

Gills, growth and activity across fishes

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Abstract

Life history theory suggests that maximum size and growth evolve to maximize fitness. In contrast, the Gill Oxygen Limitation Theory (GOLT) suggests that growth and maximum size in fishes and other aquatic, water-breathing organisms is constrained by the body mass-scaling of gill surface area. Here, we use new data and a novel phylogenetic Bayesian multilevel modelling framework to test this idea by asking the three questions posed by the GOLT regarding maximum size, growth and gills. Across fishes, we ask whether the body mass-scaling of gill surface area explains (1) variation in the von Bertalanffy growth coefficient (k) above and beyond that explained by asymptotic size (W_∞), (2) variation in growth performance (a trait that integrates the tradeoff between k and W_∞) and (3) more variation in growth performance compared to activity (as approximated by caudal fin aspect ratio). Overall, we find that there is only a weak relationship among maximum size, growth and gill surface area across species. Indeed, the body mass-scaling of gill surface area does not explain much variation in k (especially for those species that reach the same W_∞) or growth performance. Activity explained three to five times more variation in growth performance compared to gill surface area. Our results suggest that in fishes, gill surface area is not the only factor that explains variation in maximum size and growth, and that other covariates (e.g. activity) are likely important in understanding how growth, maximum size and other life history traits vary across species.

KEY WORDS

Bayesian hierarchical modelling, ecophysiology, life history theory, metabolic ecology, trait-based approaches, von Bertalanffy growth

1 | INTRODUCTION

Formalized as life history theory, decades of work have revealed that body size and other life history traits related to growth, survival and reproduction are optimized by natural selection to maximize fitness (typically measured by reproductive output in fishes; Beverton & Holt, 1959; Hutchings, 2002; Stearns, 1992). Maximizing fitness results in trade-offs between traits (such as growth and reproduction) as competing processes draw from

the same finite pool of internal resources (e.g. time, energy; Reynolds, 2003; Roff, 1984; Stearns, 1989). One of the classic trade-offs between life history traits is the inverse relationship observed between the maximum size of a species and its change in body size over time, or growth (Beverton & Holt, 1959; Reynolds et al., 2001). This trade-off suggests that an individual (or species) generally grows faster to a smaller asymptotic (final) size or grows more slowly to a larger asymptotic size (Beverton & Holt, 1959). With respect to maximum size and growth trade-offs, life history

theory predicts that under high mortality (e.g. in an unstable environment or under high predation risk), fitness would be maximized through a faster life history strategy, one that results in a higher reproductive output earlier in life, which would select for a smaller maximum size, faster growth and earlier maturity (Reznick et al., 1996; Roff, 1984; Stearns, 1976). On the other hand, under low mortality (e.g. a stable environment or one with lower predation risk), fitness would be maximized through a slower life history strategy by waiting to reproduce until an organism reaches a larger size (as reproductive output increases with increasing size; Barneche et al., 2018; Bjørkvoll et al., 2012). This would select for a larger maximum size, slower growth and later maturity (Roff, 1984; Stearns, 1976). While life history theory and its predictions have been widely supported by both theoretical and empirical research over the last 70 years, recent work on the effect of oxygen (i.e. the balance of supply and demand) and temperature on body size and growth, especially for fishes, has inspired the resurgence of a mechanistic theory surrounding body size, growth and gills (Cheung et al., 2013; Forster et al., 2012; Pauly, 1981, 2010).

Daniel Pauly's Gill Oxygen Limitation Theory (GOLT) proposes that the maximum size, and thus also the growth, of aquatic, water-breathing organisms is mechanistically constrained by oxygen supply at the gills (Pauly, 1981, 2010, 2021). The central tenet of this theory is that the oxygen supply acquired over the surface area of the gills—which is (to a first approximation) a two-dimensional surface—cannot keep pace with the demand from a continually increasing three-dimensional volume (body mass). The proposed consequence of this mismatch in geometry is that the ontogenetic slope of the relationship of gill surface area and body mass (gill surface area slope) will always be less than 1. This means that the ratio of gill surface area to body mass (i.e. mass-specific gill surface area) will decrease with increasing body mass. Thus, when the supply of oxygen diffused over the 'diminishing' gill surface area cannot match the demand from the growing body, the organism will stop growing and its maximum size will be reached (Pauly, 2010, 2021). Importantly, the GOLT is rooted in and derived from the von Bertalanffy growth model such that growth is a function of anabolism (synthesis of material) and catabolism (breaking down of material; i.e. the von Bertalanffy growth equation prior to integration, which results in the equation used to fit length or weight vs. age; von Bertalanffy, 1957). The von Bertalanffy growth model is based on the idea that growth occurs when anabolism is greater than catabolism and growth stops when anabolism equals catabolism. The GOLT argues that because anabolism requires oxygen, and catabolism does not, growth can be thought of as a function of anabolism, which ultimately, is driven by the amount of oxygen that a fish or other water-breathing organism can diffuse over the surface area of the gills (Pauly, 1981, 2021). Thus, this theory suggests that the mechanism underlying the process of growth ceasing due to anabolism equalling catabolism is a function of oxygen supply via the gills (Pauly, 1981, 2021).

Because of this connection to the von Bertalanffy growth function, a central prediction of the GOLT is that a tight

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interrelationship exists among maximum size, growth and gill surface area (Pauly, 1981, 2010, 2021). This relationship was first tested over 40 years ago by examining whether (1) the large amount of variation in von Bertalanffy growth coefficients (k) both within and across species was related to an index of gill surface area (gill area index), such that an individual or a species can only grow fast to its asymptotic size (W_∞) if it has a larger than expected gill surface area for its body size and (2) growth performance (an index that integrates the tradeoff between k and W_∞ , $\phi = \log_{10}(k * W_\infty)$) explained variation in gill area index (Pauly, 1981, 2010). Later, Blier et al. (1997) suggested that the relationship between gill area index and growth performance could be explained by activity level, raising a third question that Pauly (2010) tested using gill area index. Although only a weak, positive relationship between gill area index and growth performance existed in the 42 fish species originally examined by Pauly (1981) and subsequently re-examined by Bigman et al. (2023), this relationship underpinned the idea that gill surface area constrains growth and maximum (or asymptotic) size in fishes and has been used, in part, to predict future changes in fish maximum size associated with ocean warming (Cheung & Pauly, 2016; Cheung et al., 2013; Pauly, 1981, 2010). Indeed, half of the predicted 14%–24% decline in maximum size for individual fish species (over generations) due to projected temperature increases through 2050 has been suggested to be mechanistically linked to oxygen

limitation, or the mismatch between oxygen supply (gill surface area) and demand (metabolic rate; Cheung et al., 2013; Pauly, 1981, 2010). This 'shrinking fishes' prediction awakened renewed interest in the GOLT (Bigman et al., 2021; Lefevre et al., 2021; Pauly, 2021; Roche et al., 2022).

Much of the interest in the GOLT is centred on the debate surrounding the mechanistic underpinnings of oxygen limitation, particularly with respect to gill surface area, growth and size (Lefevre et al., 2017, 2018; Marshall & White, 2019a, 2019b). The classical physiological view is that the surface area of respiratory organs evolves to provide the capacity needed to meet an organism's requirements, instead of (aerobic) metabolic rate being driven by, and ultimately, limited by the surface area of the gills (Lefevre et al., 2017, 2018; Marshall & White, 2019a, 2019b). Relatedly, physiologists have noted that the surface area of gills are folded surfaces and thus are not under the same strict geometric constraints as seen in spherical or cubic objects (i.e. the scaling of gill surface area and body mass can and does deviate from theoretical surface area-to-volume ratios; Bigman et al., 2018; Lefevre et al., 2017, 2021; Wegner, 2011). On a more technical note, the proxy for gill surface area originally used to test whether a relationship between growth performance and gill surface area existed—gill area index—does not capture the known (large) variability in gill surface area within and across species and is biased by the sizes at which gills were measured (see Bigman et al., 2023). Additionally, the GOLT has drawn criticism as it is derived from the von Bertalanffy growth model, a model that has been called into question (see Marshall & White, 2019a for discussion). Notwithstanding these criticisms, the GOLT has potentially far-reaching consequences if empirically supported. In addition to the idea that oxygen limitation and gill surface area may be behind the observed declines in maximum size in response to increasing temperature (temperature-size rule/Bergmann's rule/James' rule), mounting evidence from broad, cross-species studies suggests that oxygen limitation may also shape species' geographic distributions and underlie the mass- and temperature-dependence of metabolic rate (Bigman et al., 2021; Clarke et al., 2021; Deutsch et al., 2020; English et al., 2021; Essington et al., 2022; Forster et al., 2012; Rubalcaba et al., 2022).

To understand whether oxygen limitation mediated by gill surface area is indeed occurring, and affecting growth and maximum size, predictions generated by the GOLT must be tested. Yet, few predictions have been tested to date, including the generality of the relationship among maximum size, growth and gill surface area. A wealth of gill surface area and life history data have been published since these predictions were first tested, with many species possessing raw gill surface area data—or measures for multiple individuals of the same species. There has also been an advancement in statistical techniques that can incorporate additional salient factors such as evolutionary history among species and allow us to link individual variation to patterns across species. To that end, in this article, we revisit the relationship of maximum size, growth and gill surface area across fishes by leveraging more recently available gill surface area data and developing a novel phylogenetic Bayesian

multilevel model with the flexibility to scale up individual variation to assess patterns across species, as well as include salient covariates. We build off recent work (Bigman et al., 2023), which demonstrates bias associated with gill area index, and here, we examine whether the body mass-scaling of gill surface area (the gill surface area slope and intercept) explain variation in growth and maximum size. Specifically, we test the three questions surrounding the interrelationship among maximum size, growth and gill surface area in the context of the GOLT: does the body mass-scaling relationship of gill surface area explain (1) variation in k above and beyond that explained by W_∞ , (2) variation in growth performance and (3) more variation in growth performance compared to activity. Finally, as our study examines patterns across species, we also explore whether variation in life history traits (growth rate in Question 1 and growth performance in Questions 2 and 3) can be explained by evolutionary history.

2 | METHODS

2.1 | Additional data collection and sources

We compiled a data set of species-specific gill surface area estimates and their associated body masses (i.e. the body mass of the individual who's gill surface area was measured, hereafter 'measurement body mass') and von Bertalanffy growth parameters for both teleosts and elasmobranchs. An initial data set was collated for those fish species with estimates of both gill surface area and available growth parameters in Fishbase (Froese & Pauly, 2020). This initial data set was then supplemented with published gill surface area data from other sources (if a given species also had available growth parameters). These other sources of gill surface area data were Bigman et al. (2021), De Jager and Dekkers (1975), Gray (1954), Hughes and Morgan (1973), Palzenberger and Pohla (1992) and references therein. We additionally limited our data set to species that have a resolved position on a phylogenetic tree to allow for including a random effect of evolutionary history in our models.

2.2 | Gill surface area data

Gill surface area and measurement body mass data were extracted from the original study in which they were reported. Only those species with raw gill surface area data (i.e. measurements for multiple individuals of a species, each with its own measurement body mass) were included in our data set. If more than one study reported raw data for a number of individuals for a given species, we combined both data sets (this was only the case for three species: Common Thresher Shark (*Alopias vulpinus*, Alopiidae), Sandbar Shark (*Carcharhinus plumbeus*, Carcharhinidae) and Shortfin Mako (*Isurus oxyrinchus*, Lamnidae)). Any gill surface area measurement that was not directly measured (e.g. predicted from assumed geometric

relationships) was not included in this study (for further discussion, see Satora & Wegner, 2012). All gill surface area and body mass data were converted to cm^2 or g, respectively, if not already in this unit and \log_{10} -transformed prior to analyses.

2.3 | Life history data

Using the 'rfishbase' package for Fishbase, we extracted all observations of von Bertalanffy growth function parameters for each species in our data set including the growth coefficient, k (year^{-1}) and asymptotic weight (W_∞ , g) and length (L_∞ , cm) (the mean weight or length the individuals in a population would reach if they were to grow indefinitely; Boettiger et al., 2012; Froese & Pauly, 2020). For most species, the asymptotic size was reported as L_∞ and not W_∞ and thus W_∞ was estimated for each observation using length-weight regressions matched by length type and sex downloaded from Fishbase using the 'rfishbase' package (Boettiger et al., 2012). If the type of length (i.e. total length, TL, fork length, FL, etc.) was not specified for an observation of L_∞ , then that observation (both k and L_∞) could not be used and was removed from the data set. If growth data were not available in Fishbase for a species, the primary literature was searched for published age and growth data. For one species, Marbled electric ray (*Torpedo marmorata*, Torpedinidae), growth parameters were not available in Fishbase but were found in the literature. For four species, length-weight coefficients for the same length type as was used to estimate growth parameters were not available (i.e. the growth coefficient was estimated using fork length but no length-weight regression for fork length to weight was found [and no conversion from another length type was available]), and thus matching type-specific length-weight regressions were collated from the literature. Growth performance was calculated for each observation as $\phi = \log_{10}(k * W_\infty)$ following Pauly (1981). For analyses, a mean of growth performance was taken for each species.

2.4 | Activity data

To include a standardized, objective and quantitative metric of activity level in our analyses, we estimated caudal fin aspect ratio—a morphological correlate of swimming speed and ability—for each species (Bigman et al., 2018; Palomares & Pauly, 1989; Sambilay Jr., 1990). Caudal fin aspect ratio, A , was calculated for each species as $A = h^2/s$, where h is the height and s is the surface area of the caudal fin as measured from anatomically correct field guide illustrations from *Sharks of the World* (Ebert et al., 2013) for elasmobranch species or FAO field guides for teleost species (Bigman et al., 2018; Palomares & Pauly, 1989; Sambilay Jr., 1990). For some teleost species, FAO images were not available ($n = 7$), and thus, alternative field guides were used. If alternative guides were used, we generated a mean caudal fin aspect ratio from up to four field guide illustrations. Of the 32 species in our data set, caudal fin aspect ratio could only be estimated for

30 species as two species do not have traditional caudal fin morphology (one eel, European eel [*Anguilla anguilla*, Anguillidae] and one batoid, [*Torpedo marmorata*]). While we recognize that there may be shortcomings of using caudal fin aspect ratio as a metric of activity level (i.e. tail shape may change slightly with growth), this metric offers a straightforward and consistent method to quantitatively index activity level that can be obtained for most species that have an anatomically correct illustration (i.e. from field guides). In contrast, the swimming capacity index used by Pauly (2010) requires species-specific swimming speed data, which does not exist for most species.

The growth of 'aquacultured' species is known to differ from that of wild fishes (due to food *ad libitum*, reduced predation and possibly increased aeration of aquaculture ponds; Pauly, 2010). Also, fishes that breathe air (either by possessing an air-breathing organ or passive oxygen diffusion through the skin) often have a lower gill surface area for a given body size compared to their non-air-breathing counterparts (Wegner, 2011). Thus, we created two subsets of our full data set to exclude species traditionally used in aquaculture and those capable of air-breathing.

In total, our data set included 457 observations of raw gill surface area and associated measurement body mass from a total of 32 fish species (both teleosts and elasmobranchs) that have a resolved position on a published phylogeny and for which von Bertalanffy growth parameters were available (Table S1).

2.5 | Analyses

2.5.1 | Does gill surface area explain variation in k above and beyond that explained by W_∞ ?

To assess whether the body mass-scaling relationship of gill surface area explains variation in von Bertalanffy growth coefficient (k) beyond that explained by asymptotic size (W_∞) across fishes, we developed a novel Bayesian multilevel modeling framework that included two levels (Figure S1; see Supporting Information for statistical notation, conceptual diagram and more detail). The first level of the model (which is the same in all three questions) estimated the body mass-scaling relationship of gill surface area for each species, resulting in a species-specific posterior distribution of the gill surface area intercept (gill surface area at a given body mass) and a species-specific posterior distribution of the gill surface area slope (rate at which gill surface area increased with body mass). The second level of the model then examined whether the entire posterior distribution of the gill surface area intercepts or slopes explained additional variation in the relationship between k and W_∞ across species. The strength of using such a multilevel modeling approach is that the entire posterior distribution of the gill surface area slopes and intercepts that were empirically estimated in the first level of the model and, thus, the uncertainty in these coefficients, is propagated to the second level (where we test whether the gill surface area slopes and intercepts explain variation in k above and beyond

TABLE 1 Comparison of coefficients and 95% Bayesian Credible Intervals (BCI) for Question 1—whether the body mass-scaling of gill surface area explains variation in k (von Bertalanffy growth coefficient) above and beyond that explained by W_∞ (asymptomatic size).

Model parameterization of the second level	Intercept (95% CI)	W_∞ slope (95% CI)	GSA slope (95% CI)	Phylogenetic signal (λ)	Relative importance of W_∞ vs. gill surface area	Proportion of posterior distribution >0	VIF	COR
$k \sim W_\infty +$								
Gill surface area	-0.55 (-0.68 to -0.42)	-0.26 (-0.38 to -0.13)	-0.08 (-0.22 to 0.06)	-	-0.26/-0.08=3.25	Intercept=0.13	1.14	0.35
Intercept	-0.55 (-0.68 to -0.42)	-0.26 (-0.39 to -0.14)	-0.06 (-0.20 to 0.07)	0.50 (0.03 to 0.97)	-	$W_\infty=0.0004$	-	-
Gill surface area	-0.55 (-0.68 to -0.42)	-0.27 (-0.40 to -0.14)	-0.05 (-0.19 to 0.09)	-	-0.27/-0.05=5.4	Intercept=0.17	-	-
Intercept	-0.55 (-0.68 to -0.42)	-0.28 (-0.40 to -0.15)	-0.03 (-0.17 to 0.12)	0.50 (0.03 to 0.97)	-	$W_\infty=0.0003$	-	-
Gill surface area	-0.55 (-0.68 to -0.41)	-0.28 (-0.40 to -0.15)	-0.03 (-0.17 to 0.12)	-	-	$W_\infty=0.00006$	1.08	0.27
slope	-	-	-	-	-	$W_\infty=0.000006$	-	-
Gill surface area	-	-	-	-	-	$W_\infty=0.000125$	-	-
slope	-	-	-	-	-	-	-	-

Note: In this model, the response variable is k and the predictors are both W_∞ and either the gill surface area slope or intercept (estimated in the first level of the model) with and without the inclusion of a random effect of phylogeny. All models were estimated using a Bayesian multilevel modeling framework in Stan using the package *rstan* in R v4.0.2, where the first level of the model estimated species-specific gill surface area and body mass relationships for all species based on data from individuals of each species. All predictors in the second level of the model were standardized and, thus, the effect sizes for the slopes are relative to each other (see text and [Supporting Information](#)).

Abbreviations: COR, correlation matrix value; GSA, gill surface area; VIF, variance inflation factor.

that of W_∞) as each iteration of both levels of the model happens in succession. Thus, this model allows us to account for individual variation in cross-species models.

To ensure that intercepts were estimated accurately across the broad size range of species included in the data set, body mass data were centred on the mean value of body mass for all 32 species in the data set (300 g). Both predictors (the gill surface area intercept or slope and W_∞) in the second level of the model were standardized (by z-score) to facilitate comparison and infer the relative importance of a given predictor in explaining variation among k . We estimated the correlation and variance inflation factors (VIF) between the gill surface area intercept or slope and W_∞ for both models to ensure that these traits, as parameterized in our models, were not collinear or correlated.

Estimating allometric coefficients (those from a relationship with body mass, such as the body mass-scaling relationship of gill surface area) must be done with care as too few data points can produce biased coefficients (Jenkins & Quintana-Ascencio, 2020; White & Kearney, 2011). Indeed, to estimate an ontogenetic allometry (in contrast to a static allometry [individuals or species of the same size/age class] or an evolutionary allometry [across different species of different sizes] (Cheverud, 1982; Gould, 1966)), data from across a size range with multiple individuals is necessary. Previous work has shown that a threshold of eight individuals is suitable to reliably estimate ontogenetic allometric coefficients (Jenkins & Quintana-Ascencio, 2020). To ensure this was true for our data set, we simulated allometric coefficients with 3–100 data points and found that coefficients did not differ substantially past eight samples (see [Figure S2](#)).

2.5.2 | Does gill surface area explain variation in growth performance?

To assess whether the body mass-scaling relationship of gill surface area explains variation in growth performance across fishes, we fit two Bayesian multilevel models ([Figure S1](#), see supplementary for statistical notation, conceptual diagram and more information). The first level of the model estimated the body mass-scaling relationship of gill surface area for each species (same as the first level in the previous question), resulting in a species-specific posterior distribution of the gill surface area intercept (centred at 300 g, as above) and slope. The second level of both models then examined whether the gill surface area intercept or slope (and their uncertainty) explained variation in growth performance across species. In both models, the gill surface area intercepts and slopes were standardized using the z-score transformation for input in the second level of the model, which facilitated model convergence, parameter estimation and predictor comparison.

2.5.3 | Does gill surface area explain more variation in growth performance compared to activity?

To assess whether the body mass-scaling relationship of gill surface area explains more variation in growth performance compared to

activity as approximated by caudal fin aspect ratio, we again fit two multilevel Bayesian models which allowed for inferring the relative importance of each predictor (gill surface area intercept or slope vs. caudal fin aspect ratio; **Figure S1**, see supplementary for statistical notation, conceptual diagram and more detail). The first level of the model estimated the body mass-scaling relationship of gill surface area for each species (same first level as in the previous two questions), resulting in a species-specific posterior distribution of the gill surface area intercept (centred at 300g, as above) and slope. The second level then examined whether caudal fin aspect ratio or the gill surface area intercept (model 1) or the gill surface area slope (model 2), and their uncertainty, explained more variation in growth performance. All predictors were standardized and we estimated the correlation and variance inflation factors (VIF) for both models to ensure that activity level and gill surface area, as parameterized in our models, were not collinear or correlated.

We ran all models in all three questions above with and without a random effect of phylogeny to ensure our results were not biased due to species' sharing various parts of evolutionary trajectories (e.g. Felsenstein, 1985; Freckleton, 2002; Harmon, 2019). To do so, we constructed a new supertree with species from our data set using two published phylogenies—one for teleosts (Chang et al., 2019; Rabosky et al., 2018) and one for chondrichthyans (Stein et al., 2018). Models with and without a random effect of phylogeny yielded almost identical results (**Tables 1–3**; see **Supporting Information** for more detail on parameterizing the random effect of phylogeny). Additionally, we reran all models on our three subsets of data: one that excluded species traditionally used in aquaculture, one that excluded those capable of air-breathing and one that included only species for which gill surface area was measured across an order of magnitude of body size. Using these, data subsets had no effect on our results (**Tables S2–S4**).

All models described above for all three questions were fit in R using the Stan probabilistic programming language in *rstan* (R Core Team, 2020; Stan Development Team, 2019). All data (and sources) assembled for this study are archived on Github (username, jennybigman; see references section for link to data and code).

TABLE 2 Comparison of all coefficients and their 95% Bayesian Credible Intervals (BCI) for Question 2—whether the body mass-scaling relationship of gill surface area explained variation in growth performance.

Model parameterization	Intercept (95% BCI)	Slope (95% BCI)	Phylogenetic signal (λ)	Proportion of posterior distribution > 0
Growth performance ~				
Gill surface area intercept	3.08 (2.63 to 3.53)	0.36 (-0.11 to 0.83)	–	0.94
Gill surface area intercept	3.08 (2.62 to 3.52)	0.36 (-0.13 to 0.83)	0.50 (0.03–0.98)	0.93
Gill surface area slope	3.08 (2.63 to 3.53)	0.33 (-0.20 to 0.83)	–	0.89
Gill surface area slope	3.08 (2.63 to 3.52)	0.33 (-0.21 to 0.84)	0.50 (0.03–0.98)	0.89

Note: In this model, the response variable is growth performance and the predictor is either the gill surface area slope or intercept (estimated in the first level of the model) with and without the inclusion of a phylogeny. A Bayesian multilevel modeling framework was used to estimate all parameters in Stan using the package *rstan* in R v4.0.2, where the first level of the model estimated species-specific gill surface area and body mass relationships for all species based on data from individuals of each species. All intercepts and slopes were standardized in the model prior to the second level (see text and **Supporting Information**).

3 | RESULTS

3.1 | Does gill surface area explain variation in k above and beyond that explained by W_∞ ?

The body mass-scaling relationship of gill surface area did not explain much variation in k across species. The 95% Bayesian Credible Intervals (BCI) of the gill surface area metric in each model overlapped with zero and a relatively small proportion of the posterior distributions of the effect sizes for the gill surface area intercept and slope were greater than zero (intercept: 13%, slope: 25%; (**Table 1**, **Figure 1**)). In contrast, W_∞ explained substantial variation in growth coefficients across species in both models with none of the posterior distributions overlapping zero (as expected based on the inverse relationship between k and W_∞ ; **Table 1**, **Figure 1**). Based on the mean effect size estimates (slope values in **Table 1**), W_∞ explained 3.25 times more variation in k than the gill surface area intercept and 5.4 times more variation than the gill surface area slope. Additionally, no multicollinearity or correlation was detected between gill surface area and W_∞ in any of the three models (**Table 1**).

3.2 | Does gill surface area explain variation in growth performance?

The relationship between gill surface area and growth performance was weakly positive for both metrics of gill surface area—the gill surface area intercept and slope (**Table 2**, **Figure 2**). The 95% BCI of the effect sizes of the gill surface area metric in both models (the gill surface area intercept and slope) crossed zero and the mean effect size for both was positive (and similar). Additionally, a large proportion of the posterior distributions for both gill surface area metrics were greater than zero. For the relationship of growth performance and the gill surface area intercept, 93.5% of the posterior distribution was greater than zero (the mean slope = 0.36; 95% BCI -0.11 to 0.83, **Table 2**, **Figure 2**) and for the relationship of growth performance and the gill surface area slope, 89.1% of the posterior distribution was greater than zero (the mean slope = 0.33 (95% BCI -0.20

TABLE 3 Comparison of coefficients and their 95% Bayesian Credible Intervals (BCI) for Question 3—whether the body mass-scaling of gill surface area explains more variation in growth performance compared to activity.

Model parameterization Of the second level	Intercept (95% CI)	CFAR slope (95% CI)	GSA slope (95% CI)	Phylogenetic signal (λ)	Relative importance of CFAR vs. gill surface area	VIF	COR
Growth performance~activity level +							
Gill surface area intercept	2.95 (2.51 to 3.38)	0.60 (0.21 to 1.00)	0.11 (-0.35 to 0.58)	—	0.60/0.11=5.5	1.16	0.29
Gill surface area intercept	2.95 (2.52 to 3.39)	0.60 (0.20 to 1.00)	0.11 (-0.38 to 0.58)	0.50 (0.03–0.98)	—	—	—
Gill surface area slope	2.95 (2.52 to 3.38)	0.62 (0.25 to 0.99)	0.19 (-0.29 to 0.67)	—	0.62/0.19=3.3	1.02	0.25
Gill surface area slope	2.95 (2.52 to 3.39)	0.62 (0.24 to 0.99)	0.19 (-0.29 to 0.65)	0.50 (0.02–0.98)	—	—	—

Note: In this model, the response variable is growth performance and the predictors are activity level (as approximated by caudal fin aspect ratio) and either the gill surface area slope or intercept (estimated in the first level of the model) with and without the inclusion of a phylogeny. All models were estimated using a Bayesian multilevel modeling framework in Stan using the package *rstan* in R v4.0.2, where the first level of the model estimated species-specific gill surface area and body mass relationships for all species based on data from individuals of each species. All predictors in the second level of the model were standardized and, thus, the effect sizes for the slopes are relative to each other (see text and [Supporting Information](#)).

Abbreviations: CFAR, caudal fin aspect ratio; COR, correlation matrix value; GSA, gill surface area; VIF, variance inflation factor.

to 0.83, [Table 2, Figure 2](#)). When considering all three aspects of model output (whether or not the posterior distribution crossed 0, the proportion of the distribution greater than zero and the mean effect size), the body mass-scaling relationship of gill surface area did not explain much variation in growth performance across species.

3.3 | Does gill surface area explain more variation in growth performance compared to activity?

Again, the body mass-scaling relationship of gill surface area did not explain much variation in growth performance across species, especially compared to activity ([Figure 3, Table 3](#)). Indeed, in both models, caudal fin aspect ratio explained more variation in growth performance across fishes compared to the gill surface area intercept or slope ([Figure 3, Table 3](#)). Based on the mean effect size estimates (slope values in [Table 3](#)), caudal fin aspect ratio explained 5.5 times more variation in growth performance than the gill surface area intercept and 3.3 times more variation than the gill surface area slope. The 95% BCI of the effect sizes for the gill surface area intercept and slope overlapped with zero and a fairly large proportion of the posterior distribution was greater than zero (68.3% and 79.6% for the gill surface area intercept and slope respectively; [[Figure 3, Table 3](#)]). For caudal fin aspect ratio, 99.8% and 99.9% of the posterior distribution in the model with the gill surface area intercept and slope, respectively, was greater than zero ([Figure 3](#)). No multicollinearity or correlation was detected for any model that included both caudal fin aspect ratio and either metric of gill surface area based on variance inflation factor (VIF) or correlation indices ([Table 3](#)).

4 | DISCUSSION

Overall, we found that while gill surface area does explain some variation in growth and maximum size, this relationship is weak. While we used several models that progressively built on each other for each question, all models were in agreement and supported the idea that variation in growth and maximum size across fishes cannot simply be explained by gill surface area alone, as the GOLT purports. We do note, however, that all models were quite noisy and had a great deal of residual error. This may provide further support that additional factors, such as those tested here (activity) or others that remain to be tested (environmental temperature, food availability, reproduction, other metrics of growth and other morphological traits related to gill surface area and oxygen), may play a larger role in fish growth compared to gill surface area (Audzijonyte et al., [2019](#); Morais & Bellwood, [2018](#); van Denderen et al., [2020](#)). We next discuss what our results mean in the context of the GOLT, what additional factors may be important in explaining variation in growth and maximum size, the pull between ecology and evolutionary history in shaping life history traits, the strengths of our modelling approach, and finally, end with suggested areas for future research.

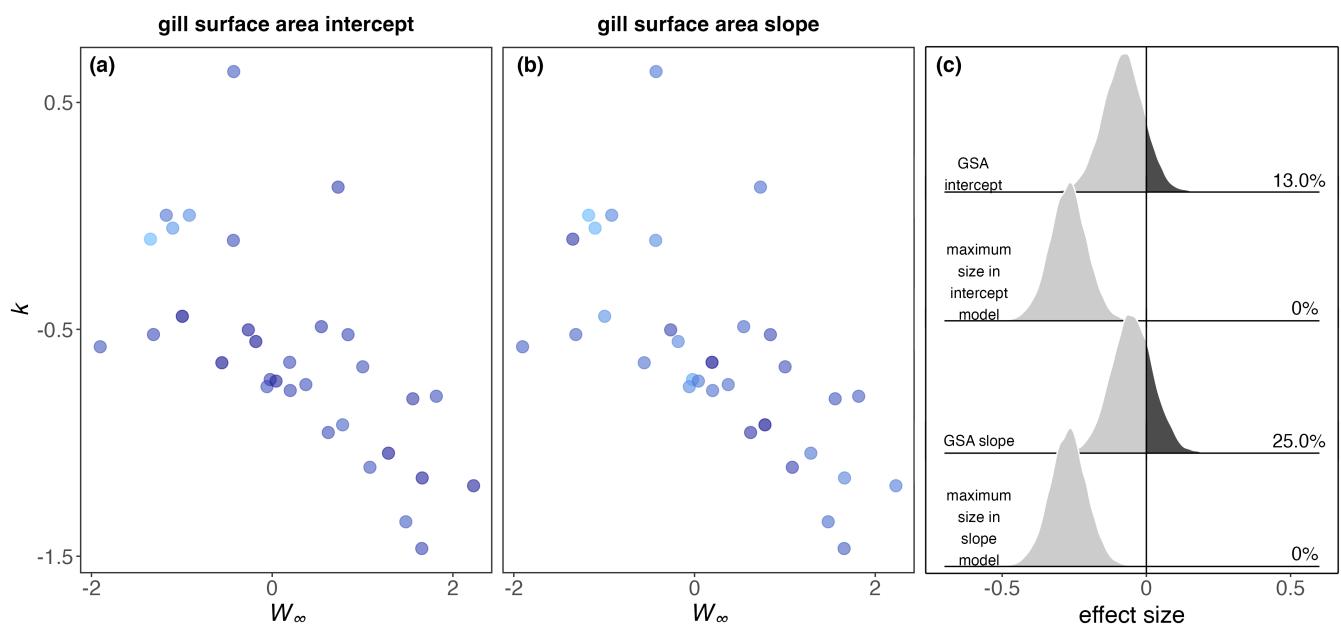


FIGURE 1 The body mass-scaling relationship of gill surface area explains little variation in growth across species. The (a) gill surface area intercept or the (b) gill surface area slope from the relationship of gill surface area and body mass differs across fishes with different von Bertalanffy growth coefficients (k , year $^{-1}$) and asymptotic sizes (W_∞ , g). Gill surface area is indicated by a gradient of colour, with darker blue indicating a greater intercept or slope, and lighter blue indicating a lower intercept or slope. Species-specific gill surface area intercepts and slopes and their relationships with k and W_∞ were estimated in a Bayesian multilevel model where the first level estimated species-specific gill surface area intercepts and slopes and the second level estimated the relationship of k , W_∞ and the intercept or slope. In this figure (and in the models), k and W_∞ were \log_{10} -transformed and W_∞ was standardized (in this figure, y-axis units are \log_{10} of k and x-axis units are standard deviation of the intercept or slope). (c) The entire posterior distribution of each effect size, as well as the per cent greater than zero (shaded dark grey), for both models in (a) and (b).

From a life history perspective, our study suggests that gill surface area alone is not the sole limiting factor determining growth and maximum size in fishes, as predicted by the GOLT (if it were, a much stronger relationship would be expected). Thus, other mechanisms appear to underlie or contribute to the suggested pattern of oxygen limitation on growth under warmer temperatures (especially at larger sizes; Audzijonyte et al., 2019; Hoefnagel & Verberk, 2015; Rubalcaba et al., 2022). Additionally, oxygen acquisition at the gills is the first of many steps in the 'oxygen cascade' as oxygen is removed from the environment and transported through the body to the cells where it is ultimately utilized (Weibel et al., 1991). The GOLT is multifaceted and while we tested three questions surrounding the central prediction, there are other aspects of this theory (i.e. ideas on protein denaturation, efficiency of assimilation, etc.), particularly those that have come to light as it has evolved since the 1980s—that remain to be evaluated (Pauly, 1981, 2010, 2021). For example, the GOLT was recently expanded to encompass predictions surrounding spawning and maturation (Morbey & Pauly, 2022; Pauly, 2022; Pauly & Liang, 2022a, 2022b). In addition, there remains much to explore regarding oxygen limitation more broadly, as well as the role of oxygen in shaping body size and other life history traits (Atkinson, 1995; Audzijonyte et al., 2019; Pauly, 1981, 2010, 2021). Wong et al. (2021) found a weak relationship between resting metabolic rate (oxygen consumption) and growth performance and Bigman et al. (2018) found a strong relationship between gill surface area (in particular,

the gill surface area intercept), maximum size, habitat type and activity level (or collectively, 'ecological lifestyle'). Further, populations and species with greater than expected scaling between metabolic rate and mass had larger gill surface area (Kuparinen et al., 2022). However, a multigenerational experiment on zebrafish revealed that metabolic rate was not linked to body size reductions under higher temperature (Wootton et al., 2021). Clearly, the interrelationships among oxygen consumption and demand (metabolic rate and gill surface area) activity, and growth are difficult to test directly, especially in the context of heterogeneity in environmental temperature.

We found that although evolutionary history did not improve our understanding of variation in growth and maximum size, activity level—as approximated by the aspect ratio of the caudal fin—did. Taken together, these results suggest that ecology (here, activity) likely explains more variation in life history compared to evolutionary history (at least for growth and maximum size). It is no surprise that activity explains variation in life history as activity is intertwined with life history traits (e.g. body size and growth), habitat and even gill surface area (Bigman et al., 2018; Gray, 1954; Hughes, 1984; Wegner, 2011). It is non-trivial to partition variance between activity and gill surface area as they are undoubtedly related, which may be reflected in our results despite the low correlation found between the specific predictors used for gill surface area and growth performance for the species in our data set. In terms of evolutionary history, it may be that relatedness truly does not explain remaining variation in growth and

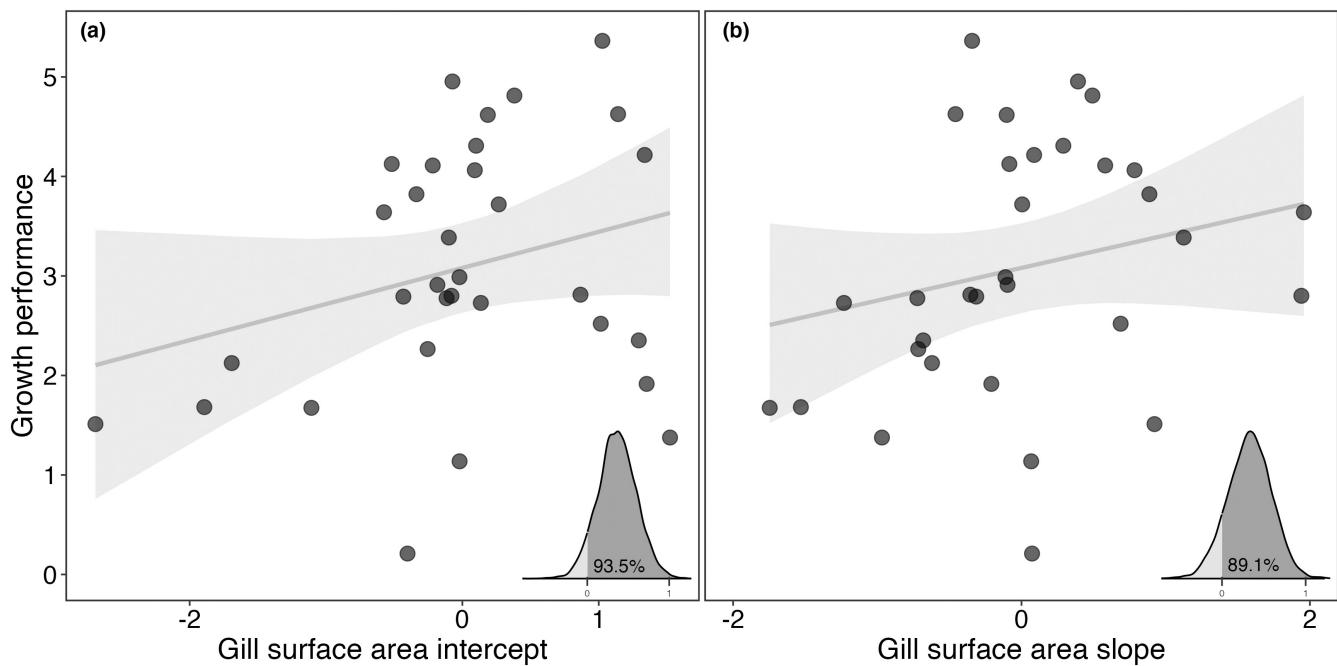


FIGURE 2 The body mass-scaling relationship of gill surface area explains little variation in growth performance across fishes. The relationship between growth performance and (a) the gill surface area intercept and (b) gill surface area slope. Species-specific intercepts and slopes and their relationships with growth performance were estimated in a Bayesian multilevel model where the first level estimated species-specific gill surface area intercepts and slopes and the second level estimated the relationship of growth performance and either the intercept or the slope. In this figure (and in the models), growth performance was \log_{10} -transformed and the intercepts and slopes were standardized (in this figure, the y-axis units are \log_{10} growth performance and x-axis units are standard deviation of the intercept or slope). In all panels, the fit lines represent the fitted growth performance for each value of the respective gill surface area measure, and the grey shaded region represents the 95% Bayesian Confidence Interval (BCI). The 95% BCIs for all models overlapped with zero but a fairly large proportion of the posterior distribution was positive (see Table 2 and inset in each panel).

maximum size, which instead, may be entirely related to ecological and physiological processes that are the result of local adaptations and independent of shared ancestry. However, the lack of variance explained by the underlying phylogenetic structure in this relationship could also be due to the model of evolution implemented to account for underlying phylogenetic structure in data sets. Typically, phylogenetic comparative methods (including ours developed and employed here) rely on the Brownian motion model of trait evolution to model the expected variance and covariance between species (Felsenstein, 1985; Freckleton, 2009; Harmon, 2019). This model of evolution assumes that traits evolve along the phylogenetic tree through a random-walk process (Harmon, 2019). Thus, species that are more closely related have had less time to diverge and thus will have trait values that are more similar (i.e. they co-vary) compared to distantly related species whose trait values have been randomly drifting for a longer period of time (Symonds & Blomberg, 2014). Other, and perhaps better, models of trait evolution exist, yet implementing them in practice is nontrivial (Harmon, 2019). However, rapid advancements in the implementation of more complex comparative methods are occurring, which will undoubtedly open the door to exploring trait evolution in a broader sense, to include employing other models of trait evolution (Pennell & Harmon, 2013). To further explore the interplay between ecology and evolutionary history, future work examining other measures of activity level (e.g.

swimming speed, aerobic scope), growth (we used von Bertalanffy growth coefficients) and other models of trait evolution may shed more light on the relationship of gill surface area, activity and growth in the context of evolution.

For example, species-level models of growth, including the von Bertalanffy growth model, have been called into question (for a more thorough discussion, see Marshall & White, 2019a). For the von Bertalanffy model specifically, issues have been raised concerning the underlying assumptions of catabolism and anabolism, lack of inclusion of reproduction and incompatibility with (top-down) phenomenological models of growth (e.g. life history models; Lester et al., 2004; Quince et al., 2008; Renner-Martin et al., 2018). This includes its use in the GOLT, adding another reason why, on top of the weak relationship among maximum size, growth and gill surface area found in this study, caution should be taken if using this theory to predict growth, size, distribution, population dynamics, etc. (Cheung et al., 2013; Clarke et al., 2021; Marshall & White, 2019a). Despite the issues with the von Bertalanffy growth model, it is the single, most widely used model of fish growth across fields including fisheries science and management and population dynamics, for example, (Beverton & Holt, 1993), life history theory (e.g. Charnov et al., 2013), ecology (e.g. Ikpewei et al., 2021), physiology (e.g. van der Meer, 2006), comparative biology (e.g. Morais & Bellwood, 2018) and climate change science (e.g. Cheung et al., 2013). Nonetheless,

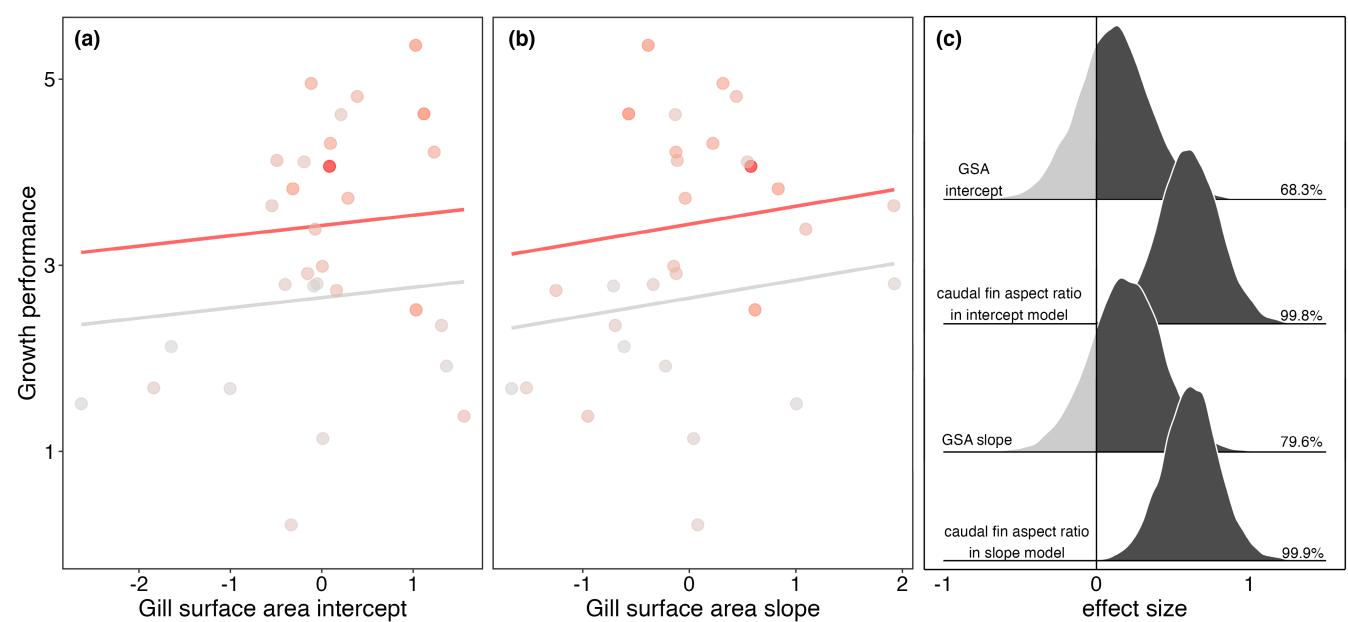


FIGURE 3 Activity explains more variation in growth performance compared to the body mass-scaling relationship of gill surface area. The relationship of growth performance and (a) the gill surface area intercept and (b) the gill surface area slope with various caudal fin aspect ratios (red = high caudal fin aspect ratio, high activity, grey = low caudal fin aspect ratio, low activity). The fit lines in both plots correspond to the predicted growth performance at a given value of the respective gill surface area metric for a high (red) and low (grey) activity level. Species-specific gill surface area intercepts and slopes and their relationships with growth performance and caudal fin aspect ratio were estimated in a Bayesian multilevel model where the first level estimated species-specific gill surface area intercepts and slopes and the second level estimated the relationship of growth performance, caudal fin aspect ratio and either the intercept or the slope. In this figure (and in the models), growth performance and caudal fin aspect ratio were \log_{10} -transformed and the slopes and intercepts were standardized (in figure, y-axis units are \log_{10} of growth performance and x-axis units are standard deviation of the intercept or slope). (c) The entire posterior distribution of each effect size, as well as the proportion greater than zero (shaded in dark grey) for both models in (a) and (b).

future work could identify other models or metrics of growth (see below) that may relate more to the scaling of gill surface area.

With this caveat aside, a major strength of our study and general approach is the ability to examine the entire body mass-scaling relationship of gill surface area with respect to growth and size across species. Indeed, the central tenet of the GOLT is that the body mass-scaling relationship of gill surface area limits the supply of oxygen for growth as an organism increases in size, ultimately determining its maximum size (Pauly, 1981, 2010, 2021). Thus, it is necessary to examine the relationship of growth and maximum size to gill surface area in the context of its scaling relationship (allometry), as opposed to using a metric such as gill area index or a mass-specific measure of gill surface area (Bigman et al., 2018, 2023; Pauly, 1981, 2010, 2021). Another important reason why an allometric scaling approach is necessary is evident when considering scale: the GOLT is focused on how the scaling of gill surface area within species drives patterns across species, while other theories surrounding the role that oxygen plays in structuring life histories, population dynamics and ecosystem functioning, among other processes, are largely centred on species-level mean data (i.e. the Metabolic Theory of Ecology; Brown et al., 2004). A combined approach that has the flexibility to incorporate raw and mean data, such as the modelling approach developed and used here, will go a long way in helping us to understand how raw data, and the allometric scaling relationships they confer, scale up to structure patterns across species, communities

and ecosystems. Indeed, understanding the role that oxygen plays in the ecology, physiology and evolution of fishes will require an integrated approach that allows us to scale up individual-level physiological and ecological data to species- and ecosystem-level patterns.

To this end, we outline four areas for future research that would help us to understand the role that oxygen may play in growth, maximum size, and more broadly, the life histories of fishes. First, there is an underappreciated complexity in estimating accurate and reliable allometric regression coefficients. Ideally, species-specific raw data spanning the entire body size range would be used to estimate an allometric slope, yet these data are rarely available. Estimating accurate slope values is central to testing whether the scaling of gill surface area (or other size-dependent traits such as metabolic rate) affect ecological, physiological and evolutionary patterns across species. Here, we took care to identify the number of individuals of a given species that were required to produce a reliable and reasonable slope estimate, and only used data to estimate allometric regression coefficients for species that had the minimum number of individuals. We urge other researchers to take a similar approach when estimating such slope values. Future work could build off our simulations to identify the minimum proportion of a species' size range needed to estimate a reliable and reasonable slope value. Second, in addition to the variation in gill surface area with size within species, there is variation in von Bertalanffy parameters within species (e.g. among populations in different thermal habitats) and variation in activity

with size. Although variation for both will be less than an allometric trait such as gill surface area, it would be ideal to incorporate such variability. Future work could extend our modelling framework to do so.

Third, future studies could examine other factors and traits (e.g. environmental temperature, food availability, metabolic rate and other physiological and morphological features related to oxygen consumption and delivery) that may underlie life history traits and maximum size across species (Audzijonyte et al., 2019; Verberk et al., 2021; Wong et al., 2021; Wootton et al., 2021). Indeed, we have not dealt with environmental temperature, a factor known to be important in explaining variation in growth across fishes (e.g. van Denderen et al., 2020). Fourth, exploring other metrics of growth with respect to gill surface area may prove fruitful. Here, we used k and W_{∞} from von Bertalanffy growth models because (1) the GOLT is derived from this growth model and (2) our goal was to explicitly test questions posed by Pauly (1981, 2010). Importantly, the GOLT attempts to characterize patterns across species, and thus, species-level metrics of growth (i.e. traits that characterize growth across a species' entire lifetime such as k and growth performance) are relevant despite drawbacks (i.e. growth and size can easily be over- and underestimated as such metrics do not capture individuals removed from the population due to natural mortality, fishing, etc.). On the other hand, the rate at which gill surface area increases with size—the central tenet of the GOLT—may be more closely linked to individual-level, physiological metrics of growth such as the change in weight over time. Measuring growth in this way is best suited to a laboratory and is logistically challenging (growth would have to be measured across the full size range) and would be limited in its ability to draw conclusions across species. However, such experimental work, particularly if it can manipulate abiotic factors such as oxygen, temperature and food availability, has the added benefit of helping to identify the mechanisms that confer the observed correlational patterns such as those uncovered here (Audzijonyte et al., 2019; Bigman et al., 2021; Wootton et al., 2022). Marrying macroecological and experimental work will help us understand the role that the balance between oxygen demand and use plays in informing growth and other life history characteristics, and more broadly, the ecology, physiology and evolution of organisms (Audzijonyte et al., 2019; Wootton et al., 2022). Such work is incredibly timely in light of the uncertainty regarding how the physiology and ecology of fishes will determine the response of species to continued global environmental change (Lefevre et al., 2021; Verberk et al., 2021).

AUTHOR CONTRIBUTIONS

Jennifer S. Bigman and Nicholas K. Dulvy conceived and designed the project and analysis. Jennifer S. Bigman collected the data and performed all analyses and visualizations. All authors contributed to the interpretation of results. Jennifer S. Bigman drafted the article and supplementary information, and created the figures, with input from all authors. Nicholas K. Dulvy supervised the project.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no competing interests.

DATA AVAILABILITY STATEMENT

All data and code necessary to reproduce the results in this study are archived on Figshare (data; <https://doi.org/10.6084/m9.figshare.21685892>) and Github (<https://github.com/jennybigman/gill-surface-area-max-size-growth>). We place no restrictions on data or code availability.

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