Breathing Easy in an Oligoxic World:
Vampyroteuthis infernalis (Phy. Mollusca, Cl. Cephalopoda) Adaptations to the Oxygen Minimum Zone

Deanna Steckler

Abstract
This review explores the existing literature on the Vampire Squid from Hell, Vampyroteuthis infernalis (Phylum Mollusca, Class Cephalopoda, Order Vampyromorpha). They are largely unstudied deep water cephalopods found in the oxygen minimum zone (OMZ) throughout the world's temperate and tropical oceans. Their unique morphology and genetic ambiguity has contributed to scientific debate regarding their phylogenetic relationships, to which there is still no definitive answer. Vampyroteuthis are so well adapted to life in the OMZ that foraging, locomotion, and antipredator behaviours are entirely unique among cephalopods. Despite a lack of direct research, inferences are made to determine the effects of anthropogenic disturbance on the vampire squid.

Most regions of the Earth have been thoroughly explored and mapped. However, one massive region that is still largely unknown is the deep sea (Berger 2009). Scientists are regularly discovering new organisms in this alien environment (Berger 2009), and those that have been identified are still largely mysterious (Healy 1989). One animal that fits into this category is Vampyroteuthis infernalis, the Vampire Squid from Hell. This species is remarkable because it differs greatly from any other member of its taxonomic class in metabolic rate, locomotion (Seibel et al. 1997), feeding (Hoving & Robison 2012), and anti-predator behaviours (Robison, Reisenbichler et al. 2003; Young, 1972). Even though the vampire squid was first discovered in 1903, many of its basic biological and behavioural characteristics, such as reproduction, are still unknown (Hoving & Robison 2012; Lindgren, Giribet, & Nishiguchi 2004; Seibel et al. 1997). As researchers continue to study Vampyroteuthis, more fascinating qualities of this species are being revealed (Hoving & Robison 2012; Robison et al. 2003).

Vampyroteuthis is a Mollusc in the class Cephalopoda, which includes octopuses, cuttlefish, nautilus, and squid. "Vampire squid" is a misleading name because Vampyroteuthis are neither true squid, nor vampires (Seibel et al. 1997; Young 1967). Early researchers named the species for its dark red to black coloured skin, glowing red eyes, and spiny webbed arms (Seibel et al. 1997). There is scientific debate regarding their phylogeny; because, analysis of morphological or genetic evidence render different conclusions (Healy 1989; Lindgren et al. 2004; Yokobori et al. 2007; Young et al. 1998).

Similar to nautilus and cuttlefish, Vampyroteuthis has been categorized into its own order, Vampyromorpha, within the class Cephalopoda (Young et al. 1998). Originally, their eight webbed arms, fleshy spines (cirri), and two anterior fins resulted in them being grouped within the octopod suborder Cirrata (finned octopods) (Young et al. 1998). This relationship was supported by sperm analysis conducted by Healy (1989). However, Vampyroteuthis possess two specialized feeding arms (retractile filaments) visually similar to squid feeding tentacles (Young et al. 1998). Comparative analysis conducted on both animals determined structural and developmental differences, which suggests Vampyroteuthis and squid likely diverged prior to the evolution of both species' feeding appendages (Young 1967). The presence of the filaments was the definitive characteristic that determined its elevation to Vampyromorpha, and the species is currently considered an intermediate between octopods and squid (Young et al. 1998).

More recently, scientists have attempted to determine the sister taxon to Vampyroteuthis with genetic evidence. Nautilus and cuttlefish have been shown to be monophyletic with squid (Lindgren et al. 2004), but several studies have reported that the vampire squid can be more closely related to either squid or octopods depending on the genetic parameters tested (Lindgren et al. 2004; Yokobori et al. 2007). Therefore, there is still no conclusive answer to the closest relative of Vampyroteuthis. Often, for simplicity's sake, researchers will base their studies on a Vampyromorpha and Octopoda monophyly regardless of the controversy (Carlini et al. 2001; Lindgren et al. 2012). Further research is needed on this enigmatic animal to determine its evolutionary history.

Not all aspects of Vampyroteuthis are so controversial. They are free-swimming, midwater organisms found throughout the world's temperate and tropical oceans at depths up to 3000m, though 600 to 1000m is most common (Siebel et al. 1997). The species resides in a hostile environment known as the oxygen minimum zone (OMZ). While there are cephalopods that spend part of their lives in the OMZ, Vampyroteuthis is the only species identified to live in this habitat for its entire life cycle (Siebel et al. 1997).

The OMZ is the deep water layer that contains lower oxygen concentrations than any other ocean layer. It varies by location, but typically lies 20 to 1000m below the surface situated between the highly wind-mixed surface waters and the oxygen saturated deep waters (Wright et al. 2012). The deepest water in our oceans originates at the polar regions. It is cold, dense, and high in oxygen. The dense water sinks and travels around the world via currents. It retains much of its oxygen due to a lack of organic matter (Wright et al. 2012). Nearly 90% of organic matter falling from the surface waters is decomposed within the first 1000m; therefore, in the deepest water there is little oxygen consumption. The OMZ has the greatest amount of decomposition and creates a midwater band of depleted oxygen (Wright et al. 2012). Organisms that live in the OMZ for their entire lives are referred to as oligoaerobics (oligo = too little or few, aerobic = uses oxygen) because they use oxygen, but in tiny concentrations (Siebel et al.

1997). Oligoaerobics, such as Vampyroteuthis, are highly specialized in maximizing oxygen intake, reducing its use, and conserving energy (Siebel et al. 1997), all qualities necessary to survive the suffocating environment.

The pressures related to living in low amounts of oxygen have selected for several adaptations in Vampyroteuthis. They highly regulate their oxygen consumption via an extremely low metabolic rate (mean = 0.06 μmol O_2 g^{-1} h^{-1}) (Siebel et al., 1997). One individual from the Siebel et al. (1997) study was measured to have the lowest metabolic rate of any cephalopod on record (0.02 μmol O_2 g^{-1} h^{-1}). To put this in perspective, the species' metabolic rate is more comparable to that of structurally simpler jellyfish (0.09 μmol O_2 g^{-1} h^{-1}) (Thuesen & Childress, 1994), than to squid (0.59 μmol O_2 g^{-1} h^{-1}) occupying similar depths (Siebel et al. 1997).

In order to maximize metabolic efficiency in the OMZ, Vampyroteuthis have adapted energetically conservative methods of locomotion. Most open-water cephalopods travel by means of jet propulsion; they pass water quickly through their outcurrent siphons (Siebel et al. 1997). This method of propulsion is efficient in terms of speed, but the amount of oxygen required to be extracted by the gills is large. As a result, adult Vampyroteuthis use jet propulsion rarely and only as a last resort to escape predators (Young & Vecchione 1999). Most often, they use the two large fins on their mantle to "fly" horizontally through the water (Siebel et al., 1997; Young & Vecchione 1999). Secondarily, they are also known to use their webbed arms to "bell-swim," similar to the locomotion of jellyfish. This movement also requires little oxygen (Siebel et al. 1997). Vampyroteuthis are experts at maximizing reduced oxygen concentrations by limiting energetically expensive locomotion. This trend is mirrored in most other facets of their specialized adaptations, particularly foraging behaviour.

Due to the rarity of vampire squid and the depth at which they thrive, the dietary choices of the species had eluded scientists until recently (Seibel et al. 1997; Young 1967; Young 1972). The OMZ has fewer predators than other environments, but this also means fewer prey organisms as well (Hoving & Robison 2012). Cephalopods that spend time in the OMZ traditionally predate upon the low abundance of fish, cnidarian, shrimp, and squid. The food evidence found in Vampyroteuthis was often too decomposed to suggest predatory behaviours. Hoving and Robison (2012), studied wild-caught specimens in their lab as well as wild individuals with a remote operated underwater vehicle. They observed that both groups of organisms fed upon the marine snow—dead organic matter (detritus)—constantly floating down from shallower depths. The research demonstrates that Vampyroteuthis eat whatever detritus they encounter, including decomposing zooplankton, crustaceans, fecal matter, and discarded mollusc shells. They are the only cephalopod known to exclusively scavenge detritus instead of predate upon other organisms (Hoving & Robison 2012).

Vampyroteuthis feeding mechanism is also unique in that unlike squid, the species lack feeding tentacles and possesses instead sensory retractile filaments (Hoving & Robison 2012). Scientists have been puzzled about the purpose of these structures for decades. They were originally thought to assist in either predator detection or in the hunting of prey (Young 1967). Hoving and Robison (2012) found that they are essential in scavenging, rather than predation. Due to the essential need to conserve energy in the OMZ, Vampyroteuthis projects its extremely long filaments and waits. When a piece of detritus touches a filament, the vampire squid retracts it. Instead of pulling the long structure to its mouth, it touches the food to the oral surface of one of the arms. The arms secrete mucus, which gathers the food and transports it to the mouth via the cirri. These feeding filaments allow Vampyroteuthis to remain essentially motionless in the water column, conserving energy while feeding (Hoving & Robison 2012). The vampire squid are not simply scavengers, but the only filter feeding cephalopod known to date. This specialized adaptation developed solely due to living in the OMZ.

Surviving in environments with a low oxygen concentration is a major difficulty for many organisms. The OMZ has such low oxygen that most species must migrate to an oxygen richer habitat on a regular basis (Seibel et al. 1997). This restriction results in few predators, which benefits Vampyroteuthis. Because of the inhospitable environment, and few studies conducted, Vampyroteuthis have very few known predators. They are rarely found in the stomachs of larger organisms (Hoving & Robison 2012). They have been found in the stomachs of deep-water fish such as the Giant Grenadier, Albatrossia pectoralis (Drazen et al. 2001) as well as in pinnipeds and cetaceans (Robison et al. 2003). A large study by Markaida and Sosa-Nishizaki (2010) found that Vampyroteuthis is a common prey item of the blue shark, Prionace glauca. Possibly more interesting than the predators of Vampyroteuthis are the anti-predation mechanisms they use to evade being eaten.

Vampyroteuthis have evolved extremely sophisticated antipredator behaviours. If threatened the first line of defense is to curl its webbed arms up around its head. The oral surface of the web is lined with fleshy spines (cirri) and this curling behaviour projects them outwards (Robison et al. 2003). While assumed to be a defensive posture by scientists, it is considered a bluff because the cirri are soft, not hard or sharpened (Robison et al. 2003; Yokobori et al. 2007).

A more dramatic anti-predator behaviour is achieved by the use of bioluminescent photophores in various locations on its body (Young 1972). Photophores are light-producing organs common to many marine organisms (Robison et al., 2003), such as comb jellies (ctenophores) (Johnson et al. 2012) and lantern sharks (Etmopterus spinax) (Renwart et al. 2014). The most dramatic photophores possessed by Vampyroteuthis are their two extremely large glowing eyes (Young 1972). Vampire squid have the ability to completely control the light produced by their eyes. They can adjust brightness as well as diameter of the photophores. Similar to the previously mentioned feeding filaments, scientists originally thought that the bioluminescence was to attract prey (Young 1972), but it is now agreed upon that the primary purpose is to confuse predators (Robison et al. 2003). In addition to their eyes, Vampyroteuthis also have a photophore at the end of each of their eight arms. These can be moved and manipulated in very dramatic ways, which likely confuses predators in the no light environment (Robison et al. 2003). As a last line of defense, vampire squid can release bioluminescent mucus from their oral surface, similar to the ink sac of other cephalopods. This creates a cloud of light around its body that serves as a distraction while it uses jet propulsion to escape (Robison et al. 2003). Even avoiding predation is conducted using as little energy as possible, which highlights Vampyroteuthis' specialization to the OMZ.

For an organism so well adapted its environment, it may be assumed that any human alteration to the OMZ would negatively affect Vampyroteuthis. While there is no information reported on how humans affect the vampire squid directly, the opposite may be true. Evidence suggests that human activity may have a positive effect on the range and food supply of Vampyroteuthis. Agricultural run-off and sewage deposits increase the amount of algal growth and decomposition that occurs in the shallow depths (Wright et al. 2012). This decomposition lowers the oxygen concentration which expands the OMZ upwards. As the oxygen is depleted, many organisms die from suffocation and drift down as detritus (Wright et al. 2012), which may in turn increase the food availability of Vampyroteuthis.

Ocean acidification may have a similar effect. Decreased pH of seawater, a result of excess CO_2 in the atmosphere, corresponds to decreased dissolved oxygen levels in the water column (Wallace et al. 2014). This can lead to increased organism mortality of non-adapted organisms (Wallace et al. 2014) which may increase Vampyroteuthis potential food supply. It is possible that expansion of the OMZ can lead to anoxic environments (locations of no oxygen) (Wright et al. 2012) which would be detrimental to Vampyroteuthis; however, there are no studies published that suggest that they would not simply move to a more suitable oxygenated environment. Unlike most marine habitats, human impact on the ocean may actually increase the survivability of Vampyroteuthis.

Vampyroteuthis infernalis is an extraordinary creature that has evolved to live in one of the least hospitable environments on Earth. Every aspect of its life is perfectly adapted to conserve energy (Hoving & Robison 2012; Robison et al. 2003; Siebel et al. 1997). Unlike other cephalopods, they "fly" through the water column using fins or bell-swim like a jellyfish (Siebel et al. 1997), and they are the only filter-feeding scavenging detritivore in the class (Hoving & Robison 2012). Lastly, vampire squid use their morphology and bioluminescent qualities to demonstrate a wide range of distinctive antipredator behaviours (Robison et al. 2003; Young 1972). There is still much to learn about even its most basic biology and evolution, so it is impossible to guess what other unique secrets

Vampyroteuthis possesses. Further research is required to determine the direct effects humans have on it, but evidence suggests (Wallace et al. 2014; Wright et al. 2012) its specialization to the OMZ may buffer it against the harshest anthropogenic influences.

References

Berger, W. H. 2009. Ocean: Reflections on a Century of Exploration. Oakland (CA): University of California Press.

Carlini, D. B., Young, R. E., & Vecchione, M. 2001. A molecular phylogeny of the Octopoda (Mollusca: Cephalopoda) evaluated in light of morphological evidence. Molecular phylogenetics and evolution. 21: 388-397.

Drazen, J. C., Buckley, T. W., & Hoff, G.R. 2001. The feeding habits of slope dwelling macrourid fishes in the eastern North Pacific. Deep sea research part I: Oceanographic research. 3: 909-935.

Healy, J. M. 1989. Spermatozoa of the deep-sea cephalopod Vampyroteuthis infernalis Chun: Ultrastructure and possible phylogenetic significance. Philosophical transactions of the royal society of London B. 323: 589-600.

Hoving, J. T. & Robison, B. H. 2012. Vampire squid: Detritivores in the oxygen minimum zone. Proceedings of the royal society B. 279: 4559-4567.

Johnson, W. S., Allen, D. M., & Fylling, M. 2012. Ctenophores: Comb jellies and sea walnuts. In Zooplankton of the Atlantic and Gulf Coasts: A Guide to Their Identification and Ecology (pp. 124-129) Baltimore (MD): John Hopkins University Press.

Lindgren, A. R., Giribet, G., & Nishiguchi, M. K. 2004. A combined approach to the phylogeny of Cephalopoda (Mollusca). Cladistics. 20: 454-486.

Lindgren, A. R., Pankey, M. S., Hochber, F. G, & Oakley, T. H. 2012. A multi-gene phylogeny of Cephalopoda supports convergent morphological evolution in association with multiple habitat shifts in the marine environment. BMC evolutionary biology. 12: 1-15.

Markaida, U. & Sosa-Nishizaki, O. 2010. Food and feeding habitats of the blue shark Prionace glauca caught off Ensenada, Baja California, Mexico, with a review on its feeding. Journal of the marine biological association of the United Kingdom. 90: 977-994.

Renwart, M., Delroisse, J., Claes, J., & Mallefet, J. 2014. Ultrastructural organization of lantern shark (Etmopterus spinax Linnaeus, 1758) photophores. Zoomorphology. 133: 405-416.

Robison, B. H., Reisenbichler, K. R., Hunt, J. C., & Haddock, S. H. 2003. Light production by the arm tips of the deep-sea cephalopod Vampyroteuthis infernalis. The biological bulletin. 205; 102-109.

Seibel, B. A., Thuesen, E. V., Childress, J. J., & Gorodezzky, L. A. 1997. Decline in pelagic cephalopod metabolism with habitat depth reflects differences in locomotion efficiency. The biological bulletin. 192: 262-278.

Thuesen, E. V. & Childress, J. J. 1994. Oxygen consumption rate and metabolic enzyme activities of oceanic California medusa in relation to body size and habitat depth. The biological bulletin. 187: 84-98.

Wallace, R. B., Baumann, H., Grear, J. S., Aller, R. C., & Gobler, C. J. 2014. Coastal ocean acidification: the other eutrophication problem. Estuarine, Coastal and shelf science. 148: 1-13.

Wright, J. J., Konwar, K. M., & Hallam, S. J. 2012. Microbial ecology of expanding oxygen minimum zones. Nature reviews microbiology. 10: 381-394.

Yokobori, S., Lindsay, D. J., Yoshida, M., Tsuchiya, K., Yamagishi, A., Maruyama, T., & Oshima, T. 2007. Mitochondrial genome structure and evolution in the living fossil vampire squid, Vampyroteuthis infernalis, and extant cephalopods. Molecular phylogenetics and evolution. 44: 898-910.

Young, R. E. 1967. Homology of retractile filaments of vampire squid. Science. 156: 1633-1634.

Young, R. E. 1972. Function of extra-ocular photoreceptors in bathypelagic cephalopods. Deep sea research. 19: 651-660.

Young, R. E., Vecchione, M., & Donovan, D. T. 1998. The evolution of coleoid cephalopods and their present biodiversity and ecology. South African journal of marine science. 20: 393-420.

Young, R. E. & Vecchione, M. 1999. Morphological observations on a hatchling and a paralarva of the vampire squid, Vampyroteuthis infernalis chun (mollusca: cephalopoda). Proceedings of the biological society of Washington. 112: 661-666.