

## Seasonal Nitrogen Dynamics in Chesapeake Bay: a Network Approach

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The input, exchange, recycling and export of nitrogen in the mesohaline region of Chesapeake Bay have been assessed in this study. The seasonal rate of exchanges between the 36 most important components and the roles of these in the recycling process of nitrogen in the ecosystem have been quantified. Results show that the demand for nitrogen by phytoplankton, bacteria and benthic algae is the highest in summer ( $418 \text{ mg N m}^{-2} \text{ day}^{-1}$ ) and lowest in winter ( $90 \text{ mg N m}^{-2} \text{ day}^{-1}$ ). The supply of dissolved nitrogen however, is highest in spring ( $289 \text{ mg N m}^{-2} \text{ day}^{-1}$ ), with the lowest exogenous supply of 'new' nitrogen during summer ( $53 \text{ mg N m}^{-2} \text{ day}^{-1}$ ). The seasonal variation in supply and demand suggest that spring nitrogen loadings continue to sustain the high nitrogen demand in summer when this nutrient appears to be in short supply. Results also show that the efflux of nitrogen from the sediments to the overlying water dominates the recycling process and is abetted by water column regeneration, mostly by the smaller biota ( $<200 \mu\text{m}$ ). Mesozooplankton, suspension-feeders and fish as a whole contribute relatively little on a seasonal or annual basis to the total amount of regenerated nitrogen. Network analysis of the seasonal dynamics of nitrogen indicates that the pathways over which nitrogen is recycled are considerably more complicated and numerous than those which retain carbon in the system. The Finn Cycling Index (FCI) reveals that the rate of nitrogen recycling during summer approximates 70% of the total system activity compared with the 34–46% range during other seasons. In contrast, the FCI for carbon was almost a constant 20% over all seasons. As regards the pelagic microbiota, which functioned more as a shunt to convey excess carbon out of the system, analysis indicates they comprise very significant pathways for the retention of nitrogen in the system.

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### Introduction

Nitrogen is an important element in ecological systems. Not only is it an essential component of animal tissue, but quite often it is a controlling factor in plant nutrition and productivity. A wide variety of nitrogenous compounds occurs in ecosystems, and

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together with nitrogen they generate the complex pattern of nitrogen cycling that can be regulated by a number of physical, chemical and biological processes. Nitrogen, like many other elements, is imported, transferred through the food-web, recycled and exported from an ecosystem. When in short supply, nitrogen may limit the productivity of the system as a whole.

The importance of nitrogen in the marine and estuarine environments has received considerable attention (cf. Carpenter & Capone, 1983; Blackburn & Sorenson, 1988; Wada & Hattori, 1991), and the significance of nitrogenous nutrients to phytoplankton and heterotrophic bacterial production has long been recognized (Eppley *et al.*, 1977; Wheeler & Kirchman, 1986; Glibert, 1988). In particular, the cycling of nitrogen, inherent in all aquatic ecosystems, has been studied extensively (for example see Blackburn & Sorenson, 1988), because the regeneration of inorganic nitrogen is essential for continued primary production. Those processes that contribute to the biogeochemical cycling of nitrogen in coastal marine environments include biological uptake, remineralization, nitrification, denitrification, and burial of nitrogen in the sediments. Numerous and extensive studies have addressed these processes in general (for reviews see Carpenter & Capone, 1983; Blackburn & Sorenson, 1988), whereas others describe nitrogen cycling in particular systems, such as bays (e.g. Nixon & Pilson, 1983; Owens *et al.*, 1986; Mantoura *et al.* 1988), the open ocean (Harrison *et al.*, 1983; Newell *et al.* 1988), mesocosms (Roman *et al.*, 1988) and estuaries (Boynton & Kemp, 1985). Nitrogen dynamics in Chesapeake Bay have been studied rather intensively over the past two decades, particularly the benthic-pelagic exchanges (Boynton & Kemp, 1985; Kemp *et al.* 1990; Kemp & Boynton, 1992), and the influence of nitrogen availability upon the magnitude of phytoplankton productivity (McCarthy *et al.*, 1977; Malone *et al.* 1986, 1988).

Our aims in this study were to (1) present a quantitative picture of the seasonal exchanges of nitrogen among the various living and non-living components of Chesapeake Bay ecosystem, and (2) apply network analysis to the seasonal flow models thus depicted. Creating the networks requires data on the biomass of each component, as well as on their dietary requirements and excretion rates. Once constructed, the network allows one to evaluate the regeneration of nitrogen by various living compartments, the contribution of nitrogen inputs from the main tributaries, and the biochemical transformations of nitrogen in an ecosystem context. The formal procedures of network analysis were used to assess the structure and magnitude of nitrogen recycling and to derive whole ecosystem properties such as ascendancy, throughput and development capacity (Ulanowicz, 1986; Kay *et al.*, 1989).

The measurement and analysis of energy and carbon flows in ecosystems reveal the rates and efficiencies of transfer, assimilation and dissipation, as well as significant information about the overall structure and function of the ecosystem (Ulanowicz & Platt, 1985; Ulanowicz, 1986; Wulff *et al.*, 1989; Baird *et al.*, 1991). There are, however, few models depicting nitrogen flow and cycling in estuarine ecosystems. This is probably because few studies focus on nitrogen as an ecosystem currency in estuaries (Wetzel & Wiegert, 1983). More recently, however, Owens *et al.* (1986), Billen and Lancelot (1988), Kremer (1989), Wulff *et al.* (1990) and Christian *et al.* (1992) have described and analysed models of nitrogen flows and cycling in estuaries and shallow coastal environments. Kremer's (1989) network analysis of nitrogen focused on the zooplankton component of Narragansett Bay, whilst Christian *et al.* (1992) considered the entire Neuse River estuary system. All these studies were concerned with aggregated and/or

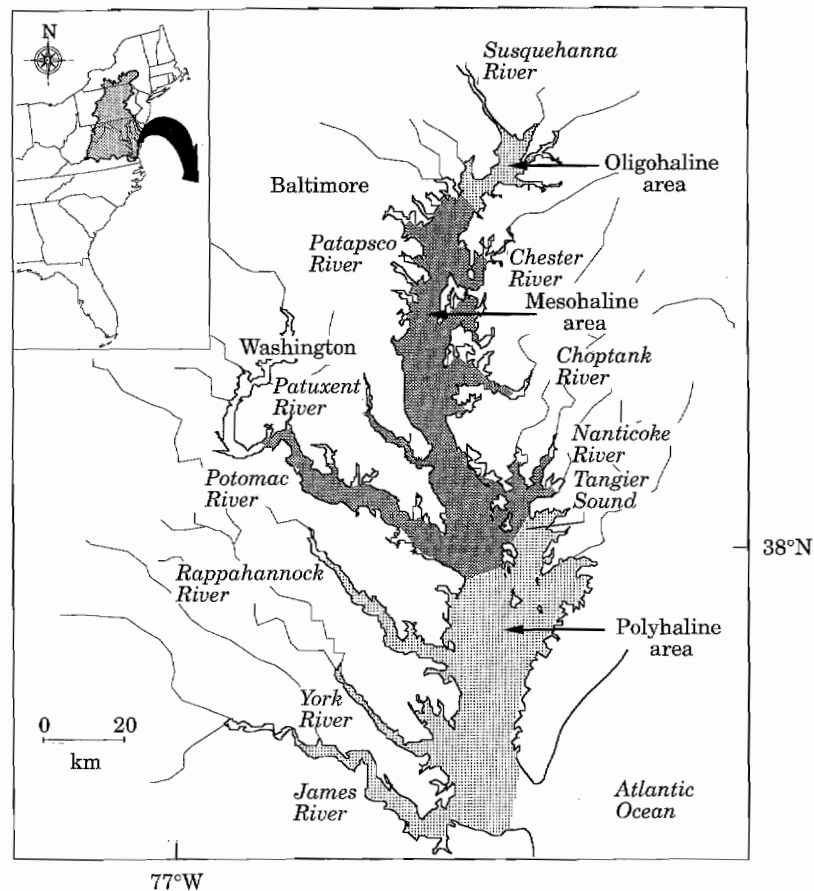


Figure 1. The location of Chesapeake Bay along the east coast of the U.S.A. and the extent of the mesohaline region within the bay.

abbreviated food-webs, whereas this paper considers relatively detailed taxonomy and provides seasonal networks.

In this study we present our generalized concept of nitrogen behaviour in an estuarine ecosystem. In doing so we quantify the input of 'new' nitrogen, the regeneration (or cycling) of nitrogen within the system by all components, the utilization of nitrogen, and the export of nitrogen on a seasonal basis.

The nitrogen networks represent the mesohaline portion of Chesapeake Bay, situated along the Atlantic coast of the United States (Figure 1). This region comprises approximately 48% of the total surface area of the bay, and about 47% of its total volume. The salinity ranges between 6 and 18, and the surface water temperatures from 21.4 to 28.9 °C in summer, 13.1 to 23.3 °C in autumn, 2.3 to 5.7 °C in winter and 6.2 to 16.7 °C in spring (Baird & Ulanowicz, 1989). The mesohaline region is characterized by moderate stratification (Boynton & Kemp, 1985) and hypoxic conditions often occur in bottom waters during summer (Kemp & Boynton, 1992). Freshwater flowing into the region imports nutrients in various amounts during each season (see Boynton *et al.*, 1991, 1992). The average depth of the mesohaline region is about 7 m.

### Estimates and assumptions

The number of compartments and the interactions between the trophic elements are patterned after the detailed seasonal carbon models of the mesohaline region of Chesapeake Bay developed by Baird and Ulanowicz (1989). The standing stocks of the nitrogen in trophic components and the fluxes of nitrogen between compartments were derived from the carbon models of Baird and Ulanowicz (1989) by applying appropriate C:N ratios to their carbon counterpart where applicable. Biomass data were updated whenever more recent information became available. Exchanges of nitrogen between compartments also followed Baird and Ulanowicz (1989) insofar as the diet composition of each consumer, its rate of production, and its faecal excretion were concerned. The estimation of dissolved inorganic nitrogen excretion by the various biotic components is described below.

#### *Nitrogen concentrations and nitrogen inputs into the mesohaline area*

The mean annual concentrations of dissolved organic and inorganic nitrogen (DON and DIN) were obtained from Boynton *et al.* (1991). Seasonal values for the total dissolved nitrogen into the mainstem of the mesohaline portion of the Bay (from the main tributaries, point, diffuse and atmospheric sources as averaged over the 7-year period 1983–90) were obtained from Boynton *et al.* (1991, 1992).

The seasonal fluxes of ammonium from the sediment to the dissolved nitrogen pool in the overlying waters were obtained from Boynton *et al.* (1991, 1992). The methods by which this flux was measured are described in detail by Boynton (1988), Kemp *et al.* (1990) and Boynton *et al.* (1991). The exchanges include ammonium excretion from sediment bacteria as well as from the infaunal species (compartments 14–18 in Figures 2–5). The ammonium excretion rates of the various macrofaunal compartments were calculated separately, and the difference between the aggregate faunal excretions and the total sediment flux as measured by Boynton *et al.* (1991, 1992) was ascribed to nitrogen remineralization by sediment bacteria. The amount of nitrogen lost as  $N_2$  from the system via denitrification was obtained from Boynton *et al.* (1991) and is shown in Figures 2–5 as 'export' from the system. Mean seasonal rates of particulate carbon deposition from the water column to the sediment were determined for the period 1987–90 by Boynton *et al.* (1991). These carbon rates were then converted into their nitrogenous counterparts using seasonal C:N molar ratios (7.96 for winter, 6.19 for spring, 6.38 for summer and 6.57 for fall; Boynton *et al.*, 1991). This deposition consists mainly of faecal excretions. Independent phytoplankton deposition rates were available from chlorophyll *a* measurements. Seasonal values for suspended particulate nitrogen concentration in the water column (compartment 34) and nitrogen standing stocks in the sediment (compartment 36) were obtained from Boynton *et al.* (1991).

The conversion of carbon biomass, production and faeces into nitrogen, and estimates of nitrogen excretion/regeneration rates of all the living components of the system were taken from published information. The relevant C:N ratios and data sources are listed in Table 1.

#### *Primary producers*

Phytoplankton nitrogenous biomass and production were determined from corresponding carbon stocks and rates as measured by Magnien *et al.* (1992) and converted using

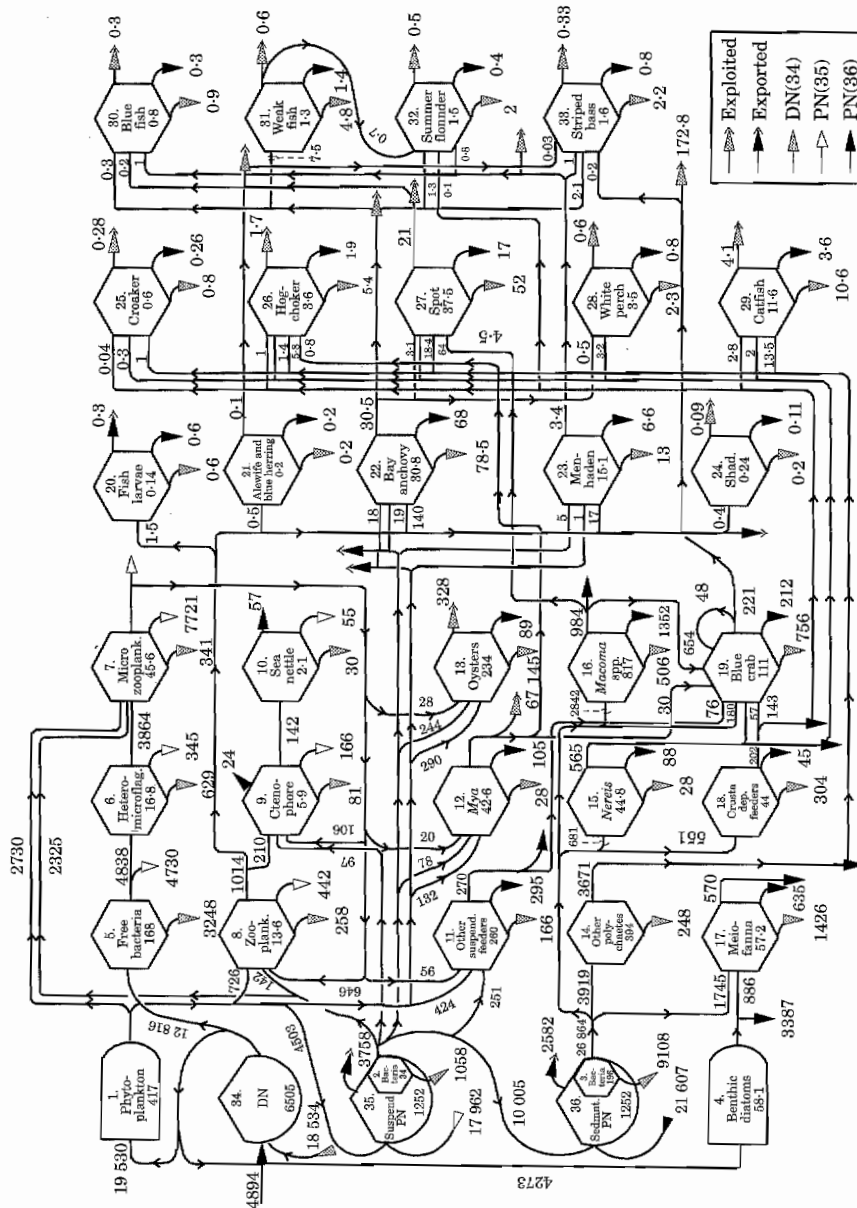


Figure 2. Summertime exchanges of nitrogen among the 36 major compartments of the mesohaline Chesapeake Bay ecosystem. Flows are in  $\text{mg N m}^{-2}$  aggregated over the 91-day season. Numbers at the inside bottom of the boxes are the standing stocks (in  $\text{mg N m}^{-2}$ ). Numbers at the inside top of the boxes represent the placement of the taxon in matrix and vector arrays. The major source of DN is shown flowing into compartment 34. Sinks and recycle flows are explained in the legend.

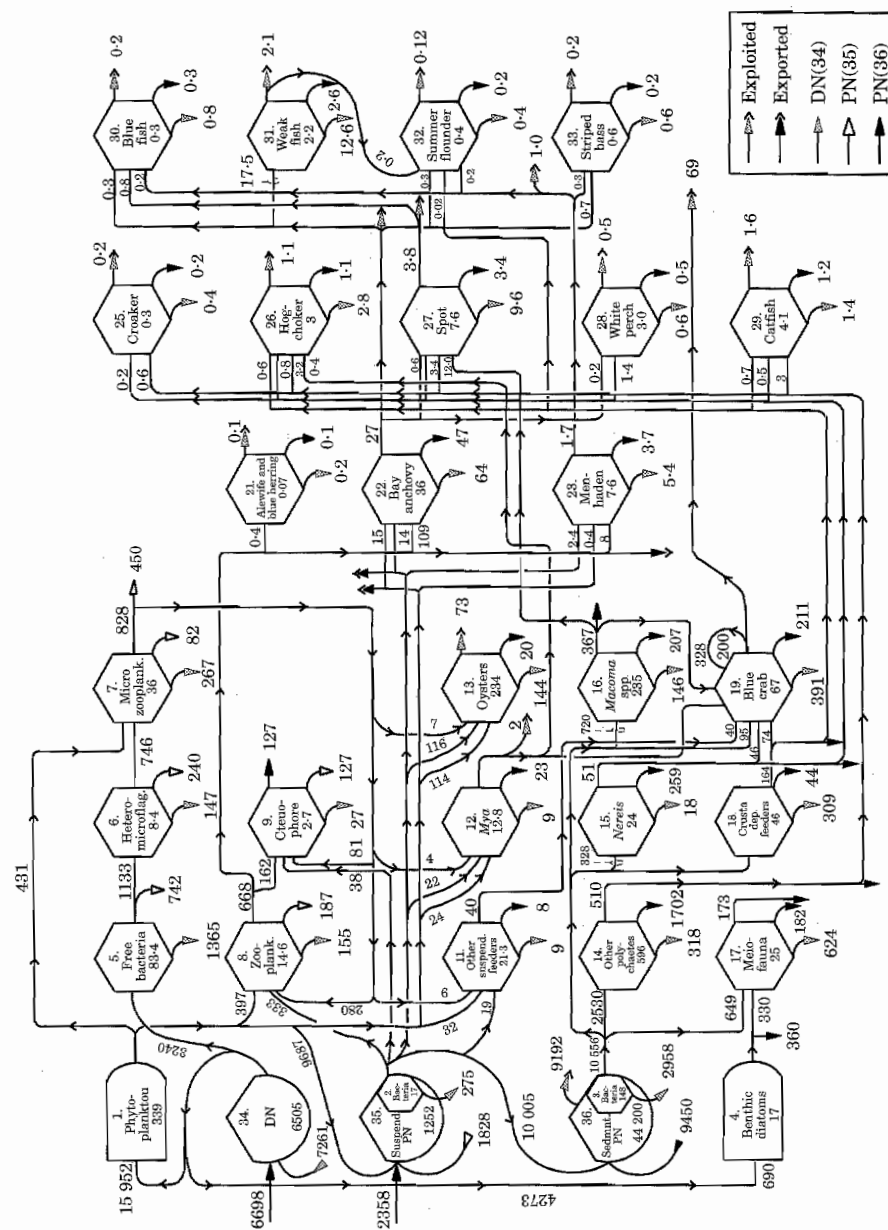


Figure 3. Autumn exchanges of nitrogen among the 36 major compartments of the mesohaline Chesapeake Bay ecosystem. Flows are in  $\text{mg N m}^{-2}$  aggregated over the 91-day season. Numbers at the inside bottom of the boxes are the standing stocks (in  $\text{mg N m}^{-2}$ ). Numbers at the inside top of the boxes represent the placement of the taxon in matrix and vector arrays. The major source of DN is shown flowing into compartment 34. Sinks and recycle flows are explained in the legend.

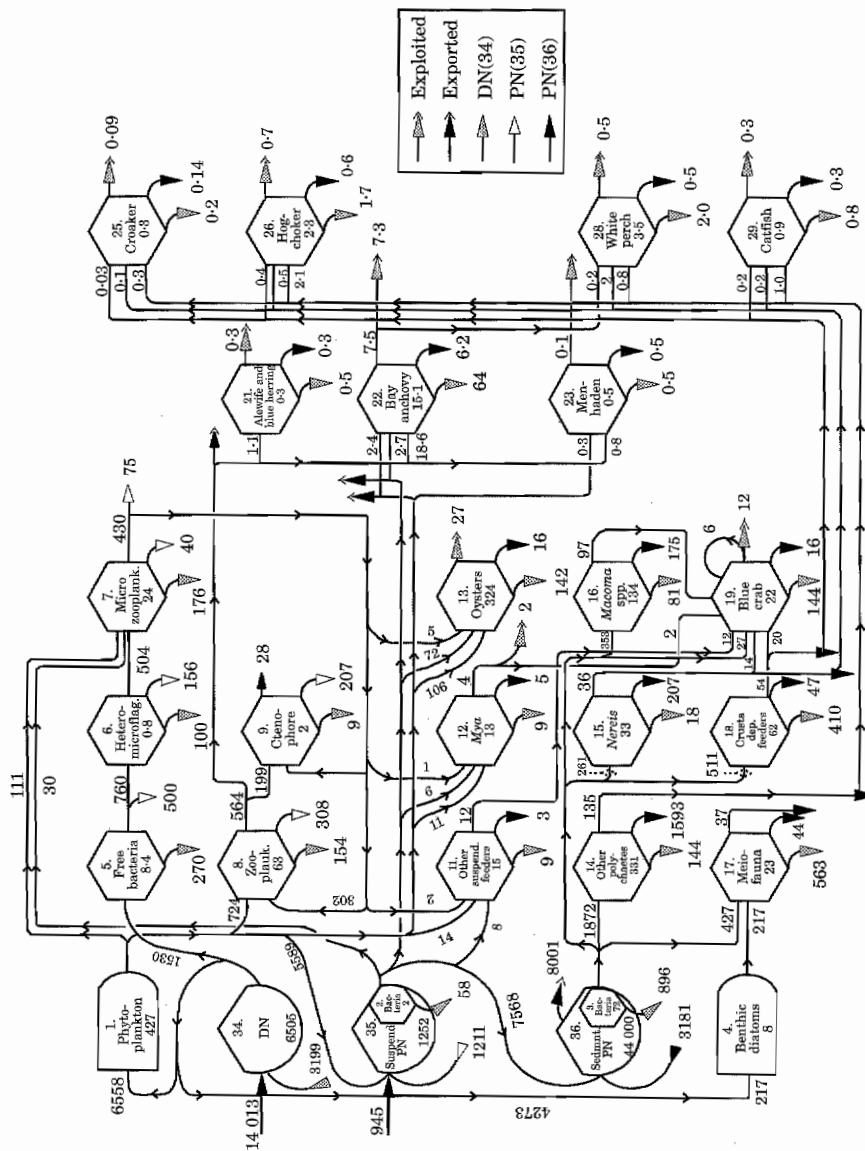


Figure 4. Wintertime exchanges of nitrogen among the 36 major compartments of the mesohaline Chesapeake Bay ecosystem. Flows are in  $\text{mg N m}^{-2}$  aggregated over the 91-day season. Numbers at the inside bottom of the boxes are the standing stocks (in  $\text{mg N m}^{-2}$ ). Numbers at the inside top of the boxes represent the placement of the taxon in matrix and vector arrays. The major source of DN is shown flowing into compartment 34. Sinks and recycle flows are explained in the legend.

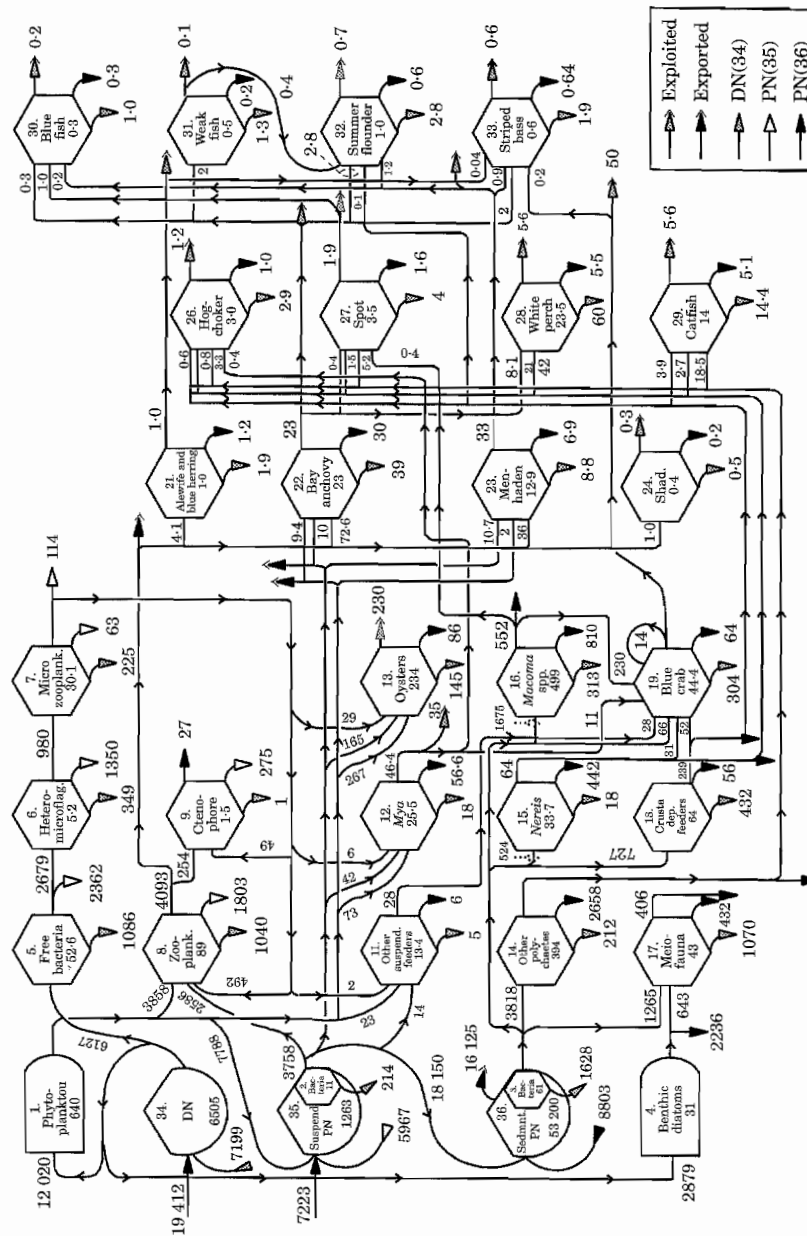


Figure 5. Springtime exchanges of nitrogen among the 36 major compartments of the mesohaline Chesapeake Bay ecosystem. Flows are in  $\text{mg N m}^{-2}$  aggregated over the 91-day season. Numbers at the inside bottom of the boxes are the standing stocks (in  $\text{mg N m}^{-2}$ ). Numbers at the inside top of the boxes represent the placement of the taxon in matrix and vector arrays. The major source of DN is shown flowing into compartment 34. Sinks and recycle flows are explained in the legend.



TABLE 1. C:N ratios and data sources (model compartment number in parentheses)

Component (compartment no.)	Parameter C:N 5	Reference
Phytoplankton (1)	C:N 6:2	Boynton & Kemp (1985)
Benthic algae (4)	C:N 6:2	
Bacteria (2, 5)	C:N 5	Newell & Linley (1984) Goldman <i>et al.</i> (1985)
	N remineralization	Newell <i>et al.</i> (1988)
Heterotrophic microflagellates (6)	Body tissue C:N 5	Newell & Linley (1984)
	Faecal C:N 8	Turner & Ferrante (1979)
	NH <sub>4</sub> regeneration 13% of ingested N	Anderson <i>et al.</i> (1985)
Microzooplankton (7)	Body tissue C:N 4:39	Newell & Linley (1984) Holligan <i>et al.</i> (1984)
	Faecal C:N 8	Turner & Ferrante (1979)
	NH <sub>4</sub> remineralization	Mantoura <i>et al.</i> (1988)
Mesozooplankton (8)	Body tissue C:N 4:38	Newell & Linley (1984) Holligan <i>et al.</i> (1984)
	Faecal C:N 8	Turner & Ferrante (1979)
	15% of daily N intake remineralized	Morales (1987) Newell & Linley (1984)
		Newell <i>et al.</i> (1988)
Ctenophores (9) and scannettes (10)	Body tissue C:N 3:37	Kremer (1976, 1977)
	Faecal C:N 8	Assumed same as for zooplankton
	Excretion rate of N	Kremer (1977)
All mollusc spp. (11–13, 16)	Body tissue C:N 4:7	Newell (1982) Seiderer & Newell (1985)
	Faecal C:N 7:25:1	Jordan (1987)
	N excretion rates	Langdon & Newell (1990) Sma & Baggaley (1976)
Nereis (15)	Body tissue C:N 3:35	Beers (1966)
	Faecal C:N 15	Blackburn & Henrikson (1983)
	N excretion	Blackburn & Henrikson (1983)
Other polychaetes (14)	Body tissue C:N 3:35	Beers (1966)
	Faecal C:N 15	Blackburn & Henrikson (1983)
	N excretion rates	Blackburn & Henrikson (1983)
Meiofauna (17)	Nitrogen 11% of dry body weight	Jorgenson (1979)
	Faecal C:N 15	Assumed same ratio as for polychaetes
Crustacean deposit-feeders (18)	Body tissue C:N 4:5	Beers (1966)
	Faecal C:N 10:4	Frankenberg <i>et al.</i> (1967)
	NH <sub>4</sub> excretion rates 7.4% of daily body N	Mayzaud (1973)
Blue crab (19) Beers (1966)	Body tissue C:N 4:5	
	Faecal C:N 4:46	Frankenberg <i>et al.</i> (1967)
	NH <sub>4</sub> excretion rates 7.4% of daily body N	Mayzaud (1973)
Fish (20–33)	Daily dissolved N (mainly NH <sub>4</sub> ) excretion	Durbin & Durbin (1983)
Omnivorous fish (20–24)	Faecal C:N 7:3	Frankenberg & Smith (1967)
Carnivorous fish (25–33)	Faecal C:N 11:2	Darnell & Wissing (1975)

a C:N ratio of 6:2 (Boynton & Kemp, 1985). Failing any clear guidelines from the literature as to the release of photosynthate nitrogen, we assumed nitrogen production to be equal to nitrogen uptake. The chlorophyll *a* sinking rates determined by Boynton *et al.* (1991) first were converted to carbon, and then to nitrogen, using a C:N ratio of 6:2

(Boynton & Kemp, 1985). The nitrogenous biomass and production of benthic diatoms were estimated by converting the carbon data of Baird and Ulanowicz (1989) using a C:N ratio of 6.2.

#### *Bacteria*

Nitrogen uptake (mainly as  $\text{NH}_4^+$ ) by free-living bacteria is balanced by regeneration and production. Bacterial carbon biomass and production (Baird & Ulanowicz, 1989; compartments 2 and 5 in Figures 2–5) were converted to nitrogen using a C:N ratio of 5:1 (Newell & Linley, 1984; Goldman *et al.*, 1985), whilst the ratio of nitrogen regeneration was estimated from a bacterial biomass/ammonium regeneration relationship (Newell *et al.*, 1988). Unutilized free-living and attached bacterial productions were assumed to remain in the water column as particulate nitrogen (compartment 35), whilst, unutilized sediment bacterial production remains in the sediment also as particulate N. As mentioned above, sediment microbial ammonium production was inferred from the difference between the total net flux of dissolved nitrogen out of the sediment and the regeneration of ammonium by the infaunal community.

#### *Faunal communities*

The generalized nitrogen budget for all faunal species is given as  $C_n = P_n + F_n + U_n$ , where  $C_n$  (total nitrogen consumption) is equal to  $P_n$  (secondary production in terms of nitrogen) plus  $F_n$  (particulate faecal nitrogen) and  $U_n$  (dissolved ammonium excretion) (Newell & Linley, 1984). The biomass and production values (in carbon, from Baird & Ulanowicz, 1989) for each faunal compartment were converted to nitrogen using appropriate C:N ratios, whilst faecal nitrogen production was estimated from published C:N ratios of faecal material. The rates of dissolved inorganic nitrogen excretion for each invertebrate component were estimated from published information. C:N ratios of body tissue and faecal material, and sources for dissolved nitrogen excretion rates by invertebrates are given in Table 1. It is virtually impossible to find the complete bioenergetic and physiological profile of every species in each and every ecosystem. Thus, in a number of cases we followed common practice and assumed that results obtained on a particular species elsewhere pertained to closely related taxonomic entities in Chesapeake Bay.

The nitrogen budgets for the fish components (20–33) were estimated as follows: faecal carbon excretion (from Baird & Ulanowicz, 1989) of omnivorous (20–24) and carnivorous (25–33) fish were converted to particulate nitrogen using C:N ratios of 7.3 and 11.2, respectively (Frankenberg & Smith, 1967; Darnell & Wissing, 1975). The nitrogen fraction of the tissue of each fish species was calculated from the relationship, nitrogen biomass = percent protein content of raw fish tissue/6.25 (Darnell & Wissing, 1975; Seiderer & Newell, 1985). Combining this value with the carbon stocks (as estimated in Baird & Ulanowicz, 1989) yields the C:N ratios as they apply to both biomass and production. The protein content of each fish species was obtained from Sidwell *et al.* (1974). The daily nitrogen excretion rates of fish were calculated from the relationship  $U_n = 0.616C_n + 0.237$ , where  $U_n$  equals the dissolved nitrogen (mainly ammonium) excretion in mg N ( $\text{g dry w}^{-1}$ )  $\text{day}^{-1}$  and  $C_n$  the total nitrogen intake in the same units (Durbin & Durbin, 1983). The daily nitrogen intake by each fish species was calculated according to its diet composition. For example, the diet of the hogchoker (26) consists mainly of deposit-feeding crustaceans (12%), *Nereis* (14%), other polychaetes (60%) and *Mya* (12%) (Baird & Ulanowicz, 1989). The quantities of

each prey consumed (in carbon, Baird & Ulanowicz, 1989) were converted to nitrogen by means of the C:N ratios of these different prey species, and in turn the sum of these was substituted as  $C_n$  into the above equation for  $U_n$ . The sum of  $U_n$ ,  $F_n$  and  $P_n$  is equal to the total daily nitrogen uptake of that particular fish component.

Seasonal standing stocks of and exchanges among the major biotic and abiotic components of the mesohaline region of Chesapeake Bay are shown in Figures 2–5, and mean annual biomasses and flows in Figure 6. The input into each producer, consumer and storage compartment is shown, as are their respective outputs in terms of production (compartments 1–33), faecal egesta (as particulate nitrogen), dissolved nitrogen excretion (for compartments 2, 3, 5–33), flows to other compartments, or exports from the system. The living compartments are numbered 1–33, and the passive storages 34–36. The biomasses, inputs and outputs from suspended particulate nitrogen (SPN; compartment 35), associated attached bacteria (compartment 2), sediment particulate nitrogen (Sed PN) and sediment bacteria (3) are contained in Figures 2–6. These values also are listed in Table 2 for clarity. Inputs to compartment 35 include faecal excretions (from compartments 5–10) and exogenous inputs, whilst outputs consist of PN deposition to the sediment, nitrogen absorbed by attached bacteria and passive exports from the systems. Flows to sediment nitrogen include deposition from 35, faecal PN from compartments 11–33 and the incorporation of unutilized production of benthic fauna into sediment PN. Flows from sediment PN include exports (see below) and nourishment to sediment bacteria.

The primary sources of dissolved and particulate nitrogen are (a) inputs from the upper bay, tributaries and other sources, and (b) heterotrophic regeneration of dissolved and particulate nitrogen in the water column and in the sediments. Nitrogen from the former source (a) is termed 'new' nitrogen, because it has its origin outside the mesohaline region of the bay. Both sources are necessary to sustain primary production and bacterial growth in the bay system

## Results

The mean seasonal inputs of total nitrogen (dissolved and particulate) for the period 1984–90 vary seasonally (Boynton *et al.*, 1991, 1992). The highest inputs occur during spring ( $274.8 \text{ mg N m}^{-2} \text{ day}^{-1}$ ) and winter ( $217.8 \text{ mg N m}^{-2} \text{ day}^{-1}$ ), whilst those during summer ( $84 \text{ mg N m}^{-2} \text{ day}^{-1}$ ) and autumn ( $106.4 \text{ mg N m}^{-2} \text{ day}^{-1}$ ) are much lower. The fraction of total nitrogen input available for plant and bacterial growth (as dissolved nitrogen) also varies seasonally from about  $211.0 \text{ mg N m}^{-2} \text{ day}^{-1}$  in spring to  $53.2$  in summer,  $73.6$  in autumn and  $166$  in winter (see Table 3). In general, nitrogen fixation accounts for less than 5% of total nitrogen circulation in the Chesapeake ecosystem (Marsho *et al.*, 1975).

The regeneration of dissolved nitrogen within the system is mediated by the excretion of dissolved nitrogen (mainly in the form of ammonium) by animals and by microbes in the water column and sediments. The total amount of dissolved inorganic nitrogen regenerated during each season by the major biotic communities is summarized in Table 3. This table reveals that the sediment–water column efflux of dissolved nitrogen accounts for a large proportion of regenerated nitrogen in Chesapeake Bay. About  $126.3 \text{ mg N m}^{-2} \text{ day}^{-1}$  is released from the sediments to the overlying waters during summer, and *c.*  $48.1$ ,  $23.5$  and  $40 \text{ mg N m}^{-2} \text{ day}^{-1}$  during the autumn, winter and spring, respectively. Of these amounts about  $27.3$  (21.6%),  $15.6$  (32.0%),  $13.6$  (57.6%)

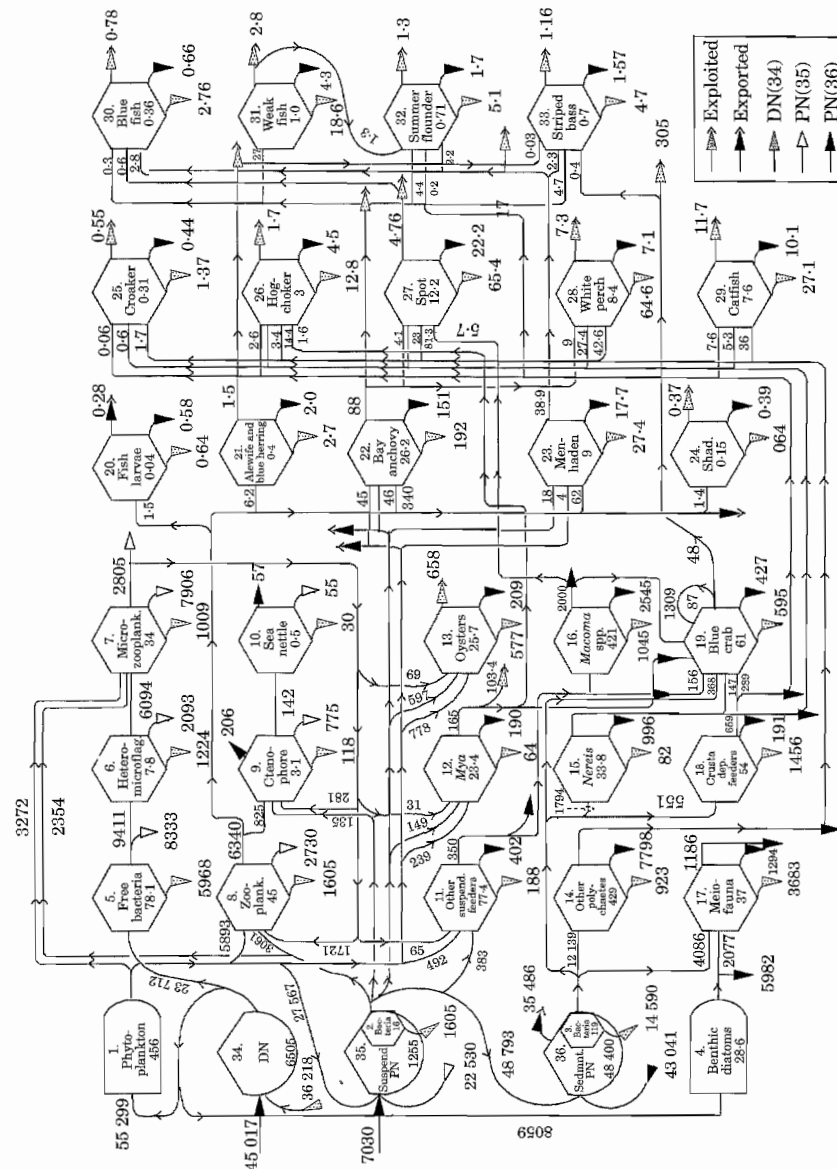


Figure 6. Annual exchanges of nitrogen among the 36 major compartments of the mesohaline Chesapeake Bay ecosystem. Flows are in  $\text{mg N m}^{-2} \text{ year}^{-1}$ . Numbers at the inside bottom of the boxes are the standing stocks (in  $\text{mg N m}^{-2}$ ). Numbers at the inside top of the boxes represent the placement of the taxon in matrix and vector arrays. The major source of DN is shown flowing into compartment 34. Sinks and recycle flows are explained in the legend.

TABLE 2. Biomass (in  $\text{mg N m}^{-2}$ ) inputs and flows (in  $\text{mg N m}^{-2} \text{ day}^{-1}$ ) of suspended (2) and sediment bacteria (3), suspended (35) and sediment particulate nitrogen (36) (compartment numbers in parentheses)

Biomass and flows ( <i>i, j</i> )	Summer	Autumn	Winter	Spring
<b>Biomass</b>				
2	34.0	16.8	1.8	10.6
3	195.5	148.5	71.7	61.0
35	1315	1242	930	1136
36	52 000	44 200	44 000	53 200
<b>Flows</b>				
to 35	195.2	153.4	86.0	235.8
35, 2	28.3	8.1	1.0	8.0
35 to	126.3	145.3	85.0	227.8
35 exp.	40.6	0	0	0
2 to	28.3	8.1	1.0	8.0
to 30	418.0	247.9	119.0	309.1
36, 3	393.6	148.5	57.4	117.7
36 exp	24.4	99.4	61.6	191.4
2 to	393.6	148.5	57.4	117.7

'to' compartment *n* refers to all inputs to compartment, compartment *n* 'to' refers to all outflows from compartment *n* to all other compartments, and compartment *n* 'exp' to exports from compartment.

TABLE 3. Seasonal demand and supply of nitrogen in the mesohaline region of Chesapeake Bay (all values in  $\text{mg N m}^{-2} \text{ day}^{-1}$  except percent values; numbers in parentheses refer to compartment numbers of Figures 2-5)

Seasonal N demand by phytoplankton diatoms and bacteria	Amount of regeneration of N by various components						'New' N
	Water column (2, 5-7)	Zooplankton (8-10)	Suspended feeders (11-13)	Scavengers (19)	Fish (20-33)	Benthic (3, 14-18)	
<b>Summer</b>							
418.3	57.4	4.0	3.7	8.2	1.9	126.3	53.2
% <sup>a</sup>	13.7	1.0	0.9	2.0	0.5	30.2	12.7
<b>Autumn</b>							
218.5	22.6	2.0	1.8	4.3	1.1	48.1	73.6
% <sup>a</sup>	10.3	0.9	0.8	2.0	0.5	22.0	33.7
<b>Winter</b>							
90.4	6.7	1.8	1.8	1.6	0.2	23.5	166.2
% <sup>a</sup>	7.4	2.0	2.0	1.8	0.2	26.0	183.8
<b>Spring</b>							
228.5	20.4	11.4	1.8	3.3	1.5	40.0	211.0
% <sup>a</sup>	8.9	5.0	0.8	1.4	0.7	17.5	92.3

<sup>a</sup>Percent contributions to N demand.

and 22.2 (55.6%)  $\text{mg N m}^{-2} \text{ day}^{-1}$  of the total sediment flux is regenerated during the same four seasons by the macroinfauna (compartments 14-18). The balance is due to microbial regeneration of nitrogen in the sediment. Sediment-regenerated nitrogen contributes between 66 and 51% (annual average 60%) to the total amount of nitrogen regenerated within the system. Regeneration in the water column (by compartments 2

and 5–10 collectively) amounts to  $61.4 \text{ mg N m}^{-2} \text{ day}^{-1}$  in summer,  $24.6$  in autumn,  $8.5$  in winter and  $31.8$  in spring. The planktonic contribution to the total amount regenerated per season ranges between  $40.6$  and  $23.9\%$  (annual mean  $31\%$ ).

Oxygen measurements by Smith (1992) to determine planktonic community respiration and production suggest that net planktonic nitrogen regeneration may approximate that via sediment efflux. The planktonic community investigated by Smith (1992) presumably included all organisms up to the size of copepods, so that the values presented here may underestimate the regeneration rates in the water column. The apportionment of oxygen production and respiration among the various size fractions, however, was not attempted by Smith (1992). To maintain consistency among the mass balance models presented here, we did not attempt to include Smith's data in the networks.

The remineralization of nitrogen by bacteria (compartments 2 and 5) is maximal in summer ( $46.8 \text{ mg N m}^{-2} \text{ day}^{-1}$ ), when it accounts for  $76\%$  of all nitrogen recycled in the water column, or about  $23\%$  of the total recycle of nitrogen. Remineralization by bacteria is much lower during the other seasons, namely  $18.0$ ,  $3.6$  and  $14.1 \text{ mg N m}^{-2} \text{ day}^{-1}$  during autumn, winter and spring, respectively (see Figures 2–5). In autumn, winter and spring, bacteria contribute about  $23$ ,  $10$  and  $18\%$ , respectively, to the total amount of recycled nitrogen. Bacteria remineralize, on average, about  $60\%$  of the annual amount of water column regenerated nitrogen, and nearly  $20\%$  of the total amount of recycled nitrogen in Chesapeake Bay.

Biomass and production of heterotrophic microflagellates (6), micro- (7) and mesozooplankton (8–10) are highest in summer, with the exception of zooplankton (8), which peaks in spring. Ammonium regeneration rates for heterotrophic microflagellates (6) were obtained from Anderson *et al.* (1985), and those for microzooplankton from Mantoura *et al.* (1988). Published rates of nitrogen excretion by zooplankton vary from  $11$  to  $38\%$  of the body weight of nitrogen per day (Butler *et al.*, 1969, 1970; Mantoura *et al.*, 1988). We have followed Newell and Linley (1984) in assuming that about  $15\%$  of the ingested nitrogen is remineralized as ammonium. Seasonal rates for nitrogen excretion by ctenophores (9) and sea nettles (10) were given by Kremer (1977) as a percentage of nitrogen turnover (*c.*  $80\%$ ) at various temperatures.

The combined nitrogen regeneration rate of heterotrophic microflagellates (6) and microzooplankton (7) ( $<200 \mu\text{m}$  in size) is highest in summer ( $10.6 \text{ mg N m}^{-2} \text{ day}^{-1}$ ), whereas it is  $4.5$ ,  $3.1$  and  $6.3 \text{ mg N m}^{-2} \text{ day}^{-1}$  in autumn, winter and spring, respectively. Their contribution to the total amount recycled fluctuates between a high of  $8.7\%$  in winter to a low of  $5.3\%$  in summer, with an annual contribution of about  $7\%$ . Microzooplankton ( $>200 \mu\text{m}$ ; compartments 8–10) regenerate nitrogen at approximately the same rates as mesozooplankton, but the highest values occur in spring ( $11.4 \text{ mg N m}^{-2} \text{ day}^{-1}$ ), and decrease through summer ( $4.0 \text{ mg N m}^{-2} \text{ day}^{-1}$ ) and autumn ( $2.0 \text{ mg N m}^{-2} \text{ day}^{-1}$ ) to winter ( $1.8 \text{ mg N m}^{-2} \text{ day}^{-1}$ ). Mesozooplankton, in particular copepods (8), contribute minimally in spring to the total amount of recycled nitrogen ( $15\%$ ), and considerably less ( $2.0$ ,  $2.5$  and  $5.1\%$ ) during the following three seasons. Mesozooplankton contribute about  $6\%$  to the annual recycled nitrogen.

Filter- and deposit-feeding species (11–13 and 19) comprise the benthic community in Chesapeake Bay. The nitrogen regenerated by these fauna is relatively small and varies between  $8\%$  in summer to  $10\%$  in winter (see Figures 2–5, Table 3). These figures are based on estimates by Langdon and Newell (1990) of an average excretion rate by oysters of  $30 \mu\text{g N h}^{-1}$  ( $\text{g dry weight}^{-1}$ ). Newell (pers. comm.) feels this rate applies to other molluscs as well.

Seasonal changes in the species composition and stocks of the fish community in Chesapeake Bay are discussed in detail by Baird and Ulanowicz (1989). The diets of the different fish species are taken from the same source. The particulate nitrogen in fish faeces is assumed to settle to the bottom. The rate of dissolved nitrogen (mainly ammonium) excreted by fish was obtained from Durbin and Durbin (1983). Collectively, fish regenerate the most nitrogen in summer ( $1.9 \text{ mg N m}^{-2} \text{ day}^{-1}$ ) and the least in winter ( $0.2 \text{ mg N m}^{-2} \text{ day}^{-1}$ ). The percentage contribution by fish to the total nitrogen regenerated in the system ranges between a high of 2.0% in spring to a low of 0.6% in winter. It thus appears that the nitrogen regenerated in Chesapeake Bay by the fish community as a whole is of distinctly lesser importance than that recycled by the invertebrate groups.

The rates of deposition of chlorophyll *a* and faecal material from the water column have been measured by Boynton *et al.* (1991, 1992), and mean seasonal values are given in Figures 2–6. The rate of deposition of chlorophyll *a* and other nitrogenous material oscillates from a high in spring ( $202 \text{ mg N m}^{-2} \text{ day}^{-1}$ ), then drops in summer ( $108 \text{ mg N m}^{-2} \text{ day}^{-1}$ ), increases again during autumn ( $143 \text{ mg N m}^{-2} \text{ day}^{-1}$ ), and reaches its nadir in winter ( $84 \text{ mg N m}^{-2} \text{ day}^{-1}$ ). Chlorophyll *a* (chl *a*) comprises about 45% (or  $91 \text{ mg chl } a \text{ N m}^{-2} \text{ day}^{-1}$ ) of the material deposited in spring, coincident with the spring phytoplankton bloom and its associated high chlorophyll *a* stocks (Kemp & Boynton, 1992). In summer, chlorophyll *a* comprises about 45% of nitrogen settlement (or  $49 \text{ mg chl } a \text{ N m}^{-2} \text{ day}^{-1}$ ) and becomes a major component (77% or  $110 \text{ mg chl } a \text{ N m}^{-2} \text{ day}^{-1}$ ) of deposited material during autumn. The deposition rate drops during winter (to  $84 \text{ mg N m}^{-2} \text{ day}^{-1}$ ), although chlorophyll *a* continues to contribute about 74% ( $62 \text{ mg chl } a \text{ N m}^{-2} \text{ day}^{-1}$ ) of the deposited nitrogen. The high rate of nitrogen deposition during spring appears to sustain the elevated level of nitrogen regeneration in summer when 'new' input becomes scarce (cf. Malone *et al.*, 1988).

Nitrogen is lost from the system through internal processes, such as denitrification, burial in the sediments and fishery yields, and through emigration (of, for example, some fish species) and passive transport of material across the downstream boundary. It has been estimated that the seasonal loss of nitrogen through denitrification is about  $41.4 \text{ mg N m}^{-2} \text{ day}^{-1}$  in spring, 35.8 in autumn and 26.9 in winter. No nitrogen is lost through this process during summer, simply because nitrate is scarce then. During summer, deep water hypoxia effectively shuts down sediment nitrification of ammonium, and hence the supply of  $\text{NO}_3$  to undergo denitrification is also curtailed. At the same time  $\text{NO}_3$  from terrestrial sources is also greatly reduced as a result of low freshwater runoff (see Table 3). Export values (given in Figures 2–5) from sediment nitrogen (compartment 36) refer to the seasonal sums of denitrification and sediment burial. They vary (collectively) between 18% of the total particulate nitrogen inputs (i.e. riverine and internal deposition) onto the sediments in summer, 49% in autumn, 50% in winter, and 47% in spring.

Exports of dissolved and suspended nitrogen across the system boundaries emanate from compartments 34 and 35 in Figures 2–5. Exports of suspended PN appear to be small in autumn, winter and spring, probably because of the high fractions of the total inputs to that compartment (35) that are deposited. Losses through emigration and exploitation are shown in Figures 2–6, and vary seasonally from 8% of the total nitrogen inputs in summer, to 1.6% in autumn, 0.3% in winter and 1.5% in spring.

Phytoplankton, benthic algae and bacteria depend directly on the availability of dissolved inorganic nitrogen (mainly as ammonium) for growth and production

TABLE 4. Seasonal nitrogen demand and supply budget (in  $\text{mg N m}^{-2} \text{ day}^{-1}$ )

Demand supply	Season			
	Spring	Summer	Autumn	Winter
<b>Demand</b>				
Phytoplankton	130.7 (57%)	232.5 (56%)	175.3 (80%)	71.0 (79%)
Benthic algae	31.3 (14%)	46.5 (11%)	7.6 (4%)	2.4 (2%)
Water column bacteria	66.6 (29%)	139.3 (33%)	35.6 (16%)	17.0 (19%)
Total	228.6	418.3	218.5	90.4
<b>Supply</b>				
Regenerated N	78.4 (37%)	201.5 (80%)	79.8 (52%)	35.6 (18%)
'New' N	211.0 (63%)	53.2 (20%)	73.6 (48%)	166.2 (82%)
Total	289.4	254.7	153.4	201.8
F-ratio ( 'new' N:reg. N)	2.7	0.3	0.9	4.7

(Wheeler & Kirchman, 1986; Paasche, 1988). Their demands for nitrogen vary seasonally, coinciding with periods of high production, which occur during spring and summer (Malone *et al.*, 1988; Baird & Ulanowicz, 1989; Kemp & Boynton, 1992). Both remineralization and the input of 'new' nitrogen serve to meet these demands.

Tables 3 and 4 summarize the estimated seasonal demands for nitrogen by phytoplankton, benthic algae and bacteria, the seasonal rates of regeneration by the different biotic groups, and the input of 'new' nitrogen. Phytoplankton production showed two distinct peaks; one in spring ( $130 \text{ mg N m}^{-2} \text{ day}^{-1}$ ) and one in summer ( $232 \text{ mg N m}^{-2} \text{ day}^{-1}$ ) (Magnien *et al.*, 1992; Figures 2–5, Tables 3 and 4). Biomass and production of benthic diatoms (4) and bacteria (2, 5) similarly peak in summer and drop to their lowest values in winter (Figures 2–5). Thus, the aggregate demands for nitrogen by these groups are highest in summer ( $418 \text{ mg N m}^{-2} \text{ day}^{-1}$ ), decline through autumn and winter ( $218 \text{ mg N m}^{-2} \text{ day}^{-1}$  and  $90 \text{ mg N m}^{-2} \text{ day}^{-1}$ , respectively), and increase again in spring ( $228 \text{ mg N m}^{-2} \text{ day}^{-1}$ ; see Tables 3 and 4). Phytoplankton demand appears to exceed that of bacteria and benthic diatoms, although bacterial demand constitutes a significant proportion of the overall demand, especially during spring and summer (Table 4).

Approximately 35% of the phytoplankton production during spring and summer is consumed by a variety of species; the percent utilization declines to about 10 and 16% in autumn and winter, respectively. Unutilized phytoplankton production is either deposited on the bottom sediments or exported from the system. We assume that unutilized benthic diatom production is contributed to the sediment PN pool (36).

## Discussion

### *Seasonal nitrogen budgets and cycling*

The production of organic matter in Chesapeake Bay is dominated by phytoplankton. It is maximal in summer and drops to a low in winter (Baird & Ulanowicz, 1989). Nitrogen taken up by phytoplankton in the euphotic zone is highest in summer ( $232 \text{ mg N m}^{-2} \text{ day}^{-1}$ ), even though the biomass of phytoplankton is higher in spring ( $640 \text{ mg N m}^{-2} \text{ day}^{-1}$ ) than in summer ( $417 \text{ mg N m}^{-2} \text{ day}^{-1}$ ). In fact, the



phytoplankton/biomass ratio increases from  $0.2 \text{ day}^{-1}$  in spring to about  $0.6 \text{ day}^{-1}$  in summer. About 35% of the spring production ( $131 \text{ mg N m}^{-2} \text{ day}^{-1}$ ) is consumed directly, whilst the balance is deposited on the sediments. Less of the summer production is deposited on the sediments, although a substantial amount ( $\approx 37\%$ ) appears to be exported from the mesohaline region. Phytoplankton production and consumption decrease dramatically through autumn and winter, whereas deposition rates of nitrogen by phytoplankton were higher in autumn than they were during summer.

The benthic algae (mainly pennate diatoms) on the sediments of Chesapeake Bay form a relatively small proportion of autotroph stock and production. The biomass of benthic algae is only 14% that of phytoplankton in summer, 5% in autumn, 2.0% in winter, and 5% in spring. Its production (as a percent of phytoplankton) is about 20, 4, 3 and 24% in summer, autumn, winter and spring, respectively; hence, the demand for dissolved nitrogen to fuel primary production is mainly by phytoplankton. The relatively high deposition by phytoplankton during spring, combined with the low input rate of 'new' nitrogen during summer, implies that spring productivity contributes indirectly, via sediment nitrogen regeneration, to the high summer phytoplankton production (Kemp & Boynton, 1992).

Free-living bacteria demand significant nitrogen for growth and production (Goldman *et al.*, 1987). They also remineralize nitrogen, and their contribution to the total nitrogen is not insignificant. Nitrogen demand and regeneration by free-living bacteria fluctuate seasonally, with the highest uptake ( $139 \text{ mg N m}^{-2} \text{ day}^{-1}$ ) and remineralization ( $35.3 \text{ mg N m}^{-2} \text{ day}^{-1}$ ) occurring during summer. This demand is about 56% of the total nitrogen supply, and their release contributes about 18% to the total amount of nitrogen regenerated during summer. Therefore, bacteria may be competing with phytoplankton for nitrogen during summer. Bacteria demand smaller proportions of available nitrogen during the other seasons (23% in autumn and spring, and 8% in winter). Their remineralization contributes 19, 15 and 8% in autumn, spring and winter, respectively, to the total regeneration of nitrogen. These bacterial contributions are exceeded in spring and winter by the micro- and mesozooplankton, at which times these components (6–10) contribute 26 and 16%, respectively, to the total amount of cycled nitrogen.

Nitrogen remineralization in the water column is mediated mainly by organisms smaller than  $200 \mu\text{m}$ . These components (bacteria, heterotrophic microflagellates and microzooplankton; compartments 2 and 5–7 of the network; Figures 2–5) regenerate, on an annual basis, about 68% of the recycled nitrogen in the water column. In contrast, the mesozooplankton ( $>200 \mu\text{m}$ , compartments 8–10) regenerate only about 12% of the annual average ( $41 \text{ mg N m}^{-2} \text{ day}^{-1}$ ). The percent contribution to water column nitrogen regeneration by bacteria and microzooplankton (compartments 2, 5–7) varies seasonally from 76% in summer, to 71% in autumn, 55% in winter to 53% in spring, whilst mesozooplankton remineralize about 5% in summer, 6% in autumn, 15% in winter and 30% in spring. The inverse relationship between the regeneration of (ammonium) nitrogen by bacteria and microzooplankton on the one hand, and by mesozooplankton on the other, appears to hinge on the abundance of the mesozooplankton, as postulated by Glibert *et al.* (1992). That is, nitrogen regeneration by bacteria and microzooplankton is high during summer and autumn when mesozooplankton biomass is relatively low, but decreases when zooplankton biomass ( $>200 \mu\text{m}$  in size) increases through winter and spring (see Figures 2–5).

The small contribution by mesozooplankton to water column nitrogen remineralization relative to that by bacteria and microzooplankton appears to mirror nitrogen dynamics in other systems. For example, mesozooplankton contribute only 8% to phytoplankton ammonium demand in the Newport River estuary, North Carolina (Smith, 1978), less than 10% in the Neuse River (Christian *et al.*, 1992) and South River estuaries, North Carolina (Fisher *et al.*, 1982), about 12% in Carmarthen Bay, U.K. (Mantoura *et al.*, 1988), 10% in the Middle Atlantic Bight (Harrison *et al.*, 1983), and 9% to the total amount of regenerated nitrogen in the English Channel (Newell & Linley, 1984). In these systems, as in Chesapeake Bay, bacteria and microzooplankton account for the bulk of nitrogen regeneration.

When the aggregate demand for nitrogen (by phytoplankton, bacteria and benthic algae) is compared with its supplies (through regeneration and the input of 'new' nitrogen), it appears that there is a nitrogen deficiency during summer and autumn (see Table 4). Nitrogen limitation of algal production also has been postulated by Fisher *et al.* (1992) during summer along the major axis of Chesapeake Bay and in the Patuxent sub-estuary by D'Elia *et al.* (1986). Magnien *et al.* (1992), however, suggested that phosphorus limitation of phytoplankton production appears more likely in the mesohaline region of Chesapeake Bay. 'New' nitrogen supplies exceed internal regeneration during winter and spring, and are responsible for an excess of nitrogen during those two seasons. It has been reported, however, that water column regeneration can supply most of the phytoplankton nitrogen demand (Harrison, 1978; Caperon *et al.*, 1979; Glibert, 1982; Smith, 1992). This implies that both pelagic and benthic regeneration are important in many coastal systems (Boynton & Kemp, 1985). It is thus possible that we have underestimated water column nitrogen regeneration, and the alleged deficits for summer and autumn (Table 4) may not really exist. There also remains the question of the role that urea plays in overall nitrogen metabolism. Data exist for very few species, and it was impractical for us to include this constituent in the overall balance.

The net sediment efflux of regenerated nitrogen ranges from  $126 \text{ mg N m}^{-2} \text{ day}^{-1}$  in summer to a low of about  $23.5 \text{ mg N m}^{-2} \text{ day}^{-1}$  in winter, and supplies about 30, 22 and 18% of the total nitrogen demand (see Table 3) during summer, autumn, winter and spring, respectively. Benthic regenerated nitrogen supplies between 27 and 54% (annual mean 36%) of the phytoplankton nitrogen demand in the Chesapeake Bay, which falls within the range of 7–78% for 14 marine systems listed by Billen and Lancelot (1988). Flint *et al.* (1986) reported that as much as 90% of the phytoplankton nitrogen demand is derived from sediments in the Corpus Christi Bay estuary, Texas.

Owing to the paucity of comprehensive studies on the seasonal (or annual) dynamics of nitrogen in marine systems, detailed comparison of Chesapeake Bay with other systems is not yet possible. However, a nitrogen budget of Carmarthen Bay (Bristol Channel, U.K.) indicates that about 28% of the phytoplankton nitrogen demand is met by regeneration (mainly as ammonium) within the bay, whilst the greater balance (largely  $\text{NO}_3$ ) is ascribed to landward inputs from the Bristol Channel (Owens *et al.*, 1986; Mantoura *et al.*, 1988). According to Harrison *et al.* (1983) 33% of the total nitrogen demand on the outer shelf of the Middle Atlantic Bight is remineralized in summer, and 67% imported as 'new' nitrogen. Of that amount remineralized, 30% is ascribed to regeneration by mesozooplankton, 63% by microplankton and the balance (only 7%) by sediment efflux. Estimates of nitrogen regeneration in the English Channel by Newell and Linley (1984) indicate that 63–72% of the nitrogen supply during summer is regenerated by the heterotrophic plankton community.

The comparison of regeneration values between systems is tenuous because of their inherent differences. It is interesting to note, however, that Chesapeake bay regenerates *in situ* approximately 80% of the total nitrogen supply during summer. This percentage fluctuates during the other seasons from 52% in autumn, to 18% in winter and 27% in spring. About 44% of the total annual supply is regenerated *in situ*. This value would even be higher if the pelagic O<sub>2</sub> respiration rates of Smith (1992) were used. *In situ* nitrogen regeneration (as a percentage of total supply) varies considerably in other estuaries and marine systems. Thirty-five percent of the supply is regenerated *in situ* in Carmarthen Bay (Mantoura *et al.*, 1988); 72% in the English Channel (Newell & Linley, 1984), 48% on the outer shelf of the Middle Atlantic Bight (Harrison *et al.*, 1983), and 41% in Narragansett Bay, Rhode Island (Nixon & Pilson, 1983). The highest percentage of recycled nitrogen was reported in a detailed study on the Neuse River estuary by Christian *et al.* (1992), who estimated that *in situ* regeneration of nitrogen supplied 98 and 86% of the total nitrogen throughout summer and spring, respectively.

#### Network analysis

The four seasonal networks of nitrogen flows and their annual ensemble were analysed using the software package NETWRK (Ulanowicz & Kay, 1991). Some of the results of the analysis gave further confirmation to conclusions already drawn above, whereas others revealed new insights.

In particular, it proved useful to compare the output from the nitrogen network with those we reported earlier using the carbon flows from the same system (Baird & Ulanowicz, 1989). As one might have expected, these differences were greatest when we contrasted the patterns in which the two elements were recycled. Nitrogen is recycled to a significantly greater degree than carbon, as reflected in a more than 2-fold increase in the proportion of community activity devoted to nitrogen recycle. This proportion, known as the Finn Cycling Index (FCI), was only 21% for the annual flow of carbon, whereas it was 53% for the corresponding nitrogen network. Seasonal changes in the FCI were even more revealing. As reported by Baird and Ulanowicz (1989), the cycling index for carbon was virtually constant over the four seasons, varying by only  $\pm 2\%$ . By contrast, the FCI for nitrogen during summertime peaks at 70%, whilst the same index ranges from 34 to 46% over the other seasons. As scarce elements tend to be those retained in recycle loops, these numbers hint at nitrogen limitation during summertime.

Not only is the magnitude of nitrogen cycling greater than that of carbon, but its manifold of recycle pathways is far more elaborate as well. Baird and Ulanowicz (1989) observed how the recycling of carbon occurred within two entirely separate, or bipartite domains of the ecosystem—one that consists of the planktonic components, and the other a combination of benthic and nektonic species. This division was ascribed to the relative insignificance of resuspension of organic carbon from the sediments into the overlying water. Because there is considerable efflux of nitrogen from the sediment into the water column, no corresponding separation exists among the cycles of nitrogen. Nitrogen can course back and forth among all sectors of the ecosystem, with the consequence that the number of pathways involved in the recycle of nitrogen is enormously greater than that for carbon. Exactly 52 787 simple cycles of nitrogen were counted in the annual network, whereas only 61 such pathways were used to recycle carbon. (A simple cycle is a loop of exchanges wherein no compartment appears more than once.)

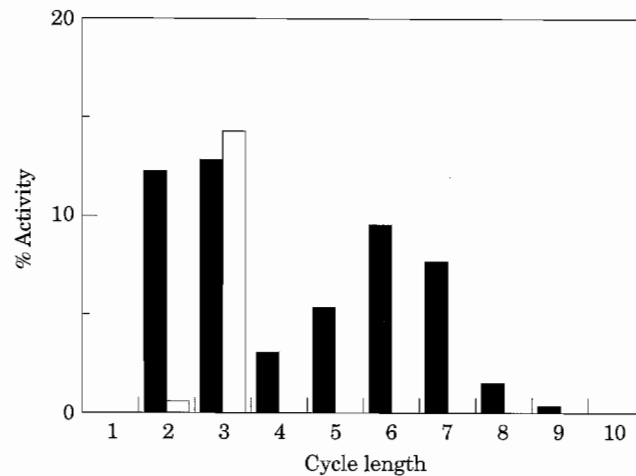


Figure 7. Percentage of total nitrogen (■) and carbon (□) transfer activity involved in recirculation over cycles with different trophic lengths.

In comparison with carbon, any individual particle of nitrogen can range over a larger domain of the ecosystem. Thus, the possibility exists that any particular limiting flow of nitrogen influences a much greater portion of the ecosystem than would be the case for carbon. The collection of all cycles that are controlled by the same trophic link constitute what in network analysis is called a 'nexus' (Ulanowicz, 1983). In the annual carbon network the nexus consisting of the most cycles was defined by the transfer of detritus from the sea nettles to the sediments and had only 11 member loops. By way of contrast, the nexus of nitrogen flows modulated by the feeding of striped bass on blue crabs counted 8030 members!

A simple example of how the influence of nitrogen feedbacks can be broader than of the corresponding returns of carbon resides in the contribution of detrital material from the zooplankton (8) to the suspended particulate matter (35). In the carbon network this flow controls only one cycle, consisting of itself and the return uptake of suspended POC by zooplankton. In the annual nitrogen network, however, the flow from compartment 8 to 35 also controls two other cycles (i.e. it defines a three-cycle nexus), which extend into the sediment and back into the water column. They encompass the sediment PN, the bacteria in the sediment, the meiofauna, the DON in the water, the phytoplankton and thence the zooplankton.

One expects many of the component cycles of these larger nitrogen nexuses to be longer (consist of more trophic transfers) than those that recycle carbon. Indeed, only a minuscule fraction of carbon recycle activity occurred over cycles composed of more than four trophic transfers. With nitrogen, however, recycle activity was spread over trophically longer pathways. A remarkable statistic is that 22% of the total transfer of nitrogen (not just recycle activity) during summer consists of nitrogen cycling over loops with six to seven trophic transfers. Baird and Ulanowicz (1989) observed a single peak of carbon cycling activity coursing over loops with three members. With nitrogen, the distribution of cycling activity as a function of cycle length was bimodal, showing one peak of activity over cycles of two to three transfer, followed by a drop in activity among four to five component cycles and finally a strong second peak at loops of length six to seven (Figure 7). What appears to be happening is that nitrogen is being passed back

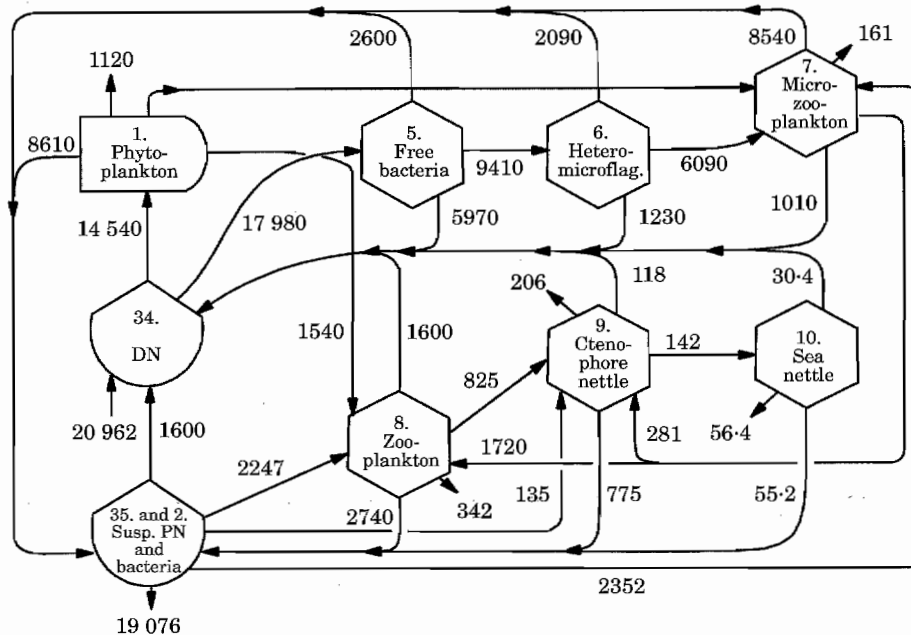


Figure 8. Cycles of flows ( $\text{mg N m}^{-2} \text{ season}^{-1} \text{ year}^{-1}$ ) of nitrogen among the components of the planktonic community in the Chesapeake mesohaline ecosystem. Arrows not pointing into (out of) any component represent aggregated exchanges of recycled nitrogen to (from) non-planktonic components.

and forth between the planktonic and benthic-nektonic domains, and within each community the characteristic cycle length (as with carbon) is about three trophic transfers.

With regard to particular structures of cycling, probably the greatest contrast between the pathways for nitrogen and carbon reuse concerned the so-called 'microbial loop', which consists of the free bacteria (5), the microheteroflagellates (6), the microzooplankton (7) and the associated dissolved and suspended non-living materials (34 and 35). What was notable about the carbon network was that three of these components (5, 6 and 24) engaged in no recycle of carbon whatsoever. With respect to carbon, the microbial pathway functions more as a shunt to convey carbon out of the system. In contrast, the microbial constituents of the plankton are integral links in the loops that keep nitrogen cycling within the ecosystem. In fact, it can be seen in Figure 8 that the pathway, DN-free bacteria-heteromicroflagellates-microzooplankton, dominates the pattern of recycle of nitrogen through the plankton. One also observes that, unlike with carbon, the cycling of nitrogen among the planktonic species is not self-contained. Most of the cycled nitrogen must leave the plankton in particulate form and return as dissolved nitrogen. Thus, for neither element do the microbial components function as a 'loop' in itself. Presumably, that might be a conclusion one would draw from a similar analysis of open-water marine systems; but, unless analysis of some other currency in the bay ecosystem shows otherwise, the 'microbial loop' continues, as regards Chesapeake Bay, to be a misnomer.

If some vehicle for retention of nitrogen in the ecosystem other than recycle were at work, it should become apparent as a difference in the trophic efficiencies of both elements as they are passed up the trophic pyramid. Ulanowicz and Kemp (1979)

developed a method for partitioning the activities of individual species among the integer levels of a Lindeman-like trophic pyramid. Ulanowicz (1995) later extended the method to handle networks that recycle (Baird & Ulanowicz, 1989, their Figure 9, for example). The trophic aggregation process allows one to calculate the underlying 'trophic efficiencies' between each level of the pyramid thus constructed (Baird & Ulanowicz, 1989, their Figure 10). We discovered that the trophic efficiencies of nitrogen flows do not differ significantly from those calculated for carbon, neither in the annual aggregate nor in any of the seasons. For example, the efficiencies of carbon transfer between the eight trophic levels were 79, 35, 11, 8, 3 and 0.8%. The corresponding values for nitrogen transfers were 77, 30, 19, 13, 11, 9 and 0.8%, respectively. Possibly, this correspondence is due to the relatively constant proportions (or 'stoichiometry') of major chemical elements within each population, but thus far we have been unable to explicitly identify any relationship.

The final step in network analysis usually is to compare the overall structures of the networks in question. Ulanowicz and Norden (1990) have described a suite of flow indices that quantify key structural attributes of a trophic network. All measures are based on what in information theory is commonly known as 'statistical entropy', but what we believe is better described as 'potential indeterminacy', i.e. an upper bound on the degrees of freedom inherent in the network. It is calculated from the flows according to the well-known 'Shannon-Wiener Index'. The potential indeterminacy for each set of flows was virtually the same (4.78 bits for the carbon *vs.* 4.82 for that of nitrogen). When this potential is scaled by the total system activity (the total amount of transfers of nitrogen or carbon), the result is called the 'development capacity'.

Conveniently, the development capacity may be decomposed algebraically into two components, the first of which is called the ascendancy. Ascendancy gauges how much of the potential indeterminacy is vanquished by the constraints that impart visible structure and form to the network. In ecological terms, ascendancy may be thought of as the ordered feedback activity that accrues as a result of predators specializing upon those prey that in their own turn are most benefited by the activity of the predator (indirect mutualism). Ulanowicz (1986) identified any increase in system ascendancy with its 'growth and development'. The second component has been named the systems' 'overhead', and it measures the residual indeterminacy, or degree of unconstrained activity, i.e. the amount of choice a typical predator has in selecting its next prey.

Remarkably, the split between ascendancy and overhead also does not vary much between the nitrogen and carbon nets. The fractions of capacity comprised by ascendancy are slightly higher for nitrogen in spring and summer. (For example, 47.2% for nitrogen *vs.* 44.3% for carbon in summer). However, things seem to balance over the course of the year, and the percentage of constrained activity (ascendancy divided by potential indeterminacy) for the annual networks is virtually identical (43.7% for carbon and 42.7% for nitrogen). Why these fractions are almost identical remains the subject of further study.

Significant differences between the information measures of the elemental carbon and nitrogen networks appear only among the components of the overhead. As with the overall development capacity, the overhead likewise may be decomposed into four separate components. Three of these are generated by indeterminacies in the exogenous transfers, namely the inputs, exports and dissipations (respirations). The fourth component reflects the degree to which pathways within the ecosystem parallel one another, and for that reason has been called the functional 'redundancy'. When the

various components were calculated for the carbon and nitrogen networks, the proportions of overall capacity encumbered by overhead on imports and usable exports turned out generally to be less than 10%. For carbon the fractions generated by inputs were decidedly higher than those associated with exports (e.g. 8.7% *vs.* 0.4% for the annual network), due, presumably, to the fact that little of the carbon entering the system leaves in organic form. The situation for nitrogen is reversed, but not as disparate. For instance, the fraction of annual capacity encumbered by nitrogen exports was 9.7%, whereas that associated with nitrogen imports was 4.2%. One might describe the differences in the first two overhead fractions as marginal, but the same cannot be said of the discrepancies in the remaining two. Because dissipation (respiration) is a significant part of carbon (and energy) activity, this fraction is considerably higher for carbon (18–20%) than for nitrogen (0.3–2.3%). On the other hand, the manifold routes for nutrient recycling and the ‘levelling’ of flow magnitudes that such recycle entails, virtually guarantees that redundancy will be more prominent in the nitrogen network. Redundancy fractions for nitrogen range over the year from 31.5% in winter to 45% in summer. The percentage of carbon activity encumbered by redundancy is quite stable over the year and ranges from a low of 26.3% to a high of 28.4% for the same two seasons.

What remains noteworthy is that the considerable variance among the seasonal components of the nitrogen overhead appears to behave in some compensatory manner, because the total overhead for any season varies by only slightly more than 2%. Furthermore, the combined overhead fractions for nitrogen are quite comparable to those for carbon. Whether such consistencies among seasons and between chemical elements are artefacts of how the flows were estimated, or whether they are indicative of some underlying organizational factor is a question deserving further study.

In conclusion, it is rare, if not unprecedented, that the ecosystem kinetics of two independent material elements are compared at the level of resolution done here. What should be obvious from this study is that any knowledge one may accrue from analysis of any single currency will always remain incomplete, and possibly even be misleading. An example concerns the microbial loop. One’s conclusions about the roles of the microbial components in the processing of carbon are radically different from what one observes as their function in the context of nitrogen flows. The implication for ecosystem research is that an adequate systems analysis should entail the study of several (or, if feasible, many) currencies before one can begin to define and appreciate the role that each individual component plays in that manifold, yet coherent, process that one calls the ecosystem.

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