

Uncoupling primary production from population growth in photosynthesizing organisms in aquatic ecosystems

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ABSTRACT

Whenever actively photosynthesizing cells are exposed to conditions where carbon fluxes exceed intakes of other essential-nutrients required for formation of new biomass, cell division is arrested, and the excess carbon is stored, excreted or directed to secondary functions. The extent of this uncoupling and its' implications in aquatic systems are discussed. We focus on three examples: the cellular level of free living phytoplankton, the ecosystem level in the microbial food web, and the highly specialized level of species interactions in the symbiotic association between zooxanthellae and corals. These examples highlight the adaptive significance of uncoupling between photosynthesis and growth in aquatic systems. Moreover, we underscore the fact that in many real-world situations, net primary productivity cannot be equated to population growth.

Roles of the “excess” carbon include photoprotective pigments and buoyancy regulating ballast. The excreted carbon compounds may protect cells or cell masses from desiccation, and fuel the microbial loop. The microbial loop increases overall nutrient extraction efficiency compared to that of which phytoplankton alone are capable.

The zooxanthellae-coelenterate symbiosis drives the nutrient and energy fluxes supporting coral reef life in the nutrient-poor tropical seas. In those mutualistic associations, since photosynthesis is normally uncoupled from cell growth, the algae excrete most of their photosynthate and that supports the metabolic activities of the host.

Introduction

Photosynthetically driven CO₂ reduction provides the energy-rich compounds that support all life processes. In aquatic ecosystems, most photosynthesis is performed by phytoplankton. The light-driven flux of carbon into photosynthesizing plankton organisms, followed by its assimilation into various organic compounds, is partitioned as follows. Respiration provides the initial taxation on the reduced carbon.

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The fraction used up by respiration varies: rapidly growing cells will respire more than slowly growing ones (Falkowski et al., 1985). Any stressors will also increase respiration, which may consume between 10% and 60% (Geider, 1992) of the initial, or gross photosynthesis. The balance of the photosynthate, or net photosynthesis, is then potentially available for the production of new cells or population growth.

All living organisms contain more than just the carbon, hydrogen and oxygen provided by photosynthesis. Without these additional elements, such as nitrogen, phosphorus, magnesium and iron, no formation of new cells can take place. Only when all necessary elements are available, can balanced cell growth be sustained. Such growth may be characterized by the maintenance of constant ratios of all elements over subsequent cell-division cycles. Thus, for instance, the carbon-specific growth rate would equal the nitrogen- (or DNA) based rates (Falkowski and Raven, 1997). Usually, the main elements restricting cell growth of phytoplankton are nitrogen and phosphorus, though in some oceanic regions and lakes, lack of iron is the principal limitation. Redfield et al. (1963), defined the “normal” C:N:P ratios characteristic of aquatic organisms and found them to be on the average 116:16:1, a ratio now known as the “Redfield ratio”. Obviously, for balanced growth to take place, the fluxes of all biomass-constituting elements into newly synthesized cells have to be such as to equal their respective ratios to the photosynthesis-driven net carbon flux.

The elaborate algal culture media used in phycology laboratories aim at providing organisms with the element-mixture that will allow them to realize their maximal potential for growth. However in nature, seasonal phenomena such as light-field variability, thermal stratification and vertical mixing of water bodies, sequestration and mineralization of compounds, pH and temperature changes cause strong fluctuations in the demand for, and availability of nutrients essential for cell growth. The capability of phytoplankton to hoard such nutrients in times of plenty, known as luxury uptake, helps them to overcome episodes of shortage, while drawing on their “cell quota” to prolong balanced growth periods (Droop, 1983). Once these stores are exhausted, cell multiplication slows down, the share of limited elements falls below their equilibrium content in the biomass, or in the case of nitrogen and phosphorus, below their Redfield ratios, and population growth inevitably ceases.

In many instances, especially in marine environments and many lakes, inorganic carbon is plentiful enough to allow for the maximal photosynthetic rates allowed by ambient light. If, under such conditions, the rate of inward flux of any biomass-constituting element falls below that required to match that of the light-driven net carbon flux, carbon assimilation rates will exceed those needed for cell building, and photosynthesis will become uncoupled from cell growth. The resulting excess photosynthate may be respired, excreted, stored or diverted to various cellular and ecosystem functions that emerged in the course of evolution.

Uncoupling of photosynthesis from growth may take place regularly or sporadically in nature, and can be induced at will in the laboratory. We shall examine some examples that illustrate the phenomenon of uncoupling and its subsequently evolved functions in a few select aquatic systems. Many of the topics presented in this review have been previously expanded in Berman-Frank and Dubinsky (1999).

I. Free Living Phytoplankton

Various studies on PDOC (photosynthetically derived dissolved organic carbon) released by phytoplankton indicate that healthy, rapidly growing cells exhibit low rates of PDOC excretion (Berman and Holm-Hansen, 1974; Sharp, 1977; Falkowski et al., 1985; Wood et al., 1992). Excretion of PDOC has been shown to increase with declining growth rates, and fluctuating and/or depleted nutrients. Zlotnik (1987) conducted a comparative study of the effects of nutrient limitation (N, P) on DOC excretion, in three phytoplankton species which represent different taxa: the freshwater *Chlorella vulgaris*, (Chlorophyceae) and *Synechococcus* sp. (Cyanophyceae) and the marine *Isochrysis galbana*, (Prymnesiophyceae). A similar response to nutrient limitation was found in the three organisms. With the increase of culture age, growth rates declined while the percentage of extracellular release increased.

In general *Synechococcus* was less stable under nutrient depletion than were the other two algae. That advantage of the algae over the cyanobacterium may stem from the ability of *Chlorella* and *Isochrysis* to mobilize a larger "cell quota" (Droop, 1983) of nutrients than those available to the much smaller *Synechococcus*. The maximum absolute size of cell quota depends on cell size (Shuter, 1978). The decline in growth rates of the two eukaryotes depended on the depletion of those quota, which is in agreement with Droop (1983). However, the growth rate of the cyanobacterium *Synechococcus* was tightly coupled to the nutrient concentration in the medium. Therefore, the progressive decline with time, in the growth rates of the three organisms is due to the gradual exhaustion of the nitrogen and phosphorus cell quota in the case of *Chlorella* and *Isochrysis*, or in the medium, in *Synechococcus*.

The results approximated a negative exponential correlation between the growth rates of the three algae and the percentage of DOC excretion. These results, which show a steep increase in excretion as growth rates decline due to nutrient limitation, demonstrate that when there is an imbalance between the rate of production of organic compounds and the rate of their utilization for growth, the algae release the excess. This is in agreement with previous studies (Wangersky, 1978; Soeder and Bolze, 1981; Fogg, 1983).

The ambient light field to which the phytoplankton are exposed also modulates excretion of PDOC. Since nutrient limitation arises whenever ratios of essential-nutrient fluxes into cells differ from their ratios in the biomass, high irradiance increases the flow of carbon, and unless that can be matched by increased flow of all other nutrients, it results in nutrient limitation and increased excretion. Thus, for instance, nitrogen or phosphorus concentrations that are sufficient for balanced growth at a depth of 50 m, may be limiting next to the surface.

In addition to its effect on PDOC excretion, as the main path for release of "excess" carbon there are several additional, or alternative, uses for growth-uncoupled photosynthate production. In times of nutrient limitation phytoplankton are known to form reserves that are mobilized when nutrients become available again and growth may resume. N-starved cells were found to accumulate starch and storage glucans that are used when nitrogen is available again, as a carbon source for amino acid synthesis (Turpin, 1991). Shortage of nitrogen favors increased synthesis of pigments lacking nitrogen compounds, such as carotenoids, rather than

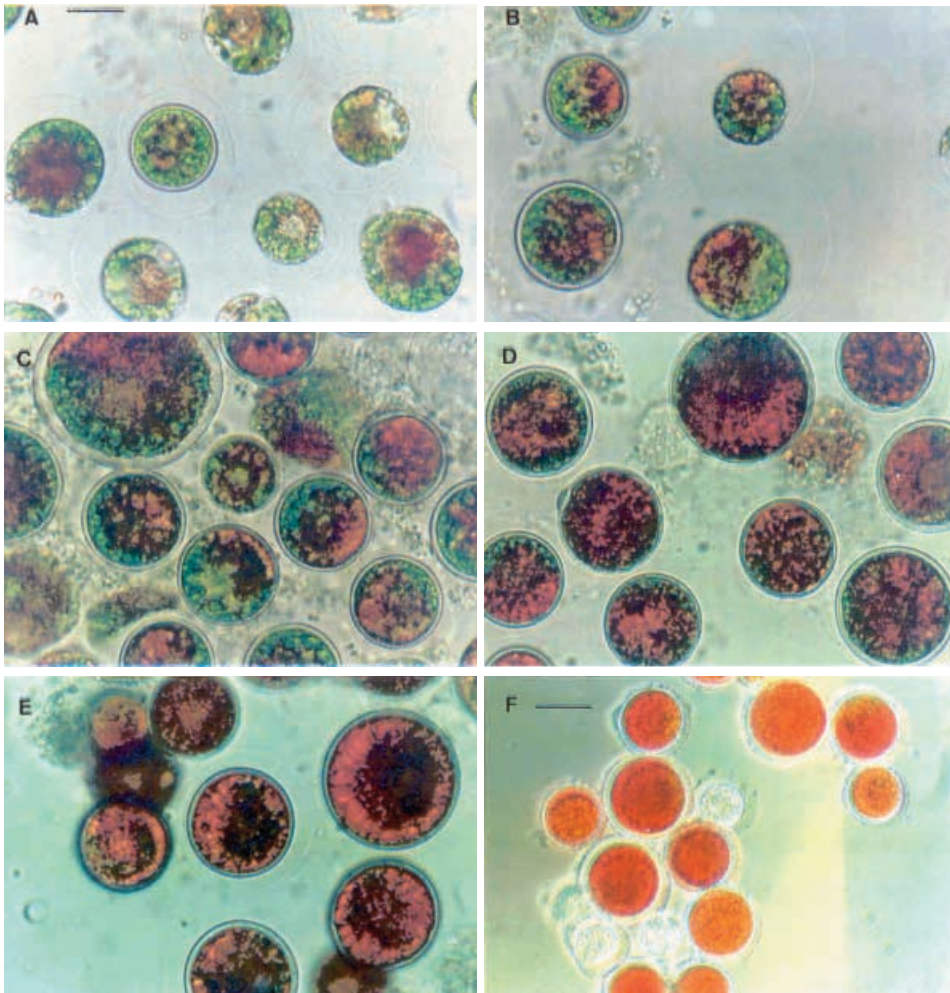


Figure 1. Phases in the differentiation of *Haematococcus pluvialis*, grown under nitrogen limitation for A, 4 d; B, 5 d; C, 6 d; D, 9 d; E, 11 d and F, 30 days, showing the accumulation of astaxanthin in the cells (Courtesy of D. Hershkowitz, Faculty of Life Sciences, Bar Ilan University, Ramat Gan, Israel)

pigments such as chlorophylls in many chlorophytes and phycobilins in cyanobacteria, and prevents the synthesis of pigment-binding proteins. *Dunaliella salina* and the “blood alga” *Haematococcus pluvialis*, both of them chlorophytes, are bright green when in balanced growth. However, when nutrient limited, *D. salina* turns orange and *H. pluvialis* red (Fig. 1). This change in color results from the accumulation of β -carotene and astaxanthin respectively (Zlotnik et al., 1993; Hershkowitz et al., 1997). In the case of the dinoflagellate *Peridinium gatunense*, towards the collapse of its annual bloom in L. Kinneret (Israel), as the nitrogen and phosphorus in the water become depleted, the cells turn increasingly orange, as they accumula-

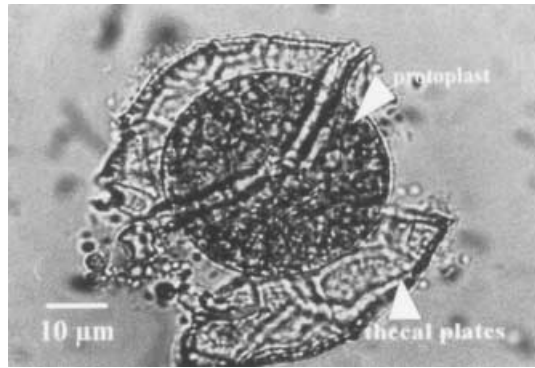


Figure 2. Nutrient stressed cell of *Peridinium gatunense*, shedding its thecae

te peridinin (Dubinsky and Polna, 1976; Dubinsky and Berman, 1976), as is seen in Fig. 2. These secondary carotenoids, besides being carbon sinks, serve as important photoprotective pigments, preventing photoinhibition and photodynamic damage. Accumulation of these pigments, which is induced by nitrogen limitation and accelerated by high irradiance is exploited for the commercial production of both pigments; β -carotene for the health food market and astaxanthin for the marine-farming of salmon and trout that otherwise grow white rather than pink. Changes in carotenoid to chlorophyll ratios change the optical characteristics of the cells (Herzig and Falkowski, 1989) to the extent that is detectable in the optical properties of the entire underwater light-field (Dubinsky and Berman, 1979; Dubinsky, 1992; Schanz et al., 1997). Additional responses to “excess” photosynthesis over cell biosynthesis were described: loss of motility and induction of the transition of flagellate cells to thick-walled aplanospores in *H. pluvialis* (Zlotnik et al., 1993).

The armored dinoflagellate *P. gatunense* normally sheds its polyglucan theca only once prior to each cell division cycle. Criscuolo et al. (1981) showed that *P. gatunense*, when maintained under stringent nutrient limitation, while otherwise conditions favored photosynthesis, responded by repeatedly shedding carbohydrate thecae, whereas cell division was arrested (Fig. 3). Under nutrient replete conditions the number of swimming cells increased in parallel to that of the empty thecae, however when deprived of essential nutrients, cell numbers remained constant while growing numbers of shed thecae accumulated at the bottom of the culture flasks. The peculiar chlorophyte *Botryococcus braunii*, when nutrient limited, also ceases to divide, and shunts photosynthate towards profuse hydrocarbon production (Rubin, 1982), which in some cases accumulated to form carbon deposits (Figs. 4 and 5). In cyanobacteria the nutrient and photosynthesis modulated carbohydrate/protein ratio acts as ballast, regulating buoyancy and the depth of the population, thereby optimizing the light exposure (Klemer et al., 1996; Klemer et al., 1982). Diatoms (Mykelstad, 1977; Jensen, 1984) and the unicellular Rhodophytes *Porphyridium sp.* and *Rhodella reticulata* (Arad et al., 1988, 1992) increase polysaccharide production and secretion under conditions forcing photosynthesis-growth imbalance. These mucous secretions may protect cells from desiccation upon exposure to air, and ward-off epiphytic attachment. Another way in which the “excess”

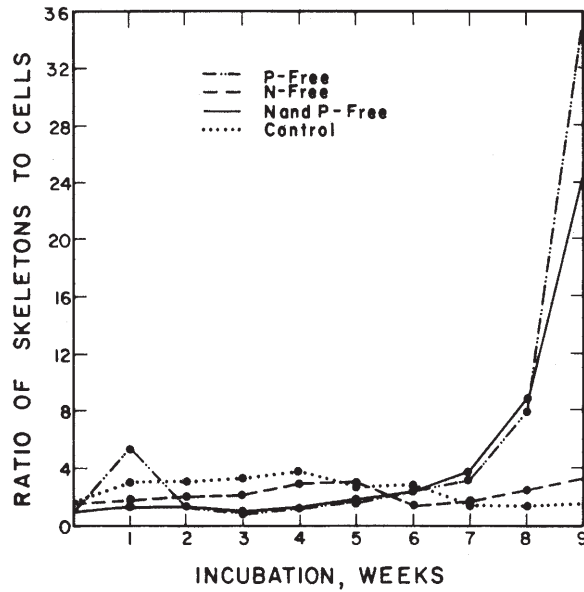


Figure 3. The ratio of empty thecae to swimming cells in axenic cultures of *Peridinium gatunense*, under different nutrient regimes (after Criscuolo et al., 1981)

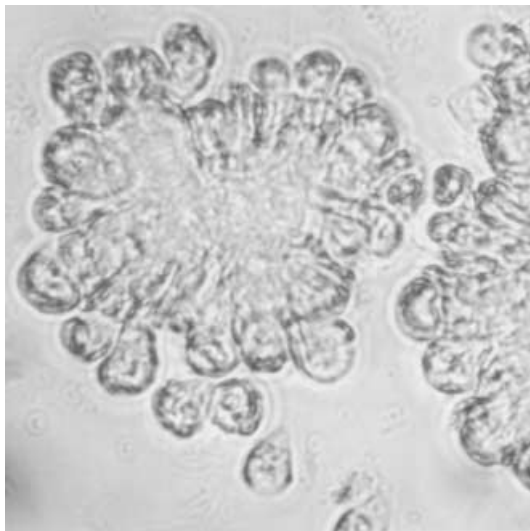


Figure 4. Light micrograph of a colony of *Botryococcus braunii* with the protoplasts embedded in a hydrocarbon matrix (Rubin, 1982)

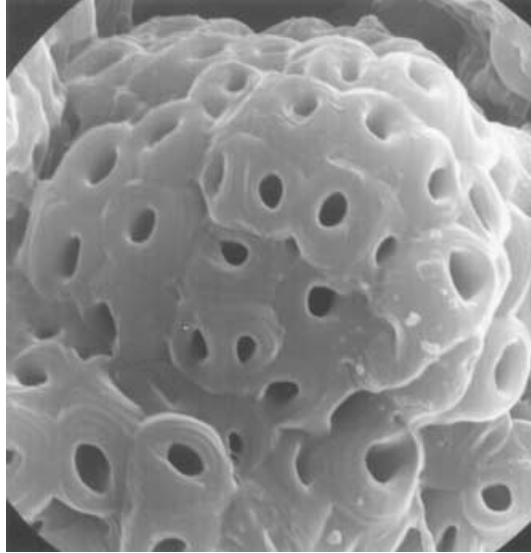


Figure 5. Scanning-electron micrograph of the empty hydrocarbon matrix of a *Botryococcus braunii* colony (Rubin, 1982)

carbon is utilized is by production and extracellular release of allelopathic compounds, as was demonstrated for a cyanobacterium under phosphorus limitation (von Elert and Juttner, 1997). Phosphorus limitation and not light controls the extracellular release of allelopathic compounds by *Trichormus doliolum* (Cyanobacteria). The allelopathic compounds reduce growth of co-occurring species and may enhance the availability of the limiting nutrient and subsequently increased growth rates.

As suggested above, small cells are likely to be more susceptible to nutrient limitation and loss of photosynthate than large cells, simply due to greater relative cell-quota. Indeed, this was confirmed in studies by Malinsky-Rushansky and Legrand (1996), who examined PDOC excretion rates by phytoplankton of different sizes and compared them with literature data. The percentage of extracellular release of dissolved carbon compared to photosynthetic uptake was higher in smaller sized cells than in larger ones. Murray (1995), had also concluded that picophytoplankton, when stressed, excrete a larger fraction of assimilated carbon than larger species. Small picophytoplankton species dominate nutrient limited environments such as oligotrophic oceans. Under such constraints their high surface/volume ratios are advantageous, allowing them access to nutrient resources that otherwise may not be available (Chisholm, 1992). When these picoplankters, mostly *Synechococcus* and *Prochloron* species, exhaust even those low-concentration nutrient resources, they stop multiplying and inevitably increase the excretion of carbon rich compounds.

Whenever photosynthetic assimilation of carbon by algae exceeds that usable for biomass synthesis, the cells synthesize various compounds containing carbon, but none of the limiting nutrients. However, these compounds have acquired in the course of evolution, or co-evolution, various advantageous cellular and community

functions. These include photoprotective pigments, ballast carbohydrates, desiccation preventing polysaccharide slimes, protective spore walls, allelopathic compounds and high-energy excretions. Thereby, the effects of uncoupling of growth from photosynthesis in aquatic photosynthesizing organisms extend beyond the individual cell and towards inter-specific interactions and associations between various trophic levels.

II. Uncoupling within the ecosystem framework

The production of PDOC is often a major input of energy supporting heterotrophic bacteria in open waters of lakes and oceans. The bacteria utilize the DOC and in turn are grazed upon by protozoa and some metazoa. That trophic path, known as the microbial loop, operates in parallel, and in some instances instead of the “conventional” one where phytoplankton are grazed upon by zooplankton (Fig. 6).

The excretion of PDOC by the algae and its subsequent utilization by heterotrophic microorganisms has been reviewed by Sherr et al. (1988), Banse (1992), Azam et al. (1995) and Azam (1998). When growth and photosynthesis become uncoupled and PDOC production increases it is used to support bacterial growth and possibly as a means of protection of phytoplankton, especially picophytoplankton, against viral infection (Murray, 1995).

Photosynthetically derived organic molecules that are excreted, secreted, or exuded, include some compounds that nevertheless remain more or less loosely attached to the cell's exterior and others that diffuse away from it. Both of these increase under conditions favoring uncoupling of growth from photosynthesis and both are available to heterotrophic bacteria. In addition to the obvious use of free organics by the bacterioplankton, the cell-bound “exudates” create a rich polysaccharide microenvironment that supports proliferation of attached bacteria. These, while using the mucus as their energy source, may extract nutrients from low concentration in the water (Bell and Mitchell, 1972; Azam and Ammermann, 1984; Azam et al., 1995), possibly raising these to levels useful for the phytoplankton. Thus, contrary to our intuitive views, aquatic environments may be characterized by inhomogeneity where “hot spots” (Azam and Smith, 1991; Azam et al., 1995) or “life support systems” (Goldman, 1984) such as “marine snow” abound. In these localized high-biomass micro regions in otherwise relatively barren oligotrophic waters, the tight ecosystem-level coupling between producer and consumer assemblages benefits both components. This association results in higher biomass levels than would have been possible without it (Cole et al., 1988), and contributes to overall carbon fluxes (Alldrige, 2000).

It has been suggested that nutrient-stressed phytoplankton may be susceptible to viral attack (Emiliani, 1996), and that PDOC may also serve for antiviral protection. Murray (1995) argues that as phytoplankton blooms exhaust the nutrients in their surroundings, photosynthesis products cannot be used for population increment and are released to the water. That PDOC stimulates the formation of an “antiviral shield”. Bacteria are attracted, multiply and inactivate the viruses, while their flagellate grazers may directly feed on them (Murray, 1995).

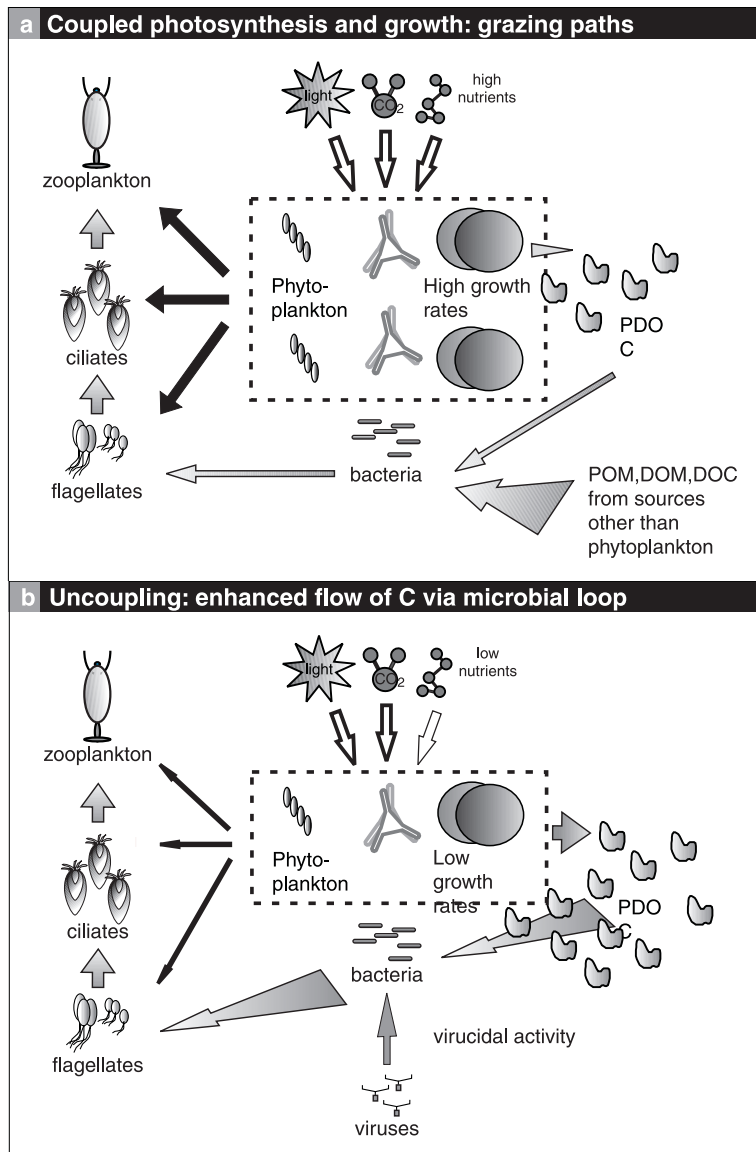


Figure 6. Scheme comparing the fluxes of carbon in: a, a nutrient-replete planktonic ecosystem, where most of the carbon is processed via the grazing pathway, and only a small fraction of the assimilated carbon is excreted by the phytoplankton and b where the low-nutrient induced uncoupling between photosynthesis and growth results in enhancement of carbon flow via the microbial loop (after Bioscience, Berman-Frank and Dubinsky, 1999)

III. “Captive phytoplankton”: Zooxanthellae/coral symbiosis

Coral reefs are one of the most puzzling ecosystems on Earth. Bathed in the “blue-desert” of the oligotrophic waters of tropical oceans, they are among the most diverse and productive biological communities. These oases teeming with life are based on the ancient mutualistic symbioses of corals, and additional invertebrates, with endocellular microalgae. The association between these dinoflagellates, or zooxanthellae, and their animal hosts is a finely tuned system, based on the “slack” between photosynthetic carbon assimilation and its retention for growth by the symbionts (Muscatine et al., 1983; Falkowski et al., 1984; Dubinsky and Jokiel, 1994). Normally, in healthy unpolluted coral reefs in transparent illuminated waters, the algae perform intensive photosynthesis; the resulting carbon flux cannot, however, be matched by the corresponding nitrogen and phosphorus fluxes that would be required if the algae were to keep the carbon and use it for new cell formation. Most of the carbon is released and “translocated” to the host, thus supporting its metabolism and providing carbon skeletons for the slow growth characteristic of corals. The excretion of the excess C by the zooxanthellae is further stimulated by putative “host factors”. The zooxanthellae themselves can increase in numbers only as fast as they acquire N and P from the water, or from prey digestion and excretion of metabolic waste products by the host. Typical doubling times of zooxanthellae *in hospice* are on the order of 70–100 days; nevertheless this slow growth rate suffices to match the concomitant extension of host tissue, and maintenance of constant population densities of the zooxanthellae. Carbon translocation from the algae to the animal may reach >95% of the net fixed carbon and supply all of the animal’s carbon needs (Muscatine et al., 1983). The energy-rich and nitrogen-poor “junk food” translocated to the coral cannot by itself support animal growth, and has to be supplemented by the active capture of the nutrient rich zooplankton-prey (Falkowski et al., 1984; Muscatine et al., 1989).

It is worth noting that as one moves from shallow water towards the deepest parts of reefs, along with the exponential decrease in available light, the nutrient status of the zooxanthellae changes from severely nutrient limited to nutrient replete. This results from the change in the rate of photosynthesis, and of the resulting carbon flux. Under the high irradiance to which near surface coral colonies are exposed, photosynthesis rates of the zooxanthellae are maximal, whereas there are no corresponding nutrient supplies. Here, the nutrient limited zooxanthellae excrete most of the carbon, as predicted. Under irradiance levels as low as 0.5–5% of subsurface levels carbon assimilation is slow, and nutrients from the water are sufficient to provide the necessary amounts to support algal growth. As a result, the nutrient replete zooxanthellae of shade adapted corals retain most of the assimilated carbon, little is translocated to the host, and the host has to depend on predation to balance its metabolic needs (Muscatine et al., 1984; Dubinsky and Jokiel, 1994)

Anthropogenic eutrophication of reef waters by forest destruction, wastewater disposal or mariculture farms, destabilizes the algae-coral association, which has coevolved over eons to cope with, and eventually monopolize, oligotrophic waters. As the zooxanthellae are presented with abundant nutrients, their multiplication is no longer restricted. They now combine the plentiful carbon skeletons from their photosynthesis with these nutrients, curtailing energy supply to the host and in-

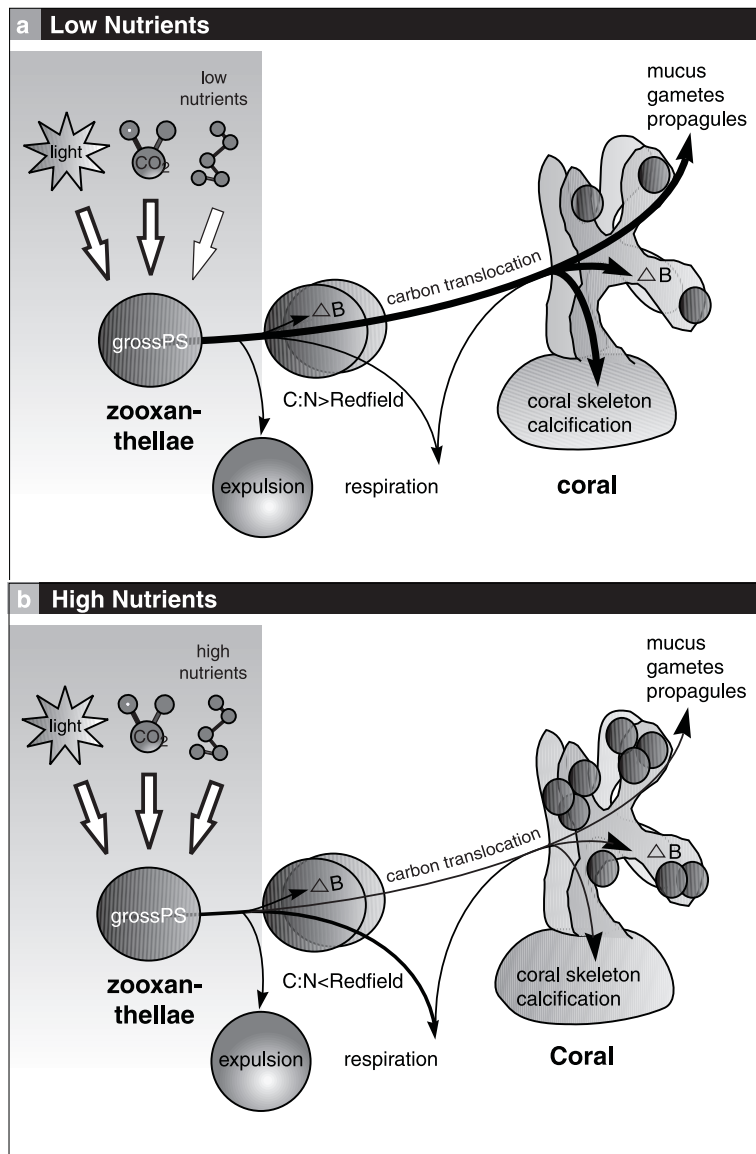


Figure 7. Scheme describing the effect of eutrophication on the flow of carbon in the mutualistic symbiosis between zooxanthellae and corals; a, under “normal” oligotrophic conditions, b, when exposed to eutrophication (after Berman-Frank and Dubinsky, 1999)

creasing their populations by up to 500% (Muscatine et al., 1989; Dubinsky and Jokiel, 1994). Thus, for a healthy coral-zooxanthellae association, uncoupling of photosynthesis and growth in the algae is necessary (and the norm) for the smooth translocation of carbohydrates from the algae to the coral (Fig. 7).

Summary and Conclusions

In phytoplankton the excess supply of carbon compounds resulting from the uncoupling between photosynthesis and biomass production may be excreted to the ambient medium, where it supports heterotrophic activity, enhancing the microbial loop. Generally the importance of the microbial loop relative to the grazing pathway increases with nutrient limitation, and the phytoplankton benefit from bacterial nutrient acquisition.

In other cases excess carbon compounds available under nutrient limited growth conditions may be retained by algal cells and given a cellular function. They may be utilized for the synthesis of photoprotective pigments like peridinin, astaxanthin and β -carotene.

Excess photosynthate can facilitate survival when used in the transformation of cells into dormant, resistant spores that will germinate once conditions allow renewed growth. Hygroscopic polysaccharides produced by the unicellular rhodophyte *Porphyridium cruentum*, various desmids, diatoms and cyanophytes protect cells from desiccation, while these organisms wait for the return of favorable conditions.

PDOC may deter grazers or lure bacteria. These may function as “shields” and protect phytoplankton from viral infections, or/and combine with the phytoplankton to form remineralization foci of limiting nutrients.

In the coral-zooxanthellae symbiosis the carbon skeletons produced by the nutrient-limited zooxanthellae are translocated to the host coral, providing the energy basis for the entire coral reef ecosystem.

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