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PICOPHYTOPLANKTON: BOTTOM-UP AND TOP-DOWN CONTROLS ON ECOLOGY AND EVOLUTION

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CHLOROPHYTA
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EUKARYA
GRAZING
PARASITISM
RESOURCE ACQUISITION
SEDIMENTATION
VIRUSES

ABSTRACT. – Picophytoplankton organisms were derived from larger ancestors in both cyanobacteria and (polyphyletically) in eukarya. There are a number of putative advantages in the acquisition of photosynthetically active radiation and nutrient solutes from resource-limited habitats, and probably of maximum specific growth rate, for very small cells relative to the situation for larger phytoplankton cells. However, there are also putative disadvantages for such small cells with respect to bottom-up factors (i.e. those limiting biomass production), including an increased potential for solute leakage and an increased metabolic cost of screening out damaging UV-B. Among top-down factors (i.e. those removing biomass), picophytoplankton may be at an advantage relative to larger phytoplankton cells in avoiding damage from eukaryotic parasites, and losses from sedimentation. However, viruses and (small) grazers can attack picophytoplankton, just as viruses and (larger) grazers can attack larger phytoplankton. Picophytoplankton may be at a disadvantage relative to larger phytoplankton in environments with temporally variable resource supply.

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RÉSUMÉ. – Les organismes du picophytoplancton dérivent d'ancêtres de plus grande taille parmi les cyanobactéries et les eucaryotes (polyphylétiquement). Ces organismes ont un nombre d'avantages potentiels dans l'acquisition de la radiation active photosynthétiquement et des éléments nutritifs solubles des habitats limités en ressources, et probablement dans le taux maximum de croissance spécifique, pour de petites cellules par rapport à la situation de cellules du phytoplancton plus grandes. Cependant, il y a aussi des désavantages potentiels pour de si petites cellules par rapport aux facteurs de croissance "bottom-up" (c.-à-d. ceux qui limitent la production de biomasse), y compris une augmentation du potentiel pour l'écoulement des substances solubles et un coût métabolique élevé pour filtrer les rayons UV-B qui causent des dommages. Parmi les facteurs « herbivores » ("top-down") (c.-à-d. ceux qui suppriment la biomasse), le picophytoplancton pourrait avoir l'avantage, par rapport aux cellules plus grandes du phytoplancton d'éviter les dommages causés par les parasites eucaryotes, et les pertes dues à la sédimentation. Cependant, les virus et les (petits) herbivores peuvent attaquer le picophytoplancton, de même que les virus et les herbivores (plus grands) peuvent attaquer le phytoplancton plus gros. Le picophytoplancton peut-être désavantagé par rapport au phytoplancton de plus forte taille dans les environnements aux ressources variables dans le temps.

INTRODUCTION

Picophytoplankton are defined here as planktonic photosynthetic organisms which are not retained by a 2 µm pore diameter filter. Molecular phylogenetic analyses show that these very small planktonic photolithotrophs were derived from larger ancestors, that, at least among eukarya, the picophytoplankton condition is polyphyletic, and that miniaturization of genomes and cells can increase the rate of evolution (Raven 1998, Moreira & López-García 2002, Vaulot *et al.* 2002, Dufresne *et al.* 2005, Giovannoni *et al*. 2005).

This paper aims to examine the possible ecological and evolutionary advantages and disadvantages of very small size for phytoplankton by comparison with larger photosynthetic plankton. These possible costs and benefits are discussed first for bottom-up factors, then for top-down factors.

BOTTOM-UP FACTORS

Non-scalable components

This heading includes any environmental factor which decreases the growth of phytoplankton. Examples include the restricted or excessive availability of photosynthetically active radiation (PAR) or of nutrient solutes, and growth rate-inhibiting fluxes of UV-B. The proportion of cell volume taken up by non-scalable components, such as the minimal suite of genes needed for photolithotrophic growth and biological membranes of constant thickness, increases as cell and genome size is reduced, potentially forcing the displacement of some protein catalysts of growth processes leading to increased specialization and a reduction in average growth rate over a range of environmental conditions (Raven 1986, 1998). In general there is an increase in maximum specific growth rate (μ_m: biomass increase per unit biomass per unit time) of organisms with decreasing body size of the form $\mu_m = a \cdot \text{biomass}^{-b}$, where a is a taxon-specific 'constant'. While b is held to have a taxon-independent value of 0.25, it may not be possible to reject the possibility of lower values of b for the members of some Phyla or Classes (Raven 1998). If the non-scalable factors restricting μ_m become significant within the size range observed for picophytoplankton, then the value of μ_m for the smallest picophytoplankton should be lower than predicted by the scaling relationship. While the smallest known photolithotrophic eukaryote, *Ostreococcus tauri*, has very high μ_m values (Fouilland *et al.* 2004), the smallest O_2-evolver, *Prochlorococcus*, has a lower μ_m than many rather larger cyanobacteria (Sullivan *et al.* 2005). Based on available observations of maximum growth rates normalized to cell volume, bigger cells appear to have higher intrinsic maximum growth rates (Table I) although there is a great deal of taxonomic and experimental variation in estimates of μ_m.

Absorption of PAR and UV-B

Turning to resource-limited growth rates, there are sound physical arguments for more effective acquisition of PAR and of nutrient solutes by smaller than by larger organisms (Fogg 1986, Raven 1986, Chisholm 1992, Raven 1998). For PAR there is less package effect in smaller than in otherwise similar larger cells, so that each pigment molecule is more effective at absorbing photons, and it takes less time for a pigment-protein complex to absorb enough photons from a given radiation field to recoup the energy cost of synthesizing the complex, in smaller cells (Raven 1984, 1998, Finkel *et al.* 2004). It is thus predicted, and observed, that the allometric coefficient b is smaller (more negative) in light-limited than in resource-saturated growth of phytoplankton organisms (Finkel & Irwin 2000, Finkel 2001, Finkel *et al.* 2004).

Table I. – Measured maximum growth rates for picophytoplankton and growth rates normalized to a cell volume of 1 μm^3.

Size and Taxonomic grouping		Cell diameter μm	Measured μ_{max} day^{-1}	Estimated μ_{max} for 1 μm^3 cell	References
Prokaryotes (Bacteria)					
Prochlorococcus spp.	Cyanobacteria	~0.7	0.99	0.7	Shalapyonok *et al.* (1988)
Synechococcus spp.	Cyanobacteria	~1	1.97	1.8	Kana and Glibert (1987)
Eukaryotes					
Ostreococcus tauri	Prasinophyceae	0.8-1.1	1.1,2.4,8*	0.9,2.4,6.5	Courties *et al.* (1998); Fouilland *et al.* (2004); Rodriguez *et al.* (2005)
Micromonas pusilla	Prasinophyceae	1.4-19	0.9,3.5*	1.1,5.0	Throndsen (1976); DuRand *et al.* (2002)
Aureococcus anophagefferens	Pelagophyceae	1.5-2	0.9,2.3*	1.1,3.0	Pustazzi *et al.* (2004); Caron *et al.* (2004)
Pycnococcus provasplii	Prasinophyceae	2.7	0.7	1.2	Ho *et al.* (2003)
Nannochloris atomus	Trebouxiophyceae	3	0.6	1.2	Ho *et al.* (2003)
Chaetoceros cf. *tenuissimus*	Bacillariophyceae	4.0	1.6	3.9	Doblin *et al.* (1999)
Thalassiosira spp.	Bacillariophyceae	~4	3*	7.2	Furnas (1991)
Small pennate spp.	Bacillariophyceae	~4	3.5*	8.5	Furnas (1991)
Small Gymnodiniaceae	Dinophyceae	~4	1.0*	2.5	Furnas (1991)
Emilinia huxleyi	Prymnesiophyceae	~4-6	1.3,1.9	3.7,5.5	Brand and Guillard (1981); Rhodes *et al.* (1995)
Skeletonema costatum	Bacillariophyceae	~8	5.9*	23.9*	Furnas (1990)
Medium Gymnodiniaceae	Dinophyceae	~10	1.0*	4.6	Furnas (1991)

*data from field study, all other data from laboratory experiments
†computed assuming allometric scaling with an exponent of –0.25
Cell size data predominantly from references indicated and Vaulot *et al.* (2004).
For Furnas (1990 and 1991) size data were not provided; the size estimates are based on an interpretation of the term "small" and "medium" for diatoms and dinoflagellates.

Furthermore, the smaller package effect in picophytoplankton than in larger organisms means that the spectral diversity among photosynthetic pigments is expressed to a greater extent in the *in vivo* absorption spectrum in the smaller organisms, which indeed have a greater diversity of photosynthetic pigments than in larger organisms (Raven 1998, Larkum & Kühl 2005, Miller *et al.* 2005). This spectral diversity of pigments is of ecological and evolutionary significance in niche partitioning among picophytoplankton species (Stomp *et al.* 2005) even if this diversity is not as important on larger evolutionary scales (Falkowski *et al.* 2004a,b).

Restriction of growth rate by UV-B radiation resembles photoinhibition by high PAR rather than limitation by low PAR. However, there is an implication of small cell size for the effectiveness of soluble intracellular UV-B screening compounds in restricting UV-B access to targets such as DNA (Raven 1998). The smaller intracellular optical path length in picophytoplankton means that a certain concentration of soluble UV-B-absorbing compounds absorbs a smaller fraction of the UV-B incident on the cell than would be the case for a larger cell, so a higher UV-B flux reaches targets (Raven 1998). Other possibilities of avoiding UV-B damage, and variations in the potential to repair UV-B damage, mean that the prediction is not obeyed universally (Raven 1998, Day & Neale 2002, Sommaruga *et al.* 2005).

Solute acquisition and loss

Smaller cells have an enhanced potential for nutrient solute influxes from low bulk phase concentrations through the diffusion boundary layers and the plasmalemma relative to the requirement for growth, granted the allometry of the potential growth rate as a function of organism size (Raven 1986, Chisholm 1992, Raven 1998). There is, however, also more potential for the loss of solutes from the smaller cells (Raven 1986, 1998). Such increased leakage can reduce the energetic efficiency of photosynthetic inorganic carbon concentrating mechanisms (CCMs) by increasing the rate constant for efflux of accumulated CO_2 (Raven 1986, 1998, Giordano *et al.* 2005). The problem is exacerbated for cyanobacteria by the low CO_2 affinity, and low CO_2/O_2 selectivity, of both the Form IA and Form IB ribulose bisphosphate carboxylase-oxygenases or Rubiscos (Horken & Tabita 1999, Badger & Price 2003, Giordano *et al.* 2005). The effectiveness of the CCM in *Synechocystis* in suppressing the oxygenase activity of Rubisco is seen by the absence of effect on growth in air-equilibrium solutions of the deletion of glycine decarboxylase, an enzyme of the photorespiratory carbon oxidation cycle which is required to consume glycolate (Hagemann *et al.* 2005). Another potential problem for resource acquisition, in this case N_2 fixation, is that of keeping oxygen away from, the nitrogenase – nitrogenase reductase complex. Even with nitrogen fixation limited to the dark phase there is a higher energy cost of removing oxygen per unit nitrogenase activity in picocyanobacteria (and other picoplankton) than in larger diazotrophs. Despite this, picophytoplanktonic cyanobacteria in which nitrogen fixation has been demonstrated, or in which have the genetic potential for nitrogen fixation, occur in the ocean (Zehr *et al.* 1998 Falcon *et al.* 2005).

Implications of the streamlining of genome

The smallest O_2-evolving photolithotrophs (*Prochlorococcus* strains) have lost a number of functions, e.g. the ability to use certain oxidized nitrogen sources (Hess 2004). Such gene loss, with genome streamlining, characterizes not only picophytoplanktonic but also the picochemoorganotrophic bacteria of the open ocean (Bryant 2002, Giovannoni *et al.* 2005). This reduction in the size of the genome offsets considerations of scalability, but ultimately the minimum size of cell and genome would mean a greater fraction of biomass is occupied by DNA, with a corresponding decrease in cellular C:N and C:P relative to the Redfield Ratio (see Table I of Geider & La Roche 2002). An increased fraction of plasmalemma in smaller cells would, as a result of the high protein and phospholipid content of the membrane, also decrease C:N and C:P relative to the Redfield Ratio (Geider & La Roche 2002). However, the observation is that C:N and C:P ratios in these very small cells may be higher than the Redfield Ratio average for larger phytoplankton cells (Geider & La Roche 2002), with the additional organic C helping to further increase the surface area per unit N or P in the small cells (reviewed by Raven *et al.* 2005, Thingstad *et al.* 2005). A further possibility for increasing surface area per unit N or P is to have a more dilute cytoplasm (see Raven *et al.* 2005). The option of vacuolation is not used by the smallest phytoplankton cells (Raven 1998), with their resource storage role taken by the essentially particulate polymers rather than dissolved monomers, with an order of magnitude smaller volume required to store unit N or P (Table II). Overall (Raven 1998, Table 6), there is the potential for a more effective use of already-acquired resources in obtaining further resources in picophytoplankton than in larger phytoplankton cells both at resource saturation and when resources are limiting. There is, however, the proviso that at the lowest sizes of picophytoplankton the fraction of the cell taken up by non-scalable components may decrease the effectiveness of already-acquired resources in obtaining further resources. Small and large cells

Table II. – Volume needed per mol P or N stored in vacuoles isosmotic with seawater, or as particulate polyphosphate or polypeptide.

Element stored, chemical form	$m^3 mol^{-1}$	References
P as KH_2PO_4	1.54	Weast (1969/1970)
P as polyphosphate, assuming density is identical to that of solid calcium pyrophosphate	0.041	Weast (1969/1970)
P as polyphosphate at the highest concentration measured in acidicalcisomes	0.125	Docampo and Moreno (2001)
N as KNO_3	1.52	Weast (1969/1970)
N as cyanophycin, the polypeptide N storage compound (1 arginine:1 aspartate) of cyanobacteria, assuming the same density as protein	0.042	Boyd and Gradmann (2002)

alike may be able to store nutrients when they are supplied in excess of need, despite using different storage strategies, but the characteristics of the temporal pulse will favour one size over others; small cells with insufficient biomass-normalized storage ability will not be able to take full advantage of large nutrient pulses.

TOP-DOWN FACTORS

Sinking

Sinking of live cells out of the euphotic zone is one factor removing biomass from a phytoplankton population. Stokes' Law shows that, if a 50 μm radius spherical cell with density 50 kg m^{-3} greater than the surrounding water sinks at 26 m day^{-1} relative to the surrounding water, an otherwise similar cell of 0.5 μm radius cell would only sink 2.6 mm day^{-1} (Raven 1998). We shall return to sinking in the context of parasitism. Coagulation of particles can dramatically change the size distribution and sinking fluxes, probably increasing the flux due to small particles above a Stokes' law prediction (Stemmann *et al.* 2004a).

Biophagy: eukaryotic parasitoids

Raven (1998) points out that picophytoplankton organisms are very unlikely to support eukaryotic parasites (parasitoids): see Raven & Waite (2004). The smallest known eukaryote is the picophytoplankton organism *Ostreococcus tauri*, with a volume of $5.24 \cdot 10^{-19}$ m^3; the largest spherical picophytoplankton cell has a volume of $4.19 \cdot 10^{-18}$ m^3. A hypothetical parasitoid with the same volume as *Ostreococcus* infecting the largest picophytoplankton organism as host could produce only four new parasitoid cells per infecting parasitoid if only half of the host biomass is converted into new parasitoids (the rest being unusable, or respired). No such parasitoid is known. Clearly no eukaryotic parasitoid, even as small as the hypothetical example used above, could have the smallest picophytoplanktonic cyanobacteria as hosts.

Biophagy: viruses

Viruses are widespread top-down factors in cyanobacterial (Sullivan *et al.* 2005) and eukaryotic (Wilson *et al.* 2005) phytoplankton, including picophytoplankton. This view is supported by the recent characterisation of two viruses of diatoms, a major phytoplankton taxon for which there had been no previous characterisation of viruses (Nagasaki *et al.* 2004, 2005). Viruses may be involved in bloom termination in cyanobacterial and eukaryotic picophytoplankton (Evans *et al.* 2003). While viruses are much smaller than eukaryotic parasitoids, viral reproduction requires significant quantities of P and the cell quota of P is very low in P-starved *Prochlorococcus* cells (Bertilsson *et al.* 2003). Furthermore, Wilson *et al.* (1996) showed that viruses infecting a *Synechococcus* culture which was starved of P had substantially reduced burst sizes. With half of the cell quota of 0.36 fg P in the 1.65 Mbp genome, the burst size of

cyanomyophage P-SSM2, with a 0.252 Mbp genome (Sullivan *et al.* 2005), can only be 13, while if a phage was as large as the 0.407 Mbp coccolithovirus (Wilson *et al.* 2005) the burst size would only be 8. Could this be a constraint on the size of cyanophages infecting the smallest picophytoplankton cells? A similar suggestion, with much more extensive documentation, has been made independently by C Brown and collaborators (personal communication; manuscript submitted).

The top-down factor of viral infection may interact with bottom-up effects independently through the recycling of nutrients by cell lysis. The *Prochlorococcus* phages P-SSM2 and P-SSM4 each have copies of two cyanobacterial genes (*phoH* and *pstS*) that are expressed under P deficiency, while the *Synechococcus* phage S-PM2 has, in addition, *phoH*; could this be related to their infection of P-depleted cells (Sullivan *et al.* 2005)? *Prochlorococcus* (Sullivan *et al.* 2005) and *Synechococcus* (Mann *et al.* 2005) phages also contain genes related to photosynthesis, another possible interaction between top-down and bottom-up factors.

There is the possibility that increased sinking rates of phytoplankton damaged by parasitoid or virus infection could be a means of purging healthy surface-dwelling populations by the faster sinking of infected organisms (Lawrence & Suttle 2004, Raven & Waite 2004). Even for larger phytoplankton cells the evolution and operation of such a mechanism has several constraints, e.g. host specificity of the parasitoid or virus, and the hydrodynamic regime of the upper mixed layer (Lawrence & Suttle 2004, Raven & Waite 2004), while the sinking rate of picophytoplankton is so small as to eliminate this mechanism for removing infected cells (Waite *et al.* 1997, Raven 1998, Raven & Waite 2004).

Biophagy: grazers

Finally we address the impact of grazers. Picophytoplankton escape grazing by larger grazers, but can be consumed by smaller grazers (see Raven 1998, Chrisaki *et al.* 1999, Fouilland *et al.* 2004); there are now known to be grazers of picoplankton size which have higher maximum specific growth rates than *Prochlorococcus*, and so could exert control over this picocyanobacterium (Gouillou *et al.* 1999). There can be significant discrimination among picophytoplankton by grazers, e.g. between *Prochlorococcus* and *Synechococcus* (Christaki *et al.* 1999, Worden *et al.* 2004). There is thus the frequent interposition of another trophic level, i.e. ciliate and flagellate grazers, between the primary producers and the many larger zooplankton grazers for picophytoplankton but not for larger phytoplankton, possibly causing a reversal in the direction of top-down effects on different size categories of phytoplankton by, for example, changes in the populations of the organisms consuming the larger phytoplankton.

CONCLUSIONS

Many of the ecological and evolutionary aspects of picophytoplankton can be related to their small size. However, 'biology' complicates almost all of the arguments made purely on the basis of cell size (Table I).

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