

Quick guide

MacropinnaSönke Johnsen^{1,*}
and Steven H.D. Haddock²

What is Macropinna and what does it tell us about how we understand the deep sea? Deep-sea biology, especially in the water column, is like quantum mechanics, in that the very act of observing this dark, featureless world disturbs the system. So, we are left doing 'forensic biology', in which we try to understand the life of an animal without ever seeing it behave naturally. The deep-sea opisthoproctid fish *Macropinna microstoma* is an example of this (Figure 1). This north Pacific fish, found at 600–800 meters, has only been observed seven times in 30 years by the remotely operated vehicles (ROVs) of the Monterey Bay Aquarium Research Institute (MBARI). Although a quick glance might suggest two small mournful eyes near the mouth, closer inspection shows those to be olfactory

organs. The real eyes are enormous, with two green spheres for lenses, encased in a fully transparent head like the pilot and co-pilot in a small plane. The few observations, all under bright ROV lights that likely affected the animal's behavior, tell us little, and instead scientists from MBARI have had to piece together a picture based on a few lab observations, morphology, and an understanding of how animals try to see in the dark.

Why is it hard to see in the deep sea? The obvious answer of course is that it's dark, but it's astonishing how dark the ocean actually gets. Light levels in the sea drop exponentially with depth at a rate that depends strongly on wavelength. Even in the absolute clearest tropical waters, the blue-green light that is attenuated the least drops to 1% of its surface value by 100 meters, and then by about 10-fold for every 100 meters below that. At 300 meters, the illumination is about equivalent to a full moon, and by 850 meters it's like an overcast moon-less night, which is the limit of our vision. The average ocean

depth is approximately 4000 meters, so even in the clearest waters, the vast majority of the habitat is no brighter than night. The top 200 meters of the ocean in many places is also not clear, being filled with phytoplankton, dissolved organic material, and possibly sediment, making the ocean underneath it even darker. Outside of the blue-green wavelengths, there is really no light at all, other than the lights that organisms bring with them in the form of bioluminescence. So animals in most of the ocean have to fight for every photon.

How do deep-sea animals manage to see then? Even though eyes of oceanic animals come in wondrous diversity of forms, it's useful to think of them as digital cameras. Using this analogy, there are only four ways to increase their sensitivity: (1) use a better sensor; (2) take a longer exposure; (3) have bigger pixels; or (4) have a larger pupil and lens. Retinas, the sensors, are already about as good as they can be — able to count individual photons — so there's little room for improvement there. Having a



Figure 1. The deep-sea opisthoproctid fish *Macropinna microstoma*.

Note the unique transparent shield surrounding the dorsal half of the head, encasing two large tubular eyes that contain green lenses. © MBARI 2015.

longer exposure is known as temporal summation, and double the exposure makes the eye twice as sensitive. Some deep-sea starfish have exposure times as long as two seconds, but this comes at the expense of smearing the image. Having larger pixels is what is known as spatial summation, where multiple photoreceptor cells are tied together into one super-pixel. Doubling the width and height of the super-pixel makes the eye four times as sensitive. We do this with our own rods at night, but — as anyone who bought an early model digital camera knows — fewer pixels means less detail.

Finally, one can simply make the pupil and lens larger. Like the race to place ever larger mirrors in telescopes, natural selection has often favored large lenses in the eyes of deep-sea animals. A lens that is twice the diameter makes the eye four times as sensitive. Unfortunately, this often demands that the eye has eight times the volume. This increases metabolic costs, and in any case there is only so much room in a head. As with owls, the eyes of many deep-sea fish are so large that they touch in the middle of the head, and the eyes of certain deep-sea crustaceans are so large as to be the entire head.

How is *Macropinna's* solution to this problem special? *Macropinna* has a suite of solutions to seeing at depth, two that are relatively common, and two that so far appear unique. First, *Macropinna* has eyes that are not spheres but instead thick tubes that connect a large lens with a patch of retina. This provides the sensitivity of a large eye without the metabolic cost and space requirements. The downside is permanent tunnel vision, which we'll get to in a moment.

Second, the lenses of *Macropinna* are a vivid green, which has been seen in several other deep-sea fish. As with many things in the deep-sea, we don't 'know' what the coloration is for but have a guess. Many deep-sea species are bioluminescent and a number (especially fish, crustaceans, and cephalopods) use ventral bioluminescence to hide their silhouette, continually adjusting the output of the light organs to match the downwelling light via an unknown feedback mechanism. This clever camouflage has a weakness — the spectrum of the emitted light tends

to be wider than the spectrum of the downwelling light. Therefore, a green filter that lets through some of this greener emitted light, but not the background light, could allow *Macropinna* to see these otherwise camouflaged animals.

Third, the tubular eyes of *Macropinna* can rotate, going from looking up to looking forward. This has never been seen before in a tubular-eyed deep-sea animal and is quite useful. Most tubular-eyed deep-sea animals spend their lives looking straight up, which — along with their large lenses — is partially what makes them look so ghoulish. This makes sense, because downwelling light is 50 times brighter than the horizontal light, but then when the animal swims up to investigate a passing silhouette, its eyes are now facing the wrong direction. Like the tiny arms of *Tyrannosaurus rex*, the vertical tubular eyes of deep-sea fish seem ungainly. *Macropinna's* ability to rotate their eyes, which took delicate collection of this animal by an MBARI ROV to observe, seems an obvious solution but was unexpected.

Finally, the entire rotating apparatus of these two large eyes is encased in a transparent shield. The function of this shield, which again required ROV collection to observe (it falls off in trawl-caught specimens), is unknown, but the working hypothesis is that it protects the two protruding eyes from damage from the stinging tentacles of *Macropinna's* gelatinous prey. Normally these eyes would be encased in the head, but the rotation requires that they be outside and vulnerable.

Where can I find out more?

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¹Department of Biology, Duke University, Durham, NC 27708, USA. ²Monterey Bay Aquarium Research Institute, Moss Landing, CA 95039, USA.

*E-mail: sjohnsen@duke.edu

Primer

The gut microbiome

Gavin A. Kuziel
and Seth Rakoff-Nahoum*

All animals, from cnidarians to humans, are colonized with microbes, and the greatest diversity and magnitude of these host-associated microorganisms resides within the intestine. Referred to as the gut microbiome, membership can be as simple as one species of bacteria or can be composed of hundreds to thousands of different microbes across the domains of life. The relationship between the gut microbiome and host span from beneficial to detrimental; interactions may be context-dependent and occur across host physiology and organ systems. In this Primer, we focus on the mammalian host to discuss basic mechanisms by which the gut microbiome impacts the host and review mechanisms by which hosts and the environment shape the microbiome. We end by highlighting key concepts and discussing future directions for the field that will be critical for generating the next generation of knowledge of the gut microbiome.

The gut microbiome — what's in there?

Perhaps the first description of the gut microbiome dates to the late 17th century, by Antonie van Leeuwenhoek (Figure 1) and resulting from the development of microscopes. Leeuwenhoek examined diverse environmental samples and saw bacteria and protozoa, organisms he referred to as *animalcules*. Two centuries later, advances in the cultivation of microbes allowed us to 'see' without microscopes and enabled mechanistic studies of microbial physiology. Though many dominant, gut-microbiome community members (mostly obligate anaerobes) remain recalcitrant to cultivation, recent innovations in culturing methods have increased the breadth of the microbiota amenable to study. The observation that many microbes in the gut microbiome cannot be cultivated is known as the 'great plate count

