

Some comments on picoplankton and its importance in the pelagic ecosystem

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ABSTRACT: Picoplankton is an integral component of a microbial community, termed the ultraplankton, which seems to be ubiquitous in all seas and lakes. The picophytoplankton and heterotrophic bacterioplankton produce the bulk of the biomass in the community and their consumption by predators with matching growth rates results in a highly dynamic and self-contained system with efficient recycling of mineral nutrients and dissolved organic matter. Given adequate radiant energy the population levels of the component organisms are largely determined by the internal dynamics of the community rather than by external factors. Only when concentrations of mineral nutrients rise above those set by dynamics of the ultraplankton can larger phytoplankton compete effectively and multiply. There is a sharp distinction in form and dynamics between ultra- and microplankton. The metabolism of the ultraplankton commonly dominates in pelagic ecosystems, although it seems to contribute little organic matter to higher trophic levels, and must be taken into account in the determination of primary productivity.

KEY WORDS: Picoplankton · Ultraplankton · Microplankton · Microbial loop · Recycling · Primary production

INTRODUCTION

Picoplankton includes all those organisms, both phototrophic and heterotrophic, which fall into the size class 0.2 to 2.0 μm . In this paper I propose to comment on some aspects of the ecology of these micro-organisms, elaborating a point of view already advanced by Sieburth (1984). My object will be to emphasize the remarkable characteristics of the marine microbial community of which the picoplankton forms an integral part. This community has been called the 'microlitersphere' by Sieburth & Davis (1982) but I prefer to use the older term 'ultraplankton'. The upper size level of this, put between 10 and 20 μm so as to include nanoplankton (but see Shapiro & Guillard 1986), seems, as I hope to show, to mark a natural discontinuity between it and the microplanktonic community familiar from the textbooks. A community related to the ultraplankton is to be found in marine snow (Silver et al. 1986) but, although it undoubtedly has important interactions with both the free-living ultraplankton and the microplankton, this will not be dealt with here.

COSMOPOLITAN NATURE AND STABILITY IN COMPOSITION OF PICOPLANKTON

Numerous studies suggest that picoplankton is cosmopolitan in distribution in the surface waters of both freshwater lakes and the sea, with numbers of organisms commonly around 10^6 ml^{-1} for heterotrophic bacteria, 10^4 ml^{-1} for cyanobacteria (Fogg 1986a, 1987, Nagata 1988, Stockner 1988, Kudoh et al. 1990, Caron et al. 1991), 10^3 ml^{-1} for eukaryotes and up to 10^5 ml^{-1} for prochlorophytes (Campbell & Vaulot 1993). This is so for Mediterranean waters as for other seas (Maugeri et al. 1992, Wood et al. in press). Population densities do not usually vary very much but fluctuations of several orders of magnitude have been reported, e.g. for a Welsh lake (Happay Wood 1991) and for Lakes Faro and Ganzirri near Messina (Acosta Pomar et al. 1988, Bruni et al. 1990), but these are relatively small water bodies subject to abrupt changes in water quality and may be regarded as special cases. Another component of the ultraplankton, the nanoplanktonic phagotrophic flagellates, also shows a relative stability of population

density at around 10^3 ml^{-1} (Sherr & Sherr 1984), as perhaps virus particles at up to 10^8 ml^{-1} do as well (Bergh et al. 1989, Proctor & Fuhrman 1990).

Types, if not species, of picoplankton seem to be cosmopolitan. *Synechococcus* spp. seem ubiquitous in open waters, whether fresh or salt. Kennaway (1989) isolated from a Welsh lake a *Synechococcus* which was morphologically similar to the Type 1 described by Johnson & Sieburth (1979) from seawater. On the other hand, considerable genetic and biochemical differences have been found between morphologically identical strains of marine *Synechococcus* (Glibert et al. 1986, Glibert & Ray 1990, Wood & Townsend 1990). Picoplanktonic prochlorophytes (with which can probably be included the 'very small red fluorescing bodies' referred to by several authors) were reported as abundant in North Atlantic waters by Chisholm et al. (1988) and are evidently widely distributed. They are present in the coastal waters of Italy (Li et al. 1991) and in the northwestern (Vaultot & Partensky 1992) and eastern Mediterranean Sea (Wood et al. in press). It is uncertain as yet whether there is any floristic similarity in prochlorophyte or eukaryotic picophytoplankton from freshwaters and the sea. The bacterioplankton flora is still largely uncharacterized, evidently because it has so far evaded isolation in culture. Analysis of bacterial 16S ribosomal genes from natural populations in the Sargasso Sea shows the presence of many undescribed and so far uncultivated species (Giovannoni et al. 1990).

There are striking variations, however, in the composition of the picophytoplankton as seen in the relative numbers of the prokaryotic and eukaryotic components in relation to temperature and irradiance. In both Lake Ontario (Caron et al. 1985) and the Irish Sea (Fogg 1986b) a logarithmic increase in cell numbers of picoplanktonic cyanobacteria with temperature, corresponding roughly to a doubling for every 2.5°C rise, has been reported. On a transect between Australia and Antarctica cyanobacterial picoplankton decreased with increasing latitude in a manner which suggested that temperature was the determining factor, a minimum concentration of 10 cells ml^{-1} being found at -1°C (Marchant et al. 1987). It should be noted, however, that strains of marine picoplanktonic cyanobacteria tolerant to low temperature do exist (Neuer 1992). Heterotrophic picoplankton shows a less marked decrease in population density with decreasing temperature (Egan & Floodgate 1985) and eukaryotic numbers tend to increase at lower temperatures (Murphy & Haugen 1985).

Variations in composition in relation to irradiance are seen as one goes down the water column. Towards the bottom of the euphotic zone maxima of cyanobacterial, eukaryotic and prochlorophyte populations

occur at progressively greater depths, a separation which seems to be explained by the respective efficiencies of their photosynthetic pigments in utilizing the wavelengths which penetrate to these depths (Li & Wood 1988, Lande et al. 1989, Wood 1990, Campbell & Vaultot 1993). Orientated cell motility may contribute to the positioning in the water column of the small eukaryotes (Lande et al. 1989).

Population densities of both phototrophic and heterotrophic picoplankton have been found to increase by perhaps an order of magnitude between oligotrophic and moderately eutrophic waters (see e.g. El Hag & Fogg 1986 for the marine situation and Berninger et al. 1991 for freshwaters). Otherwise the population characteristics seem little affected by nutrient availability or hydrographic features.

The impression is that these characteristics of picoplankton populations depend more on the internal dynamics of the ultraplanktonic community than on environmental factors. This idea is supported by what we know of the growth kinetics and trophic relationships of the component organisms, which seem essentially the same in freshwaters and the sea (Berninger et al. 1991). There are considerable differences in estimates of population growth rates according to the methods used (Sheldon et al. 1992) but the general position seems clear. Heterotrophic bacteria and the picophytoplankton have doubling times of a few hours (Van Es & Meyer-Reil 1982) and around 16 h (Stockner & Antia 1986) or 12 h (Sheldon et al. 1992) respectively. The principal predators on both these types of micro-organism, the phagotrophic flagellates and ciliates, have doubling times of the order of 24 h (Goldman & Caron 1985, Berninger et al. 1991, Sheldon et al. 1992). Since autotrophs do not grow during the night, growth rates of predator and prey are effectively equal (Sheldon et al. 1992). There is thus a rapid response of predator to increase in prey and equilibrium is established rapidly, as has been demonstrated, for example, in laboratory experiments by Johnson et al. (1982) and by Caron et al. (1991), biomass of prey and predator being thus tightly coupled (Kudoh et al. 1990). In seawaters (Hagström et al. 1988) and freshwaters (Berninger et al. 1991) bacterial production and consumption have sometimes been found to be nearly equal but some investigators have observed that predation rates fall appreciably short of estimated total mortalities (e.g. Lochte & Turley 1985). A steady state model based on the assumption that bacterial losses are caused by grazing, sinking and turbulent mixing gives predictions which match well with actual observations save that it consistently and substantially overestimates bacterial biomass (Taylor & Joint 1990). It has been suggested that lysis by viral action, to which

cyanobacteria as well as eubacteria are susceptible, may account for such discrepancies (Bergh et al. 1989). Viral particles must have high production rates and correspondingly high decay rates have been demonstrated in coastal and lake waters (Heldal & Bratbak 1991).

The total picture is thus one of a highly dynamic and responsive system tending towards equilibrium. The effect of temperature noted above is presumably due to differential effects on rates of production and predation of cyanobacteria and eukaryotic picophytoplankton. The effects of irradiance are due to differential effects on the growth rates of different types of phototrophs combined with migration to favourable levels in the water column by motile forms.

TURNOVER OF MATERIALS IN THE ULTRAPLANKTONIC COMMUNITY

This rapid turnover of populations of the various microbial components must be paralleled by rapid cycling of nutrient elements and rapid flow of energy through the system. To understand this we must first look at the physical background. The linear dimensions of all the organisms which we are considering and the spacing between them lie in the domain of very low Reynolds number in which molecular diffusion, rather than eddy diffusion, is the predominant agency for transfer of materials. Inertia is irrelevant so that the motility of organisms is of a different kind from that of the microplankton and macroscopic forms of life (Purcell 1977). The small radius of curvature of the surfaces of the individual organism effectively steepens concentration gradients, the total steady state flux becoming inversely proportional to the square of the radius (Pasciak & Gavis 1974). Episodic concentration gradients are dissipated in milliseconds. Together with the high surface area available for exchange relative to volume of protoplasm this results in the potential flux of nutrient ions or molecules from concentrations such as are usually encountered in natural waters into picoplankton cells being much in excess of what is required to maintain maximum growth rates (Raven 1986). In natural populations high specific growth rates are maintained even under poor nutrient conditions (Kudoh et al. 1990). Surrounded as it is by a cloud of efficiently absorbing picoplankton cells, a microplanktonic organism with much less efficient uptake is poorly situated and can presumably survive only when nutrient concentrations are in excess of those required by the picoplankton. Most planktonic bacteria are motile and their swimming speeds are such that they can move into the vicinity of a cell releasing organic material in a few seconds. Likewise the swimming

speeds of the nanoplanktonic flagellates enable them to encounter their prey sufficiently frequently to support their high growth rates (for references see Fogg 1986a).

Growth and predation in the ultraplanktonic community involve considerable turnover in organic matter. Release of organic carbon from picophytoplankton during photosynthesis is appreciable (Wood et al. 1992). Phagotrophic flagellates are generally 'sloppy feeders', releasing free amino acids and, presumably, other soluble organic substances, perhaps amounting to as much as half of the ingested carbon, whilst grazing on bacteria (Andersson et al. 1985, Hagström et al. 1988). Many nanoflagellates, being capable of both photosynthesis and phagotrophy, presumably contribute dissolved organic matter by either of these routes as circumstances dictate. Viral lysis of bacteria and cyanobacteria also, of course, releases dissolved organic matter. Heldal & Bratbak (1991), who found that 'phages may lyse 2 to 24% of the bacterial population per hour in coastal and lake waters', consider that this provides a major pathway for carbon flow back into the bacteria. Viral particles themselves are subject to rapid decay (Heldal & Bratbak 1991) and the protein and nucleic acids from them must enter the general pool of dissolved organic matter. Bacterioplankton is able to utilize effectively the low concentrations of substrates available in natural waters (Ammerman et al. 1984) and turnover times may be very short (Table 1). Mineral cycling is coupled to this traffic in organic carbon and turnover times of nitrogen and phosphorus are correspondingly short. For example, Suttle et al. (1980), using the sensitive tracer ^{13}N in studies of ammonium uptake by natural phytoplankton populations in Long Island Sound, found turnover times of tens of hours in April to early June falling to a fraction of an hour between mid-June and late July. Similar results were obtained in parallel studies on phosphorus uptake. The implication of picoplankton in this flux was shown by the observation that up to 50% of the flux of ^{13}N from ambient ammonium concentrations was into particles of less than 1 μm size. However, it begins to appear that the nanoplanktonic flagellate

Table 1. Turnover times of dissolved organic substances in the photic zone of the sea

Substance	Time (d)	Source
Glucose	0.4–100	Andrews & Williams (1971)
Acetate	0.34–69	Billen et al. (1980)
Lactate	2.1–104	Billen et al. (1980)
Glycollate	0.04–37	Edenborn & Litchfield (1987)
Free amino acids	ca 0.02	Fuhrman (1987)

fraction is the main agent in mineralization, not bacteria as classically supposed. Thus Van Wambeke & Bianchi (1985a, b) found rates of ammonium regeneration to be nearly 4 times as great per unit dry mass of micro-organism for heterotrophic flagellates as for bacteria. Similarly, Anderson et al. (1986) found in grazing experiments in batch cultures of a marine flagellate that this was responsible for the bulk of phosphate regeneration, bacteria making a negligible contribution.

INPUT FROM THE ULTRAPLANKTONIC COMMUNITY INTO HIGHER TROPHIC LEVELS

The extent to which the ultraplanktonic community contributes to the sustenance of larger organisms has been a matter for controversy. Picophytoplankton are responsible for most of the primary production in oligotrophic waters and a substantial proportion of that in eutrophic waters (see Fogg 1986a). It was supposed by Gray et al. (1984) that, additionally, the 'microbial loop' as it is often called in this connexion, is important in returning energy and materials to the classical pelagic food chain via the heterotrophic bacterioplankton. Separation of the microbial loop from other ultraplanktonic processes now seems artificial; cyanobacteria may contribute almost as much as heterotrophic bacteria to the sustenance of bacterivores (Caron et al. 1991) and remineralization, as we have just seen, is probably more actively carried out by flagellates and protozoa than by bacteria. The importance of the microbial loop in providing energy for higher levels of the food chain was questioned by, amongst others, Ducklow et al. (1986), who found that in an enclosed seawater column in which the bacterioplankton was labelled with ^{14}C , only 2% of the label was present in larger organisms after 13 d although about 20% remained in particles, presumably bacteria, of less than 1 μm size. Their conclusion that the microbial loop did not contribute appreciably to higher order consumers in the planktonic food web was contested by Sherr et al. (1987) on various grounds but principally because one should not generalize from a single experiment done under somewhat artificial conditions. However, the consensus which seems to be emerging is that the contribution is generally slight. Hagström et al. (1988) from an attempt to quantify organic fluxes in oligotrophic Mediterranean water using the minicell recapture technique concluded that only 6% of the total autotrophic production reaches the higher trophic levels. Wikner & Hagström (1988) using the same technique demonstrated a predator-prey link between flagellates of 1 to 3 μm size and bacteria which was tightly controlled through a chain of 4 trophic levels. Passage

through this number of levels inevitably implies that only a small proportion of the original production can reach the highest level.

RELATIONSHIP OF THE ULTRAPLANKTONIC AND MICROPLANKTONIC COMMUNITIES

From all this emerges a picture of the ultraplankton as a dynamic system, approaching equilibrium, within which materials are tightly cycled so that given the necessary light for photosynthesis it can maintain itself indefinitely. There are parallels here with the coral reef and the tropical rain forest. Losses by sedimentation are minimal and any material lost to higher trophic levels can be regained from the excretory or decomposition products of the larger organisms. Phenotypic adaptation is rapid, as, for example, in the response of a marine *Synechococcus* to a transient nanomolecular increase in surface layer nitrate concentration (Glover et al. 1988). Picoplankton also has the advantage that the large population sizes, short generation times and asexual propagation enable fast evolutionary response to environmental change (Lynch et al. 1991). Rare genotypes may become dominant within weeks or days if generation times are short and selection pressures high (Wood 1990) and the genetic structure of the ultraplankton is likely to be in constant flux.

The small size and adaptability of the picoplankton endow it with a superior capacity for uptake of dissolved materials so that in this respect it can out-compete larger organisms. The microplankton can only exist when concentration of nutrients are above those set by the internal dynamics of picoplankton. Ample evidence of this is seen in the dominance of picophytoplankton in oligotrophic seas but is also forthcoming from experiment. Takahashi et al. (1982) determined photosynthetic rates in different size fractions of plankton in enclosed columns in the CEPEX Foodweb 1 experiment at Saanich Inlet, British Columbia, and found that under nutrient-poor conditions most photosynthesis was carried out by the size fraction less than 3 μm . With added nutrients the picture changed, the biomass and photosynthesis of the less than 3 μm fraction remaining about the same but those of fractions between 35 and 202 μm increasing greatly. It is to be noted that the 3–55 μm fraction gained little from the increased nutrient supply. Evidence of a different sort came from the experiments, already mentioned, of Suttle et al. (1990) with ^{15}N as a tracer of ammonium uptake. A slight increase of ammonium concentration over the ambient level resulted in uptake in the particulate fraction retained by a 3 μm filter increasing from 33 to 80% of the total accompanied by more carbon being transferred to the higher level consumers.

Table 2. Comparison of the characteristics of ultraphytoplankton and microphytoplankton

	Ultraplankton	Microplankton
Size	0.2–20 μm	20–200 μm
Main physical process determining nutrient supply	Molecular diffusion	Turbulence, motion relative to water
Form	Simple, unicellular	Elaborate, often colonial
Gas vacuoles in cyanobacteria	Absent	Present
Generation time	Hours	Days
Relative generation time of predators	Equal	Much longer
Variations in natural population densities	10^{-10^2}	10^3-10^5

The larger phytoplankton escape the predation by the nanoflagellates which limits the picoplankton but achieve this at the expense of becoming less efficient in nutrient uptake and more liable to sedimentation so that remaining in the water column becomes a problem. They also have to exist in a different domain, in which turbulence rather than viscous flow becomes the controlling physical factor. The thought occurs that it may be biologically disadvantageous to live in the no-man's-land between the regimes of viscous flow and turbulence. Bimodal distributions of biomass, with a trough in the 10–55 μm region, which have been reported by several observers (for references see Fogg 1991), seem to support this idea. There are examples in which there clearly is not such a trough in the biomass distribution curve (e.g. Li & Wood 1988, Sheldon et al. 1992) but these are from oligotrophic waters in which the concentrations of organisms of size greater than 20 μm would be expected to be low. Takahashi et al. (1982) found in experimental enclosures that there was a gap in the distribution of photosynthetic activity and chlorophyll according to particle size between 3 and 30 μm and that addition of nitrate increased the growth of phytoplankton of the larger size classes, accentuating the bimodal distribution. There is certainly a radical change in passing from one regime to the other (Fogg 1991) and, as others before me (e.g. Sournia 1982) have pointed out, ultraphytoplankton and microplankton differ in many important respects (Table 2). As we have just seen, the microphytoplankton can only grow when nutrient concentrations are above a minimum level set by the ultraplanktonic community. This means that their multiplication is opportunistic with different species being favoured according to circumstances. Because the zooplankton which graze on them are larger and more complex than the single-celled phagotrophic flagellates and ciliates, their development is slower and generation times much longer. Thus there is a considerable lag between the development of a microphytoplankton population and that of the zooplankton predators so that population densities are less tightly controlled than those of the picoplankton and variations may be up to 5 orders

of magnitude. The microplanktonic community is thus non-equilibrium in its dynamics, a conclusion to which the late G. E. Hutchinson was forced in resolving the 'paradox of the plankton' (1961).

CONCLUSIONS

I suggest therefore that the picoplankton should be considered as an integral component of a basic, ubiquitous and nearly self-contained pelagic community. Especially in oligotrophic waters but to a considerable extent under eutrophic conditions too, its metabolism is dominant and that of larger organisms is merely superimposed on it. This has to be taken into account, for example, when interpreting determinations of primary production. The use in the radiocarbon technique of filters which do not retain picophytoplankton will result in an underestimate of total primary productivity but will give a more realistic estimate of the proportion which is available for the higher trophic levels. Another practical point is that the ultraplanktonic community, being a highly dynamic system in which some of the components, for example the nanoflagellates, are extremely fragile, may be profoundly disturbed and its metabolism altered by manipulative procedures. Enclosure of a sample in a bottle, or a change in temperature, sometimes produce effects which seem explicable only on such a basis (Fogg & Bajpai 1988, Fogg & Calvario-Martinez 1989, Kudoh et al. 1990). Beyond this, as pointed out by Smith et al. (1984), the presence of a large heterotrophic component — the bacteria — in oceanic waters has a profound regulatory effect on the metabolism of the whole plankton system, as judged by both the oxygen and carbon dioxide fluxes. Failure to recognize this when making comparisons between *in vitro* carbon uptake and oxygen evolution will severely limit the value of information about productivity in the sea.

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LITERATURE CITED

- Acosta Pomar L, Bruni V, Decembrini F, Giuffrè G, Maugeri TL (1988) Distribution and activity of picophytoplankton in a brackish environment. *Prog Oceanogr* 21:129–138
- Ammerman JW, Fuhrman JA, Hagström Å, Azam F (1984) Bacterioplankton growth in seawater. I. Growth kinetics and cellular characteristics in seawater cultures. *Mar Ecol Prog Ser* 18:31–39
- Anderson OK, Goldman JC, Caron DA, Dennett MR (1986) Nutrient cycling in a microflagellate food chain. III. Phosphorus dynamics. *Mar Ecol Prog Ser* 31:47–55
- Andersson A, Lee C, Azam F, Hagström Å (1985) Release of amino acids and inorganic nutrients by heterotrophic marine micro-flagellates. *Mar Ecol Prog Ser* 23:99–106
- Andrews P, Williams PJLeB (1971) Heterotrophic utilization of dissolved organic compounds in the sea. III. Measurement of the oxidation rates and concentrations of glucose and amino acids in sea water. *J mar biol Ass UK* 51:111–125
- Bergh Ø, Borsheim KY, Bratbak G, Heldal M (1989) High abundance of viruses found in aquatic environments. *Nature* 340:467–468
- Berninger UG, Finlay BJ, Kuuppo-Leinikki P (1991) Protozoan control of bacterial abundances in freshwater. *Limnol Oceanogr* 36:139–147
- Billen G, Joiris C, Wijnant J, Gillain G (1980) Concentration and microbiological utilisation of small organic molecules in the Scheldt estuary, the Belgian coastal zone of the North Sea and the English Channel. *Estuar coast mar Sci* 11:279–294
- Bruni V, Acosta Pomar MLC, Giuffrè G (1990) Picoplankton and picophytoplankton in a brackish environment (Lake of Ganzirri-Messina). *Rapp Comm int Mer Médit* 32(1): 137
- Campbell L, Vaulot D (1993) Photosynthetic community structure in the subtropical North Pacific Ocean near Hawaii (station ALOHA). *Deep Sea Res* 40:2043–2060
- Caron DA, Pick FR, Lean DRS (1985) Chroococcoid cyanobacteria in Lake Ontario: vertical and seasonal distributions during 1982. *J Phycol* 21:171–175
- Caron DA, Ee Lin Lim, Miceli G, Waterbury JB, Valois FW (1991) Grazing and utilization of chroococcoid cyanobacteria and heterotrophic bacteria by protozoa in laboratory cultures and a coastal plankton community. *Mar Ecol Prog Ser* 76:205–217
- Chisholm SW, Olson RJ, Zettler ER, Goericke R, Waterbury JB, Welschmeyer NA (1988) A novel free-living prochlorophyte abundant in the oceanic euphotic zone. *Nature* 334:340–343
- Ducklow HW, Purdie DA, Williams PJLeB, Davies JM (1986) Bacterioplankton: a sink for carbon in a coastal marine plankton community. *Science* 232:865–867
- Edenborn HM, Litchfield CD (1987) Glycolate turnover in the water column of the New York Bight apex. *Mar Biol* 95: 459–467
- Egan B, Floodgate GD (1985) Biological studies in the vicinity of a shallow-sea tidal mixing front. II. The distribution of bacteria. *Phil Trans R Soc Lond B* 310:435–444
- El Hag AGD, Fogg GE (1986) The distribution of coccoid blue-green algae (cyanobacteria) in the Menai Straits and the Irish Sea. *Br Phycol J* 21:45–54
- Fogg GE (1986a) Picoplankton. *Proc R Soc Lond B* 228:1–30
- Fogg GE (1986b) Picoplankton. In: Megusar F, Gantar M (eds) Perspectives in microbial ecology. Slovene Society for Microbiology, Ljubljana, p 96–100
- Fogg GE (1987) Marine planktonic cyanobacteria. In: Fay P (ed) *The Cyanobacteria*. Elsevier, Amsterdam, p 393–414
- Fogg GE (1991) The phytoplanktonic ways of life. *New Phytol* 118:191–232
- Fogg GE, Bajpai SP (1988) Temperature effects on natural phytoplankton populations. In: Round FE (ed) *Algae and the aquatic environment*. Biopress, Bristol, p 197–204
- Fogg GE, Calvario-Martinez O (1989) Effects of bottle size in determinations of primary productivity by phytoplankton. *Hydrobiologia* 173:89–94
- Fuhrman J (1987) Close coupling between release and uptake of dissolved free amino acids in seawater studied by an isotope dilution approach. *Mar Ecol Prog Ser* 37:45–52
- Giovannoni SJ, Britschgi TB, Moyer CL, Field KG (1990) Genetic diversity in Sargasso Sea bacterioplankton. *Nature* 345:60–63
- Glibert PM, Kana TM, Olson RJ, Kirchman DL, Alberte RS (1986) Clonal comparisons of growth and photosynthetic responses to nitrogen availability in marine *Synechococcus* spp. *J exp mar Biol Ecol* 101:199–208
- Glibert PM, Ray RT (1990) Different patterns of growth and nitrogen uptake in two clones of marine *Synechococcus* spp. *Mar Biol* 107:273–280
- Glover HE, Prézélin BB, Campbell L, Wyman M, Garside C (1988) A nitrate-dependant *Synechococcus* bloom in surface Sargasso Sea water. *Nature* 331:161–163
- Goldman JC, Caron DA (1985) Experimental studies on an omnivorous micro-flagellate: implications for grazing and nutrient regeneration in the marine microbial food chain. *Deep Sea Res* 32:899–915
- Gray JS, Field JG, Azam F, Fenchel T, Meyer-Reil LA, Thingstad F (1984) The role of free bacteria and bacterivory. In: Fasham M (ed) *Flows of energy and materials in marine ecosystems*. Plenum Press, New York, p 707–723
- Hagström Å, Azam F, Andersson A, Wikner J, Rassoulzadegan F (1988) Microbial loop in an oligotrophic pelagic marine ecosystem: possible roles of cyanobacteria and nanoflagellates in the organic fluxes. *Mar Ecol Prog Ser* 49:171–178
- Happley Wood CM (1991) Temporal and spatial patterns in the distribution and abundance of pico, nano and micro-phytoplankton in an upland lake. *Freshwater Biol* 26: 455–480
- Heldal M, Bratbak G (1981) Production and decay of viruses in aquatic environments. *Mar Ecol Prog Ser* 72:205–212
- Hutchinson GE (1961) The paradox of the plankton. *Am Nat* 95:137–145
- Johnson PW, Sieburth JMcN (1979) Chroococcoid cyanobacteria in the sea: a ubiquitous and diverse phototrophic biomass. *Limnol Oceanogr* 24:928–935
- Johnson PW, Xu H, Sieburth JMcN (1982) The utilization of chroococcoid cyanobacteria by marine protozooplankters but not by calanoid copepods. *Annls Inst océanogr, Paris* 58(S):297–308
- Kennaway GMA (1989) The population biology of freshwater picoplankton. PhD thesis, University of Wales
- Kudoh S, Kanda J, Takahashi M (1990) Specific growth rates and grazing mortality of chroococcoid cyanobacteria *Synechococcus* spp. in pelagic surface waters in the sea. *J exp mar Biol Ecol* 142:201–212
- Lande R, Li WKW, Horne EPW, Wood AM (1989) Phytoplankton growth rates estimated from depth profiles of cell concentration and turbulent diffusion. *Deep Sea Res* 36: 1141–1159
- Li WKW, Lewis MR, Lister A (1991) Picoplankton in the Gulf of Policastro. *Signal & Noise: Individual Particle Analysis in Aquatic Sciences* 4(2):3
- Li WKW, Wood AM (1988) Vertical distribution of North Atlantic ultraphytoplankton: analysis by flow cytometry

- and epifluorescence microscopy. *Deep Sea Res* 35: 1615–1638
- Lochte K, Turley CM (1985) Heterotrophic activity and carbon flow via bacteria in waters associated with a tidal mixing front. In: Gibbs PE (ed) *Proc 19th Eur Mar Biol Symp*. University Press, Cambridge, p 73–85
- Lynch M, Gabriel W, Wood AM (1991) Adaptive and demographic responses of plankton populations to environmental change. *Limnol Oceanogr* 36:1301–1312
- Marchant HJ, Davidson AT, Wright SW (1987) The distribution and abundance of chroococcoid cyanobacteria in the Southern Ocean. *Proc NIPR Symp Polar Biol* 1:1–9
- Maugeri TL, Acosta Pomar MLC, Bruni V, Salomone L (1992) Picoplankton and picophytoplankton in the Ligurian Sea and Straits of Messina (Mediterranean Sea). *Botanica mar* 35:495–502
- Murphy LS, Haugen EM (1985) The distribution and abundance of phototrophic ultraplankton in the North Atlantic. *Limnol Oceanogr* 30:47–58
- Nagata T (1988) The microflagellate-picoplankton food linkage in the water column of Lake Biwa. *Limnol Oceanogr* 33:504–517
- Neuer S (1992) Growth dynamics of marine *Synechococcus* spp. in the Gulf of Alaska. *Mar Ecol Prog Ser* 83:251–562
- Pasciak WJ, Gavis J (1974) Transport limitation of nutrient uptake in phytoplankton. *Limnol Oceanogr* 19:881–888
- Proctor LM, Fuhrman JA (1990) Viral mortality of marine bacteria and cyanobacteria. *Nature* 343:60–62
- Purcell EM (1977) Life at low Reynolds number. *Am J Phys* 45: 3–11
- Raven JA (1986) Physiological consequences of extremely small size for autotrophic organisms in the sea. *Can Bull Fish Aquat Sci* 214:1–70
- Shapiro LP, Guillard RLR (1986) Physiology and ecology of the marine eukaryotic ultraplankton. *Can Bull Fish Aquat Sci* 214:371–389
- Sheldon RW, Rassoulzadegan F, Azam F, Berman T, Bezanson DS, Bianchi M, Bonin D, Hagström Å, Laval-Peuto M, Neveux J, Raimbault P, Rivier A, Sherr B, Sherr E, Van Wambeke F, Wikner J, Wood AM, Yentsch CM (1992) Nano- and picoplankton growth and production in the Bay of Villefranche-sur-Mer (NW Mediterranean). *Hydrobiologia* 241:91–106
- Sherr BF, Sherr EB (1984) Role of heterotrophic protozoa in carbon and energy flow in aquatic ecosystems. In: Klug MJ, Reddy CA (eds) *Current perspectives in microbial ecology*. Am Soc Microbiol, Washington, DC, p 412–423
- Sherr EB, Sherr BF, Albright LJ (1987) Bacteria: link or sink? *Science* 235:88–89
- Sieburth JMcN (1984) Protozoan bacterivory in pelagic marine waters. In: Hobbie JE, Williams PJeB (eds) *Heterotrophic activity in the sea*. Plenum Press, New York, p 405–444
- Sieburth JMcN, Davis PG (1982) The role of heterotrophic nanoplankton in the grazing and nurturing of planktonic bacteria in the Sargasso and Caribbean Seas. *Annl Inst océanogr, Paris* 58(S):285–296
- Silver MW, Gowing MM, Davoll PJ (1986) The association of photosynthetic picoplankton and ultraplankton with pelagic detritus through the water column (0–2000 m). *Can Bull Fish Aquat Sci* 214:311–341
- Smith REH, Geider RJ, Platt Y (1984). Microplankton productivity in the oligotrophic ocean. *Nature* 311:252–254
- Sournia A (1982) Form and function in marine phytoplankton. *Biol Rev* 57:347–394
- Stockner JG (1988) Phototrophic picoplankton: an overview from marine and freshwater systems. *Limnol Oceanogr* 33: 765–775
- Stockner JG, Antia NJ (1986) Algal picoplankton from marine and freshwater ecosystems: a multidisciplinary perspective. *Can J Fish Aquat Sci* 43:2472–2503
- Suttle CA, Fuhrman JA, Capone DG (1990) Rapid ammonium cycling and concentration-dependent partitioning of ammonium and phosphate: implications for carbon transfer in planktonic communities. *Limnol Oceanogr* 35:424–433
- Takahashi M, Koike I, Iseki K, Bienfang PK, Hattori A (1982) Phytoplankton species' responses to nutrient changes in experimental enclosures and coastal waters. In: Grice GD, Reeve MR (eds) *Marine mesocosms*. Springer-Verlag, New York, p 333–340
- Taylor AH, Joint I (1990) A steady-state analysis of the 'microbial loop' in stratified systems. *Mar Ecol Prog Ser* 59:1–17
- Van Es FB, Meyer-Reil LA (1982) Biomass and metabolic activity of heterotrophic marine bacteria. *Adv Microb Ecol* 6:111–170
- Van Wambeke F, Bianchi MA (1985a) Bacterial biomass production and ammonium regeneration in Mediterranean sea water supplemented with amino acids. 1. Correlations between bacterial biomass, bacterial activities and environmental parameters. *Mar Ecol Prog Ser* 23:107–115
- Van Wambeke F, Bianchi MA (1985b) Bacterial biomass production and ammonium regeneration in Mediterranean sea water supplemented with amino acids. 2. Nitrogen flux through heterotrophic microplankton food chain. *Mar Ecol Prog Ser* 23:117–128
- Vaulot D, Partensky F (1992) Cell cycle distributions of prochlorophytes in the north western Mediterranean Sea. *Deep Sea Res* 39:727–742
- Wikner J, Hagström Å (1988) Evidence for a tightly coupled nanoplanktonic predator-prey link regulating the bacterivores in the marine environment. *Mar Ecol Prog Ser* 50: 137–145
- Wood AM (1990) Ultraphytoplankton community structure and evolution in the seasonal thermocline. In: Hattori T, Ishida Y, Maruyama Y, Morita RY, Uchida A (eds) *Recent advances in microbial ecology*. Proc 5th Int Symp Microbial Ecology, Japan Scientific Societies Press, p 336–340
- Wood AM, Neveux J, Sondergaard M, Yacobi YZ (in press) Vertical distribution of prochlorophytes, *Synechococcus*, eucaryotic ultraphytoplankton, and associated pigments in a warm-core eddy in the eastern Mediterranean Sea. *Deep Sea Res*
- Wood AM, Rai H, Garnier J, Kairesalo T, Gresens S, Orive E, Ravail B (1992) Practical approaches to algal excretion. *Mar microb Food Webs* 6:21–38
- Wood AM, Townsend D (1990) DNA polymorphism within the WH7803 serogroup of marine *Synechococcus* spp. (Cyanobacteria). *J Phycol* 26:576–585