Nitrogen Cycling in Coastal Marine Environments
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CHAPTER 15

Nitrogen Models at the Community Level: plant–animal–microbe interactions

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15.1 INTRODUCTION

The significance of heterotrophic processes in the regeneration of nutrients necessary to support primary production has been widely recognized in recent years (for reviews see Pomeroy *et al.*, 1981; Field, 1984). Most studies of shallow-water coastal communities suggest that remineralization of nitrogen by the heterotrophic activity of both the microbiota and the larger macrofauna may be of importance in supporting primary production both in phytoplankton-dominated systems and in those where macrophytes are the dominant source of primary production (Rowe *et al.*, 1975; Nixon *et al.*, 1976; Rowe and Smith, 1977; Billen, 1978; Blackburn and Henriksen, 1983; Kautsky and Wallentinus, 1980; Nixon, 1980; Pilson and Nixon, 1980; Raine and Patching, 1980; Jansson *et al.*, 1982; La Roche, 1983; Newell and Field, 1983a,b; Hargrave *et al.*, 1985).

Estimates of carbon and nitrogen flux through intertidal communities indicate that remineralization of nitrogen through the heterotrophs may also be primarily responsible for the maintenance of rich diatom blooms which occur in the surf zone adjacent to 'high-energy' sandy shores (McLachlan *et al.*, 1981; see also Pearse *et al.*, 1942; Lewin *et al.*, 1975). Analysis of the trophic structure and fluxes of carbon in shelf waters of the North Sea by Joiris *et al.* (1982) suggests that as much as 50% of the annual phytoplankton production sinks to the sea bed as detritus and is supplemented by the faecal pellets of the zooplankton (see also Smetacek, 1984). The benthos is thus heavily implicated in carbon flow in several coastal systems, over 35% of the phytoplankton net production in the Belgian waters of the North Sea being utilized by bacteria (Joiris *et al.*, 1982).

Whether the high carbon flux through the microbial community results in a net remineralization of nutrients in this and other systems is, however, an open and exciting question. The answer to this question reflies on understanding the flux of materials through a community whose biomass and contribution to secondary

production has been recognized only relatively recently. The object of our review is to synthesize some recent developments in our understanding of material flux through the microbial community, and to show how apparently conflicting results for carbon and nitrogen flux can be united to develop a more coherent understanding of the role of the microheterotrophic community in the maintenance of primary production in marine environments.

15.2 OUTLINE OF CONCEPTUAL MODEL

The role of the microheterotrophic community of bacteria and protozoa in marine systems has attracted considerable attention, particularly since it is now known that the biomass of bacteria may comprise a significant and sometimes dominant proportion of the total biomass of all heterotrophic consumer organisms in the water column (Sorokin, 1975, 1981; Sieburth *et al.*, 1978; Holligan *et al.*, 1984; Newell and Linley, 1984). Sorokin and Mikheev (1979), in a comprehensive study of energy flow through the pelagic community associated with the Peruvian upwelling system have estimated that as much as 70–80% of the total energy flux occurs through the microheterotrophic community of bacteria, heterotrophic flagellates and ciliates. Pace *et al.* (1984) have simulated continental shelf food webs on a seasonal scale and have shown that, contrary to previous models where all phytoplankton were considered to be grazed by zooplankton (see Steele, 1974), only slightly more than 50% of annual net production may be grazed (see also Williams, 1981). A similar rather high carbon flow of approximately 60% of primary production has also been estimated to flow into the microheterotrophic decomposer pathway at the end of a phytoplankton bloom in mixed waters of the English Channel, with an associated nitrogen regeneration of approximately 70% of that required for primary production (Newell and Linley, 1984).

Other estimates for the Atlantic Ocean suggest that the microbial contribution to regenerated nitrogen is less than might be supposed from their relatively high biomass and small cell size. Walsh *et al.* (1978) constructed an annual nitrogen budget for the Atlanic continental shelf which suggested that approximately 46% of primary production is supported by nutrient recycling. Zooplankton were responsible for 38% of the regenerated nitrogen, benthos 38% and bacteria 24%. Thus bacterial remineralization accounted for only 11% of the requirements of primary production (see also Smith and Whitledge, 1977). Harrison *et al.* (1983) have made similar estimates for the outer shelf of the Middle Atlanic Bight in summer and reported that regenerated nitrogen accounted for 33% of the total nitrogen requirements of primary production. Of this, zooplankton were responsible for the regeneration of 30%, benthos 7%, microplankton $> 1\ \mu m$ 16% and microplankton $< 1\ \mu M$ 47%. Although the bacteria were of more importance in nitrogen regeneration than the other components, they nevertheless accounted

for only 23% of the requirements of primary production at the time of the survey.

To a large extent these differences relate to probable spatial and temporal differences in the water masses at the time of the surveys (Newell *et al.*, 1985). Most conceptual models of material flow through marine systems are based on quasi-'steady-state' assumptions. Material flux is estimated from the results of experimental studies on the flux of carbon, and sometimes other elements, through key components of the community. Such estimations are a necessary part of the development of more complex systems models, yet their shortcomings are generally obvious. A recent simulation model by Moloney *et al.* (1986) avoids some of the problems associated with temporal changes in the plankton community. The model shows that following an initial pulse of 'new' NO_3^--N, remineralization by bacteria and protozoa is important in sustaining the middle phase of a phytoplankton bloom, but that regeneration by crustacean zooplankton is increasingly important towards the end of a bloom (see also Dugdale and Goering, 1967; Yentsch *et al.*, 1977). Estimates of the relative importance of microheterotrophs and larger consumers in nutrient regeneration, and indeed the absolute requirements of the phytoplankton, are therefore mainly dependent on the phase of the phytoplankton bloom which may vary on a short-term time scale in upwelling areas (see Andrews and Hutchings, 1980; Wulff and Field, 1983), seasonally in temperate seas, or on a longer time scale in stratified tropical waters (see also Newell *et al.*, 1985).

Marked differences in the quality and quantity of substrate, and in the types of microbial community associated with them, also occur on relatively small time and space scales (Koop *et al.*, 1982a; Davis *et al.*, 1983; Fukami *et al.*, 1985b). Recent evidence suggests that production by the bacterial community in surface waters may be closely coupled with extracellular release of photosynthetically produced dissolved organic carbon (PDOC; see Bell and Mitchell, 1972; Waite and Duthie, 1975; Wright and Shah, 1975; Nalewajko and Schindler, 1976; Wiebe and Smith, 1977; Smith *et al.*, 1977; Cole *et al.*, 1982; Larsson and Hagström, 1982) and in some cases shows a diel rhythm probably related to pulses in PDOC release by the phytoplankton (Turley and Lochte, 1986). The microbial community associated with the pycnocline, and that which characterizes environments dominated by macrophyte communities may, however, be primarily adapted to exploit particulate organic detritus and may show very different generation times and growth yields from those obtained in low concentrations of ^{14}C-labelled simple organic substrates (Payne, 1970; Lucas *et al.*, 1981; Newell *et al.*, 1981, 1983; Turley and Lochte, 1986).

The development of any conceptual models for material fluxes through the community as a whole must therefore address two main questions: (a) What substrates do various bacteria utilize under natural conditions? (b) What is the flux of materials through bacteria using the natural substrates available in the sea?

15.2.1 What substrates do bacteria utilize under natural conditions?

One of the problems in studying uptake of dissolved organic matter by marine bacteria is that the concentrations required to simulate natural conditions must be very low. The incorporation of ^{14}C-labelled simple organic molecules has been widely used to estimate the kinetics of uptake by bacteria (Wright and Hobbie, 1965; Hobbie, 1967; Hobbie and Crawford, 1969; Gordon *et al.*, 1973; Crawford *et al.*, 1974; Azam and Hodson, 1981; Wolter, 1982; Cole *et al.*, 1982; Azam *et al.*, 1983). Generally, marine bacteria incorporate such molecules with a high efficiency of at least 65% (for reviews, see Payne, 1970; Fenchel and Jørgensen, 1976; Joint and Morris, 1982), and it is now generally agreed that 10–30% of carbon flow from primary production is channelled through the extracellular leachates (PDOC) into bacteria (Larsson and Hagström, 1982; Cole *et al.*, 1982).

Figure 15.1 shows depth profiles for a station in the Southern Benguela upwelling system (latitude 32.4 °S: longitude 18.5 °E) and a similar profile for Antarctic waters (latitude 63°S: longtitude 60 °E; based on data from Painting *et al.*, 1985a,b; Lucas *et al.*, 1986, 1987). Primary production by the phytoplankton (mg $C\,m^{-3}\,d^{-1}$) and a mean of bacterial production estimated by both the [^{3}H]thymidine incorporation method of Fuhrman and Azam (1980) and from the incremental increase in biomass of bacteria in predator-free incubations (see

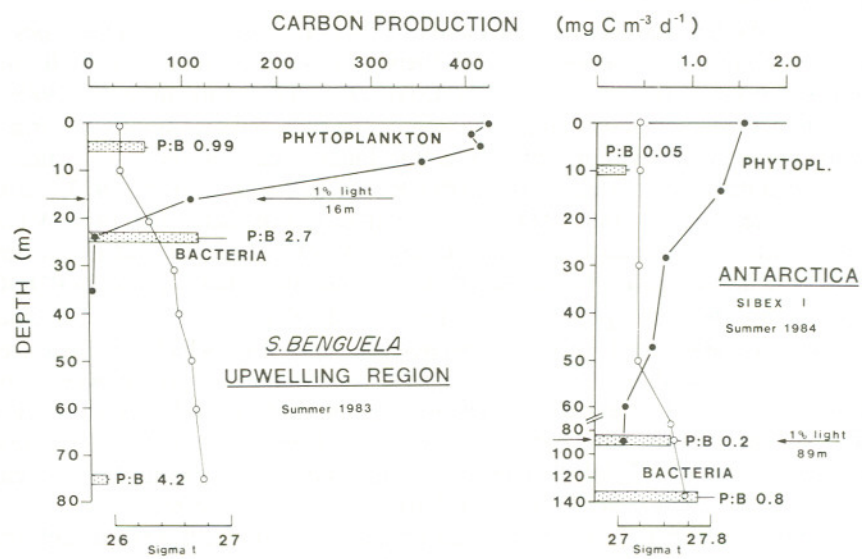

Figure 15.1. Depth profiles for primary production and bacterial production (mg $C\,m^{-3}\,d^{-1}$) estimated as a mean of both the [^{3}H]thymidine incorporation method and from predator-free incubations in the Benguela upwelling system and in Antarctic waters (lat. 63 °S; long. 60 °E). Values for sigma-*t* are also shown. (Based on Painting *et al.*, 1985, 1987.)

Lucas *et al.*, 1986) are superimposed on to values for sigma-*t*. It will be seen that production by the bacteria in the surface waters amounts to 14% of primary production in the Benguela depth profile and to 23% in the profile taken in Antarctic waters. Note that there are also major differences in the levels of primary production and microbial production in the two systems. In both cases, however, and in accordance with the conclusions summarized above, bacterial production in the euphotic zone could be supported by PDOC release amounting to 20–33% of primary production at a conversion efficiency of 70%.

It is important to notice, however, that production by bacteria at the pycnocline and below considerably exceeds primary production, and is in fact sustained at depths where net primary production is zero. Bacterial production can also exceed primary production during the collapse phase of phytoplankton blooms (Newell *et al.*, 1985; Lucas *et al.*, 1986; Painting *et al.*, 1987). In these cases, bacterial production is likely to be sustained by utilization of particulate organic matter as a primary carbon resource (see also Newell and Linley, 1984) and a good correlation is obtained between bacterial biomass and POC in the water column (Lucas *et al.*, 1986; see also Figure 15.2). Indeed, many studies have now shown that bacterial production values similar to the maximum recorded in coastal waters can be obtained by incubation of natural communities of marine bacteria in the presence of detrital substrates from a variety of sources (Lucas *et al.*, 1981; Stuart *et al.*, 1981, 1982b; Newell *et al.*, 1981, 1983; for review, Linley and Newell, 1985).

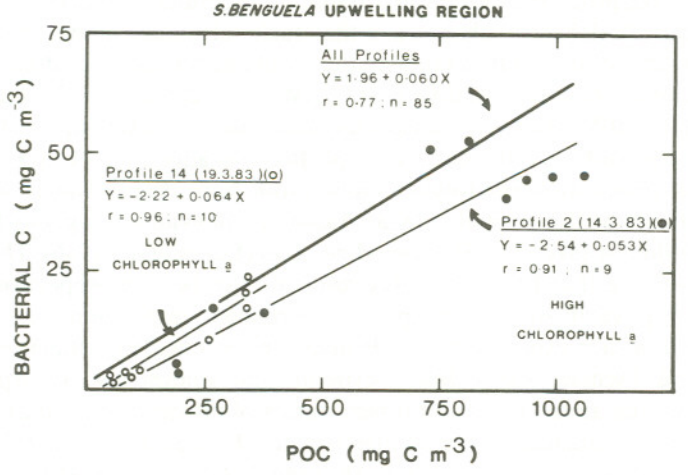

Figure 15.2 The relationship between bacterial biomass (mg C/m^3) and particulate organic carbon (POC; mg C/m^3) for two separate profiles (2 and 14) from the S. Benguela region at the beginning and end of a phytoplankton bloom. The relationship is shown also for all profiles (2–18) during the course of a bloom. (After Lucas *et al.*, 1986.)

Although subunit models for particular phases of a phytoplankton bloom in surface waters could thus be based principally on carbon flow from phytoplankton via dissolved leachates into the microbial community, it is clear that any time- or depth-integrated model must be based on the incorporation of simple organic leachates as well as the more complex and refractory molecules which make up the bulk of the material entering the detrital pathway.

15.2.2 What is the flux of materials through bacteria?

The second question, which must be addressed in any conceptual model of material flow through marine systems, is the amount material which is incorporated into microbial biomass relative to the amount fluxed. Williams (1973) pointed out that the 'apparent growth yield' (α) of simple ^{14}C-labelled organic substrates could be estimated from the net ^{14}C incorporated into the microheterotrophs divided by the sum of the ^{14}C incorporated and the ^{14}C respired (i.e. the total flux). Values for the growth yields of a variety of heterotrophs have been given by Calow (1977) and Payne and Wiebe (1978); more recently, Joint and Morris (1982) have summarized values for marine bacteria. In general, the growth yield for actively growing cultures of marine bacteria in the presence of simple ^{14}C-labelled organic substrates is approximately 60–70%, although in some cases much lower values than this have been obtained with heterogeneous populations of marine bacteria in the southern North Sea (Billen *et al.*, 1980; see also Wiebe and Smith, 1977; Cole *et al.*, 1982).

One of the problems with the extrapolation of results from experiments based on simple ^{14}C-labelled substrates is that such substances commonly comprise only 10–25% of the total organic matter available for bacterial decomposition, and may even represent as little as 0.1% (Wiebe and Smith, 1977; Larsson and Hagström, 1979). Different substrates may also be taken up with differing efficiency according to the bacterial type. Bacteria adjacent to kelp beds are, for example, primarily mannitolytic, whilst those from deeper waters are mainly glucolytic forms (Koop *et al.*, 1982a). Again, recent evidence suggests that flavobacteria do not take up [^{3}H] thymidine at all (Lucas *et al.*, 1986). There is also some evidence that because $^{14}CO_2$ respired may be non-proportional to the $^{12}CO_2$ respired in short-term uptake experiments, respiration may be underestimated in such experiments (see Hanson and Wiebe, 1977; Billen *et al.*, 1980; King and Berman, 1984). Many experimental studies also incorporate the addition of casamino acids and other sources of nitrogen to facilitate bacterial uptake of ^{14}C-labelled carbon sources (see also Payne and Wiebe, 1978). As will be shown below, this may radically alter the flux of nitrogen associated with a measured carbon incorporation by the microheterotrophs. The 'growth yield', the proportion of primary production represented by simple organic molecules released as exudates, and the C:N ratio of the substrates, as well as the size of the nitrogen pool, thus need to be taken into account in estimation of coupled carbon

and nitrogen flux through the PDOC pathway (see Billen and Lancelot, this volume).

The problem of estimating 'growth yield' for the particulate pathway is less complicated than that for PDOC, since in general concentrations of POC are relatively high in detritus-dominated systems. The utilization of carbon from batch cultures can therefore be followed by routine CHN analysis. We have made simultaneous CHN analyses and direct measurements of bacterial production by the incremental growth method in incubations with detritus from kelp (Newell *et al.*, 1980; Linley and Newell, 1981; Linley *et al.*, 1981; Newell and Lucas, 1981; Stuart *et al.*, 1981, 1982b; Koop *et al.*, 1982a,b), phytoplankton (Newell *et al.*, 1981) and saltmarsh grasses (Newell *et al.*, 1983). The numbers of microorganisms can be estimated by acridine orange direct counts (ADOC; see Hobbie *et al.*, 1977; Daley, 1979) whilst the size of the cells, and hence the mean cell volume, can be estimated either from AODC (Fuhrman, 1981) or from scanning electron microscopy (Dempsey, 1981; Linley *et al.*, 1981). The net growth yield, or amount of material which is incorporated into bacterial growth, is then obtained directly in terms of carbon or nitrogen by division of the carbon and nitrogen equivalents of bacterial biomass by that utilized from the detrital substrate.

We have referred to these values as the 'carbon conversion efficiency' and 'nitrogen conversion efficiency' (see Newell, 1984; Linley and Newell, 1985) but essentially they represent the carbon and nitrogen equivalents of the net growth yields. The values obtained for particulate detrital material incubated under laboratory and field conditions is, in all instances, much lower than that reported above for the PDOC pathway. We have obtained mean values for the carbon conversion efficiency of natural heterogeneous bacterial populations on phytoplankton debris from various sources of 9.9% (Newell *et al.*, 1981), macroalgae 8.8% (Newell and Lucas, 1981; Stuart *et al.*, 1982a; Koop *et al.*, 1982b) and saltmarsh grasses of 9.7% (Newell *et al.*, 1983; see also Robertson *et al.*, 1982). Similar high rates of respiratory losses have been reported for the degradation of phytoplankton detritus by Bauerfeind (1985), who found that 70–80% of the carbon consumed by bacteria is respired. That is, the carbon conversion efficiency could in this case not have exceeded 20–30%.

In general, a carbon conversion efficiency or net growth yield in terms of carbon of only 10–15% has been obtained when no nitrogen has been added to the media. This value is increased to 37% under natural conditions when ammonia regeneration occurs (Koop *et al.*, 1982c) or when nitrate and phosphate have been added to cultures (Newell *et al.*, 1983). These higher values conform with those obtained by Robinson *et al.* (1982) for fresh kelp detritus, but are still much lower than those recorded for simple ^{14}C-labelled compounds. The experimental evidence suggests, therefore, that models of carbon flow and associated nitrogen flux through the microheterotrophic community should be based on a small proportion of material (less than 30%), representing PDOC as leachates which are converted with a high efficiency, and a larger proportion

probably amounting to as much as 70% of primary production, being converted as senescent detrital biomass with a low efficiency by marine bacterial communities after a time lag.

Fenchel and Blackburn (1979), Billen (1984) and more recently Linley and Newell (1985) have shown that the absolute values of carbon and nitrogen incorporation and the resultant flux of these elements is dependent to a large extent on the C:N ratio of the substrate relative to that of the bacteria. Figure 15.3 shows the theoretical net growth yield for bacteria which have an assumed maximal C:N ratio of 6.0 and a minimal ratio of 2.7 (C/N_b). The theoretical maximal growth yields is given by the C:N ratio of the bacteria

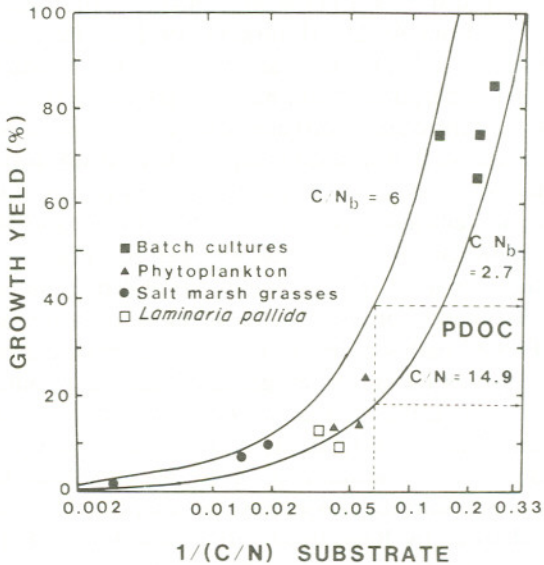

Figure 15.3. The theoretical potential growth yield (Y_g) of bacteria on idealized substrates with known C:N ratios (C/N_s). The extreme C:N ratios of bacteria (C/N_b) have been taken to be 2.7 and 6.0, and the growth yield (Y_g) obtained from $Y_g = (C/N_b)/(C/N_s)$ (see Fenchel and Blackburn, 1979). Experimentally determined growth yields for detritus are shown plotted against the approximate carbon to utilizable nitrogen ratio of the substrates. Values for batch cultures on enriched media obtained by Payne and Williams (1976) are shown for comparison. The estimated growth yield of bacteria on PDOC from kelp (C:N = 14.9) is also shown. (After Linley and Newell, 1985.)

divided by the C:N ratio of the substrate:

$$Y_g = \frac{C/N_b}{C/N_s} \quad (1)$$

Thus if the C:N ratio of the substrate is identical to that of the bacteria, a maximal growth yield of as much as 90% could be obtained if only 10% of the carbon were dissipated through respiration. On the other hand, where the C:N ratio is high, as in the case of most detrital substrates forming the POC pool, the amount of carbon fluxed through the bacteria will need to be great before sufficient nitrogen, or other limiting elements, are obtained to meet the requirements for biosynthesis and growth. The C:N ratio of some macrophytes reaches 35:1 or even 75:1 (Russell-Hunter, 1970) so that, in the absence of a large nitrogen pool, major fluxes of carbon and an efficient conservation of nitrogen are to be anticipated in macrophyte POC-dominated systems (Billen and Lancelot, this volume).

In accordance with this prediction we have obtained nitrogen conversion efficiency values both in field-based studies and in experimental microcosms as high as 83–94% with kelp debris and faecal material from mussels (Koop *et al.*, 1982c; Stuart *et al.*, 1982a). The corresponding carbon conversion efficiency in these experiments was only 9–12%. A similar high conversion efficiency for nitrogen compared with that for carbon has also recently been described for microbial conversion of phytoplankton by marine bacteria (Fukami *et al.*, 1985a).

Some of the growth yields obtained in batch cultures of marine bacteria incubated with various substrates of varying C:N ratio are summarized in Figure 15.3 (after Linley and Newell, 1985). The absolute values for nitrogen have been corrected where possible for refractory humic compounds, and have been termed 'utilizable nitrogen'. Where simple organic carbon sources have been used the nitrogen content of the casamino acids and other co-factors added to the experimental medium has been used to estimate the C:N ratio of the medium as a whole. The general correspondence between the theoretical growth yields based on equation (1) and the results of experimental incubations with a wide variety of both simple organic carbon sources and more complex components of structural particulate debris is clear.

What emerges from these studies is that there are good theoretical reasons why major differences in the carbon growth yields should be obtained from experiments using dissolved and particulate substrates, particularly when nitrogen additives have been supplied to facilitate uptake of ^{14}C-labelled compounds at low substrate concentrations. It is also apparent that fluxes of carbon and nitrogen through both the PDOC and POC pathways form an integral part of our understanding of material flow through the system as a whole. Provided we know the C:N ratio of the components in the food web it becomes possible to incorporate the quantitative differences between the PDOC and POC pathways, as well as the different growth yields of bacteria based on them, into

some simple holistic models of carbon and nitrogen flux through marine systems which are nitrogen limited. That is, through systems where uptake of nitrogen from the abiotic N-pool is small compared with flux through the biotic pool.

15.3 A SIMPLE CONCEPTUAL MODEL FOR A MACROPHYTE COMMUNITY

15.3.1 The fate of different components of kelp

In our earlier work on the flow of carbon from kelp into bacteria we were able to estimate the proportion of flow via particulate matter and cell contents released during the fragmentation process, as well as the proportion of extracellular leachates. The latter comprise significant quantities of the primary photosynthate D-mannitol, although more complex polymers including alginates and laminarins are released with mannitol during fragmentation of the tip of the fronds (Newell *et al.*, 1980; Lucas *et al.*, 1981; Newell and Lucas, 1981; Linley and Newell, 1981).

There is a considerable body of experimental data on the microbial conversion of the particulate and cell content fractions, although we have no direct measurements of microbial growth yields based on extracellular leachates (PDOC) from kelp. Since the C:N ratio of the extracellular DOM is 14.9 (Newell and Lucas, 1981; Linley, 1983), we can use Figure 15.3 to arrive at a value for the carbon conversion efficiency or growth yield of bacteria on this fraction. As can be seen from Figure 15.3, depending on the C:N ratio of the bacteria, a carbon conversion efficiency of 20–40% would be anticipated for the extracellular DOM fraction leaching from the surface of the living kelp fronds. The yields from each of these pathways for a kelp bed at Kommetjie on the west coast of the Cape Peninsula, are summarized in Figure 15.4 (from data in Newell *et al.*, 1980; Linley *et al.*, 1981; Lucas *et al.*, 1981).

From this it is clear that of the annual production of 1172 g $C\,m^{-2}\,y^{-1}$ of kelp bed at this particular study site, 574 g $C\,m^{-2}\,y^{-1}$ is estimated to flow into the POC pool and is converted with a low efficiency of 9.1% from our estimates for incubation of particulate kelp debris in seawater with natural heterogeneous bacterial populations (see Stuart *et al.*, 1982a, Newell, 1985). The cell contents (DOC) or 'mucilage' released during fragmentation are estimated to amount to 246 g $Cm^{-2}\,y^{-1}$, and are converted into bacterial carbon with a mean value of 13.2% based on our experimental incubations of both *Laminaria pallida* and *Ecklonia maxima* mucilage (for review, see Newell, 1984; Linley and Newell, 1984). Finally, the extracellular leachates (PDOC) are estimated to amount to 352 g $Cm^{-2}\,y^{-1}$, or approximately 30% of primary production (see Hatcher *et al.*, 1977; Johnston *et al.*, 1977; Newell *et al.*, 1980). From the protein analysis a C:N ratio of 14.9 gives an estimated mean carbon conversion efficiency from Figure 15.3 of 30.1%.

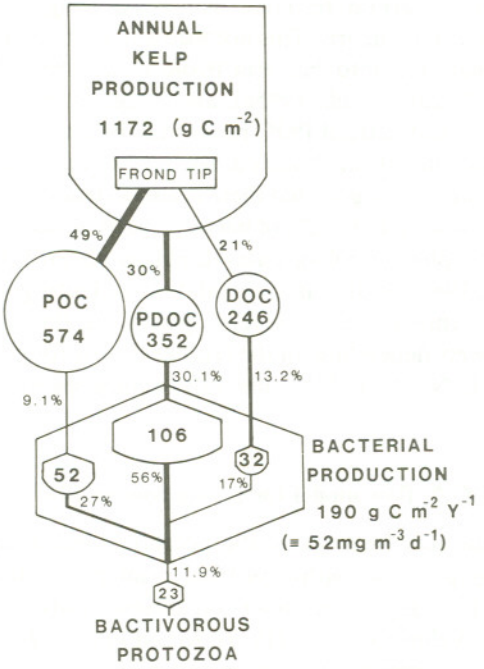

Figure 15.4 A simple model showing the flow of carbon from a kelp bed at Kommetjie, Cape Peninsula, via particulates (POC), extracellular leachates (PDOC) and cell contents (DOC) into bacteria. (Based on Linley and Newell, 1985.)

The contibution of the three different pathways to bacterial carbon production and carbon flux is therefore very different. The particulate pathway (POC) yields a bacterial production of only 52 g C m^{-2} y^{-1} and large amounts of carbon and associated elements are therefore fluxed through this pathway. Cell contents comprising more complex 'dissolved' molecules (DOC) released in mucilage during fragmentation contribute only 32 g C m^{-2} y^{-1} as bacterial production. In contrast, despite the relatively small proportion of carbon released in the extracellular leachate (PDOC) pathway, a high bacterial production of 106 g C m^{-2} y^{-1} is obtained. This gives a total of 190 g C m^{-2} y^{-1} which is equivalent to 52 mg C m^{-3} d^{-1} in the shallow water of the kelp bed. Interestingly, this figure for the estimated carbon production by the bacteria which could be supported from kelp production agrees closely with that obtained independently from direct studies of the biomass and generation time of bacteria in the water column (Mazure and Field, 1980; Linley and Field, 1981; Linley, 1983; Fenchel, this volume).

Carbon flow estimates based on kelp thus suggest that bacteria incorporate

PDOC as a primary carbon resource whilst oxidizing the more refractory components of particulate debris. This accords well with recent work on carbon flow from phytoplankton into bacteria (Cole *et al.*, 1982; Azam *et al.*, 1983; Bauerfeind, 1985; Fukami *et al.*, 1985a), and suggests that the conversion of carbon from PDOC and detrital POC pools may be only loosely coupled. Our estimates of carbon flux from bacteria to heterotrophic microflagellates in experimental incubations suggest that there is also a strong remineralization step from bacteria to protozoa, only 12% of bacterial carbon being incorporated into the grazing heterotrophic microflagellates (Linley *et al.*, 1981; Linley and Newell, 1981; Newell *et al.*, 1981, 1983). Carbon oxidation and nitrogen remineralization may therefore be anticipated at several points in the microheterotrophic decomposer food web, depending on the relative flow through PDOC and POC pathways and the C:N ratios of the substrates compared with those of bacteria and protozoa.

15.3.2 A coupled C:N flow model for a kelp community

Some estimates can now be made of the potential significance of carbon and nitrogen flow through these pathways from primary production by the kelp community into the larger consumer organisms. Earlier studies by Field *et al.* (1977, 1980), Velimirov *et al.* (1977), Mann *et al.* (1979) and Dieckmann (1980) established the primary production and biomass of key consumers in the kelp communities of the Cape Peninsula, South Africa. Subsequent work showed that there were few grazing herbivores, and that the system is dominated by filter-feeders (Newell, 1982, 1984). The energetics of the principle consumers (for review, see Field, 1984) allow some estimates to be made of the carbon and nitrogen requirements of the consumer community in relation to supply from phyto-plankton, bacteria and detrital resources.

Newell *et al.* (1982) Drew up an energy budget based on these studies, which indicated that primary production in the kelp beds was approximately equal to the energy requirements of the consumers under steady-state conditions. Wulff and Field (1984) developed a simulation model which subsequently allowed some estimates to be made of the effects of the intermittent pulses of water transport associated with the upwelling and downwelling conditions which characterize the Southern Benguela system. This model showed that during strong upwelling conditions there was a net transport of particulate debris offshore, and the community then showed a deficit in carbon balance. During downwelling conditions imported phytoplankton became an important carbon source, whilst during the 'steady-state' conditions between periods of water exchange, the sums of both phytoplankton and detrital pools were of importance as energy resources. To a large extent these predictions have been validated in subsequent studies on the phytoplankton, bacterial and detrital resources during upwelling: downwell-ing cycles on the Cape Peninsula (Seiderer and Newell, 1985; see also Table 15.2).

Table 15.1. Carbon flow from phytoplankton and macrophytes through a typical kelp community on the west coast of the Cape Peninsula, South Africa. All units in g carbon per $m^2 y^{-1}$

	Phytoplankton	Macrophytes	Total
Primary production	501	917	1418
PDOC at 30% of primary production	150	275	425
Bacterial incorporation of PDOC at 65% carbon conversion efficiency	98	179	277
Bacterial incorporation via detrital pathway	32	83	115
Total incorporation into bacterial biomass	130	262	392

After Newell and Field, 1983a, b.

The estimated microbial carbon yield from phytoplankton and macrophytes in a generalized west coast kelp bed is summarized from Newell and Field (1983b) in Table 15.1. From this it can be seen that when microbial conversion of both the carbon from the POC pool and the PDOC from primary production is taken into account, approximately 392 g C $m^{-2} y^{-1}$ is incorporated into microbial biomass. Microbial carbon thus amounts to only 27% of that available for exploitation by direct consumption of phytoplankton and particulate debris from macrophytes. It represents only 30% of the 1297 g C $m^{-2} y^{-1}$ required by the consumer community (Newell and Field, 1983a,b). Carbon is thus inferred to flow directly from primary production into the filter-feeding consumer organisms rather than via bacteria in the kelp bed system. The standing stocks of bacteria are also thought to be an insignificant carbon resource for several deposit feeders in saltmarsh–wetland ecosystems including molluscs and the polychaete *Nereis succinea* (Baker and Bradnam, 1976; Tunnicliffe and Risk, 1977; Wetzel, 1977; Cammen, 1980a,b; Jensen and Siegismund, 1980). Experimental studies on mussels from the kelp beds support the inferences made from the carbon flow model. *Aulacomya ater*, for example, is capable of absorption of structural detritus with an efficiency comparable to that for phytoplankton (Stuart, 1982; Stuart *et al.*, 1982a; see also Seiderer *et al.*, 1982).

The corresponding flux of nitrogen through the kelp community can be estimated from these carbon flow values provided the C:N ratio of the key consumers as well as that of their food and faeces is known. A generalized flow diagram for carbon and nitrogen through the kelp community is shown in Figure 15.5. Respiratory losses of carbon from the filter feeders and bacteria are shown as well as the flow of carbon through fragmentation leachates (DOC) and from extracellular PDOC. The important point is that although losses of carbon are high from this system which is supported primarily on particulate material with a high C:N ratio, nitrogen (indicated by black arrows) is efficiently conserved by the bacteria associated with the particulate matter and in the water column. Bacterial incorporation of nitrogen from dissolved and metabolized

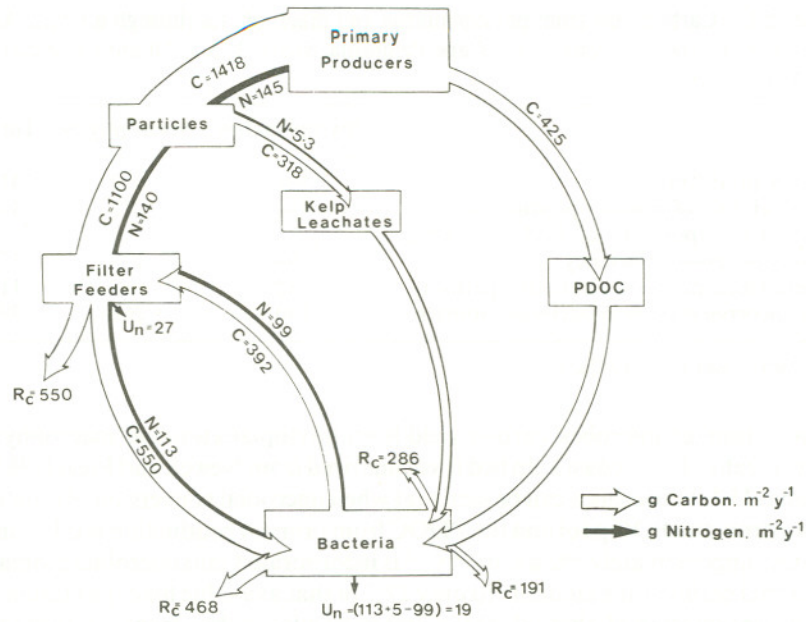

Figure 15.5 A coupled carbon and nitrogen flow diagram for a typical kelp bed community on the west coast of the Cape Peninsula, South Africa. All flows are in $g\,m^{-2}\,y^{-1}$. Primary producers are phytoplankton and macroalgae; the latter fragment into particles giving off leachates which are converted into bacterial carbon at 10% efficiency. The living primary producers are assumed to exude an additional 30% of net primary production as photosynthetic dissolved organic carbon (PDOC) which is converted at 65% efficiency into bacterial carbon. Filter feeders absorb particles at 50% efficiency and void faeces with mucus and excreta which are utilized by bacteria. Bacterial production is shown in the 'detrital loop' feeding back carbon and nitrogen to filter feeders. Respired carbon (R_c) and nitrogen excreted but not accounted for by bacteria (U_n) are shown. (After Newell and Field, 1983b.)

losses by the consumer organisms amounts to $99\,g\,m^{-2}\,y^{-1}$ (Newell and Field, 1983a) and this represents approximately 70% of the $140\,g\,N\,m^{-2}\,y^{-1}$ which flows directly from primary production.

15.3.3 Evaluation and significance of the model

The conclusion from a coupled C:N mass balance model of this sort is that because of the low efficiency with which carbon is converted from the particulate pool into microbial biomass, bacteria are relatively unimportant as a carbon resource compared with phytoplankton and particulate matter from macrophytes. But because of the high efficiency of incorporation of nitrogen by the bacteria (see Koop *et al.*, 1982c), their relative significance as a nitrogen resource

is much greater than that for carbon. Because the nitrogen is effectively conserved in this detritus-dominated system, it follows that remineralization losses from the bacteria in kelp communities are likely to be small and that primary production is probably sustained by regular input of nitrogen from outside the system during periods of upwelling (see also Wulff and Field, 1984; Field, 1984; Probyn and McQuaid, 1985).

Recent studies on the relative significance of detritus, phytoplankton and bacteria in kelp communities tend to support the predictions made from the coupled C:N mass balance estimates made above. Seiderer and Newell (1985) have recently shown that the standing stocks of phytoplankton in the kelp beds are very variable, depending among other factors on whether clear nutrient rich upwelled water is entering the kelp bed system during periods of south-easterly winds or whether downwelled phytoplankton rich surface water is present. The detrital component also varies according to the phase of upwelling and downwelling cycle, but the bacterial community is less variable.

Table 15.2 shows the mean values for carbon and nitrogen resources represented by phytoplankton, bacteria and detritus during upwelling and downwelling conditions on the west coast of the Cape Peninsula, South Africa, and on the east coast. The importance of phytoplankton and detrital pools as a carbon resource is very clear. It will also be noticed that in accordance with the inferences from the mass balance model shown in Figure 15.5, bacteria represent an important nitrogen resource which may even exceed that of the phytoplankton. Relatively high nitrogen values for the natural detrital material suggest in addition that attached bacteria may have some importance as a potential nitrogen resource for consumer organisms.

Recent measurements of ^{15}N-flux in waters of the kelp bed also tend to support the inference made from the coupled C:N mass balance for the system. Probyn (unpublished) has found no evidence of a measurable NH_4^+-N remineralization in the $< 10\,\mu M$ and $< 1\,\mu M$ size classes of kelp bed water, despite the fact that

Table 15.2. Mean values for carbon and nitrogen resources in phytoplankton, bacteria and detritus in nearshore waters of the Cape Peninsula, South Africa (data expressed as $\mu g/l$)

	Phytoplankton		Bacteria		Detritus		Total	
Site	C	N	C	N	C	N	C	N
West Coast								
Upwelling	129.5	19.7	58.2	15.6	124.9	11.5	307.1	46.2
Downwelling	209.9	31.8	75.3	21.5	173.1	17.8	458.3	71.1
False Bay	121.7	18.4	82.3	23.5	113.4	6.0	317.4	47.9

From Seiderer and Newell, 1985.

identical fractionation techniques show strong remineralization in other systems (see below).

Carbon and nitrogen flow thus appear to be only loosely coupled in the kelp bed, with a major flux of carbon but tight conservation of nitrogen apparently characterizing systems with a high C:N ratio and in which nitrogen is therefore limiting (see also Field, 1984). We may turn our attention now to a mass balance model based on a similar approach to carbon and nitrogen flux through a very different system in which the C:N ratios are much lower.

15.4 A NITROGEN FLOW MODEL FOR A PELAGIC SYSTEM

15.4.1 Presentation of the model

Values for the biomass of the main components of the plankton may be combined with estimates of their physiological energetics to arrive at a mass balance for carbon. From this, in much the same way as the kelp bed model, estimates can be made for the associated nitrogen flux through the system provided that the C:N ratios of the components are known (Newell and Linley, 1984).

A carbon mass balance diagram for a mixed water station in the English Channel based on data from Holligan *et al.* (1984) is shown in Figure 15.6. Flow from the phytoplankton to the grazing zooplankton is estimated from the integrated biomass of meso- and microzooplankton (mainly copepods and copepodites) down to the sea floor and literature values for their consumption, absorption efficiency and respiratory losses. That to the bacteria is based on the integrated biomass and on the conversion of PDOC (30% of primary production) at an efficiency of 0.65 (see Joint and Morris, 1982) and a lower value of 0.16, representing the mean of all our estimates for conversion of the 70% of primary production represented by particulate components (Newell *et al.*, 1981; Linley *et al.*, 1983). Bacterial consumption requirements are thus calculated from a mean conversion efficiency of $P/0.31$.

Several features of interest emerge from this simple mass balance model. First, there is a relatively strong flow of approximately 61% of carbon from primary production to the microheterotrophic community of bacteria and protozoa. This estimate in general conforms with that of Andrews and Williams (1971) who concluded that up to 50% of net phytoplankton production is taken up by the microheterotrophic community (see also Sorokin and Mikheev, 1979). It is rather higher than the 25–30% of carbon from primary production estimated by Wiebe and Smith (1977) and Hagström *et al.* (1979) for surface waters because we have included all the consumers from below the thermocline into our estimates of heterotrophic demand, which is thus in addition to the 30% calculated for surface waters. It will also be noted that the carbon requirements of the flagellates are in equilibrium with production by the bacteria, so that bacterial biomass is likely to

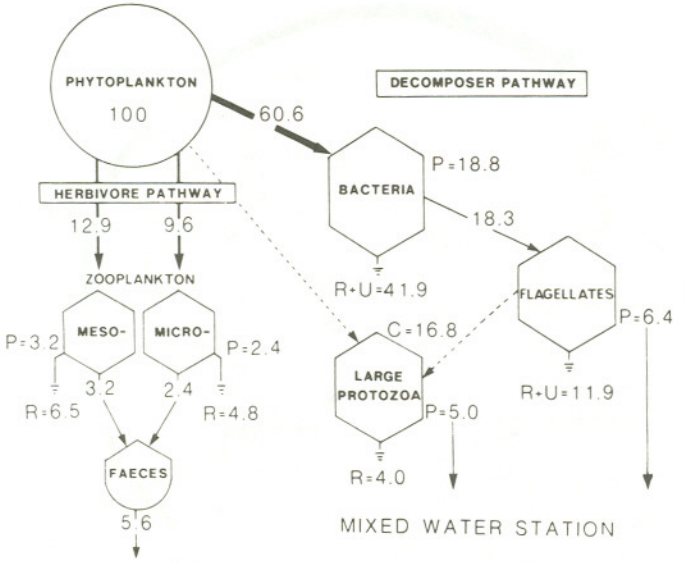

Figure 15.6 Net carbon budget estimated from biomass data of a plankton community at a mixed water station (*M*) in the western English Channel. All values expressed as a percentage of total carbon flow through the consumer community obtained from the component biomass and balanced carbon budgets of the consumers (consumption production + respiration + faeces + soluble excretion). (After Newell and Linley, 1984.)

be held more-or-less constant by the grazing of the heterotrophic microflagellates (see also Lucas *et al.*, 1985b).

The corresponding nitrogen mass balance diagram shown in Figure 15.7 has been calculated from C:N ratio of the substrate, that incorporated into production (*P*) and that in the faeces. The values for dissolved losses have been estimated from the difference between the nitrogen entering the microheterotrophic community from primary production and that incorporated into production. It is immediately apparent that under the particular conditions at which the samples were taken (see Holligan *et al.*, 1984; Newell and Linley, 1984; Fenchel this volume), and unlike the nitrogen-limited kelp detrital system, there is likely to be a strong remineralization of nitrogen through the planktonic microheterotrophic community when the starting material is phytoplankton with a relatively low C:N ratio of approximately 6.0 (see also Glibert, 1982).

The absolute values for nitrogen remineralization amount to 0.02 mg at NH_4-N m^{-3} h^{-1} for mixed water station M, 0.013 mg at NH_4-N m^{-3} h^{-1} for a frontal station F and 0.008 mg at NH_4-N m^{-3} h^{-1} for a deeper stratified water station E5 off the western approaches to the English Channel. They suggest that towards to

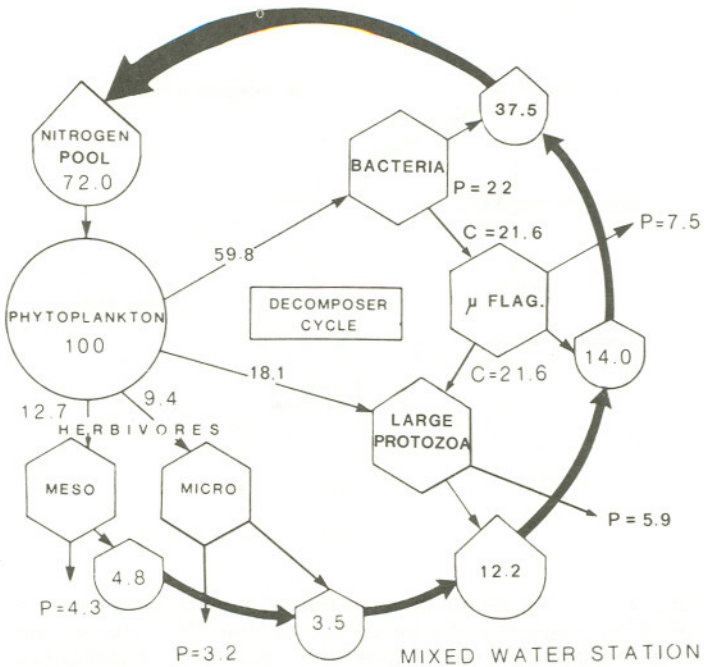

Figure 15.7. Pathways of nitrogen regeneration through the plankton community at mixed water station (*M*) in the western English Channel. Values expressed as percentage of total nitrogen flow through the consumer community during decomposition of a phytoplankton bloom. (After Newell and Linley, 1984.)

end of a phytoplankton bloom, remineralization processes through the micro-heterotrophic community may play an important part in regenerating nitrogen necessary to support further primary production. These inferences are in general agreement with data for size fractionated water samples in the Southern California Bight (Harrison, 1978) and in shelf waters of the UK (Burkill *et al.*, 1983). Glibert (1982) provided evidence from ^{15}N studies in Chesapeake Bay that the importance of the $< 1\ \mu M$ (apparently bacterial) fraction increases with the decline of a diatom bloom.

It is important to point out, however, that at other times the zooplankton may have a greater relative biomass than that recorded in the survey at the end of a *Gyrodinium* bloom in August in the English Channel (Holligan *et al.*, 1984). Under these conditions a very different role may be ascribed to the zooplankton in both carbon flow and in nitrogen regeneration (see Walsh *et al.*, 1978). Partly because of the problem of the steady-state assumptions required for mass balance estimates of this kind, Moloney *et al.* (1986) have developed a simulation model from the same data as those used for Figure 15.6 to investigate nitrogen fluxes

associated with plankton assemblages during the build-up and decline of phytoplankton blooms after a mixing or upwelling event.

An output from the model is shown in Figure 15.8 in which the effects of remineralization have been included (above) and excluded (below). The development of a phytoplankton bloom, with an initial increase in bacteria and a later increase in the zooplankton, appears to be a typical sequence in temperate coastal waters (see Sorokin, 1977). The general trend is for the microbial community to be an important component of the biomass near the beginning and again at the end of the simulated bloom and for the zooplankton to be more important at the end of the bloom. The relative significance of heterotrophic components, and the different roles ascribed to them in particular sea areas may thus reflect to a large extent the phase in the bloom at which samples are taken (see also Newell *et al.*, 1985).

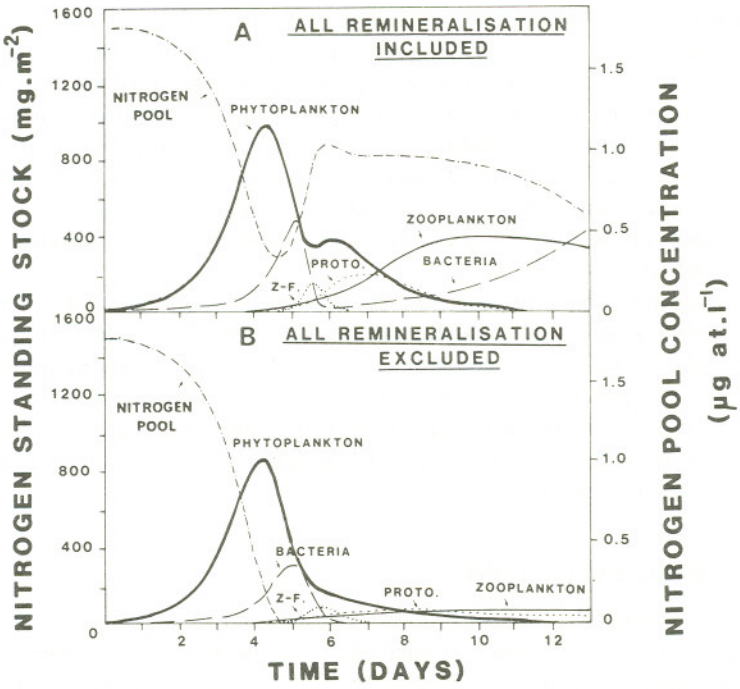

Figure 15.8. Simulation results showing the development and decay of a phytoplankton bloom and the changes in the standing stocks of the associated heterotrophic compartments (ZF = zooflagellates) when the nitrogen remineralized is excluded from the abiotic nitrogen pool. (a) all remineralization included; (b) all remineralization excluded. Axes show standing stocks (mg N/m^2 integrated over 60 m depth) and the nitrogen pool concentration (μg-at/l). (From Moloney *et al.*, 1986.)

The large peaks of standing stocks simulated in the model accord with values recorded by Sorokin (1975, 1981), Sieburth *et al.* (1978) and more recently by Holligan *et al.* (1984) for frontal and mixed waters of the English Channel. The simulated bacterial populations eventually decline due to control imposed by grazing zooflagellates (see also Pomeroy and Johannes, 1968; Sieburth *et al.*, 1978; Haas and Webb, 1979; Fenchel, 1982; Azam *et al.*, 1983). In the model, when 10% or more sedimentation of phytoplankton and faeces is simulated, micro- and mesozooplankton standing stocks assume greater importance than those of protozoa and bacteria from day 9 onwards. This may correspond to the quasi-steady-state conditions which occur in temperate stratified waters during the late summer.

The two phytoplankton peaks generated by the model correspond to the 'new production' and 'regenerated production' defined by Dugdale and Goering (1967). The first peak occurs as a result of the pulse of nitrate into the system and the second peak as the result of nitrogen regeneration by the heterotrophs (see also Yentsch *et al.*, 1977) which is excluded in the simulation shown in the lower part of Figure 15.8. The microheterotrophic component is found to be most important in remineralizing nitrogen and making it available to support further phytoplankton growth. This is brought about both by direct remineralization by bacteria and by indirect effects via other components, protozoa contributing a significant amount during the phytoplankton bloom. In contrast, the micro- and mesozooplankton are found to regenerate nitrogen in large amounts only at the end of a phytoplankton bloom when zooplankton are at their highest levels.

The simulation model thus depicts a continuum of events, many of which have been observed in isolation in coastal, oceanic and upwelling systems. It ascribes variable significance to nitrogen regeneration by the microheterotrophic community according to the time after an upwelling or mixing event. Remineralization may thus vary on a time scale of days in upwelling areas, seasonally in temperate waters or on a longer term in the quasi steady-state conditions of stratified oceanic waters.

15.4.2 Validation of the model

Figure 15.9 shows the depth profiles for the NH_4^+-N pool and NH_4^+-N regeneration at a shelf station (St Helena Bay) on the west coast of South Africa and at an oceanic station at 33°20′S; 16°49.0′E. Values for sigma-*t* are also shown. It can be seen that in shelf waters there was a high NH_4^+-N regeneration amounting to as much as 0.045 mg-at NH_4^+-N m^{-3} h^{-1} in the surface waters declining to approximately 0.02 mg-at NH_4^+-N m^{-3} h^{-1} at the pycnocline. At depth, nitrogen regeneration amounted to 0.005–0.01 mg-at NH_4^+-N m^{-3} h^{-1}. At the same time it will be noted that the ammonia nitrogen pool (NH_4^+-N mg-at m^{-3}) was at a maximum at, or just below, the pycnocline. This implies a strong

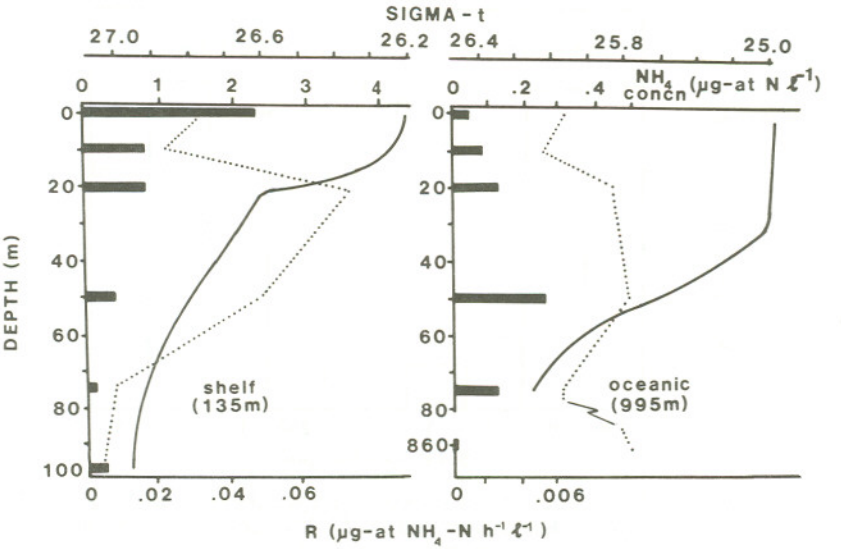

Figure 15.9. Nitrogen remineralization (mg at $NH_4^+ - N\,m^{-3}\,h^{-1}$) and ammonium concentration (NH_4 mg-at m^{-3}) in relation to depth at a shelf station (St Helena Bay) on the west coast of South Africa and at an oceanic station (33°20′S; 16°49.0′E). Values for sigma-*t* are also shown. (Probyn, unpublished.)

uptake of regenerated NH_4^+-N in the surface waters and regeneration in the pycnocline region and emphasizes the need for measurements of flux of NH_4^+-N rather than merely concentration.

In the ocean water station, the NH_4^+-N pool and the regeneration were an order of magnitude lower than in the coastal waters, and in this case maximum regeneration rates of approximately 0.006 mg-at NH_4^+-N $m^{-3}\,h^{-1}$ were reached at 50 m just above the pycnocline. Both the rates of nitrogen regeneration for shelf waters and the reduced values for deeper waters therefore accord well with those predicted from the nitrogen mass balance model shown in Figure 15.7. Nitrogen remineralization rates are an order of magnitude lower in Antarctic waters than in the Southern Benguela upwelling region whilst bacterial biomass and production are 1–2 orders of magnitude lower in the Antarctic region relative to the Southern Benguela upwelling system (Lucas *et al.*, 1986, 1987; Painting *et al.*, 1985, 1987). Nitrogen regeneration is thus apparently coupled to microbial biomass and production—a relationship which appears to be generally true for sea areas as widely separated as the English Chennel and southern sub-polar seas.

Figure 15.10 shows the rate of nitrogen regeneration (µg-at NH_4^+-N $h^{-1}\,l^{-1}$) in surface waters and at the 1% light level (27 m) a shelf oceanic station 29°43.7′S; 15°40.9′E where the water depth was 178 m. Values for nitrogen regeneration are

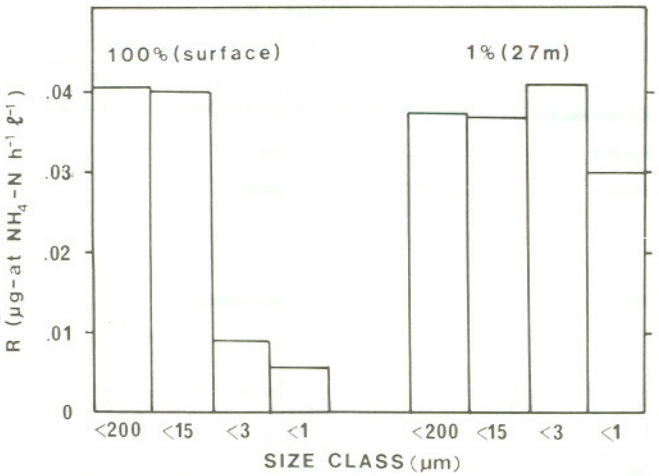

Figure 15.10. The rate of nitrogen regeneration (μg-at NH_4^+-N $h^{-1} l^{-1}$) in surface waters and at the 1% light level (27 m) in water fractionated through 200 μm, 15 μm, 3 μm and 1 μm filters at an oceanic station at 29°43.7′S; 15°40.9′E. The water depth was 178 m, salinity 35.02‰ and temperature 17.1 °C. Ammonia N flux established by ^{15}N isotopic dilution using the Blackburn–Caperon model:

$$r = \ln(R_t/R_0)/\ln(S_t/S_0)\cdot(S_0 - S_t)/T$$

where T = time, S_0 = initial NH_4^+ conc., S_t = final NH_4^+ conc.; R_0 = initial ^{15}N enrichment of aqueous NH_4^+; R_t = final ^{15}N enrichment of aqueous NH_4^+. (Probyn, unpublished.)

shown in plankton which was passed through filters of 200 μm, 15 μm, 3 μm and 1 μm respectively. It can be seen that in the surface waters a regeneration rate of 0.04 μg-at NH_4^+-N $h^{-1} l^{-1}$ occurred in both the < 200 μm filtered seawater and in the < 15 μm fraction but that regeneration fell to less than 0.01 μg-at NH_4^+-N $h^{-1} l^{-1}$ in the < 3 μm fraction. This implies that in the surface waters organisms of the size range 3–15 μm diameter were of dominant importance in nitrogen remineralization.

This contrasts sharply with the results for size-fractionated water collected from the 1% light level at 27 m. It is clear that here NH_4-N regeneration by the < 1 μm size fraction was approximately 75% of that in the larger size fractions. Remineralization at or near the pycnocline thus can be achieved principally by bacteria, whilst that in the euphotic zone may represent remineralization at the second step in the food web from bacteria to protozoa (see also Azam *et al.*, 1983).

A plot of NH_4^+ regeneration rates from Figure 15.9 and bacterial biomass at different depths shows a strong correlation between the two (Figure 15.11). Such a relationship can be interpreted as evidence for a direct role of bacteria in NH_4^+

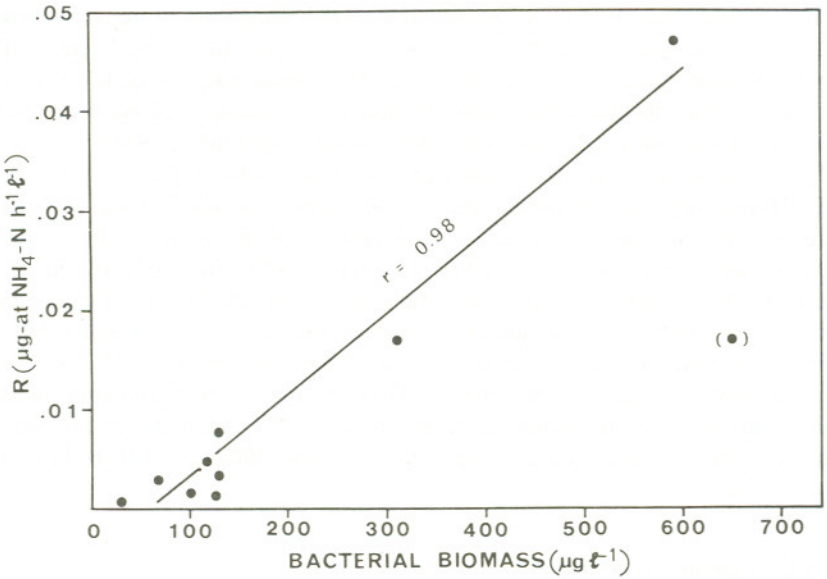

Figure 15.11. The relationship between NH_4^+-N regeneration rates (μg-at NH_4^+-N $h^{-1} l^{-1}$) and bacterial biomass (μg/l) in waters off the Cape Peninsula, South Africa. (Probyn, unpublished.)

recycling, or an indirect role through regeneration by bactivorous protozoa. Values as high as 0.05 μg-at NH_4^+-N $h^{-1} l^{-1}$ were obtained at a bacterial biomass of 600 μg/l, but the bulk of the data suggests a relatively uniform bacterial biomass of approximately 100 μg/l which corresponded to a regeneration of approximately 0.005 μg-at NH_4^+-N $h^{-1} l^{-1}$ throughout much of the water column. These values correspond well with estimates based on the nitrogen mass balance model for the English Channel.

15.5 REQUIREMENTS FOR A BETTER MODEL: SPATIAL AND TEMPORAL 'DECOUPLING' OF C AND N FLOW

Experimental validation of the model for planktonic systems thus confirms that the micro-heterotrophic community is of dominant importance in NH_4^+-N regeneration, but indicates that interesting and potentially important differences in the source of such remineralization occur with depth in the water column. Direct measurements of NH_4^+ flux in size-fractionated water suggest that in the surface waters, where the conversion of PDOC to bacterial biomass is an efficient process, the main regenerative step may be from bacteria to grazing protozoa which are of dominant importance in controlling bacterial prey density (see Fenchel this volume; also Azam *et al.*, 1983). In the deeper waters below the euphotic zone,

however, regeneration may be associated with the major flux of materials linked with the transformation of POM of still low C:N ratio (6–10) by bacteria. The results for deeper waters thus conform closely to the mass balance model developed for the detritus-dominated community during the collapse phase of a phytoplankton bloom in the English Channel (Newell and Linley, 1984).

Whereas the nitrogen fluxes associated with a depth-integrated model have been largely supported experimentally at sea, a more realistic model for deeper waters, especially where there is a marked thermocline, may thus involve separating or 'decoupling' the PDOC-driven model for the euphotic zone from the POC-driven model for the pycnocline and below. In this case, flux through the surface communities would be based on PDOC representing 10–30% of primary production (see Larsson and Hagström, 1979; Cole *et al.*, 1982) and converted with a high efficiency of 0.65. That through the bacterial communities below the euphotic zone would be based on up to 70% of primary production as detrital POC or faeces being converted with a low efficiency of 0.16 (Pomeroy *et al.*, 1984).

15.5.1 Euphotic zone model

The following assumptions were made for the development of a simple model of nitrogen standing stocks and flux through the heterotrophic community above the pycnocline.

(a) Bacteria obtain their carbon requirements from PDOC released as exudates from living phytoplankton. Their growth is essentially carbon-limited at this point since, as can be seen from the output in Figure 15.12, there is a large nitrogen pool available at the beginning of the simulation.
(b) Bacterial production in the model is nitrogen-limited, but because of the carbon-limiting assumption made above, the nitrogen available to bacteria is made the exact equivalent (1N = 1C) of PDOC, here assumed to be 30% of primary production. It should be noted that, as a result of this, the nitrogen fixed by the bacteria would require the assimilation of more carbon than is available in the PDOC alone, given that the net growth yield or carbon conversion efficiency is $< 100\%$. The uptake of nitrogen by bacteria from the nitrogen pool is then determined by Michaelis–Menten uptake kinetics.
(c) The bacteria receive no nitrogen from the phytoplankton compartment.
(d) Bacteria incorporate nitrogen with a high efficiency in the surface waters where the system is nitrogen-limited, only 5% per day of ingested nitrogen being remineralized. The following values for nitrogen remineralization were assumed for the heterotrophic compartments in the model: bacteria 5% per day, zooflagellates 65%, large protozoa 67% and micro-mesozooplankton 15% (see Newell and Linley, 1984).
(e) Phytoplankton and zooplankton faeces sediment at a rate of 30% per day of accumulated biomass due to production. This represents the input for the

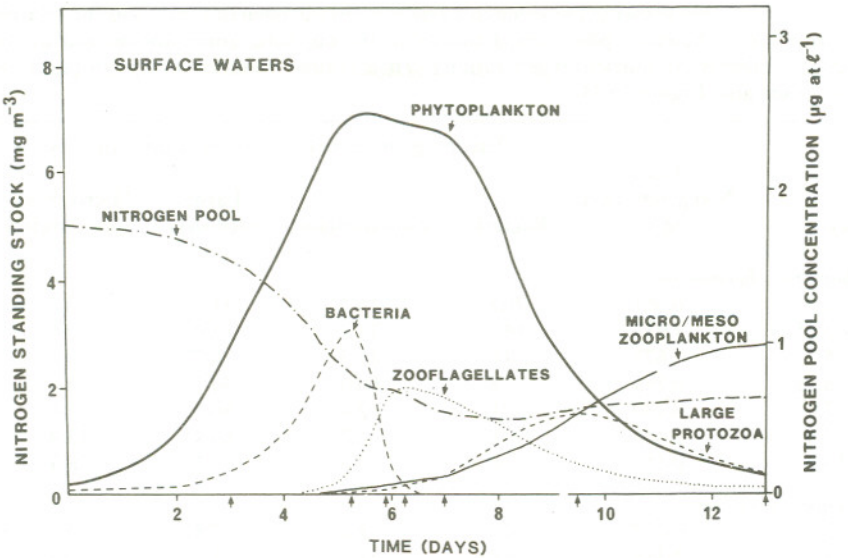

Figure 15.12. Nitrogen standing stocks of phytoplankton and the heterotrophic consumer community of bacteria, zooflagellates, large protozoa and micro/mesozooplankton (mg N m^{-3}) over a period of 13 days. The nitrogen pool concentration is also shown (μg-at/l). The biotic compartments were assigned low initial values eg. 0.1 mg/m^3 for bacteria. Values were assigned to the other compartments in similar proportions to those described by Linley *et al.* (1984) and Holligan *et al.* (1984) for the standing stocks of consumers in the western English Channel. A large initial nitrogen pool (1.8 μg-at/l) simulated the mixing of nitrogen-rich water into the euphotic zone, using nitrate concentrations for a stratified water station in the English Channel (Holligan *et al.*, 1984). Vertical arrows represent instantaneous values where the amount of remineralized nitrogen and the percentage contribution by each of the consumer compartments was calculated for Figure 15.14

POC-driven model simulating fluxes through the heterotrophic community at the pycnocline, although here we have kept the imput constant (see below).

An output from the simulation model is shown in Figure 15.12, which shows the nitrogen standing stocks (mg N/m^3) of phytoplankton, the heterotrophic consumer community and the nitrogen pool concentration (μg-at/l) over a period of 13 days. It can be seen that a large initial nitrogen pool of 1.8 μg-at/l simulated the mixing of nitrogen-rich water into the euphotic zone. This was followed by an increase in the phytoplankton, bacteria, zooflagellates and large protozoa, much as has been described for both natural waters and experimental microcosms (for reviews, see Newell, 1984; Linley and Newell, 1985). Larger zooplankton became important after the initial bloom of phytoplankton had declined. The nitrogen pool was thus sustained by successive heterotrophic compartments.

Table 15.3. Table showing the values for regenerated nitrogen (mg/m^3) and the relative contribution of heterotrophic compartments in the euphotic zone (above) and at the pycnocline (below) to nutrient regeneration (%) in a simulation model of a phytoplankton bloom (see also Figure 15.14)

Day	Total N-regeneration (mg/m^3)	Percentage from heterotrophic compartments			
		Bacteria	Zooflagellates	Large protozoa	Micro/meso-zooplankton
Above the thermocline					
3.0	0.061	70.8	15.1	11.5	2.6
5.25	1.931	18.3	77.1	4.0	0.6
5.9	2.678	4.0	88.5	6.7	0.8
6.25	0.798	1.8	60.0	34.7	3.5
7.0	0.739	0.0	12.6	80.8	6.6
9.5	1.038	0.0	2.7	84.4	12.9
13.0	0.155	0.0	3.6	38.1	58.3
Pycnocline region					
2.5	0.424	94.5	2.2	2.8	0.5
5.2	2.333	75.6	22.6	1.5	0.3
6.8	0.432	24.6	50.4	22.4	2.6
8.5	0.287	0.2	15.6	76.7	7.5
11.0	0.658	0.0	3.5	86.8	9.7
13.0	0.772	0.0	1.2	81.4	17.4

Sections through the sequence are shown in Table 15.3 and Figure 15.14a. Here it can be seen that remineralization was dominated by the zooflagellates up to day 6.25, after which the larger protozoa and, later, the micro/mesozooplankton became of increasing importance. Remineration by the bacteria was significant only in the earlier stages of the sequence (see also Figure 15.10).

15.5.2 Pycnocline zone model

As has been shown in Figures 15.1 and 15.2, bacterial production at or below the thermocline is likely to be driven by the POC supply. The following assumptions were made to simulate conditions at the pycnocline:

(a) Bacteria obtain nitrogen from both phytoplankton detritus and the nitrogen pool.
(b) Because of the large flux of material through the bacteria when POC is exploited as a carbon resource and the large nitrogen pool, bacteria are assumed to remineralize 63% per day of ingested nitrogen, zooflagellates 65%, large protozoa 67% and micro-/mesozooplankton 15% (see Newell and Linley, 1984).
(c) There is a constant phytoplankton detritus input of $1\,mg\,m^{-3}\,d^{-1}$. This is

roughly one-sixth of the maximum phytoplankton standing stock (biomass and production) above the pycnocline. The detrital input to the model in the pycnocline is therefore not related in a continuous time sequence to production in the euphotic zone above.

(d) Phytoplankton detritus and zooplankton faeces sediment out at a rate of 30% per day of the accumulated biomass due to production.

(e) Except for the pathways from the nitrogen pool to bacteria, nitrogen pool to phytoplankton and phytoplankton to bacteria, all other fluxes are assumed to be the same as for the euphotic zone flux model.

An output from the simulation model for nitrogen flux through the heterotrophic community in the pycnocline region is shown in Figure 15.13. Since, for simplicity, detritus input is continuous at 1 mg $N\,m^{-3}\,d^{-1}$ for a 13-day period, the model is not closely coupled with the one for conditions in the euphotic zone, although it is possible to incorporate a variable time sequence of coupling between them. The points at which instantaneous rates of nitrogen regeneration have been estimated for Table 15.3 and Figure 15.14 are also shown.

Here it can be seen that a similar succession of the heterotrophic community develops following a pulse of detritus into the system. Nitrogen regeneration by the

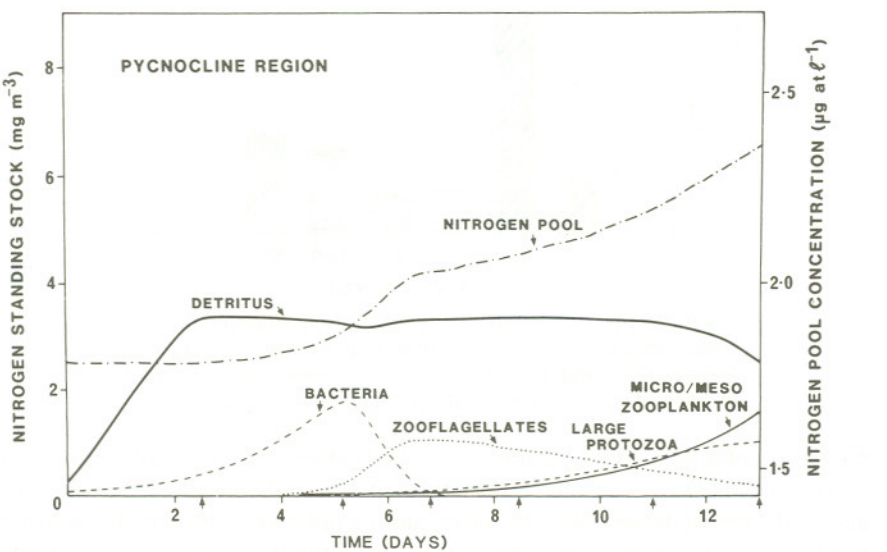

Figure 15.13. A simulation output for the nitrogen standing stocks of the heterotrophic consumer community of bacteria, zooflagellates, large protozoa and micro/mesozooplankton (mg N/m^3) over a period of 13 days at the pycnocline. The nitrogen pool (μg-at/l) is shown. Detritus input is continuous at 1 mg $N\,m^{-3}\,d^{-1}$ for the 13-day period. For simplicity, the model is therefore not directly coupled to the one shown in Figure 15.12 for conditions above the pycnocline, since absolute sedimentation values would then have been coupled to primary production

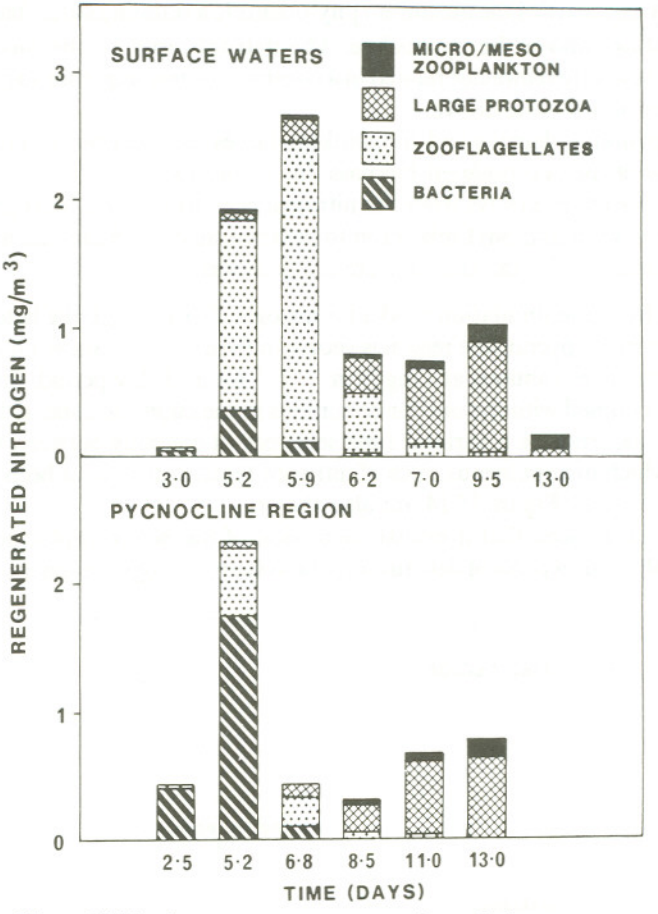

Figure 15.14. Instantaneous concentrations of nitrogen regenerated (mg/m^3) at the times indicated by vertical arrows in Figures 15.13 and 15.14. The relative proportions contributed by each of the consumer compartments are also shown

bacteria is of dominant importance in the early stages of the microheterotrophic succession, followed by an increasing importance of zooflagellates, larger protozoa and, at the end of the sequence, by micro/mesozooplankton. Because the nitrogen is not taken up for photosynthesis below the euphotic zone, the nitrogen pool increases continuously until a mixing event renews the sequence.

15.6 CONCLUSIONS

Our review thus suggests that the flux of nitrogen through the microheterotrophic community of bacteria and protozoa is dependent to a large extent on the C:N

ratio of the natural substrates available for utilization, the amount of NO_3^-, NH_4^+ and urea present, as well as on the ease of degradation of the substrates. Where the C:N ratio is high and the N-pool is small, as in many detritus-dominated macrophyte systems, nitrogen is limiting, and large fluxes of carbon may be associated with an efficient conservation of nitrogen and little nutrient regeneration. In phytoplankton-based systems, however, where the C:N values are closer to the Redfield ratio, a major regeneration of nitrogen can occur through the microheterotrophic community of bacteria and protozoa. In this case the relative importance of the microheterotrophs and the larger crustacean zooplankton depends on the relative biomass of each compartment and varies during the course of a phytoplankton bloom.

In surface waters, where exudates (PDOC) are efficiently converted in the first step of the microheterotrophic pathway, nitrogen may be principally regenerated by protozoa which are in approximate equilibrium with bacterial production (see Figure 15.6, also Azam *et al.*, 1983). Regenerated nitrogen is then rapidly taken up by phytoplankton so that the surface NH_4^+-N pool remains low (see Figure 15.12). At the pycnocline and below, however, the bacteria may utilize POC as a carbon resource, and are also able to exploit the nitrogen advected from below the euphotic zone. In this case, and in accordance with the experimental data for NH_4-N flux shown in Figure 15.10, the simulation models suggest a major regeneration of nitrogen associated with the microbial community at the pycnocline, especially during the initial phase of the microheterotrophic succession (Figures 15.13 and 15.14). Since the nitrogen remineralized at the pycnocline is not taken up for photosynthesis, the community is a net mineralizer accounting for the NH_4-N maximum commonly recorded below the thermocline (see Figure 15.9).

Clearly the rate at which regenerated nitrogen is made available to phytoplankton in the surface waters—that is, the degree of coupling of the two subsystems—will be of importance in controlling the levels of primary production which can be sustained before nitrogen becomes limiting in the euphtoic zone. The two subsystems must also be linked in the long term to preserve the C:N balance of the water column as a whole. Temporal 'decoupling' on time scales of days between upwelling events, seasonally in temperate waters, or on longer time scales in stratified waters, may, however, do much to explain regional differences in the level of primary production which can be sustained from nutrient regeneration by the heterotrophic community.

The models which we have described for carbon and nitrogen fluxes through surface waters are thus mainly dominated by vertical processes. It is clear, however, that larger scale models need to incorporate wider interactions to couple this pelagic subunit model both to the benthos and horizontally to shallow shelf systems where active nutrient regeneration and entrainment make an important contribution to the mass balance of the system as a whole. Some models incorporating processes at the sediment–water interface have been described in Chapter 14, but little comparable work has yet been attempted to describe the

complex and variable pulses of phytoplankton growth and decline which characterize the Southern Benguela upwelling system.

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