Nitrogen Cycling in Coastal Marine Environments
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CHAPTER 2

Pelagic Primary Production in Nearshore Waters

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2.1 INTRODUCTION

Given an over-all plankton chemical composition of 6.6 carbon atoms per nitrogen atom (Redfield *et al.*, 1963), autotrophic nitrogen assimilitation in the pelagic environment must by and large follow planktonic photosynthesis. Actual measurements of nitrogen uptake by marine phytoplankton are too few to permit the construction of worldwide maps or tables analogous to those representing areas of high and low primary photosynthetic production (Koblentz-Mishke *et al.*, 1970; Ryther, 1969). Still, likely average daily or yearly nitrogen uptake rates in nearshore and offshore regions can be predicted, with reasonable precision, once photosynthetic rates have been gauged correctly. The introduction of isotope methods allowing rates of ammonium and nitrate uptake to be measured experimentally in the water column (Dugdale and Goering, 1967) was important, not because it made for better estimates of the global flux of nitrogen through the primary producers but rather because it opened a way into the unravelling of the various pathways by which nitrogen is made available to them.

The interpretation of nitrogen uptake measurements in coastal water is more complicated than in the open sea, because the origin of each of the major inorganic nitrogen sources or substrates (nitrate, ammonium, urea) is less easily established. At the same time, the need for understanding the pathways of nitrogen transport within coastal ecosystems is particularly pressing. It is now widely accepted that nitrogen, rather than phosphorus, is the nutrient element likely to limit primary production in the oceans in general (Ryther and Dunstan, 1971; McCarthy and Carpenter, 1983). More recently one has realized that this general tendency is likely to be reinforced in many inshore waters because nitrogen is continually lost by the process of microbial denitrification (Nixon, 1981; Nixon and Pilson, 1983). Opposing this is an influx of excess quantities of inorganic nitrogen in the form of ammonium and nitrate, and of organic nitrogen, which may be locally very considerable (Meybeck, 1982; Sharp, 1983). The role of nitrogen as opposed to phosphorus in regulating estuarine plankton production

is still debated (Jaworski, 1981; Nixon, 1981; Schindler, 1981). Nevertheless, it is probably true of most nearshore environments that a full understanding of the dynamics of primary production must ultimately build upon an analysis of the pathways of nitrogen supply.

The following discussion will be limited to nearshore temperate waters where ^{15}N isotope methodology has been applied, with a few remarks on additional situations not so far investigated in this manner. The survey includes examples of estuaries, coastal lagoons, fjords and shelf areas. Tropical and high-latitude seas are not considered, nor are the great upwelling systems along the west coasts of continents. As the reader will notice, generalizations are made difficult by the great variety of environments considered, as well as by a scarcity of relevant studies and by methodological problems encountered in the course of these studies.

The nitrogen sources of interest in studies of nearshore nitrogen primary productivity are ammonium, nitrate, urea and, in exceptional cases, nitrite. Some microalgae will take up amino acids or other organic compounds (Wheeler, 1983) but there is no reason to believe that organic nitrogen sources, other than urea, are used by authentic plankton algae in their own environment. Cyanobacteria (blue-green algae) may fix dissolved dinitrogen gas but these organisms play a very subordinate role in nearshore temperate water, except in brackish localities.

2.2 CONCENTRATIONS OF NITROGEN IN THE PELAGIC ENVIRONMENT

Nitrate concentrations in coastal waters vary from undetectable in bloom situations away from the shore to 100 μM or more in estuaries of rivers draining agricultural and urbanized areas (Sharp, 1983). Ammonium concentrations vary similarly and, again, concentrations during blooms, even in highly productive waters, are frequently so low (0.1–0.3 μM or less) as to make precise determinations very difficult. There are fewer data on urea. Reported concentrations for shelf waters are in the range 0–0.6 μM N (= 0–0.3 μM urea) (McCarthy, 1972; Aminot and Kerouel, 1982) and for polluted estuaries and bays, 0.1–10 μM (Remsen, 1971; Kaufman *et al.*, 1983; Kristiansen, 1983). Urea is sometimes more abundantly present than ammonium in polluted water (Kaufman *et al.*, 1983; Kristiansen, 1983). Nitrite concentrations in near-surface waters are usually very low but in some shallow estuaries, such as Chesapeake Bay, USA, may reach 7–7 μM (McCarthy *et al.*, 1984).

The importance of ammonium, urea and nitrate in phytoplankton nitrogen nutrition is generally acknowledged while, with the exception of Chesapeake Bay (McCarthy *et al.*, 1977), nitrite was mostly ignored. Ambient concentrations represent the balance of rates of supply and consumption, so that low concentrations may well mask a rapid flux of nitrogen through the primary producers and high turnover rates of the dissolved inorganic nutrient pools. Thus

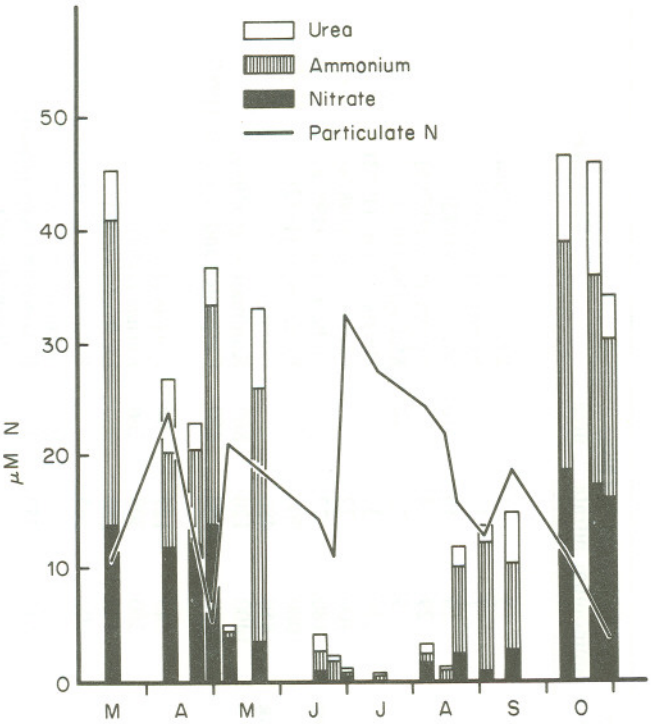

Figure 2.1. Yearly cycle of dissolved nitrogen nutrients and of particulate nitrogen just outside the harbour of Oslo, Norway in 1980. (Data from Paasche and Kristiansen, 1982a and Kristiansen, 1983).

nearshore concentrations of nitrate, ammonium and urea are generally at their lowest in the summer when high quantum flux densities support a vigorous photosynthesis (Nixon and Pilson, 1983). An example of this is given in Figure 2.1, showing the seasonal cycle of nitrogen nutrients in the most polluted part of the inner Oslofjord, Norway. In spite of a great nutrient load here, midsummer concentrations of all nitrogen nutrients at times approach the limit of detection, and there may be thirty times as much nitrogen in the plankton algae as in the dissolved nitrogen pool (Figure 2.1).

2.3 NITROGEN UPTAKE RATES AND NITROGEN PRIMARY PRODUCTION

The transformation of nitrogen in soluble substrate form into cellular nitrogen bound in plankton algae is usually referred to as nitrogen uptake. Published uptake rates for nearshore and estuarine waters are shown in Table 2.1. It is likely

Table 2.1. Greatest reported rates of nitrogen uptake by coastal phytoplankton. Unit: nanomoles N per litre and hour, where 1 nanomole/litre = 1 nM ammonium or nitrate or 0.5 nM urea

Area	Incubation time (h)	Isotope enrichment	Max. rate (nM N/h) ammonium	nitrate	urea	References
Southern California Bight						
offshore	24	trace	5	3		Eppley *et al.* (1979b)
inshore	24	trace	7	31		Eppley *et al.* (1979b)
inshore	24	trace	10	16	10	McCarthy (1972)
near sewer outfall	24	trace	29	4		Eppley *et al.* (1979b)
near sewer outfall	24	trace	9	22	14	McCarthy (1972)
Middle Atlantic Bight, inshore	6	trace	236	33		Harrison *et al.* (1983)
Vineyard Sound, Mass.	1–2	trace	100	22		Glibert *et al.* (1982a)
Vineyard Sound, Mass.	1–2	saturating	180	22		Glibert *et al.* (1982a)
North Carolina estuaries	n.r.	n.r.	1000	700		Fisher *et al.* (1982b)
New York Bight, apex	2–8	saturating	850	480		Garside (1981)
Great South Bay, N.Y.	2–3	trace	1400	120	860	Kaufman *et al.* (1983)
Carmans Estuary, N.Y.	2	trace	7590	7240	450	Carpenter and Dunham (1985)
Narragansett Bay, R.I.						
winter	3–9	trace	745	127	84	Furnas (1983)
summer	3–9	trace	360	308	266	Furnas (1983)
Bedford Basin, Nova Scotia	4	trace	420	280		La Roche (1983)
Oslofjord, Norway	3–5	trace	403	265		Paasche and Kristiansen (1982a)
Oslofjord, Norway	3–5	trace			229	Kristiansen (1983)
Oslofjord, Norway	3–5	saturating	840	357	375	Paasche and Kristiansen (unpublished)

n.r. = not reported.

that reported rates by and large represent nitrogen that was assimilated and incorporated into protein, and so should be comparable to photosynthetic carbon assimilation rates. The table includes only the highest rates recorded in each of the cited reports, so allowance should be made for the very considerable seasonal variation that has been documented in numerous ^{14}C primary production studies from similar environments. Moreover, not all of the investigations on which Table 2.1 is based comprise a full yearly cycle. With very few exceptions (e.g. Harrison *et al.*, 1983), ^{15}N studies have not produced sufficient data to calculate integrated water column production rates in terms of nitrogen assimilated per unit sea surface area. The values in Table 2.1 are all reported on a per-volume basis and can give only a rough estimate of the relative productivity of the various localities. However, they confirm expectations that the highest nitrogen primary productivities are to be found in eutrophic inshore waters. A covariance of nitrogen uptake with phytoplankton standing stock can be derived from the data in many of the studies quoted in Table 2.1. A statistical proof of such covariance was adduced in the study by Eppley *et al.* (1979b).

A closer examination of the information in Table 2.1 brings up two important aspects of ^{15}N uptake studies. One concerns the relative importance of the various nitrogen substrates. This will be discussed below (Sections 2.4–2.6). The other concerns the question of how representative measured rates are of the true flow of nitrogen through the primary producers.

Methodological aspects and problems of interpretation will be only briefly touched upon here, since they are treated in Glibert (this volume), besides having been dealt with in a number of recent reviews (e.g. McCarthy, 1981; Goldman and Glibert, 1983; Harrison, 1983). In most ^{15}N studies in coastal and inshore waters (Table 2.1), as well as in offshore regions, one has endeavoured to approximate the ideal tracer experiment by adding only a small ('trace'; see Table 2.1) amount of labelled substrate. This introduces risks of underestimation of rates resulting from substrate exhaustion in the course of incubation (Fisher *et al.*, 1981). This problem may be crucially important in nearshore productive waters. It is usually dealt with by reducing the incubation period to 3–5 hours or even 1–2 hours (Table 2.1); however, during phytoplankton blooms in the summer, when substrate concentrations are low and specific uptake rates are high (Fisher *et al.*, 1982b; Paasche and Kristiansen, 1982a), even this may be too long. Another source of uncertainty is the local turnover of dissolved substrate pools in the water samples enclosed for incubation. Heterotrophs may recycle ^{14}N which dilutes the ^{15}N label (Glibert, this volume). This particular source of error will seriously affect calculated rates of uptake for ammonium, much less if at all for urea, and not at all for nitrate. No correction for substrate exhaustion or isotope dilution was applied to the uptake rates listed in Table 2.1.

The addition of a large ('saturating'; see Table 2.1) excess of ^{15}N-labelled substrate eliminates some of these uncertainties, and has been practised in several cases (Table 2.1). The rates thus obtained are always greater than the rates based

on 'trace' additions, provided ambient substrate concentrations are less than about 0.5 μM (Glibert *et al.*, 1982a; Paasche and Kristiansen, 1982a; Glibert and McCarthy, 1984). At higher ambient substrate concentrations, rates obtained with 'trace' and 'saturating' ^{15}N enrichments tend to converge, as illustrated for nitrate uptake by Glibert *et al.* (1982a). The interpretation of saturated uptake rates is complicated, since they may entail a perturbation of the steady state (Glibert, this volume). However, in situations of low ambient nutrient concentrations and short turnover times there is a general uncertainty as to whether steady-state kinetics apply to phytoplankton nutrient uptake *in situ* (McCarthy, 1981; Harris, 1983; Currie, 1984). As long as this question has not been settled there is little to choose between rates of nitrogen uptake based on 'trace' and on 'saturating' substrate additions.

The above difficulties in interpreting ^{15}N measurements loom large in the recent literature. Comparatively less attention has been given to the fact that nitrogen uptake is not as straightforwardly related to light as is photosynthetic carbon assimilation. The dependence of nitrogen uptake on light can be inferred from nitrogen uptake profiles (Figure 2.2), and has been tested experimentally with naturally occurring phytoplankton (Dugdale and Goering, 1967; MacIsaac and Dugdale, 1972; Eppley *et al.*, 1979b; Conway and Whitledge, 1979; Fisher *et al.*, 1982b; Nalewajko and Garside, 1983; Price *et al.*, 1985). As might be expected from laboratory work on plankton algae (Syrett, 1981; Paasche *et al.*, 1984), nitrate uptake usually is more dependent on light than is ammonium uptake (Figure 2.2), though an absolute light requirement may be rare even with nitrate, and may depend on the degree of nitrogen sufficiency of the plankton as

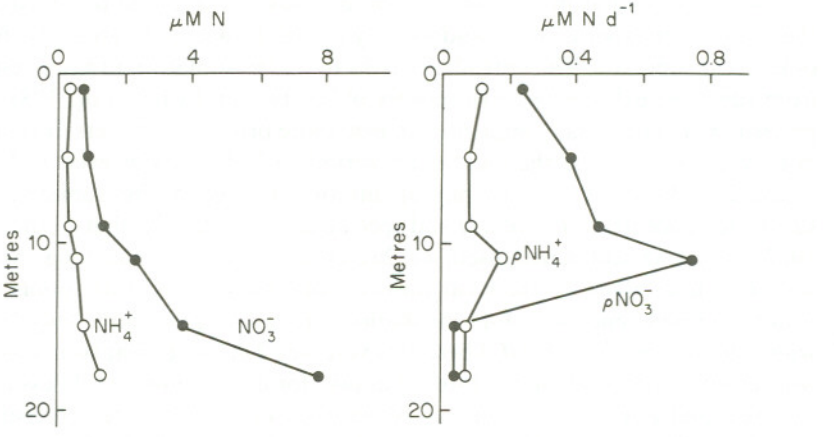

Figure 2.2. Vertical distribution of ammonium and nitrate (left) and vertical variation in nitrate and ammonium uptake rates (right) at a nearshore station in Southern California Bight, February 1975. (Based on data in Eppley *et al.*, 1979b, Table 2, p. 502.)

well as on species composition (Paasche *et al.*, 1984). In consequence of this, nitrogen uptake measurements should be extended through the entire day-and-night cycle in order to make them comparable to photosynthetic productivity estimates. Brief (daytime) incubations (Table 2.1), though mandatory for other reasons, are clearly inadequate in this regard. This is well illustrated by data presented by Fisher *et al.* (1982b). A complete 24-hour cycle of ammonium uptake was laboriously pieced together from consecutive short-term incubations, and was supplemented with ^{14}C photosynthesis measurements. The diel patterns of nitrogen and carbon incorporation are strikingly different (Figure 2.3).

Ratios of carbon uptake (measured by ^{14}C) to nitrogen uptake (by ^{15}N) from studies in estuarine, coastal and offshore waters have been summarized by Fisher *et al.* (1982b). Additional values from shelf and nearshore environments are found in papers by Harrison *et al.* (1983), La Roche (1983) and Carpenter and Dunham (1985). Comparisons are made difficult by differences in the length of incubation periods, in the number of nitrogen sources considered, and so on. The atomic C:N uptake ratios vary between a lower limit of about 3 and an upper limit of 30 or more. Values above the 'Redfield ratio' of 6.6 are the rule rather than the exception. Much of this variation is likely to be due to a choice of unrepresenta-

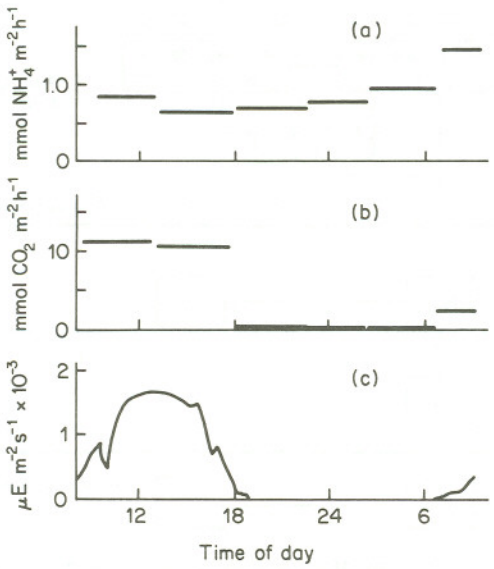

Figure 2.3. Diel cycle of (a) ammonium uptake rate, (b) carbon uptake rate, and (c) insolation at a station in South River Estuary, North Carolina, 26–27 September 1978. (Modified after Fisher *et al.*, 1982b.)

tive incubation times in the ^{15}N experiments, but a host of other factors, not all of them connected with ^{15}N methodology, may have contributed. The organic matter in nutrient-sufficient plankton algae has an atomic C:N ratio of 6–9. Uptake ratios greater than 9, if representative of the full diel cycle and including all nitrogen substrates, could be indicative of nitrogen-limited phytoplankton growth. However, even providing for 24-hour average values of total N uptake, C:N uptake ratios tend to vary much more than the compositional ratio, and in a rather unsystematic manner (Eppley *et al.*, 1979a). In so far as this variation is not due to experimental error, it may reflect 'unbalanced growth' (Eppley, 1981) causing short-term oscillations in C:N uptake ratios that are averaged out in determinations of a more constant chemical composition.

2.4 INDICES OF NITROGEN NUTRITION AND THEIR USE IN COASTAL WATERS

The concept of new and regenerated production (Dugdale and Goering, 1967; Eppley and Peterson, 1979; Glibert, this volume) finds its most straightforward application in conjunction with a simple physical model of a two-layer ocean where the pycnocline coincides with the bottom of the euphotic zone (Figure 2.4).

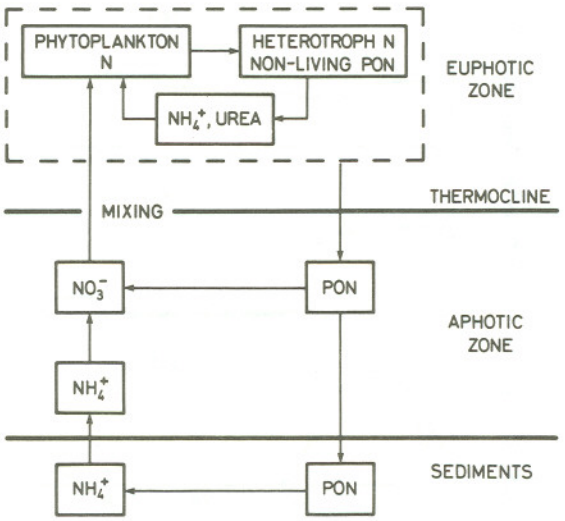

Figure 2.4. The nitrogen cycle in a two-layered ocean including underlying sediments, considered as a closed system. PON = particulate organic nitrogen. 'Regenerated production' depends on nitrogen recycled within the box marked by – – –. (Adapted from Eppley *et al.*, 1983.)

Influx of new nitrogen as nitrate can then be referred to vertical eddy diffusion through the pycnocline or to the periodic breakdown of the same through physical events. Following Eppley and Peterson (1979), the relative contribution of new and regenerated nitrogen to primary production can be estimated as:

$$f = \frac{\rho_{NO_3}}{\rho_{NO_3} + \rho_{NH_4} + \rho_{urea}}$$

where ρ_{NO_3}, ρ_{NH_4} and ρ_{urea} are the rates of uptake of nitrate, ammonium and urea, respectively. Eppley and Peterson showed that f increases from a value of 0.05 in extremely oligotrophic water offshore to a value of 0.5 in highly productive upwelling areas having an annual primary production in excess of 200 g C/m^2. At the same time they pointed out that the relationship cannot be used in shelf waters of less than 200 m depth or in inshore waters, since new nitrogen entering the water column from sediments, benthos, or land may be in the form of reduced nitrogen compounds (ammonium and urea). Thus the high rates of primary production typically measured in many inshore areas are supported largely by reduced nitrogen, as is apparent from their low f values (Section 2.5.2). Conversely, in more offshore water characterized by relatively larger f values, primary production may be seasonally low, as illustrated for southern California shelf waters by Eppley *et al.* (1979a; see Figure 2.5).

In this study by Eppley and co-workers urea uptake was not measured, so the

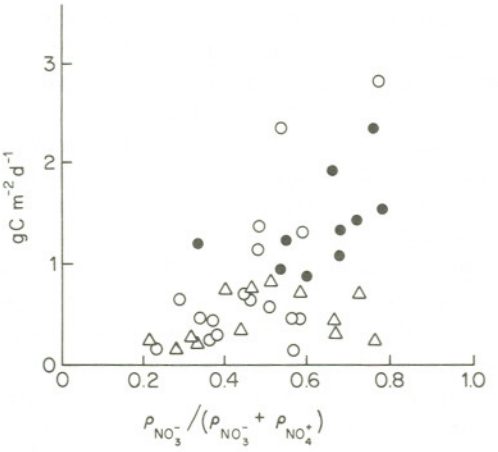

Figure 2.5. Primary production in southern California waters vs. f' (nitrate uptake rate divided by nitrate uptake rate plus ammonium uptake rate). △ = winter; ○ = spring; ● = summer. (Modified after Eppley *et al.*, 1979a.)

relative nitrate utilization in Figure 2.5 is shown simply as

$$f' = \frac{\rho_{NO_3}}{\rho_{NO_3} + \rho_{NH_4}}$$

Since the majority of pelagic ^{15}N uptake studies have not included urea, the simplified index, f', will be used in the following text. In coastal water, indices such as f or f' merely serve to indicate the contribution of nitrate to total nitrogen utilization. Clearly they can provide no clue by themselves as to how much of the reduced nitrogen available to the plankton actually is 'regenerated', i.e. originates within the euphotic zone. Similarly, the nitrate that is used does not have to be of deep-water origin, since river water frequently carries as much nitrate as ammonium (Meybeck, 1982; Sharp, 1983). However, when interpreted in conjunction with additional information on hydrographic events, on turnover times of dissolved inorganic nitrogen pools, on physiological features of phytoplankton nitrogen nutrition, and so on, they may be of some help in analyzing the nutritional basis for the elevated primary production in coastal environments.

McCarthy *et al.* (1977) introduced a relative preference index (RPI) as a more comprehensive way of describing nitrogen utilization relative to nitrogen availability. The RPI for a given substrate, N_1, is defined as

$$RPI_{N_1} = \frac{\rho_{N_1}}{\rho_{N_1} + \rho_{N_2} + \ldots + \rho_{N_i}} \Big/ \frac{(N_1)}{(N_1) + (N_2) + \ldots + (N_i)}$$

where ρ_{N_i} is the uptake rate and (N_i) the concentration of the ith substrate. McCarthy *et al.*, calculated RPI values for four substrates: ammonium, urea, nitrite and nitrate. An example is given in Figure 2.6. Calculations of RPI have been included in several recent reports (Eppley *et al.*, 1979b; Glibert *et al.*, 1982a; Harrison *et al.*, 1982; Furnas, 1983; Kaufman *et al.*, 1983; Carpenter and Dunham, 1985), although nitrite and sometimes also urea have been omitted. When the RPI for nitrate is based on only ammonium and nitrate measurements, it reduces to the f' value (see above) for ambient ammonium concentrations approaching zero (Glibert *et al.*, 1982a).

McCarthy *et al.* (1977), using data from Chesapeake Bay, showed that when both nitrate and ammonium are abundant the RPI for nitrate strikingly reflects the inhibition of nitrate uptake by ambient ammonium concentrations (Figure 2.6). This is an effect that has been amply confirmed in a number of field and laboratory investigations (Section 2.5.2). A further use of the RPI was suggested by the same authors, in that RPI values for all substrates could be expected to be close to unity as long as nitrogen is limiting, while a departure from unity specifically for nitrate, in the negative direction, would indicate a nitrogen-sufficient plankton. This departure of the nitrate RPI occurs at an ammonium concentration of about 0.5 μM, which is also the ammonium concentration at which inhibition of nitrate uptake begins to be clearly discernible in field work.

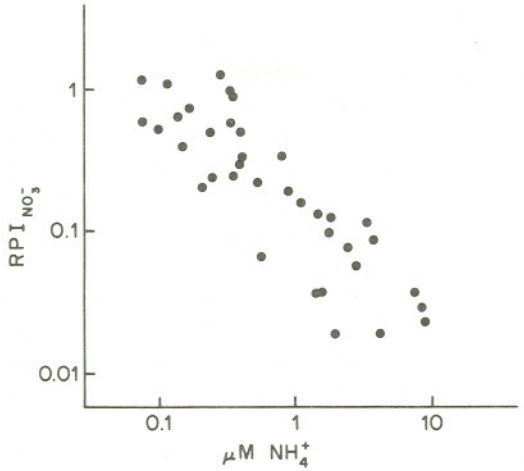

Figure 2.6. The relative preference index of nitrate vs. ammonium concentration in Chesapeake Bay. (Modified after McCarthy *et al.*, 1977.)

According to McCarthy *et al.* (1977), all nitrogen sources would be used simultaneously and in proportion to their concentrations at ammonium concentrations less than 0.5 μM. Conversely, the demand for nitrogen by the plankton would be fully satisfied by ammonium, or by ammonium and urea, at ammonium concentrations above this value. Useful as this might seem, it is difficult to reconcile the application of the RPI as a test for nitrogen limitation with the extremely high affinity of algal cells for ammonium that has been demonstrated in laboratory experiments (Goldman and Glibert, 1983).

Depending on circumstances, the RPI may or may not reflect physiologically important characteristics such as ammonium inhibition of nitrate uptake, or nitrogen limitation. It should not be used uncritically, since its numerical value is also very sensitive simply to variations in the ambient concentrations of the respective substrates. For example, given constant and equal rates of (saturated) nitrate and ammonium uptake and a low (non-inhibiting) ammonium concentration of 0.2 μM, the RPI for ammonium can be made to increase 25-fold merely by increasing the ambient nitrate concentrations from 0.2 to 10 μM. In this case variations in the RPI have no physiological basis and no ecological meaning.

2.5 SUPPLY AND UTILIZATION OF 'NEW' NITROGEN

2.5.1 Open shelf waters

Generally speaking, the elevated primary production of open coastal waters, as compared to offshore waters (Ryther, 1969; Eppley and Peterson, 1979), is a

consequence of greater admixture of deep water. Hence this increase ultimately depends on nitrate. However, not all of it represents 'new production', since it has been shown by Eppley and co-workers (Eppley *et al.*, 1979a; Eppley and Peterson, 1979) that the increased use of nitrate near the coast is accompanied by an increase in water-column recycling of nitrogen, so that production based on regenerated ammonium and urea nitrogen is also greater in absolute terms than is the case offshore. In other words, the physical mixing processes operating on the coast act as a driving force for both new and regenerated pelagic production. This description is valid as long as the input of inorganic nitrogen from sediments or from land remains insignificant. Further generalizations are hardly possible. A variety of physical mechanisms and events, such as tidal mixing, local upwelling, vertical eddy diffusion and seasonal breakdown of the pycnocline, have a profound effect on the upward transport of nitrate. A few examples from randomly selected coastal areas (Pingree *et al.*, 1975; Eppley *et al.*, 1978; Fournier *et al.*, 1984) suffice to show that the physical regimes governing the admixture of nitrogen from deep water vary appreciably from one place to another, and are not always easy to analyze.

Direct (^{15}N) measurements of ammonium and nitrate uptake have been carried out at all seasons in the southern California Bight (33° N) by Eppley *et al.* (1979a, b). The two substrates were found to contribute about equally, on the average, to phytoplankton nitrogen nutrition there ($f' = 0.48$; Table 2.2). A correction was made for urea uptake, which was not measured, and this gave a mean f value of 0.35.

With regard to temperate shelf waters at somewhat higher latitudes, evidence as to the importance of nitrate for primary production is largely indirect. The only ^{15}N studies appear to be those of Conway and Whitledge (1979) from the New York Bight (40° N) and Harrison *et al.* (1983) from the Middle Atlantic Bight (35–40° N), dealing with spring and summer situations, respectively. The latter investigation brings out the important point that the euphotic zone in stratified water may extend below the pycnocline to include nitrate-rich water harbouring growing phytoplankton populations. The mean value of the nitrate utilization index, f', was lower in the investigation by Conway and Whitledge (1979) than in the other shelf studies (Table 2.2). On the whole, however, the mean and minimum f' values of shelf waters, whether based on year-round or summer data sets, indicate that nitrate plays a more important role in phytoplankton nitrogen nutrition than is the case in either oligotrophic water (f' less than 0.1: Eppley and Peterson, 1979) or nutrient-rich inshore bays and estuaries (Table 2.2). The basis for this is probably not only the influence of vertical mixing through the physical mechanisms referred to above, but also the relatively minor impact of reduced nitrogen compounds from the bottom, from the shore or from land. This is confirmed by a study from Vineyard Sound (40° N), an inshore locality which may be relatively strongly influenced by water exchange with the

Table 2.2. Reported values of f' (nitrate uptake divided by sum of nitrate and ammonium uptakes) for coastal and inshore waters. The numerical values in part were abstracted from tables and figures in the original reports

Area	f' Value			References
	Minimum	Maximum	Mean	
Shelf waters:				
Southern California Bight	0.22	0.78	0.48	Eppley *et al.* (1979a, b)
Middle Atlantic Bight*	0.35	0.86	0.59	Harrison *et al.* (1983)
New York Bight*	0.23	0.45	0.32	Conway and Whitledge (1979)
Vineyard Sound, Mass.	0	0.94	0.60	Glibert *et al.* (1982a)
Inshore waters:				
Pamlico River, North Carolina*	0	0.49	0.18	Kuenzler *et al.* (1979)
Chesapeake Bay	0	1.00	0.30	McCarthy *et al.* (1977)
New York Bight, apex	0	0.88	—	Garside (1981)
Carmans Estuary, N.Y.	<0.05	>0.95	0.51	Carpenter and Dunham (1985)
Narragansett Bay, R.I.	0	0.67	0.29	Furnas (1983)
Bedford Basin, Nova Scotia	0	0.87	0.39	La Roche (1983)
Oslofjord, Norway	0	0.76	0.21	Paasche and Kristiansen (1982a)

* Integrated value for euphotic zone.

open shelf, and where drainage from land is modest, with a mean annual f' value of 0.60 (Glibert *et al.*, 1982a; Table 2.2).

Seasonal studies using ^{15}N remain to be carried out in open shelf waters at higher latitudes (40–60°) with a pronounced yearly cycle in insolation and thermal stratification of the water column. The well-known disappearance of nitrate from the euphotic zone concurrently with the vernal blooming of the phytoplankton (e.g. Butler *et al.*, 1979) surely signifies a major role of nitrate in phytoplankton nutrition during that period. However, depending on the development of the zooplankton, ammonium may form a significant fraction of the total. An analogy may be drawn with Antarctic waters where nitrate concentrations remain as high as, or higher than, typical winter nitrate concentrations in northern temperate shelf water. Several studies have shown that, in spite of the abundance of nitrate, this nutrient often contributes less than half, sometimes as little as 20%, of the total nitrogen flux through the Antarctic primary producers (Olson, 1980; Glibert *et al.*, 1982b; Rönner *et al.*, 1983).

In the summer, thermal stratification is a regular feature in many temperate shelf regions, and may be of profound importance for the nitrogen turnover in the water column. Recycling of nitrogen may then be essential for continued phytoplankton growth (Harrison *et al.*, 1983; Holligan *et al.*, 1984a; see Section 2.6). Conditions in the upper mixed layer have not been studied with ^{15}N except by Harrison *et al.* (1983), nor have the subsurface biomass maxima that appear to be a widespread feature of shelf waters (Cullen and Eppley, 1981; Harrison *et al.*, 1983; Holligan *et al.*, 1984a, b). These subsurface plankton communities may be more important in primary production and nitrogen turnover than has been generally realized. They are found quite regularly near the thermocline and may depend on nitrate-rich deep water for growth. Holligan *et al.* (1984a) made a detailed study of the nitrogen budget of such a situation in the vicinity of a shallow-water tidal front in the western English Channel. By means of temperature–nitrate plots, they showed that nitrate utilization near the thermocline, coupled with a net upward transport of nitrogen by swimming algal cells, could account for the eventual development of heavy plankton blooms (30–50 μg chlorophyll *a* per liter) in the entire water column above the thermocline. The organism responsible, the dinoflagellate *Gyrodinium aureolum*, apparently is not eaten to any great extent (Holligan *et al.*, 1984a) so that rates of ammonium regeneration in the upper strata would be low. Any f' value calculated for this kind of situation would be very high, and would signify preponderantly new production in the sense of Eppley and Peterson (1979). The lesson to be learned from this is that an analysis of the properties and capabilities of the primary producers themselves may be as crucial as an analysis of the physical oceanography for an understanding of how the system operates in relation to the nitrogen supply. Future work may lead to a much more diversified view of nitrogen cycling in shelf waters than can be formulated on the basis of ^{15}N work that has been carried out up to the present time.

2.5.2 Inshore waters

Ammonium and nitrate uptake rates have been measured in a sufficient number of bays and estuaries (Table 2.2) to allow some generalizations. The mean f' values tend to be lower than those for shelf waters (Table 2.2) and lower than the mean value of 0.6 ($f = 0.5$) predicted by Eppley and Peterson (1979) for coastal upwelling zones. This is an indication that inshore primary production is, for the greater part, based on nitrogen in the reduced (ammonium and urea) forms, a conclusion that was reached in the pioneering studies by McCarthy *et al.* (1975, 1977) in Chesapeake Bay. Furthermore, seeing that rivers and terrestrial runoff, as well as benthos and sediments, may supply much nitrogen in the form of ammonium to the inshore pelagic environment, the prevalence of low f' values is readily understood. Yet the total range of f' values appears to be at least as great as on the open shelf (Table 2.2), reflecting the variety of hydrographic conditions encountered inshore. Even in an extremely sheltered area such as the inner Oslofjord, f' values at some distance from land approach unity early in the growth season as a consequence of in- and upflow of nitrate-rich water from the adjacent shelf (Paasche and Kristiansen, 1982a). Another example of high (> 0.95) f' values in an enclosed environment is the Carmans Estuary, Long Island, New York, where ammonium depletion upstream enables the phytoplankton at points further downstream to use nitrate as the main substrate (Carpenter and Dunham, 1985).

In the summer, situations are frequently encountered in which no nitrate is analytically detectable in the water. Somewhat depending on how authors have back-calculated the rates of ^{15}N-nitrate uptake to *in situ* uptake rates at ambient nitrate concentrations, reported values of $f' = 0$ (Table 2.2), reflecting 'zero' nitrate uptake, may be accounted for by 'zero' concentrations. The precise physiological meaning of such situations is not always clear: however, in inshore waters they probably imply that nitrate is used continually or intermittently, since some nitrate is likely to be transported into the productive layer from land, from sediments or from deep water, depending on the local conditions. Physiological studies of marine diatoms have shown that if ammonium is also in short supply, the enzymatic apparatus for nitrate uptake and reduction may remain activated even if no nitrate is around (Cresswell and Syrett, 1981; Dortch and Conway, 1984). In accordance with this, it is commonly observed that inshore plankton in apparently nitrate-free water retains the ability to assimilate nitrate upon the addition of this substrate (Glibert and McCarthy, 1984; Paasche and Kristiansen, 1982a; and unpublished observations).

On the other hand, and again in agreement with laboratory findings (Conway, 1977; Dortch and Conway, 1984), a number of investigations of inshore localities (McCarthy *et al.*, 1975, 1977; Kuenzler *et al.*, 1979; Garside, 1981; Paasche and Kristiansen, 1982a) have shown that nitrate uptake even at high nitrate concentrations is largely inhibited ($f' < 0.2$) by ammonium concentrations

greater than about 1 μM. A much higher ammonium inhibition threshold has been claimed for microalgae in experimental ponds (Maestrini *et al.*, 1982) but not so far for phytoplankton in the free water column, although there is evidence that the inhibition can be partly reversed at extremely high (40–60 μM) nitrate concentrations (Carpenter and Dunham, 1985). Ammonium concentrations rarely if ever reach 1 μM in the upper mixed layer overlying the open shelf or deep ocean, whereas this level is frequently exceeded in estuaries and bays, and concentrations that are greater by an order of magnitude are found in polluted areas. Ammonium inhibition of nitrate utilization is clearly one aspect that distinguishes phytoplankton nitrogen nutrition inshore from that in the oceans generally. In some areas with a heavy influx of both nitrate and ammonium from land, such as points close to the shore in the inner Oslofjord, this condition may persist through much of the growth season and may be relieved only during the summer, when ammonium concentrations are low (Figure 2.1). This is then the only time when nitrate contributes significantly to phytoplankton nitrogen nutrition (Paasche and Kristiansen, 1982a).

Chesapeake Bay is the only locality where the contribution of the other possible form of oxidized, new nitrogen, nitrite, has been studied. On a yearly basis this nutrient was found to account for about 7% of all nitrogen used (McCarthy *et al.*, 1977). At certain times of the year, in the autumn, nitrite-based phytoplakton growth seems to be a prominent feature in this area, and is due to large ambient nitrite concentrations produced by nitrification in the water column when the pycnocline breaks down and ammonium-rich deep water is mixed into the oxygenated upper layer (McCarthy *et al.*, 1984). More than half of the nitrogen taken up by the phytoplankton may then be in the form of nitrite (McCarthy *et al.*, 1977). Similar situations could occur elsewhere, especially in shallow estuaries subject to cultural eutrophication and periods of anoxic conditions below the pycnocline.

The rule that all oxidized forms of inorganic nitrogen represent new nitrogen in the sense of Dugdale and Goering (1967) can be assumed to apply even to extreme inshore situations. The real difficulty is in distinguishing new and regenerated nitrogen when both are in a reduced form, as ammonium or urea. Such nitrogen may originate from land; from microbial processes in sediments, in stagnating deep basins, or in the free water column; and from excretion by animals on the bottom or in the water. As far as ammonium is concerned it is possible, in theory at least, to make a distinction between the (regenerated) fraction arising in the euphotic zone and the (new) fraction being mixed in by horizontal and vertical transport. This presupposes that measurements of *in situ* ammonium regeneration are performed by means of existing ^{15}N methodology (Glibert, this volume; see also Section 2.6). With urea there is as yet no available isotopic method for doing this, and any attempt to partition urea utilization between new and regenerated fractions must be based on indirect evidence.

Although urea was omitted from several large studies among those discussed

above (Table 2.2), there is no doubt that plankton algae capable of using this nutrient are ubiquitous in coastal water. Urea uptake was given particular attention in investigations by McCarthy *et al.* (1977), Furnas (1983), Kaufman *et al.* (1983), and Kristiansen (1983). It seems likely that much of the urea occurring in solution in the semi-enclosed environments studied by these authors was of terrestrial origin, thus representing a source of new nitrogen. McCarthy *et al.* (1977) and Kristiansen (1983) estimated that urea contributed about 20% of the total nitrogen uptake by plankton in Chesapeake Bay and in the inner Oslofjord, respectively. A corresponding estimate for Carmans Estuary, Long Island, New York, was 12% (Carpenter and Dunham, 1985). However, the share of urea in total nitrogen uptake varies considerably and, on occasions when urea concentrations are equal to or higher than ammonium concentrations, may reach 50% or more (McCarthy *et al.*, 1977; Furnas, 1983; Kristiansen, 1983). In a 2-year study of Great South Bay, Long Island, New York, Kaufman *et al.* (1983) found this to be the prevailing state of affairs. Kristiansen (1983) showed that urea uptake in the Oslofjord was clearly depressed at ammonium concentrations above 1–2 μM, in accordance with earlier field and laboratory findings (McCarthy, 1981). Kaufman *et al.* (1983) conversely measured high ammonium uptake rates only at low (2 μM N) urea concentrations. However, they acknowledged that this could be a reflection of the relative availability of the two substrates, rather than of urea interfering with ammonium uptake. Still the rather unusual composition of the plankton in this bay, with a preponderance of green algae and cyanobacteria, suggests a selection of forms especially well suited to growth in a high-urea environment (Kaufman *et al.*, 1983).

Cultural eutrophication of an estuary or other inshore water body is generally accompanied by increased nitrogen recycling. This certainly is true of the system as a whole (Nixon and Pilson 1983), and may be true of the euphotic portion of the water column if this is looked upon as a separate subsystem. However, if one is sufficiently close to the source or point of influx, the immediate response of the phytoplankton to new nitrogen introduced from land can be studied directly. As an example, data representing a gradient away from a point of sewage efflux in the inner Oslofjord are shown in Table 2.3. These data, which form part of a year-round investigation (Paasche and Kristiansen, 1982a), are mean values from six sampling dates in the summer, when there was a strong pycnocline at 10 m depth preventing an upward transport of nutrients at points removed from the shore. Along the nutrient loading gradient, ambient nutrient concentrations as well as nutrient uptake rates increased two-fold, phytoplankton (particulate nitrogen) concentrations four-fold, and chlorophyll concentrations eight-fold. The interpretation of this is that the great quantities of phytoplankton cells close to the source of nitrogen input acted as a filter removing much of the dissolved nitrogen nutrient; however, the density of algal cells was such that maximum growth rates and complete nutrient utilization could not be realized because of shelf-shading. The evidence for this was a reduction of the euphotic zone to a thickness of 2–3 m,

Table 2.3. Nitrogen dynamics along a pollution gradient in inner Oslofjord, Norway. Mean values ± S.D. for six dates in June–August 1980. Data from Paasche and Kristiansen (1982a) and Kristiansen (1983)

	Station 3	Station 2	Station 1
Distance (km) from nearest major sewage entry point	0.5	3	12
Dissolved substrate (μM N):			
ammonium	1.33 ± 0.64	0.70 ± 0.17	0.53 ± 0.10
nitrate	0.46 ± 0.56	0.19 ± 0.17	0.24 ± 0.20
urea	0.63 ± 0.52	0.24 ± 0.06	0.40 ± 0.20
Nitrogen uptake rate (nM/h):			
ammonium	> 222 ± 118	> 135 ± 92	86 ± 59
nitrate	> 78 ± 104	> 35 ± 30	30 ± 26
urea	116 ± 67	55 ± 15	59 ± 44
Turnover time (h):			
ammonium	< 6.9 ± 3.9	< 6.1 ± 1.8	8.6 ± 4.8
nitrate	< 7.5 ± 4.3	< 5.2 ± 1.9	9.6 ± 2.9
urea	7.7 ± 9.7	4.8 ± 2.1	14.8 ± 8.2
f' (nitrate uptake rate/ nitrate + ammonium uptake rate)	0.18 ± 0.17	0.24 ± 0.20	0.26 ± 0.24
Particulate N (μM)	22.0 ± 8.1	10.1 ± 2.3	6.1 ± 1.5
Particulate N/sum of dissolved substrate N (atom/atom)	11.9 ± 11.5	8.2 ± 1.6	5.1 ± 1.7
Chlorophyll *a* (μg/l)	43.7 ± 17.5	10.4 ± 2.1	5.5 ± 1.6
Particulate N/chlorophyll *a* (g/g)	7.2 ± 1.8	13.9 ± 3.7	15.6 ± 4.0

and an increased chlorophyll content (decreased nitrogen:chlorophyll *a* ratio) of the phytoplankton (Table 2.3). The nitrogen that was not used by these massive populations of light-limited cells was carried further out and diluted by some ill-defined horizontal advection process, representing a source of new nitrogen for the phytoplankton farther away from the shore. Turnover times and the relative utilization of nitrate (expressed as *f'*; Section 2.4) appeared to be fairly independent of the immediate nitrogen load (Table 2.3). This may be too simplistic a picture, and the short turnover times for dissolved nutrients (which may even have been overestimated) would lead one to expect rapid water column regeneration of ammonium to be important at the station farthest away from the shore. However, this was not borne out in a separate study, where regenerated ammonium was found to make up no more than a small fraction of total nitrogen consumption (Paasche and Kristiansen, 1982b; Section 2.6). A full understanding of this and similar situations appears possible only if the biological and chemical measurements are accompanied by a detailed analysis of physical transport mechanisms.

2.6 SUPPLY AND UTILIZATION OF 'REGENERATED' NITROGEN

Harrison (1980) has presented an exhaustive review of nitrogen nutrient regeneration in the sea and the subject is further analysed in Fenchel (this volume). Aspects having a bearing on the nitrogen supply to nearshore phytoplankton will be briefly summarized here.

In the absence of information on urea regeneration rates it will be assumed that all nitrogen returned to the dissolved inorganic pool by heterotrophic activity in the euphotic zone is in the form of ammonium. Most of this ammonium may be produced by 'microheterotrophs', i.e. by bacteria and by eukaryotic organisms belonging to the same size classes as the primary producers and feeding directly or indirectly on these (Glibert, this volume). Grazing by larger zooplankton shows much temporal and spatial variation (e.g. Dagg and Turner, 1982; Holligan *et al.*, 1984a) but there is some evidence that this category of plankton heterotrophs contributes less to total grazing, and hence to ammonium regeneration, close to the coast than near the shelf break or continental slope (Conway and Whitledge, 1979; Cosper and Stepien, 1984; see reviews by Harrison, 1980, and Bidigare, 1983). In very shallow water, nitrogen recycled to ammonium by benthic microbial and animal communities is important to phytoplankton, and may provide most or all of the nitrogen consumed in the water column (Billen, 1978; Zeitzschel, 1980; Fisher *et al.*, 1982a; Nixon and Pilson, 1983; Flint and Kamykowski, 1984). When the bottom is in direct contact with the water harbouring the growing phytoplankton, the distinction between new and regenerated nitrogen, in the sense of Eppley and Peterson (1979), can no longer be upheld. In view of the close coupling between water column and bottom metabolism in shallow estuaries and bays, new nitrogen is then best defined as nitrogen that is not regenerated locally but is introduced into the system from land, or from water farther out (Nixon, 1981; Nixon and Pilson, 1983). Any nitrate released from sediments (Fisher *et al.*, 1982a; Nixon and Pilson, 1983) would then by definition represent regenerated nitrogen.

While microheterotrophic regeneration of ammonium in the euphotic zone frequently matches the uptake of ammonium nitrogen by primary producers in open shelf water (Harrison, 1978; Harrison *et al.*, 1983), this route of nitrogen supply generally does not seem to meet the demand in the semi-enclosed waters of Bedford Basin (La Roche, 1983) and the inner Oslofjord (Paasche and Kristiansen, 1982a). A graphic representation of the data from these latter two studies, together with that of Harrison *et al.* (1983), suggests an increasing discrepancy between productive-layer ammonium production and ammonium consumption as one moves from open shelf waters to polluted water inshore (Figure 2.7). This is what one would expect if the ammonium available in the latter type of environment largely represents new nitrogen supplied from land or from nearshore sediments.

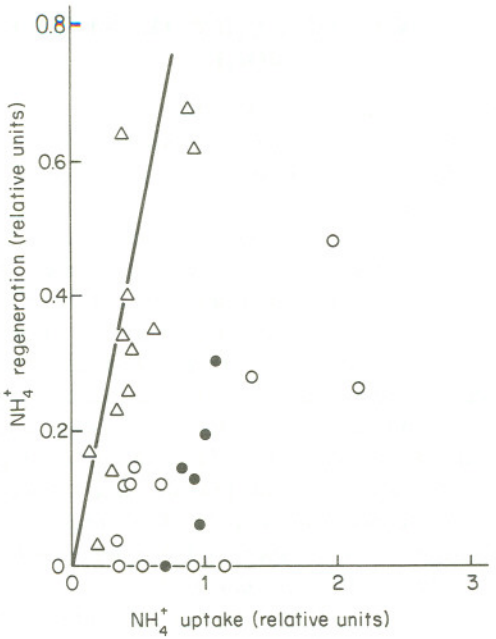

Figure 2.7. Rates of microheterotrophic ammonium regeneration vs. rates of ammonium uptake by phytoplankton in stratified water (summer situations) in the Middle Atlantic Bight (△), Bedford Basin, Nova Scotia (○), and inner Oslofjord, Norway (●). Straight line represents a 1:1 relationship. One relative unit equals 1 μM/d for the Middle Atlantic Bight, and 0.2 μM/h for Bedford Basin and the Oslofjord. (Based on data in Harrison *et al.*, 1983; La Roche, 1983; and Paasche and Kristiansen, 1982b.)

Wherever heterotrophic ammonium production has not been determined experimentally, calculations of the turnover time (depletion time) of the dissolved ammonium pool may be helpful in deciding on the probable routes of nitrogen supply. In Chesapeake Bay, for example, a rapid turnover of ammonium was thought to argue for a local origin of this nutrient rather than for an influx with river water (McCarthy *et al.*, 1975). Estimated turnover times for ammonium in shelf water are upwards of 9 hours (Harrison *et al.*, 1983). In inshore eutrophic waters they may be appreciably shorter, and ammonium turnover times of 1–3 hours have been reported from Chesapeake Bay (McCarthy *et al.*, 1975), the apex of New York Bight (Garside, 1981) and the inner Oslofjord (Paasche and Kristiansen, 1982b). Urea may be turned over similarly rapidly (Kaufman *et al.*,

1983; Kristiansen, 1983; Carpenter and Dunham, 1985). Fast turnover of dissolved inorganic nitrogen is characteristic of summer situations when standing stocks of phytoplankton are large and inorganic nutrient pools are at their minimum (Figure 2.1), and is then promoted by prevailing high temperatures making for rapid specific uptake and growth rates (Fisher *et al.*, 1982b; Glibert *et al.*, 1982a; Paasche and Kristiansen, 1982a; Carpenter and Dunham, 1985) and, presumably, by favourable light conditions.

However, a very rapid depletion rate for dissolved ammonium is not necessarily matched by a high ammonium regeneration rate. In the inner Oslofjord, Paasche and Kristiansen (1982b) estimated ammonium turnover times of 1–2 hours in the summer season; yet ammonium regeneration by microheterotrophs and larger zooplankon never accounted for more than 30% of the nitrogen consumed by the phytoplankton, and on some occasions no heterotrophic release of ammonium could be measured at all. In a similar study in Bedford Basin, La Roche (1983) concluded that the nitrogen making up the balance could originate from water below the pycnocline; in the inner Oslofjord this explanation seemed somewhat less likely (Paasche and Kristiansen, 1982b; and see Section 2.5.2).

2.7 CONCLUSIONS

The phytoplankton inshore uses nitrogen largely in reduced form (ammonium and urea). Much of this may be derived from land or from sediments and benthic animals, and nitrogen recycling within the water column is then correspondingly less important, relatively speaking, in sustaining high levels of pelagic production. Moreover, oxidized nitrogen (nitrate) from land or from deep water may, at times, be the major nitrogen source here.

Farther offshore, on the shelf, the oxidized form (nitrate), originating from deep water, contributes up to half the nitrogen consumed by the primary producers. There may be substantial regional and seasonal variation but, on the whole, nitrate is a much more important nitrogen source on the shelf than either inshore or in the open ocean.

Nitrogen uptake rate measurements form the basis for these broad conclusions, but do not by themselves lead to an understanding of the pathways involved. The routes of nitrogen supply to the plankton are ultimately determined by the local hydrography in conjunction with the growth and behaviour of the organisms, as demonstrated, for example, in studies of dinoflagellate plankton on the continental shelf (Holligan *et al.*, 1984a). Future work will have to take these aspects into account. At the same time, improvements in ^{15}N techniques and related methodology are likely to lead to a more refined description of coastal nitrogen cycling. There is a clear need for distinguishing between allochthonous and autochthonous supplies of ammonium and urea in coastal waters. Rapid ^{15}N methods for measuring *in situ*

regeneration of ammonium and of urea should be of particular interest in this context.

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CHAPTER 3

Microfauna in Pelagic Food Chains

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3.1 INTRODUCTION

This chapter will consider the phagotrophic pelagic organisms within the size range of about 3 to 200 μm, which corresponds to the heterotrophic nanoplankton (2–20 μm) plus microplankton (20–200 μm) in the terminology of Sieburth (1979). The group so defined is quantitatively and qualitatively dominated by representatives of a variety of protozoan taxa, in particular flagellates and ciliates, but also amoebae, heliozoans, radiolarians, acantharians, and foraminifera. However, the microplankton also includes some metazoa, in particular rotifera and juvenile copepods. The distinction between the phagotrophic and autotrophic components of the micro- and nanoplankton is not always sharp: some flagellate species are at the same time phagotrophs and photosynthetic and some pelagic protozoa (radiolaria, foraminiferans and some ciliates such as *Mesodinium rubrum*) harbour photosynthetic cells which effectively render the symbiotic associations into photoautotrophic organisms.

Recent recognition of the quantitative role of the phagotrophic nano- and microplankton is an integral part of what has been called a 'new paradigm of the planktonic food web (Azam *et al.*, 1983; Ducklow, 1983; Sorokin, 1977; Williams, 1981). This also includes the discovery of the large role of heterotrophic bacteria in the pelagic carbon cycle and the role played by eukaryote nanoplankton and by prokaryote photosynthetic organisms for the primary production of the sea. In this picture of the pelagic food web the role of the phagotrophic nano- and microplankton is to form a link in the food chain between bacteria and nano- and picoplankton primary producers on the one hand and the macroplankton on the other. In fact, the size range covered by the phagotrophic nano- and microplankton means that they themselves constitute two or three links in the food chains. This last observation is particularly relevant when their role as remineralizers of mineral nutrients is under discussion.

3.2 DISTRIBUTION PATTERNS AND QUANTITATIVE ROLE

Representatives of a variety of groups of non-photosynthetic flagellates dominate the phagotrophic nanoplankton although amoebae (see Davis *et al.*, 1978) may

also play a role. During the past 5 years several studies have quantified heterotrophic flagellates in seawater samples from a variety of locations. This has mainly been accomplished by the use of epifluorescence microscopy, a technique which allows the distinction between pigmented and non-pigmented forms and often identification to at least the generic level (Davis and Sieburth, 1982; Fenchel, 1982b; Haas, 1982). These quantitative data are reviewed in Fenchel (1986a). The flagellates measure 3–10 μm and typically occur at densities of round 10^3/ml in surface (0–30 m) waters. As an average number this holds for oligotrophic as well as for eutrophic waters. However, while flagellate (and bacterial) numbers seem rather constant over time in the former type of habitats, oscillating numbers are characteristic of more eutrophic situations. Thus, during the summer in the Limfjord, flagellate numbers vary between 2×10^2 and 1.4×10^4/ml. Peaks in flagellate numbers seem to follow peaks in bacterial numbers with a more or less regular periodicity of 10–20 days.

Several types of heterotrophic flagellates have been isolated into pure cultures, and this has greatly facilitated the quantification of grazing rates and other parameters of ecological bioenergetics (Fenchel, 1982a, 1986a, b; Goldman *et al.*, 1985; Sherr *et al.*, 1983). Such data have also been obtained from incubations of freshly collected seawater samples (Andersen and Fenchel, 1985; Sherr *et al.*, 1984) to approximate *in situ* conditions. The flagellates depend on suspended bacteria (including cyanobacteria) and the most minute nanoplankton organisms for food. The flagellates typically clear a volume of water of about 10^5 times their own cell volume per h or from 5×10^{-6}–5×10^{-5} ml/h (20 °C) depending on size. Most forms, and in particular the often dominating choanoflagellates, are capable of retaining even the smallest prokaryote cells. The flagellates seem to be able to maintain balanced growth at generation times from about 3.5 h and up to about 24 h (20 °C); bacterial densities below around 10^6/ml do not seem to sustain flagellate growth.

These findings together allow the estimation of *in situ* grazing rates. It seems that in most offshore and coastal waters (during summer), zooflagellates on the average clear 20–50% of the water for bacteria per 24 h, although great temporal variation due to varying population sizes occur. Altogether, available evidence shows that phagotrophic flagellates constitute the dominating consumers of bacterial production and control their numbers.

The other dominating group of the planktonic microfauna is constituted by the ciliates. While the presence of the tintinnid oligotrichs has been recognized for a long time, recent studies based on more gentle sampling and fixation techniques have revealed that other ciliates, and in particular non-loricate oligotrichs, often play a substantial role.

Several quantitative studies prior to 1980 are reviewed by Taylor (1982). Other recent studies include Capriulo and Carpenter (1980), Hargraves (1981), Heinbokel and Beers (1979), and Rassoulzadegan (1977).

Ciliates typically number 0.1–10/ml seawater; since they are mostly much

larger than flagellates (15–200 μm for most plankton forms) the two groups on the average represent a similar biomass (0.1–10 mg c/m^3). Like flagellates, the numbers of ciliates fluctuate temporally. In eutrophic areas mass occurrence of ciliates may follow blooms of nanoplankton algae (e.g. > 100/ml have been found in the Limfjord during summer; see Andersen and Sørensen, 1986).

The dominating planktonic ciliates feed on photo- and heterotrophic nanoplankton cells, or on constituents of the microplankton such as dinoglagellates, diatoms or other ciliates. Bacterivorous ciliates play a small role in the plankton (see also Fenchel, 1980, 1984). Exceptions to this are very eutrophic waters (Burkill, 1982) and the microfauna associated with suspended detrital or flocculent material (Caron *et al.*, 1982).

Values of clearance for ciliates which filter larger (> 2 μm) particles are around 10^5 times cell volume per hour (Fenchel, 1986b) and this allows crude estimates of the grazing impact of ciliates. Estimates of ciliate grazing based on *in situ* measurements are still few and not easily compared. Heinbokel and Beers (1979) found that tintinnids consumed from 4 to 20% of the primary production off the California coast; since tintinnids usually constitute less than 50% of planktonic ciliates the total grazing impact of ciliates must have been larger. Capriulo and Carpenter (1980) found that ciliates (mainly tintinnids) consumed up to 41% of the standing crop of chorophyll per day in Long Island Sound. Both these studies ignore the grazing impact on non-photosynthetic cells.

Although still incomplete in some respects, a new picture of the planktonic food web has emerged during the past decade. In this picture the production of small cells (prokaryotes and photosynthetic nanoplankton) makes up for a much larger productivity than previously believed, and this production is largely mineralized through several trophic levels constituted by phagotrophic organisms in the 2 to 200 μm size range.

3.3 MINERALIZATION OF C, N AND P

Johannes (1964, 1965) was among the first to emphasize the role of the microfauna in the regeneration of mineral nutrients, a role traditionally assigned mainly to bacteria in aquatic environments. Several other studies ensued, most of which are reviewed in Taylor (1982). These were mostly carried out with some sort of batch cultures or with microcosms which did not allow balanced growth or steady-state conditions. Consequently the results could not easily be applied to natural conditions. However, the studies did make the point that bacteria often grow on organic substrates poor in mineral nutrients. Consequently, net mineralization of nitrogen and phosphorus is low, or the bacteria may even assimilate mineral nutrients in order to grow and compete with photosynthetic organisms. Grazers of bacteria, on the other hand, feed on particles with C:N and C:P ratios similar to their own cells, and since their growth efficiency is below unity they would regenerate mineral nutrients.

The role of phagotrophs in the cycling of mineral nutrients is, in most respects, much simpler than that of prokaryotes and photosynthetic organisms. This is because phagotrophs do not assimilate dissolved inorganic nutrients, but acquire N and P together with their food particles which have a rather constant composition. Assimilatory or dissimilatory reductions or oxidations of N-compounds do not occur (but see Finlay *et al.*, 1983). In small animals and in protozoa, metabolic rate is closely coupled to growth (Fenchel and Finlay, 1983) so that the regeneration of nutrients by small phagotrophs must be proportional to their metabolic rate, and is thus a simple function of the C:N (or C:P) ratio of the food and of the growth efficiency.

Using the 'IBP terminology' the consumption (on a carbon basis) equals $R + P + F + U$, where R is respiration, P is growth and F and U represent the egested and excreted organic carbon, respectively. Let $A = P + R$ and net growth efficiency becomes $E_n = P/A$. Finally let ρ_f and ρ_p represent the C:N ratio of the food particles and the predator, respectively. If $\rho_f = \rho_p = \rho$, then the excretion of

$$\mathrm{N} = R/\rho = A[1 - E_n]\rho^{-1}$$

If $\rho_f \neq \rho_p$, then regenerated nitrogen will equal the consumed N not egested or excreted as organic N minus that assimilated into cells, or

$$A/\rho_f - P/\rho_p = A[\rho_f^{-1} - E_n\rho^{-1p}]$$

The net growth efficiency of protozoa is 50–60% (Fenchel, 1982a; Fenchel and Finlay, 1983) while gross growth efficiency probably varies much more. Fenchel (1982a) found values of 30–40% of the ingested bacterial carbon was either egested or excreted in two heterotrophic flagellates. We may assume that values of the C:N ratio for bacteria as well as for protozoa are within the range 4–6, while in phytoplankton values between 6 and 10 are found (Finlay and Uhlig, 1981; Wheeler, 1983).

If the above listed values are considered to be correct in general, then it can be seen that in a protozoan food chain around 30–40% of the ingested organic N is excreted as mineral N at each trophic level. An exception may be forms grazing on phytoplankton cells; depending on the C:N ratio of the food particles the figure may be considerably lower. A similar argument, of course, applies to the regeneration of phosphate.

The experiments of Sherr *et al.* (1983) illustrate the considerations given above. These authors measured ammonia excretion in a culture of a heterotrophic flagellate during balanced growth at a known rate. Calculations on their results in conjunction with reasonable assumptions on growth efficiency accord with the simple equations given above (Fenchel, 1986a). The detailed study by Goldman *et al.* (1985) on the nitrogen excretion of another heterotrophic flagellate also accords with the principles outlined above.

The general conclusion of this is that the share of the remineralization of N by the nano- and microplankton must be nearly proportional to their share of the

carbon mineralization. Since probably the entire bacterial production, and a large part of the photosynthetic production, is consumed by the phagotrophic nano- and microplankton organisms, and since this pelagic constituent represents two or more trophic levels, its share in the entire remineralization must be considerable, a point also made recently by Ducklow (1983).

Another approach to the question is to measure remineralization directly in size-fractionated plankton samples. In general these studies suggest that plankton organisms $< 200\,\mu m$ are responsible for the largest part of the NH_4^+ regeneration in the water column. The details of the results, however, differ in some respects. Glibert (1982) found for a number of areas that the $< 10\,\mu m$ fraction generally yielded the largest contribution to N-remineralization only sometimes exceeded by the 10–35 μm or the 35–130 μm fraction. Harrison (1978) found that 39% of the NH_4^+ excretion was due to the $< 1\,\mu m$ (bacterial) fraction, 50% to the 1–35 μm and only 11% to the $> 35\,\mu m$ fraction. In contrast, Paasche and Kristiansen (1982) found that the microplankton (45–200 μm) consisting of heterotrophic dinoflagellates, ciliates, rotifers and copepod nauplii, yielded the largest contribution to the NH_4^+ regeneration. The studies also differ in terms of the degree to which the measured regeneration rate could meet the demands of the phytoplankton; thus Glibert (1982) found a close coupling and balance between remineralization and uptake, whereas Paasche and Kristiansen (1982) found that the regeneration of nutrients could only account for 28% or less of the rate of assimilation.

These discrepancies probably to some extent reflect real differences between the nutrient cycles in different areas. They probably also reflect the complex successional patterns and rapid oscillations in numbers of different functional groups of the plankton maintained by predator–prey interactions. These processes must necessarily also induce fluctuations in nutrient fluxes with similar time scales. While the question of rates of remineralization of N and P of phagotrophs is mainly one of understanding their role in the carbon cycle, the most challenging problem in the ecology of plankton will be to understand the population dynamics of a system which is never in a steady state.

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