Size-invariant aerobic scope across ontogeny in a giant deep-sea scavenger

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Abstract

Aerobic scope defines the energetic margin available for activity beyond maintenance and plays a central role in ecological performance. In many organisms, increasing body size or environmental stress can reduce this margin, a pattern often described as having "little left in the tank". However, species that rely on episodic but intense activity may require sufficient aerobic capacity from early life stages onward, particularly when individuals are relatively large at hatching or birth. Here, we examined the ontogenetic scaling of resting metabolic rate (RMR) and active metabolic rate (AMR) in the giant deep-sea scavenger *Bathynomus doederleini* across a broad size range (1.7-48.4 g) using intermittent-flow respirometry at 10 °C. RMR and AMR increased with body mass and exhibited nearly identical scaling exponents, resulting in a size-invariant factorial aerobic scope (median = 2.83). This pattern suggests that aerobic capacity is established early and maintained proportionally with maintenance costs, supporting locomotion and scavenging throughout ontogeny in an energy-limited environment.

Key words: aerobic scope; metabolic scaling; deep sea; scavenger; crustacean

Introduction

Aerobic scope represents the metabolic capacity available for activity beyond maintenance and provides a key link between physiological performance and ecological function (Fry, 1971; Claireaux and Lefrançois, 2007). Across taxa, both resting and maximal aerobic metabolic rates increase with body mass, yet the relative scaling of these components varies substantially among species and contexts (Brett, 1965; Clark et al., 2013; Glazier, 2010). When activity-related metabolism scales more steeply than maintenance metabolism, absolute aerobic scope (the difference between maximal and resting rates) increases disproportionately with size, implying that larger individuals possess greater absolute capacity for aerobic activity (Glazier, 2005, 2009). However, this pattern is not universal and cannot be assumed a priori.

A central question is therefore how aerobic capacity is organized across ontogeny. Growth alters body size, locomotor demands, and ecological roles, and the scaling of resting and activity-related metabolism can follow at least two contrasting ontogenetic outcomes. First, active metabolic rate may increase more steeply than resting metabolic rate, yielding size-dependent changes in aerobic scope. Alternatively, resting and activity-related metabolism may scale proportionally across body sizes, resulting in size-invariant aerobic scope. These alternative outcomes can lead to similar absolute capacities at a given size range but fundamentally different constraints on performance and energy allocation. Determining which outcome applies, and under what ecological conditions, remains an unresolved issue in comparative physiology.

Deep-sea scavengers provide a particularly relevant system for examining these ideas. They experience chronic food limitation and often alternate between prolonged inactivity and brief episodes of intense locomotion associated with the exploitation of unpredictable food falls (Dayton and Hessler, 1972; Smith et al., 2018). Under such conditions, selection may favor metabolic organization that preserves sufficient aerobic capacity for essential locomotor events while minimizing energetic costs associated with maintaining excess unused capacity (Seibel and Drazen, 2007). The giant deep-sea isopod Bathynomus doederleini exemplifies this lifestyle: it hatches at a relatively large size and rapidly aggregates at carrion sources, yet can tolerate extended fasting.

Here, we quantify the ontogenetic scaling of resting and activity-related aerobic metabolism in B. doederleini across a broad body-mass range. We estimate resting metabolic rate from the lowest stable oxygen consumption observed under standardized conditions and estimate peak post-exercise oxygen consumption as an ecologically relevant measure of activity-related aerobic metabolism. Using these measures, we test whether resting and activity-related metabolism scale proportionally across ontogeny, which would predict size-invariant factorial aerobic scope, or whether scaling exponents diverge, which would predict size dependence in aerobic scope. By placing ontogenetic metabolic scaling in an explicit life-history context, we aim to refine understanding of how aerobic capacity is maintained in energy-limited deep-sea environments.

Materials and Methods

Animals and collection

Giant deep-sea isopods (*Bathynomus doederleini*) were collected between April 2024 and August 2025 from depths of 201–764 m off the Goto Islands, Japan. Sampling was conducted during research cruises of the training vessel Kakuyo-maru (Nagasaki University) using baited traps deployed on the seafloor. This method effectively captures actively foraging individuals of this species, which exhibits prolonged fasting tolerance and rapid locomotor responses to food-related stimuli (Anzai et al., 2025).

After recovery, individuals were transferred into chilled seawater (10 °C) and transported to the laboratory in insulated containers. Isopods were maintained in filtered seawater at 10 °C under continuous darkness. To standardize physiological condition

and eliminate the effects of specific dynamic action, all individuals were fasted for four weeks prior to metabolic measurements, a duration well within the normal physiological tolerance of this species (Tanaka et al., 2023; Anzai et al., 2025). A total of 29 individuals spanning a wide ontogenetic size range (body mass 1.7–48.4 g) were used.

All experimental procedures were approved by the Animal Experiment Committee of the Faculty of Fisheries, Nagasaki University (approval no. NF-0095).

Respirometry and metabolic measurements

Oxygen consumption rates were measured using intermittent-flow respirometry following established guidelines for aquatic ectotherms (Killen et al., 2021). Individuals were placed in acrylic respirometry chambers matched to body size and allowed to acclimate for 7–12 h prior to measurements. Dissolved oxygen concentration was recorded at 30 s intervals using optical oxygen sensors (WTW, Germany) at a constant temperature of 10.0 ± 0.2 °C.

Resting metabolic rate (RMR) was estimated during resting measurement cycles and defined as the lowest oxygen consumption rate recorded for each individual, using only measurement intervals with a coefficient of determination (R^2) ≥ 0.90. Background microbial respiration was quantified in empty chambers and subtracted from all measurements.

To elicit maximal activity, individuals were removed from the chamber and subjected to 5 min of forced swimming at the same temperature, a protocol commonly used to induce high aerobic metabolic rates in crustaceans (Ern et al., 2015). Immediately following exercise, individuals were returned to the chamber, and oxygen consumption was recorded continuously. Active metabolic rate (AMR) was defined as the highest oxygen consumption rate measured during the first valid post-exercise interval. We interpret AMR as an ecologically relevant maximum metabolic rate rather than an absolute physiological maximum.

Data analysis

Relationships between metabolic rate and body mass were analyzed using allometric models of the form $\dot{M}O_2 = aM^b$ after $\log_{10}$ transformation. Differences between RMR and AMR scaling relationships were tested using analysis of covariance (ANCOVA), with metabolic state as a factor and body mass as a covariate. When interaction terms were non-significant, common-slope models were fitted. Factorial aerobic scope (FAS) was calculated as the ratio of AMR to RMR for each individual and regressed against body mass to test for size dependence. All statistical analyses were conducted in R (version 4.4.2), with significance assessed at $\alpha = 0.05$. Individual-level data for body mass, standard metabolic rate, active metabolic rate, and factorial aerobic scope are provided in Supplementary Table S1.

Results and Discussion

Resting metabolic rate (RMR) and post-exercise peak oxygen consumption (hereafter AMR) both increased significantly with body mass in Bathynomus doederleini (Fig. 1). On log–log scales, the scaling exponent did not differ between metabolic states (ANCOVA interaction, $p = 0.83$), yielding a common exponent of 0.77. Intercepts differed significantly, with AMR exceeding RMR by approximately 3.3-fold across the size range examined. Together, these results indicate proportional ontogenetic scaling of maintenance and activity-related aerobic metabolism in this species.

As a consequence of this proportional scaling, factorial aerobic scope (FAS = AMR/RMR) showed no significant relationship with body mass ($R^2 = 0.002$, $p = 0.81$; Fig. 2). Median FAS was 2.83 (interquartile range: 1.47–5.96), indicating that individuals maintained a broadly consistent aerobic margin across nearly two orders of magnitude in body mass, despite substantial inter-individual variation. Importantly, the absence of a size trend in FAS implies that individual differences in aerobic capacity did not translate into systematic ontogenetic change over the size range examined.

This pattern provides insight into how aerobic capacity may be organized across growth in deep-sea scavengers. In many organisms, aerobic margins can erode with increasing size or under environmental stress, potentially constraining performance (Norin and Metcalfe, 2019). In contrast, B. doederleini maintained proportional scaling between RMR and AMR, preserving a relatively constant aerobic margin across ontogeny. Such organization is consistent with a lifestyle in which individuals require a baseline level of aerobic capacity for episodic but essential locomotor events—such as rapid approach to carrion falls—while living in a chronically food-limited environment (Dayton and Hessler, 1972; Seibel and Drazen, 2007; Smith et al., 2018). Under these conditions, maintaining an aerobic margin that scales in parallel with maintenance costs may provide sufficient capacity for necessary activity without incurring disproportionate energetic costs of large unused aerobic reserves.

Several considerations support the robustness of this inference. First, proportional scaling was evident in both the exponent similarity and the relatively stable AMR:RMR ratio across sizes. Second, while AMR here was estimated using forced swimming and therefore represents a peak post-exercise aerobic metabolic rate rather than a verified absolute maximum, this approach is widely used to capture ecologically relevant upper aerobic performance in aquatic ectotherms (Ern et al., 2015; Killen et al., 2021). Our goal was not to define a strict physiological maximum but to compare how activity-related oxygen demand scales relative to maintenance across ontogeny under standardized stimulation. The consistent scaling relationships across individuals and the lack of a size trend in FAS argue against a simple methodological artifact such as systematically weaker exercise induction in certain size classes.

At the same time, we avoid interpreting size-invariant FAS as evidence that aerobic capacity is never limiting in this species. Rather, our results suggest that ontogenetic increases in body size do not, by themselves, progressively reduce aerobic margins under the conditions measured. Future work can extend this framework by testing whether proportional scaling persists across environmental gradients relevant to the deep sea (e.g. temperature, oxygen availability) and across behavioral contexts that more closely mimic natural bursts of locomotion and recovery dynamics. Such tests would help determine whether the observed metabolic organization is a general feature of deep-sea scavenging strategies or depends on specific ecological circumstances and physiological states.

Together, these findings demonstrate that aerobic scope can remain invariant across ontogeny in a large-bodied deep-sea scavenger

and emphasize that size alone is insufficient to predict ontogenetic constraints on aerobic performance. Incorporating life-history strategy and ecological context is therefore essential for interpreting metabolic scaling and its consequences for performance limitation in extreme environments (Seibel and Drazen, 2007; Farrell, 2016).

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Competing Interests

The authors have no competing interests to declare.

Ethics Approval

The research required no permit approvals.

Author Contributions

MY Conceptualization, Methodology, Investigation, Writing – original draft, Supervision, Funding acquisition, Visualization. SA Investigation, Writing – original draft, Visualization, Funding acquisition.

Supporting Information

Additional supporting information can be found online in the Supporting Information.

Data Availability

Data has been provided as Supplementary Material.

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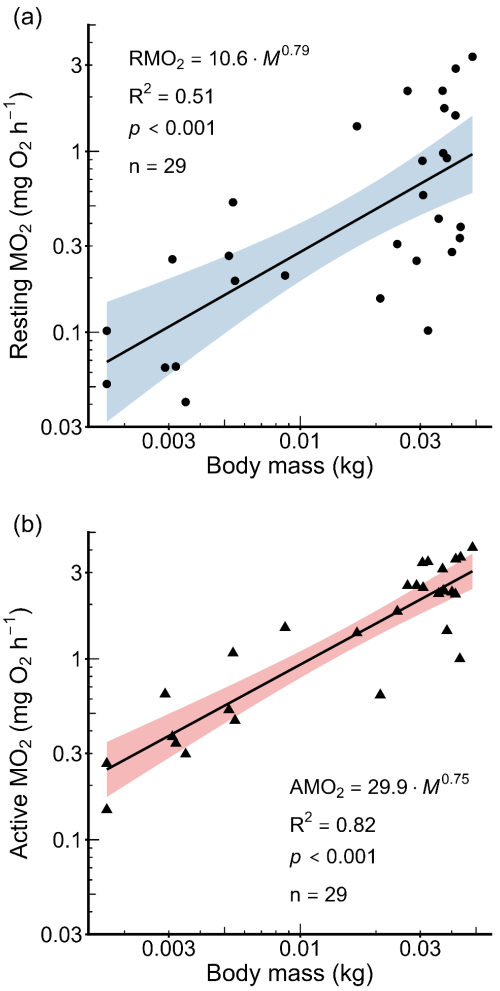

Fig. 1 Allometric relationships between body mass and oxygen consumption rate in the giant deep-sea isopod. (a) Resting metabolic rate and (b) active metabolic rate. Solid black lines indicate fitted regression lines, and shaded areas represent 95% confidence intervals. The scaling exponent was 0.79 under resting conditions (95% CI: 0.48–1.10) and 0.75 under active conditions (95% CI: 0.61–0.90), indicating significant positive relationships between body mass and oxygen consumption rate in both conditions.

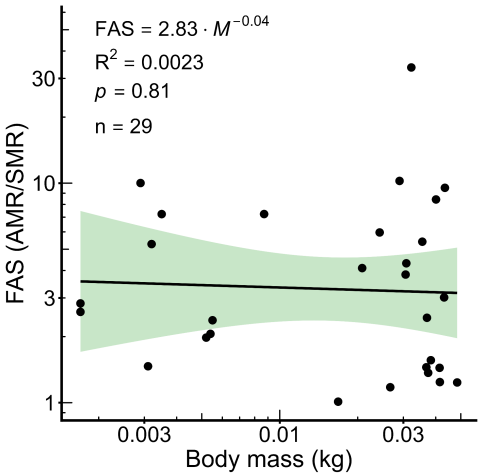

Fig. 2 Relationship between body mass and factorial aerobic scope in the giant deep-sea isopod. Factorial aerobic scope (FAS), calculated as the ratio of active to resting metabolic rate, showed no significant relationship with body mass (R^2 = 0.002, P = 0.81). The median FAS was 2.83, with substantial inter-individual variability, indicating that aerobic scope remained invariant across nearly two orders of magnitude in body mass.