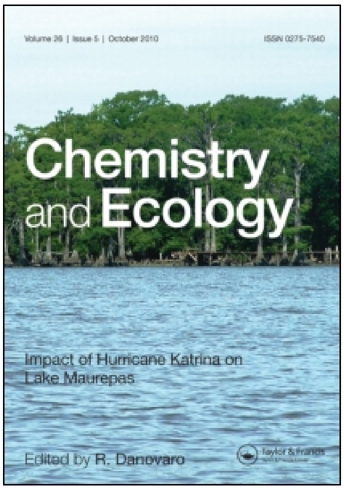

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INTERACTION BETWEEN NUTRIENT AND PREDATOR LIMITATION OF PRODUCTION IN THE MARINE EUPHOTIC ZONE

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Nutrient limitation of phytoplankton growth in nature is a complex phenomenon. The timing of nutrient limitation is a product of matching of algal growth with abiotic and/or biotic events regenerating nutrients, and mismatching with predator activity. The extent of production is governed by the concentration of atomic constituents which, in turn, is a function of the rapidity and quantity of nutrient regeneration by heterotrophs. Excess phytoplankton production over heterotroph demand is lost from the euphotic zone by sinking and from the ecosphere by sedimentation. Phytoplankton growth is therefore always limited by the size and activity of the regenerative food web, either directly through predation, or indirectly by inadequate nutrient regeneration. The open water column is a habitat deplete environment for metazoa, incapable of supporting simultaneous high predator and prey densities. Because of the incompatibility of the temporal and spatial scales of microbial and metazoan processes, and the presence of micro-habitats which can support a full recycling food web on microbial scales, the microbial loop is an important component of euphotic zone ecology. The total marine ecosystem runs at a nutrient sufficient level with nutrient deplete and replete phases dependent on matching of production with predation throughout the food web and subject to abiotic events. Man's release of N and P into coastal waters, if coupled with an increased incidence of mismatch resulting from climatic variation induced by the "greenhouse effect", could have catastrophic effects on marine ecosystems.

KEY WORDS Primary production, nutrients, predation.

INTRODUCTION

It is often stated that marine primary production (Flynn, 1988a) is nutrient limited. Much of the evidence for nutrient limitation comes from the chemical analysis of bulk volumes of sea water, usually only measuring a few nutrients which are deemed to be the most important, and from experimental tests of the physiology of the phytoplankton using questionable methods (Flynn, 1988b).

Nutrient limitation is most likely in stratified water columns and the root cause usually suggested is an absence of physical events, such as upwelling, which would replenish the nutrient stock in the euphotic zone. This thesis has two flaws. One is that large scale physical events cannot simply "fertilize" the upper waters because the nutrient-rich upwelling displaces the surface water from its geographical location (analogous in terrestrial terms to ploughing up a field rather than scattering fertilizer on an established crop). The second flaw is that nutrient cycling is a biologically mediated event in which the role of mass transport is redistribution. If phytoplankton become nutrient limited then the rate limiting step is primarily that of regeneration of nutrients by the activity of other organisms, especially those in the euphotic zone.

The presence of physical factors is of secondary importance for the redistribution of what has been regenerated in the subeuphotic zone. There can be no such condition as simple nutrient limitation brought about solely by the absence of major physical events except in an artificial environment containing one organism (such as a laboratory culture). The term "new production", used to describe production using nutrients brought to surface waters by upwelling as opposed to that using nutrients regenerated in the euphotic zone, is anomalous. Although some production may indeed result from the input of "new" nutrients (from N_2-fixation or agricultural runoff), most nutrients are regenerated in the water column. "New" production and recycling are coupled by a nutrient cycle of long duration in deep waters (Eppley *et al.*, 1983).

Despite the fact that almost all nutrients are ultimately recycled, and hence linked to total biological activity, explanations for the occurrence of nutrient limitation are rarely sought. Over geological time the balance of nutrients can be expected to reflect biological activity with an excess being lost by inefficient regeneration. This is the basis of Redfield's (1958) classic work. The important question is perhaps why phytoplankton production is *not* predator limited rather than why it is nutrient limited. Until we answer the first question our understanding of marine ecology will be incomplete.

This paper will take a fresh look at these issues: a) how does nutrient limitation occur?; b) why should production be limited to the level that it is?; c) is the survival of nutrient limited organisms put at risk?; d) how may man's activities alter the operation of the ecosystem?

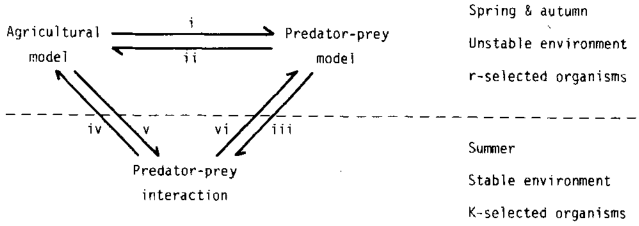
1. THE AGRICULTURAL AND PREDATOR–PREY MODELS

Two models have been proposed for the control of phototrophic production (Cushing, 1975). The agricultural model describes a system in which production is nutrient limited. In the sea these nutrients are usually considered to be dissolved inorganic N (DIN) or P (DIP). The predator-prey model argues for predator limitation of phytoplankton growth, at least during the spring bloom in temperate waters. Later production may become nutrient limited but the timing will depend on the availability of regenerated nutrients (Cushing, 1963). Predators not only reduce phytoplankton numbers but regenerate the nutrients (as do all heterotrophs) required by the algae; heterotrophic activity and nutrient regeneration are inextricably linked.

Although the agricultural model is rarely formulated in these terms, nutrient limitation is commonly the intuitive basis of many models and for explanations of the distribution and magnitude of marine production (for examples see Carpenter and Capone 1983, Hobbie and Williams 1982, Nihoul 1986). The models of Legendre *et al.* (1986) (phytoplankton production is maximal at locations of physical discontinuity or at energy gradients, such as fronts and thermoclines) imply nutrient-algal production interaction with physical phenomena with no direct involvement of predators. Despite Cushing's (1975) and Cushing and Dickson's (1976) arguments that increased levels of production at upwellings are *not* solely due to "fertilization", but more to the support of a continuous "temperate spring bloom", the nutrient mechanism is popularly used to explain enhanced production.

The implications of the agricultural model appear elsewhere. Goldman *et al.* (1987) say that the "rate by which nutrients cycle in the (microbial) loop is set by the maximum growth rate of the phytoplankton". A contrasting view would be that the rate of phytoplankton growth is dependent on the rate of regeneration of atomic constituents by other members of the food web which, as this seems to be the rate limiting step, appears more apt.

As a compromise, an alternative model can be offered which involves the predator-prey and agricultural models at extremes, and a predator-prey interaction component (Figures 1 and 2). By the predator-prey interaction model, production is limited either by excess predation or by inadequate predation resulting in nutrient limitation due to a lack of regenerated nutrients. In such systems the flux of key components will be high and concentrations low because of efficient interaction between organisms. There is also an interaction between phototrophic and heterotrophic microbial production, in which both may compete for common nutrients although the latter is ultimately dependent on the former of energy (Flynn, 1988b). Flynn (1988a) argues that the term "primary production" in marine ecology should include both phototrophic and microheterotrophic components.



Transition	Production	Dominant N-source	Limiter of production
i	$P < h_1 >= h_2$	NO_3^-	predator
ii	$P > h_1 <> h_2$	NO_3^-	nutrient
iii	$P >= h_1 >= h_2$	NH_4^+ & DON	carrying capacity of ecosystem
iv	$P > h_1 <> h_2$	NH_4^+ & DON	nutrient
V	$P =< h_1 >= h_2$	NH_4^+ & DON	carrying capacity of ecosystem
vi	$P < h_1 >= h_2$	NH_4^+ & DON	predator

Figure 1 Predator–prey interaction. Growth of phototrophs (P) may be limited by heterotrophic predators (h_1) or by nutrients; growth of predators h_1 may be limited by h_2 and so on throughout the food chain (see Figure 2). The dominant N-source is usually either NO_3^-, regenerated in the subeuphotic zone and redistributed by physical factors, or NH_4^+ and dissolved organic N (DON) regenerated in the euphotic zone. The "carrying capacity of the ecosystem" is set by the total amount of atomic constituents available and requirements for habitats (niche availability and spatial interactions). Over geological time these factors will interact; see text.

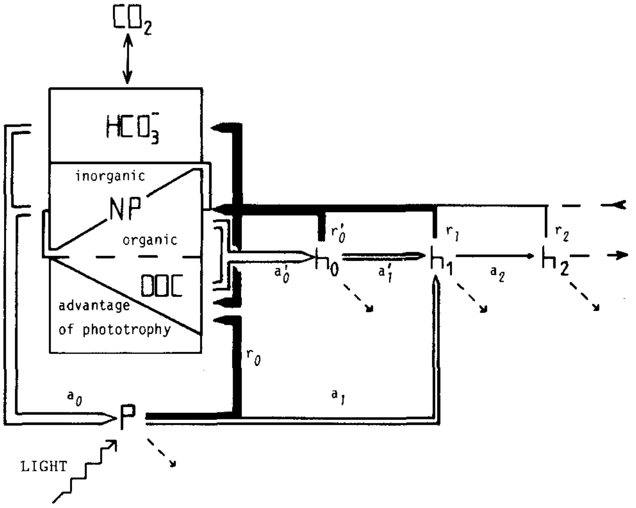


Figure 2 Suggested interaction between phototrophic and heterotrophic microbial production and interaction with activities of other organisms. Nutrients are inorganic C, dissolved organic C (DOC), and inorganic and organic nitrogenous and phosphorus compounds (NP). The biota comprises phototrophs (P), free bacteria (h_0) and other heterotrophs ($h_1, h_2 \cdots$) with assimilatory processes (a) and regenerative/release processes (r). Sedimentation ($\rightarrow$) of organisms whose populations starve and die may occur because predation fails to keep it in check, and also of material associated with feeding (debris and faeces). Decay mediated processes, performed by attached bacteria, are not shown; these organisms assimilate organic matter from various release processes, regenerating nutrients and are preyed upon by various heterotrophs. As levels of DOC increase (mostly produced by phototrophs), the advantage of phototrophy lessens and bacterial activity (a_0') increases. Both phototrophs (P) and bacteria (h_0) produce biomass at the expense of dissolved compounds, but because organic nutrients are a subset of DOC there may be no competitive advantage for phototrophs in evolving mechanisms for the use of organic nutrients (see Flynn 1988b). Phototrophic production (P) becomes nutrient limited if $a_0 > (r_0 + r_1 + r_2 \cdots) - a_0'$, this in turn will be affected by differential predation by h_1 and P (a_1) and on h_0 (a_1').

2. HABITAT LIMITATION

For predator-prey interaction to operate at maximum efficiency, the organisms must live in close proximity. This is especially important if the generation times of the organisms are significantly different. If they are not in close proximity, and efficiency is lost (e.g. mismatching occurs and death due to nutrient deprivation or starvation results in the sinking of whole organisms), then there will be a loss of material from the euphotic zone which will require physical intervention to return the atomic constituents back into surface waters. Matching, the coincidence of predator growth with that of the prey, is an important requirement for efficient predator–prey interaction.

Phytoplankton production, provided that there is sufficient energy (light and heat) and nutrients for it to start, may be considered as always limited ultimately by the activity of other members of the ecosystem, be they predators or other regenerators. Nutrient limitation of phototrophic production can arise in two environments;

1) in a habitat-sufficient environment where growth (timing and/or extent) of

other populations, especially that of predators of the phytoplankton, is not limited by spatial needs or by climatic events. Addition of the limiting nutrient would be expected to raise total production.

2) in a habitat-limited environment in which, for example, predators cannot attain a population large enough and/or quickly enough to limit the growth of their phototrophic prey before nutrient limitation occurs. Addition of the limiting nutrient would result in inefficiency and a loss of particulates from the euphotic zone.

The open water column is a dangerous environment for organisms which are hunted by the use of visual and compression wave detection methods typical of vertebrates and invertebrates (Marshall, 1979), or by chemosensory detection as used by microflagellates (Sibbald *et al.*, 1987) and copepods (Gill and Poulet, 1988). One explanation for shoaling is that it creates a pseudo habitat for the individual decreasing the likelihood of predation (Brock and Riffenburgh, 1960). In the absence of physical habitats shoaling provides a mechanism for maintaining high population densities with the associated advantages of higher possible recombination of genetic data.

Predation in the water column is often by shoaling organisms (coelenterates, crustacea, cephalopods, fish) or by colonial forms such as Thaliaceans, although "shoaling" of plankton may be as likely an accident of fate as an active process of swimming together. Predation and therefore nutrient regeneration by these organisms is inevitably discontinuous, increasing the likelihood of alternate periods of nutrient and predator limitation of their prey. The effect this may have on phototrophic production may be minimized by the slower growth rates and nutrient accumulation capabilities (sustaining growth until another nutrient pulse is encountered—Collos 1986) typical of *K*-select species.

The effect of physical habitats on the biota is obvious to fishermen and divers who know that the density and diversity of life around a shipwreck, or submarine outcrop, is higher than that away from it. In the Norfolk Broads (U.K.), where phosphate eutrophication has led to algal blooms, tests are being conducted on the use of specially constructed havens for cladocerans at risk from fish predation in the open waters; the result is the effective control of algal growth by cladoceran grazing (Moss, 1987).

Turbulence of the water column (such as Langmuir cells) may create microhabitats for microbes by bringing particles together, and turbulence is also likely to affect sensory detection by predators. Convergent fronts are areas where debris and planktonic species collect. Le Fèvre (1986) questions the popular view that increased biomass (suggesting elevated rates of production) results from the physical input of nutrients, but rather that at least a proportion of the organisms have grown in the surrounding area and have been brought together at the front.

The sea-surface microlayer, and other fluid/fluid and fluid/solid boundaries, provides a niche because of the accumulation of particles (living and dead), and resultant organic materials (Henrichs and Williams 1985) at the interface. Such material at the sea surface supports populations of bacteria, algae and zooplankton far in excess of that found in the water just below (Sieburth 1971, Sieburth *et al.*, 1976). Even so, Paerl and Carlton (1988) suggest that the absence of suitable habitats may explain why levels of N_2-fixation by cyanobacteria in open waters are so low.

Biological activity also creates habitats for microbes. The activity of pelagic

Urochordates results in a conditioning of the water column creating aggregates of small particles (Pomeroy and Deibel 1980), and bacterial activity on algal debris is also associated with aggregate formation (Newell *et al.*, 1981). The formation of aggregates and flocs makes material previously too small for capture available to some zooplankton but also provides a habitat for attached microbes and their associated predators. Complete microbial foodwebs (the "microbial loop"—Azam *et al.*, 1983) of phototrophs, microheterotrophs (bacteria) and microbivores attached to aggregates of marine "snow" have been suggested (Pomeroy and Deibel, 1980; Goldman, 1984). Common methods of investigation take no account of such community structure. Kranck and Milligan (1988) warn that methods used to sample natural populations destroy such delicate assemblages. A scientists will routinely shake a flask or bottle in order to break up clumps and to ensure that the sample represents an average component of the population. Filter fractionation techniques will also break aggregates and flocs. The fact that the organisms may be stressed by doing so is rarely noted.

With the passing of successive generations and resulting evolution, ecological niche and habitat needs may be expected to interact with food/nutrient supply. In an environment in which phototrophic production is inadequate to support the food web which could in theory develop there, the spatial requirements of the predators may increase in order to ensure that sufficient food will be within range. The predator's ecological niche may widen, their diet becoming less specialized. Such changes would only be limiting when energy requirements needed to locate and capture food in competition with other organisms exceed that obtained from its assimilation. Is the low biological activity in some waters a consequence of low phototrophic production, or are levels of this production low because past predation has been inadequate resulting in a loss of particulates, and hence of atomic constituents, out of the euphotic zone? This condition applies throughout the nutrient cycle. If any step occurs at a rate which exceeds that of the next then there is the possible loss of atomic constituents from the ecosystem, possibly for ever if it enters the sediment undegraded. The present quasi-equilibrium is the result of millions of years of interaction between the biota and the environment.

The open water column appears to be a habitat-deplete environment for metazoa and, because mismatching of predator and prey is likely, food webs including metazoa may be inefficient. Such mismatch is even more likely between metazoan predators and microbial prey because of the difference in generation times. Metazoan activity also produces particulates (debris and faeces) which sink out of surface waters. It is because these processes of mismatch and inefficient metazoan activities result in the loss of atomic constitutents from surface waters that upwelling is so important in determining the distribution of phytoplankton. If there was no loss of atomic constituents there would be no dependence on upwelling; physical processes returning nutrients to surface waters are a prerequisite for continued metazoan production.

Physical processes, through the redistribution of atomic constituents in both time and space, will play a major part in the control of the extent of production at any one location. The return of nutrients to surface waters from the immediate vicinity may be seasonal in enclosed seas, but in major upwellings the water bearing nutrients may have travelled many thousands of kilometres through the abyss over periods of tens or even hundreds of years and may have last entered phytoplankton biomass at a different geographical location. During this time, water masses from different areas become mixed and the concentration of nutrients will tend to become uniform. This alone is likely to result in areas which, in theory could support a high biomass, being supplied with only a limiting supply of nutrients.

3. MATCH AND MIS-MATCH: CONTROL OF PRODUCTION BY THE ECOSYSTEM

A mature ecosystem can function only in an environment which is free from major physical perturbation. In such systems net production will be zero, balanced by respiration. In areas of perturbation, opportunistic species (*r*-select organisms) predominate, diversity of life is low, and predator–prey interaction is likely to be less efficient. The highest net production is by *r*-select organisms growing in an immature ecosystem. Because plankton drift with the currents, those in mid-oceanic waters may be considered to be separated in time as well as in space from those at upwellings. A spatial transect from an upwelling to the centre of the ocean may be considered analogous to a temporal transect from early spring to late summer in temperate waters. This is the basis for Cushing and Dickson's (1976) explanation for high productivity at upwellings. The traditional food web (e.g. microphytoplankton, copepods and fish), which we could call the "metazoan loop", has the microbial loop as a subset. Whereas the microbial loop may operate independently of the metazoan loop, the reverse is not possible.

As upwelling water containing nutrients regenerated in deep water (Fogg, 1982) nears the surface, net photosynthesis becomes possible (Cushing, 1975). The microphytoplankton, typically diatoms, begin to grow in the absence of effective predation. The tight coupling of microbial loop production is evidenced by the fact that the larger algae bloom at all, else surely the ubiquitous picophytoplankton which are held to be so efficient at nutrient uptake and photosynthesis at low light (Fogg, 1986) would outcompete them. Depending on the mismatch between the growth of microalgae and of their metazoan predators, the algae may or may not become nutrient limited. Such mismatch is less likely in an upwelling as the role of the climate in matching is less important than for the temperate spring bloom.

The interplay required for predator–prey interaction is complicated by the inflexible timing of metazoan reproductive cycles in comparison with that of algae which bloom as soon, or as late, as climatic and water conditions dictate. The larger microalgae (e.g. diatoms) which dominate temperate spring blooms are predated by larger zooplankton (e.g. copepods). These predators are longer lived and have a long reproductive cycle (say 40 d—Marshall and Orr, 1972) relative to that of their prey (1–3 d), compensated by the high fecundity of the predator. The consequence of these facts is that once the copepods have reproduced to a population sufficient to limit microalgal populations, and because copepods appear to be able to withstand periods of starvation between grazing (Cowey and Corner, 1963; Marshall and Orr, 1972), the post-spring bloom microphytoplankton population may remain predator limited for the duration of the production cycle unless copepod predation by fish is extreme.

The match and mismatch of algal and copepod growth is discussed in considerable detail by Cushing and Dickson (1976), and appears to depend on factors such as climatic conditions. For example, between 1948 and 1972 the timing of the spring bloom in the NE Atlantic shifted from March to April with the result that copepod populations, whose reproductive cycle is less flexible, mismatched repeatedly, leading to a fall in copepod numbers (Cushing and Dickson, 1976). It would be interesting to know if nutrient deprivation of algae was more frequent in those years than in years of closer matching. Climatic events such as wind velocity affecting depth of mixing, hours of sunlight, and especially shifts in cold and warm water currents affecting nutrient and predator distributions, can have dramatic consequences (Cushing and Dickson, 1976; Southward, 1980). However, the most robust and successful populations are the most fecund which, whilst expensive energetically, are able to survive through years of particularly bad mismatch. A failure of predators to evolve a match with algal blooms at fortnightly releases of nutrients at fronts is suggested by Le Fèvre (1986). If this is so, then either we are ignorant of some factor, or there is no evolutionary advantage to potential predators in evolving a generation time to match this occurrence which takes place on a small scale compared with the distribution range of the predators.

The shoaling of metazoan predators results in a patchy distribution of predator and prey which in turn results in poor predator–prey interaction in the metazoan loop. In open waters, the metazoan loop can probably exist only in an immature ecosystem (usually associated with the occurrence of physical processes such as upwelling). Paradoxically, this probably increases metazoan production because it results in a greater probability of nutrient exhaustion of the prey, rather than predator limitation in the presence of surplus nutrients. It could be argued that, as predators may have to survive periods of starvation, the consumption of nutrient deprived prey with high C/N would not be disadvantageous as the extra C could be laid down as reserves. Poulet and Martin-Jézéquel (1983) suggest that copepods are attracted to large blooms of algae which leak free amino acids when they end exponential growth. Once grazing starts, the regenerated nutrients will be taken up rapidly by nutrient deprived microbes; the concentration of nutrients in bulk volumes of water may remain low even though the algae are not then deprived of nutrients (see Figure 3; Flynn and Fielder, 1989).

If the efficient inter-relationships between organisms, needed to ensure that nutrient regeneration and utilization are closely coupled, do not develop, then the availability of most forms of regenerated nutrients, organic as well as inorganic, for the growth of phytoplankton may become crucial to avoid nutrient limitation (see Flynn and Butler, 1986). Superfluous grazing by copepods (breakage of algal cells with inefficient ingestion and digestion) is important as the liberation of organics and particles support other food webs leading to eventual nutrient regeneration beyond that possible by the copepods alone (Cushing and Vucetic, 1963). If this did not happen then the relatively dense whole algal cells would sink out of the euphotic zone at death.

Whilst a proportion of the particulate organic matter produced by the immature ecosystem (dead algae, copepod faecal pellets and other debris) will be lost from the euphotic zone by sinking, there is reason to suspect that such loss is less in more stable waters with more mature ecosystems, or where mismatch of predator and prey is less extreme. Faecal pellets from copepods are not as heavy as when the copepods are not indulging in superfluous feeding, and so they sink slowly (Dagg and Walser, 1986). Populations of bacteria emerge on the pellets

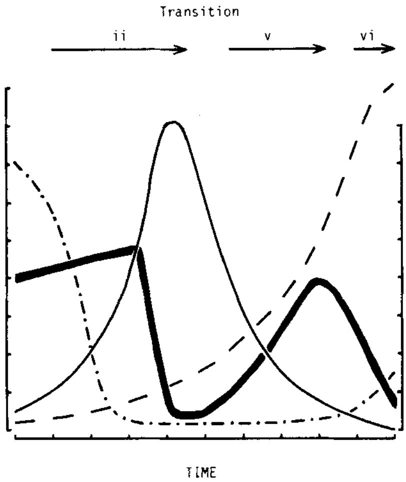


Figure 3 An illustration of predator–prey interaction in a simple two component ecosystem. In a laboratory experiment, a phototroph (——) grew using ammonium (—·—) as the sole N-source; the microflagellate predator (– – –) regenerated ammonium. The ratio of intracellular glutamine/glutamate, GLN/GLU, (═══) was used as an index of the nutrient status of the phototroph. The delay (mismatch) in response of the predator to increased prey resulted in nutrient limitation of the phototroph (transition ii; see Figure 1) as ammonium was exhausted; GLN/GLU fell rapidly indicating nitrogen limitation of phototrophic growth. As predator numbers increased, ammonium was regenerated but because uptake by the phototrophs was rapid an increase in levels of ammonium was not detected. However GLN/GLU increased, indicating the improved nutrient status of the phototrophs as predator–prey interaction developed (transition v; Figure 1). In the absence of a higher predator, predation of the phototrophs increased, eventually leading to predator limitation (transition vi; Figure 1) of the phototrophs; the level of ammonium increased as regeneration exceeded demand. GLN/GLU decreased as the phototroph population was eliminated. Units are arbitrary. Adapted from Flynn and Fielder (1989).

and on other particles, regenerating nutrients and comprising parts of other food webs. Bacterial activity possibly makes some components more readily available to zooplankton digestion. For metazoa, the existence of suitably sized particles is important, rather than the production rates at each level of the microbial loop and there may be little difference in the nutritional value of microalgae and detritus for zooplankton (Cowey and Corner, 1963). Successive metazoan activities clear the water column, releasing faeces and other debris associated with feeding, but however efficient this process is, there will inevitably be a loss from the euphotic zone by sinking or export by nekton.

As the ecosystem develops towards a climax state, in the temperate summer and in mid-oceanic waters, there is a shift in dominance to the smaller plankton. During this development there is also a shift in dominance from inorganic to organic dissolved nutrients (Butler *et al.*, 1979; Jackson and Williams, 1985); inorganic nutrients are cycled rapidly and competition between phototrophs and bacteria for common nutrients may occur (Flynn, 1988b; Figure 2). Free bacteria use dissolved organic carbon (DOC) released by phytoplankton (Lancelot and Billen, 1985) as a source of energy. The water column is stable with little transference across the thermocline or pycnocline, and components of the microbial loop can exist in isolation from larger organisms (Williams, 1984; Fogg, 1986). Regeneration of nutrients within the microbial loop must be rapid if nutrient limitation is not to occur.

In contrast with the diatom–copepod relationship, the difference between the generation times of ciliates (say 0.5 d—Turley *et al.*, 1986), flagellates (0.5 d—Sieburth, 1984) and salps (say 2 d—Heron, 1972) which may graze the nano- and picophytoplankton (1–2 d—Joint and Pomeroy, 1986) as part of the microbial loop (Azam *et al.*, 1983) is generally small. This similarity can enable a closer coupling of predator–prey populations (Fenchel, 1982; Sieburth, 1984). These predators may graze on heterotrophic and phototrophic picoplankton (Goldman and Caron, 1985; Goldman *et al.*, 1985), especially as the activity of attached bacteria is associated with the formation of bacterio-particulate aggregates (Newell *et al.*, 1981). It would appear more appropriate to refer to such predators as microbivores rather than attempt to differentiate between herbivores (an outmoded term) and bacterivores. It is not clear if populations of bacteria are limited by nutrients or by predation with the population densities of bacteria representing threshold levels for clearance by predators (Albright *et al.*, 1987; Andersen and Fenchel, 1985; Andersson *et al.*, 1986; Pomeroy, 1984; Rassoulzadegan and Sheldon, 1986). The importance of Urochordates and of microflagellates (both predators of picoplankton) has probably been underestimated because the routine use of trawls destroys the organisms during sampling (Harbison and Gilmer, 1976; Goldman, 1984; Wiebe *et al.*, 1979).

Populations of microflagellates and their bacterial prey oscillate with a time scale of 4 d (Fenchel, 1982) so that phytoplankton may have to survive several days of nutrient deprivation. Because of the similarity between bacterial and bacteriovore C/N ratios, a greater proportion of regeneration may not occur until the bacterivores are themselves eaten. Nutrient limited algae have increased C/N and C/P ratios, so regeneration of N and P by their predators is also slower than when feeding on nutrient replete algae (Goldman *et al.*, 1987). Coccoid cyanobacteria, which live higher in the water column than the eukaryote picophytoplankton, may maintain growth at the expense of phycoerythrin used as a N-reserve (Fogg, 1986), whilst the eukaryotes live nearer the thermocline (Glover *et al.*, 1986) in Sieburth's (1987) "pseudobenthos" in which anoxic nutrient regeneration may occur within particles of marine "snow" in the oxygenated water column. Interaction within the microbial loop is clearly complex (Pengerud *et al.*, 1987) but because the organisms are so small, even if the system fails, there may be little significant loss of material from the euphotic zone attributable to such an ecosystem except by the activity of metazoa such as salps (Wiebe *et al.*, 1979).

Episodic events, such as the breaking of internal waves and even rainfall (Mopper and Zika, 1987) which provide an input of nutrients, may promote localized outbursts of algal growth (Glover *et al.*, 1988). The perturbation caused by metazoan activity and its associated respiration and regeneration of nutrients may also lead to enhanced phototrophic production, a process which then oscillates with other microbial activities, restarting the microbial loop. The existence of such communities is consistent with the C/N/P ratios reported by Goldman *et al.* (1979) for oceanic algae which suggests that, although living in an apparently nutrient-deplete environment, such algae are actually growing at near maximum rates.

Because of the efficiency of the microbial loop (Andersen and Fenchel, 1985;

Goldman and Caron, 1985) and its scale, which is incompatible with methods typically used in field studies (Goldman *et al.* 1981, Goldman, 1984; Harris, 1984), there will be a rapid flux of atomic constituents. The categorization of these mid oceanic waters as oligotrophic, by observation of very low levels of inorganic nutrients in bulk volumes, appears meaningless. By this criterion, any climax community will live in oligotrophic conditions, but it does not mean that the growth of individual organisms is limited by nutrient availability in a simple fashion.

4. PREDATOR–PREY INTERACTION AND MAN

The activity of Man has at least two possible major effects on eutrophic ecology, in addition to overfishing. One is the increase in nutrients, especially of nitrate and phosphate, entering coastal waters by way of runoff from intensive agriculture. The other is the increase in atmospheric CO_2 concentrations leading to the "greenhouse effect".

Claims of nutrient limitation of phytoplankton production may be taken to imply that addition of that nutrient will increase overall production. There do not appear to be any data with which to correlate nutrient availability and levels of metazoan production in such a simple fashion. Whilst a correlation may be found for levels of nutrients and CO_2 fixation, and between CO_2 fixation and fishery yield, there is no evidence that man could increase fish production by the addition of fertilizers to the oceans (Nixon and Pilso, 1983; Le Fèvre, 1986; see Post and McQueen, 1987). It is more probable that extra particulate organic matter derived from algae would be lost from the euphotic zone when death occurs and enrich the benthos. In situations where eutrophication occurs, the natural balance of nutrient sufficiency is disturbed. A large scale example of this is the southern North Sea where increased incidence of phytoplankton blooms, and subsequent mass mortality leading to localized deoxygenation of the water column, is thought to be due in part to increased input of nutrients (Milesi, 1987).

Blooms of *Phaeocystis* have become common in recent years, especially off the Belgian and Dutch coasts (Lancelot *et al.*, 1986), whilst a new problem has been encountered off Scandinavia with blooms of *Chrysochromulina* (previously an insignificant component of the plankton) during late spring 1988. How common such events have been in previous centuries we do not know. To some extent they may occur with a natural periodicity and perhaps only the use of modern communications and remote sensing by satellites indicates the full extent of blooms. What is apparent is that once conditions are right, the presence of larger amounts of N and P is likely to result in the formation of a larger biomass before nutrient limitation, or some other event such as self-shading or toxin production, intervenes. It is also possible that other chemicals released by Man may inhibit growth of less harmful phytoplankters or affect recruitment of predators.

Elevated levels of atmospheric CO_2 are of increasing concern; Brewer (1983) discusses the role of the oceans in the C-cycle. Can the biota respond by sinking the extra C, and can it do so quickly enough? The expected increase in temperature will in turn lead to changes in the climate and eventually in the movement of water masses. The stability of stratified water columns will also increase, thus restricting still further the exchange of nutrients into the euphotic zone. Another result will be that periods of mismatch of phytoplankton and metazoan predators leading to algal blooms may become more likely; climatic events have been proposed as significant in matching of production (Cushing and Dickson, 1976; Southward, 1980). Mismatching should result in the sinking of more C due to inefficient transfer of energy through the food chain. In the absence of increased nutrients, the size and frequency of blooms would be limited to similar levels to those at present. However, in coastal waters where eutrophication occurs, massive blooms may occur, leading to the conditions reported for the North Sea.

Coccolithophorids develop large blooms (Holligan *et al.,* 1983) but these organisms play an additional role in the C cycle because of the calcareous plates which cover the cells during part of the life cycle. Over geological time sedimentation of such organisms has resulted in the formation of limestones (Westbroek *et al.,* 1984). Coccolithophorids are also suggested to be major producers of dimethylsulphide (DMS), a volatile chemical which, on conversion to sulphates in the upper atmosphere, leads to the creation of cloud condensation nuclei and hence to cloud formation (Charlson *et al.,* 1987). At present we have insufficient data on the physiology of coccolithophorids to be able to predict how their growth may be affected by the greenhouse effect; whether calcification may be promoted and if DMS production will increase.

CONCLUSIONS

We now return to the questions posed in the introduction.

How does nutrient limitation occur; why does it occur at the observed level?

Given that nutrient limitation may be considered a consequence of inadequate predation, nutrient limitation of microbial production appears as much a consequence as a cause of limitation of metazoan production (if there is such a simple link). Shoaling of metazoa inevitably results in patchiness of nutrient regeneration. Such patchiness is further exaggerated by the incompatible temporal and spatial scales of microbial and metazoan production which result not only in mismatch of predator and prey but in mismatch of metazoan nutrient regeneration and microbial requirements. The euphotic zone appears barren with respect to habitat diversity for all but microbes. It is perhaps no coincidence that the microbial loop is of such importance in open water ecology for only on a microbial scale can a complete regenerative food web exist on a time scale compatible with algal growth dynamics.

Production runs at its present level because of two factors. One is that continued excess production over demand has resulted in the removal of atomic constituents into the sediments so that a sufficiency of nutrients now exists. The other factor is the averaging effect of the spatial and temporal redistribution of nutrients regenerated in deep water due to the physical flow of water around the planet.

Does nutrient limitation affect metazoan production adversely?; does it indicate a local surplus of supply over demand?

Mismatch of predator and prey is probably not a bad thing for the individual species. It is important to stress that the only "role" that any organism has is reproduction. It is not to support the growth of other organisms by supplying a source of food; that is a teleological argument. Clearly in order to maximize reproduction all available atomic constituents need to be assimilated by one species. That species will inevitably become nutrient depleted, or starved, but it is that very condition that often stimulates sexual reproduction or spore formation which coupled with maximum cell density, assures the greatest probability of survival of the species by genetic recombination.

The feeding of predators, from their standpoint, is more efficient in terms of energy gained by digestion exceeding that expended in capture when feeding on prey at high cell densities. In addition, the excess C in nutrient deprived prey may furnish the predator with an extra source of C needed for survival until the next patch of prey is encountered. However, if algal production became limited at higher cell densities and death occurred before predation, then anoxia in the subeuphotic zone and in sediments may cause the death not only of organisms responsible for nutrient regeneration but even of the resting stages of the algae themselves. This situation would be worse if the algae, such as some dinoflagellates (red tides) and prymnesiophytes, release toxins which directly kill metazoa.

How does human activity perturb this ecosystem?

The input of nutrients into coastal waters and the effect of global warming by the increased levels of the "greenhouse" gases (CH_4, and especially CO_2) may have catastrophic effects. Whether or not the biota respond quickly enough to counteract global warming, the result will probably follow the geological pattern of removing the excess atomic constituents to the sediments. This can only be achieved by an over-loading of the ecosystem and eutrophication will only exaggerate the outcome.

If recent blooms of phytoplankton in the North Sea are any indication of what is to come, then coastal marine ecology and, especially important for Man, the associated fisheries, may be devastated. It is too late to prevent at least some global warming, even if all fossil fuel combustion were to be replaced by other power sources (with all their associated problems), but at least steps might be taken to control the release of N and P into coastal waters so as to limit any mismatch in production of predator and prey.

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