Aquatic Ecology 33: 17–27, 1999.

The role of C, N and P in dissolved and particulate organic matter as a nutrient source for phytoplankton growth, including toxic species

Edna Granéli, Per Carlsson and Catherine Legrand
Department of Marine Sciences, University of Kalmar, Box 905, S-391 29, Kalmar, Sweden

Accepted 27 January 1999

Key words: dissolved organic substances, harmful phytoplankton, macronutrients, mixotrophy, osmotrophy, phagotrophy

Abstract

Phytoplankton have traditionally been regarded as strictly phototrophic, with a well defined position at the base of pelagic food webs. However, recently we have learned that the nutritional demands of a growing number of phytoplankton species can be met, at least partially, or under specific environmental conditions, through heterotrophy. Mixotrophy is the ability of an organism to be both phototrophic and heterotrophic, in the latter case utilizing either organic particles (phagotrophy) or dissolved organic substances (osmotrophy). This finding has direct implications for our view on algal survival strategies, particularly for harmful species, and energy- and nutrient flow in pelagic food webs. Mixotrophic species may outcompete strict autotrophs, e.g. in waters poor in inorganic nutrients or under low light. In the traditional view of the 'microbial loop' DOC is thought to be channeled from algal photosynthesis to bacteria and then up the food chain through heterotrophic flagellates, ciliates and mesozooplankton. Are mixotrophic phytoplankton that feed on bacteria also significantly contributing to this transport of photosynthetic carbon up the food chain? How can we estimate the fluxes of carbon and nutrients between different trophic levels in the plankton food web involving phagotrophic algae? These questions largely remain unanswered. In this review we treat evidence for both osmotrophy and phagotrophy in phytoplankton, especially toxic marine species, and some ecological implications of mixotrophy.

Introduction

Whether phytoplankton can utilize dissolved organic matter as a significant source of carbon and other macronutrients such as nitrogen (N) and phosphorus (P) at naturally-occurring concentrations is still an open question. That some cultured phytoplankton species can grow heterotrophically on dissolved organic carbon (DOC) in the dark has been known for some time (Droop, 1974; Ukeles & Rose, 1976). However, growth of phytoplankton in the dark based on DOC as the sole carbon source requires very high substrate concentrations, concentrations that do not occur in natural waters (Droop, 1974; Richardson & Fogg, 1982). Also, under light conditions, DOC can increase the growth of some phytoplankton species (Combres et al., 1994). However, as for dark-mediated heterotrophic growth, high concentrations of substrate are required. Experiments with naturally-occurring concentrations of DOC did not show any significant stimulation of either growth or survival of axenic algal cultures (Richardson & Fogg, 1982). These results have lead to the conclusion that microalgal utilization of carbon in dissolved organic matter (DOM) can be considered as insignificant.

Heterotrophic growth of microalgae in the dark on low-molecular carbon compounds has been demonstrated for several diatom species (Hellebust & Lewin, 1977). Amino acids can be used directly by phytoplankton as a nitrogen source (e.g. Flynn & Butler, 1986). Some studies using trace concentrations of isotopes, have shown that some phytoplankton species are able to take up dissolved organic nitrogen (DON) at naturally-representative (Paerl, 1991). Many harmful phytoplankton species have been shown to use amino acids as nitrogen sources. *Prymnesium parvum*

is able to grow with the amino acids ethionine or methionine as the only nitrogen source (Rahat & Hochberg, 1971). Baden & Mende (1979) showed that the toxic dinoflagellate *Gymnodinium breve* had K_s values of 110 and 150 μmol l^{-1} for the two amino acids glycine and valine respectively. Such high half saturation constants for amino acid uptake indicate that *G. breve* should not be able to use amino acids in its normal environment. However, other experiments have shown much lower half-saturation constants (0.6–2 μmol l^{-1}) for phytoplankton growth on amino acids as nitrogen sources (Flynn & Syrett, 1986).

Soil extracts have been known for a long time to stimulate the growth of phytoplankton in cultures (e.g. Provasoli et al., 1957). Prakash & Rashid (1968) and Prakash et al. (1973) found that DOM in the form of humic substances increased both yield and growth rates of marine dinoflagellates and diatoms (Prakash & Rashid, 1968; Prakash et al., 1973). Although the reason for the growth stimulating effect could not be adequately explained, the authors suggested that the humic substances acted as chelators, enhancing trace metal availability, a conclusion shared by Anderson & Morel (1982). The N and P content of humic substances were considered to be of minor importance (Prakash & Rashid, 1968).

Other experiments have indicated that organic N in soil extracts is beneficial for phytoplankton. Morrill & Loeblich (1979) found that growth of *Peridinium foliaceum* in N limited axenic cultures increased when supplied with sterile soil extracts, probably because of the humic substances in the extract containing organic N. Granéli et al. (1985) showed that the biomass yield of the toxic dinoflagellate *Prorocentrum minimum* increased considerably when humic substances and phosphate were added to the medium. *Prorocentrum minimum* cells grown with additions of humic substances contained similar concentrations of N as cells grown with inorganic N (Granéli et al., 1985).

Concentrations of inorganic N and P usually become very low in both off shore and coastal marine waters during summer months, while concentrations of DON are high. Thus, a relatively large part of the N and P pools in the sea are found as dissolved organic molecules. It would be a great competitive advantage for the phytoplankton if they could use even a smaller part of the DON pool. Organic P can be utilized by phytoplankton through the action of phosphatases, a well known process (e.g. Berman, 1970). However, parallel utilization of different forms of organic N other than urea or amino acids is less well known (Antia et al., 1991), which is unfortunate since marine phytoplankton are usually thought to be N, and not P, limited. In rainfall DON also constitutes a quantitatively important source of N, which at least in part is biologically available (Peierls & Paerl, 1997).

The idea that photosynthetic organisms might be able to utilize organic particles is not new. Early observations of phagotrophy typically relied on conventional light microscopy. Hofeneder (1930) reported that the freshwater dinoflagellate *Ceratium hirundinella* engulfed prey using a pseudopodium. Although algal phagotrophy has been known for decades through such descriptive microscopic observations, attempts to quantify the ecological significance of phagotrophy in the marine environment are relatively recent. Current studies of mixotrophy have been stimulated by new methods for the quantification of grazing by small plankton organisms and by the reconceptualization of the pelagic food chain to include the 'microbial loop' (Azam & Smith, 1991). This includes the importance of bacterivory by heterotrophic and mixotrophic microflagellates for the carbon flow and nutrient cycling. Especially important are methodological innovations such as the techniques based on fluorescently- or radioactively-labelled particles (Lessard & Swift, 1985; Sherr et al., 1987; Havskum & Riemann, 1996; Li et al., 1996). Detection of phagotrophy in the freshwater chrysophyte *Dinobryon* spp. was possible using fluorescent latex beads (Bird & Kalff, 1986). This investigation has spurred many subsequent studies of algal phagotrophy in both marine and freshwater pelagic communities.

However, the significance of phagotrophy in the ecology of phytoplankton is still largely unknown. Many questions concerning numerical and biomass abundance, carbon flux, feeding rates, nutrient regeneration rates, etc., are directly analogous to those asked by zooplankton ecologists (Boraas et al., 1988). Phagotrophy can be seen as an important factor regulating population dynamics, and some of the important issues that need to be further pursued are: (1) The detection, characterization and quantification of phagotrophy among members of the different phytoplankton taxonomic groups. (2) The importance of phagotrophic uptake of C, N, P, trace metals, or special organic compounds (such as some vitamins that the algae cannot synthesize) for the growth of these organisms. (3) The environmental conditions that trigger phagotrophic behavior. (4) The competitive advantage of being a photosynthetic phagotroph compared

to solely autotrophic or heterotrophic during certain environmental conditions (e. g. different light and nutrient regimes). Phagotrophy may also be only a remnant of an ancient, formerly important behavior among planktonic organisms, that has little ecological significance.

This review on phytoplankton mixotrophy focuses on the utilization of organic matter as a source of macronutrients C, N and P for phytoplankton growth, and its consequences for phytoplankton ecology as well as for the view of the microbial food web. The first part of the review is focused on the uptake of dissolved organic nutrients and the second on ingestion of particles (bacteria, other phytoplankton cells or even zooplankton) by phytoplankton cells.

Osmotrophy and phytoplankton growth

Importance of DON as a nutrient source

The pool of DON in natural waters is composed of a large number of components and a large fraction of the DON has not yet been characterized (Sharp, 1983). Rapidly cycling small organic compounds (e.g. amino acids, amines, urea) account only for a minor fraction (10–20%) of total DON in marine waters (Sharp, 1983; McCarthy et al., 1996). The major part of DON is probably resistant to biological degradation (McCarthy et al., 1996). In coastal waters, DON originates from several sources: such as riverine loading, atmospheric deposition, and to a minor extent sediment-water exchange and groundwater (Figure 1). These two later sources of DON constitute a large part of the flux of N from land to sea, often making up more than 50% of the total dissolved N export (Meybeck, 1982). The N content of riverine humic substances is usually 1–3% (by weight) and the P content is about 0.2% (Thurman, 1985; Hedges, 1987). In marine rainfall, DON also constitutes a quantitatively important source of N. Atmospheric N deposition originates mostly from fossil fuel combustion and agriculture, and is mainly composed of nitrogen oxides (Likens et al., 1974), ammonia (Buijsman et al., 1987), and DON (i.e. urea, amino acids) (Timperley et al., 1985; Mopper & Zika, 1987). Rainwater also contains other elements necessary for phytoplankton such as P and metals (Duce et al., 1991). A large part of DON in rainfall is biologically available to microbial and phytoplankton growth (Peierls & Paerl, 1997) since dissolved amino acids and urea can constitute up to

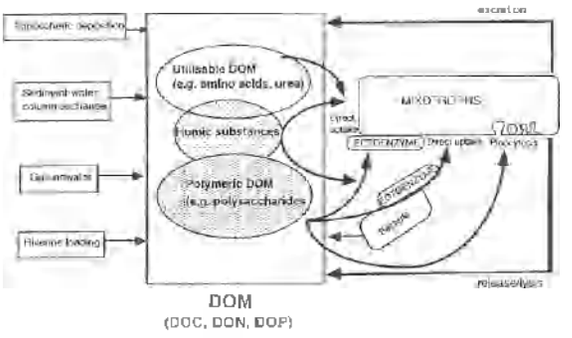

Figure 1. Sources and utilization of DOM (Osmotrophy) by mixotrophic phytoplankton.

50% of DON (Mopper & Zika, 1987; Timperley et al., 1985). DON concentrations in marine waters are usually thought to be in the range from 3 to 5 μmol l^{-1} (Sharp, 1983). However, Suzuki et al. (1985) reported DON concentrations of 20–40 μmol l^{-1} in surface oceanic waters using a high-temperature catalytic oxidation method. However, Hansell (1993) found DON concentrations in nearshore and open-ocean waters consistently lower than 10 μmol l^{-1}, also using high-temperature catalytic oxidation. Irrespective of the exact amount of DON present in marine waters, the DON pool is substantially larger than that of dissolved inorganic N (DIN) in most stratified waters during the productive season.

When management of eutrophicated coastal areas is considered, DON is usually not considered as part of the nutrient pool available for phytoplankton. Several studies have shown, however, that DON can stimulate phytoplankton production. *Chlorella* spp. and the freshwater *Pediastrum biwae* were shown to grow using DON from precipitation as the only N source (Timperley et al., 1985). Ammonium and DON release by *Trichodesmium* spp. enhanced the total phytoplankton production in the subtropical North Pacific Ocean (Letelier & Karl, 1996). In Shinnecock Bay, Long Island, blooms of *Aureococcus anophagellereas* were connected to the urea concentration in the water (Berg et al., 1997).

Abiotic and enzymatic breakdown of DOM

Dissolved organic matter entering marine waters can be broken down by light and or bacteria (Kieber et al., 1990). The half-life of oceanic DOC has traditionally been estimated to be very long, up to thousands of years (Williams & Druffel, 1988). However, for riverine DOC reaching coastal waters calculations based on

photodegradation of DOM are substantially lower, between 1 and 5 years (Kieber et al., 1990). Through the action of UV-radiation biologically available inorganic N may be produced from DOM (Bushaw et al., 1996).

The ecological significance of abiotic, photoproduction of DIN from DOM in marine waters is still largely unknown, while enzymatic utilization of other nutrients in DOM, especially P, has been more extensively studied. Both bacteria and phytoplankton are able to produce extracellular phosphatases that hydrolyse organic phosphorus compounds, and release phosphates that are taken up by the cells (Myklestad & Sakshaug, 1983; Combella et al., 1985). With respect to N, leucine aminopeptidase (an enzyme that is widely distributed in aquatic environments and that hydrolyses a large number of peptides and amides) can degrade macromolecules with peptide bonds (Hoppe et al., 1988). However, extracellular or cell surface peptidases seem to be produced only by bacteria (Rosso & Azam, 1987) and there are no reports of phytoplankton utilization of these enzymes. Associated with the cell membrane are the bacterial exoenzymes, and the products from their activity should be mainly available for the bacteria and not phytoplankton. Consequently, the activity of aminopeptidase is often low in 0.2 μm filtrates where bacteria are not present (e.g. Chróst, 1989). However, when bacteria are associated with phytoplankton, algal cells might utilize monomers derived from bacterial exoenzymatic activity (Figure 1). None of the phytoplankton species tested by Palenik & Morel (1990) did possess cell-surface or extracellular peptidases. Extracellular enzymes can be washed away from the periplasmic space, liberated by lysis or damage of cells by grazers. Even the intracellular enzymes may become dissolved in the water by cell lysis or grazing (Chróst, 1991). High aminopeptidase activities (10–90% of total activity) have also been reported in 0.2 μm filtrates (Jacobsen & Rai, 1991), which would produce free amino acids also available for phytoplankton uptake. It is thus possible that phytoplankton, to some extent, are using amino acids produced by the action of bacterial peptidases.

The toxic haptophyte *Prymnesium parvum* possesses cell-surface L-amino acid oxidases that oxidize amino acids and primary amines, producing ammonium that is taken up by the cell, peroxide and a-keto acids (from amino acids) or aldehydes (from primary amines) (Palenik & Morel, 1990).

Indirect utilization of DOM by phytoplankton – the role of bacteria and regeneration of inorganic nutrients

Through grazing of heterotrophic flagellates on bacteria, inorganic nutrients are regenerated (Caron & Goldman, 1990). The regenerated inorganic P and N are then available both for bacteria and phytoplankton. Bacteria are considered to be the dominant organisms using DOM as substrate. Since bacterial C:N ratios (about 3–7 (Bratbak, 1985; Nagata, 1986)) are lower than those for phytoplankton (6–20 (Darley, 1977)), bacteria need more N per unit biomass than phytoplankton. In marine waters, DOM has a high C:N ratio, about 15 by weight (Benner et al., 1992), while riverine DOM that enters coastal waters often has much higher ratios (about 50 (Malcolm, 1985)). Bacteria may thus retain the N from DOM and not regenerate it in inorganic form available for phytoplankton (Goldman & Caron, 1985). However, when bacteria are grazed, e.g. by heterotrophic nanoflagellates and ciliates, DIN is released (e.g. Caron & Goldman, 1990) in amounts between 10 to 50% of the ingested bacterial N (Andersson et al., 1985).

Granéli et al. (1985) have shown that cell numbers of the dinoflagellate *Prorocentrum minimum* increased when humic acid was added to cultures. That the cells were able to utilize N in the humic material, was indicated through similar levels of intracellular N in these cells as in cells grown with DIN. However, the mechanism behind the utilization of humic-bound nitrogen was not clear. In similar experiments with a natural plankton community, total algal and bacterial biomass, the number of bacterivores and DIN concentration became significantly higher when DOM was added (Carlsson et al. 1993). This suggested that the DOM was used by bacteria and that DIN was later regenerated by the bacterivores grazing on the bacteria and used by the phytoplankton.

Direct uptake of high-molecular weight compounds

Polymeric compounds are considered too large to pass the cytoplasmic membrane by simple diffusion (Payne, 1980). Nevertheless, a mechanism to take up high molecular weight compounds is by pinocytosis, which is an active transport system where the macromolecules are accumulated in small vesicles inside the cell membrane (Figure 1). This process has only been studied to a minor extent in phytoplankton (Kivic & Vesk, 1974; Klut et al., 1987). The uptake of macromolecule markers (e.g. lectins, peroxidases,

dextrans) has been demonstrated in the flagellates *Amphidinium carterae* and *Prorocentrum micans* (Klut et al., 1987) and *Alexandrium catenella* (Legrand & Carlsson, 1998a). These phytoplankton cells probably ingested the macromolecules by pinocytosis. However, the potential significance of pinocytosis in phytoplankton nutrition remains to be elucidated.

Algal blooms and the input of DOM from terrestrial origin

Prakash & Rashid (1968) suggested that most, if not all, dinoflagellate blooms in coastal waters depend on humic or other nutritional factors entering the waters after heavy rainfalls or land drainage. River waters draining agricultural soil, rich in inorganic N and P, stimulate growth of diatoms, while river waters from forest areas, rich in humic substances, increase growth of dinoflagellates (Granéli & Moreira, 1990). Coastal waters can be heavily influenced by river run-off containing both inorganic and organic nutrients. In coastal areas influenced by rivers draining forested land, the contribution of organically bound N can be very high.

Worldwide nitrogenous compounds have increased in atmospheric emissions largely uncontrolled over the last 4 decades (Duce et al., 1991). From 20 to >40% of coastal DIN + DON loading is attributed to atmospheric deposition alone, thus equaling or exceeding riverine inputs (Paerl, 1995).

A large increase in the discharge of humic substances by rivers into Swedish coastal waters seen during the last 20 years (Andersson et al., 1991; Forsberg, 1992) coincides with increased number and intensity of dinoflagellate blooms in the same area (Granéli et al., 1989). Zhang (1994) suggested a correlation between atmospheric deposition of nutrients and harmful blooms.

Significance of phagotrophy for phytoplankton growth

External abiotic or biotic factors influencing cell physiological state presumably regulate phagotrophy among algae (Figure 2). If light is insufficient to allow for sufficient CO_2 fixation to meet metabolic demands of the cell, phagotrophy can supplement or even substitute for photosynthesis as a source of organic carbon (Andersson et al., 1989; Sanders et al., 1990). Phagotrophy may be explained in the same way with respect to nutrients, i.e. phagotrophy may supply

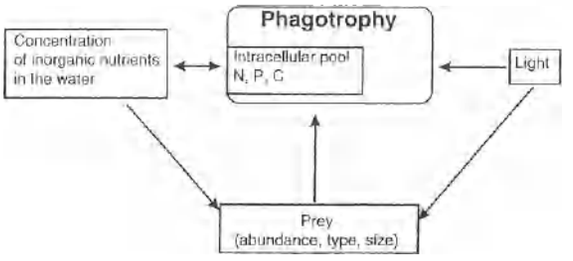

Figure 2. Possible environmental factors regulating phagotrophy in mixotrophic phytoplankton.

the organism with N or P or some micronutrient if dissolved sources have been exhausted (Kimura & Ishida, 1985; Caron et al., 1993; Nygaard & Tobiesen, 1993). For phagotrophy to be effective, there has to be a sufficient supply of suitable organic particles (prey organisms). Thus, in environments where the organism encounters a high concentration of prey, e.g. bacteria, phagotrophy might be induced. The three most important triggering/regulating factors for phagotrophy might then be nutrient availability, prey abundance, and light (Figure 2).

It is natural to assume that algae use phagotrophy to obtain macro- (N, P) and micro-nutrients (e.g. metals, vitamins), when dissolved inorganic or organic nutrients are growth-limiting (Aaronson, 1974; Kimura & Ishida, 1985; Sanders & Porter, 1988). Mixotrophy may thus be a primitive trait, a notion that is supported by the fact that groups with many phagotrophs are ancient (Porter, 1988). It has been proposed that some phagotrophic algae have evolved from primitive heterotrophs, while others are 'secondary' phagotrophs, where the character has evolved from strict phototrophy (Jones, 1994). This author suggested that mixotrophy should not be viewed as a single strategy developed by planktonic organisms, placed between the dominant forms of nutrition (autotrophy and heterotrophy), but instead as a continuous gradient between true autotrophs and heterotrophs. For some organisms phagotrophy will only initiate if high quantities of prey are present (Andersson et al., 1989; Sanders et al., 1990), whereas for others phagotrophy appears to be more dependent on abiotic factors, such as light (Caron et al., 1993; Jones et al., 1993, 1995; Keller et al., 1994). Some algae may be efficient phagotrophs but poor phototrophs (Caron et al., 1990), whereas others may be obligate photoautotrophs, still capable of phagotrophy (Caron et al., 1993). From an ecological point of view, it is expected that there is a trade-off between photosynthesis and phagotrophy. The simul-

taneous ability to perform both modes of nutrition has high costs, but enables the organism to outcompete heterotrophic or strictly photosynthetic species under certain environmental conditions (Rothhaupt, 1996a; Thingstad et al., 1996).

Phagotrophy among photosynthetic plankton has been studied mainly for phytoflagellates, including chrysophytes in freshwater environments and dinoflagellates in the marine environment (with a few studies on chrysophytes and haptophytes in marine/estuarine waters). Among dinoflagellates, there are species that are strictly heterotrophic (lacking photosynthetic pigments), whereas closely related species are photosynthetic or mixotrophic, e.g. in the genus *Gyrodinium* (Gaines & Elbrächter, 1987). Also there are colorless species which after ingesting their prey may retain their actively working chloroplasts ('cleptochloroplasts').

Phagotrophy exists in several harmful/toxic marine phytoplankton species. The toxic *Chrysochromulina polylepis*, *Heterosigma akashiwo* and *Alexandrium tamarense* are able to ingest radioactively labelled bacteria at high rates (Nygaard & Tobiesen, 1993). Also, food vacuoles have been observed in the toxic *Dinophysis acuminata* and *Dinophysis norvegica* (Jabobson & Andersen, 1994). These results indicate that phagotrophy may be an important mode of nutrition for these potentially toxic algae. Several other harmful dinoflagellates species (e.g. *Gymnodinium sanguineum*, *Gyrodinium uncatenatum*, *Ceratium furca*, *P. minimum*, *P. micans*) have been observed with ingested prey (Li et al., 1996; Stoecker et al., 1997; Jacobson & Anderson, 1996).

Phagotrophy in relation to environmental conditions

Light, nutrient availability, and prey concentration may interact to regulate phagotrophy in complicated ways (Figure 2). It is also possible that physiological adaptation is involved when switching modes of nutrition. If this is true, then the mode of nutrition may not immediately track changes in environmental conditions, as is the case for physiological changes taking place when a phytoplankton cell is exposed to variable light regimes.

An example of the decoupling of light and prey availability in phagotrophy of a photosynthetic organism was found by Rothhaupt (1996b) for *Ochromonas* sp. This species increased its ingestion rate with increasing bacterial density, independent of light conditions. Growth rate also increased in proportion to an increase in bacterial density, independent of light regime. However, at low bacterial densities, growth rates were slightly higher when *Ochromonas* sp. was growing in light than in the dark. Prey concentrations had no effect on the ingestion rates or chlorophyll concentrations of *Chrysochromulina brevifilum*, while low light intensity increased cellular chlorophyll content and ingestion rates (Jones et al., 1995).

Intuitively, one expects low light to be a major factor triggering induction of phagotrophy in phytoplankton (Granéli et al., 1997; Jones et al., 1993, 1995; McKenzie et al., 1995; Legrand et al., 1998). There may be a stimulation of phagotrophy in low light/darkness (Bird & Kalff, 1986; Jones et al., 1995; Legrand et al., 1998). Maximum ingestion rates and highest photosynthetic rates occurred simultaneously at 40 μmol m^{-2} s^{-1} for the chrysophyte *Poterioochromonas malhamensis* (Porter, 1988). The ingestion of fluorescently labelled flagellates (3 μm) by the dinoflagellate *Heterocapsa triquetra* was higher in darkness than in light (100 μmol m^{-2} s^{-1}) in short-term (24 h) experiments. However, in longer experiments (4–5 d) light was necessary to sustain phagotrophy in this dinoflagellate (Legrand et al., 1998). In the genus *Chrysochromulina* 16 species were tested for phagotrophy under low and high light, and with live and dead prey (Jones et al., 1993). Only 5 of the 16 species did not become phagotrophic, at least in response to some of the offered prey. *C. brevifilum* showed an inverse relation between phagotrophy and light, which was re-confirmed in further experiments (Jones et al., 1993). Phagotrophy increased at low light intensity, and the number of *C. brevifilum* cells grown at low light (45 μmol m^{-2} s^{-1}) was much higher when algal prey was provided as food. This is an example where phagotrophy seems to have substituted for photosynthesis as the dominant source of organic carbon at low light intensities. However, the opposite has also been found. For example inhibition of bacterivory in a freshwater chrysophyte exposed to darkness or low light was found by Caron et al. (1993).

Some phytoplankton species that are not good competitors for the limiting nutrient at low concentrations may have retained or re-developed the capacity to prey on other plankton organisms in order to obtain the required nutrients (see Schöllhorn & Granéli, 1996). Use of an alternative nutrient source may enable these species to coexist with, or outcompete, species that rely strictly on dissolved nutrients (Rothhaupt, 1996b).

An increase in bacterivory in several species of toxic flagellates was observed when the cells were grown in P deficient medium (Nygaard & Tobiesen, 1993). *C. polylepis* was grown under N- or P-deficiency and under nutrient sufficient conditions (Legrand et al., 1996). The disappearance of fluorescently labelled algae (FLA) from the medium in P-deficient treatments was higher than for other treatments. Thus, *C. polylepis* cells might have been using FLA as a P source. The same authors found phagotrophy in *C. polylepis* to correspond to a maximum of 5% of the carbon intake. However, since dead cells were presented as prey, these ingestion rates may have been significantly underestimated.

Ingestion of bacteria, which are rich in P, may be a mechanism for phagotrophic dinoflagellates/flagellates to obtain this critical element (Nygaard & Tobiesen, 1993). The chrysophyte *Ochromonas* sp. switched from uptake to excretion of SRP (soluble reactive phosphorus) when growing autotrophically and phagotrophically respectively, indicating that phagotrophy can decrease or even exceed the demand for SRP (Rothhaupt, 1996a). This enables the phagotrophic species to coexist with phototrophic species, which must rely on SRP or dissolved organic P (Rothhaupt, 1996b). The chrysophyte *Uroglena* sp. assimilate inorganic P through phototrophy, and it is also able to take up phospholipids via ingestion of bacteria (Kimura & Ishida, 1985). According to Keller et al. (1994), *Ochromonas* sp. used phagotrophy to supplement its nutrition when light or inorganic nutrients were limiting. However, there was an apparent threshold of response, as phagotrophy decreased or even ceased after periods of prolonged darkness.

The freshwater chrysophyte *Dinobryon cylindricum* could satisfy 25% of its C, N and P need through ingestion of bacteria (Caron et al., 1993). Up to 50% of the C demand by *Dinobryon sertularia* can be met by phagotrophy (Bird & Kalff, 1989). Assuming an assimilation efficiency of 60% for C (Calow, 1977) and close to 100% for N, Bird & Kalff (1989) estimated that nearly 100% of the N demand by *Dinobryon sertularia* could be met by phagotrophy. For the marine red-tide dinoflagellate *G. sanguineum*, Bockstahler & Coats (1993a) calculated that natural populations of this algae in the Chesapeake Bay were able to meet their N requirement by ingesting small nanociliates (<20 μm).

The ecological significance of phagotrophy

Phagotrophy has been considered a significant loss rate in ecosystem energy budgets. Phagotrophic C uptake as a percentage of total (photosynthesis plus phagotrophy) C incorporation varies widely in the literature, from a few percent (Tranvik et al., 1989; Legrand et al., 1996) to more than 50% (Porter, 1988; Bird & Kalff, 1989; Caron et al., 1993). This variation can occur within the same algal group (genus). Bird & Kalff (1989) showed that C assimilation by phagotrophic chrysomonads in the deeper waters (below 6 m) of Lac Gilbert can be equal to or higher than photosynthetic fixation. Tranvik et al. (1989), however, reported that bacterivory by *Cryptomonas* sp. was not an important C source for this phytoflagellate, representing less than 2% of the C intake.

Control of bacterial densities in lakes and marine waters has, until recently, been attributed mostly to heterotrophic flagellates. Some phytoplankton species have similar or sometimes higher grazing rates than heterotrophic flagellates, controlling not only bacteria but even heterotrophs of the same size as the algae themselves (Sanders & Porter, 1988; Bockstahler & Coats, 1993a, 1993b; Skovgaard, 1996). Phagotrophic phytoflagellates are reported to be responsible for a major part of the grazing pressure on bacteria in some lakes (Bird & Kalff, 1986; Berninger et al., 1992). Sanders & Porter (1988) reported clearance rates between 2.5–8.4 nl hr^{-1} for phytoflagellates in Lake Oglethorpe. Similar values were found for marine flagellate/dinoflagellate species such as *C. polylepis* (Nygaard & Tobiesen, 1993). The occurrence of food vacuoles in *G. sanguineum* was positively correlated to ciliate densities (Bockstahler & Coats, 1993a). The daily removal of these nanociliates by *G. sanguineum* accounted from 6 to 67% of the <20 μm ciliate standing stock (Bockstahler & Coats, 1993a).

These contradictory results show that the contribution by phagotrophy of mixotrophic algae to the control of biomass of bacteria or other plankton organisms is highly variable, depending on the algal species and the environmental conditions encountered by the algae. However, it is clear that losses due to pigmented flagellates must be considered when estimating grazing rates on bacteria, algae and microzooplankton in lakes or marine waters.

Summary

Substantial experimental evidence shows that phytoplankton utilize DOM as a nutrient source in natural environments, which are either organic substances present in seawater or DOM reaching coastal zones with rivers and rainfall. This growth stimulating effect may be caused either by trace metal complexation by the organic molecules, and/or direct utilization of organic bound N occurring in small molecules such as urea and amino acids. Indirect utilization of organic bound N via remineralization by bacterivores cropping on bacteria that used the DOM as a substrate, is also a mechanism for phytoplankton to access the N in DOM. Direct ingestion of high-molecular weight organic molecules by phytoplankton seems to be a potentially important but largely overlooked mechanism. Dissolved organic matter in river water entering coastal waters is subjected to two major breakdown processes: bacterial degradation, and photochemical transformations that increase their availability to bacteria. In coastal waters largely influenced by river runoff and rainfall, increased growth of phytoplankton, including blooms of harmful algal species, might therefore occur as an effect of indirect utilization of N previously bound to DOM.

Phagotrophy is widespread in certain groups of photosynthetic organisms, especially among various phytoflagellates including important toxic or harmful species, such as *C. polylepis*, *Pfiesteria piscicida*, *H. akashiwo*, *A. tamarense*, *Dinophysis* spp., *Gyrodinium galateanum* and *H. triquetra*. Phagotrophic algae prey on bacteria, other algae, and even microzooplankton. Phagotrophy may substitute for photosynthesis, and thus may be an alternative way of acquiring reduced C, as well as macronutrients (P, N), metals, vitamins or other organic substances that the organism cannot synthesize itself. Both low light and nutrient deficiency promote phagotrophy, with grazing rates generally dependent on prey concentration. However, some phagotrophic algae graze independent of light conditions. There is a wide range in degree of mixotrophy, from species that can only supplement their nutrition with phagotrophy to species that are able to grow phagotrophically in complete darkness. Mixotrophic organisms may have a competitive advantage over strict heterotrophs or strict photoautotrophs under specific environmental conditions. However, there is most likely a cost attached to being mixotrophic that makes phagotrophic algae photosynthetically less efficient than obligate autotrophs, and less efficient grazers than heterotrophic unicellular organisms. Under certain conditions phagotrophic algae can be the primary bacterivores of the microbial food web. Phagotrophy among algae was 'rediscovered' only about 10 years ago, and the ecological significance of this mode of nutrition at the organism and ecosystem level is yet to be elucidated.

Acknowledgements

Financial support from the Swedish Natural Science Research Council (NFR), the Swedish Board for Agricultural and Forestry Research (SJFR), the Swedish Environmental Protection Agency (SNV) (recipients Per Carlsson and Edna Granéli) and the European Mobility and Training Research Program (contract nr MAS2-CT93-5010 to Catherine Legrand) is gratefully acknowledged.

References

Aaronson S (1974) The biology and ultrastructure of phagotrophy in *Ochromonas danica* (Chrysophyceae: Chrysomonadida). J Microbiol 83: 21–9

Anderson MA and Morel FMM (1982) The influence of aqueous iron chemistry on the uptake of iron by the coastal diatom *Thalassiosira weissflogii*. Limnol Oceanogr 27: 789–813

Andersson A, Falk S, Samuelsson G and Hagström Å (1989) Nutritional characteristics of mixotrophic nanoflagellate. *Ochromonas* sp. Microb Ecol 17: 251–262

Andersson A, Lee C, Azam F and Hagstrom A (1985) Release of amino acids and inorganic nutrients by heterotrophic marine microflagellates. Mar Ecol Prog Ser 23: 99–10

Andersson T, Nilsson Å and Jansson M (1991) Coloured substances in Swedish rivers-temporal variation and regulating factors. In: Allard B, Borén H and Grimvall A (eds.) Humic Substances in the Aquatic and Terrestrial Environment. Lecture notes in Earth Sciences, Vol. 33 (pp. 243–253) Springer-Verlag, Berlin-Heidelberg

Antia NJ, Harrison PJ and Oliveira L (1991) The role of dissolved organic nitrogen in phytoplankton nutrition, cell biology and ecology. Phycologia 30: 1–89

Azam F and Smith DC (1991) Bacterial influence: on the variability in the ocean's biogeochemical state: a mechanistic view. In: Demers S (ed.) Particles Analysis in Oceanography, NATO ASI Series Vol G127 (pp. 213–236) Springer-Verlag, Berlin

Baden DG and Mende TJ (1979) Amino acid utilization by *Gymnodinium breve*. Phytochemistry 18: 247–252

Benner R, Pakulski JD, McCarthy M, Hedges JI and Hatcher PG (1992) Bulk chemical characteristics of dissolved organic matter in the ocean. Science 255: 1561–1564

Berg GM, Glibert PM, Lomas MW and Burford MA (1997) Organic nitrogen uptake and growth by the chrysophyte *Aureococcus anophagefferens* during a brown tide event. Mar Biol 129 377–387

Berman T (1970) Alkaline phosphatases and phosphorus availability in Lake Kinneret. Limnol Oceanogr 15: 663–674

Berninger UG, Caron DA, and Sanders RW (1992) Mixotrophic algae in three ice-covered lakes of the Pocono Mountains, U.S.A. Freshwater Biol 28: 263–272

Bird DF and Kalff J (1986) Bacterial grazing by planktonic lake algae. Science 231: 493–495

Bird DF and Kalff J (1989) Phagotrophic sustenance of a metalimnetic phytoplankton peak. Limnol Oceanogr 34: 155–162

Bockstahler KR and Coats DW (1993a) Spatial and temporal aspects of mixotrophy in Chesapeake Bay dinoflagellates. J Euk Microbiol 40: 46–60

Bockstahler KR and Coats DW (1993b) Grazing of the mixotrophic dinoflagellate *Gymnodinium sanguineum* on ciliate populations of Chesapeake Bay. Mar Biol 116: 477–487

Boraas ME, Estep KW, Johnson PW and Sieburth JM (1988) Phagotrophic phototrophs: the ecological significance of Mixotrophy. J Protozool 35: 249–252

Brathak G (1985) Bacterial biovolume and biomass estimation. Appl Environ Microbiol 49: 1488–1493

Buijsman E, Maas HFM, and Asmen WAH (1987) Anthropogenic ammonia emissions in Europe. Atmos Environ 21: 1009–1020

Bushaw KL, Zepp RG, Tarr MA, Schulz-Jander D, Bourbonniere RA, Hodson RE, Miller WL, Bronk DA and Moran MA (1996) Photochemical release of biologically available nitrogen from dissolved organic matter. Nature 381:404–407

Calow P (1977) Conversion efficiencies in heterotrophic organisms. Biol Rev 52: 385–409

Carlsson P, Segatto AZ and Granéli E (1993) Nitrogen bound to humic matter of terrestrial origin – a nitrogen pool for coastal phytoplankton? Mar Ecol Prog Ser 97: 105–111

Caron DA and Goldman JC (1990) Protozoan nutrient generation. In: Capriulo GM (ed.) Ecology of Marine Protozoa (pp. 283–306) Oxford University Press, New York

Caron DA, Porter KG and Sanders RW (1990) Carbon, nitrogen and phosphorus budgets for the mixotrophic phytoflagellate *Poterioochromonas malhamensis* (Chrysophyceae) during bacterial ingestion. Limnol Oceanogr 35: 433–443

Caron DA, Sanders RW and Lim EL (1993) Light-dependent phagotrophy in the freshwater mixotrophic Chrysophyte *Dinobryon cylindricum*. Microb Ecol 25: 93–111

Cembella AD, Antia NJ and Harrison PJ (1985) The utilization of inorganic and organic phosphorus compounds as nutrients by eucaryouc microalgae: A multidisciplinary perspective. Part 2. CRC Critical Reviews in Microbiology 11: 13–81

Cheng UY and Antia NJ (1970) Enhancement by glycerol of phototrophic growth of marine planktonic algae and its significance to the ecology of glycerol pollution. J Fish Res Board Can 27: 335–346

Chróst RJ (1989) Characterization and significance of b-glucosidase activity in lake water. Limnol Oceanogr 34: 660–672

Chróst RJ (1991) Environmental control of the synthesis and activity of aquatic microbial enzymes. In: Chróst RJ (ed.) Microbial Enzymes in Aquatic Environments (pp. 29–59) Springer-Verlag, New York

Combres C, Laliberté G, Sevrin Reyssac J and de la Noüe J (1994) Effect on acetate on growth and ammonium uptake in the microalga *Scenedesmus obliquus*. Physiol Plant 91: 729–734

Darley WM (1977) Biochemical composition. In: Werner D (ed.) The Biology of Diatoms. Botanical Monographs Vol 13 (pp. 198–223) Univ. California Press, Los Angeles

Droop MR (1974) Heterotrophy of carbon. In: Stewart WDP (ed.) Algal Physiology and Biochemistry (pp. 530–559) Univ. California Press, Los Angeles

Duce RA, Liss PS, Merrill JT, Atlas EL, Bautmenard P, Hicks BB, Miller JM, Prospero JM, Arimoto R, Church TM, Ellis W, Galloway JN, Hansen L, Jickells TD, Knap AH, Reinhardt KH, Schneider B, Soudine A, Tokos JJ, Tsunogai S, Wollast R and Zhou M (1991) The atmospheric input of trace species to the world ocean. Global Biogeochem Cycles 5: 193–259

Flynn KJ and Syrett PJ (1986) Utilization of L-Lysine and L-arginine by the diatom *Phaeodactylum tricornutum*. Mar Biol 90: 159–164

Flynn KJ and Butler I (1986) Nitrogen sources for the growth of marine microalgae: role of dissolved free amino acids. Mar Ecol Prog Ser 34: 281–304

Forsberg C (1992) Will an increased greenhouse impact in Fennoscandia give rise to more humic and coloured lakes? Hydrobiologia 229: 51–58

Gaines G and Elbrächter M (1987) Heterotrophic nutrition. In: Taylor FJR (ed.) The Biology of Dinoflagellates (pp. 224–268) Blackwell Scientific Publications, Oxford

Goldman JC and Caron D (1985) Experimental studies on an omnivorous microflagellate: Implications for grazing and nutrient regeneration in the marine microbial food chain. Deep Sea Res 8: 899–915

Granéli E, Anderson DM, Carlsson P, Finenko G and Maestrini SY (1997) Light and dark carbon fixation by *Dinophysis*-species in comparison to other photosynthetic and heterotrophic dinoflagellates. Aquat Microb Ecol 13:177–186

Granéli E, Edler L, Gedziorowska D and Nyman U (1985) Influence of humic and fulvic acids on *Prorocentrum minimum* Pav.) J. Schiller. In: Anderson DM, White AW and Baden DG (eds) Toxic Dinoflagellates (pp. 201–206) Elsevier Sci Publ, New York

Granéli E and Moreira MO (1990) Effects of river water of different origin on the growth of marine dinoflagellates and diatoms in laboratory cultures. J Exp Mar Biol Ecol 136: 89–106

Granéli E, Carlsson P, Olsson P, Sundström B, Granéli W and Lindahl O (1989) From anoxia to fish poisoning: the last ten years of phytoplankton blooms in Swedish marine waters. In: Cosper EM, Bricelj VM and Carpenter EJ (eds.) Novel Phytoplankton Blooms–Causes and impacts of recurrent brown tides and other unusual blooms (pp. 407–427) Springer-Verlag, New York

Hansell D (1993) Results and observations from the measurement of DOC and DON in seawater using a high-temperature catalytic oxidation technique. Mar Chem 41: 195–202

Havskum H and Riemann B (1996) Ecological importance of bacterivorous, pigmented flagellates (mixotrophs) in the Bay of Aarhus.Mar Ecol Prog Ser 137: 251–263

Hedges JI (1987) Organic matter in sea water. Nature 330: 205–206

Hellebust JA and Lewin J (1977) Heterotrophic nutrition. In: Werner D (ed.) The Biology of Diatoms (pp. 169–197) Blackwell Scientific Publ., Oxford

Hofeneder H (1930) Über die animalische Ernährung von *Ceratium hirundinella* O.F. Muller und über die Rolle des kernes bei dieser Zellfunktion. Arch Protistenkd 71: 1–32

Hoppe HG, Kim SJ and Gocke K (1988) Microbial decomposition in aquatic environments: combined processes of extracellular enzyme activity and substrate uptake. Appl Environ Microbiol 54: 784–790

Jacobsen TR and Rai H (1991) Aminopeptidase activity in lakes of differing eutrophication. In: Chróst RJ (ed.) Microbial Enzymes in Aquatic Environments (pp. 155–164) Springer-Verlag, New York

Jacobson DM and Anderson RA (1994) The discovery of mixotrophy in photosynthetic species of *Dinophysis* (Dinophyceae): light and electron microscopical observations of food vacuoles in *Dinophysis acuminata*, *D. norvegica* and two heterotrophic dinophysoid dinoflagellates. Phycologia 33: 97–110

Jacobson DM and Anderson DM (1996) Widespread phagocytosis of ciliates and other protists by marine mixotrophic and heterotrophic thecate dinoflagellates. J Phycol 32: 279–285

Jones HLJ, Durjun P, Leadbeater BSC and Green JC (1995) The relationship between photoacclimation and phagotrophy with respect to chlorophyll a, carbon and nitrogen content, and cell size of *Chrysochromulina brevifilum* (Prymnesiophyceae). Phycologia 34: 128–134

Jones RI (1994) Mixotrophy in planktonic protists as a spectrum of nutritional strategies. Mar Microb Food Webs 8: 87–96

Jones HLJ, Leadbeater BSC and Green JC (1993) Mixotrophy in marine species of *Chrysochromulina* (Prymnesiophyceae): ingestion and digestion of a small green flagellate. J Mar Biol Ass UK 73: 283–296

Keller MD, Shapiro LP, Haugen EM, Cucci TL and Sherr EB (1994) Phagotrophy of fluorescently labelled bacteria by an oceanic phytoplankter. Microb Ecol 28: 39–52

Kieber RJ, Zhou X and Mopper K (1990) Formation of carbonyl compounds from UV-induced photodegradation of humic substances in natural waters: Fate of riverine carbon in the sea. Limnol Oceanogr 35: 1503–1515

Kimura B and Ishida Y (1985) Photophagotrophy in *Uroglena americana*, Chrysophyceae. Jap J Limnol 46: 315–318

Kivic PA and Vesk M (1974) Pinocytotic uptake of protein from the reservoir in *Euglena*. Arch Microbiol 96: 155–159

Klut ME, Bisalputra T and Antia NJ (1987) Some observations on the structure and function of the dinoflagellate pusule. Can J Bot 65: 736–744

Legrand C and Carlsson P (1998) Uptake of high molecular weight dextran by the dinoflagellate *Alexandrium catenella*. Aquat Microb Ecol 16: 81–86

Legrand C, Granéli E and Carlsson P (1998) Induced phagotrophy in the photosynthetic dinoflagellate *Heterocapsa triquetra*. Aquat Microb Ecol 15: 65–75

Legrand C, Sæmundsdottir S and Granéli E (1996) Phagotrophy in *Chrysochromulina polylepis* (Prymnesiophyceae): ingestion of C(FI.A) under different nutrient conditions. In: Yasumoto T, Oshima Y and Fukuyo Y (eds.) Harmful and Toxic Algal Blooms (pp. 339–342) Intergovernmental Oceanographic Commission of UNESCO

Lessard EJ and Swift E (1985) Species-specific grazing rates of heterotrophic dinoflagellates in oceanic waters, measured with a dual-label radioisotope technique. Mar Biol 87: 289–296

Letelier RM and Karl DM (1996) Role of *Trichodesmium* spp. in the productivity of the subtropical North Pacific Ocean. Mar Ecol Prog Ser 133: 263–273

Li A, Stoecker DK, Coats W and Adam EJ (1996) Ingestion of fluorescently labelled and phycoerythrin-containing prey by mixotrophic dinoflagellates. Aquat Microb Ecol 10: 139–147

Likens GE, Borman FH and Johnson NM (1974) Acid rain. Environment 14: 33–40

Malcolm RL (1985) Geochemistry of stream fulvic and humic substances. In: Aiken GR, McKnight DM and Wershaw RL (eds) Humic Substances in Soil, Sediment, and Water (pp. 181–210) John Wiley & Sons, New York

McCarthy M, Pratum T, Hedges J and Benner R (1997) Chemical composition of dissolved organic nitrogen in the ocean. Nature 390: 150–153

McKenzie CH, Deibel D, Paranjape MA and Thompson RJ (1995) The marine mixotroph *Dinobryon balticum* (Chrysophyceae): phagotrophy and survival in a cold ocean. J Phycol 31: 19–24

Meybeck M (1982) Carbon, nitrogen and phosphorus transport by world rivers. Am J Sci 282: 401–450

Mopper K and Zika RG (1987) Free amino acids in marine rains: evidence for oxidation and potential role in nitrogen cycling. Nature 325: 246–249

Morrill LC and Loeblich AR (1979) An investigation of heterotrophic and photoheterotrophic capabilities in marine Pyrrhophyta. Phycologia 18: 394–404

Myklestad S and Sakshaug E (1983) Alkaline phosphatase activity of *Skeletonema costatum* populations in the Trondheims Fjord Norway. J Plankton Res 5: 557–564

Nagata T (1986) Carbon and nitrogen content of natural planktonic bacteria. Appl Environ Microbiol 52: 28–32

Nygaard K and Tobiesen A (1993) Bacterivory in algae: a survival strategy during nutrient limitation. Limnol Oceanogr 38: 273–279

Paerl HW (1991) Ecophysiological and trophic implications of light-stimulated amino acid utilzation in marine phytoplankton. Appl Environ Microbiol 57: 473–479

Paerl HW (1995) Coastal eutrophication in relation to atmospheric nitrogen deposition: Current perspectives. Ophelia 41: 237–259

Palenik B and Morel FMM (1990) Comparison of cell-surface L-amino acid oxidases from several marine phytoplankton. Mar Ecol Prog Ser 59: 195–201

Payne JW (1980) Microorganisms and nitrogen sources. J Wiley and Sons, New York. 764 pp.

Peierls BL and Paerl HW (1997) Bioavailability of atmospheric organic nitrogen deposition to coastal phytoplankton. Limnol Oceanogr 42: 1819–1823

Porter KG (1988) Phagotrophic phytoflagellates in microbial food webs. Hydrobiologia 159: 89–97

Prakash A and Rashid MA (1968) Influence of humic substances on the growth of marine phytoplankton: dinoflagellates. Limnol Oceanogr 13: 598–606

Prakash A, Rashid MA, Jensen A and Subba Rao DV (1973) Influence of humic substances on the growth of marine phytoplankton: diatoms. Limnol Oceanogr 18: 516–524

Provasoli L, McLaughlin JJA and Droop MR (1957) The development of artificial media for marine algae. Arch Microbiol 25: 392–428

Rahat M and Hochberg A (1971) Ethionine and methionine metabolism by the chrysomonad flagellate *Prymnesium parvum*. J Protozool 18: 378–382

Richardson K and Fogg GE (1982) The role of dissolved organic material in the nutrition and survival of marine dinoflagellates. Phycologia 21: 17–26

Rosso AL and Azam F (1987) Proteolytic activity in coastal oceanic waters: depth distribution and relationship to bacterial populations. Mar Ecol Prog Ser 41: 231–240

Rothhaupt KO (1996a) Laboratory experiments with a mixotrophic chrysophyte and obligately phagotrophic and photorophic competitors. Ecology 77: 716–724

Rothhaupt KO (1996b) Utilization of substitutable carbon and phosphorus sources by the mixotrophic chrysophyte *Ochromonas* sp. Ecology 77: 706–715

Sanders RW, Porter KG and Caron DA (1990) Relationship between phototrophy and phagotrophy in the mixotrophic chrysophyte *Poterioochromonas malhamensis*. Microb Ecol 19: 97–109

Sanders RW and Porter KG (1988) Phagotrophic phytoflagellates. Advances Microb Ecol 10: 167–192

Schöllhorn S and Granéli E (1996) Influence of different nitrogen to silica ratios and artificial mixing on the structure of a summer phytoplankton community from the Swedish West Coast (Gullmar Fjord). J Sea Res 35: 159–167

Sharp JH (1983) The distributions of inorganic nitrogen and dissolved and particulate organic nitrogen in the sea. In: Carpenter

EJ and Capone DG (eds) Nitrogen in the Marine Environment (pp 1–35) Academic Press, New York

Sherr EB, Sherr BF and Fallon RD (1987) Use of monodispersed fluorescently labelled bacteria to estimate *in situ* protozoan bacterivory. Appl Environ Mirobiol 53: 958–965

Skovgaard A (1996) Mixotrophy in *Fragilidium subglobosum* (Dinophyceae): growth and grazing responses as functions of light intensity. Mar Ecol Prog Ser 143: 247–253

Stoecker DK, Li A, Coats DW, Gustafson DE and Nannen MK (1997) Mixotrophy in the dinoflagellate*Prorocentrum minimum*. Mar Ecol Prog Ser 152: 1–12

Suzuki Y, Sugimura Y and Itoh T (1985) A catalytic oxidation method for the determination of total nitrogen dissolved in seawater. Mar Chem 16: 83–97

Thingstad TF, Havskum H, Garde K and Riemann B (1996) On the strategy of 'eating your competitor'. A mathematical analysis of algal mixotrophy. Ecology 77: 39–49

Thurman EM (1985) Organic geochemistry of natural waters. Nijhoff/Junk, Boston. 687 pp.

Timperley MH, Vigor-Brown R, Kawashima M and Ishigami M (1985) Organic nitrogen compounds in atmospheric precipitation: their chemistry and availability to phytoplankton. Can J Fish Aquat Sci 42: 1171–1177

Tranvik L, Porter KG and Sieburth JM (1989) Occurrence of bacterivory in *Cryptomonas*, a common freshwater phytoplankter. Oecologia 78: 473–476

Ukeles R and Rose WE (1976) Observations on organic carbon utilization by photosynthetic marine microalgae. Mar Biol 37: 11–28

Williams PM and Druffel ERM (1988) Dissolved organic matter in the ocean: Comments on a controversy. Oceanography 1: 14–17

Zhang J (1994) Atmospheric wet deposition of nutrient elements: correlation with harmful biological blooms in Northwest Pacific coastal zones. Ambio 23: 464–468