



ASSEMBLING THE PROTIST PUZZLE

Nowhere in aquatic science has the revolution of understanding in recent decades been greater than when it comes to protists, their interactions, and their importance for ecology and biogeochemical cycling. In the late 1800s, the German physiologist Hensen (1911) recognized that the “blood of the sea” (which he coined “plankton”) was somehow related to fish production. From that point on, scientific interest became focused on these tiny organisms but, essentially only on their role as a food source for larger organisms. It was here – with the notable exception of a few taxonomy enthusiasts that lovingly examined and christened all of the organisms they encountered, that scientific focus remained for about a century. Aside from the role of plankton in the production of fish, little or no consideration was given to what – if any – role these organisms might have in the functioning of aquatic ecosystems or the relationships between these organisms. This began to change in the early 1980s, with the identification of the “microbial loop” (Azam et al. 1983), where it was recognized that the small plankton that cannot be directly eaten by the larger zooplankton also have a potential role to play in aquatic food webs and carbon cycling. Nevertheless, this loop was still largely promoted as being a mechanism whereby the dissolved organic carbon (DOC) that otherwise would be “lost” could be shunted back into the fisheries-relevant food web.

During the last decade, however, the world of the protists (and the role of DOC) has been blown open for us; no longer are they only interesting to scientists in terms of their abilities to directly supply food to organisms occupying higher trophic levels. What we now know about these tiny organisms has totally changed our understanding of autotrophy and heterotrophy. Where these designations were before considered as being distinct “boxes” to which different species could be assigned, we now recognize that they merely describe quantitative traits which many species can express at different times or under different conditions. While we still refer to the chlorophyll containing protists as “primary” producers, it appears that, with the exception of the diatoms and cyanobacteria, organisms practicing

both autotrophy and heterotrophy (i.e., mixotrophs) occur in all phytoplankton groups and are common in several (Flynn et al. 2012). Although some studies of grazing rate suggest mixotrophic grazers may have the potential under field conditions to regulate the concentrations of their prey species (Jeong et al. 2005), we are in reality only just beginning to understand the potential importance of mixotrophy under natural conditions.

From laboratory studies, it appears that light is a prerequisite for many of these mixotrophs to utilize their heterotrophic food sources. As counterintuitive as it may seem, this can mean for some species that the greater the light intensity, the less important photosynthesis is in supporting their total energy budgets (Li et al. 2000). Some species are highly specific (Fig. 1) with respect to the organisms they can prey upon and others less so (Park et al. 2007). Intriguingly, mixotrophs can sometimes utilize organisms much larger than themselves for their nutrition. Indeed, working together in groups, some dinoflagellates can even attack and consume copepods (Berge et al. 2012); while other dinoflagellates have been shown to be detrital feeders using copepod fecal pellets as a food source (Poulsen et al. 2011).

We have long assumed that turbulence always results in well-mixed water columns where species are forced into contact with one another. However, we now know that, under some conditions, different species can occupy very narrow and distinct vertical strata in the ocean; strata that are far too narrow to be resolved using standard sampling bottles (Mouritsen and Richardson 2003). This strict stratification may suggest that some species are deliberately avoiding (or preying) on others. Indeed, we also know that some species have allelopathic effects on others (Granéli and Hansen 2006) although the ecological importance of this allelopathy is still unclear (Poulsen et al. 2010). Most intriguingly, it is also clear that some species retain and use (Stoecker et al. 2009) and can even photoacclimate with (Moeller et al. 2011) the chloroplasts they have “borrowed” from their prey. One has to wonder how the cells “know” which parts of their prey are to be digested

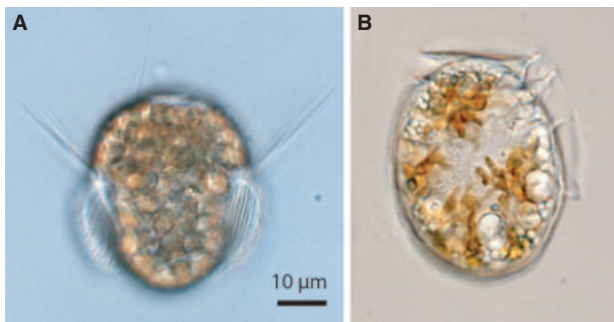


FIG. 1. (A) *Mesodinium major*, a recently described mixotrophic ciliate containing numerous reddish-brown colored chloroplasts of cryptophyte origin. *Mesodinium* collects cryptophytes on their tentacles and later ingests them. This is the first record of *M. major* from Arctic waters. (B) *Dinophysis acuminata*, the mixotrophic dinoflagellate that gets its chloroplasts from *Mesodinium* spp. by the use of a feeding tube. Both species were collected in the same sample, July 2010 at Disko Bay (Western Greenland) using a 20 µm plankton. Microphotos: Niels Daugbjerg.

and which can be put to work and whether these temporary relationships with borrowed chloroplasts represent an evolutionary transition stage en route to a more permanent symbiotic relationship. Recently, it has also been suggested that protists and the interactions between them that produce recalcitrant forms of DOC may represent a powerful sink for carbon in the global carbon cycle via what has been dubbed the “microbial carbon pump” (Jiao et al. 2010).

The paper in this issue by Collos et al. “Discrepancies between net particulate carbon production and ^{13}C -labeled bicarbonate uptake by *Alexandrium catenella* (Dinophyceae): grazing controls the balance between autotrophic and non autotrophic carbon acquisition” places yet another piece of the protist puzzle in place and begins to clarify how interactions in natural environments can feed-back on an organism’s nutritional strategy. These workers show that the importance of autotrophy as nutritional form decreases as grazing on a mixotrophic dinoflagellate increases. The suggestion is that the DOC released through the grazing process is utilized by the dinoflagellate to increase the component of its growth that is supported by the uptake of organic substrates. Once again, one has to marvel at nature’s innovative capacity. It is certainly not hard to imagine evolution providing a selective advantage to organisms that can feed on the byproducts of their own predators!

The study further reminds us that carbon budgets for pelagic food webs are likely to be flawed when they are based on the autotrophic uptake of radioactively labeled CO_2 . Under the heaviest grazing pressure, autotrophic DIC uptake supported less than half of the particulate carbon production of *A. catenella*. As I read the paper, the many pelagic carbon budgets that I have seen over the years where grazers appear to have a carbon demand that exceeds primary production began to fall into place.

There are still many pieces of the protist puzzle missing and, right now, we can only marvel at the contours of the picture emerging from the pieces already in place. Nevertheless, as we assemble the rest of the puzzle, it seems likely that we will find answers to many of the questions we ponder concerning evolution, ecology and even biogeochemical cycling in the Earth System.

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