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 energetic margin available for activity beyond maintenance and is a key link between physiological capacity and ecological performance (Claireaux and Lefrançois, 2007; Farrell, 2016). In many organisms, increases in body size or environmental stress are associated with reduced aerobic margins, a pattern often conceptualized as having "little left in the tank" (Killen et al., 2016). This framework has been particularly influential in studies examining how metabolic constraints shape performance under challenging environmental conditions.

However, this perspective does not imply that all large-bodied organisms inevitably experience progressive metabolic limitation. Life-history traits can strongly influence how aerobic capacity is organized across ontogeny. In species that depend on episodic but intense activity, selection may favor the early establishment of sufficient aerobic capacity to meet locomotor and foraging demands, rather than maximizing excess capacity later in life (Norin and Metcalfe, 2019). Such strategies may be especially relevant in energy-limited environments, where maintaining unused metabolic capacity could incur unnecessary energetic costs (Seibel and Drazen, 2007).

Deep-sea scavengers provide a compelling system in which to examine these ideas. These organisms typically experience prolonged periods of inactivity punctuated by brief, high-intensity locomotor events associated with the exploitation of unpredictable food falls (Dayton and Hessler, 1972; Smith et al., 2018). The giant isopod *Bathynomus doederleini*, which hatches at a relatively large size and exhibits rapid aggregation at carrion sources, exemplifies this lifestyle. Here, we test whether aerobic scope declines with body size in *B. doederleini* by quantifying the ontogenetic scaling of resting and active metabolic rates across a broad size range.

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 active metabolic rate (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. Similar proportional scaling of maintenance and activity-related metabolism has been reported in other aquatic ectotherms under conditions where locomotor performance must be maintained across body sizes (Claireaux and Lefrançois, 2007; Farrell, 2016). Intercepts differed significantly, with AMR exceeding SMR by approximately 3.3-fold across the entire size range examined, indicating a consistent capacity for activity relative to maintenance demands.

As a consequence of this proportional scaling, factorial aerobic scope (FAS) 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), demonstrating that individuals maintained a consistent aerobic margin across nearly two orders of magnitude in body mass. Although factorial aerobic scope exhibited substantial inter-individual variability, no systematic relationship with body mass was detected, indicating that individual variation did not translate into a size-dependent trend. Size-invariant aerobic scope has been observed in some taxa where aerobic capacity is tightly linked to essential behaviors rather than excess performance (Norin and Metcalfe, 2019).

This pattern has important implications for understanding how aerobic capacity is organized across ontogeny in deep-sea scavengers. In many organisms, increases in body size or environmental stress can erode aerobic margins, potentially leading to a state described as having "little left in the tank" (Killen et al., 2016). However, our results indicate that *B. doederleini* does not experience progressive erosion of aerobic scope with growth. Instead, aerobic capacity appears to be established early and scaled in parallel with maintenance costs, maintaining the metabolic margin required for locomotion and scavenging throughout ontogeny.

Such an arrangement is consistent with the life-history characteristics of this species and of deep-sea scavengers more generally. These organisms typically experience prolonged periods of inactivity punctuated by brief, high-intensity locomotor events associated with the exploitation of unpredictable food falls (Dayton and Hessler, 1972; Smith et al., 2018). In this ecological context, selection may favor the early acquisition of sufficient aerobic capacity to meet minimum activity requirements, rather than the maintenance of large unused aerobic reserves, which would be energetically costly in chronically food-limited environments (Seibel and Drazen, 2007).

Importantly, this interpretation does not contradict the conceptual framework underlying "little left in the tank" (Killen et al., 2016). Rather, it suggests that the extent to which aerobic margins are reduced with increasing size depends on life-history strategy and ecological context. In species where activity demands increase disproportionately with size or environmental stress, aerobic scope may indeed become limiting (Norin and Metcalfe, 2019). In contrast, species such as *B. doederleini* that hatch at relatively large sizes and require a baseline level of locomotor capacity from early life stages may maintain proportional scaling of maintenance and maximal metabolism, preserving aerobic scope across growth.

Although AMR in this study was estimated using forced swimming and thus represents an ecologically relevant maximum rather than an absolute physiological maximum, this approach is appropriate for evaluating relative aerobic capacity associated with locomotion and scavenging, as commonly applied in studies of aquatic ectotherms (Ern et al., 2015; Killen et al., 2021). The consistent scaling relationships observed across individuals further suggest that methodological constraints are unlikely to explain the absence of size dependence in aerobic scope.

Together, these findings demonstrate that aerobic scope can remain invariant across ontogeny in a large-bodied deep-sea scavenger and emphasize the importance of considering life-history strategy when evaluating size-related metabolic constraints. Extreme environments such as the deep sea therefore provide valuable systems for refining general models of metabolic organization and performance limitation (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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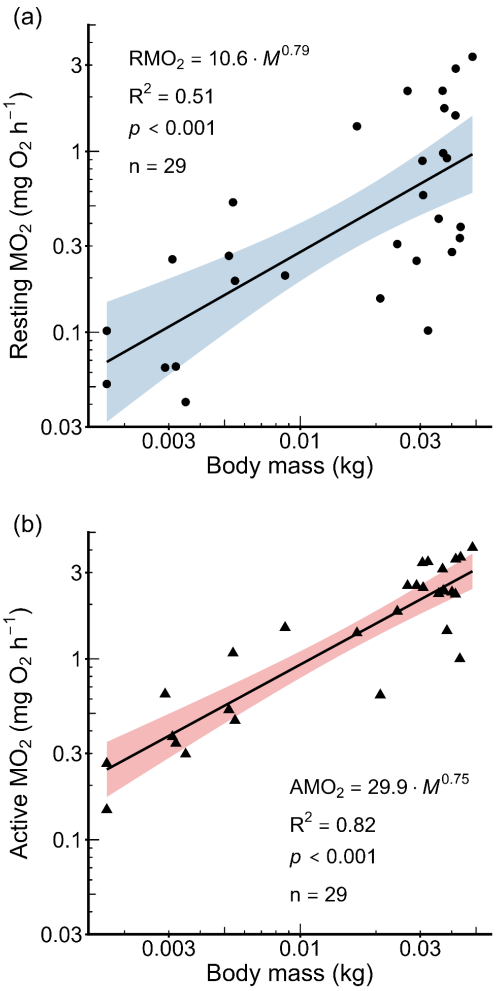

Fig. 1 Allometric relationships between body mass and oxygen consumption rate in the giant deep-sea isopod. (a) Resting metabolic rate and (b) active metabolic rate. Solid black lines indicate fitted regression lines, and shaded areas represent 95% confidence intervals. The scaling exponent was 0.79 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.

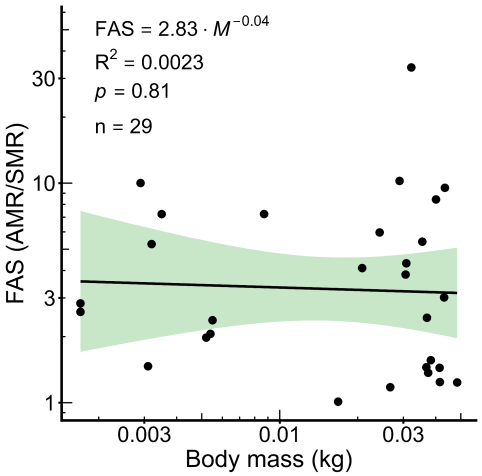

Fig. 2 Relationship between body mass and factorial aerobic scope in the giant deep-sea isopod. Factorial aerobic scope (FAS), calculated as the ratio of active to resting metabolic rate, showed no significant relationship with body mass (R^2 = 0.002, P = 0.81). The median FAS was 2.83, with substantial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