Forbes & a Filter-Feeder

By Zach Hancock

The portrait of Edward Forbes by J.H. Maguire in 1850 portrays a slightly bemused man, clean-shaven with wavy long hair, arm perched comfortably on the back of the chair. Across his lap is an untitled book closed partially around his narrow fingers, as if Maguire had arrived unannounced, interrupting Forbes' reading. Nine years prior, the naturalist and English father of marine biology sets out on an 18-month expedition aboard the HMS *Beacon*. The vessel surveyed the depths of the Aegean Sea with a crude, basket-like dredge. According to Anderson & Rice (2006), this was hard-work as the ship—driven almost entirely by wind-power—struggled to maintain constant speed, and these dredges often rapidly filled with mud making hauling them up laborious. Despite, the crew hauled 100 dredges over the course of the voyage to depths of 420 m. Anderson & Rice report that at night, the captain and some crew members would pitch-in to help Forbes dissect and preserve the specimens collected from the dredges; though he certainly made important drawings of his findings, his comical cartoon depiction of the tiny dredge surrounded by grinning sea critters all avoiding its net is perhaps more telling. Indeed, Forbes would later formulate his 'abyssus theory,' that there was a decreasing abundance of life at increasing ocean depths, an idea supported by his observations aboard the *Beacon*.

On the surface, the idea seems intuitive—indeed, Forbes was influenced by work by Alexander von Humboldt, who, in 1850, published *Views of Nature*, which recorded the tendency for life to decrease at higher altitudes. A marked decrease in temperature and lack of nutrients at such environmental extremes seemed a useful analogy for Forbes—the dark, cold abyssal depths of the ocean seemed to mirror the apex of a mountain. How could life possibly survive without light or nutrients?

Obviously, Forbes could not have known about the energy-rich deep-sea hydrothermal vents that support a wide diversity of life (for examples, see Portail *et al.* 2016), but contradictory evidence existed during his time. For example, the vessel *Isabella*, captained by John Ross, had collected specimens such as the amazing basket-star, *Gorgonocephalus arcticus* (Leach 1814), from depths of ~1,000 m (Anderson & Rice point out that Ross initially miscalculated his sampling depth as 1,465 m). Perhaps Forbes' reliance upon the 'uninhabitable mountaintop' analogy, as appealing as it was, biased him against the possibility of deep-sea life. Indeed, a key difference exists between Humboldt's mountaintop and Forbes' abyssus—what field ecologist William Beebe would call 'marine snow.'

Marine snow is descending organic matter—when things above die or defecate, a portion of that content will slowly sink to the ocean depths. Here, in the dark, cold abyss, a multitude of life exists by filtering these particles from the water or scraping them from the ocean floor.

Life in the deep-sea is still poorly known, largely owing to the difficulty of adequately sampling at such great depths. Many specimens collected from the deep-sea are brought-up in trawls—not too different from Forbes' dredges. Often biologists are forced to describe species by the fractured parts that survive the haul.

Organizations such as the Monterrey Bay Aquarium Research Institute (MBARI) and the U.S. National Oceanographic and Atmospheric Administration (NOAA) have launched various initiatives with the hopes of closing the gap in our knowledge of the deep-sea. Recently, an expedition titled “2016 Exploration of the Marianas” deployed a remote-operated vehicle—the *Deep Discoverer*—to photograph and collect samples of fauna from the Mariana Trench. The trench is a colossal ocean valley to the east of the Mariana Islands, running about 1,500 miles in length and a maximum recorded depth of almost 11,000 meters (Nakanishi & Hashimoto 2010).

On June 30, 2016, at a sight known as “Twin Peaks,” the *Deep Discoverer*, while at depths of 4,800 m, moseying along the seafloor, encountered an odd crustacean that appeared immobile and facing the current. The vehicle halted for several moments, snapping photographs of the shrimp and capturing its behavior on video. The shrimp was ~120 mm in length with a dull, splotchy red carapace. After remaining completely still for a time, probably spooked by the vehicle’s thrusters that toss-up the clay sediment, the shrimp then flayed its anterior legs into the current. This action revealed rows of setae lining the first three legs (called ‘pereopods’). For the remainder of the observation, the shrimp faced the current as if offering it a hug.

Video footage and photographs were streamed from the expedition to collaborators around the world, including Dr. Mary Wicksten, an EEB-associated faculty member at Texas A&M University, College Station. She immediately recognized the shrimp as a member of the family Stylodactylidae—a group that includes several known deep-sea caridean shrimp. However, only a handful of specimens exist, and are in poor condition. There is a single specimen of the benthic shrimp *Bathystylodactylus bathyalis*, recovered from a trawl in the Coral Sea, missing all its legs. None of the group have ever been captured alive.

This footage thus represents the first-ever look at a living deep-sea caridean. And what of the odd intimate gesture the shrimp offered the current? Wicksten *et al.* (2017) propose that this behavior is analogous to the ‘filter-basket’ formed by euphausiaceans. However, the euphausiaceans actively pump water, whereas the stylodactylid appeared to capture the marine snow passively. In a conversation with Dr. Wicksten, she explained to me that these shrimps have sophisticated anatomical specializations that allow them to differentiate at several stages of feeding between edible particles and sandy debris. For example, the potential food particle is captured by the setae on pereopods 1-3 and then passed up to the highly modified maxillipeds, of which decapods have three. Each of these post-oral mouthparts are armed with an ‘exopod’ and an ‘endopod,’ a scissor-like split of the appendage itself. This allows each of these segments to be further modified independently—the endopod, for instance, is usually heavily setose and can chemically ‘taste’ the food particles. If something distasteful is discovered, it will pass the particle to the exopod, which then flicks it away. A similar process occurs at the 1$^{st}$ and 2$^{nd}$ maxilla, which add additional food processing. The complex procedure is beneficial for a passive filter feeder like the *B. bathyalis* filmed by *Deep Discoverer* as it can avoid wastefully digesting clay sediment stirred up by ROVs.

This is not the first interesting finding that Dr. Wicksten has made with the help of the NOAA-sponsored expedition. In 2016, she described the first-ever recording of a deep-sea snail (*Gaza sp.*) ‘tumbling’ away after being startled by the ROV (Wicksten 2016). Forbes would undoubtedly be impressed—Anderson & Rice note that his true passion was for mollusks. His drawings of British nudibranchs with Hanley are impressive, a far-cry from his cartoon dredges. *Deep Discoverer* has captured an amazing variety of organisms either previously unknown or poorly known to science—including long-legged isopods, a giant purple hemichordate (acorn worm), and a gaping tunicate.

Humboldt's barren mountainside analogy clearly isn't manifest in the deep-sea as Forbes hypothesized. His skepticism about marine life at abyssal depths is not unfounded, by any means, but he—and many of his contemporaries—underestimated the creative power of natural selection to mold specializations to overcome the unique challenges of the deep-sea. This filter-feeding stylodactylid shrimp is but one example of the incredible adaptability of living forms.

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