Misuse of the phytoplankton–zooplankton dichotomy: the need to assign organisms as mixotrophs within plankton functional types

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The classic portrayal of plankton is dominated by phytoplanktonic primary producers and zooplanktonic secondary producers. In reality, many if not most plankton traditionally labelled as phytoplankton or microzooplankton should be identified as mixotrophs, contributing to both primary and secondary production. Mixotrophic protists (i.e. single-celled eukaryotes that perform photosynthesis and graze on particles) do not represent a minor component of the plankton, as some form of inferior representatives of the past evolution of protists; they represent a major component of the extant protist plankton, and one which could become more dominant with climate change. The implications for this mistaken identification, of
the incorrect labelling of mixotrophs as “phytoplankton” or “microzooplankton”, are great. It extends from the (mis)use of photopigments as indicators of primary production performed by strict photoautotrophs rather than also (co)locating mixotrophic activity, through to the inadequacy of plankton functional type descriptions in models (noting that mixotrophic production in the individual organism is not a simple sum of phototrophy and heterotrophy). We propose that mixotrophy should be recognized as a major contributor to plankton dynamics, with due effort expended in field and laboratory studies, and should no longer be side-lined in conceptual food webs or in mathematical models.

KEYWORDS: phytoplankton; microzooplankton; primary production; secondary production; mixotroph; model; plankton functional type

INTRODUCTION: DEFINING TERMS IN PLANKTON ECOLOGY

In both teaching and research, the open water planktonic food web is typically characterized as containing predominantly bacteria, phytoplankton, microzooplankton and mesozooplankton. We all know what these terms mean; or do we? And does our terminology and use of these terms reflect our current state of knowledge? We commence by considering the meaning of common descriptors in plankton research, for it is within that framework that the mixotrophic protists, which are the subject of this commentary, reside.

Bacteria as a group should be readily and clearly defined, and yet, depending on the application, this group may or may not include cyanobacteria, which may or may not be included within phytoplankton; cyanobacteria (usually, but not always, considered functionally to include Prochlorococcus) may, or may not, be accorded their own group. Phytoplankton, i.e. the planktonic photosynthetic eukaryotes and prokaryotes, are often (at least colloquially) considered to perform a role analogous to that of higher plants in terrestrial ecology. In older texts, phytoplankton biomass may even be given units of “plant pigments” (Cushing, 1975), and are thus fed upon by “herbivorous” zooplankton (Cushing, 1975; Fasham, 1995). Microzooplankton and mesozooplankton are, according to the prefix of each term, delimited by size. In practical terms, as divided using filters and meshes, the range for microzooplankton is generally considered to be 20–200 μm (nanoplankton at 2–20 μm), with mesozooplankton in the range of 200–2000 μm; these sizes equate to wet weight ranges (nanoplankton weigh nanogram, microplankton weigh microgram etc.) (Gifford and Caron, 2000). However, the term “microzooplankton” can also be taken to mean unicellular zooplankton, and thus refer to protists that feed on particles through phagotrophy. This conflicts with the allometric division because some “microzooplankton” are larger than early life stages of many “mesozooplankton”; they may, unlike metazoan zooplankton, also predate much larger particles than themselves (including mesozooplankton and large detritus particles (Poulsen et al., 2011; Berge et al., 2012) and so disturb conventional expectations of allometric scaling in trophic dynamics. Despite the fact that protist-microzooplankton grazing on “phytoplankton” is at least as important as that undertaken by mesozooplankton (Calbet and Landry, 2004), and that copepods (and their allies) obtain much of their food by grazing on protists (Calbet and Saiz, 2003; Fileman et al., 2010), it is the copepods that are still typically accorded the term “herbivore”, suggesting that they are the major secondary producers.

Adding to this complexity (and confusion) are the terms “microbe” and “microbial loop”. A microbe is an organism that is microscopic, which by definition includes all of the above-mentioned organisms (excepting the larger mesozooplankton), and not just bacteria or a bacterial-centric trophic pathway. The term “microbial loop” (Azam et al., 1983; Jiao et al., 2010) encapsulates the concept of return of dissolved organic carbon to higher trophic level via its incorporation into bacterial biomass, but it is really a description of organic carbon recycling through the microbial food web consisting of bacteria, cyanobacteria, viruses and protists.

Then there are the physiological terms of “autotroph” and “heterotroph”. The meanings of autotrophy and heterotrophy have clear definitions, and groups of plankton are typically described (or assumed) as being solely of one or other nutritional (functional) type. However, confusion arises when both nutritional pathways co-occur within a single organism, i.e. within the “mixotrophs”. The term “mixotroph” is used here to describe an organism that undertakes some...
combination of both photoautotrophic and heterotrophic activity. Technically, the heterotrophic component may involve osmotrophy (using dissolved organic substrates) and/or phagotrophy. However, almost certainly, all “phytoplankton” (eukaryote and prokaryote) are in part osmotrophs, not least by virtue of being auxotrophic; many need external sources of one or more vitamins (Croft et al., 2006). Further, in the majority that have been surveyed, “phytoplankton” exhibit significant levels of non-auxotrophic osmotrophy, especially with respect to the uptake of amino acids and other primary metabolite compounds (Flynn and Butler, 1986; Berman and Bronk, 2003; Mulholland et al., 2003; Gilbert and Legrand, 2006; Lindehoff et al., 2011). Likewise, protist “microzooplankton” can also engage in osmotrophy (Droop, 1959; Sanders, 1992). The use of osmotrophy as a discriminating feature of mixotrophy in planktonic protists thus appears weak (de facto all phytoplankton are mixotrophs by such a definition), and hence in practice, phagotrophy coupled with phototrophy is a more useful discriminator. (In passing, it should be noted that phagotrophy is not a processes seen in prokaryotes, thus cyanobacteria could not be considered as mixotrophs by virtue of phototrophy + phagotrophy.) Phagotrophy, especially when it involves the death of another organism, not only has implications for the growth of the mixotroph, but it also has other important impacts on trophic dynamics.

Clearly, the terminology we use in our science has not evolved in step with our understanding of plankton ecophysiology, and certainly not with advances in our appreciation of nutritional diversity in protists. Emerging out of concepts in which planktonic “plants” and “animals” were thought to be easily distinguished, the research arena now has a mess of sloppy, loosely defined, terms with which we typically describe members of plankton and their processes. As we shall see, it is becoming increasingly apparent that photosynthetic protists should by default be regarded as mixotrophs and not as phototrophs. That this situation has not been given its due appreciation in the past is most likely due in large measure to problems in nomenclature enforcing the retention of stereotypes in functionality. The mixotrophic protists combine all the complexities of phototrophs, osmotrophs and phagotrophs, together within a single cell, and yet packaged in a bewildering array of functional and taxonomic groups (Jones, 1997; Stoecker, 1998; Stoecker et al., 2009; Granéli et al., 2012). In a subject in which the search for scientific clarity is a prime motivator, one may be excused for glossing over these organisms with their complex and often perplexing physiology. However, here we argue the importance of mixotrophy needs to be acknowledged and clarifying their descriptions (and indeed that of their planktonic consorts) is as good a place as any to start.

THE MIXOTROPHIC PROTISTS

In teaching and research in aquatic ecology, limnology and oceanography, the term “mixotroph” only occasionally surfaces, typically as a curio, not least to fascinate students with videos of protists eating other protists, and with the spectre of potentially harmful algal bloom (HAB) species in the field eating other plankton, if not killing organisms at higher trophic levels. The group most closely aligned with the term “mixotrophs” are the dinoflagellates (Burkholder et al., 2008; Jeong et al., 2010b; Hansen, 2011). Generally, however, in the science literature and in textbooks, the protists are distributed between “phytoplankton” and “microzooplankton”, between those that cannot eat and those that can (Sarmiento and Gruber, 2006; Miller and Wheeler, 2010). This categorization, conveniently for ecologists and modellers, also splits protists between primary and secondary producers (Fig. 1). In fact, however, the protists that inhabit illuminated waters are far from being distributed cleanly between primary and secondary producers (Fig. 1), but are smeared across a continuum (Fig. 2). Mixotrophy is not limited to a few groups, such as the dinoflagellates, it is almost everywhere in the illuminated water column, for much of the time (e.g. Hartmann et al., 2012). Or at least, it is potentially there; the organisms are there though their mode of operation at any instant is rarely characterized and will likely depend on the presence of conditions conducive to one or other, or both, nutritional pathways.

**Fig. 1.** Schematic showing the classic misrepresentation of the functional classification of planktonic protists as contributors to primary production (on the right) or to secondary production (on the left). Only some dinoflagellates, forams, radiolaria and acantharia are accorded a mixotrophic status, and these are down-played (usually ignored) in models.
Fig. 2. Schematic of the functional classification of planktonic protists as contributors to primary production (on the right) and/or to secondary production (on the left). Note that in contrast to the classic misrepresentation (Fig. 1), the potential for individual organisms to contribute both to primary and secondary production is now acknowledged. References in support of this description are as follows: Acantharia (Caron et al., 1995; Stoecker et al., 1996); Chrysophyceae (Kristiansen, 2003) with mixotrophy common in Chrysophyceae *sensu stricto*, i.e. excluding the photolithophytic Synurophyceae (Bhatti and Colman, 2008); Ciliates (Bernard and Rassoulzadegan, 1994; Stoecker et al., 1996, 2009; Perez et al., 1997; Esteban et al., 2010); Cryptophyta (Laybourn-Parry et al., 2005; Callieri et al., 2006), Dinoflagellates (Callieri et al., 2006; Park et al., 2010; Jeong et al., 2010b; Hansen, 2011; Minnhagen et al., 2011); Foraminifera (Caron et al., 1995; Stoecker et al., 1996, 2009); Pavlovophyceae (Callieri et al., 2006); Prasinophyceae (Bell and Laybourn-Parry, 2003), though mixotrophy appears rare in the Prasinophyceae, Prymnesiophyceae (Hansen and Hjorth, 2002; Carvalho and Granéli, 2010; Granéli et al., 2012; Rokitta et al., 2011), though mixotrophy is very rare in coccolithophores, occurring only in some non-calcified species, it is common in the sister class Pavlovophyceae; Radiolaria (Caron et al., 1995). Also, not shown in the figure: mixotrophy occurs in the Chlororaphidophyta (Calderon-Suarez and Schnetter, 1989) and Raphidophyceae (Jeong et al., 2010a; Jeong, 2011). For an overview of the phylogenetic occurrence of mixotrophy, see Table II of Raven et al. (Raven et al., 2009).

An analysis of the organisms traditionally termed eukaryote “phytoplankton” reveals that, not only are they all osmotrophs, but that the majority are to a lesser or greater degree potentially also phagotrophic (Fig. 2). Certainly, studies over the last decade have shown that many flagellate species are ferocious phagotrophs, such as the haptophyte *Prymnesium parvum* (Carvalho and Granéli, 2010; Granéli et al., 2012). The mixotrophic status may even include both haploid and diploid *Emiliania huxleyi*, which appear capable of phagotrophy late in batch culture (Rokitta et al., 2011). Likewise, many organisms traditionally termed “microzooplankton” have been shown to exhibit some level of phagotrophic activity [typically through kleptoplastidy or endosymbiosis (Stoecker et al., 2009a)] and hence also exhibit mixotrophic capabilities (Fig. 2, cf. Fig. 1).

It must be said that the concept of a continuum of mixotrophy within aquatic protists is not new (Sanders, 1991, 1992, 2011; Jones, 1994; Stoecker, 1998). However, the message, and the critical importance of it in our understanding of the system, has failed to enter mainstream plankton research. Why this is so is not clear. While there is a time and place for all concepts, maybe part of the problem has been that previous commentaries have been directed at the mixotroph researchers and at the breadth of diversity within mixotrophs, rather than at the full breadth of plankton scientists (from laboratory to field to modellers) and at the breadth of diversity within aquatic protists. Doubtless, the issue has also not been helped by the sheer diversity of mixotrophic strategies that are described in these earlier works, together with the stereotypical descriptors used in plankton research discussed earlier.

The core point that we make here is that the default expectation for photosynthetic protists living in illuminated water is that they are mixotrophs. The exceptions (in total contrast to commonly voiced wisdom) are those species that cannot also engage in phagocytosis, and not those that can eat. That the default nutritional expectation should indeed be mixotrophy is underscored by the fact that a notable feature of the protists is their remarkable series of repeated evolutionary gains and losses of phototrophic potential (Sanchez-Puerta and Delwiche, 2008). A defining feature of protist evolution has been genetic (re)combination and exchange of functionality supported through mixotrophy. The implication is that mixotrophy has, and continues to be, an important nutritional option for these planktonic protists.

Alas, our detailed understanding of protist ecophysiology is not aided by the emphasis on axenic clones of mixotrophic protists held in culture collection, a practice which will select against mixotrophy. Meanwhile, those protists deemed to be heterotrophs are held under conditions selecting for that mode of nutrition. It is also notable that organisms that are strongly mixotrophic (in some instances, obligate mixotrophs) are rarely held in culture collections for any period of time; we do not understand enough about their nutritional needs, further hindered by the emphasis towards maintaining axenic cultures.

All this leads to a circular situation; because we do not know how important the process is, it is difficult to justify studying it, and yet we will never know how important it is, unless we do expend that research effort. What we can be sure of is that the factors stimulating mixotrophy need not be simply the supply of C (which lies at the heart of the classic definition of “mixotrophy”), but that the acquisition of other nutrients is likely to be at least as important. Indeed, the contribution of C could be minor, but that of other N, P and Fe could be highly significant both for mixotroph nutrition and for trophic dynamics (Maranger et al., 1998; Smalley et al., 2003; Stoecker et al., 2006; Zubkov and Tarhan, 2013).
ORGANISM CHARACTERIZATIONS AND TROPHIC FUNCTIONALITY

Not only does the classic characterization of protists divide them neatly into “phytoplankton” and “microzooplankton”, but it further distinguishes between those contributing to primary production and to secondary production (Fig. 1). As may be deduced from the corrected revised portrayal (Fig. 2), our mistaken categorization of protist plankton as either “phytoplankton” or “microzooplankton” has various ramifications and implications for key questions in plankton ecology and oceanography. Critically, it now becomes clear that many, if not on occasion most, protists in the photic zone contribute to both primary and secondary production simultaneously, in the same single-celled organism. While it is without doubt that the existence of mixotrophic protists is well known, and that these organisms have been included within various conceptual food webs and mathematical models (e.g. Thingstad et al., 1996; Baretta-Bekker et al., 1998; Stickney et al., 2000; Hammer and Pitchford, 2005; Jeong et al., 2010b), more typically mixotrophs are hardly mentioned. As examples, mixotrophs are absent from a recent review of the microbial loop (Jiao et al., 2010), and from recent text books and compendia (e.g. Sarmiento and Gruber, 2006; Steele et al., 2010). Inevitably, then, discussion and analysis of rate processes of primary and secondary production typically ignores the role of mixotrophy.

The greatest emphasis in biological oceanography is on primary producers, and primary production. In part through convenience, and because of the ways in which field analyses are conducted, from molecular analyses to remote sensing technologies, there has been a blurring of the descriptors “phytoplankton”, “primary production” and “chlorophyll”. The result is that the rate process of “primary production” has become uncritically associated, almost as a synonym, with the state variable “phytoplankton”. Further, “chlorophyll” all-too-often has become synonymous with “phytoplankton biomass”. Indeed, because of the operational difficulty in measuring phytoplankton biomass in the field, colloquially at least, “chlorophyll” is phytoplankton biomass (Falkowski and Kiefer, 1985; Aiken et al., 2008).

Whether some significant fraction of the pigment signature, and thus a fraction of the process of primary production, is associated with organisms that are actually mixotrophs invariably does not enter into the analysis. Certainly, when considering the process of C-fixation, it does not matter so much, but when we need to understand, and model, the processes of primary production (which is more than just photosynthesis) then it certainly does matter. This is because it affects our understanding of the flow of nutrients supporting primary production, affecting the classic perception that primary production is supported by only inorganic nutrition. On the contrary, it appears that primary production in many ocean areas is actually supported by P and Fe derived directly from phagocytosis (Maranger et al., 1998; Hartmann et al., 2012). It also affects our understanding of the support and fate of secondary production. The situation is exacerbated on acceptance that a significant part of the classic “microzooplankton” fraction is also photosynthetic (Figs 1 versus 2). Just as primary production is uncritically linked to phytoplankton, so the term “predation” has also become uncritically linked to a group of organisms rather than properly remaining as a descriptor of a rate process.

The net result of all this is a perpetuation of the perception of the pelagic ecosystem as one dominated by the groups phytoplankton and microzooplankton (perhaps with minor inclusion of mixotrophs), rather than dominated by the processes of phototrophy and phagotrophy (which may or may not operate concurrently in the same organism). The problem does not only reside with the use of chlorophyll as a marker for characterization of protist functionality; molecular screening approaches also need careful interpretation, not least because of the complexity of protist evolution (Sanchez-Puerta and Delwiche, 2008; Stoecker et al., 2009) which results in genomic and proteomic signatures being smeared across protist groups.

Where researchers have specifically sought to identify mixotrophy, and/or to identify and hence characterize actual organisms, the contributions of mixotrophs to system dynamics and functionality have been shown to be important (Stoecker et al., 1997; Jeong et al., 1999, 2005a, b, 2010a, b; Gisselson et al., 2002; Smalley et al., 2003; Zubkov and Tarran, 2008; Gilbert et al., 2009; Rokitta et al., 2011; Hartmann et al., 2012). The implication is that the more we look, the more we will find evidence for mixotrophy. It is perhaps ironic that in the situations where mixotrophs are best known to be of importance (Burkholder et al., 2008), our terminology lets us down; “HAB” is a rather unfortunate descriptor in this capacity, with the term “algae”, like “phytoplankton”, being synonymous with a plant-like phototrophic
life style (perhaps with some osmotrophy, but not with phagotrophy).

GETTING IT RIGHT

Does it matter that the ecosystem functionality of protists is incorrectly assigned, that so many organisms that are actually mixotrophs are put into the wrong bucket, so to speak? On point of principle, yes of course, it matters. It is beheld on scientists to describe and characterize the workings of nature correctly. That is all the more so when an incorrect characterization may lead to a deeper misunderstanding of how systems function, and in the modern context, to a potential misunderstanding of the consequences of climate change. If there are to be simplifications, then they need to be well argued and evidence-based. Who is to say how the balance of protist nutrition (and which nutrition; C, N, P, Fe) may change in the future, between phototrophic versus phagotrophic versus mixotrophic modes?

The proper identification of the organisms responsible for biogeochemical processes, for supporting primary and secondary production (etc.) affects our perception of nutrient cycling, of what proportion of primary production flows from regenerated production (low f-ratio) and of how much regeneration is short-circuited directly from secondary production to primary production within the same organism functional type. It affects our understanding of who eats who, and the drivers for that interaction. It affects our understanding of the “microbial loop”. A recognition of mixotrophy is also critically important in understanding how microbes moderate stoichiometric imbalances within the plankton, likely making primary production packaged within a mixotroph better balanced (less extreme) than that packaged within a strict non-phototrophic phototroph (e.g. Gilbert and Burkholder, 2011). If, as we suggest, it is important to correctly identify the organisms responsible for biogeochemical processes and for production, then surely this perception should also affect how we model these ecosystems.

Models of planktonic systems traditionally (and usually still do) have as state variables parameters that describe organisms performing strict phototrophy and strict grazing (the phytoplankton “P” and zooplankton “Z” boxes, respectively; Fasham et al., 1990; Fasham, 1995). The major mechanism for the truthing of the biological component of plankton models is by the use of data from the monitoring of photopigments (mainly chlorophyll), either by in situ or remote monitoring (Lochte et al., 1993; Aiken et al., 2008). These data have been used to derive estimates for the “biomass” of primary producers, which are used to tune and validate the P box. Data for the biomass of grazers, and for grazing activity, are far fewer in number and scope (e.g. Lochte et al., 1993), and are less robust. We thus rely critically on the structure of the model to infer what trophic levels above primary production are doing: and that feeds back around the loop through predator–prey cycles, through nutrient regeneration and sedimentation processes. The problem that now becomes clear is that the chlorophyll signal originates from functionally rather diverse organisms. Yes, it is associated with primary production, but often it is also associated with secondary production within the same organism, if not (for kleptochloroplastidic protists) associated with a complex interaction between primary producers and phagotrophs (Park et al., 2010; Minnhagen et al., 2011; Hansen et al., 2012).

As we move increasingly towards the development and the use of so-called plankton functional type models, with all the challenges that presents (Flynn, 2006), where are the state variables for the organism groups shown in Fig. 2? Where are these mixotrophs? Where are the state variables for the organism groups shown in Fig. 2? Where are these mixotrophs? Where are the rate processes for mixotrophy? And where does this throw the concept of adaptive modelling, of considering trait tradeoffs based upon resource optimization? There are profound differences between the individual processes of primary and secondary production occurring within the same organism, rather than in separate organisms. Within a mixotroph, the two processes do not simply add up, and neither do they simply compete; rather there is a level of cooperation between them (Flynn and Mitra, 2009; Mitra and Flynn, 2010). The implication is that the activity of mixotrophs certainly cannot be summed by adding together the contents and activities of the strict phototrophic “P” and strict phagotrophic “Z” boxes in models. Or to be pragmatic, we certainly should not assume that they can be summed unless we have proven it. One thing is for certain; we lack complete data sets to critically test models of mixotrophy. That includes not only data for the mixotroph itself, but for its prey (Flynn and Mitra, 2009).

When such a large fraction of the primary production signal (as photopigment) is incorrectly assigned within the model structure, how sure can we be of the reliability of the whole model? Hindcasts provide a validation method for climate change models (Ciavatta et al., 2011), but to accept that as a methodology, we need to assume that under climate change, the balance of strict phototrophs, mixotrophs and strict phagotrophs remains unchanged. We clearly cannot do that with any surety.

One could argue that there are enough problems, enough challenges, in marine science without introducing mixotrophs as a plankton functional type. Others
would surely argue that this is a challenge that should be met, that mixotrophs cannot continue to be sidelined as throwback freaks, as extant representatives of the evolution between phagotrophic protists and strict phototrophic (or perhaps more accurately strict non-phagotrophic) protists. The fact is that, a very significant minority if not the majority (depending on the time and place) of the protist plankton are actively mixotrophic (Caron et al., 1995; Stoecker et al., 1996, 2009; Jeong et al., 2010b; Jeong, 2011; Hartmann et al., 2012).

It is not that a group of organisms new to science has been identified; it is that members of existing groups have been widely misidentified with respect to their functionally. While it may be argued that the term “mixotroph” is unfortunate as it does not distinguish between those photoautotrophs that have heterotrophic tendencies and those heterotrophs that have autotrophic tendencies, the critical issue is that we recognize that among the photic-zone dwelling planktonic microbes, there are few strict photoautotrophic or strict heterotrophic protists. (Indeed, including osmotrophy to support growth in non-phagotrophs such as diatoms would identify all phototrophic protists as mixotrophs.)

Once we achieve that recognition for mixotrophy in protists, then we can determine the contribution, the fluxes of C, N, P, Fe (etc.), that flows through them. Accordingly, we suggest that it is time to recognize the role of mixotrophy in field work, to reflect it in laboratory studies and describe it in conceptual and mathematical models.

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