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Review

Evolution of Phytoplankton in Relation to Their Physiological Traits

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Abstract: Defining the physiological traits that characterise phytoplankton involves comparison with related organisms in benthic habitats. Comparison of survival time in darkness under natural conditions requires more information. Gas vesicles and flagella as mechanisms of upward movement relative to surrounding water, allowing periodic vertical migration, are not confined to plankton, although buoyancy changes related to compositional changes of a large central vacuole may be restricted to plankton. Benthic microalgae have the same range of photosynthetic pigments as do phytoplankton; it is not clear if there are differences in the rate of regulation and acclimation of photosynthetic machinery to variations in irradiance for phytoplankton and for microphytobenthos. There are inadequate data to determine if responses to variations in frequency or magnitude of changes in the supply of inorganic carbon, nitrogen or phosphorus differ between phytoplankton and benthic microalgae. Phagophotomixotrophy and osmophotomixotrophy, occur in both phytoplankton and benthic microalgae. Further progress in identifying physiological traits specific to phytoplankton requires more experimentation on benthic microalgae that are closely related to planktonic microalgae, with attention to whether the benthic algae examined have, as far as can be determined, never been planktonic during their evolution or are derived from planktonic ancestors.

Keywords: buoyancy; carbon concentrating mechanisms; dark survival; flagella; gas vesicles; nutrients; photosynthetic pigments; sinking; vitamins

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1. Introduction

In considering the evolution of physiological traits of phytoplankton, it is necessary to take into account the habitat of the ancestors of the planktonic organisms and their physiological traits. Is a given trait an evolutionary result of life in the plankton, or was it inherited from adaptation to whatever environments that they occupied previously? This is not always considered, as exemplified by a quotation from Sabir et al. [1] in their review of the history of the 'accidental phytoplankton' *Phaeodactylum tricornutum*: "Despite the many observations suggesting a benthic component of this diatom's life history, it continues to be discussed explicitly or explicitly as a model diatom in the context of planktonic environments". Consequently, in this review, we have focussed on examining what physiological traits might be ascribed to the planktonic habitat by comparison to those of cyanobacteria and algae found in other environments, especially the benthic habitat.

2. Molecular Phylogenetic and Fossil Evidence on the Ancestral Habitat of Extant Phytoplankton

According to molecular phylogeny, the basal extant cyanobacterium is the thylakoidless terrestrial *Gloeobacter* [2], and benthic (i.e., coastal) marine (and terrestrial?) cyanobacteria were the oxygen-producing components which, combined with organic C burial,

resulted in the Global Oxidation Event ~2.3–2.4 Ga ago [2–4]. Again, from molecular phylogeny, planktonic marine cyanobacteria did not occur until the Neoproterozoic (1000–542 Ma ago), when marine planktonic cyanobacteria with eukaryotic phytoplankton were the oxygen-producing component of the Neoproterozoic Oxidation Event 800–600 Ma ago [2,3]. The molecular phylogenetic studies for the Proterozoic are not, however, related to fossils from deep ocean sediments. This absence of evidence is, of course, not evidence of absence. However, the turnover of ocean crust means there is little chance of finding open ocean fossils; Hynes [5] suggested that occurrences of early Palaeozoic ocean crust exposed at the surface of the Earth are very rare, and Granot [6] reports 'old' oceanic crust at 340 Ma ago in the eastern Mediterranean. Notwithstanding these suggestions, there are reports of exposed ocean crust from 1.9 Ga ago [7] and 2.1 Ga ago [8], but without fossils.

The fossil evidence of eukaryotes that are thought to be marine phytoplankton are acanthomorphic acritarchs from as far back as 1811 Ma [9]. Some acritarchs (e.g., *Tappania*) have been attributed to the phycoma stage of the Prasinophyceae (Chlorophyta) [10]. Other Proterozoic photosynthetic eukaryotes from 1600 Ma onwards [9,11] are mainly benthic macrophytes. These fossils occur in what was inundated coastal continental crust. Very little ocean crust older than 340 Ma remains [5,6], and what little occurs is not fossiliferous [7,8], so there are no data on open ocean biota (if there was any) in the Proterozoic, including any 'ghost clades' that have no extant descendants.

Basal diatoms may have lived on land in ephemeral water bodies, then sequentially invaded the benthos of marine coastal waters, marine plankton with some reversion to the marine benthos (see Figure 6 of Reference [12]), and finally, the plankton and benthos of inland waters [12–14]. A bias in the fossil record of marine organisms in favour of coastal waters that increases with age of the fossil is the turnover of ocean crust with a half-life of ~110 Ma (see previous paragraph); this is less important for diatoms (with a fossil record from the upper Jurassic onwards) than for older taxa [12]. A further problem with fossilisation of diatoms is that the ocean has been undersaturated with respect to silica precipitation since well before the time of the earliest fossil diatoms. For a given size, shape and degree of silicification of a diatom, and hence sinking rate, for a greater distance that the cells sink from the illuminated surface water to the ocean floor where fossilisation can occur means longer for bacterial removal of the organic layer around the silicified frustules that limits silica dissolution, and hence a greater possibility of complete dissolution before reaching the ocean floor [12].

In considering the evolution of the physiology of planktonic diatoms, it is worth bearing in mind the analysis in Vincent and Bowler [15] who considered the global distribution of planktonic diatoms in relation to abiotic (resource availability, water movements, temperature) and biotic (competitors, grazers and pathogens) environmental attributes. Vincent and Bowler [15] found that only 13% of the distribution of diatoms could be accounted for by abiotic factors: the remaining 87% is accounted for by the distribution of competitors, grazers and pathogens. Physiology underpins the only slowly modifiable structural (silicified wall, sometimes with spines) defences against grazing, and the more immediate response of expressing chemical defences (allelochemicals) against grazers and pathogens [15]. These findings might indicate the relative selection pressures imposed by abiotic and by biotic factors on algal physiology.

Nakov et al. [16,17] and Medlin [18] analyse diversification rates of diatoms, the most speciose class of microalgae. The diversification rate is higher for freshwater than marine diatoms [17], and highest for raphid benthic diatoms that have gliding motility on surfaces, giving greater vegetative growth and sexual reproduction opportunities [16], but see [19,20], at a small resource cost of motility [21]. The (derived) marine benthic diatoms have a photoprotective capacity that is dictated by growth form rather than phylogeny [22]. Kooistra et al. [23] showed that the benthic centric diatom *Toxarium* is, like many pennate diatoms, elongate, benthic and motile through mucilage secretion. Kooistra et al. [24] show that araphid pennate diatoms are ancestrally benthic, and have become planktonic at three, possibly four, times; whereas decreased silicification relative to benthic

araphids is common to all planktonic araphids, there are no changes in morphology that are common to all of the planktonic araphid diatoms. Whereas many planktonic pennate diatoms are colonial, colonial forms are also known among benthic pennate diatoms [25–27]. The genome sequence of the benthic pennate diatom *Seminavis robusta* allows comparison with sequenced planktonic pennate diatoms [28]. Among the expanded gene families are those related to motility and adhesion, and also globins related to O_2 sensing, and rhodopsins and phytochromes related to light sensing, reflecting the greater spatial and temporal variation in O_2 and light in benthic habitats [28].

The almost entirely marine haptophytes have an eponymous organelle, the haptonema, as a synapomorphy [29]. Because the haptonema is putatively related to prey capture, it is hypothesised that the earliest Haptophyta were phagophotomixotrophs [29]. If the haptophytes acquired phototrophy by endosymbiosis independently of other algae with plastids derived from red algae, compatible with the analysis of Strassert et al. [30], then the haptonema could have pre-dated phototrophy in haptophytes.

The basal dinoflagellates, and their sister taxon the chromerids, are alveolates, and, like haptophytes, cryptophytes and stramenopiles, photosynthesise using plastids derived from red algal endophytes [31]. All known chromerids and many dinoflagellates are benthic, sometimes endosymbionts, in the ocean [31]. Others are planktonic in the ocean, or benthic or planktonic in inland waters [31]. There have been multiple losses of photosynthesis in dinoflagellates, and replacement over varying timespans with kleptoplastids retained after phagotrophy, with varying extents of retention of quantities of extra-plastidial genetic material from the ingested phototroph [32]. The upper extremes of genome retention, other than retention of entire cells, potentially capable of free-living growth and survival, are the diatom endosymbionts as 'dinotoms'; there are also cyanobacterial symbionts [32].

Turning to changes in ocean conditions relevant to cyanobacterial and eukaryotic algal physiology, these have changed significantly over the more than 2 billion years for which benthic and planktonic oxygenic phototrophs have existed. As a result, oxygenic phototrophs today are adapted to different conditions from those found earlier. An example of such a secondary adaptation is the very low Cu concentration in the Proterozoic ocean [33] that would have greatly limited the ability of cyanobacteria to produce the Cu-containing photosynthetic redox protein plastocyanin [34] and the Cu-containing terminal oxidase cytochrome aa_3 [35]. These oxidation–reduction compounds can be produced in many habitats today [34,35]. In the Proterozoic, the reactions catalysed by plastocyanin could have been replaced with the Fe-containing cytochrome c_6, and cytochrome bd-quinol and/or the alternative oxidase, respectively. In extant cyanobacteria, the Cu-containing redox catalysts can be produced when Cu is available [34,35], provided Cu toxicity in much of the current ocean is ameliorated by production of Cu-chelating compounds [33].

The Permian–Triassic transition, i.e., the beginning of the Mesozoic, more or less coincides with the origin of the fossil record of marine coccolithophores and dinocysts; fossil diatoms came later (see reference [36]). Differences in the elemental stoichiometry of marine phytoplankton grown under resource-sufficient conditions show that cyanobacteria plus the green line of eukaryotic algae are differentiated from the red line, mainly in their trace metal content [36–38]. Similar patterns were found when the data set was extended to include more species, including those from freshwater [39]. Attempts have been made to relate the increased occurrence of red line marine phytoplankton, with their particular trace element content, to the changes in the availability of trace elements during the Mesozoic, e.g., ocean anoxic episodes [36]. As well as problems with hindcasting the change in trace element composition of the marine photic zone at the P:T transition, the data on elemental content relate to the content of elements, not the cellular requirement, i.e., they do not take 'luxury accumulation' into account. A further problem is that the elemental analyses focus on planktonic microalgae, so the specificity of any changes to planktonic rather than benthic algae is not clear.

A further resource supply change for marine phytoplankton in the Mesozoic is the supply of sulfur, which apparently increased in the Mesozoic ocean relative the Phanero-

zoic [40,41]. Ratti et al. [41] showed that growth of the cyanobacterium and green alga tested was not increased by concentrations of SO_4^{2-} higher than 1 mole m^{-3}, whereas the 'red line' diatom, dinoflagellate and coccolithophore tested showed increased growth up to 10 mole m^{-3}. However, Giordano et al. [40] and Ratti et al. [41] emphasise the importance of other changes in the abiotic and biotic environment in the evolution of marine phytoplankton post-Permian. Furthermore, the organisms tested are all from the marine phytoplankton, and similar changes in sulfur supply presumably occurred in the habitat of benthic algae; data are needed on how the sulfur supply varied in the habitats of inland water phytoplankton and microphytobenthos.

It is difficult to determine the rate at which physiological traits change. These changes, except to the limited extent to which the changes physiological traits can be inferred from changed morphology, cannot be inferred from fossils. An example of what can inferred from fossils is the decrease in mean cell size of vegetative size of diatoms and, from the size of their cysts, dinoflagellates, and correlations, or lack thereof, with environmental changes [42,43]. The decrease in mean size means a greater capacity for light harvesting and nutrient uptake per unit biomass under resource limitation, and a small decrease in specific growth rate with increasing cell size [42–44]. Experimental evolution studies on microalgae focus on phytoplankton and show, for instance, that trait correlations limit adaptation to high CO_2 [45,46].

3. Physiological Traits Potentially Limited to Planktonic Microalgae

3.1. Prolonged Dark Survival

Besides the physiological traits involved in growth-related processes, such as resource acquisition, allocation and retention, and limitation of losses by sinking, grazing and parasitism, some cyanobacterial and algal plankton have recognisable resting stages [47,48]. Some morphologically distinct resting stages can remain viable, in the case of dinoflagellates, for over a century under conditions in which growth is impossible [49], and the akinetes of the cyanobacterium, *Anabaena*, in the Baltic Sea can survive at least 40 years in coastal sediments and over 400 years in open sea sediments [48]. Dinoflagellate cysts in sediment from a Swedish fjord survived 37 years, whereas spores of diatoms such as *Chaetoceros* remain viable for decades [50]. The transition from fossils of dinoflagellate cysts to diatom resting spores, predominantly *Chaetoceros*, occurred [51] in the late Paleogene-early Neogene. Some diatom resting spores can survive for millennia [52]. However, not all phytoplankton resting stages are morphologically distinct from vegetative cells. It should be noted that the Parmales (Class Bolidophyceae, sister group of the diatoms), whose silicified non-motile cells were previously thought to be a non-growing resting stage, in one case have been shown to be capable of growth without morphological change, and to continue growth in a non-silicified form in Si-free media [53].

Arctic marine phytoplankton must be able to survive months without sunlight [54]. Phytoplankton in high latitude temperate open oceans have very limited productivity in winter with lower temperatures, shorter photoperiods and deeper mixing (see, e.g., [55]). Perhaps winter survival of sufficient phytoplankton cells to 'seed' the spring bloom is enhanced by limited photosynthesis when cells in the upper mixed layer are briefly close to the sea surface in their vertical circulation. Whereas the chlorophyll *a* per volume of seawater in the upper mixed layer can be an order of magnitude lower at the lowest value in winter than at the peak of the spring bloom [55], it is the chlorophyll *a* per cell and the functionality of photochemistry and downstream metabolism that is important in providing the 'seed' for the spring bloom.

However, the extent to which there is a requirement for specific resting stages in winter by benthic microalgae at higher latitudes, or elsewhere, is not clear, so cysts and spores as resting stages may not be a plankton-specific trait among microalgae. The nearest to a morphologically distinct (from vegetative cells) resting stage in benthic microalgae seems to be the hypnozygotes of the benthic dinoflagellate *Ostreopsis* that can germinate after 5 months in unspecified conditions [56]. Survival of Antarctic benthic diatoms for 64 days

of darkness occurs without morphologically distinct resting stages [57]. Veuger and van Oevelen [58] found that a small fraction of benthic diatoms survived a year of darkness. Kamp et al. [59] compared the dark anoxic survival of three planktonic diatoms with that of three benthic diatoms as a function of the nitrate concentration stored in the cells during their photoautotrophic growth. Greater nitrate storage and was correlated with the length of dark anoxic survival, with longer survival (up to the end of the experiment at 13 weeks) for high nitrate storage for benthic diatoms, than for planktonic diatoms (6 and 9 weeks), with the organisms apparently using dissimilatory nitrate reduction as an energy source in the transition to a resting state. On the basis of present data, benthic microalga cannot survive darkness as long as some planktonic algae.

Based on limited data for benthic microalga, at least some phytoplankton have much longer survival times in the dark than do benthic microalgae, and morphologically distinct resting stages appear to be limited to certain phytoplankton.

3.2. Directed and Undirected Movement Relative to Surrounding Water and Diffusion Boundary Layers

A starting point for considering movement by phytoplankton is that they generally have a higher density than the aqueous environment [60]. This is particularly the case for freshwater, where the medium has a lower density than does seawater [38]. Particles that are more dense than the medium sink according to the Navier–Stokes equation [38]. An important point about particles that have a higher density than the surrounding water is that they sink faster in turbulent than in still water, contrary to the qualitative conclusion from the effect of stirring a vessel, in which dense particles have settled at the bottom and stirring temporarily causes the particles to swirl around [61,62]. However, this analysis [61] is for an upper mixed layer with a constant vertical distribution of turbulence. For the environmentally relevant case of decreased turbulence with greater depth in the upper mixed layer, turbulence promoted the retention of non-motile particles in the upper mixed layer [63]. Oceanic turbulence has multiple influences on the interactions of motile plankton with other planktonic organisms, e.g., chemical trails left behind by moving organisms [64].

Phytoplankton with flagella can swim upwards even when the cells have a density greater than that of the surrounding water [21]. Three-dimensional phototaxis is a characteristic of flagellate phytoplankton, and also of the flagellate stages of macroalgae, that are not shared with benthic algal flagellates, or benthic algae that are motile by gliding mobility [65]. Open ocean marine *Synechococcus* strains that are motile (by an as yet uncharacterised mechanism) do not exhibit phototaxis, but show a chemotactic response to several nitrogen compounds at concentrations found in the oligotrophic ocean [21,66]. Periodic vertical migration can occur by means of flagella motility in eukaryotes (marine and freshwater, benthic and planktonic), by variations in cell density in cyanobacteria as a result of variations in gas vesicle volume and in ballast content (marine and freshwater; planktonic). It can also occur in larger vacuolate cells by changes in the solute composition of the vacuole, possible supplemented by active water transport, and in ballast components (marine, planktonic) for some diatoms, a prasinophyte and a dinoflagellate [21]. Gliding motility only functions in freshwater and marine benthic microalgae [21]. Periodic vertical migration in phytoplankton occurs with diel, or longer (several days), periodicity [21].

The movement traits that might be expected to be limited to cyanobacteria and algae from planktonic environments is buoyancy, i.e., having a density that is lower than that of the surrounding water, and periodic vertical migration related to changes in buoyancy. These traits involve cyanobacterial gas vesicles in freshwaters and the ocean, and buoyancy and periodic migration involving changes in the density of aqueous vacuoles in seawater [21,67]. It is of interest that the smallest photoautotrophic organism, the marine planktonic cyanobacterium *Prochlorococcus*, lacks gas vesicles (see, e.g., [68]), although the predicted sinking rate of *Prochlorococcus* relative to the surrounding water is only 2.6 mm per day [69,70]. However, in non-photosynthetic bacterial gas vesicles are not confined to plankton, occurring in a psychrophilic methanotroph in tundra soil [71] and

an enterobacterium from a temperate salt marsh [72]. The enterobacterium *Serratia* sp. ATCC 3900 can express bacterial flagella as well as gas vesicles, albeit not at the same time; a quorum-sensing molecule acts as a morphogen promoting gas vesicle production [73]. Downregulating the TrkH potassium transporter upregulates gas vesicle expression and downregulates flagella expression in *Serratia* sp. ATCC 3900 [74]. Ramsay and Salmond [72] point out that aggregates of cells can rise more rapidly to the water–air interface than can single cells with gas vesicles, or even single flagellate cells [67]. The distribution of gas vesicles, or rather their expression as seen by transmission electron microscopy, does not always relate to a planktonic lifestyle. Whereas the cyanobiont in coralloid roots of the cycad *Encephalartos transversosus* lacks gas vesicles [75], these structures do occur in a cyanobacterium from desert crusts [76] and in benthic strains of the predominately planktonic cyanobacterium *Planktothrix* [77]. The benthic strains of *Planktothrix* are ancestral in the genus [77]. Furthermore, the cyanobiont, *Richelia intracellularis*, of the planktonic diatom *Rhizosolenia* lacks contractile vacuoles [78], although here the small fraction of the holobiont volume occupied by *Richelia* means that contractile vacuoles could not significantly influence holobiont density. Furthermore, some *Rhizosolenia* species exhibit periodic vertical migration in the water column with buoyancy related to the composition of the (aqueous) vacuole of *Rhizosolenia* [21]. In addition to buoyancy, gas vesicles increase the cell surface area per unit cytosol volume for a cell of a given size and shape [77], and increase light scattering [67].

For non-flagellate eukaryotes, density can be manipulated by altering ballast components (such as polysaccharides versus lipids; mineral deposits) and altering the solutes in the (aqueous) vacuole to give a range of densities; in both cases, positive buoyancy can only be obtained in seawater, which has a higher density than freshwater [21,60,79]. Organic carbon reserves change phenotypically, as can silica and calcite deposits, as a function of environmental conditions. For diatoms, there is a genotypic decrease of silicification on a cell volume basis that changes the cell density when other ballast and solute change effects are allowed for, such that larger cells have a lower density, showing that the sinking rate is proportional to radius$^{1.6}$ rather than the Stokes law prediction for constant density of radius^{2} [80]. Phenotypic variation in density can decrease the exponent to 1.2 [80].

The last eukaryote common ancestor was most probably a flagellate [81–83]. Flagellar motility in algae is not unique to phytoplankton, but open water rather than sediment, as is the case of benthic microalgae, presents different opportunities and challenges for flagellated algae. Examples of freshwater volvocine phytoplankton are the unicellular *Chlamydomonas* [84] and the multicellular (cells at the surface of a sphere) *Volvox* [85]. Tam and Hosoi [84] showed that the most energetically efficient speed of swimming, e.g., chemotactically from lower to high nutrient concentration patches, is not the same as the speed causing maximum advective flux of nutrients to the cell surface from low bulk phase nutrient concentrations. Short et al. [85] modelled the role of flagella activity in increasing advective flux of nutrients from a low-nutrient bulk phase to *Volvox* cells that permits the *Volvox* life form to grow in nutrient-poor water at a higher rate than would be the case for similar non-flagellate organisms. *Volvox* can also exhibit diel, vertical migration between nutrient acquisition at night from the higher nutrient concentrations at the chemocline and the photosynthetically active radiation near the lake surface in a poorly mixed nutrient-poor epilimnion during the photoperiod when photosynthesis occurs; here, maximising the speed of movement could be advantageous in increasing the acquisition of nutrients and light, increasing the growth rate [21]. Another example of flagellate phytoplanktonic eukaryotes undergoing diel vertical migration is found among the marine and freshwater dinoflagellates [21], although here diel vertical migration sometimes occurs when the epilimnion is nutrient-replete [86]. The energetic cost of vertical migration has been calculated as both the work done against friction as a minimum estimate, and the maximum energy that can be expended as ATP hydrolysis based on the number of ATPase molecules per unit length of flagellum, the length of the flagella, and the in vivo free energy of hydrolysis of ATP, as well the energy cost of synthesis of flagella [87]. However, the

pay-off is thought to be nutrient harvesting from the thermocline, supplementing the nutrients available from a nutrient-depleted upper mixed layer. This nutrient gain is not readily expressed in terms of energy. A possible method would be to use the minimum energy cost of cell growth (mol absorbed photons per g dry matter gain [88]) scaled to the intracellular nitrogen (or phosphorus). A full energetic cost–benefit analysis was not achieved [87], despite the title of the paper.

An example of periodic (several days for a cycle) vertical migration related to inverse gradients of light and nutrients is that of large-celled marine planktonic centric diatoms such as *Ethmodiscus rex* [89,90] and some *Rhizosolenia* spp. [90,91], as well as the dinoflagellate *Pyrocystis* and the phycoma stage of *Halosphaera* and some other prasinophytes [90]. These periodic vertical migrations have a significant role in nitrate transfer from the nutricline to the oligotrophic ocean [90]. Periodic vertical migration can only occur for large cells with a large fraction of the cell occupied by a vacuole in the sea, where vacuolar density can be modified to values substantially lower than that of seawater by an as-yet incompletely understood mechanism, including changed inorganic ion composition and synthesis of organic solutes forming low-density solutions, and possibly active water transport, the result of modifying pre-existing mechanisms [21,79,90]. Such periodic vertical migrations are confined to marine habitats because (a) the lower density of freshwater than seawater would amplify the problems of decreasing cell density relative to that of the medium [79], (b) freshwater phytoplankton cells do not reach the large sizes found for the largest marine phytoplankton cells (for diatoms, see [92]) and (c) only for diatoms, the greater silicification of freshwater than marine cells of a comparable size [93].

Benthic microalgae live attached to or glide over rocks, or are attached to, glide over or swim (if flagellate) between smaller particles of sand or mud; gliding motility can function in benthic microalgae but not in phytoplankton [21]. Gliding motility has been shown to occur in some benthic cyanobacteria, benthic raphid pennate diatoms, a benthic araphid diatom, and some benthic desmids (Zygnematophyceae) [21,94,95]. Disturbance, e.g., wave action or bioturbation, can release benthic microalgae into the water body, which can facilitate dispersal, especially for epipsammic or epipelic species [1,21]. Vertical migration in benthic algae occurs over millimetres and follows diel, sometimes modulated by tidal, cycles, as found, for example, for the flagellate *Euglena* [96], and gliding diatoms [97].

In conclusion, flagellar motility occurs in some benthic microalgae and some phytoplankton. Gliding motility occurs in some benthic microalgae, but cannot occur in phytoplankton in the absence of a surface on which gliding can occur. Gas vesicles occur in some benthic and terrestrial cyanobacteria, although a function in movement has not been shown; gas vesicles are clearly involved in upward movement in planktonic cyanobacteria. Vertical movement in non-flagellate eukaryotic phytoplankton by cell density variations, including upward movement, has only been sought, and demonstrated, in some larger phytoplankton cells.

3.3. Variations in Spectral Distribution of Photosynthetically Active Radiation

Another aspect of the difference between the habitats of deep-growing microalgae in marine and freshwater planktonic and benthic habitats and those living on land is the spectral distribution of photosynthetically active radiation (PAR). For phytoplankton, the photic zone can be more than 100 m deep. Among the phytoplankton, those growing at the deep chlorophyll maximum are of special interest, because they are not subject to circulation through the light gradient in the upper mixed layer/epilimnion, and so are in a habitat with more constant, low photon flux density of photosynthetically active radiation [98,99]. The deep chlorophyll maximum near the thermocline can be at depths as great as 140 m in the ocean and lakes [100–103]. Fennel and Boss [101] point out that the deep chlorophyll maximum is at greater depths than the phytoplankton biomass as a result of increased chlorophyll per unit biomass with depth. With a low depth-integrated pigment content per m^2 surface area of habitat, the spectral distribution of PAR incident on the deep chlorophyll maximum is the outcome of the greater attenuation by water of longer,

red wavelengths, more than green and, especially, blue wavelengths [98,99,104,105]. In some coastal waters, there is attenuation of shorter, blue, wavelengths by dissolved organic compounds (gilvin or gelbstoff) [99,106].

Deep-growing benthic microalgae are also subject to the attenuation processes outlined in the previous paragraph. Benthic microalgal chlorophyll in the ocean occurs as deep as 191 m (Table 1 of [107]), although for epipsammic and epipelic microalgae, the extent to which the cells and the particles to which they are attached could have moved down-slope is not always clear. A crustose coralline red macroalga attached to a rocky substrate is even deeper growing (274 m): see [108].

In contrast, the photic zone of cyanobacteria and microalgae in terrestrial (e.g., desert crust) and microalgal mats in shallow benthic habitats is of the order of 1 mm deep, with PAR attenuation dominated by inorganic particles and cyanobacterial and microalgal pigments and, when the bottom of the euphotic zone is anoxic, bacteriochlorophyll. Towards the bottom of the photic zone, blue and, to a lesser extent, red wavelengths have been largely removed with, for overlying cyanobacteria, greater decreases in intermediate wavelengths [104,105,109,110].

What is the evidence of selection for different photosynthetic pigments in planktonic microalgae from those in benthic microalgae? For isolated cells, a greater spectral diversity of pigments has a greater influence on per cell absorptance of PAR in a given light field for smaller cells, because of the smaller package effect [111,112]. This argument can be extended to light-harvesting carotenoids and phycobilins [111,112]. In principle, a sufficient diversity of absorption maxima of pigments, and extent to which the different pigments are expressed, could produce a cell that absorbs a constant fraction of incident radiation at all wavelengths. However, no such cell has been reported; it would require a complex set of apoproteins binding the pigments that would allow energetically efficient excitation energy transfer from the range of light-harvesting pigment–protein complexes to Photosystem I or Photosystem II. In relation to minimizing self-shading, it is worth noting that the smallest known cyanobacterium, *Prochlorococcus*, is planktonic, occurs in the deep chlorophyll maximum, and has divinylchlorophyll *a* as well as chlorophyll *a*, and Mg 3,8 divinyl-pheoporphyrin a_5 (MgDVP) [113], and negligible expression of phycobilins that absorb in the trough between the blue and red peaks of the chlorophylls and MgDVP [114]. In contrast, the slightly larger *Synechococcus*, also from the oligotrophic ocean, has chlorophylls *a* + *b* and phycobilins, and less PAR absorbed per unit pigment than in *Prochlorococcus* [115]. The smallest photosynthetic eukaryote, the planktonic mamiellophycean *Ostreococcus*, has chlorophylls *a* + *b* and MgDVP [116].

As well as the absorption maxima of the pigments, an important factor for photon absorption is the specific absorption coefficient (units of m^2 (mole pigment)$^{-1}$); higher values mean a larger fraction of the incident photons are absorbed. For chlorophylls (and probably MgDVP), absorption at the blue absorption peak decreases in the order chlorophylls c_1, and/or c_2 and/or c_3, depending on the organism, and MgDVP), > chlorophyll *b* > chlorophyll *a*; this order is reversed for absorption at the red absorption peak [111,112]. Deep in the ocean, where there is limited absorption of blue radiation by gilvin (gelbstoff) and blue wavelengths penetrate deepest, chlorophylls *c* (and MgDVP) and, to a lesser extent, chlorophyll *b*, are more effective in photon absorption than chlorophyll *a*. Chlorophyll *c* occurs in almost all red line microalgae, including the major marine phytoplankton diatoms, haptophytes and (basal) dinoflagellates [98,108,117–119]. Several evolutionarily derived dinoflagellates contain kleptoplastids, dinotoms or cyanobacterial symbionts, yielding a range of light-harvesting pigments [108]. The blue light absorption by chlorophyll *c* in red line microalgae could be related to the enrichment of deep ocean water in blue wavelengths, especially in the deep chlorophyll maximum where microalgae have permanent blue light enrichment in the photoperiod. Also relevant are the light-harvesting carotenoids, peridinin in basal dinoflagellates [120], and fucoxanthin and its butanoyl- and hexanoyl-derivatives in diatoms and haptophytes, that extend the blue absorption into the blue-green more than the light-harvesting carotenoids of chloro-

phyll *a* + *b* organisms [121–123]. Latasa et al. [124] show that, within the deep chlorophyll maximum, the order of taxa with increasing depth are *Prochlorococcus*, dinoflagellates, *Synechococcus*, small haptophytes, coccolithophores, chlorophytes, pelagophytes and diatoms. Thus, chlorophylls c_1 and/or c_2 and/or c_3 (depending on the organism). and/or MgDVP. occur throughout the deep chlorophyll maximum. Chlorophyll *c* also occurs in deep-growing benthic diatoms living attached to sediments to 40 m depth in the Dogger Bank of the North Sea [125] and to 191 m in the western North Atlantic [81]. Whereas chlorophyll *c* occurs in some of the deepest growing planktonic and benthic microalgae, this light-harvesting pigment also occurs in microalgae growing in high light environments, as well as in the intertidal and subtidal macroalgal Phaeophyceae, where the package effect decreases the significance of the individual light-harvesting pigments [111]. Furthermore, the deepest growing benthic macroalga is a crustose coralline red alga with chlorophyll *a* and phycobilins as the photosynthetic pigments [108].

There were two secondary endosymbioses of green algal plastids producing the photosynthetic euglenids and chlorarachniophytes [126]. However, the number, and timing, of the secondary endosymbioses of red algal plastids leading to the photosynthetic alveolates, cryptophytes, haptophytes and stramenopiles is not clear [126,127]. Additionally, the timing of the evolutionary origin of the various light-harvesting and photoprotective pigments other than chlorophyll a, and the loss of pigments, such as phycobilins in all but the cryptophytes, in which phycobilins occur in the thylakoid lumen rather than in phycobilisomes on the outer surface of the thylakoids as in cyanobacteria, glaucophytes and red algae [128], is poorly understood [126]. This is also the case for differences in pigments within diatoms where there have been transitions from planktonic to benthic or vice versa.

In conclusion, there seems to be no differences in photosynthetic light-harvesting pigments between benthic and planktonic representatives of any clade on microalgae for which there are adequate data.

3.4. Variations in Incident PAR during the Photoperiod for Phytoplankton Entrained in Vertical Water Circulation in the Upper Mixed Layer/Epilimnion

A further aspect of photosynthetically active radiation availability to plankton that has no obvious analogue in benthic microalgae is vertical movement in water circulation in the upper mixed layer/epilimnion that is not offset by motion relative to the surrounding water by flagella motility and changes in buoyancy [129–134]. The physics of water movement in the upper mixed layer/epilimnion is very complex, but there seems to be a general inverse relation between the frequency of variation in PAR in the photoperiod and the magnitude of the variation. This relationship means that the high frequency (minutes) but low magnitude variations in Langmuir circulations near the surface only permit regulatory changes in photosynthesis, i.e., alterations in the functioning of the proteome [135] in state transitions and non-photochemical quenching. Lower-frequency (hours) but higher-magnitude changes, such as deep mixing, permit acclimation, i.e., changes in the proteome [135]. Increases in the ratio of chromophore–protein light-harvesting complexes to photochemical reactions centres and downstream redox catalysts and enzymes occur in low PAR episodes and vice versa in high PAR episodes. Benthic microalgae are also exposed to variation in PAR as a result of diel and tidal migration, wave focusing, changes in turbidity, and of shading by movement of any overlying seaweed fronds or seagrass leaves. What is not clear is whether there are differences between planktonic and benthic cyanobacteria and microalgae in the frequency and magnitude of the regulatory and acclimatory processes that depend on adaptive (genomic) differences [135] between planktonic and benthic photosynthetic micro-organisms.

The limited data do not allow conclusions on possible differences in repose to mean PAR, or in the frequency of variation in PAR between related benthic and planktonic microalga.

3.5. CO_2 and O_2 Concentration

As well as the compressed (relative to plankton) depth of the photic zone, the habitat of benthic cyanobacteria and microalgae has a larger diffusion boundary layer [136,137] than what is the case for planktonic cyanobacteria and microalgae (see Section 3.2 above). This greater limitation to diffusion results in a larger CO_2 depletion and O_2 enrichment in the light in cyanobacterial hypersaline mats and marine diatom mats [136–138] than is the case for planktonic photosynthetic organisms [139,140]. The widespread occurrence of inorganic carbon concentrating mechanisms (CCMs), in planktonic eukaryotic algae, and the universal occurrence of CCMs in photosynthetically competent cyanobacteria [32,140] and basal, peridinin-containing dinoflagellates [23], shows that the greater perceived need for CCMs in benthic microbial oxygenic photosynthetic organisms does not distinguish phytoplankton from microphytobenthos with respect to the occurrence of CCMs. The CCMs are almost all based on active transport of bicarbonate, some on active transport of protons, and with little evidence of a role for C_4-like metabolism [32,140]. The limited data do not permit differentiation of inorganic carbon acquisition mechanisms in planktonic and benthic microalgae [32,140,141]. The evolution of CCMs in photoautotrophs in relation to geological changes in atmospheric CO_2 and O_2, and also temperature that alters the kinetics of Rubisco as well as the solubility of CO_2 and O_2, are discussed in [140,142–145]. The timing of the origins of CCMs can only be defined within broad limits, but the CCMs of cyanobacteria could have evolved in the Proterozoic, and occur in all cyanobacteria today [140]. CCMs of eukaryotes could have evolved as late as the Carboniferous high O_2/CO_2 ratio [140]. For those eukaryotes with Form IB or Form ID Rubisco, but not dinoflagellates and chromerids with Form II Rubisco, there could have been problems with retention of CCMs in high CO_2 episodes [140]. It should be emphasised that some photosynthetic eukaryotes lack CCMs [140]. A recent finding is that the carboxysomes, intracellular compartments containing all of the Rubisco in cyanobacteria, and the pyrenoids containing the Rubisco of many eukaryotes with CCMs [142], have Rubisco as a phase-separated liquid related to the presence of an intrinsically disordered protein [146–148]. This phase separation cannot be essential for eukaryote CCMs, since a number of CCM-expressing eukaryotic algae lack pyrenoids [142].

To conclude, as indicated above, the limited data do not permit differentiation of inorganic carbon acquisition mechanisms in planktonic from those of benthic microalgae [32,140].

3.6. Availability of Nitrogen, Phosphorus and Iron

These three essential nutrients are considered here because they are the main elemental resources that limit planktonic primary productivity in the ocean, whereas phosphorus and nitrogen are the main elemental resources limiting growth in inland waters. Figure 3 of Moore et al. [149] shows the global distribution of N, P and Fe limitations of marine phytoplankton productivity. Thus, even with small diffusion boundary layers (see Section 3.2 above), N, P and Fe limitation of primary productivity is widespread among marine phytoplankton. N limitation has also been shown for benthic marine diatoms in the oligotrophic western Baltic Sea [150]. For freshwater habitats, Maberly et al. [151] examined nutrient limitation in an upland lake in the UK, and showed N limitation, P limitation and PN co-limitation to similar extents in phytoplankton and periphyton (microphytobenthos plus multicellular benthic algae and mosses). Thus, as expected, microphytobenthos as well as phytoplankton are similarly N and P limited in the same N and P environment. Again, there is no evidence of greater capacity to acquire N or P in phytoplankton than in the microphytobenthos. There seems to be no data comparing the kinetics of nutrient uptake by phytoplanktonic and microphytobenthic cells under conditions with similar thicknesses of the diffusion boundary layer.

Are there differences between planktonic and benthic microalgae in the nitrogen and phosphorus sources that can be used? Dissolved organic N, including urea, is used by many phytoplankton species, e.g., the harmful algal bloom dinoflagellate *Prorocentrum minimum* and the pelagophycean *Aurecococcus anophageffens* [152]. Rivkin and Putt [153] showed

that Antarctic planktonic, benthic and sea ice diatoms are all able to take up amino acids. Whereas most microalgae can use nitrate and nitrite, some strains of the planktonic cyanobacterium *Prochlorococcus* cannot use one or both of these oxidised nitrogen species [154]. It is not clear whether there are benthic microalgae that are unable to use nitrate or nitrite. There are diazotrophic cyanobacteria in the plankton and benthos, with symbioses as well as free-living examples [155]. Phosphate is almost invariably taken up as inorganic phosphate; organic phosphate esters are hydrolysed by external phosphatase prior to inorganic phosphate uptake [156]. An exception to inorganic phosphate uptake is for certain cyanobacteria where organic phosphonates are taken up and intracellular phosphonatases produce inorganic phosphate in planktonic [156,157] and benthic [158] cyanobacteria.

The available data do not permit conclusions as to differences in acquisition in non-carbon nutrients between benthic and planktonic microalgae.

3.7. Phagophotomixotrophy

Much attention has been given to phagophotomixotrophy of phytoplankton [159,160] that occurs in Dinophyta, Chrysophyceae, Cryptophyta, Haptophyta and Prasinophyceae. Much less attention has been given to benthic microalgae, but phagomixotrophy has been found in benthic dinoflagellates in several locations [161–163]. The ancestral eukaryotic algae, for both primary endosymbioses of a cyanobacterium resulting, separately, in Archaeplastida and *Paulinella*, and for secondary endosymbiosis of a green or red eukaryote yielding other photosynthetic eukaryotes, had the capacity for phagotrophy, so phagophotomixotrophy is apparently ancestral in algae [164]. Furthermore, molecular phylogenetic studies suggest that the benthic freshwater *Gloeomargarita* is the closest extant cyanobacterium to the ancestor of plastids of the Archaeplastida [165,166], so benthic phagophototrophy may be the ancestral state of photosynthetic eukaryotes. However, extant eukaryotes have a diversity of endocytotic mechanisms, and polyphyly is likely [167,168]. Phagophotomixotrophy is widespread in extant microalgae [169]. Whether phagophotomixotrphy in benthic dinoflagellates is ancestral or derived from planktonic phagophotomixotrophs is unclear. Diatoms, like many other algae, are subject to viral attack [170], so their silicified walls do not protect them from viruses, but do prevent them from ingesting much larger organic particles in phagophotomixotrophy.

As well as phagotrophy by photosynthetic microalgae in plankton and benthos, photosynthetic microalgae can act as the photosymbionts in phagoorganotrophic plankton. Some dinoflagellates are endosymbionts with planktonic rhizarians such as some foraminifera, radiolaria and acantharia [32] and the planktonic cnidarian *Cassiopeia* [171], and, with a photosynthetic haptophyte, in one species of polycystine acantharian [172]. In 25 species of polycystine acantharians, a haptophyte is the only photosymbiont [172]. Endosymbiosis of photosynthetic dinoflagellates occurs in some phagotrophic benthic Cnidaria and Porifera [32].

The other mode of microalgal mixotrophy is osmophotomixotrophy, i.e., the influx and use in growth of dissolved organic carbon compounds by a photosynthetically competent organism. Benner and Amon [173] point out that 98% of the 56 Pmole organic carbon in the global ocean is dissolved organic carbon. However, most of this is refractory organic carbon with turnover times of centuries to millennia; the rest are semi-labile (turnover time months to years) and labile (turnover time days to weeks) [173,174].

Some microalgae are obligate photoautotrophs in that none of the organic solutes tested can contribute to growth, although in the case of the tychoplanktonic *Phaeodactylum tricornutum*, the expression of the human or the *Chlorella* glucose transporter allows glucose to contribute to growth [175]. Osmophotomixotrophy has been demonstrated in several microalgae, although with higher organic solute concentrations higher than those found in nature, with the exception of some eutrophic habitats [176]. Wright and Hobbie [177] showed that phytoplankton in Lake Erken in Sweden were very poor competitors for the use of acetate and glucose compared with co-existing bacteria. The experiment involved adding

^{14}C-labelled glucose at 5.5–55 mmole m^{-3}, and ^{14}C-labelled acetate at 16–160 mmole m^{-3} to samples of lake water [177]. The ^{14}C found in phytoplankton was less than 10% of that in bacteria, despite the phytoplankton biomass that was at least an order of magnitude greater than that of bacteria [177].

Additional evidence that osmophotomixotrophy by microalgae is of very limited significance in the environment comes from measurements of the fraction of organic carbon produced in microalgal photosynthesis that is lost from the organism as dissolved organic carbon. This ranges from 1.5 to 27% during exponential growth [178,179]; see also [180]. So far, there have been no experiments examining the influx of ^{13}C- or ^{14}C-labelled organic carbon by microalgae at the same time as efflux of ^{12}C dissolved organic carbon. Such experiments would preferably use ^{13}C- or ^{14}C-labelled excreted organic C produced in a separate experiment with microalgae photosynthesising with ^{13}C- or ^{14}C-labelled inorganic carbon.

The available evidence suggests a limited role for osmophotomixotrophy in microalgae in either plankton or benthos.

Uptake of organic compounds by microalgae occurs in the form of vitamins that the organisms need but cannot synthesise. No eukaryote can synthesise vitamin B12, and microalgae such as *Thalassiosira pseudonana* that rely on the vitamin B12-dependent enzyme *MetH* of the pathway of methionine synthesis require an external supply of vitamin B12 [181]. Some microalgae such as *Phaeodactylum tricornutum* have, in addition to *MetH*, *MetE*, which catalyses the same reaction as *MetH* but does not require Vitamin B_{12}, and so do not need Vitamin B12 for growth. Whereas *Thalassiosira pseudonana* is planktonic, and *Phaeodactylum tricornutum* is tychoplanktonic, these data cannot be extrapolated to Vitamin B_{12}-dependence of eukaryotic phytoplankton and Vitamin B12-independence of benthic eukaryotic microalgae.

It is not possible to distinguish benthic from planktonic microalgae on the basis present knowledge of the extent of phagophotomixotrophy, osmophotomixotrophy, and dependence on exogenous vitamins.

3.8. Allelopathy and Other Physiological Processes Related to Competition with Other Phototrophs and Defence against Grazers and Parasites

Specific allelochemicals produced by some phytoplankton organisms can decrease the growth rate, and even threaten the survival, of other species of phytoplankton [182]. Dilution of allelochemicals in planktonic environments means that allelopathic interactions might be favoured in environments with high cell densities, such as harmful algal blooms [183]. The enhancement of allelochemical production by N, P and light limitation can be interpreted as limiting competition for N and P, and also for light in dense cultures when shading by other phototrophs is significant; the functional significance, if any, of increased allelochemical production at low temperature or low pH is not clear [182].

The outcome of long-term competition experiments with co-cultured *Oscillatoria* sp. that produces allelochemicals, and *Ankistrodesmus falcatus*, a superior competitor for NO_3^-, depends on the initial abundances of the two species: the outcome can be either dominance of the superior competitor for NO_3^-, oscillatory co-existence, or dominance of the allelochemical producer [182]. Allelopathy can limit competition and promote phytoplankton diversity [184–186], a part of the solution to the 'Paradox of the Plankton' [187].

For benthic microalgal habitats, there have been fewer reports of allelopathic interactions, with significant methodological constraints on such investigation [188]. Modelling of the evolution of allelopathy suggests that this can only occur in a structured, benthic environment [189]. Toxin-producing benthic dinoflagellates occur, e.g., *Fukuyoa*, *Gambierdiscus*, and *Ostreopsis* are known, with most research focussed on the effects on metazoa [56,190], with no reports of allelopathic effects in benthic microalgae. However, filtrates of benthic diatoms inhibit the growth of *Ostreopsis* [56,182,190].

As well as interactions among phototrophs, allelopathy also involves interactions of phototrophs with grazers and parasites. Studies of the effects of the planktonic *Synechococcus* sp., *Tetraselmis susica, and Thalassospia weissfloggi* on either of the grazers *Euplotes* sp.

and *Acartia tonsa* (copepod) showed that toxins produced by the cyanobacterium, and to a lesser extent by the diatom, were inhibitory of *Euplotes*, but not *Acartia* [191].

Another physiological aspect of defence of microalgae against grazers is strengthened cell wall [191,192]. The silicified frustules of diatoms have considerable resistance to external pressure, with implications for access by grazers to the cell contents [193]. The presence of the grazing copepod *Acartia* increased silicification [191], and presumably frustule resistance to external pressure by copepods [194], of the diatom *Thalassiosira weissflogii* by 4–6 fold, with no effect of the protist grazer *Euplotes* [191].

Euplotes, with no opposable hard parts, is expected not to depend on crushing diatoms for their digestion. However, that the benthic formaniferan *Haynesina*, also with no opposable hard parts, could bring about extracellular breakage of the diatom *Pleurosigma*. [195]. This phenomenon is currently unexplained.

4. Conclusions

What physiological traits of microalgae can be specifically related to the phytoplanktonic habitat? Survival of some phytoplankton cells in darkness following sinking of plankton below the photic zone can extend to decades or even centuries. Much less information is available for benthic microalgae; the longest period of darkness tested was one year, with survival of some cells. For mechanisms of upward movement relative to surrounding water, some planktonic cyanobacteria have gas vesicles, and some eukaryotes (e.g., dinoflagellates) have flagella. These mechanisms permit periodic vertical migration when the photic zone has sufficiently small vertical water movement, allowing use of the inverse vertical gradients of the resources, photosynthetically active radiation and nutrients. However, some benthic cyanobacteria also have gas vesicles and some benthic microalgae growing in sand or mud are flagellate, and show periodic vertical migration in diel rhythms as moderated, in tidal habitats, by tidal cycles. Some benthic cyanobacteria, diatoms and desmids also show motility. The only motility mechanism confined to phytoplankton is buoyancy related to changes in the composition of a large central vacuole of large cells of diatoms, prasinophyte phycomata, and a (non-flagellate) dinoflagellate, again allowing use of the inverse vertical gradients of the resources, photosynthetically active radiation and nutrients.

Phytoplankton photosynthetic pigments, and downstream photosynthetic processes, are not unique to phytoplankton as some clades also have benthic representatives, e.g., cyanobacteria, diatoms and dinoflagellates. Whereas some pigments (e.g., chlorophyll *c* and MgDVP) can be construed as particularly useful in photon absorption in blue-enriched light at the bottom of the photic zone, this is the case not only for plankton but also for deep-growing benthic algae. Also, some deep chlorophyll maximum plankton lack chlorophyll *c* and MgDVP. For phytoplankton entrained in vertical water movement, there are regulatory and acclimatory changes during cyclic variations in photosynthetically active radiation as a function of depth superimposed on the diel variation in photosynthetically active radiation at a given depth. It is not clear if this requires different time scales of responses to those found in diel–tidal vertical migration, in some cases, modulated by variable shading by overlying seagrass leaves or macroalgal fronds.

There are inadequate data to determine if variations in inorganic carbon supply, or nitrogen and phosphorus supply, in frequency or magnitude, are different in phytoplankton from those in benthic microalgae. Phagophotomixotrophy and (to the extent that it occurs) osmophotomixotrophy occur in both phytoplankton and benthic microalgae. Finally, allelopathy involving interactions of microscopic photoautotrophs, and between photoautotrophs and grazers, occur in plankton and benthos.

Further progress in identifying physiological traits found only in phytoplankton needs further investigation of benthic microalgae that are closely related to planktonic microalgae. Particular attention is needed on whether the phylogeny of benthic algae shows, as far as can be determined, a planktonic period, or whether they are derived from planktonic ancestors.

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