Effects of Foraging Strategies on Metabolic Rates in Epipelagic Squids

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Trueblood LA, Seibel B. 2014. Slow swimming, fast strikes: effects of feeding behavior on scaling of anaerobic metabolism in epipelagic squid. *Journal of Experimental Biology* 217: 2710-2716.

The marine epipelagic zone, located within the upper photic zone, is one of the largest and most productive habitats on Earth (Lewallen et al. 2010). The epipelagic zone supports a wide variety of organisms from zooplankton to predatory fish to massive blue whales. Given this diversity, many pelagic fishes rely on specialized feeding behaviors, supported by high metabolic rates and anaerobic metabolic capacity, to outcompete others for prey. Epipelagic squids have been shown to have the highest metabolic rates in the oceans because of their demanding foraging strategies and the use of jet propulsion (Trueblood and Seibel 2014). In the open ocean, there is very little opportunity to stalk prey by hiding, and thus the predator must rely on bursts of speed to cover larger distances and avoid detection. The ability to maintain high speeds depends on the amount of white and red muscle within predatory fish. White, fast-twitch muscles make up the bulk of these fish, whereas red, slow-twitch muscles are found only in a small midlateral band under the skin (Zhang et al. 2010). In order to swim for prolonged periods at high speeds, an organism uses dominantly white muscle and eventually fatigues. Although squid aren't fish, per say, they do express similar feeding behaviors to predatory fish like tuna and cod, including engaging prey at high speed. Based on this, squid must also have some amount of white muscle within their musculature to support jet propulsion. In addition to the presence of white muscle, the use of tentacles, selection of prey, body shape, and size determine the efficiency of an epipelagic squid to capture prey. Depending on the efficiency of the hunt, a squid's metabolic capacity is directly affected (Trueblood and Seibel 2014).

Trueblood and Seibel (2014) examined the enzymatic proxies of anaerobic metabolism in two species of pelagic squid, *Dosidicus gigas* and *Doryteuthis pealeii*, over a size range of six orders of magnitude. *D. gigas* is a relatively large squid found along the west coast of North and South America, with ranges extending out into the equatorial Pacific. *D.* pealeii is a smaller Atlantic coastal squid. The data for *D. gigas* in this experiment forms one of the largest intraspecific studies performed to date because of the use of six sizes of the organism. By incorporating different sizes of squid, Trueblood and Seibel tested their main question: would activity of the anaerobically poised enzymes be high during prey-capture and increase with size (as found in other ecologically similar fishes)? They also questioned whether or not additional cephalopod-specific traits (using tentacles, body shape, etc.) would create a diminished reliance on anaerobically based fueled burst activity during feeding.

The squids were captured using a few different methods based on their size: hand lines were utilized for the largest animals, while squid jigs, dip nets, and trawls were employed for increasingly smaller organisms. Samples of *D. gigas* were captured in Guaymas Basin, Gulf of

California whereas *D. pealeii* were collected from Newport, Rhode Island. After tissue samples were taken for enzyme analysis from the anterior ventral mantel, all animals were weighed and immediately frozen in liquid nitrogen. Not only did the tissue samples serve to determine the octopine dehydrogenase (ODH) activity (the anaerobic metabolic potential was estimated from ODH activity measurements according to the methods of a 1980 study by Baldwin and England), they also proved insightful into the discovery of the amounts of red and white muscle within the squids. The specimens were maintained at -80 degrees Celsius until they were assayed.

Trueblood and Seibel's data shows that *D. gigas* has some of the highest capacities for anaerobic metabolism amongst cephalopods with a large range of ODH activities. *D.* gigas's ODH activity seemed to support the original hypothesis up until a breakpoint at 17.76 grams (Focus Figure 1.). Any squid larger than this displayed a clear decrease in anaerobic capacity. In order to evaluate these enzymatic activities fully, the scientists looked at the tissue composition of *D. gigas*. They found that citrate synthase activity in *D. gigas* decreases with increasing size, which supports the possibility of increased relative red muscle mass with size. Because of the increased displacement of white muscle at larger sizes, the squid has a reduced burst locomotory capacity. That being said, however, the scientists found an overall negative scaling trend of ODH for both *D. gigas* and *D. pealeii.* as their size increased. This scaling trend differs from those reported for other pelagic vertebrates (Fig. 1).

In regards to the other cephalopod-specific traits and whether or not they created a diminished reliance on anaerobic energy sources during prey capture, the scientists uncovered some results in support of their hypothesis. By relying on tentacles, squid do not have to swim as far or as fast to reach their prey. Therefore, as size increases, larger squid will have a longer reach with their tentacles and decrease the need for extended bursts of speed while swimming. In terms of prey selection, *D. gigas,* regardless of their own size, generally feed on small fish, ranging from 2-7 cm in length, and zooplankton. By selecting small-sized prey, the burst speed and power required to match prey speed decreases drastically. Lastly, having a body shape that places the largest dorso-ventral body depth as far posterior to the mouth as possible provides an advantage during prey capture and diminishes closure time. All three of these qualities have the ability to reduce a squid's reliance on anaerobic energy sources!

Based on their results, Trueblood and Seibel demonstrated that anaerobic metabolic capacity in these two squids scale negatively with body mass. This discovery disproves their original hypothesis. Despite the thorough tests employed and careful equations used to determine enzyme activity, this study raises some important questions. How would the results differ if the squid were measured in their own natural environment as opposed to a controlled lab environment? Would additional physiological or behavioral factors influence metabolism? How do the metabolisms of squid, or other similar organisms, function in different water temperatures? Lastly, do certain species of squid exhibit varying levels of white versus red muscle that may make them more efficient hunters than others? Studying these organisms further will give scientists and researchers more insight into epipelagic squid feeding behaviors and ultimately help us to understand just a few of the wide variety of species that inhabit the oceans of the world.

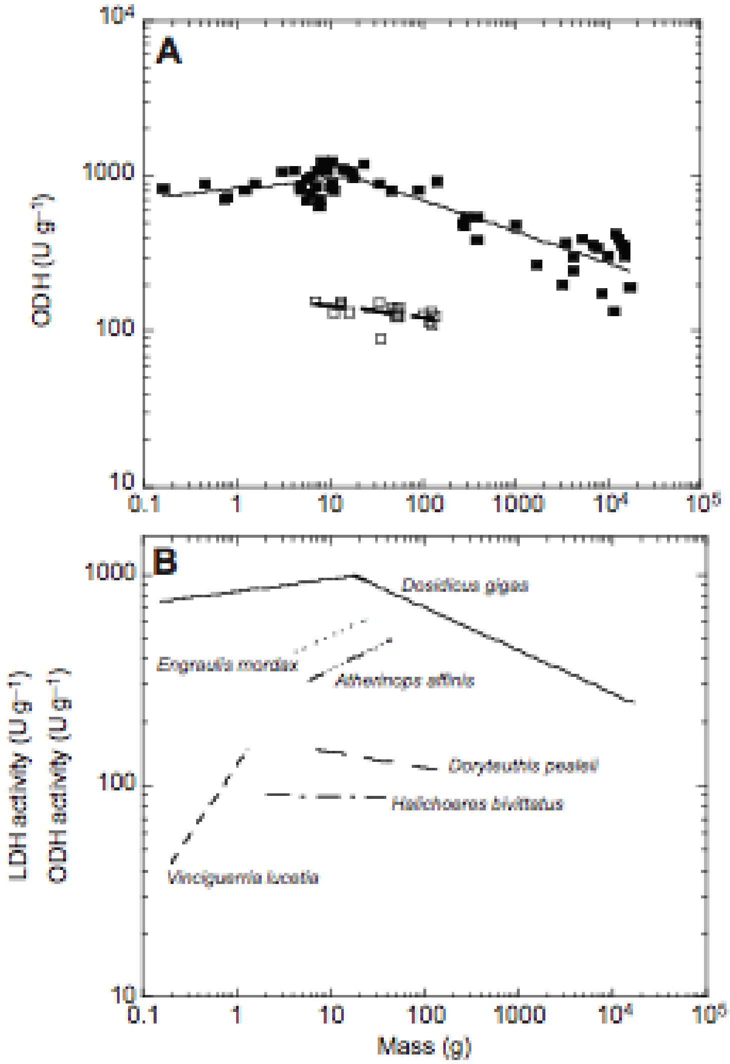

Fig. 1. Scaling of anaerobic activity. (A) Effect of body mass on octopine dehydrogenase (ODH) activity in *Dosidicus gigas* (filled squares) and *Dorteuthis pealeii* (open squares). In both squids, there is an overall negative scaling effect with the ODH. *D. gigas* shows a breakpoint at 17.76 g, at which the ODH activity begins to downturn whereas *D. pealeii* never experiences any increase in ODH. (B) Comparative lactate dehydrogenase (LDH) activity for other species of epipelagic fish compared with ODH activity in the two squid. Most of the fish experience a positive scaling trend in which the larger the fish is, the higher the LDH activity is.

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