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Original Article

Metabolic scaling in adult white-spotted pygmy filefish (*Rudarius ercodes*) from a wild population in Japan

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Abstract: Metabolic rate is a critical determinant of energy flux in organisms, influencing both physiological and ecological performance. Despite its importance, intraspecific metabolic scaling in wild adult populations remains poorly understood. This study measured whole-animal metabolic rate in wild-caught adult white-spotted pygmy filefish (*Rudarius ercodes*) to assess metabolic scaling under natural conditions. The results indicated that whole-animal metabolic rate increased with body mass, following a pattern of negative allometry. This suggests that larger individuals have a lower metabolic demand relative to their body mass compared to smaller individuals. Consistent with this observation, mass-specific metabolic rate decreased with increasing body size. Although body mass explained some of the variation in metabolic rate, significant inter-individual heterogeneity was observed among individuals of similar size, highlighting substantial physiological diversity beyond the effects of body size. These findings provide population-level evidence for size-dependent metabolic structuring in a natural adult fish population and support a context-dependent interpretation of metabolic scaling exponents. By incorporating individual-level variation observed under ecologically realistic conditions, this study offers empirically grounded insights that refine metabolic scaling theory beyond idealized interspecific comparisons or captive-derived datasets.

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Introduction

The metabolic rate, which is the rate at which organisms convert energy to sustain life, underpins growth, survival, and reproductive performance in all animals (Kozłowski and Teriokhin, 1999; Czarnołęski et al., 2003; Hou et al., 2008). In fish, metabolic processes are particularly sensitive to body mass and environmental temperature, making metabolic scaling a central framework for understanding the physiological, ecological, and evolutionary dynamics of aquatic systems (Ohlberger et al., 2012; Li et al., 2018). Classic allometric theory predicts that the whole-organism metabolic rate scales with body mass according to a power-law relationship, with exponents near 3/4 (Kleiber's law) or 2/3, depending on surface-area constraints (Farrell-Gray and Gotelli, 2005; Savage et al., 2004; White et al., 2007). However, growing empirical evidence demonstrates that metabolic scaling exponents vary substantially across taxonomic groups, life stages, ecological contexts, and analytical scales, challenging their universality (Darveau et al., 2002; Capellini et al., 2010; Hulbert, 2014; Ballesteros et al., 2018). Recent syntheses have emphasized that intraspecific metabolic scaling, particularly within restricted body mass ranges, often deviates from interspecific predictions derived from metabolic theory (Chown et al., 2007; Glazier, 2009; Sieg et al., 2009; Killen et al., 2010). Such deviations are increasingly interpreted not as violations of theory but as reflections of biological constraints, ontogenetic transitions, and ecological specialization. In fish, metabolic scaling is known to change dynamically across ontogeny, with steeper exponents typically observed during early developmental stages and shallower relationships emerging as morphological and physiological systems mature (Moran and Wells, 2007; Sánchez-González and Nicieza, 2023).

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Notably, much of the debate surrounding metabolic scaling has focused on broad interspecific comparisons or pronounced ontogenetic transitions (Rosén et al., 2026; White and Kearney, 2011); in contrast, relatively little attention has been paid to whether detectable mass-dependent patterns persist within narrow ranges of adult body mass (Glazier, 2015; Thommen et al., 2019; Rosén et al., 2026). In such restricted size intervals, classical allometric expectations predict only modest variations in metabolic rate, raising the possibility that individual-level heterogeneity may obscure underlying scaling relationships (Rasmussen and Izard, 1988; Thommen et al., 2019). Therefore, determining whether body mass continues to structure metabolic variation during adulthood, even within limited size ranges, is critical for evaluating the extent to which metabolic scaling operates as a continuous physiological constraint rather than as a pattern confined to early development or broad taxonomic contrasts.

Despite the growing recognition of context-dependent metabolic scaling, empirical data from wild adult fish alone are surprisingly scarce. Most metabolic studies rely on laboratory-reared or long-term captive individuals owing to the logistical constraints and methodological challenges associated with measuring the metabolic rate in small, active species (Cooke et al., 2016; Nelson, 2016). However, captive rearing is known to alter physiological traits through relaxed selection, reduced environmental variability, and domestication effects, potentially leading to a systematic underestimation of metabolic demand in natural populations of these fish. Consequently, extrapolating metabolic parameters from cultured stocks to wild populations may bias bioenergetic models and ecological predictions (Evans et al., 2014; Horreo et al., 2019).

The white-spotted pygmy filefish (*Rudarius ercodes*), a small coastal species widely distributed in temperate marine environments, represents an ideal system for examining metabolic scaling in wild adult fish. This species exhibits a relatively narrow adult body size range (approximately 2-6 g), limited post-juvenile morphological changes, and strong exposure to natural environmental heterogeneity (Ishida and Tanaka, 1983). Such characteristics allow the isolation of adult-stage intraspecific metabolic scaling without the confounding effects of rapid ontogenetic remodeling, which dominates larval and early juvenile phases. However, to date, no study has quantified the body mass–metabolic rate relationship in this species in the wild.

Here, the relationship between body mass and metabolic rate was quantified in wild-caught adult white-spotted pygmy filefish. Specifically, I tested whether metabolic rate scales predictably with body mass within a restricted adult size range and assessed how the resulting scaling exponent compares with classical allometric expectations. By focusing exclusively on wild individuals at a later ontogenetic stage, this study provides ecologically relevant baseline data and adds to growing evidence that metabolic scaling is shaped by life history, environmental context, and methodological framework rather than governed by a single universal law.

Materials and Methods

Fish preparation

Collection of wild fish: White-spotted pygmy filefish were collected from the coastal waters of northern Kyushu, Japan (33°47′N, 130°27′E), off the Fukuoka Prefecture (Fig. 1A, B). The sampling site is a nearshore habitat characterized by recurrent accumulations of drifting macroalgae that provide a structural refuge for small coastal fish. The collections were conducted between May and August 2014.

Fish associated with drifting seaweed were identified visually in situ and captured using a hand net without vessel-based trawling or enclosure gear. This approach minimizes habitat disturbance and is widely used to sample small-bodied fishes inhabiting floating algal mats. Immediately after capture, the fish were transferred to aerated containers filled with ambient seawater and transported to the laboratory for subsequent experiments. A total of 12 individuals were included in all experimental analyses.

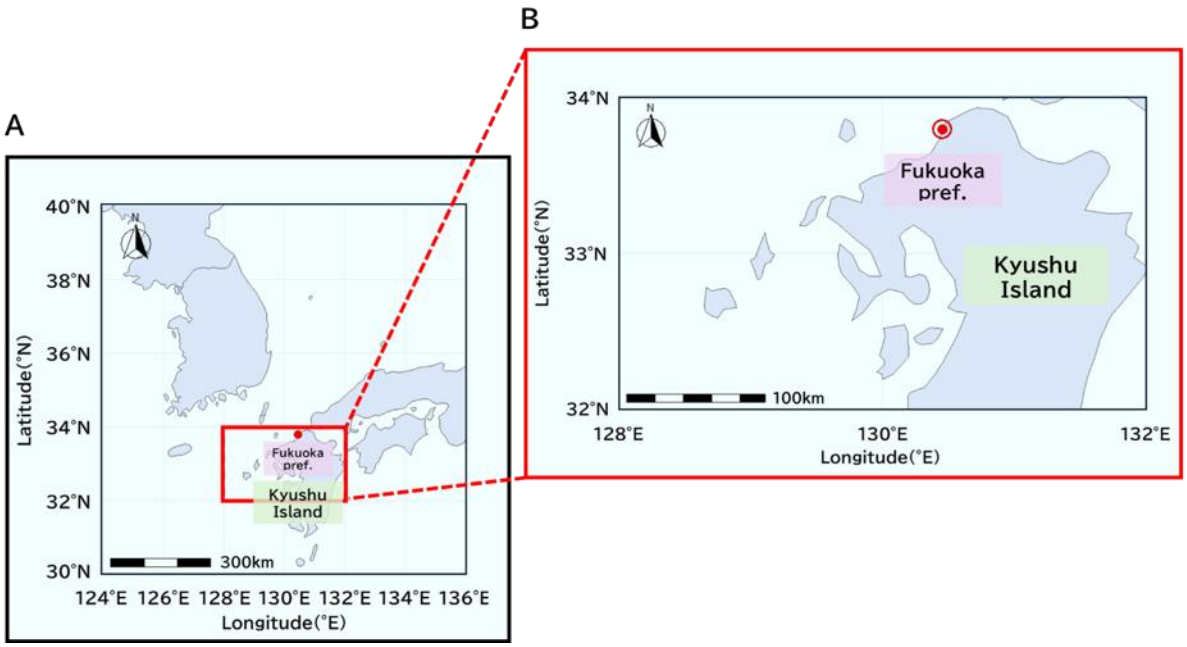

Figure 1. Sampling location of white-spotted pygmy filefish in northern Kyushu, Japan. (A) Regional map of East Asia showing the study area. (B) Close-up map of northern Kyushu showing the sampling site (red circle; 33°47′N, 130°27′E) off the coast of Fukuoka Prefecture, Japan. Scale bars are shown in each panel.

Holding and acclimation conditions: Immediately after capture, the fish were transported to an on-site experimental facility and transferred to a 200-L cylindrical polycarbonate tank supplied with continuously aerated seawater. Individuals were acclimated for approximately two weeks under ambient environmental conditions to minimize handling, stress, and artificial influences. During the acclimation period, the water temperature followed the natural seasonal variation typical of coastal waters off Kyushu between May and August (approximately 1828 °C), and salinity was maintained at 32-33 psu. The fish were kept under a natural photoperiod without artificial lighting. Throughout acclimation, the fish were fed a commercially formulated diet three times daily.

Respirometry

Respirometry apparatus: The metabolic rate was defined as the rate of oxygen consumption, and the whole-animal metabolic rate ($\dot{M}O_2$) specifically refers to the oxygen consumption rate of an individual fish. The metabolic rate was quantified using a parallel constant-flow respirometry system maintained at 20°C. The system consisted of two identical cylindrical acrylic chambers (internal volume: 200 ml each): one respiration chamber containing a single fish and one blank chamber without a fish to account for background oxygen dynamics (Table 1). Both chambers were supplied simultaneously from a common header tank to ensure identical inflow conditions. The header tank was equipped with a submersible heater to maintain a constant water temperature throughout the experiment. Seawater from the header tank was delivered to each chamber at equal and constant flow rates (26-34 ml min^{-1}) using precision inline flow-control valves (Table 1).

Flow rates were verified volumetrically before and after each measurement period and maintained within a 2% deviation between chambers. The flow conditions were selected to generate measurable oxygen differentials between the chambers while preventing excessive oxygen depletion within the respiration chamber (Table 1).

Pre-measurement procedures: All individuals were fasted for 24 h prior to measurements to ensure a post-absorptive metabolic state and eliminate the influence of specific dynamic action. The fish were carefully transferred to the respiration chamber to minimize handling stress.

Following the introduction, individuals were

Table 1. Summary of the respirometry system based on the constant-flow respirometry system at 20°C.

Range of Body mass (g)	Chamber volume (mL)	Flow rate (mL min^{-1})	O_2 in water in mL L^{-1} (Mean ± S.D.)	
			Initial or at inflowing water	Final or outflowing water
2.73-3.98	200	33.7-33.9	4.64±0.09	4.38±0.08
4.42-4.65	200	27.0-33.0	4.44±0.21	4.15±0.19
5.06-6.73	200	30.3-37.9	4.66±0.08	4.28±0.09

maintained under continuous-flow conditions to allow complete renewal of the chamber water, equilibration of the water chemistry, and recovery from handling disturbance. Individuals were subsequently allowed to acclimate within the respiration chamber for 1-2 h prior to data collection to ensure their physiological stabilization. Oxygen consumption measurements were conducted for 1-3 h under continuous flow conditions.

Quantification of oxygen consumption: Dissolved oxygen concentrations were determined from the outflow streams of both respiration and blank chambers using the Winkler titration method (Oikawa et al., 1991). Because both chambers received water from the same header tank under identical flow conditions, the oxygen consumption rate ($\dot{M}O_2$) was calculated from the difference in dissolved oxygen concentration between the blank and respiration chambers: $\dot{M}O_2 = F \times (C_{blank} - C_{fish})$, where F represents the flow rate (ml min^{-1}), and C_{blank} and C_{fish} denote the dissolved oxygen concentrations in the blank and respiration chamber outflows, respectively.

Immediately after the completion of the respirometry measurements, each individual was removed from the chamber, gently blotted to remove excess surface moisture, and weighed using an analytical balance (Sartorius CP225D, Sartorius, Goettingen, Germany; resolution ±0.01 mg). Body mass measurements were used to calculate the mass-specific metabolic rate ($\dot{M}O_2$, μL O_2 g^{-1} min^{-1}) by dividing the whole-animal metabolic rate ($\dot{M}O_2$) by individual body mass (M). The system's configuration and analytical framework followed established principles of constant-flow respirometry (Oikawa and Itazawa 1995).

Statistical analyses

Descriptive statistics: All statistical analyses were conducted to quantify the relationship between body mass and oxygen consumption rate in wild-caught adult white-spotted pygmy filefish. The whole-animal metabolic rate ($\dot{M}O_2$, μL O_2 fish^{-1} min^{-1}) and body mass (M, g) were summarized using the mean, standard deviation (SD), and inter-individual variability was assessed using the coefficient of variation (CV). The mass-specific metabolic rate ($\dot{M}O_2/M$, μL O_2 g^{-1} min^{-1}) was derived directly from the whole-animal metabolic rate ($\dot{M}O_2$) and summarized descriptively.

Allometric scaling analysis: The relationship between body mass (M) and whole-animal metabolic rate ($\dot{M}O_2$) was examined using log–log linear regression. Both variables were $\log_{10}$-transformed prior to analysis to linearize the allometric relationship as follows: $\log_{10}(\dot{M}O_2) = a + b \log_{10}(M)$, where a represents the intercept of the log–log regression and b represents the slope (i.e., scaling exponent). Because the mass-specific metabolic rate ($\dot{M}O_2/M$) is mathematically derived from the whole-animal metabolic rate ($\dot{M}O_2$), its dependence on body mass can be interpreted in the context of the estimated scaling exponent ($b - 1$).

Model significance was evaluated using t-tests on the regression coefficients, and goodness-of-fit was assessed using the coefficient of determination (R^2). Model assumptions were verified by visually inspecting residual plots to confirm homoscedasticity, normality, and the absence of systematic trends across the observed body mass range. All statistical analyses were performed using RStudio (RStudio 2023.12.1 Build 402 “Ocean Storm” for Windows; Posit Software, PBC, Boston, MA, USA). Statistical significance was set at $\alpha = 0.05$.

Results

Descriptive statistics of body mass and metabolic traits: The body mass of the white-spotted pygmy filefish ranged from 2.73 to 6.73 g (4.62±1.18 g; CV = 25.5%), indicating a relatively constrained size distribution within the adult life stage (Table 2, Fig. 2A, B). Within this narrow size range, the whole-animal metabolic rate ($\dot{M}O_2$) varied from 7.25 to 14.42 (11.46±2.20; CV = 19.2%) (Table 2, Fig. 2A). The mass-specific metabolic rate ($\dot{M}O_2/M$) ranged from 1.76 to 3.57 (2.58±0.59; CV = 22.7%) (Table 2, Fig. 2B). Importantly, the magnitude of metabolic variation was comparable to that of the body mass. These descriptive statistics indicate that substantial inter-individual metabolic variability exists even within a restricted adult size range, suggesting that

Table 2. Descriptive statistics of body mass and metabolic traits in white-spotted pygmy filefish. Minimum, maximum, mean, and standard deviation (SD) are shown for wet body mass, whole-animal metabolic rate ($\dot{M}O_2$), and mass-specific metabolic rate ($\dot{M}O_2/M$). Coefficients of variation (CV, %) are provided as a measure of inter-individual variability. All measurements were conducted on wild-caught adult individuals at 20°C under post-absorptive conditions.

Variable	Min	Max	Mean	S.D.	CV (%)
Body mass (M)	2.73	6.73	4.61	1.18	25.5
Whole-animal metabolic rate ($\dot{M}O_2$)	7.25	14.42	11.46	2.20	19.2
Mass-specific metabolic rate ($\dot{M}O_2/M$)	1.76	3.57	2.58	0.59	22.7

Table 3. Log–log scaling relationships between body mass and metabolic traits in white-spotted pygmy filefish. Scaling relationships were estimated using linear regression on $\log_{10}$-transformed data according to the equation: $\log_{10}(\dot{M}O_2) = a + b\log_{10}(M)$, where a is the intercept and b is the scaling exponent (slope). $\dot{M}O_2$ denotes whole-animal metabolic rate (μL O_2 fish^{-1} min^{-1}), and M denotes body mass (g). Values of b are presented as mean ± S.E.M. R^2 indicates the proportion of variance explained by the regression model. P-values test whether the scaling exponent differs from unity using a two-tailed Student's t-test. N denotes sample size.

Variable	N	Intercept (a)	Slope (b)	R^2	P-value
Whole-animal metabolic rate ($\dot{M}O_2$)	12	5.81	0.440±0.215	0.296	2.61×10^{-2}
Mass-specific metabolic rate ($\dot{M}O_2/M$)	12	5.81	–0.560±0.215	0.404	2.70×10^{-5}

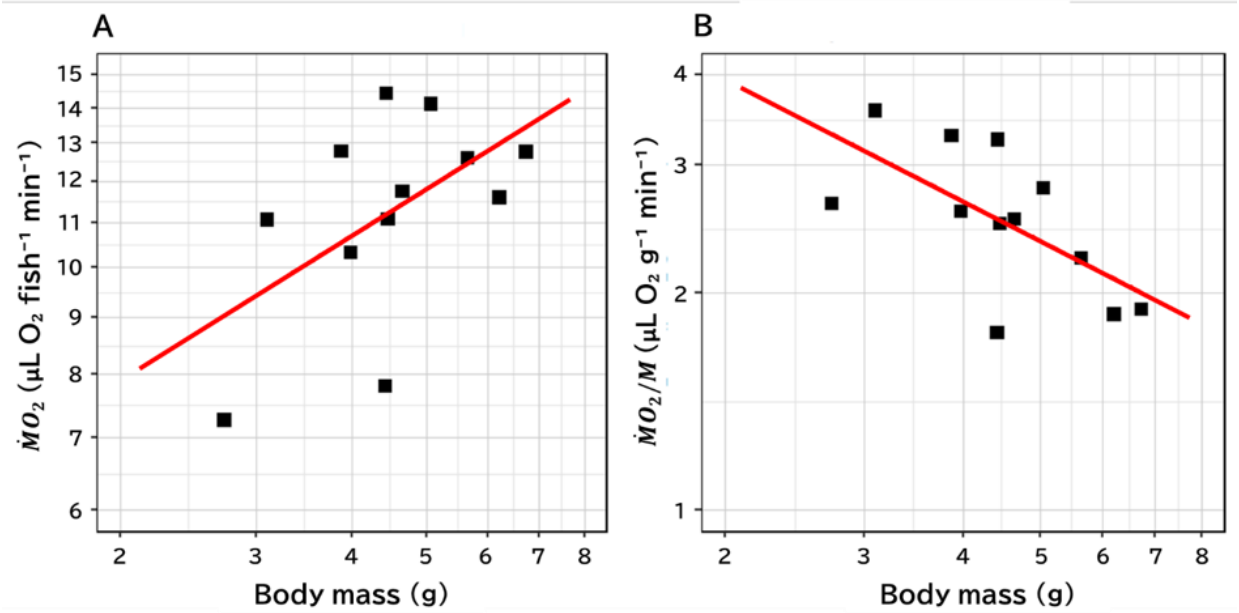

Figure 2. Metabolic scaling in wild adult white-spotted pygmy filefish. (A) The relationship between body mass and whole-animal metabolic rate ($\dot{M}O_2$). (B) The relationship between body mass and mass-specific metabolic rate ($\dot{M}O_2$/M). Each square represents an individual wild-caught adult fish (N = 12). Metabolic rate was measured at 20°C using a constant-flow respirometry system. Red lines indicate ordinary least-squares regressions fitted to $\log_{10}$-transformed data, corresponding to the allometric relationship $\dot{M}O_2 = aM^b$. The whole-animal metabolic rate ($\dot{M}O_2$) increased with body mass, whereas the mass-specific metabolic rate decreased with increasing body mass, indicating sublinear metabolic scaling across the examined adult size range.

factors beyond body size may contribute to metabolic heterogeneity.

Scaling relationships between body mass and metabolic traits: To quantify the contribution of body mass to metabolic variation, log–log regression analysis was conducted (Table 3, Fig. 2A, B). The whole-animal metabolic rate ($\dot{M}O_2$) scaled positively with body mass, with an estimated exponent of b = 0.440±0.215 (S.E.M., N = 12). Body mass explained 29.6% of the variance in $\dot{M}O_2$ (R^2 = 0.296) (Table 3, Fig. 2A). The exponent was significantly lower than unity (two-tailed Student's t-test, $P = 2.61\times10^{-2}$), rejecting isometric scaling and indicating a negative allometry (Table 3, Fig. 2A). Consistent with this result, the mass-specific metabolic rate ($\dot{M}O_2/M$) declined significantly with increasing body mass (b = –0.560±0.215; R^2 = 0.404; $P = 2.70\times10^{-5}$), reflecting the mathematical consequence of sublinear whole-animal scaling (Table 3, Fig. 2B).

Together, these analyses demonstrate that oxygen consumption increased with body size in the white-spotted pygmy filefish, but not in proportion, resulting in a systematic decline in mass-specific metabolism as body mass increased. Although body mass exerted a statistically significant influence on the metabolic rate, its explanatory power was moderate (R^2 = 0.296 for $\dot{M}O_2$; R^2 = 0.404 for $\dot{M}O_2/M$) (Table 3, Fig. 2A, B). Considerable dispersion remained among individuals within comparable size classes, indicating that metabolic variation was not fully captured by body size. Thus, while allometric scaling was detectable at the population level, substantial inter-individual variability persisted beyond the effect of mass.

Discussions

Body mass–metabolic rate relationships in wild adult fishes: Understanding how metabolic rate scales with body mass within natural populations remains a central challenge in ecological physiology. In the present study, the whole-animal metabolic rate ($\dot{M}O_2$) of the white-spotted pygmy filefish exhibited a positive scaling relationship with body mass, even across a relatively narrow adult size range. The estimated scaling exponent (b = 0.440 ± 0.215) was significantly lower than unity ($P = 2.61\times10^{-2}$), indicating negative allometry. Thus, although metabolic demand increased with increasing body mass, the increase was disproportionately slow relative to isometric expectations.

Body mass accounted for a measurable but moderate proportion of the observed metabolic variation (R^2 = 0.296). This magnitude of explanatory power indicates that while body size contributes to the structuring of metabolic variation, substantial inter-individual variability remains beyond the effect of mass alone. This residual dispersion is consistent with the multifactorial determinants of metabolic performance in wild fish.

Nevertheless, the detection of a significant mass-dependent scaling trend within a natural adult population provides quantitative evidence of intraspecific metabolic allometry under ecologically realistic conditions. The persistence of this pattern, despite limited variation in body size, suggests that body mass continues to exert a detectable influence on metabolic variability during the adult life stage. These findings provide empirically grounded data to ongoing discussions of metabolic scaling theory and establish a foundation for future studies that incorporate broader size ranges and larger sample sizes.

Body mass is widely recognized as a primary determinant of metabolic demand in fish; however, the strength and form of this relationship vary considerably among taxa, life stages, and environmental contexts (Killen et al., 2010). By focusing exclusively on wild individuals, the present study avoided potential confounding effects associated with long-term captive rearing and artificial selection, thereby providing insight into naturally surviving adult fish (Glazier et al., 2011). Moreover, the persistence of a size-dependent metabolic pattern after major ontogenetic transitions suggests that body size remains an influential variable throughout adulthood rather than a determinant restricted to early development (Norin and Gamperl, 2018; Glazier et al., 2020).

In parallel with the whole-animal metabolic rate

($\dot{M}O_2$), the mass-specific metabolic rate ($\dot{M}O_2/M$) declines significantly with increasing body mass, reflecting the mathematical consequence of sublinear whole-animal scaling. This negative scaling of mass-specific metabolism is consistent with the patterns documented across diverse fish taxa (Post and Lee, 1996; Clarke and Johnston, 1999; Nilsson and Östlund-Nilsson, 2008). Such declines have been attributed to disproportionate increases in metabolically inert tissues, reduced maintenance costs per unit mass, and scaling constraints in oxygen transport and delivery systems (Oikawa et al., 1992; Clarke and Johnston, 1999; Glazier, 2005, 2014; Harrison et al., 2022). The persistence of this relationship within a restricted adult size window is consistent with the continued operation of fundamental physiological scaling principles beyond early ontogeny.

Interpretation of the metabolic scaling exponent: The estimated metabolic scaling exponent for the whole-animal metabolic rate (b = 0.440±0.215) was significantly lower than unity, indicating negative allometry within this wild adult population. Although the point estimate lies below both the canonical 3/4-power scaling predicted by Kleiber's law (Kleiber, 1932) and the surface area-based 2/3 expectation, the relatively large standard error indicates limited statistical precision in resolving the differences among competing theoretical exponents. Accordingly, the present dataset does not permit definitive discrimination between these classical predictions. A growing consensus suggests that such theoretical exponents should not be treated as universal constants, particularly within species and across restricted body mass ranges (White et al., 2007; Marras et al., 2010; Norin and Malte 2012).

Rather than representing a meaningful departure from the metabolic theory, the comparatively shallow point estimate observed here likely reflects the biological and statistical constraints inherent to adult-stage intraspecific datasets. When body mass variation is limited to post-juvenile or adult stages, scaling slopes often become more variable and may appear reduced relative to broader ontogenetic analyses, as reported in multiple teleost species (Killen et al., 2010; Glazier, 2020). These findings are therefore consistent with a context-dependent view of metabolic scaling, in which scaling exponents emerge from interactions among body size, life stage, and ecological history rather than converging on a single invariant theoretical value.

Ecological significance of wild populations and intraspecific metabolic variation: Wild fish populations are generally expected to harbor greater genetic and phenotypic diversity than hatchery or aquaculture stocks because of ongoing natural selection, gene flow, and environmental heterogeneity (Chown et al., 2007; Glazier, 2009; Sieg et al., 2009; Killen et al., 2010). Such diversity can directly translate into broader variations in physiological traits, including metabolic rate. Comparative studies frequently report altered metabolic performance in captive-reared fish, likely resulting from relaxed selection pressures and homogenized rearing environments (Milot et al., 2013; Makiguchi et al., 2023; Masó et al., 2025).

In this context, focusing exclusively on wild individuals enables a more realistic assessment of metabolic traits under natural conditions. Consistent with this expectation, substantial inter-individual variation in metabolic rate was observed, despite the relatively restricted body mass distribution of the sampled adults. The whole-animal metabolic rate ($\dot{M}O_2$) ranged from 7.25 to 14.42, whereas the mass-specific metabolic rate ($\dot{M}O_2/M$) varied from 1.76 to 3.57, indicating pronounced metabolic heterogeneity even among individuals of comparable size. Such a magnitude of variation cannot be attributed solely to body mass differences and instead suggests meaningful physiological diversity within the population. Increasing evidence indicates that such intraspecific variation is biologically meaningful rather than stochastic noise, influencing behavior, growth, survival, and fitness (Burton et al., 2011; Metcalfe et al., 2016; Auer et al., 2018; Pang et al., 2021).

By explicitly incorporating wild individuals, this study not only provides ecologically relevant baseline

data that more accurately represent the metabolic characteristics of naturally persisting populations but also highlights the importance of natural metabolic diversity. Together, these findings reinforce the need to integrate individual-level variation into metabolic scaling theory, particularly when extending theoretical predictions to natural populations in the wild.

Conclusion

Using wild-caught white-spotted pygmy filefish, this study provides evidence for intraspecific metabolic scaling within a naturally structured adult population under ecologically realistic conditions. Whole-organism metabolic rate increased with body mass, whereas mass-specific metabolic rate declined, indicating that body size continues to structure metabolic organization even within a relatively narrow adult size range. Concurrently, substantial inter-individual variability highlights the physiological diversity inherent in natural populations. By focusing exclusively on wild-caught individuals, this study helps characterize metabolic scaling under natural physiological conditions, thereby minimizing potential influences associated with long-term captivity. The results support a context-dependent view of metabolic scaling, in which scaling patterns emerge from the interaction of body size, life history, and ecological experience rather than converging on a universal constant. Extending this framework across broader geographic, ontogenetic, and environmental gradients will be important for clarifying the interactions between intrinsic size-dependent processes and ecological variability. Integrating these dimensions will help move metabolic scaling theory beyond generalized patterns toward a mechanistic understanding of energy use in natural populations.

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