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**[REVIEW]**

# Dive Deep: Bioenergetic Adaptation of Deep-Sea Animals

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**The deep sea, which encompasses the largest habitat on Earth, presents a set of extreme and unique environmental conditions, including high hydrostatic pressure, near-freezing temperatures, and perpetual darkness. These conditions pose significant challenges to the survival and energy management of its inhabitants. Deep-sea organisms have evolved a range of bioenergetic adaptations to negotiate these harsh conditions, ensuring efficient energy acquisition and utilization. This review examines the multifaceted strategies employed by deep-sea animals, focusing on three key areas: energy input, digestive and absorptive efficiency, and energy consumption. We examine the physical environment of the deep sea, highlighting vertical profiles of temperature, salinity, and dissolved oxygen, which contrast sharply with surface conditions. Physiological adaptations of deep-sea species, such as specialized digestive systems and enzyme modifications that function optimally under high pressure, are explored in detail. Furthermore, we discuss behavioral adaptations, including diurnal vertical migration, which optimize energy intake and reduce metabolic costs. Comparative analyses with shallow-water species provide insights into the evolutionary pressures that have shaped these adaptations. This review also addresses the concept of "power budgeting", in which energy expenditures for specific dynamic actions (SDAs) must be balanced with other metabolic demands. This comprehensive examination of bioenergetic adaptation in deep-sea organisms enhances our understanding of their resilience and adaptability, offering glimpses into the complex interplay between environmental constraints and biological processes in one of the most challenging habitats on the planet.**

**Key words:** body size, metabolic rate, metabolism, scaling, deep sea, specific dynamic action

## INTRODUCTION

How do deep-sea organisms live in the dark, cold, and under high water pressure? Considering the space available to living organisms in three dimensions, for terrestrial organisms, the habitat area is at most 120 m above the ground, such as tall trees, whereas the oceans are up to ~11,000 m deep and occupy 99.5% of the space on Earth. The mean depth of the oceans is approximately 3800 m, and 88% of the area is deeper than 1000 m, i.e., most of the habitat occupied by living organisms is in deep-sea environments. Until the early 19th century, we assumed that the deep sea is unsurvivable for animals (Childress and Thuesen, 1995), and there is still little known about the deep sea, much less about the organisms that live there. In fact, recently, a colossal new species of the family Alepocephalidae (slickhead), *Narcetes shonanmaruae*, which grows to over 1 m long, was discovered in waters around Japan (Fujiwara et al., 2021). As the number of species generally decreases with increasing body size (May, 1988), the discovery of a new species of such size is unusual on land, but there are probably many organisms living in the deep sea that have not yet been discovered.

Living organisms have evolved adaptations to their habitats, and the physical environment shapes the morphology and physiology of individual organisms. In general, the deep sea is defined by its low light intensity. It occurs below the epipelagic zone where sunlight powers photosynthesis (i.e., 200 m below the ocean surface), and includes the mesopelagic (200 m to 1000 m) and bathypelagic (1000 to 6000 m) zones. What kind of physical environment is the deep sea? Water temperatures are higher in the surface layer, warmed by solar radiation, and decrease toward deeper layers (Fig. 1). In temperate and tropical oceans, water temperatures remain below a mean of 4°C at depths below the layer of drastically decreasing water temperatures, known as the thermocline (Fig. 1A). The standard deviation of the annual variation in water temperature decreases with depth and is 2.5°C throughout the year at depths of ≥ 2000 m (Fig. 1B). Salinity (PSU) increases slightly from around 100 m to 2000 m depth (Fig. 1A), but that of deep water is relatively homo-

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geneous, ranging from 34.6 to 34.9. Dissolved oxygen (DO) is as high as > 220 µmol/l (5 mL/L) in the surface layer, whereas in deeper layers there is a hypoxic layer at around 1000 m where DO is very low (50 µmol/L or 1.1 mL/L) due to consumption of oxygen by aerobic organisms and slow vertical mixing (Fig. 1A) (Note that oxygen minimum layers are not universal in the ocean). In general, most organisms cannot survive in an environment with little oxygen (deep oxygen minimum zone: OMZ) and therefore avoid hypoxia. However, some resident ectotherms live with reduced activity and oxygen demand in OMZs (Teal and Carey, 1967; Childress, 1968). In addition, a fish species of the family Hadacaeidae in the northwestern Indian Ocean spends the day in the OMZ and then moves to an oxygenated layer at night (Herring, 2002), clearly coping with hypoxia. Pelagic shrimp also appear in the OMZ and play dead in an inverted orientation (Burford et al., 2018). In so doing, these and other animals with high hypoxia tolerance avoid capture by visual predators. Beyond 1000 m depth, DO increases with depth to 130–220 µmol/l (3–5 mL/L) as the oxygen demand by organisms is lower (Fig. 1A). Thus, deep-sea organisms live in an environment that is significantly different from the surface layer.

As terrestrial organisms ourselves, we are often surprised by the unusual structures and functions of deep-sea organisms. For example, deep-sea goblin sharks rapidly protrude their jaws a considerable distance, possibly as a trade-off for the loss of physical strength (Nakaya et al., 2016). In addition, large body size characterizes some taxonomic groups of deep-sea organisms. The deep-sea isopod, which occurs at depths of around 400 m, differs from the wood louse of the same taxonomic group by a factor of 340 in mass (Fig. 2). The Japanese giant crab, *Macrocheira kaempferi*, which lives in deep waters around Japan, is the world's largest arthropod. These are consequences of body size evolution known as gigantism, although the mechanism remains a matter of debate (Chapelle and Peck, 1999; Collins et al., 2005; Vermeij, 2016). Some deep-sea organisms are surprisingly long-lived. The Greenland shark, *Somniosus microcephalus* (81–502 cm in length), which is widespread in the deep waters of the North Atlantic, lives from 272 to 392 years (Nielsen et al., 2016). Some deep-sea organisms engage in seasonal or diel vertical migration (DVM) (Haren and Compton, 2013; Brierley, 2014). DVM is an active migration on a large scale, at speeds of up to 300 m per hour. Some mesopelagic fish and shrimp rise to the

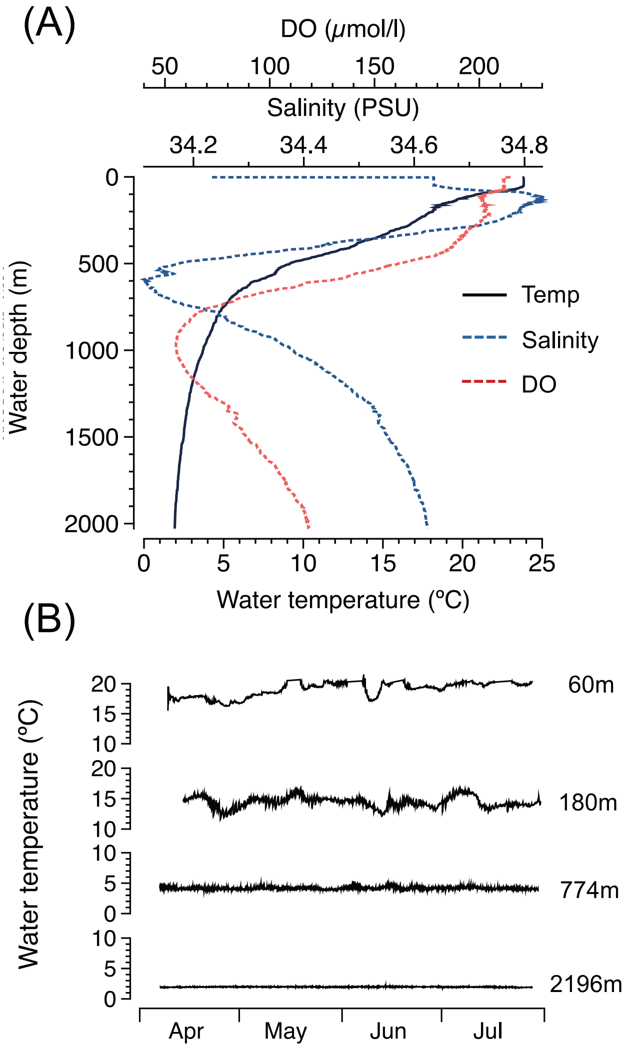

**Fig. 1.** **(A)** Vertical profiles of water temperature (Temp), salinity, and dissolved oxygen (DO) in the Pacific Ocean (22°59.4′N, 137°00.6′E) during winter 2021. The warm surface water is separated from the cold deep water by a thermocline at around 500 m. Data from the Japan Meteorological Agency (JMA). **(B)** Temporal changes in water temperatures just above the seabed in the East China Sea (60 m, 32°03.0′N, 130°06.0′E; 180 m, 31°28.3′N, 130°00.0′E) and in the Pacific Ocean (774 m, 29°24.9′N, 130°28.5′E; 2196 m, 28°39.3′N, 130°26.0′E). The standard deviation in temperature change throughout the year decreases with increasing water depth. Data from temperature loggers installed on seabed seismometers by the authors.

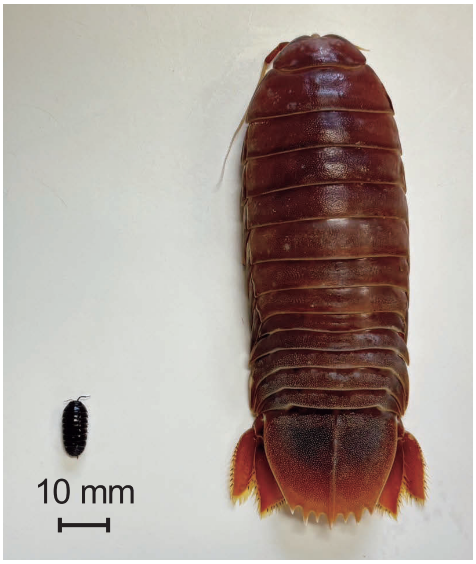

**Fig. 2.** Comparison of body size between the deep-sea isopod *Bathynomus doederleinii* (right) and the wood louse *Armadillidium vulgare* (left). Both are isopods, but differ in body weight by a factor of 340 (deep-sea isopod, 34.4 g; wood louse, 0.1 g). The deep-sea isopod is found at depths of around 400 m in temperate zones, whereas the wood louse is terrestrial.

surface and descend again around dawn (Heys, 2003). Acoustic backscattering can capture this behavior as a deep-sea scattering layer (DSL) (Plueddemann and Pinkel, 1989) (Fig. 3).

Energy management is essential for survival strategies of deep-sea organisms, comprising energy input, digestion, absorption, and metabolic conversion, and energy consumption. Deep-sea organisms must accomplish these things as efficiently as possible in severe environments. This review provides an overview of adaptations of deep-sea organisms at the individual level from a bioenergetic perspective. It also discusses the question, “How does energy metabolism of deep-sea organisms differ from that of shallow-sea organisms?”

## Energy input

Deep-sea organisms have evolved strategies for energy acquisition that allow them to take advantage of feeding opportunities. As biomass declines with depth below 200 m (Marshall, 1971; Childress, 1995; Olivar et al., 2017), deep-sea organisms have a lower probability of encountering prey than surface organisms. If they attempt to locate prey by swimming, the energy cost of the search increases (Videler, 1993), even if their body water, ion, and lipid contents are adjusted to intermediate buoyancy (Childress and Nygaard, 1974; Sanders and Childress, 1988; Yancy et al., 1989). In addition, not all feeding is predation, scavenging on carrion falls is quite important in the deep sea. In deeper oceans, many animals minimize energy expenditure by adopting ambush, rather than active hunting strategies. For example, female anglerfish employ a lure on the upper part of the head, rather than pursuing prey (Munk, 1999).

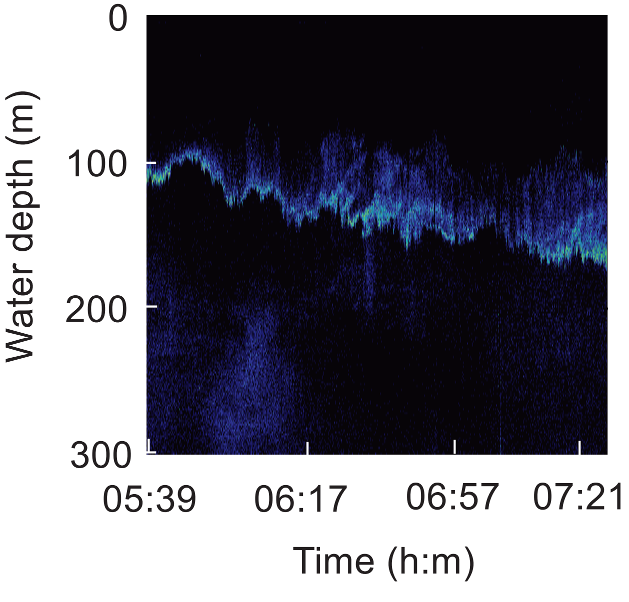

**Fig. 3.** Descending deep-water scatter layer (DSL) reflecting diurnal vertical movement (DVM) in the morning. Some DSLs migrate upward from a depth of approximately 400 m immediately before sunset and reach the surface 1 h later. They move downward again shortly before sunrise. This DSL probably reflects mesopelagic fish or shrimp species. Image supplied by the authors.

Under circumstances in which prey availability is constrained and energy is not being expended on active foraging, maximizing prey size is an appropriate strategy. Large body size would seem advantageous for storing large energy reserves; however, the matter is not so simple when considering costs of growth. In theoretical studies, it has been argued that where food is scarce, animals need to spend more time foraging, so larger prey are advantageous (Herring, 2002). Energy costs of increased foraging are offset by expending less energy on growth, so overall body size (within-fauna pattern) tends to decrease (Stefanescu et al., 1992; Herring, 2002; Moranta et al., 2004). Increasing relative mouth (jaw) size is a good way to increase prey size while keeping body size small. Indeed, many deep-sea fish tend to have larger teeth and jaws than similar-sized species at shallower depths (Ebeling and Cailliet, 1974). Some species are able to significantly increase their gapes, not only by elongating the jaws, but also by making mandibular joints flexible enough to reposition themselves dynamically. This is similar to the way snakes swallow food. Indeed, vipers can ingest food items comprising as much as 36% of their body weight (Pough and Groves, 1983) These may be examples of parallel evolution. The secret of gluttony also lies in the structure of the digestive tract. Many deep-sea fishes have evolved stomachs that can expand, and some, such as anglerfish and Chiasmodontids, can accommodate their own body masses in prey. Some deep-sea fish prey upon anything that they can capture and swallow (Hopkins and Baird, 1973), which may explain why consumption of plastics is so common in the longnose lancetfish, *Alepisaurus ferox* (Jantz et al., 2013; Gago et al., 2020).

How much food is ingested by deep-sea invertebrates is largely unknown; however, it has recently been reported that a deep-sea isopod (Fig. 2) can consume 45% of its body weight in just 10 min (Tanaka et al., 2023). Hargrave et al. (1994) reported that a deep-sea amphipod, *Eurythenes gryllus*, consumes meals greater than 75% of its body weight. Typically, a satiating meal for an organism ranges from 2 to 4% of its body weight (Elner, 1980; Robertson et al., 2002), and a meal size of 5% would be considered high for crustaceans (Curtis et al., 2010). Instead of swallowing whole organisms, deep-sea isopods scrape carrion with their mouthparts to ingest large quantities of food. Presumably, a similar strategy is used by cephalopods such as the giant squid. The deep-sea isopod has a bell-shaped abdomen, enabling it to store large quantities of food. These adaptations permit deep-sea isopods to mitigate intense competition for sporadic resources by maximizing rapid food intake, thereby reducing the risk of predation and cannibalism (Smith and Baldwin, 1982; Barradas-Ortiz et al., 2003).

## Digestion, assimilation, and specific dynamic action

Deep-sea species have evolved cold-adapted enzymes to compensate for the lower temperatures of the deep sea (Torres and Somero, 1988; White et al., 2011). High pressure also appears to have given rise to further adaptations. Water pressure affects the speed and accuracy of enzymatic catalysis and enzyme structure (Somero, 1998). Activity of some enzymes may decrease due to high pressure, whereas others may be activated by high pressure (Eisenmenger and Reyes-De-Corcuera, 2009). To investigate enzyme adaptation to water pressure, Hochachka et al. (1971a, b) determined the relationship between reaction rate and pressure for fructose diphosphatase (FRPase) in the liver of a deep-sea benthic grenadier fish *Coryphaenoides* sp. and the rainbow trout, *Salmo gairdneri*, a surface fish. The results showed that the reaction rate was greater at high pressure (500 bars) than at ambient pressure (1 bar) in *Coryphaenoides* sp. in the range of physiological substrate concentrations, whereas the reaction rate did not change in rainbow trout. In *Coryphaenoides* sp., the reduction in reaction rate due to lower water temperatures is compensated by the increase in reaction rate due to high pressure. Enzymes in deep-sea animals are generally less pressure-sensitive than their homologs in shallow-sea species, and their enzymes function at pressures that would inactivate those of shallow-sea species (Somero and Siebenaller, 1979). The key to pressure adaptation in enzymes is the ability to effectively regulate catalytic capacity and maintain protein structure, rather than maintaining the absolute rate of catalytic action. Recently, a novel digestive enzyme was discovered in the hadal amphipod *Hirondellae gigas* by testing its activity in degrading proteins and lipid polysaccharides (Kobayashi et al., 2012). These plant polysaccharide-degrading enzymes probably contribute to digestion and absorption of food fragments such as driftwood, dead leaves, and seeds at the bottom of the sea.

Waxes are esters consisting of one molecule of alcohol with a long hydrophobic side chain bonded to one molecule of fatty acid. Wax, like other lipids, has high energy content; however, it cannot be hydrolyzed by ordinary vertebrate lipases (Schmidt-Nielsen, 1990). It is therefore a food of little significance to land animals, except for some birds. In contrast, wax is extremely important to deep marine animals. Some copepods, which are the food of almost all juvenile fish, contain up to 70% of their dry weight in wax. Fish that eat copepods, such as herring, anchovies, and sardines, have lipases in their digestive tracts that degrade the wax (Sargent and Gatten, 1976). Fatty alcohols are oxidized to fatty acids, which are further converted to neutral lipids such as triglycerides, the main role of which is energy storage. However, it is unclear how much wax is digested by other fish species, as they have only a small amount of lipase. The possibility that deep-sea organisms use wax as a buoyant material further complicates matters. It is difficult to distinguish whether wax is a metabolizable reserve energy source or whether it is stored because it is not easy to metabolize when consumed. However, it is reasonable to assume that wax is available because it is contained in the fat and oil of various marine animals, including whales, and scavengers that feed on these animals when they sink to the sea floor do not excrete wax in feces.

There is not much information on the assimilation efficiency of deep-sea organisms, but it appears to be higher than that of closely related surface species. Assimilation efficiency can be determined to some extent by determining the relative amounts of food and feces and measuring their relative calories (Kooijman, 1993). Assimilation efficiency is generally higher in species with longer intestinal tracts (Robison and Bailey, 1982). A deep-sea fish, *Poromitra crassiceps*, which feeds on gelatinous zooplankton, has a very long intestinal tract to assimilate very small amounts of nutrients from water-rich substrates (Herring, 2002). In addition, the efficiency of ambush predators, which feed intermittently, is approximately 40%, compared with approximately 30% for regular feeders such as migratory lanternfish. Furthermore, the maximum assimilation rate of *Xylonora atlantica* in deep-sea wood-boring bivalves is 10- to 15-fold higher than that in shallow-sea boring bivalves, such as *Teredo navalis* (Gaudron et al., 2021). However, despite their higher assimilation efficiency, deep-sea organisms still appear to be chronically undernourished, as they have a higher water content and lower fat content than their shallow-sea relatives (Childress and Nygaard, 1973).

When food is consumed, nutrients absorbed are degraded and part of the energy is released as body heat, increasing the metabolic rate even at rest (Fig. 4). This phenomenon is known as specific dynamic action (SDA), and the rate of increase depends on the type of nutrient ingested (Secor, 2009). In ectotherms, it has been hypothesized that as water temperature decreases and food intake increases, the metabolic cost and duration of SDA rise (Wang et al., 2002). This hypothesis has been supported by various studies (Chakraborty et al., 1992; Janes and Chappell, 1995; Toledo et al., 2003).

What is the SDA of gluttonous, low-temperature deep-sea organisms? This interesting question was difficult to answer for many years due to the difficulties of long-term rearing (monitoring of metabolic rate) of deep-sea organisms. However, recently, Tanaka et al. (2023) showed a pos-

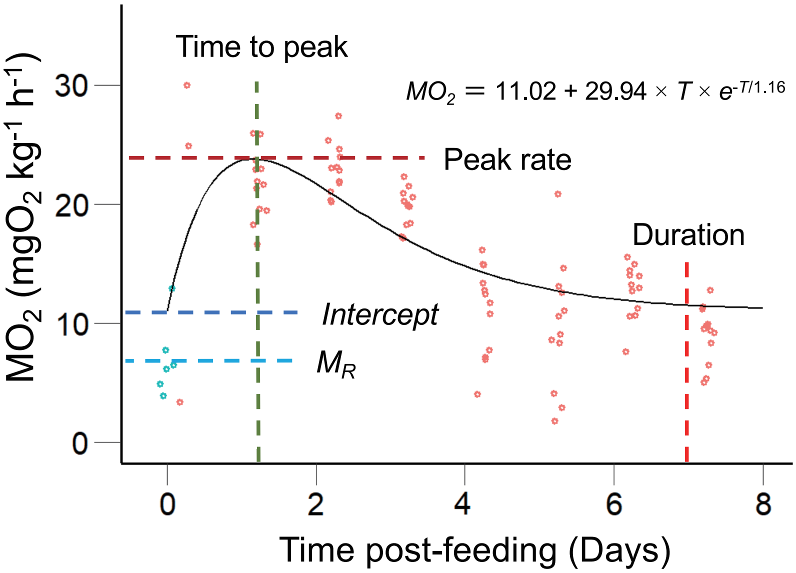

**Fig. 4.** Hypothetical postprandial metabolic profile (solid line) and plots obtained in a deep-sea isopod (circles) of metabolic rate plotted against time post-feeding. Time to peak: duration from time of feeding to peak metabolic rate, peak rate: postprandial peak in metabolism, duration: time from feeding when metabolic rate in no longer significantly greater than the intercept, *M*R: metabolic rate. (Redrawn from Tanaka et al. [2023] Fig. 1, with permission from Elsevier.)

itive correlation between SDA parameters (peak rate, time to peak, duration, and factorial scope) and meal size in deep-sea organisms (Figs. 4, 5). The duration of elevated metabolic rates in these isopods was remarkably prolonged, lasting up to 16 days (Fig. 5). This extended duration may be attributed to the substantial meal size, which is significantly larger than that of shallow-water organisms. For instance, the American crayfish, *Procambarus clarkia*, and the shallow-water crab, *Hemigrapsus nudus*, which are similar in body size to the deep-sea isopods, have maximum meal sizes of 0.5% and 3.0% of their body mass, respectively, with durations of 0.47 and 2.51 days (McGaw and Curtis, 2013). The factorial scope of this species increased significantly with larger meal sizes (Fig. 5D). Many organisms, including isopods, have factorial scopes ranging from 2.0 to 7.0 (Secor, 2009). However, this deep-sea isopod species exhibited a maximum factorial scope of 12.1. Interestingly, this increased energy expenditure for SDA may also constrain behavioral activity. Post-feeding individuals of various meal sizes tend to be rounded and immobile. McCue (2006) suggested that comparing SDA scope to maximal metabolic scope can estimate the residual capacity for activity during digestion. Jutfelt et al. (2021) also noted that the elevated oxygen consumption rate due to SDA can potentially use a significant portion of an organism's aerobic capacity, ultimately limiting what is available for other functions. A trade-off may exist if more energy is allocated to SDA, thereby constraining activity. Priede (1985) demonstrated that in some fish species, peak SDA can occupy the entire metabolic scope, necessitating that activity be scheduled between periods of digestive activity, a constraint termed "power budgeting." The link between feeding and behavior needs to be clarified in deep-sea organisms.

## Energy expenditure

Aerobic animals obtain most of their energy to carry out various functions, which they accomplish by obtaining ATP (adenosine triphosphate), by oxidizing food in the tricarboxylic acid circuit (TCA cycle). In the 18th century, Lavoisier confirmed that animals absorb oxygen and expel carbon dioxide during respiration, and ice calorimetry showed that respiration and combustion are the same phenomenon (Niklas and Kutschera, 2015). In principle, metabolic rate is best measured by the heat production of the organism as joules or calories, although oxygen consumption is an indicator (Yagi et al., 2010). Metabolic heat production per liter of oxygen consumed is approximately 4.8 kcal (0.23 kJ). This is based on the fact that regardless of the substrate being oxidized, heat production for consuming a liter of oxygen is approximately constant at 4.4–4.5 kcal for protein, 4.7 kcal for fat, and 5.0 kcal for carbohydrates (Schmidt-Nielsen, 1990). Fat has the highest energy content per gram (9.4 kcal) compared to other nutrients (protein: 4.25–4.3 kcal, carbohydrates: 4.2 kcal). Storing energy as fat is also efficient because it is hydrophobic and does not require water of hydration, as do proteins and carbohydrates. Lipid content in pelagic crustaceans ranges from 3.3 to 66% of dry weight, excluding ash, which may be related to the trend of increasing lipid content with increasing habitat depth (Childress and Nygaard, 1974).

In animals, oxygen consumption varies with the level of activity; thus, metabolic rate is defined based on the level of activity at the time of measurement. "Basal metabolism" refers to the resting state of an animal that is not growing and not processing food (i.e., they have been fasted), while "resting metabolism" refers to the resting state of an animal. "Resting

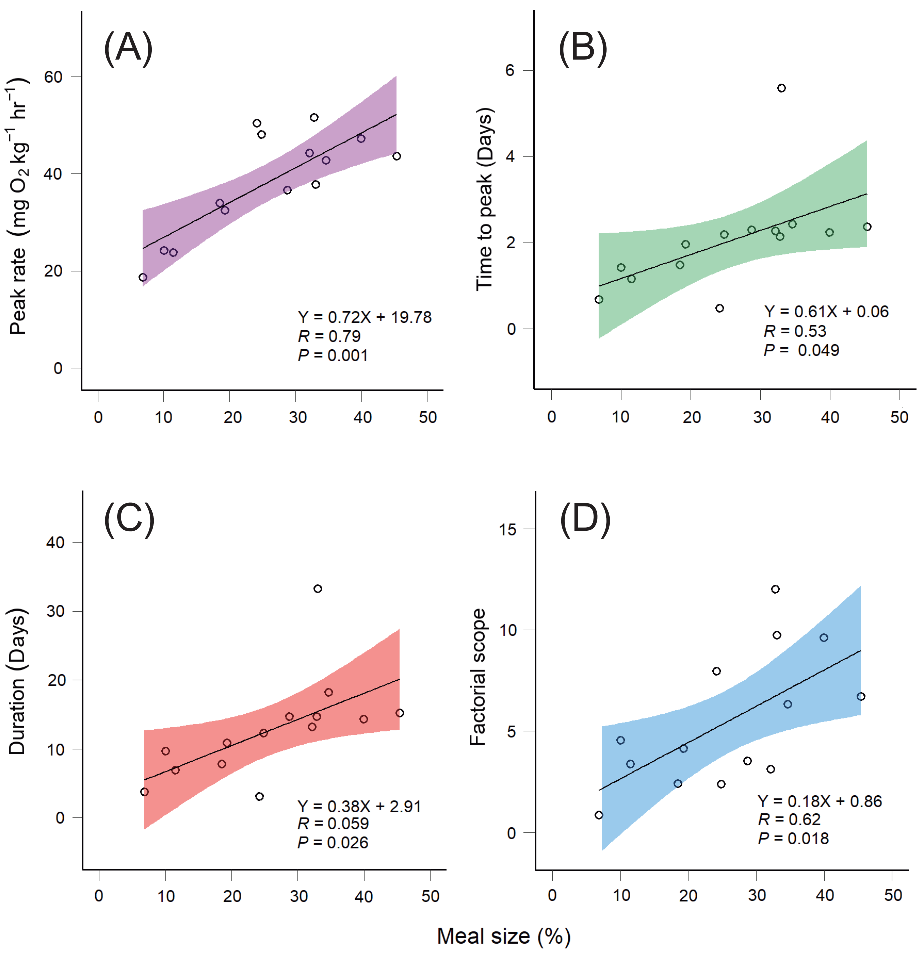

**Fig. 5.** Relationships between specific dynamic action (SDA) parameters and meal size for the deep-sea isopod *Bathynomus doederleinii.* **(A)** Peak metabolic rate. **(B)** Time to reach peak metabolic rate. **(C)** Duration of elevated metabolic rate. **(D)** Factorial scope. Shaded regions represent the 95% confidence interval for the fitted exponential curve. (Redrawn from Tanaka et al. [2023] Fig. 2, with permission from Elsevier.)

normal metabolism" is the metabolic rate of a fish that is resting, but moving its fins minimally, and "maximal active metabolism" is the metabolic rate of an animal that is engaged in activity that can be maintained only briefly (Yagi and Oikawa, 2008, 2014b). In addition, oxygen consumption measurements in any activity state should be made under fasting conditions to exclude effects of SDA (Brockington and Clarke, 2001; Clarke and Fraser, 2004). However, it is virtually impossible to apply these conditions strictly in the case of deep-sea organisms. The metabolic rate of deep-sea organisms is generally estimated from the amount of decrease in dissolved oxygen during a period of time in which individuals collected in the field are housed in sealed containers and incubated at water temperatures approximating those in their natural habitat (Omori and Ikeda, 1984; Thuessen and Childress, 1994). The dissolved oxygen content can be measured by the Winkler titration method or by an oxygen electrode (Yagi et al., 2014a; Tarallo et al., 2016). Although this method is simple, care must be taken to ensure that it reflects the physiological state of the organism in the wild. Therefore, in mid- and low-latitude areas, it is important to use a special cod-end (Childress et al., 1978) that maintains the water temperature at that of the depth collection site, so as to avoid water temperature shock during collection, and to measure the electron transfer system (ETS), citrate synthase (CS), pyruvate transferase (PK), lactate dehydrogenase (LDH), malate dehydrogenase (MDH), and other enzymes related to intermediate metabolism to confirm that the physiological state of the individual is normal (Childress, 1995; Ikeda et al., 2000). Attempts have also been made to measure oxygen consumption in situ without capturing the organism and bringing it on board (Smith, 1985; Bailey et al., 2002). On the other hand, metabolic rate experiments can be conducted under different measurement conditions in captivity for species such as deep-sea isopods, which are tolerant to pressure changes caused by open circulatory systems (Tanaka et al., 2023). In addition, some mesopelagic caecilians have been able to hatch eggs and develop to adults through normal molting (Ozaki and Ikeda, 1998). Even in deep-sea fish, metabolic rates can be measured at ambient pressure in groups that have adapted to have their wiping pouch walls covered with a thick layer of guanine or oil instead of gas.

The fire of life appears to burn with nearly the same brightness in different species if they are of similar temperature and body size. Seminal work by Hemmingsen (1960) showed that when divided into groups of endotherms, ectotherms, and unicellular organisms, they plot on a straight line proportional to the 0.75 power of body mass (Fig. 6A). This implies that the metabolic rate is approximately explained by body size. Since the slope of both logarithmic graphs is 0.75, the slope of the metabolic rate per unit body mass (mass-specific metabolic rate) is –0.25, and thus decreases with increasing body size (Fig. 6B). Why is the log-log slope 0.75? And why does the mass-specific metabolic rate decrease? These questions are much debated and still unresolved (West et al., 1997; Dodds et al., 2001; Kozlowski et al., 2005; Mori et al., 2010; Glazier, 2022). Recently, most investigators no longer regard metabolic scaling as following any single exponent (e.g., Glazier, 2005, 2006, 2022; White, 2010; Gavrilov et al., 2022). They claim that the 0.75-power law is not universal. The diversity of metabolic scaling is pervasive throughout the tree of life; it varies within and between species and higher taxa, in relation to developmental stage, activity level, body shape and composition, cellular mode of growth, ecological lifestyle, and various environmental factors (Heusner, 1982; Yagi et al., 2010, 2014a; Glazier, 2022; Glazier and Gjoni, 2024). Furthermore, recent studies show that the graph of Hemmingsen (1960) (Fig. 6) no longer accurately reflects the metabolic scaling (e.g., Phillipson, 1981; Glazier, 2009; DeLong et al., 2010; Hatton et al., 2019). Unicellular prokaryotes show hypermetric metabolic scaling (log-log slope > 1). Unicellular and multicellular eukaryotes typically show either isometric or allometric metabolic scaling (log-log slope ≤ 1).

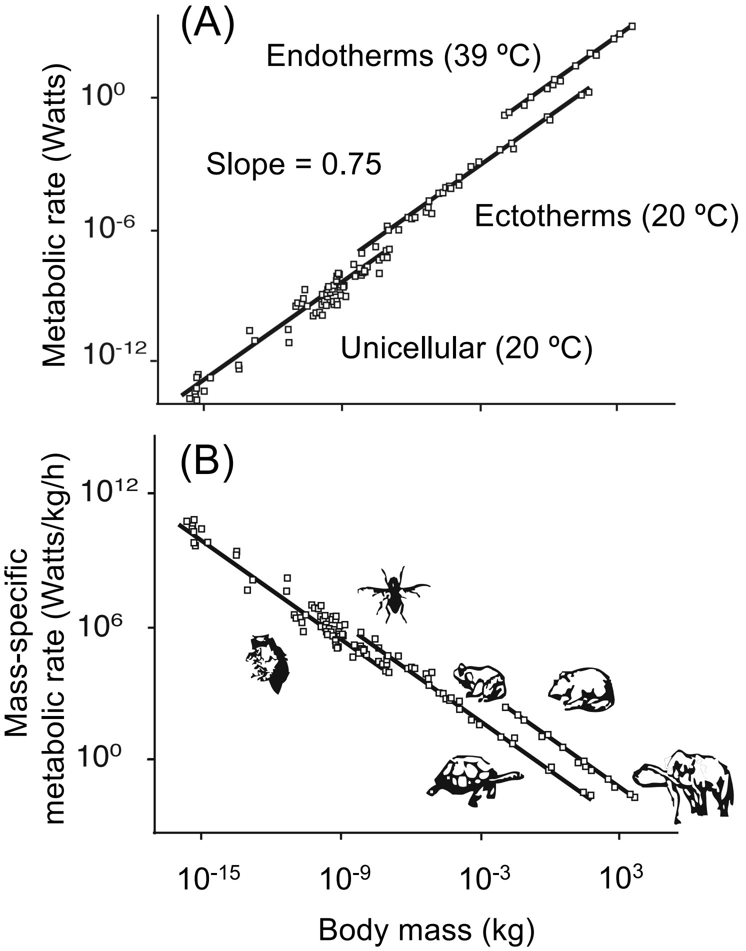

**Fig. 6.** Relationship between metabolic rate and body mass from unicellular organisms to endotherms. The extensive body size range from microorganisms to the largest mammals shows a slope of 0.75 (or –0.25) for each taxon plotted on a double-log graph. (A) Whole body metabolic rate. (B) Mass-specific metabolic rate. (Redrawn from Yagi and Oikawa [2008] Fig. 2, and Yagi and Oikawa [2014b] Fig. 8 with permissions from The Japanese Society for Comparative Physiology and Biochemistry.)

Endothermic vertebrates tend to show metabolic scaling slopes < 0.75, whereas ectothermic vertebrates tend to show metabolic scaling slopes > 0.75 (White et al., 2006; Glazier, 2010; Gavrilov et al., 2022). Information addressing metabolic scaling relationships within the same species of deep-sea organisms is limited. At any rate, these facts show that the fire burns brighter in endotherms because of their higher intercept values, is dimmer in unicellular organisms, and is intermediate between the two in ectotherms. Interestingly, the mass-specific metabolic rate is also closely related to life span, with animals with smaller body size and higher mass-specific metabolic rate living shorter lives. This relationship tends to be proportional to the 0.25 power (Schmidt-Nielsen, 1984). In other words, the mouse's candle of life is thick and short, but bright, while the elephant's is a long, thin candle with a dimmer flame than the mouse's. However, the slope for both relationships often does not follow the universal scaling relationships (Lemaître et al., 2014; Scharf et al., 2015; Szekely et al., 2015). The rate of living theory is also not generally applicable across the tree of life (e.g., de Magalhães et al., 2007; Stark et al., 2020). It is not known whether the principles of lifespan and metabolic rate also hold for deep-sea organisms.

The fire of life in deep-sea organisms is not very bright. Tanaka et al. (2023) reported that the mean metabolic rate of a deep-sea isopod, adjusted for temperature (25°C), is 63% lower than the established metabolic scaling relationship for aquatic invertebrates (Makarieva et al., 2008) (Fig. 7). Childress (1971) measured metabolic rates of 12 species, including fish of the families Liparididae and Zoarcidae, krill, mysids, amphipods, decapods, and ostracods, collected from depths ranging from 0 to 1300 meters off the coast of California at a mid-depth temperature of 5.5°C at 600 m. He reported that as collection depth increased, the mass-specific metabolic rate decreased, reaching approximately 10% of the metabolic rate at 0–400 m at depths of 900–1300 m. Smith and Hessler (1974) also measured metabolic rates of a deep-sea fish, *Coryphaenoides acrolepsis*, at 1230 m. They found that metabolic rate was 4.5% of that of the shallow-water Atlantic cod (*Gadus morhua*) at similar temperatures. A decrease in metabolic rate has also been observed in 28 species of mesopelagic crustaceans (mysids, decapods, and amphipods) as the minimum depth of occurrence (MDO: the upper limit of depth at which more than 90% of the population of the species is distributed) increases (Childress and Nygaard, 1973) (Fig. 7A). This phenomenon has been confirmed in various species throughout the sea (Torres et al., 1979; Quetin et al., 1980; Ikeda, 1988; Seibel et al., 1997; Tanaka et al., 2023). In situ measurements conducted at 4000 m, where the cod were not subjected to handling stress, also showed that their metabolic rate was approximately 14–27% of that of cod of the same temperature and body size (Bailey et al., 2002). The effect of temperature on metabolism is quantified by the $Q_{10}$ value, which represents the increase in metabolic rate caused by a 10°C rise in temperature. It typically ranges from 2 to 3 (Schmidt-Nielsen, 1990; Clarke and Johnston, 1999). This value is also observed in the deep-sea isopod ($Q_{10}$ = 2.36) (Tanaka et al., 2023). Specifically, with a $Q_{10}$ of 2.5, a 10°C decrease would result in a 40% reduction in metabolic rate. Thus, the observed decline in the metabolic rates of deep-sea organisms cannot be explained by temperature alone. Indeed, a significant decrease in metabolic rates with increasing water depth has been reported in six species of Antarctic fish, even though the water temperature in the Southern Ocean remains almost constant (0.5°C) (Fig. 8B).

Why is the metabolic rate of deep-sea organisms so exceptionally low? As mentioned above, there are significant differences in physical environments between deep and shallow water, including water pressure, light levels, and DO content. In pelagic species, Teal (1971) examined the relationship between oxygen consumption rate and water pressure for five pelagic crustacean species from the North Pacific and reported a trend of increased metabolic rates with increasing water pressure while maintaining a constant temperature. Therefore, when deep-sea organisms migrate downward due to DVM (Fig. 3), their metabolic rates decrease with the drop in temperature. However, the influence of pressure causes an increase, and these two factors offset each other, resulting in a nearly constant or slightly increasing metabolic rate to a depth of around 700 m.

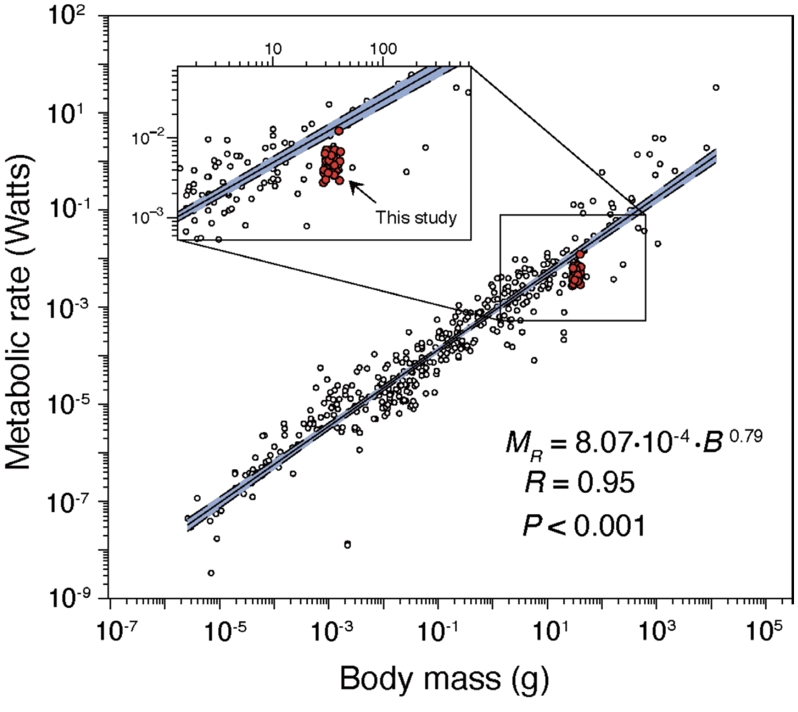

**Fig. 7.** Relationship between metabolic rate and wet body mass in the deep-sea isopod *Bathynomus doederleinii* in comparison to published interspecific comparisons (Makarieva et al., 2008) among aquatic invertebrates. Measurements from aquatic invertebrates ($n$ = 376) and our measurements of *B. doederleini* ($n$ = 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 data of the deep-sea isopod. (Data from Tanaka et al. [2023]).

Beyond this depth, metabolic rate decreases. Among organisms that perform DVM, effects of pressure and temperature compensate for each other, resulting in little change in metabolic rate, despite significant vertical migration. Therefore, the contribution of pressure to the adaptation of low metabolism is likely minimal. What about light intensity? It is true that in epipelagic copepods and euphausiids, metabolic rates are reported to be higher in the light than in the dark (Ikeda et al., 2000). However, this increase in metabolic rate is likely due to the increased swimming activity in response to light, rather than a direct effect of light on metabolism. Additionally, since metabolic rates of deep-sea organisms are typically measured in dark conditions (Tanaka et al., 2023), the impact of light is also considered minimal. On the other hand, regarding DO, Childress and Seibel (1998) noted that the metabolic rates of fish inhabiting depths deeper than the OMZ (Fig. 1) are lower than those of fish inhabiting the OMZ. They also found that metabolic rates of midwater fish species in the highly developed OMZ off California are nearly identical to those of the same species inhabiting waters off the Hawaiian Islands, where OMZ development is less pronounced, suggesting that dissolved oxygen concentration is not a primary cause of low metabolism. However, Ikeda (1988, 2009) indicated that metabolic rates of cephalopods, amphipods, euphausiids, and ostracods inhabiting the oxygen-rich intermediate layers of the Southern Ocean are higher than those of these taxa inhabiting the midwater off California where OMZ is developed, implying that oxygen concentration in the habitat influences metabolic rates. Therefore, further verification regarding DO is needed. Finally, there are reports suggesting that limited food supply is related to low metabolism (Somero et al., 1983; Priede, 2017). Indeed, laboratory experiments have shown that zooplankton exhibit decreased metabolic rates under starvation conditions (Ikeda et al., 2000). However, no significant regional differences in metabolic rates of midwater euphausiids, amphipods, and cephalopods inhabiting the food-scarce waters off Hawaii and the abundant waters off California have been observed in field studies (Cowless et al., 1991). Limitations in food supply manifest at the biomass level rather than affecting individual metabolic rates directly (Childress, 1995). Considering adaptation and evolution under low nutrient supply, it is suggested that extreme environmental factors themselves do not suppress metabolic rates at the individual level (Seibel and Drazen, 2007).

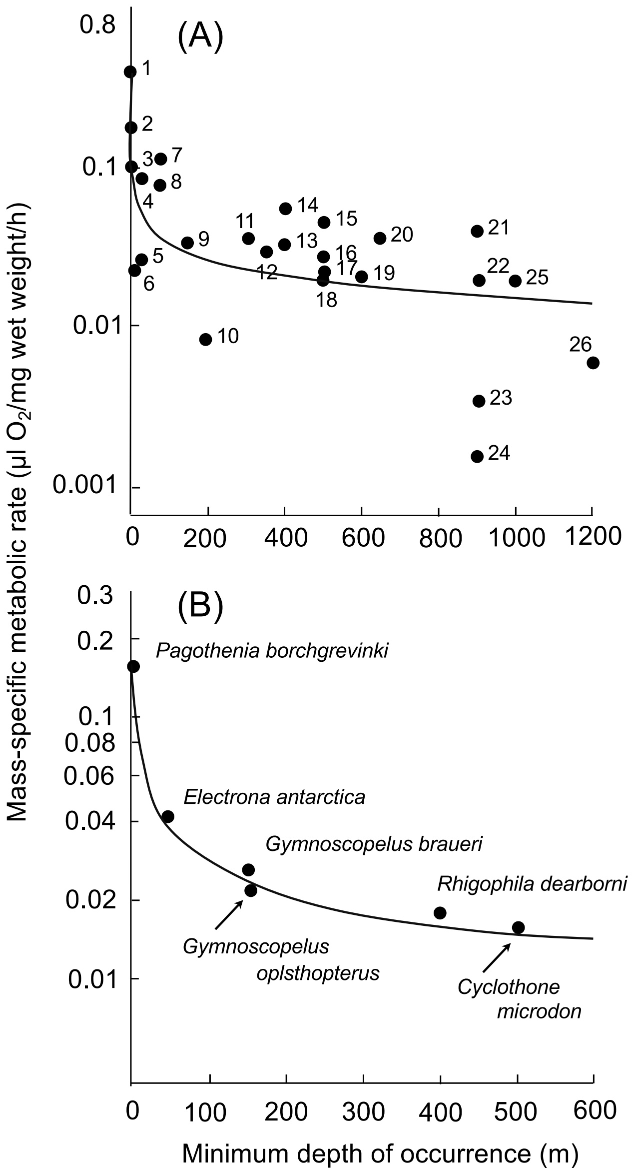

**Fig. 8.** Relationships between minimum depth of occurrence (MDO) and metabolic rates. **(A)** Crustaceans. 1: *Labidocera* sp., 2: *Euphausia pacifica*, 3: *Pleuroncodes planipes*, 4: *Hyperia galba*, 5: *Phronima Sedentaria*, 6: *Sergestes similis*, 7: *Pasiphaea chacei*, 8: *Pasiphaea pacifica*, 9: *Gaussia princeps*, 10: *Anuropus bathypelagicus,* 11: *Bathycalanus princeps*, 12: *Sergestes phorcus*, 13: *Hymenodora frontalis*, 14: *Gnathophausia ingens*, 15: *Paracallisoma coccus*, 16: *Acanthephyra curtirostris*, 17: *Boreomysis cahfornica*, 18: *Gnathophausia zoea*, 19: *Pasiphaea emarginata*, 20: *Systellaspis cristata*, 21: *Bathycalanus bradyi*, 22: *Gnathophausia gracilis*, 23: *Gnathophausia ingens*, 24: *Gigantocypris agassizii*, 25: *Gnathophausia gigas*, 26: *Notostomus* sp. **(B)** Fishes. These data indicate that the decrease in mass-specific metabolic rate with increasing depth is not a function of habitat temperature, i.e., an innate deep-sea low metabolic adaptation (Data from Childress [1975] and Torres and Somero [1988]).

Metabolic adaptation is primarily attributed to a marked decrease in enzyme activity in skeletal muscle, largely due to the low enzyme concentrations found in that tissue. Childress and Nygaard (1973, 1974) investigated not only metabolic rates, but also the body chemical composition (water content, protein, fat, carbohydrates, ash, carbon, nitrogen, energy content) of deep-sea fish species such as euphausiids, amphipods, decapods, cephalopods, and mollusks off the coast of California. As a result, it became evident that with increasing habitat depth, fish show increased water content, while crustaceans exhibit decreased nitrogen content, indicating a reduction in muscle mass (Ventura, 2006). This reduction in muscle mass likely accompanies a decrease in swimming ability. In California waters, activities of intermediate enzymes (citrate synthase [CS], pyruvate kinase [PK], malate dehydrogenase [MDH]) extracted from muscles of 24 fish species also decreased sharply with increasing depth of occurrence (MDO) (Childress and Somero, 1979). Furthermore, Drazen et al. (2015) examined the metabolic enzyme activities of 61 species of demersal fish collected from depths up to 3000 meters. Enzymes measured included CS, lactate dehydrogenase, MDH, and PK. They showed that differences in enzyme activity were observed between benthic and benthopelagic fish, with higher citrate synthase activity in benthopelagic species. Enzyme activity declined with depth in both groups. The depth-related trends were consistent across data sources, suggesting that metabolic rate is influenced by more than just body mass and temperature. These findings not only demonstrate that metabolic rates of captured organisms are not abnormal, but also suggest that the decline in swimming ability due to muscle weakening significantly contributes to their low metabolic rates. In essence, deep-sea organisms are born with low metabolic rates (Torres et al., 1979).

What would be the comparison of metabolic rates between deep-sea and related epiphytic species by adjusting metabolic rates for wet, dry body mass, carbon content, and nitrogen content? The Antarctic krill, *Euphausia superba*, have a moisture content of 88% and nitrogen content of 10–11% of dry weight, whereas salpas have body compositions of 96% and 1–3%, respectively. Comparing the metabolic rates of individuals of the same body weight in these two species, Ikeda and Mitchell (1982) reported that the former was 17 times higher than the latter in wet weight units, four times higher in dry weight units, and 0.8 times higher in nitrogen units. This requires us to consider what is appropriate to use as a unit of body weight. Traditionally, wet weight, dry weight, organic matter weight (dry weight − ash weight), carbon, and nitrogen have been used as units of weight (Zeuthen, 1947, 1953; Ivleva, 1980; Postel et al., 2000; Childress et al., 2008; Ikeda, 2008; McClain et al., 2012). It should be noted that the body composition of deep-sea organisms differs from that of shallow-sea organisms, thus the choice of body weight unit may lead to different results. In fact, when the metabolic rate of meso/bathypelagic crustaceans, fishes, cephalopods, and caecilians is converted to that of a 1 mgN individual (AMR: $\mu lO_2$ $mgN^{-0.8}$ $h^{-1}$) at 1°C, the AMR falls within a very narrow range (2 to 3) despite the large differences in body size, morphology, and swimming ability of the animal groups (Ikeda, 2009). The amount of nitrogen is proportional to the amount of protein, and thus to muscle mass. Therefore, if the reduction in metabolic rate in deep-sea organisms can be explained solely by a reduction in muscle mass, there should be no correlation between MDO and the metabolic rate per unit nitrogen content. However, contrary to this prediction, the correlation between metabolic rate per unit nitrogen and MDO remains significant, albeit slightly weaker for crustaceans and fish (Ikeda, 2009). This suggests that the decrease in oxygen consumption rate in deep-sea organisms cannot be explained solely by muscle atrophy.

The cave environment is similar to the deep-sea environment in terms of darkness, low temperature, and a constant scarcity of food. However, there are significant differences in water pressure and dissolved oxygen concentration. A comparison between cave-dwelling organisms (troglobites) and deep-sea organisms may help to evaluate the effects of water pressure and oxygen concentration on metabolic rates. Several studies have documented the metabolic rates of troglobites. For example, Paulsen and While (1969) and Paulsen (2001) reported that the metabolic rates of fish from the family Amblyopsidae are significantly lower than those of epipelagic fish, being comparable to those of deep-sea species. Additionally, their protein content seems to be intermediate between epipelagic and deep-sea fish, indicating that they retain a certain amount of muscle mass. Paulsen (2001) suggested that this is due to the necessity of swimming in response to occasional increases in water flow within the cave. On the other hand, the key differences between the cave and deep-sea environments likely lie in the ‘presence of predators’ and the ‘evolutionary timescale’. Cave fish experience almost no predation pressure within the cave environment and do not display escape behaviors. Furthermore, cave-dwelling fish have only adapted over a relatively short evolutionary period (1 to 3 million years) and show limited species diversification (Avise and Selander, 1972; Paulsen, 2001). In contrast, deep-sea fish have been evolving and adapting for over 50 million years, resulting in high species diversity (Childress, 1995). The differences in metabolic rates between these two groups may reflect evolutionary outcomes driven by predator-prey interactions.

Two hypotheses have been developed to explain the evolutionary driving mechanisms behind the low metabolism of deep-sea organisms, the “Visual Interaction Hypothesis” and the “Predation-Mediated Selection Hypothesis”. The former, proposed by Childress and Mickel (1985), suggests that organisms with functional eyes, such as amphipods, euphausiids, decapods, fish, and cephalopods, in the bright surface layers, evolved to quickly detect their prey or larger fish predators from a distance and rapidly swim to capture them or to escape. This requires well-developed muscles and consequently, a high metabolic rate. The fact that the relative heart and ventricle size decreases with depth also supports this hypothesis as an explanation for the reduced metabolic capacity of deep-sea sharks (Larsen et al., 2020). In contrast, in the dimly lit or completely dark mid- and deep-sea layers, prey cannot be seen, and predation pressure is greatly reduced, leading to a lack of selective advantage for high swimming ability. As a result, evolutionarily, muscles atrophied and metabolic rates decreased. This hypothesis predicts that species with non-functional eyes, such as copepods, chaetognaths, jellyfish, and ostracods, have metabolic rates and body chemical composition that are unaffected by habitat depth. Childress and colleagues conducted measurements on these taxa and reported that metabolic rates, CS, LDH, and PK levels remain constant regardless of MDO (Thusen and Childress, 1993, 1994; Thuesen et al., 1998), suggesting that the relationship between metabolic rates and MDO can be explained based on whether eyes are functional (Childress, 1995).

On the other hand, Ikeda et al. (2006a) carefully determined metabolic rates of more than 50 species of copepods living at depths of 500–3000 meters in the Oyashio region and found a tendency for higher metabolic rates at shallower depths. This contradicts the results of Thuesen et al. (1998) and cannot be explained by the Visual Interaction Hypothesis. Therefore, Ikeda et al. (2006a) proposed the “Predation-Mediated Selection Hypothesis”. This hypothesis posits that predation pressure is highest in bright surface layers, where species with high swimming abilities (and high metabolic rates) evolved to escape predation, regardless of visual capability. Thus, it predicts that metabolic rates decrease with increasing depth, regardless of whether the species have functional eyes. Data on the body chemical composition (water, carbon, nitrogen, ash) and energy content of copepods support this hypothesis, with only nitrogen decreasing with increasing depth (Ikeda et al., 2006b). This indicates that copepods inhabiting deep layers have lower muscle mass and lower metabolic rates per unit mass of muscle. This hypothesis should be tested in the future to examine whether increasing the swimming ability of copepods will improve their escape from faster-moving fish predators. It should also be noted that prey movement may induce more predator attacks than if the prey were stationary. In the food-scarce deep-sea environment, a lifestyle that lowers metabolic rates to make efficient use of occasional food resources is likely advantageous.

Energy balance is crucial for survival, and all biological responses are compromises among conflicting options. The copepods *Calanus pacificus* and *Calanus carinatus* remain at greater depths during periods between upwellings when food is scarce, thereby reducing their energy expenditure (Miller and Clemons, 1988). Benthic organisms also appear to adopt a strategy of lowering their basal metabolism between meals and rapidly increasing it when food becomes available (Herring, 2002). In fact, copepods enter a state of dormancy, which is thought to correspond to a phase in which metabolic rates drop significantly, similar to diapause in insects. During such a period of dormancy or hibernation, even homeothermic mammals exhibit metabolic rates that fall significantly below those predicted by size-scaling laws (Geiser, 2004). However, physiological mechanisms underlying these low metabolic responses remain unclear. Regardless of whether physiological dormancy occurs, descending into colder, deeper waters reduces metabolic demands necessary to maintain bodily functions for some groups. On the other hand, planktonic organisms such as euphausiids and hyperiid amphipods in the family Scinaidae seem to survive by simply lowering their metabolic rates and living off stored reserves, without undertaking seasonal migrations.

As mentioned at the outset, greater ocean depths result in changing physical conditions, such as water temperature. Understanding environmental and metabolic adaptations achieved through deep diving in the ocean awaits further investigation. Determining which aspects of energy use are reduced or increased necessitates considering a wide range of options. It is rare for a single option to be employed; instead, a suite of related energetic adaptations is generally employed.

## CONCLUSIONS

Much of the life on our planet exists in deep-sea environments. Deep-sea organisms are gluttonous, taking advantage of opportunities to maximize their energy intake. They increase their assimilation efficiency and live in a way that minimizes energy expenditure. However, despite their higher assimilation efficiency, deep-sea organisms still appear to be chronically undernourished, as evidenced by their higher water content. Key to pressure adaptation in enzymes is the ability to effectively regulate catalytic capacity and maintain protein structure, rather than maintaining an absolute rate of catalytic action. Although scaling laws apply to shallow-water and terrestrial animals, mass-specific metabolic rates of deep-sea animals are extremely low. Deep-sea fishes may consume oxygen at rates only 5–10% of those that characterize shallow-water species. The biochemical basis of this metabolic adaptation is a low level of enzyme activity in skeletal muscle, but not heart or brain, mainly due to the low enzyme concentrations in that tissue. With increasing minimum occurrence depth, metabolic rates decrease. However, there may be no significant difference in the metabolic rates of shallow- and deep-water benthic species (Seibel and Drazen, 2007). A unified understanding of the relationship between metabolism and habitat depth has yet to be established. On the other hand, given that the essence of metabolism is protein synthesis, it has been suggested that metabolic rates should be examined on a protein molarity basis rather than on a wet weight basis (Ventula, 2006; Ikeda, 2008). Regions investigated so far are limited, and the relationship between metabolic activity and habitat depth in benthic taxa is still not well understood. Future research should focus on ontogenetic analysis from the perspective of life history. Additionally, methods to analyze the impact of global climate change on metabolism at a global scale will also be important.

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## COMPETING INTERESTS

The authors have no competing interests to declare.

## AUTHOR CONTRIBUTIONS

MY: Conceptualization, Methodology, Investigation, Writing – original draft, Supervision, Funding acquisition, Visualization. SA: Investigation, Writing – review and editing. ST: Investigation, Writing – review and editing.

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