Environmental and Ecological Drivers of Slow Growth in Deep-Sea Demersal Fishes

A THESIS SUBMITTED TO THE GRADUATE

DIVISION OF THE UNIVERSITY OF HAWAIʻI AT

MĀNOA IN PARTIAL FULFILLMENT OF THE

REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

IN

OCEANOGRAPHY

August 2020

By Jesse Black

Thesis Committee:

Jeffrey Drazen, Chair

Anna Neuheimer

Craig Smith

ABSTRACT:

The deep sea (>500m ocean depth) is the largest habitat on the planet, characterized by near-freezing temperatures, low ambient light, and food-poor conditions relative to shallower waters. Fishes in the deep sea generally grow more slowly than those inhabiting shallow-water. This is a generalization, however, and even amongst deep-sea fishes, there is a broad continuum of growth rates. The relative importance of potential drivers of growth-rate variability amongst deep-sea species, such as temperature, food availability, oxygen concentration, metabolic rate, and phylogeny, have yet to be fully evaluated. We present a meta-analysis in which age and size data were collected for 53 species of fishes whose collective depth ranges span surface waters to 4000m. Here we focus on demersal species because much of the existing data for deep-sea fish growth is centered on commercially harvested, demersal taxa. We calculated growth metrics using both calendar and thermal age, and compared them with environmental, ecological, and phylogenetic variables. Temperature alone explains up to 30% of variation in the Von Bertalanffy growth coefficient, *K* (yr^{-1}), and 21% of the variation in the average annual increase in mass (AIM; %), a metric of growth prior to maturity. After correcting for the influence of temperature, depth was still a significant driver of growth, explaining up to 20% and 10% of the remaining variation in *K* and AIM, respectively. Oxygen concentration also explained ~11% of remaining variation in AIM following temperature-correction. Relatively minor amounts of variation may be explained by food availability and the locomotory mode of the fishes. We also found a strong correlation between growth and metabolic rate. Deeper, slower-growing stocks are generally more vulnerable to overfishing due their relatively slow growth rates, though considerable variation in growth persists, even amongst deep-sea fishes. By understanding the influence of multiple ecological and/or environmental drivers of growth rate, we can better estimate resilience to fishing mortality than from depth alone. Further disruption of fish populations and habitats may be compounded by the advent of deep-sea mining for rare minerals. Deep-sea mining may begin within the next few decades and will target a

diversity of deep-sea habitats across the globe, including seamounts, mid ocean ridges, and abyssal plains. It is therefore vital to accurately model the growth rates of deeper-living fish to evaluate their resiliency to escalating anthropogenic disturbance.

INTRODUCTION

Deep-sea fishes generally have longer times-to-maturity, slower growth rates, lower metabolic rates, and greater longevity than shallow-water fishes (Koslow 1996, Drazen and Haedrich 2012; Cailliet 2001). Despite these generalizations, life history parameters vary considerably across the depth continuum. For example, the Patagonian toothfish *Dissostichus eleginoides* (median depth of occurrence ~1100m) matures between 5 and 7 years of age (Horn et al. 2001; Everson and Murray 1999), while the black cardinal fish *Epigonus telescopus (*median depth ~800m) matures around 36 years (Horn et al. 2010). Differences in longevity, maturity and growth rate may reflect the cumulative influence of phylogeny and a variety of environmental drivers such as pressure, temperature, oxygen, and food availability, all of which change with depth in most ocean habitats.

A variety of environmental drivers, temperature and food supply in particular, may affect growth rates of shallow water fishes. Temperature has been shown to be a primary driver of growth. The growing degree-day (GDY ;°C x year), i.e., the product of habitat temperature and calendar age of fish in days, has successfully explained differences in growth rates across populations of North-Atlantic cod (*Gadus morhua*) and other fishes (Neuheimer and Taggart 2007; Venturelli et al. 2010; Neuheimer and Taggart 2010; Braaten and Guy 2011; Shackell et al. 2019). In much of the deep-sea, temperature and growth rates decline rapidly with depth, and so temperature has been frequently hypothesized to drive the observed patterns (Drazen and Haedrich 2012, McLain et al 2012). Flux of particulate organic carbon, the primary basis of the food web in the deep ocean, also declines exponentially with depth (e.g., Martin 1987; Lutz 2007). Thus, the declining availability of food with depth may also play a role in growth, as accumulating mass requires energy intake in some form and, at least in aquaculture settings, feeding level has a large influence on growth rates (reviewed in Persson and De Roos 2006). However, in the wild, ecosystem-level changes in food supply may primarily constrain population size before affecting interspecific growth rate; as available food increases, the carrying capacity of a given population increases, while the amount of energy available to individuals for growth and other biological processes may remain relatively constant, depending on relationships between average body size and foraging efficiency (McClain et al. 2012; Sebens 1987). A meta-analysis of shark growth rates by Rigby and Simpfendorfer (2015) did find differences in growth across habitat types but did not estimate the effect of food availability as an individual parameter.

Metabolic rate may also influence growth rates. The metabolic theory of ecology predicts that metabolic rate, driven by mass and temperature, determines the pace of all ecological processes (Brown 2004; McClain et al. 2012), including the distribution of biochemical resources into the processes of growth, reproduction, and survival. Temperature clearly declines with depth in most ocean basins which could then reduce metabolic rates with concurrent reductions in growth rate. Oxygen is a key reactant in aerobic metabolism, and if growth rate is indeed constrained by or linked to metabolic rate, it would follow that aerobic metabolic reactions that facilitate generation of new biomass can only operate as quickly as oxygen can be made available. However, metabolic rate has been shown to be more strongly associated with gill surface area than the ambient concentration of oxygen itself, and thus a rapid metabolism in oxygen poor waters may simply be a matter of possessing specific adaptations for efficient oxygen extraction and delivery (Friedman et al. 2012). In short, depth, temperature, food supply, and oxygen may all affect metabolic rate, depending largely on the depth in question, and may therefore be indirect but important drivers of growth if the metabolic theory of ecology is accurate. The visual interactions hypothesis suggests that after accounting for temperature and body size effects, the decline in metabolism with depth in midwater animals to a depth of about 1000m reflects a decrease in selective pressure for rapid locomotory capacity as visual predation becomes less common with decreasing light levels (Childress 1995). If links between metabolism and growth are strong, then growth might also decline.

Many of these variables change with depth, often covarying with one another, and/or varying between regions of the ocean (Paulmier and Ruiz-Pino 2008). Therefore, distinguishing the importance of one factor over another will require knowledge of life histories from multiple regions of the oceans to untangle as much covariation as possible. Studies of age and growth require extensive sampling effort, time and labor, and these logistical demands increase sharply as deeper-dwelling organisms are targeted. The progress of age and growth studies for many deep-sea species may therefore be outpaced by anthropogenic impacts, and as such, a predictive framework of growth is required in the short term. Put simply, there is not enough time to perform adequate age and growth studies on all deep-sea fish taxa before the human impact in the deep sea escalates substantially.

I seek to understand the drivers of growth and life-history parameters in deep-sea demersal fishes. To address this goal, we conducted a meta-analysis of growth and life-history parameters from studies on populations of deep-sea demersal fishes and some phylogenetically related shallow-water species. We compared these data to environmental variables from each species' habitat to establish a framework for estimating growth patterns and life histories. Similar analyses have been performed on octopods, freshwater fishes, and sharks to explain the effect of temperature and other ecological and environmental variables on life-history parameters, but to our knowledge, this is the first meta-analysis to incorporate environmental conditions in explaining growth of marine demersal fishes across depth (Schwarz et al. 2018; Rigby and Simpfendorfer 2015; Santana et al. 2020).

METHODS

Growth Data and Metrics

Data on fish growth and life history were extracted from a variety of sources (Table 1). Forty published studies and two national oceanographic institutions (Northwest Fisheries Science Center (NWFSC) operating out of the United States, and the National Institute of Water and Atmospheric Research (NIWA) out of New Zealand) also provided data. Raw data were used when possible. When raw data were unavailable, data were digitized from plots of age vs. size, or from tables containing mean size-at-age. When available, other relevant spatial and environmental data were also collected including depth, latitude and longitude, temperature and/or oxygen concentration measured on the fishing gear. We attempted to minimize the effects of covariation between depth and temperature by collecting data from a global set of locations, including the Mediterranean Sea, where temperature remains relatively constant (~13°C) across depth.

All age data in this meta-analysis originate from counts of otolith annuli. To control for the quality of age data, this analysis includes no studies that read only whole otoliths to estimate age. In order to be accepted for use in this meta-analysis, otoliths must have been at least polished/ground/broken to reveal the central nucleus before age estimation. Age data from whole otoliths and scales has been widely shown to severely underestimate actual fish age for multiple species, particularly for long-lived species (reviewed in Campana 2001). Some studies in this analysis used whole otoliths to estimate ages of young fish but switched to more accurate methods (break and burn or transverse sectioning) for fish above a particular size. Only studies with age data for at least 90 individual fish were used in this analysis. In some cases, data for more than one population of the same species was collected, and growth parameters and environmental conditions were estimated separately for these distinct populations. The only exception is *Coryphaenoides acrolepis.* Here, in order to obtain enough observations to fit growth parameters to age and size data, data were combined from Andrews et al. 1999 and Matsui et al. 1990, in which they were collected primarily from the California slope with some data from off Oregon and Washington. The catch locations for all species from the NWFSC

Groundfish Survey, which spans the entire west coast of the United States, were initially split into North and South sections to test for differences in environmental parameters and growth rates between the two regions. All these fishes are mobile, and no evidence for multiple, isolated populations of these fish along the western United States was found in the literature. Of these 7 species, only *Merluccius productus* showed significant differences in growth metrics (~30% difference) between fish from north and south of 42.5N, so these groups were parameterized as different populations (Table 1). The rest of the species from the NWFSC Groundfish Survey are parameterized as one contiguous population because no significant differences in growth parameters were found.

Growth rate in fish has been traditionally represented using the Von Bertalanffy (1938) growth curve: $L_t = L_\infty (1\text{-}e^{-K(t-t0)})$, where L_t is length of the fish at time *t*, the x intercept *t0* is the theoretical age at a length of zero, and *K* represents the exponential coefficient of growth until a maximum asymptotic length (L_∞). A larger value of *K* corresponds to a more rapid increase in length to the maximum length of the fish. These parameters were calculated for each population. Bootstrapped 95% confidence intervals were calculated for each parameter. For datasets with few young fish, this method can produce biologically improbable curves (e.g. a population with predicted lengths of ~20cm at age 0). For this meta-analysis, any Von Bertalanffy curve with a *t0* with absolute value > 2.5 years was recalculated with a *t0* fixed at -0.5. Fixing the t0 parameter at -0.1 or -0.5 has been employed in growth studies on species with a relative scarcity of juvenile data in order to ensure predicted fish length is positive and nonzero at hatching, producing more biologically realistic values of *K* (Horn and Sutton 2015; Horn et al. 2012). Here we chose -0.5 as the fixed value, though fixing at -0.1 did not yield significantly different *K* values. Still, parameter values should be observed with some caution (Lorenzen 1996). See supplemental folder “Von B Curves” and Supplementary Table 1 for growth curves and confidence intervals with and without fixed values of t0.

Growth was also calculated as an Average Increase in Mass (%; AIM) per year during the pre-maturity phase. The pre-maturity phase was chosen for this analysis to provide an estimate of the maximum rates at which each species can accumulate mass prior to experiencing the energy expenditures associated with reproduction. When available, age at 50% maturity was collected from the literature for each species (Supplemental Table 1). When age at 50% maturity was not available, we used a general time at maturity, or estimated a likely age at maturity from published lengths at maturity using Von Bertalanffy growth curves (highlighted in Table 1). If the age at maturity was different between sexes, the smaller of the two was used as the cut-off for the end of pre-maturity phase. When mass data were not available, predicted mass was calculated from fish length using published length-weight conversions (Supp. Table 1). For each species, the relationship between age and predicted or observed mass was modeled using a generalized additive model (GAM) to predict mass-at-age during the pre-maturity phase of growth (error distribution: Gamma). These GAM fits were simulated 1000 times using the R package “DHARMa” (Hartig 2019) and compared to the data to check for uniformity or outlier errors. To avoid overfitting, complexity of the curve shape was increased incrementally until simulated fits did not produce these errors. A more detailed description of how GAMs were fit can be found in the Supplemental Methods. Curves fit for the Atlantic populations of the abyssal *C. armatus,* the deepest species in our dataset, did not meet our thresholds for any fitting approach due to a small data set. However, data for this population was retained to investigate the influence of this abyssal fish on patterns in growth. Results for AIM are reported with and without inclusion of *C. armatus*. To capture only the phase of rapid growth during pre-maturity, any decline in predicted mass observed as the fish approached maturity was trimmed. The remaining values of predicted mass-at-age were then used to calculate the average annual increase in mass per year, referred to onward as AIM.

Depth ranges were collected from the literature for each species (Supp. Table 1). Whenever possible, we used published depth ranges that were estimated in the same general geographic location as the catch locations for studies used for this meta-analysis. Several of the species studied in this meta-analysis have improbably wide absolute minimum and maximum depths of occurrence. For example, *Antimora rostrata* has been observed/collected at minimum and maximum depths of 350m to 3000m, but generally lives at 1200m-2500m (Fishbase; Cohen et al. 1990). In order to constrain predictions of temperature, oxygen, and other environmental parameters to conditions likely experienced by most of the members of each species, we used these narrower, “usual”, depth ranges of high abundance for each species in our analyses, rather than the absolute historical limits of observed depth range (as in Drazen and Haedrich 2012). When modal histograms of abundance vs. depth were available in the literature, the minimum and maximum of depth range was set to where abundance was 25% of the maximum abundance. This procedure was also used if histograms of presence in percent of tows vs. depth were available (i.e. Anderson et al. 2000). The median value between minimum and maximum usual depths was also used as a predictor. Thus, for each population, this analysis includes three depth metrics: a minimum usual depth, median usual depth, and maximum usual depth.

As temperature has been shown to explain a great deal of variation in growth rate in shallow-water species, it was predicted to be a primary driver in both growth metrics, *K* and AIM. In order to decouple the effect of temperature from other potential drivers that also closely correlate with increasing depth, temperature-adjusted versions of *K* and AIM were created by calculating versions of each growth metric using growing degree-years (GDY, i.e. the integrated thermal age), instead of calendar age. Here we use the growing degree-year (GDY), the product of fish age in years and predicted temperature of habitat with a temperature threshold of -3°C, to obtain a metric of thermal age for each fish. Thermal ages were then used to create temperature-adjusted versions of *K* and AIM, denoted here as $\mathbf{K_{GDY}}$ and $\mathbf{AIM_{GDY}}$. These two temperature-adjusted metrics were analyzed alongside *K* and AIM in statistical analyses with environmental and ecological variables.

Temperature at the location of fish captures was not available in most studies. An average temperature experienced by the fish throughout their lifespan was predicted using data from World Ocean Atlas (1° horizontal resolution with 5m vertical resolution near the surface down to 100m resolution at abyssal depths, decadal averages from 1955 to 2012). Temperature observations across each species' usual depth range at the location of catch were averaged. In the initial stages of this analysis, a handful of Antarctic species were included. These fish often had near-zero or sub-zero temperatures, and so all temperatures were scaled up three degrees to avoid thermal ages that were zero or negative. In subsequent analyses, these species appear to be strong outliers in terms of temperature standardized growth, dominating any other patterns observable across the rest of the dataset. This suggests radical thermal adaptation that warrants further specific investigation in the future, and these fish were removed for the broader purpose of this meta-analysis.

Oxygen concentration (mL/L) data were gathered from World Ocean (1° horizontal resolution with 5m vertical resolution near the surface down to 100m resolution at abyssal depths, decadal averages from 1955 to 2012, https://www.nodc.noaa.gov/cgi-bin/OC5/woa13/woa13oxnu.pl). Oxygen concentration observations across each species' usual depth range at the capture locations were averaged.

Estimating food availability is a great challenge and depends upon species-specific feeding preferences and foraging strategies (Drazen and Sutton 2017) as well as prey population dynamics. This information was lacking for nearly all species in this study. Therefore, we used particulate organic carbon (POC) flux to the seafloor estimated by the Lutz model (2007) as a proxy of food availability. POC flux has been used as a proxy for food supply in similar, global meta-analyses (Wooley et al. 2016). POC flux is the basal energy source for most seafloor habitats (except chemosynthetic ecosystems), and therefore supports the production of biomass in benthic habitats, which is theoretically available for fishes to feed upon. The procedure for estimating POC flux to the seafloor for each individual species' catch location was adapted from methods described by Lutz et al. (2007). Net primary production was estimated using global Standard Vertically Generalized Production Model (VGPM) data from Oregon State University's Ocean Productivity portal (http://www.science.oregonstate.edu/ocean.productivity/custom.php) at a resolution of 1/6th of a degree. Bathymetry was extracted from the Navy ETOPO data base (ETOPO5 5x5 minutes bathymetry (http://iridl.ldeo.columbia.edu/SOURCES/.WORLDBATH/.bath/datafiles.html), and any observations of chlorophyll along the of 30m isobath or shallower were omitted to avoid unnecessary backscatter, as done in previous published estimations of primary production (Gove et al. 2016). Net primary production (NPP) at two-year intervals across the years 2007 to 2017 was averaged across each population's catch location bounds, resulting in a decadal average value of NPP for each population. Seasonal Variation Index (SVI) was calculated as described in Lutz et al. 2007. A global average euphotic zone depth of 110m was used (Lima et al. 2013). Three separate Lutz POC fluxes were predicted to the minimum, median, and maximum depths for each population within their catch boundaries.

Lutz POC flux is dependent on measurements from sediment traps, which have been found to underestimate the inputs of organic carbon to the seafloor, particularly on continental slopes (*K.* Smith et al. 1992; *K.* Smith et al. 2003; Smith and Demopoulos 2003). For this reason, we also gathered sediment community oxygen consumption (SCOC) rate data, a measure of remineralization rates of organic material that has also been used to estimate ecosystem food availability (Jahnke 1996; Stratman et al. 2019). We used the SCOC Database collated by Stratmann et al. (2019) to collect SCOC rates within the bounds of species' catch location and averaged them at 50m intervals across each species' depth range. These 50m binned averages were then averaged to provide a mean SCOC value representative of each entire habitat. As these data are sparse geographically and rely on individual measurements rather than extrapolation from satellite color data, representative lifespan SCOC rates could only be calculated for 21 species.

For a subset of fishes, published data from studies on fish metabolic rate were available for comparison to growth metrics. Specifically, published activities of citrate synthase enzyme activity for various species were collected (Drazen et al. 2015; Saavedra et al. 2015; Siebenaller et al. 1986; Sullivan and Somero 1980; Truman et al. unpublished data). Citrate synthase is an enzyme of the Kreb's cycle, and its activity has been used in past studies to as a proxy for whole animal resting aerobic metabolic rates in fishes (Somero and Childress 1980; Somero and Childress 1990; reviewed in Dalhoff 2004 and Drazen and Seibel 2007). Enzyme activities were all measured at a temperature of 10°C, and are here denoted as CS_{10}. CS_{10} values were also normalized to a mass of 500g in order to correct for the scaling effects of body mass on metabolism. These adjustments to mass were performed per the methods described in previous work (Gillooly 2001; Brown 2004). See the "Supplementary Methods and Figures" for equations used. As biochemical reaction rates increase with temperature, temperature-adjusted versions of these CS_{10} values were also calculated (denoted as CS_H) to reflect the metabolic rate at the habitat temperature experienced by each fish, per previous work (Gillooly 2001; Brown 2004; McClain et al. 2012; see Supplementary Methods and Results and "Ontogenetic migrators" section below for details and equations used).

The fishes in this meta-analysis, though all demersal, occur on a wide spectrum of activity levels, from the sluggish, sedentary *Sebastolobus alascanus* to active swimmers like *Anoplopoma fimbria*. As an additional proxy for activity level, we included a rough categorization of activity level based on locomotory mode: each fish was characterized as benthic if they predominately remain on the seafloor or benthopelagic if they are typically actively swimming above the seafloor. This descriptor was used as a factor in statistical analysis. Locomotory modes were generally assigned based on descriptions for each species in Fishbase (see Supplementary Table 1 for all sources and justifications used).

Ontogenetic migrators

Ten species in this meta-analysis are known to ontogenetically migrate deeper with age/size (highlighted in blue text in Table 1), complicating the estimation of environmental predictors. For these fishes, estimation of environmental predictors was modified to account for changes in depth across the fish's lifespan. Environmental predictors were estimated individually, based on the unique depth of each individual fish given its capture depth (or mean size-at-age data point, when only mean size-at-age was available). When individual depth-of-capture was not available, published regressions were used to estimate likely depth at a given size/age. For *S. alascanus*, published probabilities of depth by length (Jacobson et al. 2001) were used to model of predicted length vs. depth (GAM, family: gamma; link: log). When detailed depth information was available (primarily for data from NWFSC), temperature was estimated for each ontogenetic migrator by collecting WOA temperature data within each study location and using a model (GAM; family: gamma, link: log) to predict temperature based on each ontogenetic migrator's predicted or observed depth and latitude/longitude of catch. This process was repeated to estimate oxygen concentration for each migrator. Lutz POC flux was calculated at the predicted or observed depth of each individual ontogenetic migrator (or mean size-at-age datapoint when only mean data were available).

For inter-species comparisons of growth rates and environmental predictors across migrators and non-migrators, two versions **each** of average temperature, oxygen, POC flux, SCOC, and depth were created for each species: one "**pre-maturity**" average of conditions experienced by fish at or younger than their age at maturity, and one "**lifespan**" version, reflective of those experienced during the fish's entire lifespan. For non-ontogenetic migrators, these two versions are identical, as these fish are expected to be distributed relatively uniformly in age/size across their depth range. Collected SCOC rates within the catch locations and depth ranges of ontogenetic migrators were not numerous enough to create regressions of SCOC vs. depth and predict SCOC at the depth of each individual ontogenetic migrator. To resolve this, we averaged SCOC at the pre-maturity depth range of each ontogenetic migrator (average individual depth of capture or predicted depth during pre-maturity, plus and minus the standard deviation of depth of capture). Data were only sufficient to calculate these pre-maturity SCOC rates for ontogenetic migrators living along the west coast USA (*Sebastolobus alascanus* and species collected in the NWFSC Groundfish Trawl Survey; Table 1). For metabolic rate comparisons, two versions of temperature-adjusted citrate synthase activities were created by adjusting CS_{10} values to the lifespan temperature experienced by each species across its lifespan **(lifespan CS_H),** and citrate synthase activity rate adjusted to the pre-maturity temperature experienced by each species **(pre-maturity CS_H)**. These adjustments to mass were performed per the methods described in previous work (Gillooly 2001; Brown 2004; McClain et al. 2012). See the "Supplementary Methods and Figures" for equations used. In summary, the descriptor "**pre-maturity**" and "**lifespan**" are used next to environmental predictors in order to specify whether the underlying data for ontogenetic migrators reflects their early, relatively shallow-water period of life, or their entire lifespan, respectively.

In terms of calculating thermal age, fish that ontogenetically migrate deeper with age generally experience a shifting temperature regime across their lifespan, and thus GDY cannot be calculated as a simple product of age and current predicted temperature. For these fishes, a generalized linear model (GLM) was used to fit the relationship between age and predicted or observed temperature (Family: gamma, link function: log). In multiple species, males and females were observed to have statistically different ($P < 0.05$) age vs. temperature curves, suggesting different rates of downslope migration between sexes. For this reason, separate GLMs were fit to males and females for most ontogenetic migrators. In order to calculate the cumulative GDY for a fish species, the curve produced by the respective GLM equation for the fish's species and/or sex was integrated with bounds beginning from age 0 up to the individual fish age. This integration produces the area under the age vs. temperature curve, and thus calculates a thermal age for the individual fish that accounts for the shifting thermal regime encountered by these ontogenetic migrators.

Statistical Analysis

All growth metrics were compared with all available environmental predictors in two ways: pairwise generalized linear models (GLMs with gamma error distribution) each containing only one growth metric and one environmental variable, and with multivariate generalized linear mixed-models (GLMMs, gamma error distribution), each containing one growth metric, multiple environmental variables, and a random effect for phylogenetic family. The former method was used primarily to identify which versions of each predictor (i.e. maximum depth vs. median depth, pre-maturity temperature vs. lifespan temperature, etc.) best explain growth and informed which should be included in subsequent GLMM analysis. The latter was used to determine which combinations of predictors best explained the growth rate data. In these analyses a gamma error distribution was chosen, as long-term growth rates of these animals must be greater than zero, and this error distribution does not allow residuals to be negative. Due to paucity of SCOC and metabolic rate data, these predictors were only analyzed in pairwise regressions, and were not included in the full GLMM analysis. However, to see how much variation could potentially be explained by including metabolic rate data, the top model for explaining each growth rate was rerun including pre-maturity CS_H, the metabolic rate predictor with the strongest relationships with growth rate in pairwise analysis, as a predictor. Environmental predictors estimated from both the pre-maturity phase of life and across the entire lifespan were used in the pairwise regressions, as well as in GLMM analysis for K and K_{GDY}. Only pre-maturity predictors were used in multivariate analysis for AIM and AIM_{GDY}, as these growth metrics reflect only the pre-maturity phase of growth. For numerical predictors, either a log link function or inverse link function was used depending on which form of the GLM created residuals that were more evenly distributed and without clear patterns. When a clear difference in residual patterns across link functions was not observed, the model favored by Akaike Information Criterion with correction for small sample size (AICc) was chosen. AICc is a scoring method used to rank models without favoring those that are overly complex, as the

AICc is decreased with increasing explanatory power, but is increased by model complexity. Models with relatively lower AICc scores are considered to be better, though models with AICc scores within 2 of one another are assumed to be equally likely to be the “true” model. AICc was used in these analyses in the model selection process to maintain balance between overfitting and underfitting the data.

Mixed model analysis and subsequent model selection was repeated for each growth metric with and without inclusion of the abyssal grenadier *Coryphaenoides armatus*, as this is the only abyssal fish in the dataset and is thus a valuable point of comparison to other fishes, but is also notable outlier in AIM and AIM_{GDY}. For the mixed models, where there was more than one version of a predictor (i.e., minimum usual depth vs. median usual depth vs. maximum usual depth), the one that explained the most variation for each growth metric in their respective pairwise regression (Table 2) was used.

In order to reduce the influence of covariation among predictors in mixed models, predictors were removed stepwise from each GLMM until the variation inflation factor (VIF) of each predictor was below 3. VIF thresholds of lower than 10 have been suggested, with more conservative cutoffs in high-colinearity datasets set at 2 or 3 (Zuur et al. 2010). The remaining GLMs were each run through the R function “dredge”, which creates an individual GLMM for every possible permutation of predictors in the global model, and returns a table with the models ranked by AICc.

RESULTS

Seventy-four teleost growth studies or data sources were considered for this meta-analysis. Of these, 21 were eliminated due to use of only whole otoliths and/or scales in the aging process. Another 12 were eliminated for quality control reasons outlined in the methods section above. Thus, data were included from 42 sources: 40 published studies and 2 national oceanographic institutions (NIWA and NWSFC). Fifty-three species over 6 orders of teleost fishes were represented (Table 1). Among these species, 22 are shallow-water fish (maximum usual depth < 500m), with most others with median depths of 500 to 3150m, and a maximum depth of 4000m (Fig. 1). Temperatures experienced by these fishes ranged from 1.7-25 °C (endmembers, *Coryphaenoides armatus* and *Platycephalus indicus*, respectively), with 17 species inhabiting waters >10°C (Fig. 1). Average oxygen concentrations ranged from 0.5-7.0mL/L (*Anoplopoma fimbria* and *Hippoglossus hippoglossoides,* respectively, Table 2). Estimated Lutz POC fluxes to each species' habitat ranged from 1.02-26.7 g $Cm^{-2}yr^{-1}$ (Table 2). SCOC rates spanned from 0.45-13.3mmol $O_2m^{-2}d^{-1}$ (Supp. Table 1). Catch locations ranged in latitude from 80˚S to 66˚N, and from the Indian, Atlantic, Pacific, and Southern Ocean (Fig. 2). Most catch locations were focused in the North Atlantic, Northeast Pacific, and Southwest Pacific. The Mediterranean Sea is the next-most sampled region. 19 growth studies on Mediterranean populations were examined, but 15 of the 19 used whole otoliths for age estimation and were rejected for quality-control reasons. The low latitudes (~20°S to 20°N) are relatively underrepresented. This underrepresentation likely reflects the relative paucity of age and growth studies around Africa, South America, and India, as well as the difficulty in obtaining and/or translating aging studies around Asia. Phylogenetic orders are evenly dispersed across the areas of highest concentration of studies (Fig. 2) but some orders are not found in shallow water (Fig 1). The age and size data available for some of the species in this meta-analysis were insufficient to robustly compute growth metrics (*K* or AIM). These cases are highlighted with an asterisk in Table 1 and were omitted from analyses.

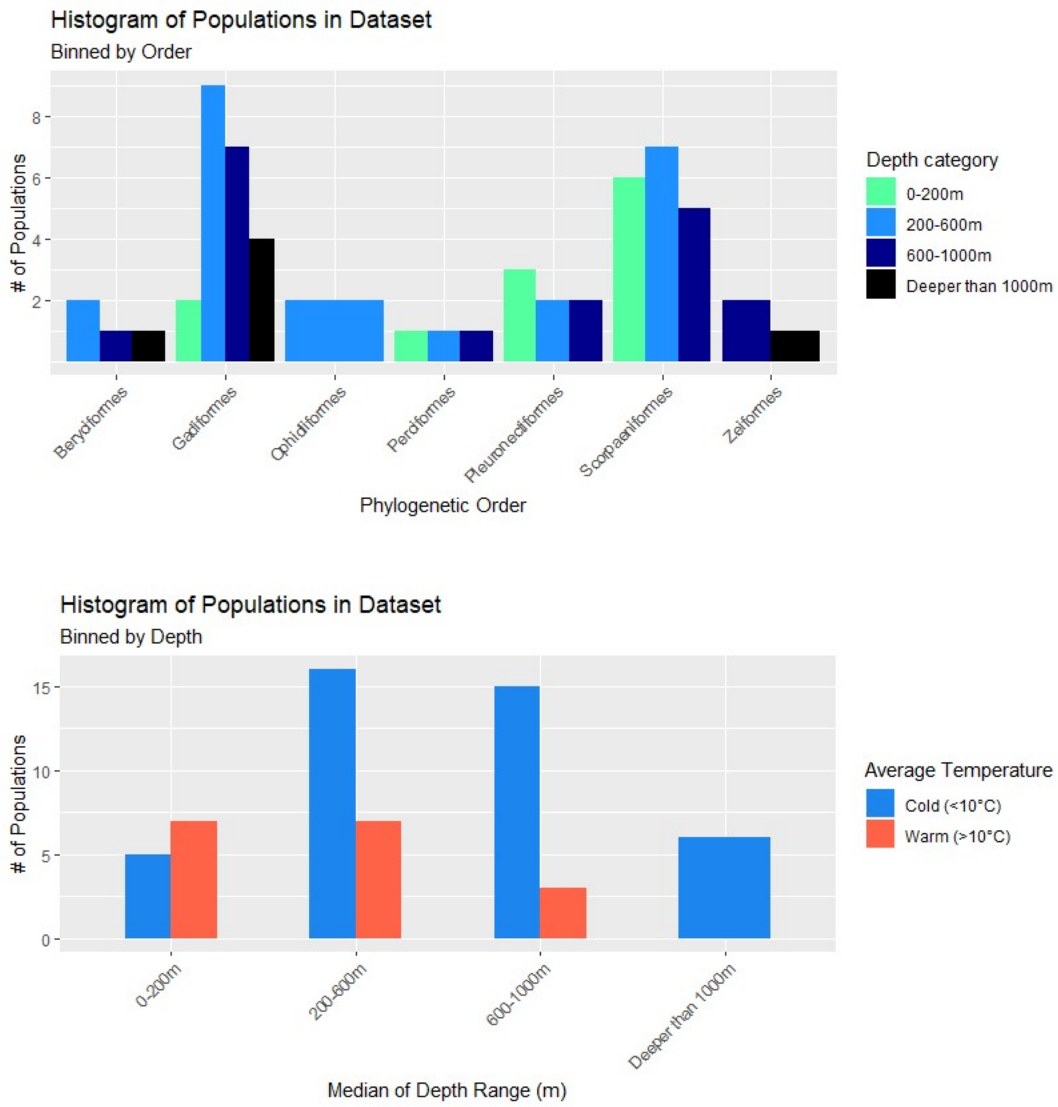


Figure 1: Numbers of populations of fishes in this study organized by lifespan average temperature **(upper)** and depth category (**lower**). Median usual depths across the entire fish lifespan were used to categorize each species.

Table 1: Depths, habitat variables and growth metrics for each fish population (see methods and Supp. Table 1 for sources and explanation of depth ranges). **A_M** is age at 50% maturity unless otherwise noted with the following subscripts: **a.** median of known minimum and maximum ages at maturity; **b.** age at

50% maturity was estimated using a published length at 50% maturity and the Von B curve; **c.** general time at maturity. **Lutz POC flux** is reported as three values separated left to right by slashes as values at minimum, median, and maximum depths. **CS_H PM** refers to citrate synthase activity (units per gram wet weight of white muscle tissue at each species' average pre-maturity temperature. **Ontogenetic migrators** are highlighted in blue, and the pre-maturity version of applicable predictors are in parentheses. Asterisks denote where there was insufficient data to calculate growth metrics. Number of fish represented in data from each study listed under ***n*.** Only observations containing both age and size are counted here. Data for *M. productus* contained many more observations of mass-at-age age than of length-at-age, denoted with (L) for length observations and (M) for mass.

	Min depth (m)	Median depth (m)	Max depth (m)	Lutz POC flux (mg C/m^{-2}d^{-1})	O$_2$ (mL/L)	T (C°)	*K*	K$_{GDY}$	AIM$_{GDY}$ (%)	AIM (%)	CS$_H$	A$_M$	*n*
Beryciformes													
Beryx decadactlyus													
Charleston Bump (Friess and Sedberry 2011)	368	432	496	7.7/7.3/7.0	4.0	15.2	0.12	0.007	*	*		4	155
Beryx splendens													
Palliser Bank (NIWA)	200	500	800	32.7/25.8/20.6	5.0	9.0	0.22	0.021	2.34	33.1	3.41	5$_b$	2310
Hoplostethus atlanticus													
Walter's Shoal (NIWA)	1000	1125	1250	6.9/6.4/5.9	4.5	5.4	0.06	0.007	*	*	0.50	22	409
Hoplostethus mediterraneus													
Eastern Mediterranean (D'Onghia et al. 1998)	388	642.5	897	8.2/7.0/6.0	4.4	13.9	0.21	0.013	4.33	72.7		4	419
Gadiformes													
Antimora rostrata													
North Atlantic (Orlov et al. 2018)	1300 (880)	1900 (960)	2500 (1045)	9.5 (12.4)	6.6	3.5 (3.7)	0.06	0.007	3.20	24.2	0.21	16	340
Coelorinchus caelorhincus													
Eastern Mediterranean (Labropoulou and Papaconstantinou 2000)	350	450	550	8.4/7.9/7.4	4.5	14.1	0.05	0.003	4.58	116.3		6	244
Coryphaenoides acrolepis													

West coast USA (Matsui et al. 1993; Andrews et al. 1999)	700	1350	2000	18.0/11.2/7.5	0.9	3.1	0.05	0.007	1.50	9.7	0.51	36_a	146
Coryphaenoides armatus													
Mid-Atlantic Ridge (Bergstad et al. 2013)	2000	3000	4000	6.9/4.0/2.8	6.3	2.9	0.04	0.007	5.23	36.5	1.04	20_c	317
Station M (Gerringer et al. 2018)	2000	3150	4300	6.3/4.3/3.5	2.7	1.7	*	*	3.04	15.3	1.04	20_c	107
Coryphaenoides rupestris													
British Isles (Allain et al. 2000)	400	950	1500	34.4/21.0/13.2	5.5	7.6	0.04	0.004	1.48	17.1	0.30	10	2814
Gadus morhua													
North Atlantic (Rideout et al. 2013)	50	125	200	33.8/31.6/29.5	6.2	3.2	0.13	0.022	6.47	40.0		5	7781062
Hymenocephalus italicus													
Eastern Mediterranean (D'Onghia et al. 2000)	305	601	897	9.7/8.0/6.6	4.4	13.9	0.18	0.011	3.46	78.0		3	408
Lepidion eques													
North Atlantic (Magnússon 2001)	500	700	900	31.4/25.9/21.4	6.1	5.8 (6.4)	0.10	0.006	3.99	43.9		9	295
Macrourus carinatus													
Heard Island (Van Wijk et al.	500	750	1000		4.4	2.3	0.07	0.013	3.43	19.3			142

2003)				11.1/8.7/6.9								11	
Macruronus novaezelandiae													
Australasia (Horn and Sullivan 1996)	200	500	800	39.4/31.1/24.7	5.1	9.2	0.17	0.014	2.94	43.0		6	9569
Merluccius australis													
West Coast South Island (NIWA)	300	700	1100	25.1/18.4/13.8	4.6	7.7	0.22	0.020	3.60	49.6		6	3884
Merluccius hubbsi													
Off Brazil (Vaz-dos-Santos and Rossi-Wongtschowski 2007)	100	150	200	16.4/15.7/15.1	5.0	18.0	0.19	0.009	5.67	261.8		2	685
Merluccius merluccius													
Iberian Peninsula (Piñeiro and Saínza 2003)	70	220	370	40.6/35.7/31.4	6.6	12.6	0.10	0.007	*	*		3	965
Merluccius productus													
Northern West Coast USA (NWFSC Groundfish Trawl Survey)	50 (120)	275 (170)	500 (220)	66.9 (67.4)	3.1 (3.0)	7.1(7.2)	0.27	0.025	7.22	122.6	1.52	3	5501 (M) 556 (L)
Southern West Coast USA (NWFSC Groundfish Trawl Survey)	50 (170)	275 (190)	500 (210)	35.5 (36.5)	2.4 (2.6)	7.5(7.9)	0.20	0.019	5.91	88.3	1.65	3	4475 (M) 687 (L)

Micromesistius australis													
Off Argentina (Cassia 2000)	70	200	620	64.1/56.1/36.8	6.4	4.5	0.17	0.023	8.16	81.2		4_b	4919
Off New Zealand (NIWA)	400	500	600	13.4/12.3/11.4	5.8	5.8	0.20	0.022	7.76	96.7		3	7920
Mora moro													
Chatham Rise (Sutton et al. 2010)	500	750	1000	22.6/18.3/14.9	5.0	6.3	0.13	0.014	3.81	42.8	0.34	8_c	294
Nezumia sclerorhynchus													
Eastern Mediterranean (Labropoulou and Papaconstantinou 2000)	350	550	750	8.4/7.4/6.6	4.5	14.1	0.15	0.009	1.97	42.5		11	200
Trachyrhynchus scabrus													
Western Mediterranean (Massutí et al. 1995)	700	875	1050	10.7/9.4/8.4	4.3	13.3	0.15	0.009	*	*		4_b	263
Ophidiiformes													
Genypterus blacodes													
Cambell Plateau (NIWA)	200	500	800	13/10.2/8	5.8	6.6	0.15	0.015	5.31	65.7		6	5254
Chatham Rise (NIWA)	200	500	800	28.3/21.8/17	5.5	7.3	0.12	0.011	5.05	66.8		6	5751
Perciformes													
Cheilodactylus spectabilis													
Tasmania (Ewing et al. 2017)	0	25	50	34.1/33.4/32.8	5.6	15.3	0.39	0.026	2.54	57.7		3	198
Epigonus telescopus													

Australasia (Tracey 2000)	500	800	1000	14.6/11.7/10.1	4.8	7.2	0.04	0.004	0.54	5.7		36	554
Hyperoglyphe perciformis													
Charleston Bump (Filer and Sedberry 2008)	200	363	526	10/8.8/7.8	4.1	16.1	0.21	0.012	0.46	9.2		6	710
Pleuronectiformes													
Atheresthes stomias													
West coast USA (NWFSC Groundfish Trawl Survey)	27 (130)	148.5 (170)	270 (210)	50.8 (55.4)	1.4 (1.7)	6.4(7.6)	0.14	0.012	2.68	33.2	0.46	7	3525
Cynoglossus zanzibarensis													
South Africa (Booth and Walmsley-Hart 2000)	30	230	430	58.5/50/42.9	4.7	14.8	0.44	0.025	4.05	100.6		2	180
Eopsetta jordani													
West coast USA (NWFSC Groundfish Trawl Survey)	160 (80)	205 (100)	250 (120)	45.5 (50.8)	3.1 (4.1)	8.4(10.6)	0.13	0.009	2.75	39.7	0.64	5	4745
Hippoglossus hippoglossus													
North Atlantic (Armsworthy and Campana 2010)	55	81.5	108	46.5/45.3/44.2	7.0	6.2	0.13	0.014	6.69	186.1		6	2429
Microstomus pacificus													
West coast USA (NWFSC Groundfish Trawl Survey)	55 (110)	777.5 (180)	1500 (250)	31.1 (43.43)	1.1 (3.3)	5.3(8.8)	0.17	0.017	2.10	23.3	0.78	7	6020
Parophrys vetulus													

West coast USA (NWFSC Groundfish Trawl Survey)	40 (70)	120 (90)	200 (110)	49.1 (50.83)	3.8 (4.2)	9.2(10.6)	0.35	0.028	3.31	61.6	0.85	4_a	772
Reinhardtius hippoglossoides													
North Atlantic (Dwyer et al. 2016)	500	750	1000	22.8/17.9/14.2	6.7	2.0	0.07	0.015	9.78	58.4		10	266
Scorpaeniformes													
Anoplopoma fimbria													
West coast USA (NWFSC Groundfish Trawl Survey)	200 (140)	600 (270)	1000 (390)	25.7 (40.17)	0.7 (2.7)	4.3 (7.4)	0.43	0.045	4.87	61.4	1.67	5	3772
Chelidonichthys capensis													
South Africa (McPhail 1998)	30	115	200	42.1/39.4/36.9	4.7	14.8	0.07	0.004	3.31	75.2		4	383
Chelidonichthys queketti													
South Africa (Booth 1997)	50	100	150	37.9/36.4/35	4.7	14.8	0.40	0.022	*	*		2	227
Helicolenus percoides													
Australasia (Paul and Horn 2009)	100	400	700	37.2/28.7/22.2	5.4	8.8	0.10	0.009	3.73	53.9		5	1338
Platycephalus indicus													
Japan (Akita and Tachihara 2019)	0	15	30	11.9/11.8/11.6	4.8	25.0	0.38	0.014	2.78	118.7		2	351
Pterois volitans													

Gulf of Mexico (Fogg 2017)	50	85	120	23.7/23/22.4	4.2	20.8	0.44	0.018	5.92	163.5		1	1576
Scorpaena notata													
Eastern Mediterranean (Scarcella et al. 2011)	30	365	700	51.2/38.1/28.6	5.1	13.4	0.32	0.019	2.85	59.0		2.5	225
Sebastes crameri													
West coast USA (Nichols 1990)	140	175	210	73.3/70.9/68.5	2.9	7.6	0.20	0.019	5.66	75.9	0.49	5	1060
Sebastes ensifer													
West coast USA (Love et al. 2018)	45	205.5	366	61.6/54/47.4	3.1	8.7	0.13	0.012	1.91	23.7		9	171
Sebastes fasciatus													
Flemish Cap (Saborido et al. 2004)	130	315	500	33.9/28.4/24	6.3	3.9	0.13	0.018	*	*		6	5174
Sebastes marinus													
Flemish Cap (Saborido et al. 2004)	100	200	300	34.8/31.7/28.8	6.3	3.9	0.07	0.009	6.15	52.1		7	6016
Sebastes melanostomus													
West coast USA (Stevens et al. 2003)	250	425	600	40/34.8/30.4	1.0	6.4	0.06	0.007	0.82	7.9	0.32	34	332
Sebastes mentella													
Irminger (Stransky et al.	300	600	900		6.7	3.8 (4.1)	0.13	0.020	1.58	10.2			359

2005)				28.7/21.5/16.2								10	
Newfoundland (Saborido et al. 2004)	300	600	900	28.8/21.9/16.7	6.5	3.7	0.11	0.016	3.64	27.8		10	8930
Sebastes mystinus													
British Isles (Laidig and Person 2003)	0	45	90	70.1/67.4/64.8	5.2	11.1	0.22	0.015	4.67	89.9	0.76	6	1245
Sebastes simulator													
West coast USA (Love et al. 2018)	99	274.5	450	58.9/51/44.3	1.7	7.8	0.10	0.009	2.53	30.4		11	156
Sebastolobus alascanus													
Off California (Kline 1996)	90 (380)	750 (380)	1500 (380)	31 (42.48)	0.5 (1.16)	4.4(6.0)	0.02	0.002	2.26	21.8	0.40	12	1140
Sebastolobus altivelis													
Off California (Kline 1996)	400	950	1500	46.5/30.3/20.5	0.7	4.2	0.06	0.008	*	*	0.21	6_c	342
Zeiformes													
Allocyttus niger													
Chatham Rise (NIWA)	700 (644)	900 (840)	1300 (1039)	17.4 (18.31)	4.8 (4.9)	3.9(4.2)	0.23	0.023	0.54	3.7		27_c	2056
Allocyttus verrucosus													
Australasia (Stewart et al. 1995)	1000	1200	1400	11.3/10/8.8	4.2	3.6	0.06	0.010	1.79	12.4		24	102

Neocyttus rhomboidalis												
South East Australia (Smith and Stewart 1994)	600	700	800	16.6/15.4/14.4	5.2	7.6	0.05	0.005	0.77	8.5		33[b]	97

Table 2: R^2 values for pairwise regressions of predictors and growth metrics, with and without *Coryphaenoides armatus*. Deeper orange colors indicate a higher magnitude of variation explained. R^2 values are highlighted in blue text when $P < 0.05$.

Predictors	**K**	**K w/o *C.a.***	**KGDY**	**KGDY w/o *C.a.***	**AIM**	**AIM w/o *C.a.***	**AIMGDY**	**AIMGDY w/o *C.a.***
Minimum Usual Depth (Pre-maturity)	37.8	34.7	19.2	18.1	23.6	28.5	1.5	8.1
Median Usual Depth (Pre-maturity)	35.8	34	16.8	16.4	26.1	33.9	2	11.5
Maximum Usual Depth (Pre-maturity)	31	29.6	13	12.3	24.3	30	1.6	9.5
Minimum Usual Depth (Lifespan)	33	29.6	16.3	14.7	22.5	24.3	1.5	6.4
Median Usual Depth (Lifespan)	33.4	30.4	13.9	12.8	29.1	32.5	2.5	10.3
Maximum Usual Depth (Lifespan)	28.6	26.1	9.9	8.7	29.1	31.4	2.6	9.8
O_2 Concentration (Pre-maturity)	0.1	0.3	1	1.4	5	4.6	12.6	11.8
O_2 Concentration (Lifespan)	0.1	0	0	0.1	5.3	5	11.8	11.1
Net Primary Production	2	1.8	2.5	2.3	0	0.1	1.3	1.2
Lutz POC flux to Min. Depth (Pre-maturity)	5	4	9.6	8.6	2.7	1.7	1.7	2.2
Lutz POC flux to Med. Depth (Pre-maturity)	7.1	5.9	11.3	10.2	4.3	3.1	2.4	3.0
Lutz POC flux to Max. Depth (Pre-maturity)	8.4	7.2	11.2	10.1	5.1	3.9	2.0	2.50
Lutz POC flux to Min. Depth (Lifespan)	4.4	3.5	7.5	6.6	3.5	2.4	2.3	2.8
Lutz POC flux to Med. Depth (Lifespan)	6.5	5.5	9.2	8.2	5.4	4.1	3.1	3.8
Lutz POC flux to Max. Depth (Lifespan)	8	6.9	9.3	8.3	6.5	5.2	2.7	3.3
Phylogenetic Order	3.6	3.4	3.5	3.5	30.6	32	39	39
Temperature (Pre-maturity)	31.1	29.9	0.2	0.1	19.7	17.7	1	1
Temperature (Lifespan)	25.2	24.1	0	0.1	20.7	18.9	0.7	0.6

CS_{10}	17.2	24.4	24.9	31.3	5.8	11.4	11.3	10.3
CS_H (Lifespan)	20.4	23.8	23.5	25.6	13.7	15.3	10.5	10.3
CS_H (Pre-maturity)	27.2	30.8	32	34.1	13.8	14.8	10.5	10.6
Locomotory mode	0.2	0	1	1.2	4.5	4	0.1	0.2
SCOC (Lifespan)	13.4	13.4	7.19	7.19	11.46	7.06	4.78	4.77
SCOC (Pre-maturity)	16.62	16.62	11.97	11.97	4.41	0.65	0.22	0.01

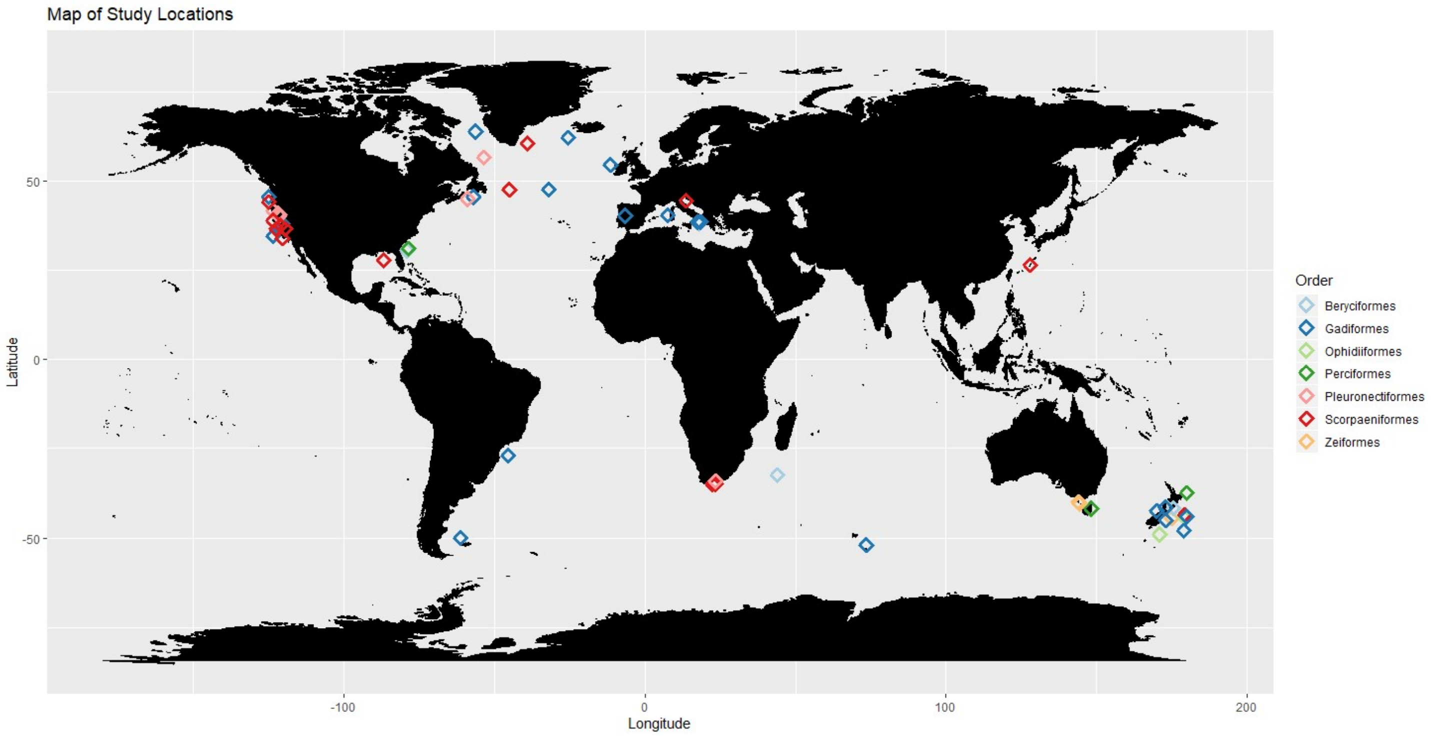
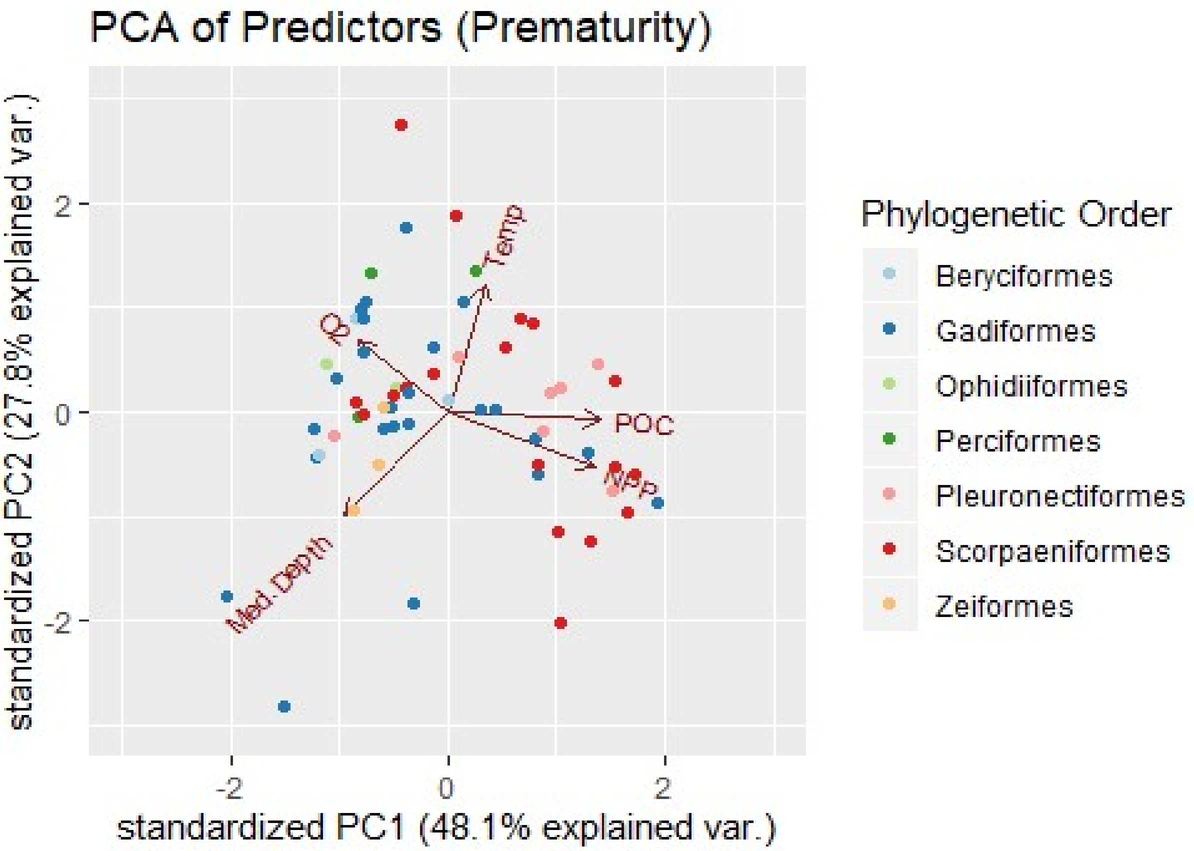
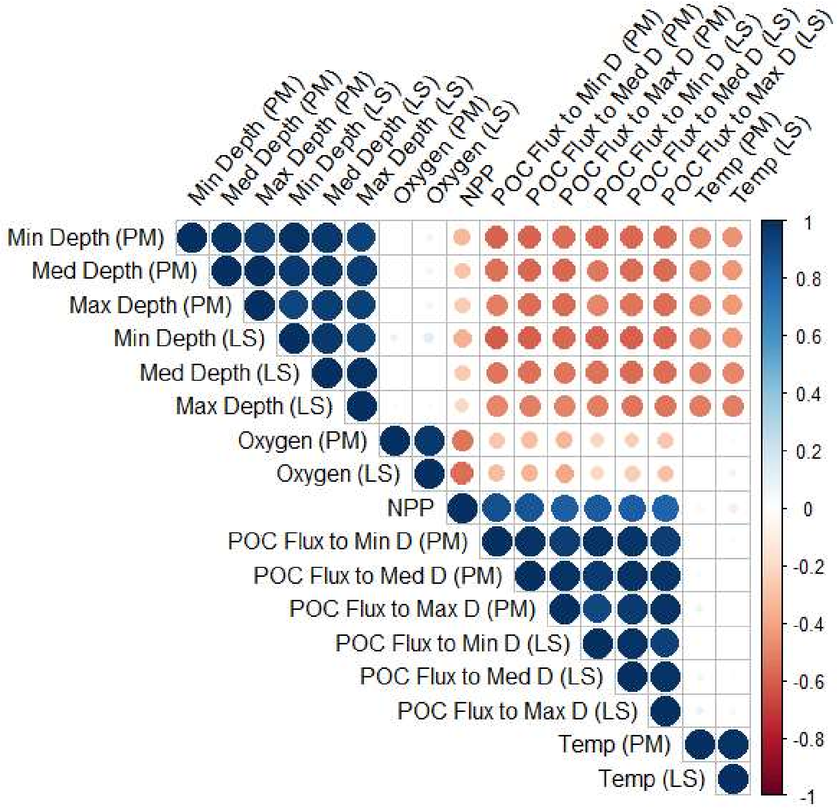


Figure 2: World map highlighted with catch locations from each study use for meta-analysis. Catch locations are colored by phylogenetic order.


PCA of Predictors (Prematurity)
standardized PC2 (27.8% explained var.)
standardized PC1 (48.1% explained var.)
2
0
-2
-2
0
2
Temp
O2
POC
NPP
Med. Depth
Phylogenetic Order
Beryciformes
Gadiformes
Ophidiiformes
Perciformes
Pleuronectiformes
Scorpaeniformes
Zeiformes


Min Depth (PM)
Med Depth (PM)
Max Depth (PM)
Min Depth (LS)
Med Depth (LS)
Max Depth (LS)
Oxygen (PM)
Oxygen (LS)
NPP
POC Flux to Min D (PM)
POC Flux to Med D (PM)
POC Flux to Max D (PM)
POC Flux to Min D (LS)
POC Flux to Med D (LS)
POC Flux to Max D (LS)
Temp (PM)
Temp (LS)
1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1

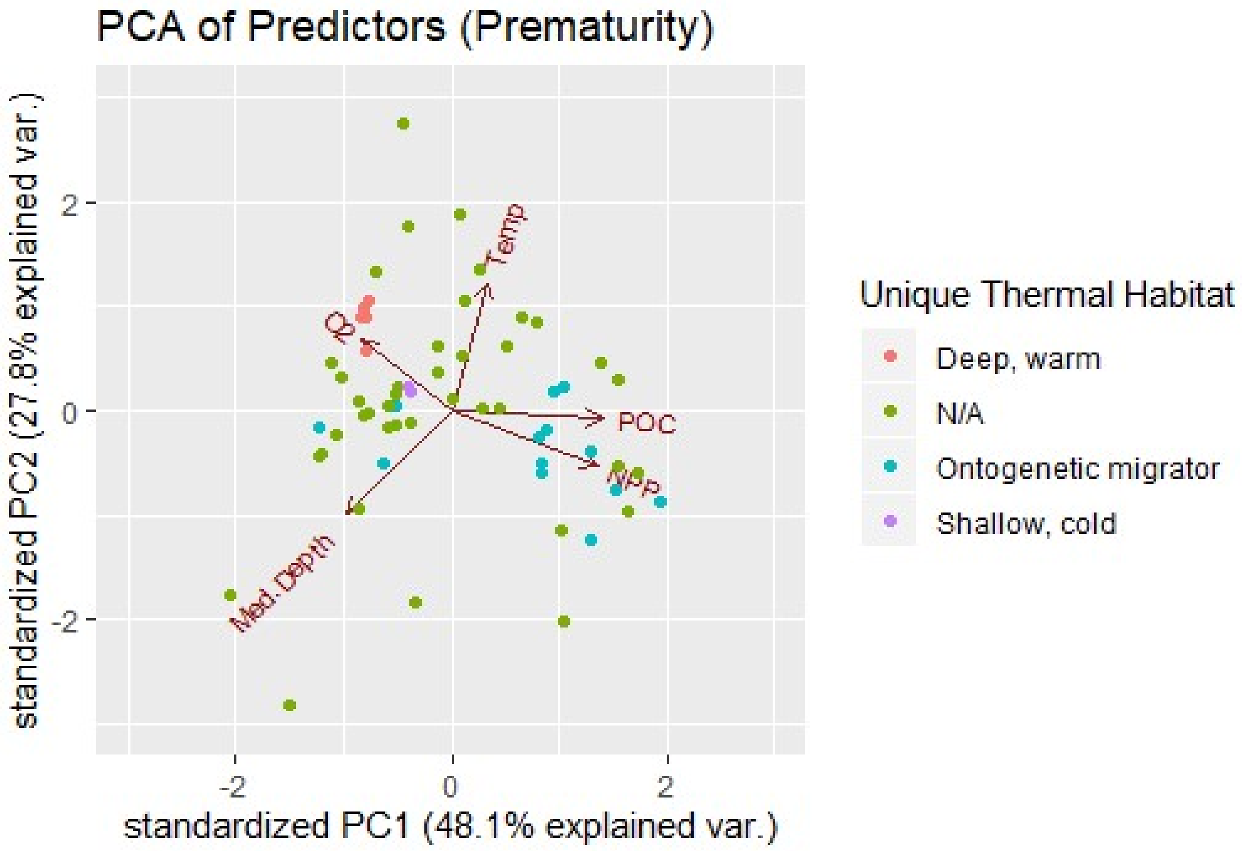


Figure 3: Top: Correlation plot of all continuous growth predictors used in this meta-analysis. Larger circles and deeper colors indicate larger magnitudes of the Pearson correlation coefficient. Blue hues indicate positive correlation, and red hues indicate negative correlation. **Middle:** PCA plot of pre-maturity predictors. Points are colored by phylogenetic order. **Bottom:** PCA plots of pre-maturity predictors. Points are colored unique thermal situations (if applicable) that contrast the typical "colder, deeper" paradigm found in the world oceans. Fish are designated as "deep, warm" if living at an average temperature above 10°C and with a minimum lifespan depth of at least 300 meters. "Shallow, cold" denotes fish living at a maximum usual depth of shallower than 300m and at average temperatures at or below 4°C.

Moderate covariation was found between some environmental predictors (Fig. 3). Pearson correlation coefficients of temperature and depth had values between -0.43 and -0.51, depending on the depth bound and whether pre-maturity or lifespan temperatures are used for ontogenetic migrators. As expected, NPP and POC metrics were all highly positively correlated (Pearson correlation coefficients: 81% to 87%). Among all predictors, POC metrics were the most strongly correlated with depth (Pearson correlation coefficients: -0.48 and -0.6). Oxygen is strongly (negatively) correlated only to NPP. Principal Component analyses of the pre-maturity predictors shows NPP and oxygen concentration oriented along the same axis (Fig. 3). Temperature and median depth are fairly aligned. PC1 and PC2 explain 48.1% and 27.8% of the variation among environmental predictors, respectively. No obvious clustering is observed among phylogenetic orders, but species inhabiting deep, warm environments (minimum usual depth > 300m and average temperature >10°C) are clustered tightly. These species were all caught in Mediterranean, likely driving their similar position across environmental characteristics. The two shallow, cold water fish, *Gadus morhua* and *Sebastes marinus* (maximum usual depth < 300m and average temperature < 4°C), are also clustered closely.

Pairwise GLM comparisons: growth rates have strong relationships to temperature, depth, and metabolic rate

K coefficients across the species showed logarithmic declines with minimum, median, and maximum usual lifespan depth ($P < 0.001$, $R^2 = 29$-33%, Table 2, Fig. 4). Interestingly, *K* with minimum, median, and maximum usual pre-maturity depth showed similar declines and explained several percent more variation overall ($P < 0.001$, $R^2 = 31$-38%, Table 2, Fig. 4). These patterns remain when the deepest fish in the meta-analysis, *C. armatus* is omitted, but with some loss of explanatory power (Table 2). *K* increased significantly with average lifespan temperature and pre-maturity temperature ($P < 0.01$; $R^2 =$ 25% and 31% respectively, Table 2, Fig. 6). In contrast, Lutz POC flux explained much less variation in *K*, and the relationships varied in statistical significance ($P = 0.11$-0.024, $R^2 = 4.4$-8.0%, Table 2, Supp. Fig. 2). Like depth, the explanatory power of Lutz POC flux is slightly reduced without the inclusions of *C. armatus* (Table 2). *K* increased with citrate synthase (CS) activity, both measured at 10°C and adjusted to each species habitat temperature ($P < 0.05$, $R^2 = 17$-31%, Table 2, Fig. 8, Supp. Fig. 2). Pre-maturity CS_H

activity explained the greatest amount of variation among the metabolic rate predictors ($P < 0.05$, R^2 = 27% with *C. armatus*, 32% without *C. armatus*). *Beryx splendens* was a notable outlier in metabolic rate relative to all metrics of growth, though particularly so for AIM and AIM_{GDY} (Fig. 8). When *B. splendens* was omitted from these analyses, the metabolic rate was a stronger predictor of *K* ($P < 0.05$ for all metabolic rate metrics, R^2 = 20%, 36%, and 41% for CS_{10}, lifespan CS_H and pre-maturity CS_H, respectively). No significant difference in *K* values was found between benthic and benthopelagic fishes. *K* was not significantly related to NPP or SCOC in pairwise regressions at the $P < 0.05$ level, but SCOC did explain up to 16% of variation, which was higher than the 4-8% explained by POC flux (Table 2).

The temperature adjusted equivalent of *K*, K_{GDY} also showed significant declines with minimum, median, and maximum pre-maturity and lifespan depths ($P < 0.05$, R^2 = 8.7-18%, Table 2; Figure 4). However, the depth metrics explained an average of 18% less variation in $K_{GDY.}$ compared to *K*. Excluding *C. armatus* did not alter this general pattern. With temperature's influence largely removed (by using K_{GDY}), this growth metric also showed significant increases with all Lutz POC flux predictors ($P < 0.05$, R^2 = 6.6-11%, Table 2). K_{GDY} displayed similar patterns as *K* in relationships to metabolic rate ($P < 0.05$, R^2 = 23-32% Table 2, Fig. 8). Citrate synthase activity adjusted to pre-maturity temperatures appears to be the most significant metric of the metabolic rate predictors. When *B. splendens* was omitted from these analysis, metabolic rate was again a stronger predictor of K_{GDY} ($P < 0.01$ for all metabolic rate metrics, R^2 = 30%, 40%, and 48% for CS_{10}, CS_H Lifespan and CS_H Pre-maturity, respectively). No significant difference was found between benthic and benthopelagic fishes in pairwise comparison with K_{GDY}. K_{GDY} was not significantly related to NPP or SCOC in pairwise regressions.

AIM also declined logarithmically with all depth metrics, with most variation explained by the lifespan metrics ($P < 0.01$, R^2 = 24-34%, Table 2, Fig. 5). When *C. armatus* is excluded, these patterns remained. Oxygen concentration and Lutz POC flux were not significantly related to AIM, with or without *C. armatus.* AIM increased with both pre-maturity and lifespan temperatures, regardless of inclusion of *C. armatus* ($P < 0.01$, $R^2 = 18$-21%, Table 2, Fig. 6). In terms of phylogenetic order, the only significant difference in AIM was found in Zeiformes, which were seen to grow slower than average compared to the other orders (Supp. Fig. 5). CS activites were not significantly related to AIM unless *B. splendens* was removed from the analysis, in which case there was a significant positive relationship between AIM and temperature adjusted metabolic rates ($P < 0.001$, $R^2 = 37$% and 34% for lifespan CS_H and pre-maturity CS_H, respectively. No significant difference was found between benthic and benthopelagic fishes in terms of AIM. AIM was not significantly related to NPP or SCOC in pairwise regressions.

When *C. armatus* was included in pairwise regressions of AIM_{GDY} and any depth metric, no significant relationship was detected. However, upon exclusion of this fish, AIM_{GDY} showed significant declines with 5 out the 6 depth metrics ($P < 0.05$, $R^2 = 6.4$-12%, Table 2, Fig. 5). Even when *C. armatus* is excluded, these depth metrics on average explain 21% less variation in AIM_{GDY} than in the non-temperature adjusted equivalent, AIM (Table 2). With or without *C. armatus*, AIM_{GDY} significantly increased with pre-maturity and lifespan oxygen concentrations ($P < 0.01$, $R^2 = 11$-13%, Table 2, Fig. 7). However, this patter seems largely driven by a cluster of OMZ dwelling fishes at oxygen concentrations less than 2mL/L. When these fishes are omitted from pairwise regressions with pre-maturity and lifespan oxygen concentrations, the relationships are no longer significant ($P > 0.05$). Similar to AIM, CS activites were not significantly related to AIM_{GDY} unless *B. splendens* was removed from the analysis, in which case there was a significant positive relationship between AIM_{GDY} ($P < 0.01$ for all metrics, $R^2 =$ 29%, 42% and 37% for CS_{10}, lifespan CS_H and pre-maturity CS_H, respectively). AIM_{GDY} was not found to significantly differ across Lutz POC flux or between benthic and benthopelagic fishes. AIM_{GDY} was not significantly related to NPP or SCOC in pairwise regressions.

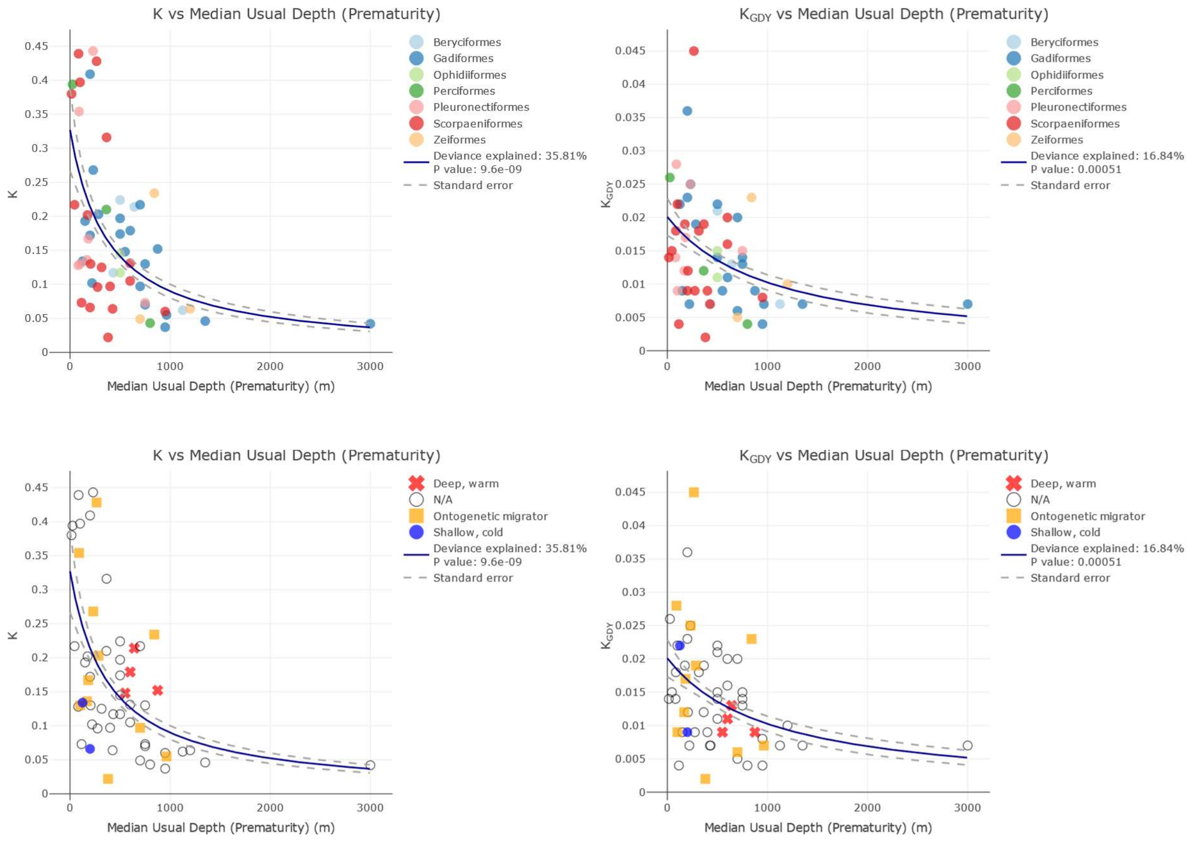


Figure 4: Von Bertalanffy *K* and temperature adjusted K_{GDY} vs. median of species' depth range. For ontogenetic migrators, the average pre-maturity depth is used. The blue lines show best-fit regression, and grey bands show the standard error. **Top row:** regressions of *K* (left) and K_{GDY} (right) against median usual depth range during pre-maturity, colored by phylogenetic order. **Bottom row:** unique thermal situations for some species are highlighted with shape and color: species that ontogenetically migrate to deeper waters are shown as yellow squares, species that live in cold, shallow water (≤ 300m maximum usual depth and < 4°C average temperature of habitat) are shown as blue circles, and species that live in deep, warm water (≥ 300m minimum usual depth and > 10°C average temperature of habitat) are denoted with as a red **X**.

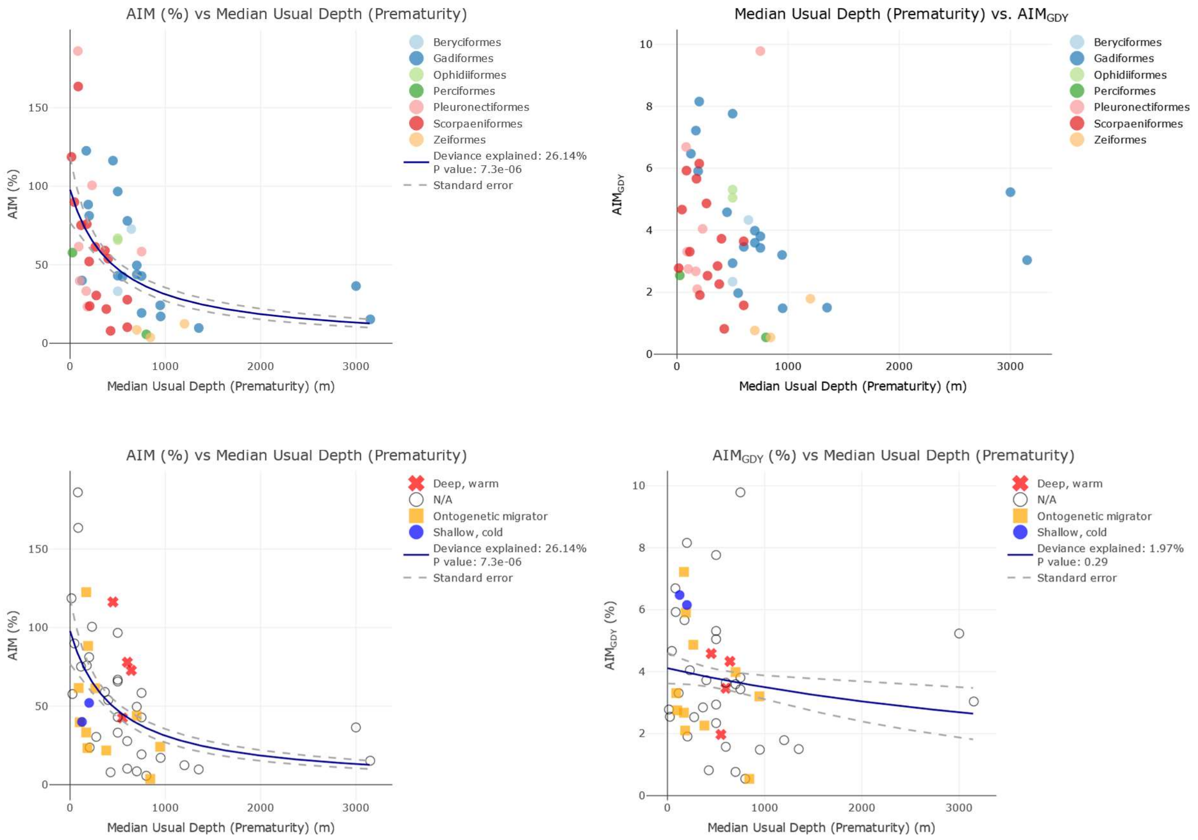


Figure 5: Von Bertalanffy AIM and temperature adjusted AIM$_{GDY}$ vs. median of species' depth range. For ontogenetic migrators, the average pre-maturity depth is shown. The blue lines show best-fit regression, and grey bands show the standard error. **Top row:** values of AIM (left) and AIM$_{GDY}$ (right) are colored by phylogenetic order. **Bottom row:** unique thermal situations for some species are highlighted with shape and color: species that ontogenetically migrate to deeper waters are shown as yellow squares, species that live in cold, shallow water (≤ 300m maximum usual depth and < 4°C average temperature of habitat) are shown as blue circles, and species that live in deep, warm water (≥ 300m minimum usual depth and > 10°C average temperature of habitat) are denoted with as a red **X**.

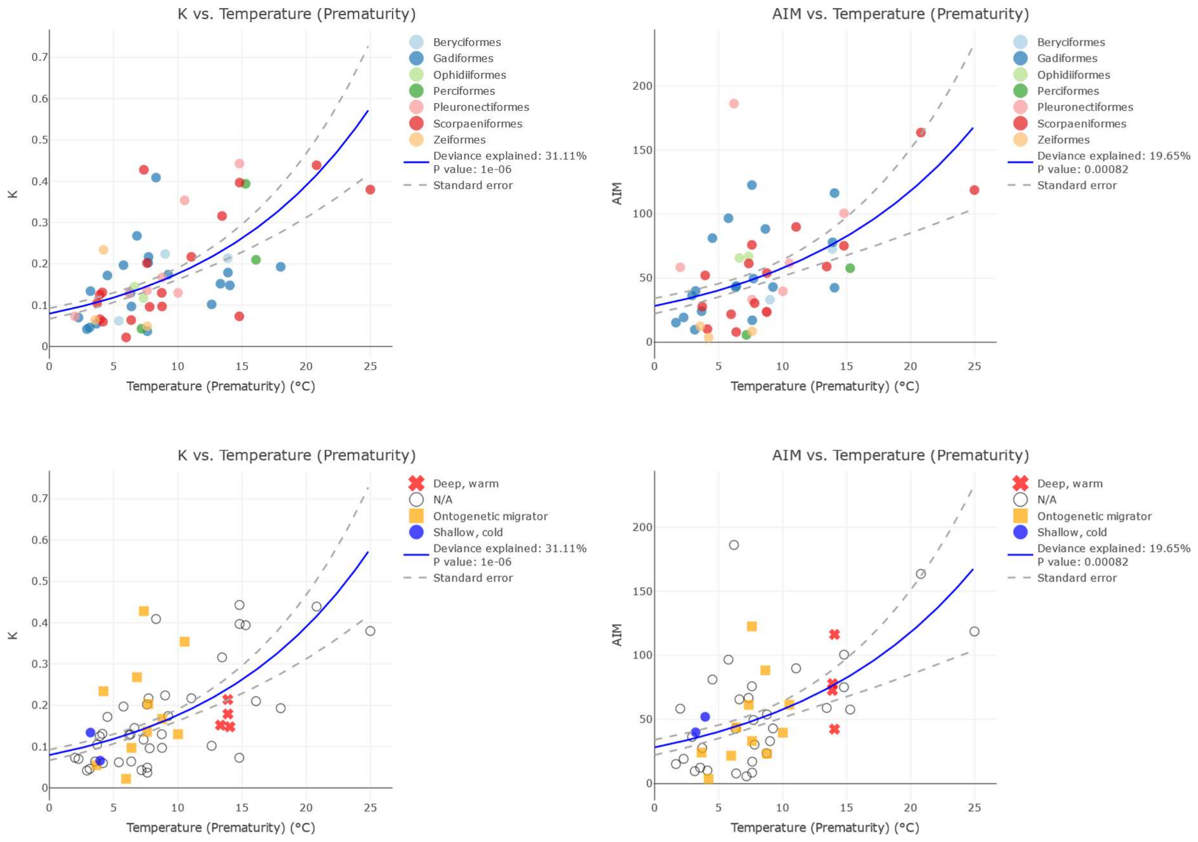


Figure 6: Von Bertalanffy *K* and AIM vs. average temperature. For ontogenetic migrators, temperatures were averaged across the **pre-maturity phase**. The blue lines show best-fit regression, and grey bands show the standard error. **Top row:** values of *K* (left) and AIM (right) vs. temperature, colored by phylogenetic order. **Bottom row:** *K* (left) and AIM (right) vs. temperature, with unique thermal situations for some species are highlighted with shape and color: species that ontogenetically migrate to deeper waters are shown as yellow squares, species that live in cold, shallow water (≤ 300m maximum usual depth and < 4°C average temperature of habitat) are shown as blue circles, and species that live in deep, warm water (≥ 300m minimum usual depth and > 10°C average temperature of habitat) are denoted with as a red **X**.

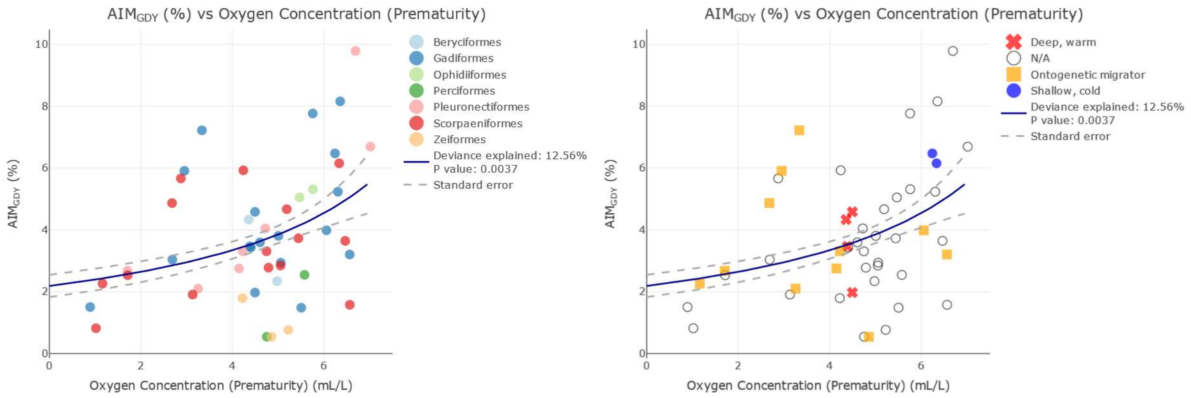
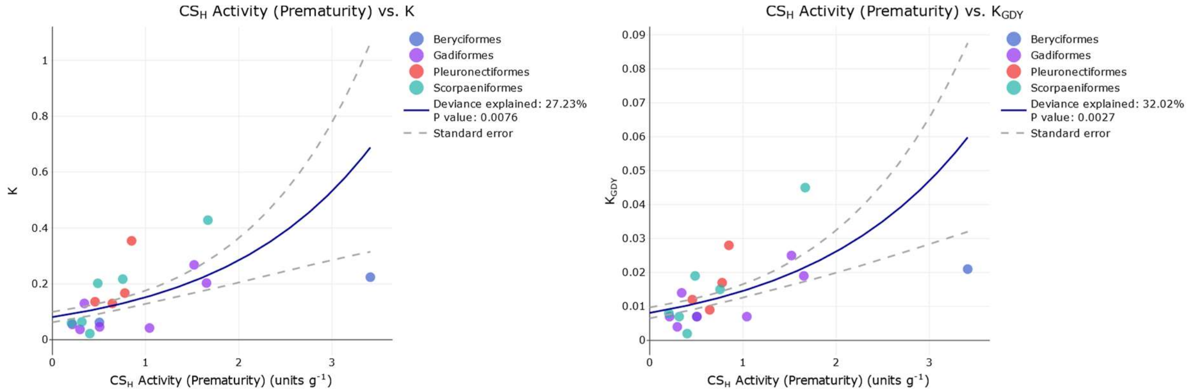


Figure 7: AIM and AIM$_{GDY}$ vs. average O_2 concentration. For ontogenetic migrators, O_2 concentrations were averaged across the **pre-maturity phase**. The blue lines show best-fit regression, and grey bands show the standard error. **Top row:** values of AIM (left) and AIM$_{GDY}$ (right) vs. O_2, colored by phylogenetic order. **Bottom row:** AIM (left) and AIM$_{GDY}$ (right) vs. O_2, with unique thermal situations for some species are highlighted with shape and color: species that ontogenetically migrate to deeper waters are shown as yellow squares, species that live in cold, shallow water (≤ 300m maximum usual depth and < 4°C average temperature of habitat) are shown as blue circles, and species that live in deep, warm water (≥ 300m minimum usual depth and > 10°C average temperature of habitat) are denoted with as a red **X**.



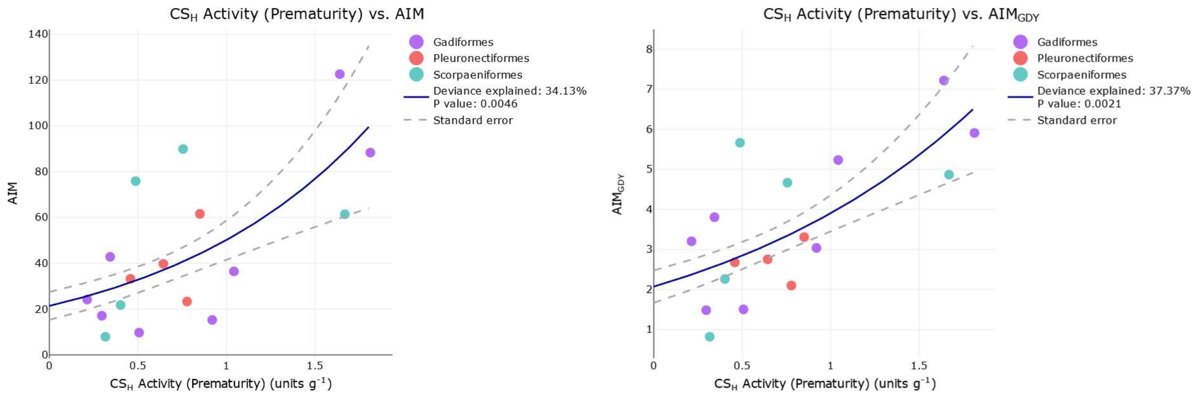


Figure 8. Growth metrics vs. citrate synthase activity adjusted to average pre-maturity temperature and normalized to a body mass of 500g. See Supplementary Methods and Results for adjustment equations. The blue lines show best-fit regression, and grey bands show the standard error. **Top row:** values of *K* (left) and K_{GDY} (right) vs. CS activity, colored by phylogenetic order. **Bottom row:** values of AIM (left) and AIM_{GDY} (right) vs. CS_H activity, colored by phylogenetic order and shown without *B. splendens*. **Note that the relationships of AIM and AIM_{GDY} vs. CS_H Activity are only significant at the P < 0.05 level when *B. splendens* omitted from the analysis.**

Multivariate GLMM analysis: the GLMM for pre-maturity analysis explained more variation in all growth metrics than that for lifespan. Therefore, we report only the pre-maturity GLMM analysis here.

K was best explained by a **negative relationship with minimum depth and a positive relationship with temperature** (R^2 = 47%, AICc = -127.9, hierarchical partitioning: 71% for depth, 28% for temperature, predictors removed: NPP). Rerunning this best model with pre-maturity CS_H as a predictor in the best model increases R^2 to 61% but limits the sample size to 19 and increases the maximum VIF of the predictors to 2.64. Five additional models were just as likely as the best model by ΔAICc < 2, including some combination of minimum depth, temperature, Lutz POC flux, and locomotory mode (see Supplemental Table 5). The second-best model indicated that *K* was nearly just as likely to be explained best by depth alone (R^2 = 45%, AICc = -127.7, predictors removed: NPP). When *C. armatus* was excluded, we saw no change in these patterns. Random-effect intercepts for each phylogenetic family all showed overlapping confidence intervals, with sebastids appearing slightly farther from the mean (Supp. Fig. 6). This is likely due to the large variability of growth rate within the family and the especially slow growth of *Sebastolobus alascanus* (Supp. Fig. 12-16). When a random effect for phylogenetic family was not included, **locomotory mode was also included, along with depth and temperature** as an important predictor in the best model, with benthopelagic fishes growing more quickly than benthic fishes (Supplementary Table 3). However, hierarchical partitioning revealed that depth and temperature were by far primary drivers (R^2 = 49%, weight = 0.36, hierarchical partitioning: 64% for depth, 30% for temperature, and 6% for locomotory mode, predictors removed: NPP).

K_{GDY} was best explained by **minimum depth and locomotory mode**, showing declines with depth and in benthic fishes in the GLMM analysis (R^2 = 27%, AICc, -399.2, hierarchical partitioning: 83% for depth, 17% for locomotory mode, weight = 0.64, predictors removed: NPP, Figure 9; Supp. Table 5; Supp. Fig. 7). Rerunning this best model with pre-maturity CS_H as a predictor increases R^2 to 47% but limits the sample size to 19. Only one additional model was equally likely by ΔAICc < 2, and contained POC flux, minimum depth, and locomotory mode as important predictors (R^2 = 29%, AICc = -398, predictors removed: NPP, Supp. Table 4). As was the case for *K*, GLMM for K_{GDY} analysis was repeated without *C. armatus,* but we observed no changes in the results chosen in models returned by dredge analysis. No changes in important predictors chosen occurred when phylogenetic family was not included in the analysis as a random effect. Random-effect intercepts for each phylogenetic family all showed overlapping confidence intervals (Supp. Fig. 7).

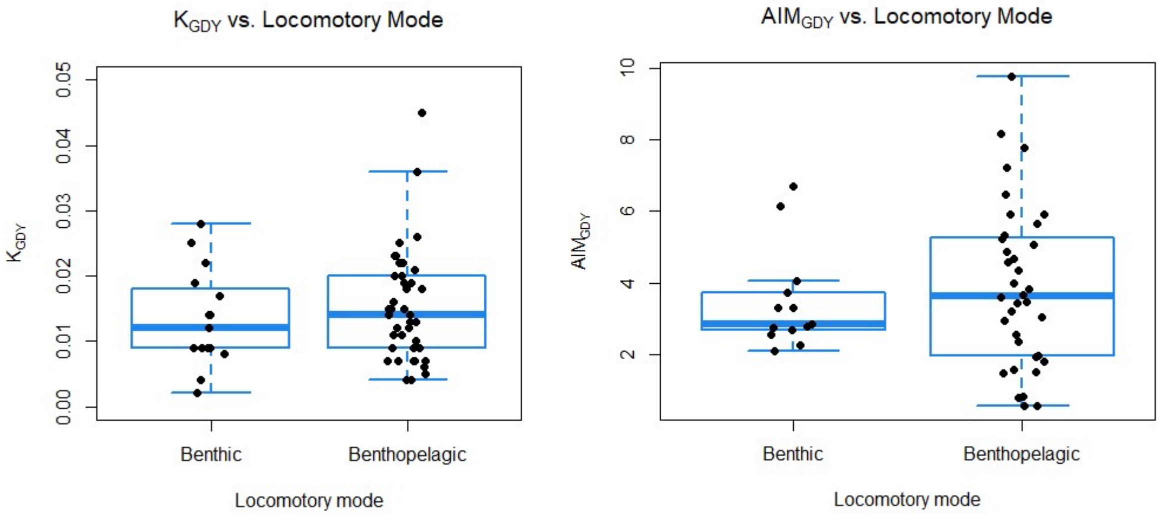


Figure 9: Box plot of K_{GDY} (**left**) and AIM_{GDY} **(right)** in benthic and benthopelagic fishes. Edges of each box represent Q1 and Q3, the center line is the median, and whiskers extend to furthest datum within 1.5 times the interquartile range. Outliers are represented as points outside the whiskers. Outliers are represented as points outside the whiskers, which for K_{GDY} is *Anoplopoma fimbria* (K_{GDY} = 0.045), and for AIM_{GDY} are the benthic fishes *S. marinus* and *H. hippoglossus* (AIM_{GDY} = 6.2% and 6.7%, respectively).

AIM was best explained by temperature and depth, but the importance of depth was sensitive to *C. armatus* inclusion. When *C. armatus* is included, GLMM analysis indicated that variation in AIM is best explained by **temperature, Lutz POC flux, and O_2 ,** in that rank order (R^2 = 38%, weight = 0.37, hierarchical partitioning: 49% for temperature, 39% for Lutz POC flux, and 12% for O_2, predictors removed: NPP). Rerunning this best model with pre-maturity CS_H as a predictor increases R^2 slightly to 40% but limited sample size of 18 prevents the use of phylogeny as a random effect, and the maximum VIF of the predictors increases to 3.11. Three additional models were equally likely by ΔAICc < 2, each containing some combination of POC flux, median depth, O_2, and temperature (R^2 = 32-38%, predictors removed: NPP, Supp. Table 5). When the random effect for phylogeny was removed, **median depth, temperature and O_2** were important predictors of variation in AIM (R^2 = 38%, weight = 0.34, hierarchical partitioning: 72% for depth, 20% for temperature, and 8% for O_2, predictors removed: NPP). There were again three additional models with ΔAICc < 2, each containing some combination of these same predictors (R^2 = 33-40%, predictors removed: NPP, Supp. Table 6). Random-effect intercepts for each phylogenetic family all showed overlapping confidence intervals (Supp. Fig. 8).

When *C. armatus* is excluded from the GLMM analysis, we found that that variation in AIM is best explained by **median depth and O_2** (R^2 = 37%, AICc = 76.3, weight = 0.61, hierarchical partitioning: 87% for depth, 13% for O_2, predictors removed: NPP). Rerunning this best model with pre-maturity CS_H as a predictor increases R^2 to 61% but limited sample size of 16. Only one additional model was equally likely by ΔAICc < 2, and contained **O_2, median depth and temperature** as important predictors (R^2 = 39%, AICc = 77.2, predictors removed: NPP, Supp. Table 7). When the random effect for phylogenetic family was removed, these patterns in the best two models were the same, but four additional models were equally as likely by ΔAICc < 2, each containing some combination of **median depth, temperature, O_2 , and locomotory mode** (Supp. Table 8). Random-effect intercepts for each phylogenetic family all showed overlapping confidence intervals (Supp. Fig. 9).

AIM_{GDY} declined with decreasing O_2, increasing depth, and in benthic fishes, but results are sensitive to *C. armatus* inclusion. When *C. armatus* was included in the analysis, AIM_{GDY} was found to be best explained by **O_2 and Lutz POC flux** (R^2 = 22%, AICc = 73.3, weight = 0.40, hierarchical partitioning: 80% for O_2, 20% for Lutz POC flux, predictors removed: NPP, Supp. Table 9). Rerunning this best model with pre-maturity CS_H as a predictor increases R^2 to 32% but limited sample size to 18. Two additional models were equally likely by ΔAICc < 2: one model containing **O_2 alone** (R^2 = 18%, AICc = 73.3, weight = 0.40, Supp. Table 9) and another model containing **O_2, Locomotory mode, and Lutz POC Flux** (R^2 = 24%, AICc = 74.7, weight = 0.20, Supp. Table 9). When random effects were excluded, these patterns were similar, but with a drop in R^2 for one of the three output models (R^2 = 13-20%, Supp. Table 10). Random-effect intercepts for each phylogenetic family all showed overlapping confidence intervals, but there are a few apparent outliers in the model residuals (Supp. Fig. 10).

When *C. armatus* was excluded, AIM_{GDY} was again best explained by **median depth, O_2, and locomotory mode,** (R^2 = 28%, weight= 0.329, hierarchical partitioning: 52% for O_2, 41% for depth, and 7% for locomotory mode, predictors removed: NPP). Rerunning this best model with pre-maturity CS_H as a predictor increases R^2 to 50% but limited sample size to 16. Three additional models were equally likely by ΔAICc < 2, each containing some combination of **median depth, O_2, Lutz POC Flux, and locomotory mode**, and with O_2 in all four models (R^2 = 17-28%, predictors removed: NPP, Supp. Table 11). When a random effect for phylogeny was excluded or if NPP is included in the analysis instead of Lutz POC flux, the important predictors in the top model were again median depth, O_2, and locomotory mode (R^2 =29%, AICc = 67.3, weight = 0.57). Only one additional model was found to be equally likely by ΔAICc < 2, with **median depth and O_2** as the important predictors (R^2 = 25%, AICc = 67.6, weight = 0.44). Random-effect intercepts for each phylogenetic family all showed overlapping confidence intervals, and there are again few apparent outliers in the model residuals (Supp. Fig. 11).

DISCUSSION

This study presents the first comprehensive examination of the environmental and physiological drivers of demersal fish growth rate across the depth continuum. The general decline in the Von Bertalanffy growth coefficient *K* with depth observed by Drazen and Haedrich (2012) is reinforced here (Table 2, Figure 4). Pre-maturity depths for ontogenetic migrators explained more variation in *K* and K_{GDY} than when lifespan-averaged depths were used (Table 2). This is not terribly surprising, given that most fish growth occurs in the pre-maturity phase of life and thus habitat variables must be matched accordingly. Average percent increase in mass during the pre-maturity phase (AIM) also declined with depth, though this was sensitive to the inclusion of *C. armatus* (Table 2, Figure 7). However, observing the depth pattern alone does not lead to an understanding of the underlying drivers because depth is not a direct ecological driver, and there is still considerable variation in growth (~60 to 90%, depending on the metric) that is unexplained by depth alone (Table 2).

Hydrostatic pressure is nearly perfectly correlated to depth, and is a variable not directly explored in this analysis. Changes in pressure are known to affect cell membrane fluidity, enzyme function and rates of biochemical reactions in fish, and deep-sea fishes possess specific adaptations to tolerate high pressures, such as increased proportions of unsaturated fatty acids in cell membranes, pressure-adapted enzymes, and high concentrations of intracellular enzyme-stablizing piezolytes (Somero 1990; Yancey and Siebenaller 2015; Gerringer et al. 2017). These adaptations, while necessary for tolerating high pressures, have been found to decrease enzyme efficiency and/or incur associated energetic costs. For example, fishes living below 500m possess versions of dehydrogenases with reduced pressure sensitivity, but at the cost of catalytic efficiency (Somero 1990). Catalytic efficiency can be increased by simply producing higher concentrations of enzyme, but this increased production requires energetic input. As growth rate is the summed product of rates of many metabolic reactions, some of the explanatory power of depth we observe in predicting growth rates may arise mechanistically from increasing energetic costs associated with maintaining enzyme function and catalytic efficiency with increasing pressure at depth. Interestingly, Gerringer et al. (2017) found hadal fishes had higher enzyme activities relative to abyssal species when tested at habitat pressure, particularly for citrate synthase and malate dehydrogenase, which they argued may be due to higher food availability in the trenches. It is unclear from our work whether these increases in enzyme activity translate to more rapid growth, as this dataset does not contain hadal fishes. It may be that the observed declines in metabolic rate with depth are a function of the visual interactions hypothesis and/o energetic costs related to Until more growth data is synthesized at abyssal and hadal depths, it is yet unclear whether

It is also worth noting that this work focuses on demersal fishes, for which most marine growth studies have focused due to their wide commercial exploitation relative to pelagic species. In the pelagic, relatively less prior research has focused on trends of growth rate and depth, though Childress et al. (1980) found K values generally followed a “slower, deeper” trend, but bathypelagic fishes grew faster than shallower mesopelagics in terms of yearly increases in caloric content. However, this study compared only 10 species and estimated age with whole otoliths, which have been shown to underestimate age particularly in deep-sea species, potentially obfuscating patterns of growth (Campana 2001). However, many of the species analyzed by Childress et al. (1980) have very small otoliths, which makes more accurate aging methods such as transverse sectioning less feasible. Regardless, further growth studies on open ocean fishes are necessary to determine whether they follow similar rates of decline in growth rate with depth as demersal fishes.

Temperature during the pre-maturity phase was found to be an important predictor of *K* and AIM (Table 2, Figures 4 and 5). Our findings reinforce the exponential increases in interspecific growth rate as a function of temperature, hypothesized in prior work (Van der Have and De Jong 1996; Jobling 1997; Neuheimer et al. 2011; Rall et al. 2012). It should be noted that the patterns with temperature in this interspecific meta-analysis do not reflect those found in intraspecific studies. While populations of a given species in warmer temperatures have been shown to grow faster than conspecifics inhabiting colder temperatures, this intraspecific growth response is unimodal: growth rate initially increases with temperature to an optimum and decreases beyond this threshold (Pörtner and Knust 2007; Thresher et al. 2007; Braaten and Guy 2011; Neuheimer and Grønkjær 2012; Rypel 2012). A similar meta-analysis of growth in freshwater fishes across South America by Santana et al. (2020) primarily focused on the effects of latitude as a proxy for temperature but did not find a significant relationship with interspecific growth rate. Though this study found that intraspecific asymptotic length decreases with latitude, the authors found no significant interspecific relationships in growth rates. Their meta-analysis does differ in that it focuses on the freshwater habitat, uses latitude as a proxy for temperature which is imprecise, and incorporates ageing methods not included here (scales, vertebrae, length-frequency analysis, etc.).

Contrary to expectations, the apparent influence of depth is still present even after the signal of temperature is accounted for with temperature-adjusted growth rates. Multivariate mixed models showed that 26% of the remaining variability in K_{GDY} is explained by depth and locomotory mode. In pairwise comparisons with K_{GDY}, depth was found to still be a statistically significant predictor, albeit less important in terms of explanatory power than that for *K*. This would suggest that temperature is not the sole driver of variation in *K* across depth. Compared to patterns seen with K_{GDY}, depth was found to be a lesser, but still important, predictor of variation in AIM_{GDY}, though only upon exclusion of *C. armatus* from the dataset. The sensitivity of these patterns in AIM and AIM_{GDY} to inclusion of *C. armatus* likely reflects inherent uncertainty as to this species' age-at-maturity, as well as a lack of data for other abyssal species, which is discussed in more detail below. Nevertheless, the persistent significance of depth in explaining K_{GDY} and AIM_{GDY} suggests the influence of additional variables associated with depth, e.g., hydrostatic pressure, in determining growth.

The estimates of food availability used here were not found to be important predictors of interspecific growth rates, regardless of the statistical approach taken (Table 2, Figure 3). Unfortunately, we were not able to include NPP in mixed model analysis with growth metrics due to high covariation with oxygen and Lutz POC flux, but as NPP was not significantly related to any growth metric in pairwise comparisons, it seems unlikely that this predictor is particularly important for explaining growth across the depth continuum. Lutz POC flux was a secondary predictor of AIM and AIM_{GDY}, but only when the outlier *C. armatus* was included. These results echo the findings of the meta-analysis by McClain et al. (2012) in which the amount of chemical energy present in the base of the food web was not found to control interspecific patterns in rockfish growth rates, but instead constrains population or ecosystem level processes such as abundance, biodiversity, and total biomass. Studies on the energetics of individual growth in fish have established that an increase in food ration leads to more rapid growth, and intraspecific variation in growth rates on short time scales such as in aquaculture settings, clearly affects fish growth rates (Persson and De Roos 2006). Despite food's importance as an intraspecific driver of growth, it appears either that interspecific patterns in growth across depth are relatively unaffected by variability in food supply, or that Lutz POC flux is not capturing the important variability in food supply and availability occurring in slope habitats. In slope habitats, food availability may be driven by many processes not captured in the Lutz model (including settling or large organic aggregates (*K*. Smith et al., 2013), downslope transport of particles (*K*. Smith et al., 1992), large organic falls (Smith and Demopoulos, 2003), vertical migrators, and very small, repackaged particles. We attempted two other possible metrics of food availability, NPP and SCOC, to attempt to overcome uncertainties in Lutz POC flux as a predictor of food availability but found no significant pairwise regressions for either predictor. However, we were unable to incorporate these two predictors into GLMM analysis due to covariation and lack of data, respectively. It is possible that, given more data on SCOC rates, one might find a significant relationship with growth. As such, we cannot conclusively say whether the observed lack of strong relationship found with our estimates of ecosystem food availability is due to dataset limitations and/or underestimates of true food availability.

Oxygen was found to be an important predictor of AIM, though relatively less so than depth and temperature. In both pairwise and GLMM analyses, O_2 only explained about 5% of variation in AIM. After correcting for temperature, the influence of O_2 was much stronger, becoming the most important predictor of AIM_{GDY} with or without the inclusion of *C. armatus*. However, this pattern with AIM_{GDY} is driven by several OMZ dwelling fishes inhabiting O_2 concentrations of less than 2mL/L. When these species are omitted in pairwise regressions of AIMGDY and O_2, there is no longer a statistically significant relationship ($P > 0.05$). Oxygen has been linked with growth in the literature: overall population biomass, maximum body size, and abundance tends to correlate with oxygen levels within oxygen minimum zones (reviewed in Gallo and Levin 2016). Intraspecific studies have shown a link between metabolism, oxygen concentration, and growth, with hypoxic conditions suppressing growth and metabolic rate in actively-swimming fishes, though the critical concentration at which suppression occurs is species-specific (reviewed in Gray et al. 2002). Moreover, the heightened longevity observed in deeper-dwelling fishes has been attributed to lower concentrations of oxygen and thus free radical damage to cells, though high longevity is not necessarily coupled to growth rate (Cailliet 2001). Generally, less is known regarding the effects of oxygen on interspecific growth rates. High O_2 demand has been associated with rapidly growing, “high performance” fishes such as tuna and mahi mahi (Brill 1996). However, prior work on demersal species has not shown a clear pattern between environmental O_2 concentration and rate of metabolism, but rather a strong positive correlation between high metabolism and mass-specific gill surface area (Friedman et al. 2012). Our analysis shows that sablefish live at low concentrations of oxygen (~0.7-2.7mL/L) and have high rates of metabolism and growth, but also were found by Friedman et al. to have relatively higher gill surface area than several of the slow growing OMZ dwellers in our dataset, such as *Sebastolobus alascanus, Sebastolobus altivelis* and *Microstomus pacificus*. The positive relationship between growth and O_2 we found is driven entirely by these slow growing OMZ-dwellers, which may indicate a threshold response in that oxygen only limits maximum growth rate at concentrations lower than about 2mL/L, and only in fishes without specific adaptations for high gill surface area. The lack of any relationship of oxygen and growth at concentrations above this threshold suggests that fish growth can be constrained by aerobic capacity (Pauly 2010) in oxygen minimum zones but is otherwise not directly driving observed growth rates, and fish can circumvent this constraint with specific adaptation for high uptake rates of oxygen.

The influence of phylogeny on growth appears to be minor, though we are unable to conclusively and quantitatively determine its effect on growth. Across phylogenetic orders, no significant differences were found in *K* or K_{GDY}. Only Zeiformes (the oreos) were found to grow significantly slower than other orders in terms of AIM and AIM_{GDY}. This may be due simply to a lack of sampling in this order because all 3 species analyzed are deep living, with median lifespan depths > 600m. We have insufficient data to correct for variability in responses to our environmental variables at the species level using random effects but were able do so at the family level. Important predictors of variation in AIM change when phylogeny is incorporated as a random effect (see results for GLMM analysis and Supplementary Fig. 6-9) but these are small shifts from one covarying factor to another (e.g. Lutz POC flux vs. depth). The effect of phylogeny is difficult to address due to data limitation, particularly because growth data are not available for shallow-water members of some deep-sea families, such as the Oreosomatidae and Macrouridae (Drazen and Haedrich 2012; Priede and Froese 2013).We also included the shallow-dwelling Ophidiid *Genypterus blacodes*, but were unable to find age and growth data for deep-sea members of this family. Similar meta-analyses on Chondrichthyan growth rates have investigated the importance of phylogeny as a predictor: Garcia et al. (2008) found correlations with growth rates and genus, and Rigby and Simpfendorfer (2015) found that after accounting for phylogeny, the influence of environmental conditions on growth was still significant. Overall, we are unable to speak conclusively to the effect of phylogeny, but its incorporation into these analyses as a random effect appears to account for some underlying variation in growth. Our findings reinforce those of Rigby and Simpfendorfer (2015), that while phylogeny can be important, other environmental drivers seem to be more so.

Temperature and depth fall out from our analyses as the primary, indirect drivers of growth and we propose that metabolic rate is the underlying, mechanistic driver of variability in fish growth rate across the depth continuum. Here we show strong, positive relationships of citrate synthase activity, a proxy for aerobic metabolic rate, with growth (Table 2, Figure 11). All three citrate synthase activity predictors: non-adjusted, adjusted to average temperature, and adjusted to average pre-maturity temperature, were found to be significantly related to nearly all the growth rates in this study at the $P < 0.05$ level, and to all of them at the $P < 0.10$ level. Generally, metabolic rate seems to explain more variation in K and K_{GDY} than in AIM and AIM_{GDY}, which was surprising given how AIM is more closely tied to accumulation of biomass and expected to be a more direct analog to biochemical processes than increase in length. Some or all of the poorer relationship to AIM is surely due to the outlier, *Beryx* *splendens,* which has a high metabolic rate considering its relatively slow growth, especially in terms of AIM and AIM_{GDY} (Fig. 8). Indeed, when this fish is removed from the analysis, the relationship with metabolic rate is stronger for all growth metrics, and the disparity in explanatory power across growth metrics is considerably smaller (see Results section for pairwise comparisons with metabolic rate). The high metabolic rate of *B. splendens,* an aggregating,seamount-associated species, fits patterns observed in other fishes with a similar lifestyle. Koslow (1996) found that metabolic rates are elevated in aggregating, seamount-associated, deep-sea fishes relative to fishes that are "dispersed" and inhabitants of weaker current regimes. Koslow posits that rapid metabolism enables the high locomotory capacity required in aggregating fishes in strong seamount-associated currents, and that these fishes grow slowly because energy is instead routed to high swimming activity rather than growth. This pattern was evident in Koslow's analysis when correcting metabolic rates for mass. Here we attempted to create adjusted metabolic rates that take into account mass *and* temperature but found them to explain less variation in every case than when correcting for temperature alone. This difference may reflect that Koslow was adjusting all metabolic rates with fishes ranging from 0.005kg to several kilograms, i.e., 1000-fold. The fishes in our dataset are closer in average size, differing at most in lifespan average mass by about 13-fold, and by pre-maturity average mass by about 170-fold. Nevertheless, we find the data for *B. splendens* support this idea that seamount-associated species have robust body forms and high metabolic rates, but with slow growth. However, our data for *Hoplostethus atlanticus,* another seamount-associated species, does not support this idea, with this species growing slowly and with a metabolic rate comparable to the "dispersed" fishes of similar depth ranges (Fig. 8). Overall, the paradigms of metabolic rate and growth in these seamount species need to be revisited, as we do not have enough data for other seamount species to speak conclusively to the dynamics of growth and metabolic for seamount-associated species.

The seamount-associated species in this dataset (*Beryx splendens, Beryx decadactylus, Hoplostethus atlanticus, Allocyttus verrucosus, Allocyttus niger, Epigonus telescopus* and *Neocyttus rhomboidalis),* appear to generally grow at similar rates to slope-dwellers of similar depth ranges in terms of K and K_{GDY} (Supp. Figure 15). However, the 5 seamount species for which AIM and AIM_{GDY} could be calculated (*Beryx splendens, Allocyttus verrucosus, Allocyttus niger, Epigonus telescopus* and *Neocyttus rhomboidalis)* appear to grow slower than slope-dwellers of similar depth ranges in terms of AIM and AIM_{GDY} (Supp. Figure 15). This disparity in K vs. K_{GDY} and AIM vs. AIM_{GDY} may result from the lack of fish younger than ~4 years for the Zeiformes and *Epigonus telescopus*, omitting a period of maximal growth rate. As AIM and AIM_{GDY} are calculated only from data from fish prior to the age of maturity, these growth rates may be more sensitive to lack of young fishes than K or K_{GDY}. Moreover, the dichotomy between "seamount-associated" and "slope-dwelling" is an oversimplification, as some of these seamount associated fishes can be found on the continental slope, and others like *Hoplostethus atlanticus* and *Allocyttus niger* are thought to have early life phases in the mesopelagic up to around 5 years (Shephard et al. 2007; Horn et al. 2019). Without metabolic rate data for more seamount-associated fishes, we are unable to speak further to the hypothesis put forth by Koslow (2001) that seamount-associated fishes devote the product of rapid metabolism to movement rather than growth.

Our findings support the idea that a high metabolic rate does not necessarily *cause* rapid growth, as seen in the example of *B. splendens*, but may be necessary to enable it, as suggested by Glazier (2015). We do not find any evidence of rapid growth at low metabolic rates. We see some evidence of a tradeoff between metabolic rate/activity levels and growth in the data for *B. splendens*, and the slightly higher growth rates seen in benthopelagic fishes. Metabolic rate has been found in prior studies to be higher in benthopelagic compared to benthic fishes (Drazen et al. 2007; Drazen et al. 2011; Drazen and Yeh 2012; Drazen et al. 2015), which if growth and metabolism are linked, would argue for higher growth rates in benthopelagic species. This would explain our finding that locomotory mode is an important predictor for several growth rates, with benthopelagic species growing faster (Fig. 9 -10). It is much simpler to characterize fish swimming capability broadly than measure species metabolic rate directly or through proxies such as CS enzyme activity, enabling a greater diversity of species to be included in these kinds of meta-analyses. Unfortunately, such a broad classification may obscure more complex relationships.

A close link between growth and metabolic rate has been observed before. The metabolic theory of ecology (MTE) posits that temperature and body mass set the pace of metabolism which in turn is the “pacemaker” of ecological processes such as growth, reproduction, and activity (Brown 2004). A recent review by Glazier (2015) challenged some of these conclusions. They argue that the MTE ignores the role of adaptive regulation of growth and metabolism via hormones and physiological signals, and that intraspecific growth and metabolism can be decoupled, and are not always positively correlated. Clearly, factors in addition to temperature and body mass are important. The authors agree, however, that metabolic rate may be a co-integrated “enabler” of growth rate: rapid delivery and transformation of chemical reactants and products is necessary for rapid creation of biomass via anabolic reactions. Furthermore, growth and metabolic rates have been connected in the literature for shallow-water fish, though intraspecific studies do not always show positive relationships between the two (Fonds et al. 1992; Peterson-Curtis 1997; Enders and Boisclair 2016; Zeng et al. 2017; reviewed in Jobling 1997; Pauly 2010; Glazier 2015).

Metabolic rate in demersal fishes declines with depth even after accounting for temperature and body size effects, and our results suggest that this also explains a substantial portion of the declines in temperature-corrected growth metrics with depth. Metabolic rates have been found to decline with depth in benthic and benthopelagic fishes, but more so than would be expected based on depth-related shifts in temperature and body size alone (Sullivan and Somero 1980; Drazen and Seibel 2007; Drazen et al. 2015). Light level, a variable unexplored directly in this analysis, also declines exponentially with depth to ~ 1000m. The visual interactions hypothesis suggests that high metabolic rates (and thus high locomotory capacity and response rate) are relatively advantageous in shallower, more illuminated habitats to facilitate prey pursuit and predator avoidance over larger distances (Childress, 1995). With increased depth, the selection pressure for rapid mobility is relaxed because these visual animals cannot see as far, reducing the distances over which they need to react to swim to avoid predators or chase down prey. With a reduced need for high locomotory power, declines in metabolic rate are observed. We suggest that temperature constrains growth rate by setting the pace of anabolic reaction kinetics, while selection pressure for rapid metabolism is relaxed with decreasing light levels with depth, per the visual interactions hypothesis, further regulating and reducing maximum rates of growth. Indeed, the most rapid decline in growth rate occurs in the first ~1000m, where the steepest gradients in light and temperature are found in the global oceans (Figure 6). It seems likely that in addition to temperature, the visual interactions hypothesis helps explain the broad declines in growth rates in fishes observed on the global scale at depths <1000m. Broadly, more growth and metabolic data is needed in depths <1000m. Moreover, there is need for more overlap in growth data with the currently existing metabolic data on families living deeper than 1000m, such as the Zoarcidae and Liparidae (Drazen et al. 2015).

The strong relationships found in this meta-analysis provide an essential first step in understanding the drivers of growth variation and in locating gaps in the current knowledge for targeted research. However, a fully predictive model of growth across the depth continuum or a complete mechanistic understanding of its drivers will require much more data, and better estimates of food availability. The potential explanatory power of metabolic rate in our dataset, though limited by sample size, is a promising step in a fully predictive framework. Adding metabolic rate data to the top mixed model increased R^2 values from 47% to 61% when explaining K, and from 27% to 47% in explaining K_{GDY}. R^2 values for explaining AIM and AIM_{GDY} also increased drastically when MR data was added (37% to 67% for AIM; 21% to 61% for AIM_{GDY}), but only when *B. splendens* was omitted and a random effect for phylogeny was not included. Overall this would suggest that while our models are not yet fully predictive due to a limited dataset, given sufficient environmental, phylogenetic, and metabolic rate data, a fully predictive framework for the growth of deep-sea demersal fishes is plausible.

A number of past studies could not be included here due to procedural issues and lack of age-validation approaches. This hampered the present analysis. For instance, further work is needed to untangle some of the covariation in depth and temperature by collecting a dataset with as many species from the Mediterranean (where temperature remain constant and relatively warm, with depth) as possible. Twenty sources of age and size data Mediterranean populations were examined, but 15 of the 20 used either whole otoliths or scales for age estimation and were rejected for quality control reasons (see Supplementary Methods). It is possible that annuli count from viewing whole otoliths indeed accurately reflect the age for some or even all of these species, but without radiometric or other independent validation of the ring periodicity, the risk of underestimation of age and overestimation of growth rate was concern enough to exclude these studies (Campana 2001). More studies of otolith sections or using age validation are needed from warm deep-sea regions.

Ultimately, we find that the deeper-living, least resilient fishes in this meta-analysis are also the most poorly understood as a group in terms of life history traits, evident by the scarcity of growth studies beyond ~1500m depth (Fig. 4-5). We found a large disparity in AIM and AIM_{GDY} between Pacific and Atlantic populations of *C. armatus*. Due to limited sampling, we are hesitant to ascribe any environmental or ecological influence on the disparity in these values across populations, as it likely reflects data limitation due to lack of radiometric validation of otolith annuli, and/or uncertainty as to the age of maturity for this fish. Nevertheless, reproductive capacity for many deep-sea species in this analysis is extremely low relative to shallow-water fishes, with ages-at-maturity of 20 years or more in *Hoplostethus atlanticus,* and the Zeiformes. As such populations of deep-sea fishes are certainly far less able to recover from acute increases in mortality and/or habitat disturbance. The strong relationships of growth rate and depth found in this global meta-analysis reinforce the notion that resilience of species to stressors and mortality decreases sharply with increasing depth. As such, we require more growth and life history data from the lower bathyal, abyssal and hadal zones to fully understand drivers of growth across the full depth gradient.

The human footprint in the deep sea continues to expand. Historically, studies of the life histories of deep-sea fish focused on direct exploitation (Koslow et al. 2000; Bailey et al. 2009). Past age and growth studies have focused on the upper bathyal (<1500m) where commercially harvested species live. However, future threats to the ocean from deep-sea mining (reviewed in Glover and Smith 2003) and climate change (Sweetman et al. 2017) will occur at greater depths and present a real need for more information. For example, deep-sea mining is likely to commence at industrial scale within the next few decades, with potentially decadal-scale disruptions to both benthic and pelagic habitats (Stratmann et al. 2018; reviewed in Glover and Smith 2003). Though the spatial and temporal extent of disruption is not yet fully clear, at current proposed depths of operation on seamounts and/or abyssal plains, it would certainly affect some of the deepest, least resilient, slowest growing species in our analyses (*C. armatus, A. rostrata, H. atlanticus,* etc.). In terms of broad-scale anthropogenic climate change, recent estimates suggest abyssal ocean temperature may increase by 1°C by the end of the century, with concurrent decreases in the flux of particulate organic carbon (POC) (Sweetman et al. 2017). Because deeper habitats are particularly stable in environmental conditions, deep-sea fishes are likely to be even more sensitive to climate driven changes than shallow-water fishes. While we found positive relationships between interspecific growth rate and temperature, climate warming may lead to drastically decreased growth performance intraspecifically, particularly in deep-sea fishes accustomed to relatively stable thermal regimes. (Pörtner and Knust 2007; Thresher et al. 2007; Braaten and Guy 2011; Neuheimer and Grønkjær 2012; Rypel 2012). Moreover, while Lutz POC flux was not found to drive growth interspecifically, the proposed constraints of food supply on population size could lead to decreasing abundances with decreasing flux of organic carbon to the seafloor (McClain 2012). Most of the life histories of deep-sea fishes remain to be described, and the impacts of anthropogenic stressors on their populations may be unseen, unpredictable, and compounding. To fully quantify the *interspecific* effect of these anthropogenic disturbances, much more data is needed on both the life histories of deep-sea fishes and their tolerances to changing conditions. Deep-sea demersal fishes fulfill critical ecological roles as mid-to-top level predators and may be responsible for direct delivery of carbon from the mesopelagic to the seafloor via consumption of vertical migrators (Truman et al. 2014; Drazen and Sutton 2017). These fishes may represent an important component of biogeochemical cycling through deep carbon deposition and burial. It is therefore essential to establish a fully predictive framework with which to gauge the susceptibility of these fishes to exploitation and future human stressors and to conserve their roles in both deep-sea ecosystems and the marine carbon cycle.

ACKNOWLEDGEMENTS

I would like to thank my committee members for their mentorship: Jeff Drazen, Anna Neuheimer, and Craig Smith. I would also like to thank my family and my wife Lucy for their support and encouragement. Thanks to Peter Horn and Di Tracey from NIWA for comments, insight, and data. I thank Allen Andrews for providing thoughts, ideas, and data for this work. I also thank Odd Bergstad for providing data for *Coryphaenoides* armatus, as well as Clive Truman and Diana Shores for their help in providing enzyme data and metadata. Finally, I must thank all the researchers that provided vital data for this meta-analysis: Alisa Abookire, Valérie Allain, Allen Andrews, Steven E. Campana, Cassandra Brooks, Graeme Ewing, Chip Cotton, Alex Fogg, Mackenzie Gerringer, Alison Gould, Sergio Ragonese, Donna Kline, Tom Laidig, Milton Love, Ana Neves, Dan Nichols, Isaac Kaplan, Margaret Finch, Cassandra Brooks, Melissa Mahoney, Nuria Raventos, Mark Belchier, David Sampson, Cara Rodgveller, Kelly Robinson and Christoph Stransky. NSF-OCE provided funding for this project (Grants #1829612 and #0727135).

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