1 **Metabolic responses to food and temperature in deep-sea isopods, *Bathynomus doederleini***

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17 **ABSTRACT**

18 Metabolic rate, the energy required per unit of time for an organism to sustain life, is influenced by

19 both intrinsic and extrinsic factors. Despite the similarities among living organisms across the various

20 domains of life, it has been observed that those adapted to deep-sea environments exhibit notable

21 distinctions from those in shallower waters, even when accounting for size and temperature. However,

22 as deep-sea organisms are infrequently kept in captivity for prolonged periods, investigations into their

23 potential metabolic responses to food and temperature have yet to be conducted. In this study, we

24 demonstrate the impact of food (specific dynamic action: *SDA*) and temperature (Q_{10}) on the metabolic

25 rate of the deep-sea isopod *Bathynomus doederleini*. Positive correlations were found between *SDA*

26 parameters (peak, time to peak, duration, and factorial scope) and meal size in deep-sea organisms.

27 The postprandial metabolic rate, at a meal size of 45.4%, increased by approximately 6.5-fold, and the

28 duration was 20 days. Within the temperature range of their natural habitat, the overall Q_{10} was 2.36,

29 indicating that a 10 ºC increase would lead to a 2.4-fold increase in resting metabolic rate. The mean

30 metabolic rate of this species, corrected for the equivalent temperature, was significantly 63% lower

31 than the metabolic scaling rule for aquatic invertebrates. This low metabolic rate suggests that deep-

32 sea isopods can survive for a year on a mere few grams of whale blubber at a water temperature of

33 10.5 ºC. This information is crucial for understanding the metabolic strategies and consequences of

34 adaptation to a deep-sea environment.

35

36 *Keywords*: Oxygen consumption, Metabolic scaling, Q_{10}, Metabolism, Specific Dynamic Action, *SDA*

37

1. Introduction

39

40   Aerobic organisms sustain themselves by utilizing oxygen to metabolize nutrients in their bodies

41   and generate energy. The metabolic rate, which is the energy expenditure per unit time required for an

42   organism to survive, is often referred to as the "fire of life." Energy metabolism is largely constrained

43   by physical and kinetic factors, such as body size and temperature (Peters, 1983; Calder, 1984;

44   Schmidt-Nielsen, 1984; Blaxter, 1989; Brown and West, 2000; Glazier, 2005). The rate of increase in

45   metabolic rate for a 10 °C increase in temperature is known as the Q_{10} (Schmidt-Nielsen, 1997). It has

46   been posited that metabolic rate may also be influenced by factors such as an organism's activity level

47   (Biro and Stamps, 2010), ontogenetic stage (Yagi et al., 2010; Yagi and Oikawa, 2014), taxonomic

48   and phylogenetic status (Hayssen and Lacy, 1985), geographic range and distribution patterns

49   (Lovegrove, 2000), habitat temperature conditions (MacMillen and Garland, 1989), and the

50   availability and preferences of resources (McNab, 1986).

51   The correlation between resting metabolic rate and body size after adjusting for temperature,

52   known as metabolic scaling, has been the subject of extensive research for a considerable period. In

53   his seminal work, Hemmingsen (1960) established that the following allometric equation could

54   adequately express the relationship between metabolic rate and body size across various taxa:

55

56     $$M_R = a_i B^b \ (i = 1\text{-}3)$$

57

58   where MR represents resting metabolic rate, B denotes body mass, a represents a scaling constant and

59   b signifies the scaling exponent. The value of i denotes the three different animal groups (homeotherms,

60   heterotherms and unicellular organisms), which exhibit distinct values for the scaling constant

61   (intercepts). Despite ongoing debate regarding the scaling exponent (Kozłowski and Konarzewski,

62   2004; O'Connor et al., 2007; Harrison, 2017; Glazier, 2022), it has been established that each of these

63   animal groups displays a consistent trend (Makarieva et al., 2008).

64   Is the "fire of life" less ardent in deep-sea organisms? The deep sea environment is characterized

65   by decreasing temperatures and increasing pressures with increasing water depth, as well as being

66   oligotrophic and having a significantly reduced light intensity (Merrett and Haedrich, 1997). Some

67   deep-sea organisms that have adapted to such conditions exhibit lower metabolic rates than their

68   shallow-water counterparts, even after accounting for temperature and body size adjustments (Seibel

69   and Drazen, 2007). The "visual-interaction hypothesis" has been proposed to explain this phenomenon

70   (Childress and Mickel, 1985; Seibel and Drazen, 2007). This hypothesis posits that visually mediated

71   predation and prey behaviour diminish with increasing depth (reduced light), rendering active

72   swimming redundant in deeper and darker environments. As a result, metabolic activity has evolved

73   to decrease with depth in visually developed organisms (Seibel and Drazen, 2007). This trend has been
74   observed in cephalopods, crustaceans with well-developed vision, and teleost fish (Sullivan and
75   Somero, 1980; Seibel et al., 1997; Seibel and Drazen, 2007).

76   Even among deep-sea organisms, metabolic reductions may not have evolved in the deep-sea
77   isopod *Bathynomus doederleini*. This species, which possesses an adult size of approximately 100 mm,
78   is primarily found in the Pacific Ocean, ranging from Japan to the Philippines at depths of 200 - 600m
79   (Sekiguchi et al., 1981). Deep-sea isopods are considered benthic scavengers and typically burrow in
80   the seafloor to evade predation (Matui et al., 2011). The "visual-interaction hypothesis" suggests that
81   animals with poor visual acuity and those inhabiting the benthos do not exhibit metabolic reductions
82   with increasing depth (Seibel and Drazen, 2007). Indeed, it has been reported that metabolic rate does
83   not decrease with increasing depth in benthic crustaceans, octopods, chaetognaths, medusa, and worms,
84   whose behaviour is not as reliant on vision (Thuesen and Childress, 1993a; Thuesen and Childress,
85   1993b; Seibel and Childress, 2000; Seibel and Drazen, 2007). However, to the best of our knowledge,
86   there are no reported metabolic rates for this deep-sea species.

87   Determining the metabolic rate of deep-sea organisms in response to environmental changes
88   presents a formidable challenge, as sudden fluctuations in water pressure can prove fatal during the
89   process of capturing and raising them to the surface. Despite the existence of reports of *in vitro* enzyme
90   activity (Childress and Somero, 1979) and measurements under high-pressure conditions (Mickel and
91   Childress, 1982) pertaining to deep-sea metabolism, the response of these organisms to varying
92   environmental conditions remains inadequately understood. Conversely, some studies have conducted
93   *in situ* measurements of metabolism in deep-sea environments, yielding intriguing insights (e.g. Bailey
94   et al., 2002). However, metabolic rates that take into account the effects of specific dynamic actions
95   (*SDA*) have yet to be determined, as the feeding state of the individuals being measured cannot be
96   controlled. *SDA* refers to the increase in metabolic rate following feeding (McCue, 2006). In order to
97   exclude the effects of *SDA*, resting metabolic rate should be measured when individuals are fasting
98   (Kleiber, 1932; Wang et al., 2006; Secor 2009). Notably, no studies on *SDA* in deep-sea organisms
99   have been conducted to date.

100 Deep-sea isopods possess a durable exoskeleton and lack a swim bladder, rendering them tolerant
101 to fluctuations in water pressure, indicating their ability to persevere for extended intervals under
102 ambient pressure, thus facilitating thorough measurements to be conducted under varying conditions.
103 The overarching objectives of the current study were to investigate: (i) the impact of food intake (*SDA*)
104 and (ii) the effect of water temperature (Q_{10}) on the metabolic rate of the deep-sea isopod. This
105 knowledge is crucial for comprehending the physiology of deep-sea organisms, specifically metabolic
106 strategies pertaining to adaptation to the deep-sea milieu, and ecological and evolutionary
107 bioenergetics.

108

2. Materials and methods

2.1. Ethics statement

All experiments were performed in conformity with Japanese Animal Care protocols and received approval from the Nagasaki University Fish and Invertebrate Experimental Ethics Committee (Ethics Approval No. NF-0069).

2.2. Animals

Deep-sea isopods were obtained through the efforts of local fishermen utilizing bait traps in Suruga Bay and off the coast of Goto Island, Japan in 2021. A total of forty-six specimens (38 from Suruga Bay and 8 from Goto Island) were conveyed in refrigerated storage to the Fish and Ships Lab, Faculty of Fisheries at Nagasaki University. Upon arrival, they were promptly transferred to a 200 L black circular tank (diameter: 0.8 m) until the initiation of experiments. The rearing tank was equipped with aeration, a filtration system (Ehim 2260, Ehime, Germany), and cooled via a cooling chiller (AZ280X, Rei-Sea, Tokyo, Japan). The deep-sea isopods were provided with sustenance in the form of swordtip squid *Uroteuthis edulis* once every two weeks, with the exception of the experimental period. The rearing water was replaced by half every seven days. The rearing room was consistently shaded, and observations and experimental settings were conducted under red light. Temperature Data Loggers (model UTBi-001, Onset Computer Corporation, MA, U.S.A.) were submerged in both the rearing and experimental tanks. During the rearing period, the mean water temperature (± S.D.) was 12.1 ± 0.2 °C and salinity ranged from 33.1 - 34.3 PSU.

2.3. Respirometory

Oxygen consumption during resting status of animals was measured as a proxy of resting metabolic rate (Yagi et al., 2010). The technique of intermittent-flow respirometry as described by Mochnac et al. (2017) was employed to measure oxygen consumption. The respirometry unit, with a volume of approximately 80 L, consisted of a respiration chamber and a water bath, the temperature of which was regulated by means of a heater and cooler, and was filled with air-saturated seawater. The respiration chamber was cylindrical in shape (90 mm x 200 mm, 930 mL), fabricated from acrylic and stirred by a magnetic stirrer. Dissolved oxygen and salinity were measured using an optical multimeter (Multi3430, Weilheim, Germany). Measurements were taken at intervals of 50-85 minutes (with close and open times of 20-45 minutes and 30-40 minutes, respectively). The dissolved oxygen never dropped below 80%. In parallel, a blank control was conducted to calculate the background respiration

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145 (which never exceeded 3%). The respiration chamber was covered with a blackout curtain during

146 measurements.

147   MO_2 (expressed in units of mgO$_2$ L^{-1} min^{-1}) was computed by taking into account the decrease in

148 dissolved oxygen in both the experimental chamber and the blank (absent of animals) as follows:

149

150 $$MO_2 = (\Delta O_{exp} - \Delta O_{blank}) \times (\text{Vch - Vsp}) / \text{BW} \times 60 \times 1000$$

151

152 where ΔO_{exp} and ΔO_{blank} (mgO$_2$ L^{-1} min^{-1}) are the gradients of linear regression of dissolved oxygen

153 in the experimental and blank respirometry in relation to the duration of incubation. V_{ch} denotes the

154 volume of the respiration chamber (930 mL), and V_{sp} represents the volume of the specimen,

155 determined from its body weight. The density of the deep-sea isopods was found to be 1.225 g mL^{-1}

156 as determined by the volumetric method utilising Archimedes' principle.

157

158 *2.4. Effects of food (SDA)*

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160   To examine the effects of food on metabolic rate (*SDA*), pre- and post-feeding oxygen consumption

161 were assessed. The measurements were conducted at a temperature of 12.1 ± 0.3 ºC for a period of 24

162 hours prior to feeding using individuals that fasted for more than 28 days. The mean wet body weight

163 (± S.D.) and body length were 33.0 ± 4.6 g and 100.0 ± 3.8 mm (n = 14), respectively. The food item

164 utilized was swordtip squid. In order to achieve significant variation in feeding rate, the feeding time

165 ranged from 2 to 10 minutes, resulting in a proportion of 6.8 - 45.4% of the body weight. The weight

166 of the feed was computed by subtracting the weight of the food prior to and after feeding. The period

167 of measurements varied from 6 to 30 days depending on food intake. During the measurement period,

168 10 L of seawater in the respiratory tank was changed daily without altering the water temperature.

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170 *2.5. Effects of temperature (Q_{10})*

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172   To investigate the effects of temperature on metabolic rate (Q_{10}), oxygen consumption was

173 measured at four distinct temperatures (15, 12, 9 and 6 ºC) which are within the temperature range in

174 which the species is found in the natural habitat (Yagi et al., unpublished data). Five individuals were

175 randomly selected from the bloodstock tank and placed in three separate 30 L black circular tanks

176 (diameter: 0.4 m) that were independent of one another. Each tank was equipped with aeration, a

177 filtration system (Eheim Classic Filter 2213, Deizisau, Germany), and a cooler (Cool Way BK110,

178 Gex, Osaka, Japan). Ten L of seawater was exchanged every week without altering the temperature in

179 each tank. Prior to the metabolic rate measurements, the individuals were acclimatized for a minimum

180 of 14 days at each temperature. The measurements were carried out in descending order from high (15

181   ºC) to low (6 ºC) temperatures, with the temperatures being decreased to 1 ºC per day. During each

182   acclimation period, the mean water temperature (± S.D.) was 15.3 ± 0.2 ºC, 12.2 ± 0.2 ºC, 9.2 ± 0.2

183   ºC, 6.2 ± 0.2 ºC. The aforementioned experiment was repeated twice in different populations.

184   Measurements were performed on a total of 25 individuals at temperatures of 15 ºC (n = 8), 12 ºC

185   (n = 10), 9 ºC (n = 8), and 6 ºC (n = 9). The mean wet body weight (± S.D.) and body length (± S.D.)

186   were 34.0 ± 2.9 g and 102.7 ± 5.6 mm (n = 25), respectively. Individuals underwent a fast of at least

187   14 days prior to the measurement. Prior to the measurements, individuals were acclimated to the

188   respiration chamber overnight and oxygen consumption was measured three times in each individual.

189

190   *2.5. Data analysis*

191

192   The variables commonly employed to quantify *SDA* - were calculated according to Secor (2009)

193   and Feher (2017), utilizing the following model equations:

194

195    $$MO_2 = M_R + F \times T \times exp^{-T/P}$$

196

197   Where MO_2 (mgO$_2$ kg^{-1} h^{-1}) represents metabolic rate, M_R denotes the resting MO_2 averaged over the

198   6 hours preceding feeding, F represents meal size (the proportion (%) of food intake (g) divided by

199   the individual body weight (g)), T (h) denotes the time elapsed since feeding, and P (h) represents the

200   time until peak. Thus, the maximum of the curve occurs at $T = P$ at an increment of $F\ T\ exp^{-1}$ (Feher,

201   2017). MO_2 data between 05:00 AM and 17:00 PM were analyzed in accordance with Roe (2004).

202   Subsequently, the four parameters were determined (Fig. 1), i.e., (i) peak; postprandial peak in

203   metabolic rate, (ii) time to peak; duration from time of feeding to peak metabolic rate, (iii) duration;

204   time from feeding when metabolic rate achieves a 5% increase in resting metabolic rate, (iv) factorial

205   scope; postprandial peak divided by resting metabolic rate. Linear relationships between *SDA*

206   parameters and meal size were analyzed by Pearson's correlation coefficient test.

207   An exponential curve was fitted to the effects of temperature on metabolic rate, with metabolic rate

208   as the dependent variable and temperature as the independent variable. Q_{10} was calculated by utilizing

209   the following equation:

210

211    $$Q_{10} = (M_{R2} / M_{R1})^{10 / (Temp_2 - Temp_1)}$$

212

213   where M_{R1} and M_{R2} are the known metabolic rates (mgO$_2$ kg^{-1} h^{-1}) at their respective temperatures,

214    $Temp_1$ and $Temp_2$ (°C) (Schmidt-Nielsen, 1997).

215   To verify the normality and homogeneity of the dataset for the application of parametric analysis,
216   Shapiro-Wilk and Bartlett tests were conducted. All statistical analyses were performed using R
217   (Version 4.2.2).

218

3. Results

219

220

221   3.1 *Effects of food (SDA)*

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223   Postprandial metabolic rates of deep-sea isopods increased (Fig. 1). Mean resting metabolic rate
224   (M_R ± S.D.) was $9.5 ± 5.6$ mgO_2 kg^{-1} h^{-1}, ranging from 3.9 to 21.6 mgO_2 kg^{-1} h^{-1} (n = 14).
225   All *SDA* parameters displayed a dependency on meal size, with statistical significance (peak; t =
226   4.39, p < 0.001, time to peak; t = 2.19, p = 0.049, duration; t = 2.53, p = 0.026, factorial scope; t =
227   2.75, P = 0.018) (Fig. 2). Peak and time to peak ranged from 18.6 to 51.6 (Fig. 2a), and 0.5 to 5.6 (Fig.
228   2b), respectively. Duration and factorial scope ranged from 3.1 to 33.3 (Fig. 2c), and from 0.9 to 12.0
229   (Fig. 2d), respectively.

230

231   3.2. *Effects of temperature (Q_{10})*

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233   The resting metabolic rate significantly increased with increasing temperature (Fig. 3). The mean
234   resting metabolic rate (± S.D.) at each temperature was $20.2 ± 4.1$ (15 ºC, n = 8), $15.8 ± 4.9$ (12 ºC, n
235   = 10), $12.6 ± 5.5$ (9 ºC, n = 8) and $9.1 ± 2.9$ mgO_2 kg^{-1} h^{-1} (6 ºC, n = 9). The overall Q_{10} was 2.36, and
236   the one at each temperature range was 2.20 (15-12 ºC), 1.80 (12-9 ºC) and 3.30 (9-6 ºC).

237

4. Discussion

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239

240   This study quantified the responses of food and temperature on metabolic rate in deep-sea isopods
241   through long-term rearing and temperature acclimation experiments. To the best of our knowledge,
242   this is the first report of a positive correlation between *SDA* parameters (peak, time to peak, duration,
243   and factorial scope) and meal size in deep-sea organisms. The postprandial metabolic rate at a meal
244   size of 45.4% increased by approximately 6.5-fold and the duration was 20 days. Within the water
245   temperature range of the species' natural habitat, the overall Q_{10} was 2.36, indicating that a 10 ºC
246   increase would result in a 2.36-fold increase in resting metabolic rate.
247   Deep-sea organisms may possess *SDA* characteristics that reflect their feeding strategy of
248   consuming large quantities of food infrequently, due to the scarcity of resources in their deep-sea
249   habitat. The postprandial increase in metabolism, known as *SDA*, reflects the energy requirements
250   associated with digestion, including the transport, absorption, and storage of nutrients, as well as

251   increased synthesis of proteins and lipids (Secor, 2009). This study confirms that deep-sea isopods

252   also possess *SDA*, similar to shallow-water organisms. The duration of *SDA* increased with increasing

253   meal size (Chakrabborty et al.,1992; Janes and Chappell, 1995; Toledo et al., 2003), which is

254   consistent with the findings of this study. However, the calculated duration of this species was notably

255   long, reaching up to 33.3 days (Fig. 2). This may reflect the substantial difference in meal size (33.0%),

256   which is an order of magnitude greater than that of shallow-water organisms. A satiating meal typically

257   ranges between 2 - 4% of an organism's body weight (Elner, 1980; Robertson et al., 2002), and a 5%

258   meal size would be considered high for crustaceans (Curtis et al., 2010). For comparison, the American

259   crayfish *Procambarus clarkii* and the shallow-water crab *Hemigrapsus nudus*, which have similar

260   body sizes to the deep-sea isopod, have been reported to have maximum meal sizes of 0.5% and 3.0%,

261   respectively, with durations of 0.47 and 2.51 days (McGaw and Curtis, 2013). Furthermore, the deep-

262   sea isopods in this study consumed a meal size of 45.4% within 10 minutes, indicating a high feeding

263   rate. These adaptations allow deep-sea isopods to cope with the intense competition for patchy

264   resources by rapidly consuming as much food as possible to avoid predation or cannibalism (Barradas-

265   Ortiz et al., 2003; Smith and Baldwin, 1982).

266   Due to their well-developed digestive systems, deep-sea isopods may adopt an energetic strategy

267   of increasing the factorial scope for a single large meal size. In this study, it was observed that the

268   factorial scope of this species increased significantly with increasing meal size (Fig. 2d). Many

269   organisms, including isopods, have been found to have a factorial scope within the range of 1.5 - 3.0

270   (Secor, 2009). However, this deep-sea isopod species exhibited a maximum factorial scope of 12.1.

271   The presence of three pairs of hepatopancreatic glands in the oesophagus, which secrete digestive

272   enzymes, and the likely use of energy-requiring absorptive processes, facilitated by a well-developed

273   circulatory system (Kihara and Kuwasawa, 1984), likely contribute to the deep-sea isopod's ability to

274   consume large meals. However, this increased energy expenditure for *SDA* may also constrain

275   behavioural activity. Indeed, post-feeding individuals of many meal sizes were observed to be rounded

276   and static. McCue (2006) suggested that *SDA* scope can be compared to maximal metabolic scope to

277   estimate the residual capacity for activity during digestion. Interestingly, it is plausible that there exists

278   a trade-off relationship where more energy is allocated towards *SDA*, and behavioural activity is

279   constrained.

280   Although deep-sea isopods inhabit deep-oceanic environments, this species exhibits a degree of

281   adaptability to a relatively broad range of temperatures. The Q_{10} coefficient, which measures the

282   sensitivity of an organism's metabolic rate to temperature fluctuations, has been observed to increase

283   in value as temperatures approach their lethal limit (Christensen et al., 2021). The Q_{10} of deep-sea

284   isopods in this study was found to be 2.36 within the temperature range of 6 - 15 ºC, a value

285   comparable to that of many other organisms, typically falling within the range of 2 - 3 (Schmidt-

286   Nielsen, 1997). However, no significant deviation in Q_{10} value was observed at temperatures

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287　approaching the lethal limit, indicating that deep-sea isopods possess a high degree of adaptability to

288　these temperature ranges. Indeed, deep-sea isopods are primarily found at depths of 200 - 600 meters

289　(Sekiguchi et al., 1981). The water temperature immediately above the seafloor in the East China Sea,

290　where this species occurs, averages 13.8 ºC at a depth of 200 meters and 6.6 ºC at 600 meters (Yagi

291　et al., unpublished). This study provides further support for the adaptive nature of this species to the

292　coastal-bathyal environment, particularly in terms of thermo-metabolic physiology.

293　　　The fire of life in deep-sea isopods was faint. The visual interaction hypothesis posits that the

294　metabolic rate of swimming crustaceans and cephalopods significantly diminishes with increasing

295　depth of habitat, in contrast to a lack of decline in benthic crustaceans and polychaetes (Seibel and

296　Drazen, 2007). Given that this particular species is benthic, it is predicted that its metabolic rate should

297　not deviate from that of shallow-water animals, according to the hypothesis. However, the mean

298　metabolic rate of this species, adjusted for temperature (25 ºC), was significantly 63% lower than the

299　established metabolic scaling relationship for the aquatic invertebrate group (Makarieva et al., 2008)

300　(Fig. 4). Decreases in metabolic rate have also been documented in benthic carrideans and crustaceans

301　with increasing depth (Company and Sarda, 1998; Seibel and Drazen, 2007), in conformity with the

302　present study. At present, additional information on metabolic rate and lifestyle is necessary to validate

303　the hypothesis (Drazen and Seibel, 2007).

304　　　According to calculations based on the low metabolic rate of the deep-sea isopod, this species may

305　survive for a year on 2.1 grams of whale blubber at a temperature of approximately 10 ºC. Given the

306　species' remarkable meal size (Fig. 2), it can be estimated that it would subsist for 6.6 years on a single

307　diet, although the energy costs associated with foraging, growth, and reproduction would be an

308　additional factor in reality. Indeed, Ginn et al. (2014) reported that the closely related giant isopod *B.*

309　*giganteus* lived for five years in aquarium captivity, even after fasting. The deep-sea, low-metabolism

310　colosal squid *Mesonychoteuthis hamiltoni* (with a body weight of 500 kg) has been estimated to

311　consume only 30 grams of fish per day, regardless of its giant body size (Rosa et al., 2010).

312　Nonetheless, the mechanisms underlying low metabolic rates in deep-sea organisms, including this

313　species, remain poorly understood. It is suggested that mechanisms that preserve low metabolic rates

314　that do not conform to metabolic scaling may exist, and further research into the metabolism of deep-

315　sea organisms is crucial.

316

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325

326   **References**

327

328   Bailey, D.M., Jamieson, A.J., Bagley, P.M., Collins, M.A., Priede, I.G., 2002. Measurement of in situ

329   oxygen consumption of deep-sea fish using an autonomous lander vehicle. Deep Sea Res. Part

330   I: Oceanogr. Res. Pap. 49, 1519–1529. http://dx.doi.org/10.3723/175605404783101567.

331   Barradas-Ortiz, C., Briones-Fourzán, P., Lozano-Álvarez, E., 2003. Seasonal reproduction and

332   feeding ecology of giant isopods *Bathynomus giganteus* from the continental slope of the

333   Yucatán peninsula. Deep Sea Res. Part I: Oceanogr. Res. Pap. 50, 495–513.

334   https://doi.org/10.1016/S0967-0637(03)00036-0

335   Biro, P.A., Stamps, J.A., 2010. Do consistent individual differences in metabolic rate promote

336   consistent individual differences in behavior? Trends Ecol. Evol. 25, 653–659.

337   https://doi.org/10.1016/j.tree.2010.08.003

338   Blaxter, K., 1989. Energy Metabolism in Animals and Man. Cambridge University Press, Cambridge.

339   Brown, J.H., West, G.B., 2000. Scaling in Biology. Oxford University Press, Oxford.

340   Company, J.B., Sardà, F., 1998. Metabolic rates and energy content of deep-sea benthic decapod

341   crustaceans in the western Mediterranean Sea. Deep. Res. Part I: Oceanogr. Res. Pap. 45, 1861-

342   1880. https://doi.org/10.1016/S0967-0637(98)00034-X

343   Calder, W.A., 1984. Size, Function, and Life History. Harvard University Press, London.

344   Chakraborty, S.C., Ross, L.G., Ross, B., 1992. Specific dynamic action and feeding metabolism in

345   common carp, *Cyprinus carpio* L. Comp. Biochem. Physiol., Part A: Mol. Integr. Physiol. 103,

346   809–815. https://doi.org/10.1016/0300-9629(92)90185-S

347   Childress, J.J., Mickel, T.J., 1985. Metabolic rates of animals from the hydrothermal vents and other

348   deep-sea habitats. Biol. Soc. Wash. Bull. 6, 249–260.

349   Childress, J.J., Somero, G.N., 1979. Depth-related enzymic activities in muscle, brain and heart of

350   deep-living pelagic marine teleosts. Mar. Biol. 52, 273–283.

351   https://doi.org/10.1007/BF00398141

352   Christensen, E.A.F., Norin. T., Tabak, I., van Deurs, M., Behrens, J.W., 2021. Effects of temperature

353   on physiological performance and behavioral thermoregulation in an invasive fish, the round

354   goby. J. Exp. Biol. 224, jeb237699. https://doi.org/10.1242/jeb.237669

355   Curtis, D.L., Vanier, C.H., McGaw, I.J., 2010. The effects of starvation and acute low salinity

356   exposure on food intake in the Dungeness crab, *Cancer magister.* Mar. Biol. 157, 603–612.

357   https://doi.org/10.1007/s00227-009-1345-4

10

358 Drazen, J.C., Seibel, B.A., 2007. Depth-related trends in metabolism of benthic and benthopelagic
359　　　 deep-sea fishes. Limnol. Oceanogr. 52, 2306–2316. https://doi.org/10.4319/lo.2007.52.5.2306

360 Elner, R.W., 1980. The influence of temperature, sex and chela size in the foraging strategy of the
361　　　 shore crab, *Carcinus maenas* (L.). Mar. Behav. Physiol. 7, 15–24.
362　　　 https://doi.org/10.1080/10236248009386968

363 Feher, J., 2017. Energy Balance and Regulation of Food Intake, in: Feher, J. (Eds.), Quantitative
364　　　 Human Physiology (Second edition) An introduction. Department of Physiology and Biophysics.
365　　　 Virginia Commonwealth University School of Medicine, pp. 834-846.
366　　　 https://doi.org/10.1016/B978-0-12-800883-6.00082-3

367 Glazier, D.S., 2005. Beyond the "3/4-power law": Variation in the intra-and interspecific scaling of
368　　　 metabolic rate in animals. Biol. Rev. Camb. Philos. Soc. 80, 611–662.
369　　　 https://doi.org/10.1017/S1464793105006834

370 Glazier, D.S., 2022. Variable metabolic scaling breaks the law: from 'Newtonian' to 'Darwinian'
371　　　 approaches. Proc. R. Soc. B Biol. Sci. 289. https://doi.org/10.1098/rspb.2022.1605

372 Ginn, F., Beisel, U., Barua, M., 2014. Flourishing with awkward creatures: togetherness, vulnerability,
373　　　 killing. Environ Humanit. 4, 113–123. https://doi.org/10.1215/22011919-3614953

374 Harrison, J.F., 2017. Do Performance–Safety Tradeoffs Cause Hypometric Metabolic Scaling in
375　　　 Animals? Trends Ecol. Evol. 32, 653–664. https://doi.org/10.1016/j.tree.2017.05.008

376 Hayssen, V., Lacy, R.C., 1985. Basal metabolic rates in mammals: Taxonomic differences in the
377　　　 allometry of BMR and body mass. Comp. Biochem. Physiol. A 81, 741-754.
378　　　 https://doi.org/10.1016/0300-9629(85)90904-1

379 Hemmingsen, A.M., 1960. Energy metabolism as related to body size and respiratory surface, and its
380　　　 evolution.Rep. Steno. Mem. Hos. 13, 1-110.

381 Jobling, M., 1994. Fish bioenergetics. Chapman & Hall, London.

382 Janes, D.N., Chappell, M.A., 1995. The effect of ration size and body size on specific dynamic action
383　　　 in Adélie penguin chicks, *Pygoscelis adeliae*, Physiol. Zool. 68, 1029–1044.
384　　　 https://doi.org/10.1086/physzool.68.6.30163792

385 Kihara, A., Kuwasawa, K., 1984. Neural control of cardiac output to the arteries in *Bathynomus*
386　　　 *doederleini*. Zool. Sei. (Tokyo). 1, 874.

387 Kleiber, M., 1932. Body size and metabolism. Hilgardia. 6, 315-353.

388 Kozłowsk, J., Konarzewski, M., 2004. Is West, Brown and Enquist's model of allometric scaling
389　　　 mathematically correct and biologically relevant? Funct. Ecol. 18, 283–289.
390　　　 https://doi.org/10.1111/j.0269-8463.2004.00830.x

391 Lovegrove, B.G., 2000. The zoogeography of mammalian basal metabolic rate. Am. Nat. 156, 201-
392　　　 219. https://doi.org/10.1086/303383

393 MacMillen, R.E., Garland, T., 1989. Adaptive physiology. in: Layne, J., Kirkland, G. (Eds.), Advances
394   in the study of *Peromyscus* (Rodentia)Texas. Technical University Press, Lubbock, pp. 143-168.

395 Makarieva, A.M., Gorshkov, V.G., Li, B.-L., Chown, S.L., Reich, P.B., Gavrilov, V.M., 2008. Mean
396   mass-specific metabolic rates are strikingly similar across life's major domains: Evidence for
397   life's metabolic optimum. Proc. Natl. Acad. Sci. 105, 16994–16999.
398   https://doi.org/10.1073/pnas.0802148105

399 Matsui, T., Moriyama, T., Kato, R., 2011. Burrow plasticity in the deep-sea isopod *Bathynomus*
400   *doederleini* (Crustacea: Isopoda: Cirolanidae). Zoolog. Sci. 28, 863–868.
401   https://doi.org/10.2108/zsj.28.863

402 McCue, M.D., 2006. Specific dynamic action: A century of investigation. Comp. Biochem. Physiol.,
403   Part A: Mol. Integr. Physiol. 144, 381–394. https://doi.org/10.1016/j.cbpa.2006.03.011

404 McGaw, I.J., Curtis, D.L., 2013. Effect of meal size and body size on specific dynamic action and
405   gastric processing in decapod crustaceans. Comp. Biochem. Physiol., Part A: Mol. Integr.
406   Physiol. 166, 414–425. https://doi.org/10.1016/j.cbpa.2013.07.023

407 McNab, B.K., 1986. The influence of food habits on the energetics of eutherian mammals. Ecol.
408   Monogr. 56, 1-19. https://doi.org/10.2307/2937268

409 Merrett, N.R., Haedrich, R.L., 1997. Deep-Sea Demersal Fish and Fisheries. Fish Fish. Ser. 23, 282.

410 Mickel, T.J., Childress, J.J., 1982. Effects of Temperature, Pressure, and Oxygen Concentration on
411   the Oxygen Consumption Rate of the Hydrothermal Vent Crab *Bythograea thermydron*
412   (Brachyura). Physiol. Biochem. Zool. https://doi.org/10.1086/physzool.55.2.30155856

413 Mochnacz, N.J., Kissinger, B.C., Deslauriers, D., Guzzo, M.M., Enders, E.C., Gary Anderson, W.,
414   Docker, M.F., Isaak, D.J., Durhack, T.C., Treberg, J.R., 2017. Development and testing of a
415   simple field-based intermittent-flow respirometry system for riverine fishes. Conserv. Physiol.
416   5, cox048. https://doi.org/10.1093/conphys/cox048

417 O'Connor, M.P., Kemp, S.J., Agosta, S.J., Hansen, F., Sieg, A.E., Wallace, B.P., McNair, J.N.,
418   Dunham, A.E., 2007. Reconsidering the mechanistic basis of the metabolic theory of ecology.
419   Oikos. 116, 1058–1072. https://doi.org/10.1111/j.0030-1299.2007.15534.x

420 Peters, R.H., 1983. The Ecological Implications of Body Size. Cambridge University Press,
421   Cambridge.

422 Robertson, R.F., Meagor, J., Taylor, E.W., 2002. Specific dynamic action in the shore crab, *Carcinus*
423   *maenas* (L.), in relation to acclimation temperature and to the onset of the Emersion response.
424   Physiol. Biochem. Zool. 75, 350–359. https://doi.org/10.1086/342801

425 Roe, J.H., Hopkins, W.A., Snodgrass, J.W., Congdon, J.D., 2004. The influence of circadian rhythms
426   on pre- and post-prandial metabolism in the snake *Lamprophis fuliginosus*. Comp. Biochem.
427   Physiol., Part A: Mol. Integr. Physiol. 139, 159-168.
428   https://doi.org/10.1016/j.cbpb.2004.08.005

429 Rosa, R., Seibel, B.A., 2010. Slow pace of life of the Antarctic colossal squid. J. Mar. Biol. Assoc.
430   U.K. 90, 1375–137.https://doi:10.1017/S0025315409991494

431 Schmidt-Nielsen, K., 1984. Scaling: Why Is Animal Size so Important? Cambridge University Press,
432   Cambridge.

433 Schmidt-Nielsen, K., 1997. Animal physiology: adaptation and environment. Cambridge University
434   Press, Cambridge.

435 Secor, S.M., 2009. Specific dynamic action: a review of the postprandial metabolic response. J. Comp.
436   Physiol., B 179, 1–56. https://doi.org/10.1007/s00360-008-0283-7

437 Seibel, B.A., Childress, J.J., 2000. Metabolism of benthic octopods (Cephalopoda) as a function of
438   habitat depth and oxygen concentration. Deep Sea Res. Part I: Oceanogr. Res. Pap. 47, 1247–
439   1260. https://doi.org/10.1016/S0967-0637(99)00103-X

440 Seibel, B.A., Drazen, J.C., 2007. The rate of metabolism in marine animals: environmental constraints,
441   ecological demands and energetic opportunities. Philos. Trans. R. Soc., B Bio. Sci. 362, 2061–
442   2078. https://doi.org/10.1098/rstb.2007.2101

443 Seibel, B.A., Thuesen, E. V., Childress, J.J., Gorodezky, L.A., 1997. Decline in pelagic cephalopod
444   metabolism with habitat depth reflects differences in locomotory efficient. Biol. Bul. 192, 262–
445   278. https://doi: 10.2307/1542720

446 Sekiguchi, H., Yamaguchi, Y., Kobayashi, H., 1981. *Bathynomus* (Isopoda: Cirolanidae) attacking
447   sharks caught in a gill-net. Bulletin of the Faculty of Fisheries Mie University. 8, 11–17.

448 Smith, K.L., Baldwin, R.J., 1982. Scavenging deep-sea amphipods: Effects of food odor on oxygen
449   consumption and a proposed metabolic strategy. Mar. Biol. 68, 287–298.
450   https://doi.org/10.1007/BF00409595

451 Sullivan, K.M., Somero, G.N., 1980. Enzyme activities of fish skeletal muscle and brain as influenced
452   by depth of occurrence and habits of feeding and locomotion. Mar. Biol. 60, 91–99.
453   https://doi.org/10.1007/BF00389152

454 Thuesen, E. V., Childress, J.J., 1993a. Enzymatic activities and metabolic rates of pelagic
455   chaetognaths: Lack of depth-related declines. Limnol. Oceanogr. 38, 935–948.
456   https://doi.org/10.4319/lo.1993.38.5.0935

457 Thuesen, E. V., Childress, J.J., 1993b. Metabolic rates, enzyme activities and chemical compositions
458   of some deep-sea pelagic worms, particularly *Nectonemertes mirabilis* (Nemertea;
459   Hoplonemertinea) and *Poeobius meseres* (Annelida; Polychaeta). Deep. Res. Part I Oceanogr.
460   Res. Pap. 40, 937–951. https://doi.org/10.1016/0967-0637(93)90082-E

461 Toledo, L.F., Abe, A.S., Andrade, D.V., 2003. Temperature and meal size effects on the postprandial
462   metabolism and energetics in a Boid snake. Physiol. Biochem. Zool. 76, 240–246.
463   https://doi:10.1086/374300

464   Wang, T., Hung, C.C.Y., Randall, D.J., 2006. The comparative physiology of food deprivation: From

465   feast   to   famine.   Annu.   Rev.   Physiol.   68,   223–251.

466   https://doi.org/10.1146/annurev.physiol.68.040104.105739

467   Yagi, M., Kanda, T., Takeda, T., Ishimatsu, A., Oikawa, S., 2010. Ontogenetic phase shifts in

468   metabolism: links to development and anti-predator adaptation. Proc. R. Soc. B Biol. Sci. 277,

469   2793–2801. https://doi.org/10.1098/rspb.2010.0583

470   Yagi, M., Oikawa, S., 2014. Trends in metabolic scaling toward integrating comparative physiology

471   and ecology: ecological theory of metabolism. Hikaku seiri seikagaku (Comparative Physiol.

472   Biochem.) 31, 20–27. https://doi.org/10.3330/hikakuseiriseika.31.20

473

474
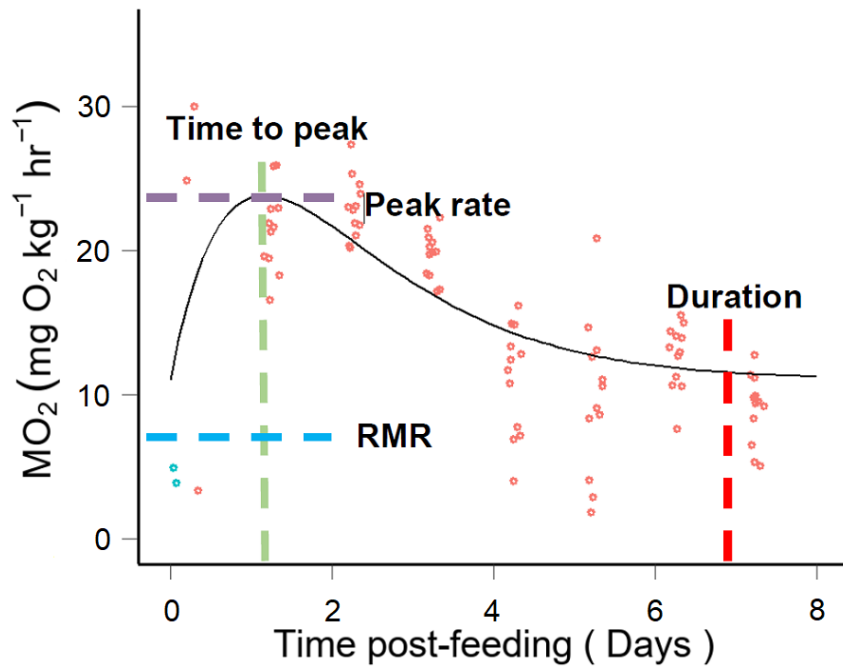
Fig. 1. Impact of food intake on the metabolic rate of the deep-sea isopod *Bathynomus doederleini*. An illustration of the postprandial metabolic profile of metabolic rate plotted against time post-feeding (meal size was 11.5 % of body weight). Quantified specific dynamic action (*SDA*) parameters are highlighted.
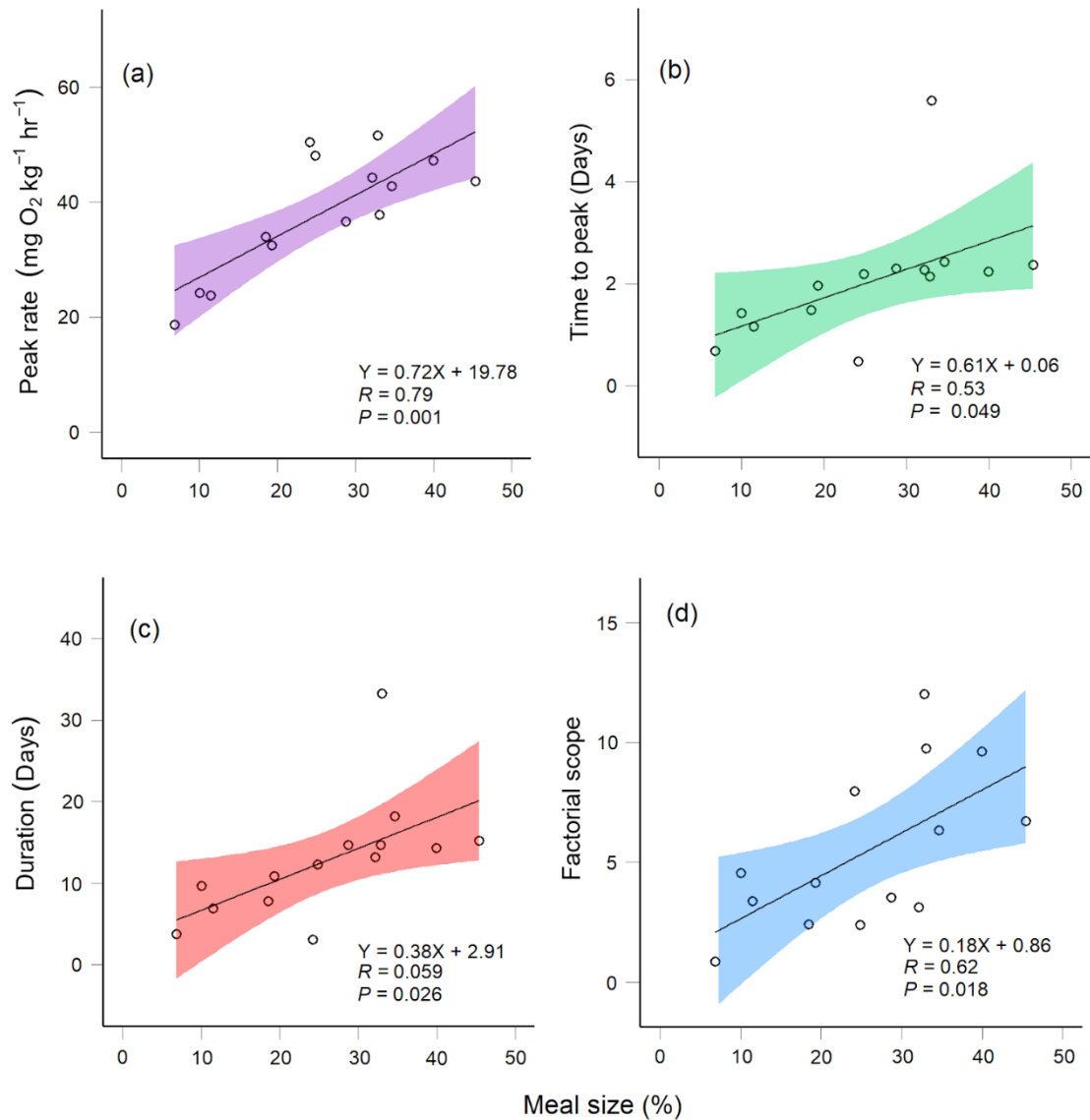
Fig. 2. Relationships between specific dynamic action (*SDA*) parameters and meal size for deep-sea isopods *Bathynomus doederleini*. (a) Peak. (b) Time to peak. (c) Duration. (d) Factorial scope. The shaded areas indicate the 95% confidence interval for the fitted exponential curve.
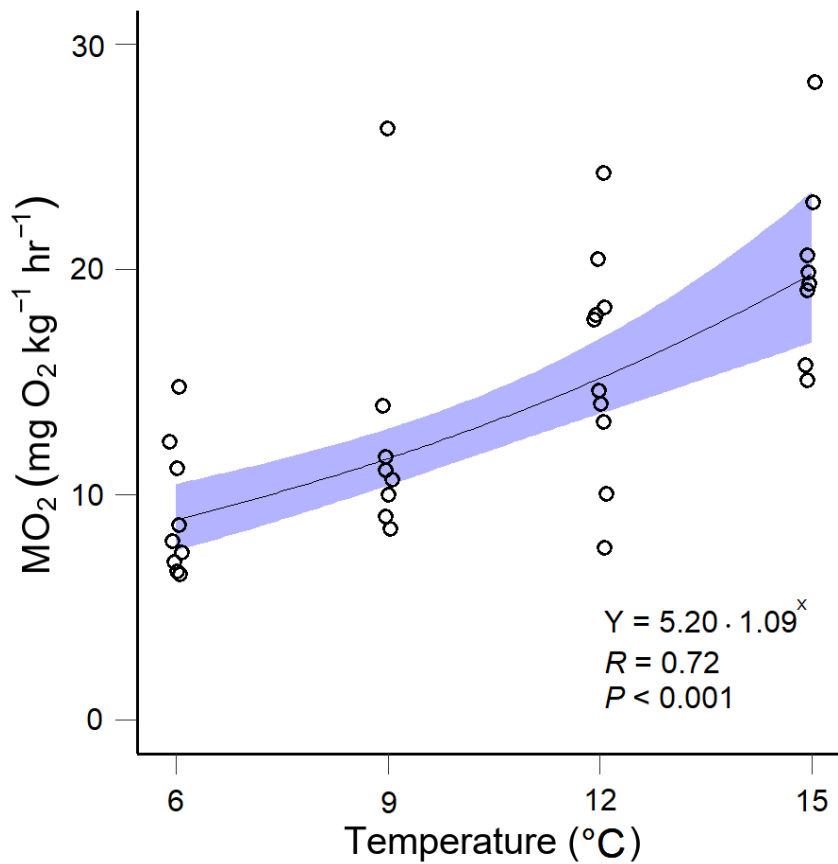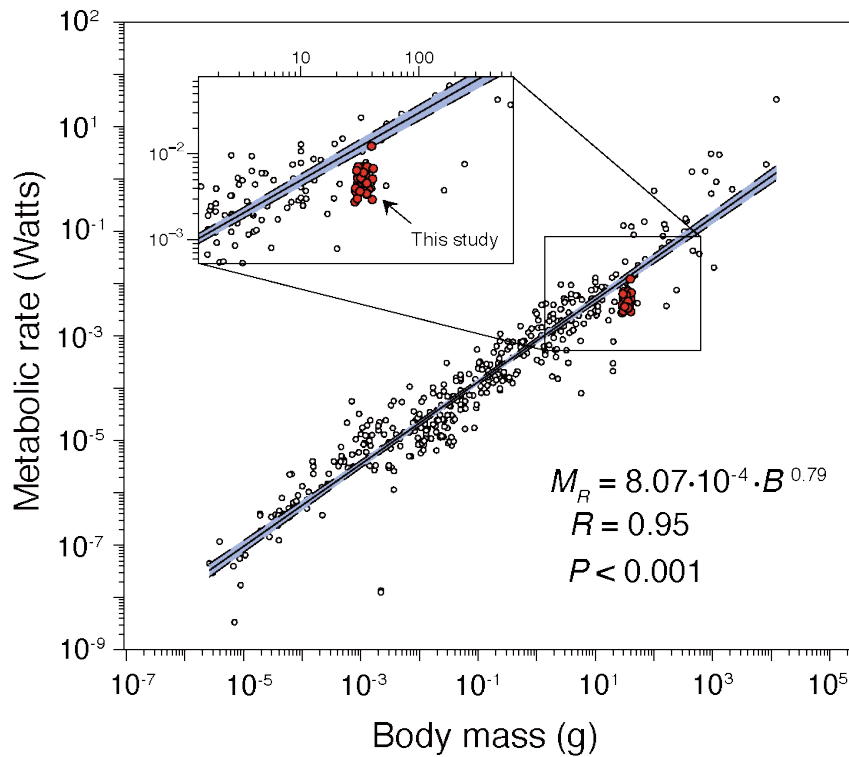
Fig. 3. Effects of temperature on resting metabolic rate (MO_2) in deep-sea isopods *Bathynomus doederleini*. The overall Q_{10} was 2.36. The shaded area indicates the 95% confidence interval for the fitted exponential curve.

Fig. 4. Metabolic scaling (the relationship between metabolic rate and wet body mass) in the deep-sea isopod *Bathynomus doederleini* in comparison to published interspecific comparisons (Makarieva et al., 2008) amongst aquatic invertebrates. Measurements from aquatic invertebrates (n = 376) and our measurements of deep-sea isopod (n = 35; represented by red circles) were adjusted to 25 °C, using the factor Q_{10} = 2, in accordance with Makarieva et al. (2008). The regression line and its 95% confidence interval (shaded area) did not encompass the data from this study.