

The Gill-Oxygen Limitation Theory and size at maturity/maximum size relationships for salmonid populations occupying flowing waters

Kevin A. Meyer  | Daniel J. Schill

Idaho Department of Fish and Game,
Nampa, Idaho

Correspondence

Kevin A. Meyer, Idaho Department of Fish and Game, 1414 E. Locust Lane, Nampa, ID, 83709, USA.
Email: kevin.meyer@idfg.idaho.gov

Funding information

Sport Fish Restoration

Abstract

The slowing of growth as fish age has long been believed to be related to energy expenditure for maturation, and this rationalization has been used to explain why, across nearly all fish species, the relationship between size at first maturity (L_m) and maximum (L_{max}) or asymptotic length (L_∞) is relatively constant. In contrast, the Gill-Oxygen Limitation Theory (GOLT) postulates that (a) fish growth slows because as they grow, their two-dimensional ability to extract oxygen from the water diminishes relative to their three-dimensional weight gain, and (b) they can only invest energy for maturation if oxygen supply at their size at first maturity (Q_m) exceeds that needed for maintenance metabolism (Q_∞). It has been reported previously across dozens of marine fish species that the relationship between Q_m and Q_∞ is linear and, further, it can be mathematically converted to L_m vs. L_∞ by raising both terms to the power of D (the gill surface factor), resulting in a slope of 1.36. If the GOLT is universal, a similar slope should exist for L_m^D vs. L_∞^D relationships for freshwater species across multiple individual populations that reside in disparate habitats, although to our knowledge this has never been evaluated. For analysis, we used existing data from previous studies conducted on 51 stream-dwelling populations of redband trout *Oncorhynchus mykiss gairdneri*, Yellowstone cutthroat trout *O. clarkii bouvieri* and mountain whitefish *Prosopium williamsoni*. The resulting L_m^D vs. L_∞^D slopes combining all data points (1.35) or for all species considered separately (range = 1.29–1.40) were indeed equivalent to the slope originally produced for the marine species from which the GOLT-derived relationship was first reported. We briefly discuss select papers both supporting and resisting various aspects of the GOLT, note that it could potentially explain shrinking sizes of marine fish, and call for more concerted research efforts combining laboratory and field expertise in fish growth research.

KEYWORDS

asymptotic length, Gill-Oxygen Limitation Theory, GOLT, size at maturity

1 | INTRODUCTION

In ecology and genetics, phenotypic plasticity refers to the ability of a single genotype to express a variety of phenotypes across a variable

environment. Such expression results in varying patterns of movement, growth, survival and reproduction within a particular species. Fishes are arguably the most diverse group of vertebrates relative to their phenotypic plasticity (Iles, 1974). One such aspect of this

variability of longstanding interest in fisheries science and management is the variation observed in age and size at first maturity and their relationships to other life history characteristics, particularly growth (e.g., Beverton & Holt, 1959; Charnov, 2008; Jensen, 1996; Pauly, 1979).

Most fish grow rapidly at a young age, with growth slowing continuously as fish approach their asymptotic length (von Bertalanffy, 1960). This slowing of growth as fish age has long been believed to be due to maturation (e.g., Hubbs, 1926; Jones, 1976; Lagler *et al.*, 1977). This view of fish growth assumes that gonadal development utilizes much of the energy previously available for body growth, leaving less energy to be converted to growth once maturation commences. Iles (1974) dubbed this growth/maturity relationship the “reproductive drain” concept although he disagreed with it and presented study results to dismiss it as a viable explanation. Nonetheless, this hypothesis regarding growth cessation and maturation remains widely accepted (e.g., Charnov, 2008; Quince, Abrams, *et al.*, 2008).

An alternate hypothesis, first put forth by Pauly (1984) and expanded upon by Pauly (2019a,b), derives from what belatedly has been called the Gill-Oxygen Limitation Theory (or GOLT). In short, the GOLT postulates that of the two primary requirements for growth – food and oxygen – the latter is much more difficult for fish to extract from their environment due to the dense medium in which they live and the reduced oxygen available to them relative to air-breathing vertebrates. The ability of fish to absorb oxygen through their gills increases as the surface of their gills increases, whereas the fish themselves increase in size volumetrically (von Bertalanffy, 1960). Since fish size increases in three dimensions while their gills increase in two dimensions, their ability to extract oxygen from the water diminishes as they grow larger, eventually reaching a point where oxygen supply is only sufficient to meet maintenance metabolism and growth ceases (L_{∞}).

Though not without controversy (Lefevre *et al.*, 2017; Marshall & White, 2019; Nilsson & Östlund-Nilsson, 2008), the GOLT proposes that length at first maturity (L_m) occurs when it does because fish can invest energy into gonadal development only if oxygen supply at first maturity (Q_m) is more than that needed for maintenance metabolism at L_{∞} (Q_{∞}). In essence, whereas the “reproductive drain” argues that fish growth slows because they start to divert energy away from somatic growth, GOLT argues that somatic growth slows due to oxygen limitation, and that stimulates fish to start reproducing. Pauly (1984, 2019a) estimated that across 56 species of fish, the relationship between Q_m and Q_{∞} is linear and has a slope of about 1.36. This Q_m vs. Q_{∞} relationship can be converted to L_m vs. L_{∞} by raising both terms to the power of D (Pauly, 1984), which is a parameter of the generalized von Bertalanffy Growth Function (VBGF) of Pauly (1979, 2019b):

$$L_t = L_{\infty} \left(1 - e^{-KD(t-t_0)} \right)^{\frac{1}{D}}$$

where L_t is size at age t , L_{∞} is the asymptotic length, t_0 is the “age” at which length would be zero if the fish had always grown as predicted

by the formula and D is the gill surface factor. D is essentially the difference between the power of length in proportion to which weight increases and the power of length in proportion to which gill surface increases, and the resulting relationship produces the same slope of 1.36 as noted above (Pauly, 1979). In short, the GOLT postulates that growth slows when gill surface area and hence oxygen availability struggle to keep up with a volumetric body size increase, resulting in marked reduction in growth and subsequent maturation. It is Pauly's longstanding contention (1979, 2019b) that GOLT defines why fish populations grow and mature as they do in all environments and also why fish may shrink in size in the face of climate change (Pauly & Cheung, 2018).

If the GOLT is indeed correct, then the relationship between Q_m and Q_{∞} (or L_m^D and L_{∞}^D), which was derived exclusively from data on marine species (Pauly, 1979), should also apply when regressing the same two variables for data derived for freshwater species, and across populations within the same species exhibiting different life history characteristics such as growth rate, size at first maturity and maximum size. To our knowledge, the latter has never been evaluated. The objective of this study was therefore to investigate whether the L_m^D vs. L_{∞}^D slope across multiple populations within the same species would approximate 1.36 for four stream-dwelling salmonids in Idaho.

2 | MATERIALS AND METHODS

In earlier research, wild salmonids from physically isolated Idaho stream populations were collected within 1–2 months of spawning so that maturity could be ascertained *via* necropsy (e.g., Downs *et al.*, 1997). Sampling occurred in 11 populations of Yellowstone cutthroat trout *Oncorhynchus clarkii bouvieri* (Jordan and Gilbert, 1883) (Meyer *et al.*, 2003), 19 populations of mountain whitefish *Prosopium williamsoni* (Girard 1856) (Meyer *et al.*, 2009), 9 populations of desert redband trout *O. mykiss gairdneri* (Richardson 1836) (Schill *et al.*, 2010) and 12 populations of montane redband trout (KAM, unpublished data; Meyer *et al.*, 2014). For all species, males were classified as immature if testes were opaque and threadlike, and mature if they were large and milky white, whereas females were classified as immature if the ovaries were small, granular and translucent, and mature if they contained well-developed eggs that filled much of the abdominal cavity. Along with maturity status, we recorded lengths (nearest mm TL) and weights (nearest g) of all fish captured. Logistic regression was used to relate fish length to immature (dummy variable of 0) or mature (dummy variable of 1) condition to estimate L_m for each individual population sampled for each species (see original papers for details). Physical characteristics and geographic locations of the streams from which these data were collected varied widely (Figure 1 and Table 1), which contributed to highly variable estimates of L_m as well as the maximum length of fish captured (L_{max}) across the 51 populations.

To estimate the slope of the L_m^D vs. L_{∞}^D relationship, it is irrelevant whether one uses L_{max} or L_{∞} as the denominator because they are nearly identical (Froese & Binohlan, 2000; Pauly, 1979; Taylor, 1962). D , the gill surface factor described

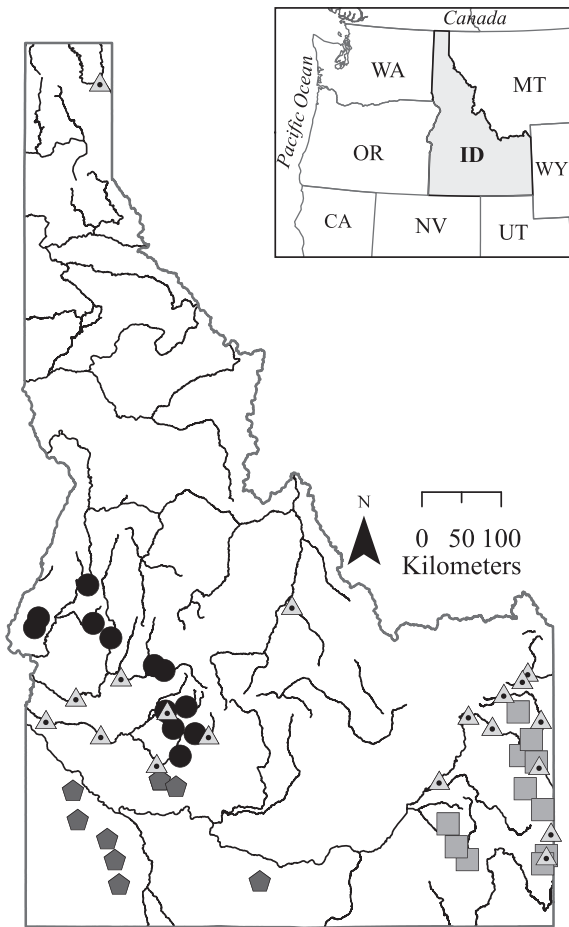


FIGURE 1 Location of streams in Idaho where length at first maturity and maximum length were obtained for populations of Yellowstone cutthroat trout *Oncorhynchus clarkii bouvieri* (YCT), mountain whitefish *Prosopium williamsoni* (MWF) and redband trout *O. mykiss gairdneri* in desert streams (dRBT) and montane streams (mRBT). (◐) dRBT, (●) mRBT, (▲) MWF, (■) YCT

above, is equal to $b \times (1 - d)$ (Pauly, 2019a), with b being the exponent of the fish length–weight relationship, which was calculated separately for each of our populations (Carlander, 1969), and d being the exponent of the gill area–weight relationship, which for trout and most other fish species is about 0.8 (De Jager & Dekkers, 1974; Pauly, 1981; Bochdansky & Leggett, 2001). The slope (and 95% CIs) of the resulting L_m^D vs. L_{\max}^D linear regression (with the intercept fitted through the origin) was estimated for each species separately, but we also fit a combined linear regression through all data points from all species combined. All analyses were conducted using the SAS statistical software package (SAS Institute, 2009).

3 | RESULTS

The exponent of the length–weight relationship (b) was close to 3.0 for all species (Table 1), indicating that growth was essentially isometric (i. e., that growth occurred in all bodily dimensions at the same rate) for

the stream-dwelling salmonid populations we included in our study. The slopes of the L_m^D vs. L_{∞}^D relationships were very similar for all species, with a slope ($\pm 95\%$ CIs) of 1.31 (1.21–1.42) for desert populations of redband trout, 1.29 (1.22–1.36) for montane populations of redband trout, 1.25 (1.18–1.32) for Yellowstone cutthroat trout and 1.40 (1.36–1.45) for mountain whitefish (Table 1 and Figure 2). Combining all data points from all species produced an overall L_m^D vs. L_{∞}^D slope of 1.35 (1.31–1.38). The individual slopes corresponded to a predicted size at first maturity occurring at 0.62 of the maximum size of fish captured for desert redband trout populations, 0.66 for montane redband trout populations, 0.70 for Yellowstone cutthroat trout populations and 0.59 for mountain whitefish populations.

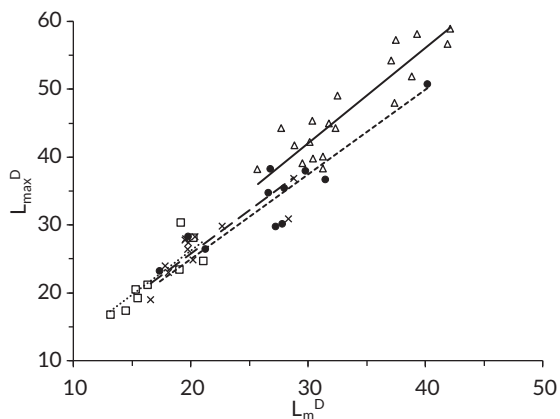
4 | DISCUSSION

The ratio L_m/L_{∞} has long been recognized to be a relatively constant ratio of about 0.6–0.7 for most fishes (Beverton & Holt, 1959; Iles, 1974; Jensen, 1996), and is one of the three life history ratios Charnov (1993) subsequently termed “invariants”. Considering that L_{\max}/L_{∞} is often about 0.95 (Froese & Binohlan, 2000; Taylor, 1962) or higher (Pauly, 1979), our mean L_m/L_{\max} ratio (0.67) concurs with this invariant. Reproduction has long been believed to channel energy away from fish growth (Charnov, 2008; Hubbs, 1926; Lagler *et al.*, 1977; Quince, Abrams, *et al.*, 2008). However, as Iles (1974) pointed out, if this L_m/L_{∞} invariance was caused by the energetic demands of producing eggs or milt, a “reproductive drain” of available metabolic energy would result in a deceleration of growth at the time of maturation. While growth does decelerate as all fish age, this deceleration appears constant throughout nearly all of their life (Cushing, 1967; Larkin *et al.*, 1957), including when they transition from immature to mature, with no inflexion point in the deceleration of growth at maturation size (Alm, 1959; Iles, 1974, but see Quince, Shuter, *et al.*, 2008). Iles (1974) suggested that the relatively constant L_m/L_{∞} ratio is an ontogenetic, pre-recorded “growth programme tied to a fish’s innate growth trajectory”, whereas Jensen (1996) suggested that the ratio could be explained by maturation occurring when the reproductive output of a cohort is maximized, a suggestion similar to that of Charnov (1993). Pauly’s GOLT theory explains the L_m/L_{∞} constancy as a simple expression of an underlying geometric reality, the invariance of the ratio Q_m/Q_{∞} (Pauly, 2019b).

Our results extend the application of the L_m^D vs. L_{∞}^D relationship from single data points for each of a broad spectrum of marine fish species (Pauly, 1984, 2019a), to broadly distributed freshwater populations within the same species that occupy widely disparate lotic environments. Our results adhere to the same general L_m^D vs. L_{∞}^D slope of 1.36 that was theorized by Pauly (1984) to be a direct consequence of the GOLT. Because the use of an L_m/L_{∞} (or L_m/L_{\max}) ratio of 0.6–0.7 or an L_m^D vs. L_{∞}^D slope of ~ 1.36 will predict essentially the same size at first maturity for any given population, we recognize that our findings, while compatible with the GOLT, do not “validate” it. Indeed, it has been well established that size at first maturity can vary greatly among populations of the same species (e.g.,

TABLE 1 Ranges in stream characteristics, length at first maturity (L_m) and maximum length (L_{max}) for several salmonids sampled in Idaho, as well as resulting L_m^D/L_{max}^D ratios

	Desert redband trout	Montane redband trout	Mountain whitefish	Yellowstone cutthroat trout
Elevation (m)	942–1749	1001–1677	549–1985	1561–2091
Conductivity ($\mu\text{S}/\text{cm}$)	33–315	35–103	62–835	183–652
Summer (June–August) water temperature ($^{\circ}\text{C}$)	14.2–18.2	NA ^a	8.1–21.0	10.4–16.1
Gradient (%)	1.3–3.8	1.5–5.0	<0.1–0.9	0.2–6.3
Stream width (m)	1.2–2.7	6.5–23.3	5.3–128	1.7–79.0
Number of populations	9	12	19	11
Number of fish	484	1155	1783	499
b (range among populations)	2.71–3.01	2.86–3.15	2.73–3.31	2.90–3.19
L_m (mm; range among populations)	110–177	118–222	193–299	97–354
L_{max} (mm; range among populations)	160–297	170–401	338–506	150–481
L_m^D/L_{max}^D slope ($\pm 95\%$ CIs)	1.31 (1.21–1.42)	1.29 (1.22–1.36)	1.40 (1.36–1.45)	1.25 (1.18–1.32)

^aNo data available.**FIGURE 2** Relationship between normalized length at first maturity (L_m^D) and normalized maximum length of fish sampled (L_{max}^D) from various populations of Yellowstone cutthroat trout *Oncorhynchus clarkii bouvieri*, mountain whitefish *Prosopium williamsoni*, and desert and montane populations of redband trout *O. mykiss gairdneri* in Idaho streams. The lines, slopes and statistics are least squares linear regressions fitted through the origin for each data set. (□) desert redband trout: $y = 1.31x$; $r^2 = 0.86$; $P < 0.001$, (×) montane redband trout: $y = 1.29x$; $r^2 = 0.90$; $P < 0.001$, (△) Yellowstone cutthroat trout: $y = 1.25x$; $r^2 = 0.89$; $P < 0.001$, (○) mountain whitefish: $y = 1.40x$; $r^2 = 0.94$; $P < 0.001$

Beamish, 1973; Jonsson *et al.*, 2001; Meyer *et al.*, 2003, 2009, 2014; Schill *et al.*, 2010; Trip *et al.*, 2014). However, the strong L_m^D vs. L_{∞}^D relationship originally derived for marine species and incorporating the gill surface factor D (recalling that $D = b \times (1 - d)$), comprises Pauly's main argument that the GOLT is directly supported by the basic geometry of fish in relation to their low-oxygen environment relative to air breathers (Pauly, 2019b). The fact that our overall slope (1.35) was virtually identical to that of Pauly's 1.36 value for marine species, and that the species-specific slopes of the L_m^D vs. L_{∞}^D

relationships obtained for several freshwater fish species across multiple populations were also quite similar to the relationship first developed for marine fish, would seem to provide at least circumstantial support for the GOLT.

Literature dealing with the GOLT is rapidly increasing, with arguments both supporting and refuting its foundations. The main underpinning of the theory – the disparity in growth between gill surface area and body mass – has long been acknowledged in the literature, beginning with von Bertalanffy, who believed that, in fish, respiration limits anabolism and thus maximal growth in fishes (von Bertalanffy, 1949, 1960). The value of the exponent d has also been well documented empirically (e.g., De Jager & Dekkers, 1974; Muir & Hughes, 1969; Palzenberger & Pohla, 1992) and most recently *via* meta-analysis (Bochdanský & Leggett, 2001). In addition, several manipulative studies provide support for the GOLT. For example, oxygen concentration (*i.e.*, dissolved oxygen, DO) was clearly shown to positively affect both food conversion and growth rate in juvenile largemouth bass *Micropterus salmoides* fed unlimited amounts of food until ambient DO levels exceeded those observed in nature, whereupon both metrics markedly declined (Stewart *et al.*, 1967). More recently, in a manipulative test directly evaluating the GOLT, Kolding *et al.* (2008) concluded that the observed differences in size at maturity of Nile tilapia *Oreochromis niloticus* reared in high, medium and low oxygen, along with several corollary observations, supported the theory.

Nonetheless, acceptance of the GOLT has not been universal. The primary critique centres on the argument that large fish are no more oxygen limited than smaller fish because organs such as fish gills evolve to provide the capacity necessary to meet an organism's requirements (e.g., Marshall & White, 2019). Lefevre *et al.* (2017, 2018) argued that the scaling of surface area to volume in gills is simply not constrained by geometry due to various specializations, including the folding of gill structures. Other physiologists have noted that many fish species have developed special adaptations to hypoxia,

such as haemoglobin with exceptionally high oxygen affinities, and have argued that larger fish have clear advantage over smaller ones during severe hypoxia (Nilsson & Östlund-Nilsson, 2008).

In recent years, debate has increased on whether the GOLT explains the shrinking size of fish that is becoming apparent across the globe and that has been linked to climate change (Daufresne *et al.*, 2009). Using anadromous salmonids as an example, a spate of recent papers have documented substantial reductions in length at ocean age and a concomitant downward shift in age at maturity for numerous Chinook salmon *O. tshawytscha* populations (Kendall & Quinn, 2011; Lewis *et al.*, 2015; McPhee *et al.*, 2016; Ohlberger *et al.*, 2018; Siegel *et al.*, 2017), with little evidence that selective harvest or excessive hatchery stocking was the cause (Lewis *et al.*, 2015; Ohlberger *et al.*, 2018). Two of these studies documented increased mean length in the youngest ocean age groups while mean sizes in older age groups declined across multidecadal scales (Ohlberger *et al.*, 2018; Siegel *et al.*, 2017). A similar “shrinking” phenomenon has also been reported in populations of Atlantic salmon *Salmo salar* (Todd *et al.*, 2008), steelhead *Oncorhynchus mykiss* (Bowersox *et al.*, 2019) and most recently for all five species of Alaska salmon (Oke *et al.*, 2020). Despite the fact that these temporal life history changes could be explained by ocean warming and the GOLT (Cheung *et al.*, 2013; Pauly & Cheung, 2018), it was only mentioned in a single one of the studies as a possible explanation. As noted by Pauly and Cheung (2018), an alternative hypothesis to the GOLT that offers a more parsimonious explanation for such fish “shrinking”, as well as a broad range of other phenomena related to fish growth, has yet to be advanced.

In strongly questioning the validity of the GOLT to explain “shrinking” marine fish as the climate warms, Lefevre *et al.* (2017) nevertheless concede that some fish will possibly become smaller in the future, and call for improved communication and congruity between fisheries scientists and fish physiologists. Indeed, as the climate continues to warm over the 21st century, understanding the cause and effect of shrinking marine ectotherms is of paramount importance. More comprehensive research is clearly needed, combining the expertise of geneticists, modellers, ecologists, physiologists and field scientists in an effort to better integrate theory and physiology with observed field and laboratory data (Audzijonyte *et al.*, 2019). Indeed, as nonphysiologists, our ability to navigate the vast and dense literature with radically opposing points of views and study conclusions regarding the intricacies of fish growth is rather limited, particularly as it seems hopelessly conflicted. As von Bertalanffy (1960) suggested, we believe a judicious amount of intellectual humility and good humour, and lack of dogmatism will go a long way in facilitating the debate regarding any theory, in this case about gills, oxygen, growth and maturation in fish.

ACKNOWLEDGEMENTS

We thank Mike Hansen for assistance thinking through various aspects of the quantity *D* and thoughtful presubmittal review of the manuscript. This work was funded in part by anglers and boaters through their purchase of Idaho fishing licences, tags and permits, and

from federal excise taxes on fishing equipment and boat fuel through the Sport Fish Restoration Program.

AUTHOR CONTRIBUTIONS

K.A.M. and D.J.S. each contributed equally to ideas, data collection, statistical analyses and interpretation, and manuscript preparation and revision.

ORCID

Kevin A. Meyer  <https://orcid.org/0000-0002-1192-3906>

REFERENCES

- Alm, G. (1959). Connection between maturity, size and age in fishes. *Institute of Freshwater Research*, 40, 5–145.
- Audzijonyte, A., Barneche, D. R., Baudron, A. R., Belmaker, J., Clark, T. D., Marshall, C. T., ... van Rijn, I. (2019). Is oxygen limitation in warming waters a valid mechanism to explain decreased body sizes in aquatic ectotherms? *Global Ecology and Biogeography*, 28, 64–77.
- Beamish, R. J. (1973). Determination of age and growth of populations of the white sucker (*Catostomus commersoni*) exhibiting a wide range in size at maturity. *Journal of the Fisheries Board of Canada*, 30, 607–616.
- Beverton, R. J. H., & Holt, S. J. (1959). A review of the lifespans and mortality rates of fish in nature, and their relation to growth and other physiological characteristics. In G. E. W. Wolstenholme & M. O'Connor (Eds.), *CIBA Foundation colloquia on ageing* (Vol. 5, pp. 142–180). London: J&A Churchill Ltd..
- Bochdanský, A. B., & Leggett, W. C. (2001). Winberg revisited: convergence of routine metabolism in larval and juvenile fish. *Canadian Journal of Fisheries and Aquatic Sciences*, 58, 220–230.
- Bowersox, B. J., Corsi, M. P., McCormick, J. L., Copeland, T., & Campbell, M. R. (2019). Examining life history shifts and genetic composition in a hatchery steelhead population, with implications for fishery and ocean selection. *Transactions of the American Fisheries Society*, 148, 1056–1068.
- Carlander, K. D. (1969). *Handbook of freshwater fishery biology* (Vol. 1). Ames: Iowa State University Press.
- Chamov, E. (1993). *Life history invariants*. New York: Oxford University Press.
- Charnov, E. L. (2008). Fish growth: Bertalanffy *k* is proportional to reproductive effort. *Environmental Biology of Fishes*, 83, 185–187.
- Cheung, W. W., Sarmiento, J. L., Dunne, J., Frölicher, T. L., Lam, V. W., Palomares, M. D., ... Pauly, D. (2013). Shrinking of fishes exacerbates impacts of global ocean changes on marine ecosystems. *Nature Climate Change*, 3, 254–258.
- Cushing, D. H. (1967). The grouping of herring populations. *Journal of the Marine Biological Association of the United Kingdom*, 47, 193–208.
- Daufresne, M., Lengfellner, K., & Sommer, U. (2009). Global warming benefits the small in aquatic ecosystems. *Proceedings of the National Academy of Sciences*, 106, 12788–12793.
- De Jager, S., & Dekkers, W. J. (1974). Relations between gill structure and activity in fish. *Netherlands Journal of Zoology*, 25, 276–308.
- Downs, C. C., White, R. G., & Shepard, B. B. (1997). Age at sexual maturity, sex ratio, fecundity and longevity of isolated headwater populations of westslope cutthroat trout. *North American Journal of Fisheries Management*, 17, 85–92.
- Froese, R., & Binohlan, C. (2000). Empirical relationships to estimate asymptotic length, length at first maturity and length at maximum yield per recruit in fishes, with a simple method to evaluate length frequency data. *Journal of Fish Biology*, 56, 758–773.
- Hubbs, C. L. (1926). The structural consequences of modifications of the developmental rate in fishes, considered in reference to certain problems of evolution. *American Naturalist*, 60, 57–81.

- Iles, T. D. (1974). The tactics and strategy of growth in fishes. In F. R. Harden Jones (Ed.), *Sea fisheries research* (pp. 331–345). London: Elek Scientific.
- Jensen, A. L. (1996). Beverton and Holt life history invariants result from optimal trade-off of reproduction and survival. *Canadian Journal of Fisheries and Aquatic Sciences*, 53, 820–822.
- Jones, R. (1976). Growth of fishes. In D. H. Cushing & J. J. Walsh (Eds.), *The ecology of the sea* (pp. 251–279). London: Blackwell Scientific.
- Jonsson, B., Jonsson, N., Brodtkorb, E., & Ingebrigtsen, P. J. (2001). Life-history traits of brown trout vary with the size of small streams. *Functional Ecology*, 15, 310–317.
- Kendall, N. W., & Quinn, T. P. (2011). Length and age trends of Chinook salmon in the Nushagak River, Alaska, related to commercial and recreational fishery selection and exploitation. *Transactions of the American Fisheries Society*, 140, 611–622.
- Kolding, J., Haug, L., & Stefansson, S. (2008). Effect of ambient oxygen on growth and reproduction in Nile tilapia (*Oreochromis niloticus*). *Canadian Journal of Fisheries and Aquatic Sciences*, 65, 1413–1424.
- Lagler, K., Bardach, J. E., Miller, R. R., & Passino, D. R. M. (1977). *Ichthyology*. New York: John Wiley and Sons.
- Larkin, P. A., Terpenning, J. G., & Parker, R. R. (1957). Size as a determinant of growth rate in rainbow trout *Salmo gairdneri*. *Transactions of the American Fisheries Society*, 86, 84–96.
- Lefevre, S., McKenzie, D. J., & Nilsson, G. E. (2017). Models projecting the fate of fish populations under climate change need to be based on valid physiological mechanisms. *Global Change Biology*, 23, 3449–3459.
- Lefevre, S., McKenzie, D. J., & Nilsson, G. E. (2018). In modelling effects of global warming, invalid assumptions lead to unrealistic projections. *Global Change Biology*, 24, 553–556.
- Lewis, B., Grant, W. S., Brenner, R. E., & Hamazaki, T. (2015). Changes in size and age of Chinook salmon *Oncorhynchus tshawytscha* returning to Alaska. *PLoS One*, 10, e0130184.
- Marshall, D. J., & White, C. R. (2019). Aquatic life history trajectories are shaped by selection, not oxygen limitation. *Trends in Ecology and Evolution*, 34, 182–184.
- McPhee, M. V., Leon, J. M., Wilson, L. I., Siegel, J. E., & Agler, B. A. (2016). Changing growth and maturity in western Alaskan Chinook salmon, *Oncorhynchus tshawytscha*, brood years 1975–2005. *North Pacific Fish Commission Bulletin*, 6, 307–327.
- Meyer, K. A., Elle, F. S., & Lamansky, J. A., Jr. (2009). Environmental factors related to the distribution, abundance, and life history characteristics of mountain whitefish in Idaho. *North American Journal of Fisheries Management*, 29, 753–767.
- Meyer, K. A., Schill, D. J., Elle, F. S., & Lamansky, J. A., Jr. (2003). Reproductive demographics and factors that influence length at sexual maturity of Yellowstone cutthroat trout in Idaho. *Transactions of the American Fisheries Society*, 132, 183–195.
- Meyer, K. A., Schill, D. J., Mamer, E. R. J. M., Kozfkay, C. C., & Campbell, M. R. (2014). Status of redband trout in the upper Snake River basin of Idaho. *North American Journal of Fisheries Management*, 34, 507–523.
- Muir, B. S., & Hughes, G. M. (1969). Gill dimensions for three species of tunny. *Journal of Experimental Biology*, 51, 271–285.
- Nilsson, G. E., & Östlund-Nilsson, S. (2008). Does size matter for hypoxia tolerance in fish? *Biological Reviews*, 83, 173–189.
- Ohlberger, J., Ward, E. J., Schindler, D. E., & Lewis, B. (2018). Demographic changes in Chinook salmon across the Northeast Pacific Ocean. *Fish and Fisheries*, 19, 533–546.
- Oke, K. B., Cunningham, C. J., Westley, P. A. H., Baskett, M. L., Carlson, S. M., Clark, J., ... Kindsvater, H. K. (2020). Recent declines in salmon body size impact ecosystems and fisheries. *Nature Communications*, 11, 4155.
- Palzenberger, M., & Pohla, H. (1992). Gill surface area of water-breathing freshwater fish. *Reviews in Fish Biology and Fisheries*, 2, 187–216.
- Pauly, D. (1979). Gill size and temperature as governing factors in fish growth: a generalization of von Bertalanffy's growth formula (Berichte aus dem Institut fuer Meereskunde 63). Kiel University, Kiel, Germany.
- Pauly, D. (1981). The relationships between gill surface area and growth performance in fish: a generalization of von Bertalanffy's theory of growth. *Berichte der Deutschen Wissenschaftlichen Kommission fur Meeresforschung*, 28, 251–282.
- Pauly, D. (1984). A mechanism for the juvenile-to-adult transition in fishes. *ICES Journal of Marine Science*, 41, 280–284.
- Pauly, D. (2019a). Gasping fish and panting squids: Oxygen, temperature and the growth of water-breathing animals. In *Excellence in ecology*, 22 (2nd ed., p. 279). Oldendorf/Luhe, Germany: International Ecology Institute.
- Pauly, D. (2019b). A précis of gill-oxygen limitation theory (GOLT), with some emphasis on the eastern Mediterranean. *Mediterranean Marine Science*, 20, 688–702.
- Pauly, D., & Cheung, W. W. L. (2018). Sound physiological knowledge and principles in modeling shrinking of fishes under climate change. *Global Change Biology*, 24, e15–e26.
- Quince, C., Abrams, P. A., Shuter, B. J., & Lester, N. P. (2008). Biphasic growth in fish I: Theoretical foundations. *Journal of Theoretical Biology*, 254, 197–206.
- Quince, C., Shuter, B. J., Abrams, P. A., & Lester, N. P. (2008). Biphasic growth in fish II: Empirical assessment. *Journal of Theoretical Biology*, 254, 207–214.
- SAS Institute Inc. (2009). *The SAS system for windows* (Release 9.2). Cary, NC: SAS Institute Inc.
- Schill, D. J., Labar, G. W., Mamer, E. R. J. M., & Meyer, K. A. (2010). Sex ratio, fecundity and models predicting length at sexual maturity of redband trout in Idaho desert streams. *North American Journal of Fisheries Management*, 30, 1352–1363.
- Siegel, J. E., McPhee, M. V., & Adkison, M. D. (2017). Evidence that marine temperatures influence growth and maturation of Western Alaskan Chinook salmon. *Marine and Coastal Fisheries*, 9, 441–456.
- Stewart, N. E., Shumway, D. L., & Doudoroff, P. (1967). Influence of oxygen concentration on the growth of juvenile largemouth bass. *Journal of the Fisheries Board of Canada*, 24, 475–494.
- Taylor, C. C. (1962). Growth equations with metabolic parameters. *ICES Journal of Marine Science*, 27, 270–286.
- Todd, C. D., Hughes, S. L., Marshall, C. T., MacLean, J. C., Lonergan, M. E., & Biuw, E. M. (2008). Detrimental effects of recent ocean surface warming on growth condition of Atlantic salmon. *Global Change Biology*, 14, 958–970.
- Trip, E. D. L., Clements, K. D., Raubenheimer, D., & Choat, J. H. (2014). Temperature-related variation in growth rate, size, maturation and life span in a marine herbivorous fish over a latitudinal gradient. *Journal of Animal Ecology*, 83, 866–875.
- von Bertalanffy, L. (1949). Problems of organic growth. *Nature*, 163, 156–158.
- von Bertalanffy, L. (1960). Principles and theory of growth. In W. W. Nowinski (Ed.), *Fundamental aspects of normal and malignant growth* (pp. 137–259). Amsterdam and New York: Elsevier.

How to cite this article: Meyer KA, Schill DJ. The Gill-Oxygen Limitation Theory and size at maturity/maximum size relationships for salmonid populations occupying flowing waters. *J Fish Biol.* 2021;98:44–49. <https://doi.org/10.1111/jfb.14555>