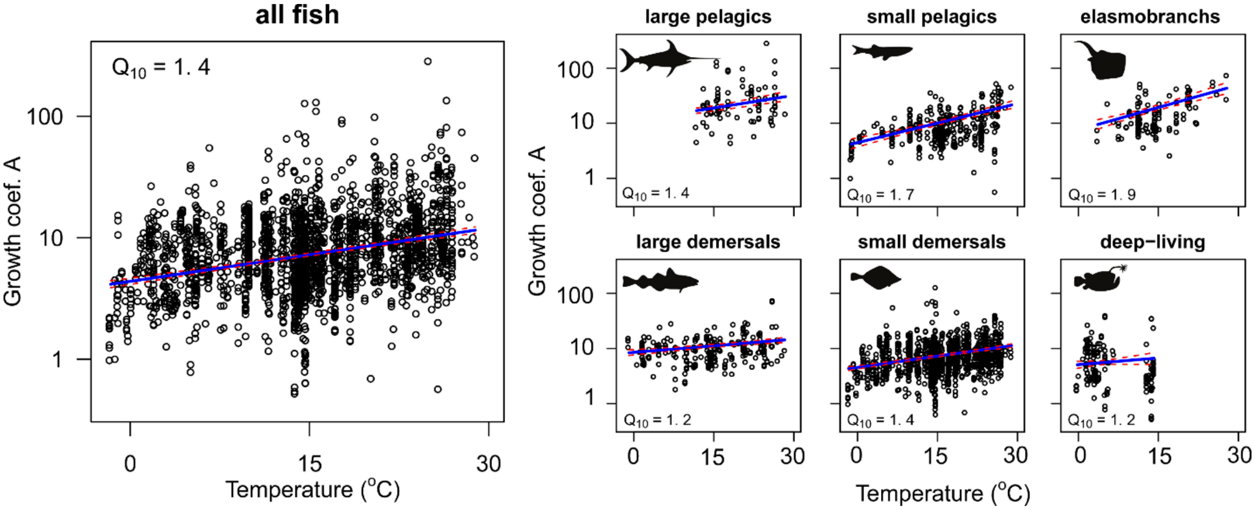
all fish
Q_{10} = 1. 4
Growth coef. A
100
10
1
0
15
30
Temperature (°C)
large pelagics
small pelagics
elasmobranchs
large demersals
small demersals
deep−living
Q_{10} = 1. 4
Q_{10} = 1. 7
Q_{10} = 1. 9
Q_{10} = 1. 2
Q_{10} = 1. 4
Q_{10} = 1. 2
Growth coef. A
100
10
1
0
15
30
Temperature (°C)

Figure 2.

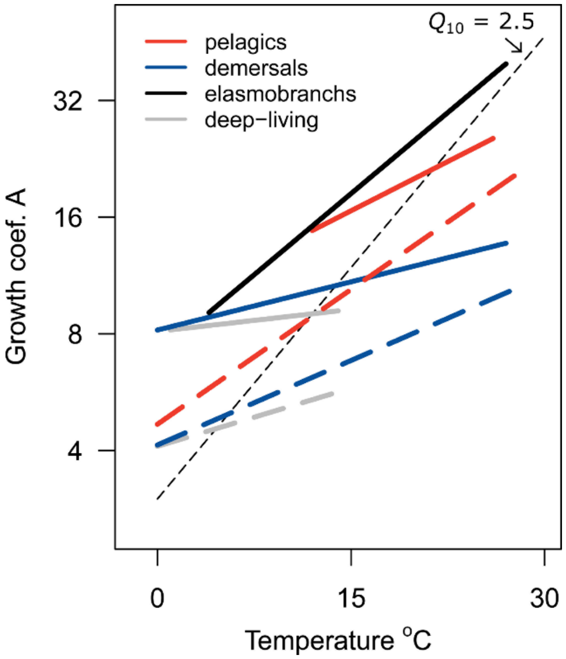
pelagics
demersals
elasmobranchs
deep−living
Q_{10} = 2.5
Growth coef. A
32
16
8
4
0
15
30
Temperature °C

Figure 3.

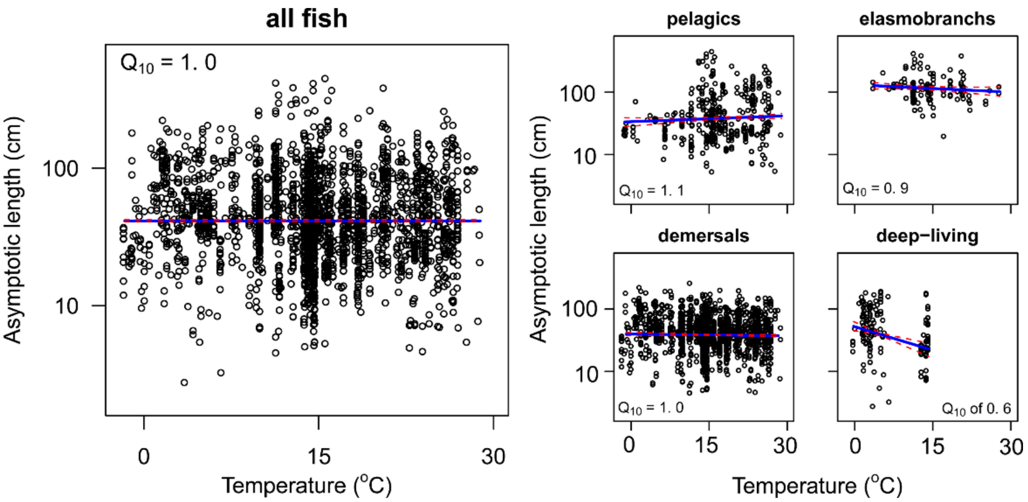
all fish
Q_{10} = 1. 0
Asymptotic length (cm)
100
10
0
15
30
Temperature (°C)
pelagics
elasmobranchs
demersals
deep−living
Q_{10} = 1. 1
Q_{10} = 0. 9
Q_{10} = 1. 0
Q_{10} of 0. 6
Asymptotic length (cm)
100
10
0
15
30
Temperature (°C)

Figure 4.

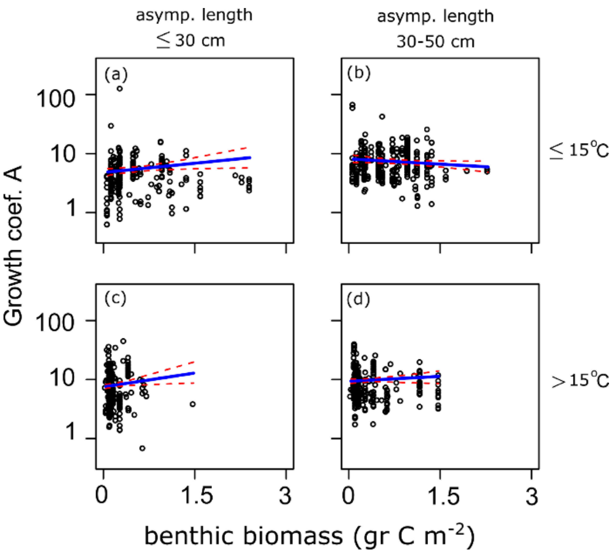
asymp. length
≤ 30 cm
asymp. length
30-50 cm
(a)
(b)
(c)
(d)
100
10
1
Growth coef. A
≤ 15°C
> 15°C
0
1.5
3
benthic biomass (gr C m-2)

Figure 5.

Appendix

Little difference in average fish growth and maximum size across temperatures

Daniël van Denderen, Henrik Gislason and Ken H. Andersen

Appendix 1 – supplementary figures and tables

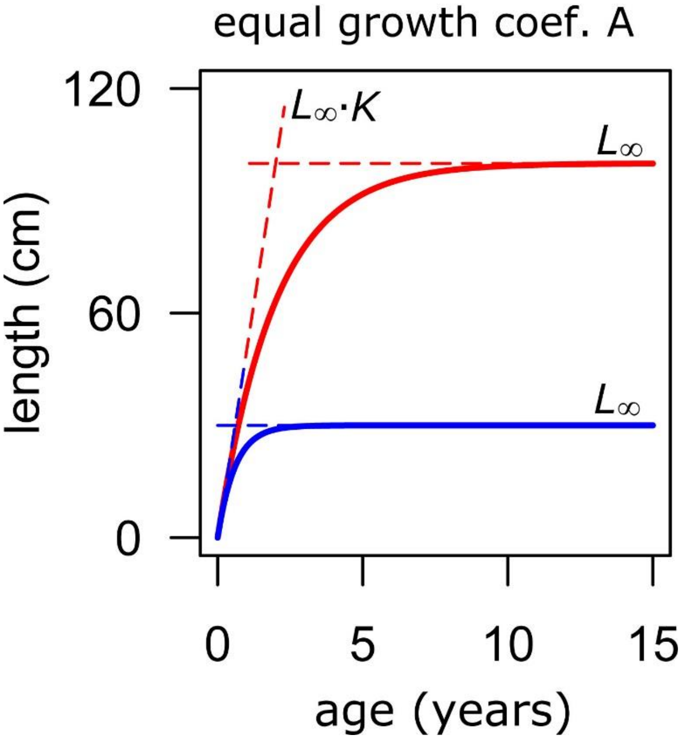

Figure A1-1. Von Bertalanffy length-at-age curves for two species with an equal growth coefficient *A* (constant $0.65 \cdot L_\infty \cdot K$) with $K = 0.5$ (red line) or 1.67 yr^{-1} (blue line) and $L_\infty = 30$ or 100 cm. The horizontal dashed lines are at L_∞, the slanted dashed lines are age multiplied by $L_\infty \cdot K$. von Bertalanffy length-at-age curves are based on length(t) = $L_\infty \cdot (1-e^{-Kt})$.

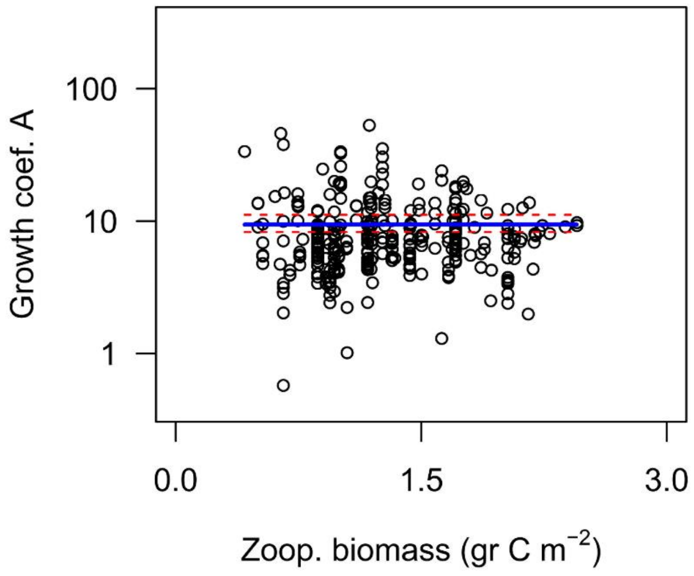

Fig. A1-2. Relationships between growth coefficient *A* and zooplankton biomass for all small pelagic fish ($L_\infty < 50$ cm) (Table 2-M5). There is no relation between growth coefficient *A* and food availability. The blue line is plotted given an average L_∞ and temperature and $t_0 = 0$ (since L_∞, temperature and t_0 affect *A*). The red dashed lines show the maximum variability as determined from the 5000 simulations.

Table A1-1. Fish classification into different guilds following the seaaroundus.org project.

Guilds	**Classification**
Pelagics	Pelagics
Demersals	Demersals, benthopelagics, flatfishes, reef-associated
Elasmobranchs	Sharks, rays
Deep-living	Bathydemersals, bathypelagics

Table A1-2. Relationships between temperature and growth coefficient *A* presented as Q_{10} following different methods of data selection. First column: similar to main manuscript; second column: all data with t_0 ± 1; third column: all unique species (based on the maximum observed growth coefficient *A* for each species across all regions); fourth column: re-sampling of observations when randomly picking 80% of the species in each sample. When selecting all data with t_0 ± 1, a three-way interaction between temperature, fish guild and asymptotic length is the most supported model. For the other two analyses, we find support for a model that is similar to the main analysis. In all analyses, the effect of temperature on the different fish guilds is comparable with our main findings as shown by limited variation in Q_{10}.

	Main document (n=2502)	**t_0 ± 1 (n=1737)**	**Highest growth rate per species (n=774)**	**Resampling of species and obs. (n = 2502)**
Pelagics L_∞ = 30 cm	1.70	1.68	1.82	1.70
Pelagics L_∞ = 100 cm	1.48	1.28	1.62	1.48
Demersals L_∞ = 30 cm	1.40	1.44	1.39	1.40
Demersals L_∞ = 100 cm	1.21	1.15	1.23	1.21
Elasmobranchs L_∞ = 30 cm	-	-	-	-
Elasmobranchs L_∞ = 100 cm	1.90	2.11	1.91	1.90
Deep-living fish L_∞ = 30 cm	1.26	1.24	1.40	1.26
Deep-living fish L_∞ = 100 cm	1.09	1.53	1.25	1.09

Table A1-3. Relationships between temperature and asymptotic length presented as Q_{10} following different methods of data selection. First column: similar to main manuscript; second column: all data with t_0 ± 1; third column: all unique species (based on the maximum observed growth coefficient *A* for each species across all regions); fourth column: re-sampling of observations when randomly picking 80% of the species in each sample. When selecting the highest growth per species, we find support for a model that is similar to the main analysis. For the other two analyses, no effect of temperature is found.

	Main document (n=2502)	***t₀* ± 1 (n=1737)**	**Highest growth rate per species (n=774)**	**Resampling of species and obs. (n = 2502)**
Pelagics	1.06	1	1.11	1
Demersals	0.99	1	1.01	1
Elasmobranchs	0.88	1	0.94	1
Deep-living fish	0.56	1	0.55	1

Table A1-4. Relationship between growth, temperature and prey production (P) instead of prey biomass for small pelagics and demersals (L_∞ < 50 cm). Prey production is estimated from the ecosystem model COBALT (see method). In the model, medium and large-sized zooplankton biomass have a density dependent closure term that represents mortality from fish predation. We use this mortality term (gr C m^{-2} day^{-1}) as an estimate of zooplankton prey production. As a proxy for benthic production, we use COBALT output on the detrital flux reaching the seabed in shallow waters (< 500 meter) (gr C m^{-2} day^{-1}). In regions without information on the detrital flux reaching the seabed < 500 (because of a small shelf in combination with a 1 degrees grid), we use the relationship between detrital flux reaching the seabed < 500 meter and >= 500 meter found in the other ecoregions to predict the value (regression analysis shows $\log_{10}(y) = 0.13 + 0.65\log_{10}(x)$; $r^2 = 0.58$). Model selection is based on the number of times a model had the lowest AIC in the 5000 simulations. R-square shows the amount of variance explained by the selected model and is based on the average adjusted R-square in the 5000 simulations. T is temperature in °C and growth coefficient A and asymptotic length are $\log_{10}$ transformed.

Model		**% lowest AIC**	**R-square**
M5_prod:	$A_{spel} \sim T \cdot L_\infty + t_0$	42	0.42
	$A_{spel} \sim T \cdot L_\infty + T \cdot P_{zoop} + t_0$	25	
M6_prod:	$A_{sdem} \sim T + L_\infty + P_{benth} + t_0$	42	0.35
	$A_{sdem} \sim T + L_\infty + t_0$	18	

Table A1-5. Model parameter estimates of Table 2 calculated as the average in the 5000 simulations. Model name corresponds to the name used in Table 1-2. T is temperature in °C and growth coefficient A and asymptotic length are $\log_{10}$ transformed. G_{pel} is pelagics guild, G_{dem} is demersals guild and G_{elas} is elasmobranchs guild (the deep-living guild is the reference level to which the other guilds are contrasted).

Model name					
M1	**intercept**	**T**			
	0.6407	0.0146			
M2	**intercept**				
	1.6172				
M3	**intercept**	**T**	**L_∞**	**G_{dem}**	**G_{pel}**
	-0.2246	0.0276	0.5671	0.0034	0.0568
	G_{elas}	**t_0**	**$T{:}L_\infty$**	**$T{:}G_{dem}$**	**$T{:}G_{pel}$**
	-0.0630	0.1356	-0.0119	0.0045	0.0132
	$T{:}G_{elas}$				
	0.0241				
M4	**intercept**	**T**	**G_{dem}**	**G_{pel}**	**G_{elas}**
	1.7176	-0.0252	-0.1194	-0.1915	0.4016
	$T{:}G_{dem}$	**$T{:}G_{pel}$**	**$T{:}G_{elas}$**		
	0.0244	0.0284	0.0212		
M5	**intercept**	**T**	**L_∞**	**t_0**	**$T{:}\ L_\infty$**
	-0.6372	0.0689	0.9039	0.1680	-0.0333
M6	**intercept**	**T**	**L_∞**	**B_{benth}**	**t_0**
	-0.9591	0.0648	1.1299	0.7797	0.1803
	$T{:}B_{benth}$	**$T{:}L_\infty$**	**$L_\infty{:}B_{benth}$**	**$T{:}L_\infty{:}B_{benth}$**	
	-0.0102	-0.0366	-0.6052	0.0136	

Appendix 2. Species-specific length-weight relationships

We derived species-specific length-weight relationships from rFishbase (Boettiger et al. 2012) for 640 fish species where data was available and we estimated growth coefficient A as:

The relationship between length and weight can be described as:

$$l = (w/c)^b.$$

Length-based growth can be transformed to weight-based growth with the chain-rule:

$$\frac{\mathrm{d}l}{\mathrm{d}t} = \frac{\mathrm{d}(w/c)^b}{\mathrm{d}t} = c^{-b}\frac{\mathrm{d}w^b}{\mathrm{d}w}\frac{\mathrm{d}w}{\mathrm{d}t} = c^{-b}bw^{b-1}\frac{\mathrm{d}w}{\mathrm{d}t}.$$

Inserting the length-based juvenile growth from the von Bertalanffy equation $\mathrm{d}l/\mathrm{d}t = KL_\infty$ (slope of the growth equation for $l << L_\infty$) and $\mathrm{d}w/\mathrm{d}t = Aw^{2/3}$ gives:

$$KL_\infty = c^{-b}bw^{b-1+2/3}A,$$

and rearranging gives:

$$A = c^b b^{-1} w^{-b+1-2/3} KL_\infty.$$

The rearrangement shows that the use of a species-specific length-weight relationship complicates the estimate of growth coefficient A as A becomes weight-dependent. However, if $b = 1/3$ then the weight dependency disappears and $A = c^{1/3}3KL_\infty = 0.65KL_\infty$ (as in the main document). The value of b is close to 1/3 (Froese 2006), so the weight dependency of A is weak. To test this, we calculated A for all fish species where species-specific length-weight relationships where available at 5 and 25 cm. We afterwards examined the effect of temperature on A and compared it with our main analysis. This shows that with the statistical model from the main analysis, the predicted temperature effects are largely similar (Table A2-1).

Table A2-1. Relationships between temperature and growth coefficient *A* presented as Q_{10} following a species-specific length-weight relationship and the calculation of *A* at 5 cm (middle column) and 25 cm (right column) with the statistical model from the main analysis (Table 2-M3).

	Main document (n=2502)	**Species specific length/weight at 5 cm (n=2266)**	**Species specific length/weight at 25 cm (n=2266)**
Pelagics L_∞ = 30 cm	1.70	1.70	1.72
Pelagics L_∞ = 100 cm	1.48	1.42	1.42
Demersals L_∞ = 30 cm	1.40	1.52	1.51
Demersals L_∞ = 100 cm	1.21	1.27	1.25
Elasmobranchs L_∞ = 30 cm	-	-	-
Elasmobranchs L_∞ = 100 cm	1.90	2.18	2.20
Deep-living fish L_∞ = 30 cm	1.26	1.38	1.37
Deep-living fish L_∞ = 100 cm	1.09	1.15	1.14

Reference

Froese 2006 Cube law, condition factor and weight–length relationships: history, meta-analysis and recommendations Journal of Applied Ichthyology 22:241-253.