Nutrient dynamics in the Sylt-Rømø Bight ecosystem, German Wadden Sea: An ecological network analysis approach

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ABSTRACT

Carbon, nitrogen, and phosphorus flow networks, consisting of 59 compartments, were constructed for the Sylt-Rømø Bight, a large shallow sea in the German Wadden Sea. These networks were analysed using ecological network analysis. Each network depicts the standing stock of each component in the ecosystem, and the flows between them. The trophic efficiency by which material is utilised in the Bight increase from 3%, to 6% to 17% for C, N and P, respectively. The number of cycles though which these elements pass increase from 1 197 for carbon, to 414 744 and 538 800 for nitrogen and phosphorus, respectively. The Finn Cycling Index, reflecting the amount of material recycled as a fraction of the total system activity, TST, increases from 17% for carbon, to 43% for nitrogen, to 81% for phosphorus. Other system level attributes such as the Average Path Length, the Average Internal Mutual Information, Relative Ascendancy, Relative and Normalized Redundancy, show an increase from the carbon to the nitrogen to the phosphorus networks. Phosphorus is tightly cycled over longer pathways than the other two elements, and also has the longest residence time in the Bight. Postulated differences between the behaviour of energy (or carbon) and biogeochemical networks in coastal ecosystems are evident from the results obtained from ecological network analysis.

1. Introduction

Three important elements in the functioning of marine and coastal ecosystems are carbon (C), nitrogen (N), and phosphorus (P). All three macronutrients are essential for biological activity, and their availability determine to a large extent the productivity and ecological health of an aquatic ecosystem. C, N and P are imported, transformed, recycled, stored and exported in varied quantities and proportions from estuaries and embayments, involving complex biological and biogeochemical processes. They occur in stoichiometric ratios, which may vary due to the rates by which they are taken up, stored in living tissue and in non-living dissolved and particulate pools in the water column and sediments, and made available through anabolic and catabolic processes.

The behaviour of C, N, and P has individually and separately received an enormous amount of research attention in order to explain their role and function in ecological systems. Several studies have examined the dynamics of C and N from an ecosystem perspective in terms of fluxes, cycling, and other system properties by means of ecological network analysis (ENA). Carbon flow networks have been constructed and analysed on spatial scales (e.g. Baird and Ulanowicz, 1993; Baird, 1998b; Baird et al., 2007; Scharler and Baird, 2005), and temporal scales (e.g. Baird and Ulanowicz, 1989; Baird et al., 1998, 2004b). Several studies examined the nitrogen flow models using ENA, for example Christian et al. (1992), Forès et al. (1994), Baird et al. (1995), Thomas and Christian (2001), Christian and Thomas (2003), and Borrett et al. (2006). However, scant attention has been given to the construction and analyses of flow networks using other nutrient elements such as phosphorus, silica. Even scarcer are studies that examined the simultaneous dynamics of nutrient networks at the ecosystem level. Ulanowicz and Baird (1999) have produced one of the few papers dealing with the dynamics of C, N and P using ENA.

The role of network analysis in comparative system ecology has gathered momentum and its application to estuarine ecosystems is reviewed by Christian et al. (2005). Ecological network analysis is a set of algorithms to evaluate the flow and cycling of energy and material through ecosystems from which a suite of system properties can be derived. The theoretical background and methodology are described in detail by Ulanowicz (1986, 2004), Wulff et al. (1989) and Kay et al. (1989).

The objective of this paper is to examine the dynamics of C, N and P based on detailed flow networks of the three elements in the Sylt-Rømø Bight ecosystem using network analysis. Using the results from the analysis of each network, we comment on the similarities

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and differences between the behaviour of C, N and P in a large coastal ecosystem.

2. Materials and methods

2.1. Study area

The Sylt-Rømø Bight (54° 52′–55° 10′ N and 8° 20′–8° 40′ E) is part of the greater Wadden Sea, a shallow coastal region of the North Sea, extending from the Netherlands to Denmark. The Bight is a semi-enclosed basin situated between the islands of Sylt, Germany, and Rømø, Denmark, and is connected to the North Sea by means of a 2.8 km wide channel between the islands (Fig. 1).

The Bight covers a surface area of 404 km^2, with an intertidal area of about 135 km^2. The salinity of Bight waters fluctuates between 28 and 32, and the water temperature between –1 °C in winter and 20 °C in summer. The tidal range in the basin is, on average, 2 m, and the average depth of the Bight is about 4.2 m at high tide. The diurnal tidal prism is about 550 million m^3, and 66 million m^3 for the intertidal area, between 8% and 12% of the waters of the Bight is exchanged per tidal cycle (Fast et al., 1999) with the adjacent northern Wadden Sea, while the water residence time ranges between 19 and 29 days. Little freshwater is discharged into the Bight with minimal nutrient inputs from the surrounding land. Nutrient concentrations in the Bight and fluxes between the sediments, mussel beds, sea grass beds, and the overlying waters received considerable attention over the past few decades (cf. Asmus and Asmus, 1993, 1998a, 2000; Asmus et al., 1998, 2000).

Plant and animal communities occur in various proportions in the different substrate types and tidal reaches. Sandy substrates are dominant in the Bight and cover a total area (inter- and subtidally) of about 360.5 km^2, while muddy substrates, *Zostera-*, and mussel beds cover approximately 27.8 km^2, 15.2 km^2, and 10.5 km^2, respectively (Asmus and Asmus, 1998b; Bayerl et al., 1998). The

Fig. 1. Sylt-Rømø Bight situated between the islands of Sylt (Germany) and Rømø (Denmark) in the northern German Wadden Sea. Speckled area in the figure indicates intertidal regions of the Bight.

deep subtidal area (>5 m depth) of about 40 km^2 consists of a sandy bottom and is poor in benthic macrofaunal species and abundance (Asmus and Asmus, 1998b).

2.2. Sources of information and assumptions

Most of the information to construct network models with carbon, nitrogen and phosphorus as currencies was obtained from the literature. A detailed carbon flow model of the Bight consisting of 59 compartments was developed by Baird et al. (2004a), which reflected the structure of the Bight ecosystem based on data collected during the period 1995–2004, and which formed the basis of the analyses of this paper. Carbon biomass, production, flows, and estimates of N and P excretion/regeneration rates of the living components were converted to N and P using C:N, C:P and N:P ratios reported in the literature. Exchanges of N and P between the compartments were calculated according to the diet composition of each consumer, its rate of production and faecal excretion according to Baird et al. (2004a). Conversion ratios, sources of N and P excretion rates, and the respective ratios between dissolved and particulate N and P excretion are given in Table 1. Concentration of dissolved and particulate C, N and P, chl a, and the flux of nutrients between the intertidal region, the Bight and the adjacent Wadden Sea was obtained from published and unpublished data sources.

The standing stocks and production in N and P of the primary producers were determined from corresponding carbon stocks and rates as reported by Baird et al. (2004a) and converted using the Redfield ratio. We assumed N and P production to be equal to N and P uptake, respectively, failing clear guidelines from the literature as to the release of photosynthate N and P.

Dissolved N and P uptake by free-living and sediment bacteria is balanced by regeneration and production. Carbon bacterial biomass and production (Baird et al., 2004a) were converted to N using a C:N ratio of 5.1 (Newell and Linley, 1984; Goldman et al., 1985), and P from a C:P ratio of 17 (Jürgens and Güde, 1990). Nitrogen regeneration was derived from a bacterial biomass/ammonium regeneration relationship (Newell et al., 1988), and that of phosphate according to Krempin et al. (1981). In the carbon network bacterial consumption of dissolved Cc was balanced by production (Pc), respiration (Rc) and excretion (Ec) (lowercase c refers to carbon), whereas bacterial uptake of dissolved N (Cn) and P (Cp) was assumed to be equal to the dissolved excretion (Un, Up) and production of N (Pn) and P (Pp) (lowercase n and p refer to N and P, respectively).

The generalized C budget for all heterotrophic organisms is the same as given for bacteria above, while the balanced budget equation for N and P is given as Cx = Px + Fx + Ux where lowercase x refers to either N or P, and where C (total N and P consumption) is equal to P (secondary production of N and P), plus F (particulate faecal N and P egestion), plus U (dissolved N and P excretion, mainly as ammonia and phosphate, respectively). Since no N or P is excreted in gaseous forms by plants and animals the respiration term is not included in the generalized N and P budget equation. However, the processes of nitrogen fixation and denitrification provide the link between the aquatic ecosystem and the atmosphere, while both processes are mediated by bacterial activity. The C:N, C:P and N:P ratios listed in Table 1 were used to convert carbon biomass, production, and faecal excretion to N and P equivalents. The ratio between particulate and dissolved faecal material was estimated from published information (see Table 1, cf. Baird et al., 1995; Baird, 1998a), or, where appropriate reference and/or ratios of Fx to Ux could not be obtained, Ux was estimated by difference i.e. Ux = Cx − Px − Fx, and where Fx was considered to be equal to Ec in the carbon budget equation. Based on these generalized budget equations for C, N and P each compartment's input equals
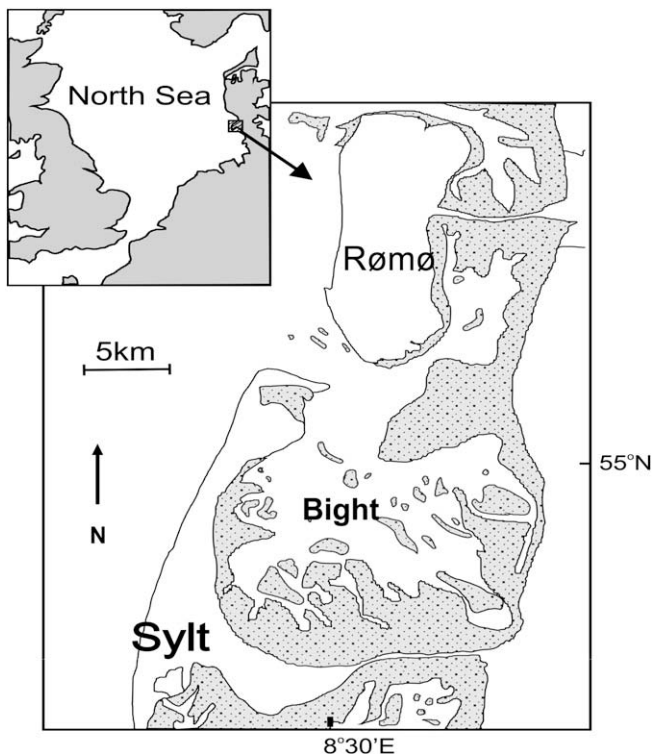
Table 1
Literature sources and C, N and P conversion ratios for the model components of the Sylt-Romo Bight (model compartment number(s) given in brackets)

Model compartment	Parameter	C, N & P conversion	Reference
Primary producers (1–3)	N & P biomass, production	Redfield ratio	
Bacteria (4, 55)	N body tissue	C:N 5.1	Newell and Linley (1984)
			Goldman et al. (1985)
	N remineralization	23% of standing stock/day	Newell et al. (1988)
			Goldman et al. (1985)
	P body tissue	C:P 17	Jurgens and Güde (1990)
	Phosphate remineralization		Krempin et al. (1981)
Zooplankton (5)	N body tissue	C:N 4.39	Newell and Linley (1984)
			Holligan et al. (1984)
	N excretion		Newell et al. (1988)
			Newell and Linley (1984)
			Anderson (1992)
			Checkley et al. (1992)
	Fecal	C:N 8	Turner and Ferrante (1979)
	P body tissue	C:P 50	Beers (1966)
	P excretion rates		Le Borgne (1982)
			Hargrave and Geen (1968)
			Lehman (1980)
			Peters and Rigley (1973)
	Fecal	N:P 9.5	Le Borgne (1982)
			Sterner (1990)
Benthic grazers (6, 7)	N body tissue	C:N 4.7	Newell (1982)
			Seiderer and Newell (1985)
	Fecal	C:N 7.25	Jordan (1987, pers. comm)
	N excretion rates		Kofoed (1975)
			Duerr (1968)
	P body tissue	C:P 29.3	Beers (1966)
	Fecal	C:P 33	Vink and Atkinson (1985)
Polychaetes (8, 9, 10, 11, 12, 14, 22, 25, 29)	N body tissue	C:N 3.35	Beers (1966)
	Fecal	C:N 15	Blackburn and Hendrikson (1983)
	N excretion		Blackburn and Hendrikson (1983)
	P body tissue	C:P 29.3	Beers (1966)
	P excretion rates	30% of P uptake	Kuenzler (1961)
			Napela et al. (1983)
	Fecal	C:P 33	Boynton (1991)
Molusks (13, 15, 19, 20, 21, 23, 24)	N body tissue	C:N 4.7	Newell (1982)
			Seiderer and Newell (1985)
	Fecal	C:N 7.5	Jordan (1987, pers. comm.)
	N excretion		Langdon and Newell (1990)
			Srna and Baggaley (1976)
	P body tissue	C:P 87	Vink and Atkinson (1985)
	Fecal	C:P 67.8	Jordan (1987, pers. comm.)
	P excretion		Kuenzler (1961)
Crustaceans (16, 17, 18, 26, 27, 28)	N body tissue	C:N 4.5	Beers (1966)
	Fecal	C:N 10.4	Frankenberg et al. (1967)
		C:N 4.46 (#27, 28)	Frankenberg et al. (1967)
	N excretion		Mayzaud (1973)
	P body tissue	C:P 29.3	Beers (1966)
	Fecal	N:P 37.7	Le Borgne (1982)
	P excretion		Le Borgne (1982)
			Sterner (1990)
Omnivorous fish (30, 31, 34)	N body tissue	C:N 2.78	Sidwell et al. (1974)
	Fecal	C:N 7.3	Frankenberg and Smith (1967)
	N excretion	80% as ammonia via gills	Durbin and Durbin (1983)
		Un:Fn 80:20	Goldstein and Forster (1970)
Carnivorous fish (32, 33, 35, 36, 37)	N body tissue	C:N ratios derived from % Protein/6.25, ranging from 2.6 to 3.0	Darnell and Wissing (1975)
	Fecal	C:N 11.2	Darnell and Wissing (1975)
	N excretion	80% as ammonia via gills	Durbin and Durbin (1983)
		Un:Fn 80:20	Goldstein and Forster (1970)
All fish spp (30–37)	P body tissue	N:P 6.5	Davis and Boyd (1978)
	P excretion	Up:Fp 90:10	Braband et al. (1990)
			Nakashime and Legget (1980)
			Kraft (1992)

Table 1 (continued)

Model compartment	Parameter	C, N & P conversion	Reference
Birds (38–54 9	N body tissue	C:N 3.5	Chilgren (1985)
	N excretion	Derived from	Portnoy (1990)
		Un = Cn − Pn	
	Particulate dissolved fecal N	Fn:Un 20:80	Smith and Johnson (1995)
			Brown (1970)
			McNabb and McNabb (1975)
	P body tissue	N:P 4	
	P excretion	Derived from	Portnoy (1990)
		Up = Cp − Pp	
	Particulate:dissolved fecal P	Fp:Up 50:50	Smith and Johnson (1995)
Meiofauna (56)	N biomass	C:N 9.1	Jorgensson (1979)
	Fecal	C:N 15	As for polychaetes
	N excretion		Baird et al. (1995)
	P biomass	C:P 29.3	Beers (1966)
	Fecal	C:P 33	Baird (1998a,b)
	P excretion	30% of P uptake	Baird (1998a,b)

its outputs and considered to be in a steady state. Biomass and the relevant bioenergetic values in C, N and P are given in Table 2.

The intake of nitrogen and phosphorus by heterotrophs was calculated according to its diet. For example, the diet of shellduck consists of 79.6% *Hydrobia ulvae*, 8.1% *Nereis diversicolor*, 11.3%

Table 2
Annual regeneration and demand of dissolved N (DN) and P (DP) in the Sylt-Rømø Bight (in mg DN or DP m^{-2} year^{-1})

(a) Nitrogen

Community (compartment numbers in brackets)	Amount of regenerated DN by various communities (mg N m^{-2} year^{-1})	Percent contribution %
Free-living bacteria (4)	170	0.5
Zooplankton	40	0.1
Benthic fauna (6–29, 56)	23 980	65.4
Sediment bacteria (55)	10 869	29.6
Fish (30–37)	66	0.2
Birds (38–54)	1536	4.2
Total regenerated DN	36 661	100.0

Community (compartment numbers in brackets)	Annual dissolved N demand by consumer communities (mg DN m^{-2} year^{-1})	Percent of DN required %
Phytoplankton (1)	20 298	30.9
Microphytobenthos (2)	37 577	57.3
Macrophytes (3)	2103	3.2
Free-living bacteria (4)	5617	8.6
Total demand of DN	65 595	100.0

(b) Phosphorous

Community (compartment numbers in brackets)	Amount of regenerated DP by various communities (m DP m^{-2} year^{-1})	Percent contribution %
Free-living bacteria (4)	579	4.7
Zooplankton	6	0.0
Benthic fauna (6–29, 56)	3466	28.3
Sediment bacteria (55)	8117	66.3
Fish (30–37)	9	0.1
Birds (38–54)	69	0.6
Total regenerated DP	12 246	100.0

Community (compartment numbers in brackets)	Annual dissolved P demand by consumer communities (mg DP m^{-2} year^{-1})	Percent of DP required %
Phytoplankton (1)	3055	28.8
Microphytobenthos (2)	5682	53.6
Macrophytes (3)	318	3.0
Free-living bacteria (4)	1544	14.6
Total demand of DP	10 599	100.0

Corophium volutator, and 1% *Cerastodule edule*. The amounts of each prey consumed in carbon (Baird et al., 2004a) were converted to N and P by means of the appropriate elemental ratios of these different prey species, and the sum equal to Cn or Cp. It was assumed that unutilized production and faecal excretions of water column bacteria and zooplankton remain in suspension, and that the unutilized production and particulate faecal material of all the other heterotrophic components contribute to sediment C, N and P.

The dissolved fraction of animal N and P excretion was assumed to contribute to the pools of dissolved N and P in the water column. The primary sources of dissolved and particulate N and P in the Bight are from remineralization processes of heterotrophs in the water column and sediments, and also from inputs from the Wadden Sea during flood tides. The input of freshwater into the Bight and associated nutrient loading is very low and do not influence or contribute to concentrations in the Bight.

2.3. Data base and network construction

A quantified carbon food web consisting of 56 living and three non-living compartments was constructed by Baird et al. (2004a) based on data from the literature and from unpublished information deposited at the Alfred Wegener Institute, Wadden Sea Station, Sylt, Germany. Standing stocks, diets of the various faunal components, and the rates of flow between the compartments in the model were based on empirical data and results contained in the numerous sources cited in this paper. Nitrogen and phosphorus values for the stocks and flows were derived using appropriate ratios as given in Table 1 and elsewhere in the text.

The concentrations and standing stocks of the non-living compartments, i.e. suspended particular organic carbon (SuspPOC), sediment particular organic carbon (SedPOC), and dissolved organic carbon (DOC), were obtained from Asmus and Asmus (1993), and Asmus and Asmus (1998a,b, 2000). Inorganic carbon, which contributes to primary production, was not included as a discrete component in the C network. Suspended and sediment particulate organic C and DOC were converted to N using C:N ratios of 6.6, 6.29, and 3.4, respectively (Boynton and Kemp, 1985; Boynton, 1991; Baird et al., 1995). Suspended particulate P was estimated from a C:P ratio of 60 (Boynton, 1991), particulate sediment P from an N:P ratio of 7.2 (Hedtkamp, pers. comm., Ph.D. thesis, 2005); and dissolved P from an N:P ratio of 44 (Baird, 1998a; Ulanowicz and Baird, 1999). Data on biomass of sediment and pelagic bacteria were obtained from Kirchman et al. (1986), Schulz (1990) and Rusch et al. (2001). The biomass, rates of gross primary (GPP) and net primary production (NPP) of the three primary

producer communities, namely phytoplankton, microphytobenthos, and macrophytes are given by Asmus and Bauerfeind (1994) and Asmus et al. (1998). Average annual biomass estimates for the various macrofaunal and fish species and communities were extracted from the published literature (cf. Asmus, 1987, 1994; Asmus and Asmus, 1990, 1993, 1998b; Asmus et al., 1998; Hermann et al., 1998) and from unpublished information (H. Asmus, unpublished data, AWI, List). Bird numbers were obtained from Scheiffarth and Nehls (1997) and Nehls and Scheiffarth (1998).

C, N and P annual averaged budgets, according to the budget equations given above, were determined for each of the three auto- and 53 heterotrophic compartments identified in the Bight ecosystem.

Diet composition for each invertebrate and vertebrate component in the food web was derived from a synthesis of published literature (Plagmann, 1939; Ehlert, 1964; Jacobsen, 1967; Höfmann and Hörschelmann, 1969; Fenchel and Kofoed, 1976; De Vlas, 1979; Fauchald and Jumars, 1979; Jensen and Siegismund, 1980; Heip et al., 1984; Pihl and Rosenberg, 1984; Pihl, 1985; Zwarts and Blomert, 1992), sources in Gätje and Reise (1998), and unpublished data at the AWI Wattermeerstation in List, Sylt.

The rate and quantity of prey consumption by each component are based on the carbon network of Baird et al. (2004a). Each network was assumed to be in a steady state where the sum of all inputs equals that of all outputs. The networks consisted of an identical number of compartments containing the estimated biomass and/or stock values, and flows between them. A general box and arrow diagram (Fig. 2) shows an aggregated model, with

compartments grouped together in trophic guilds according to Baird et al. (2004a). The diagram shows imports and exports to and from some aggregations (boxes), as well as flows indicated by arrows labelled Px (i.e. production) to consumers. Arrows labelled Fx (particulate N or P) and Ux (dissolved N or P) indicate flows to the suspended particulate or to sediment particulate N or P pools (compartments #57 and #58, respectively), while Ux indicate flows to the dissolved N or P pool (#59). The number(s) within each box refer to the relevant aggregated compartment(s).

2.4. N and P budgets

Nutrient loading into the Bight of terrestrial origin is minimal (Asmus and Asmus, 2000). Nutrients are mainly derived from mineralization processes in the Bight by fauna and from imports into the Bight by tidal currents. Asmus and Asmus (2000) and Asmus et al. (1992, 1995) provided information on the flux of dissolved N and P from and to the intertidal regions in the Bight over tidal cycles. The regeneration of dissolved nitrogen (mainly as ammonia) and phosphorus (mainly as phosphate) is due to the excretion by microbes and animals in the water column and sediment.

Rates of nitrification and denitrification vary considerably seasonally and per substrate type. Nitrification rates ranged from 1 to 17 μmol m^{-2} h^{-1} in sandy substrates and slightly higher in muddy regions ranging from 5 to 28 μmol m^{-2} h^{-1}. Nitrification rates were generally lower in all substrates during early winter and showed low rates of denitrification occurred from summer to early winter (0–8 μmol m^{-2} h^{-1}) and higher rates during late winter and spring with maximum values of 11 μmol m^{-2} h^{-1} up to 62 μmol m^{-2} h^{-1}
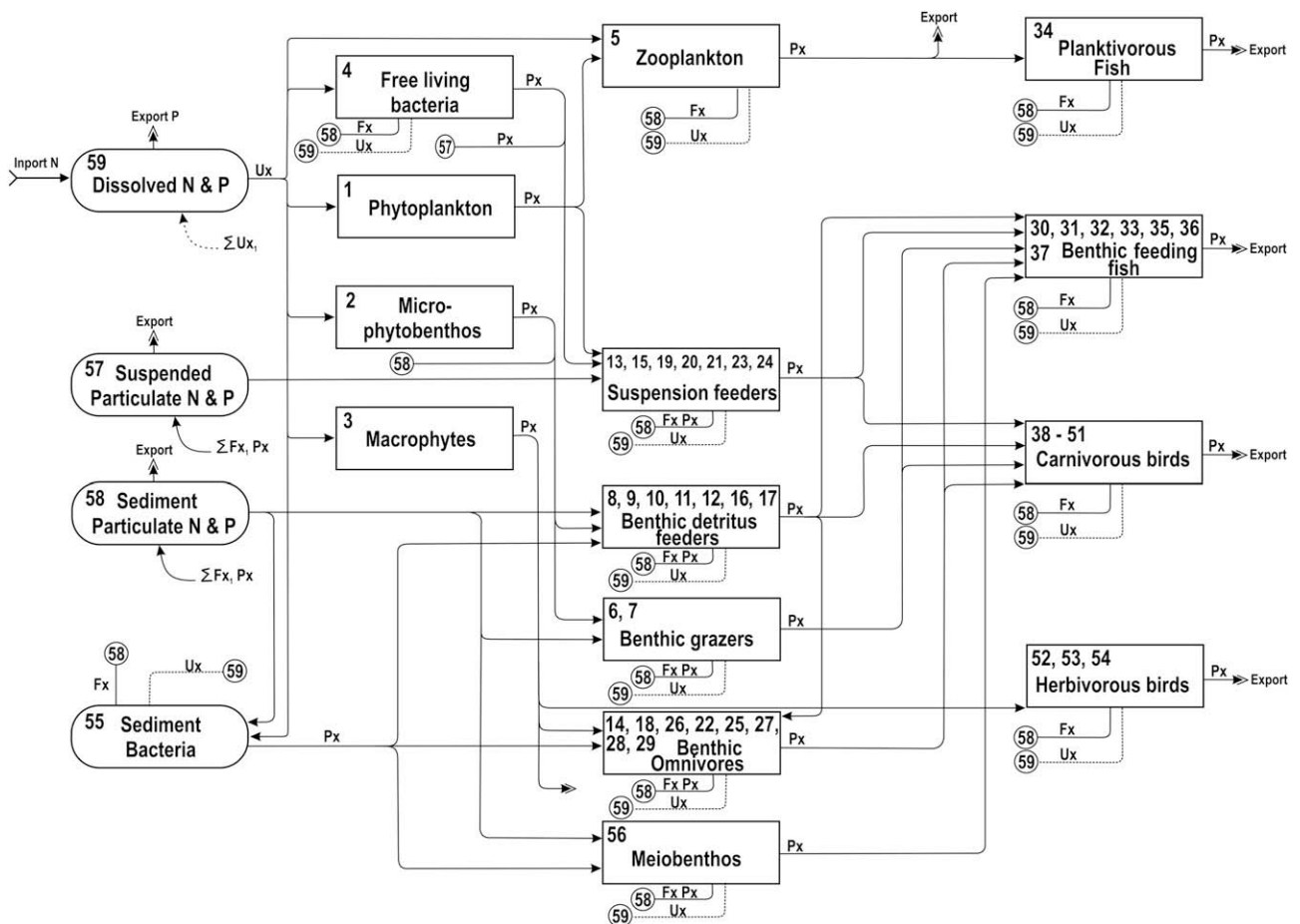

Fig. 2. Aggregated network of nitrogen and phosphorus flows in the Sylt-Rømø Bight. Numbers in boxes refer to compartments given in Table 3, Px, Fx and Ux refer to production, particulate and dissolved egesta, respectively, and lowercase x either N or P. Σ indicates the sum of inputs of Ux to compartment 59, and of Fx and Px to compartments 57 and 58.

measured in sandy and muddy substrates, respectively (Jensen et al., 1996). Denitrification of NO_3 from the overlying waters accounted for between 60% and 90% of the total denitrification during most of the year. Jensen et al. (1996) measured the annual mean dark denitrification rates to vary between 3.0 and 4.2 $\mu mol\, m^{-2}\, h^{-1}$ in sandy substrates and about 17 $\mu mol\, m^{-2}\, h^{-1}$ in muddy regions of the Bight. Weighted by area and converted to an annual rate denitrification accounts for a loss of gaseous N of approximately 520 $mg\, m^{-2}$ which was considered as an export in the N network.

The amounts of dissolved N and P regenerated by the faunal communities are summarised in Table 2, as well as annual demand of dissolved N and P by consumers. Table 2a shows that about 36 661 $mg\, DIN\, m^{-2}$ is remineralised per year by the various communities, with 95% mediated by benthic fauna and sediment bacteria. The demand for DN by autotrophs and free bacteria amounts to about 65 595 $mg\, DIN\, m^{-2}\, year^{-1}$, resulting in a shortfall of 28 934 $mg\, DIN\, m^{-2}\, year^{-1}$. Asmus and Asmus (2000) have estimated a net annual import of "new" DIN from the Wadden Sea of about 70 000 $mg\, DIN\, m^{-2}\, year^{-1}$, which compensates for the estimated shortfall which was subsequently entered as an import to the system in the N flow model.

Regenerated DP within the Bight amounts to about 12 246 $mg\, DP\, m^{-2}\, year^{-1}$ while the demand is about 10 599 $mg\, DP\, m^{-2}\, year^{-1}$ (see Table 2b). The excess in situ regeneration of DP was considered to be exported from the system which conforms with the export of DP measured by Asmus and Asmus (2000). Dissolved excretory products, remineralised and imported dissolved C, N and P comprised the dissolved pool of each element in each network (compartment 59), and from where flows were directed to the various consumers of dissolved C, N and P. Flows to and from the dissolved pools are given in Appendix A.

About 64 g of Suspended Particulate N (SusPN) is imported into the Bight $m^{-2}\, year^{-1}$ (Harald Asmus, AWI, pers. com). We have estimated that a further 5318 $mg\, SusPN\, m^{-2}\, year^{-1}$ is produced in the intertidal areas within the system through the excretion of particulate N by animals. The supply thus exceeds the demand of 3365 $mg\, SusPN\, m^{-2}\, year^{-1}$ by suspension feeders in the Bight. The demand for Suspended Particulate P (SusPP) was estimated at about 345 $mg\, SusPP\, m^{-2}\, year^{-1}$. We calculated that approximately 944 $mg\, SusPP\, m^{-2}\, year^{-1}$ is regenerated by animals in the Bight, and the excess was exported by tidal currents as also reported by Asmus and Asmus (2000).

Sediment Particulate N (SedPN) is produced in the system by particulate excretion by benthic and infaunal communities, and the decomposition of dead plants and animals. Approximately 65 869 $mg\, SedPN$ is produced $m^{-2}\, year^{-1}$ while the demand for sediment PN is about 40 713 $mg\, SedPN\, m^{-2}\, year^{-1}$; excess SedPN was assumed to be exported by tidal currents. In contrast, the uptake of Particulate Sediment P (SedPP) of about 13 545 $mg\, SedPP\, m^{-2}\, year^{-1}$ exceeded the in situ production of SedPP of 11 033 $mg\, m^{-2}\, year^{-1}$, and an amount of 2512 $mg\, SedPP\, m^{-2}\, year^{-1}$ was imported in the flow model to satisfy the demand. Secondary production of nitrogen and phosphorus, as calculated from the generalized N and P budgets, are considered to be exported from the Bight by fish and bird migration.

The standing stocks and values for the generalized C, N and P bioenergetic budgets are given in Table 3. The diet composition of each living compartment is given in detail by Baird et al. (2004a), which was used here to calculate N and P uptake by the various compartments in the flow networks.

2.5. Network analysis

Ecological network analysis, which consists of a systematic assessment of flow networks, was used to analyse the three networks with C, N and P as currencies. This analytical methodology is described in detail by Kay et al. (1989) and the software package NETWRK4.2a by Ulanowicz and Kay (1991) used for the analyses is available with supporting documentation at www.cbl.umces.edu/~ulan/ntwk/network.hmtl. The outputs from network analysis provide many useful indices and system properties of natural ecosystems, and relevant information on the interpretation of energy and nutrient flows, how these affect the structure of the ecosystem, and how one may wish to direct management or monitoring actions for the conservation or rehabilitation of biodiversity and ecosystem function (Christian and Thomas, 2003). Outputs from network analysis were used to describe the following aspects of nutrient dynamics in the Bight ecosystem:

i. Input–output analysis provides, for example, a matrix of "dependency" coefficients depicting the extended diet of a species or compartment which gives the degree to which the diet, or uptake, of any particular component depends on any other compartment in the system (Szyrmer and Ulanowicz, 1987);

ii. The Average Path Length (APL) is a system descriptor that measures the average number of compartments that a unit of C, N, or P passes through from its entry into the system until it leaves. The APL is defined by $(TST - Z)/Z$, where TST is the Total Systems Throughput (see below) and Z equals the sum of all exogenous inputs of any of the currencies (Kay et al., 1989). The Average Residence Time (ART) of material or energy in the system is the ratio between the total system biomass and the sum of all outputs (respiration and exports for C, exports for N and P) (Christensen, 1995);

iii. The Lindeman trophic aggregation routine which transforms each complex network of trophic transfers into a linear food chain with discrete trophic levels (i.e. the Lindeman Spine). The Spine illustrates the amount of material or energy that each level receives from the preceding one, as well as the fraction lost from each level through respiration and export, and the net production passed on to the next higher level. It also shows the pool of recycled detrital material, which, together with the inputs to the autotrophs, forms the first trophic level. The Lindeman Spine also allows the calculation of the efficiency of trophic transfer for each level, that is, the efficiency of transfer of energy and material from one level to the next, whilst the trophic efficiency of the whole system can be derived from the logarithmic mean of the efficiencies of each integer trophic level (Baird and Ulanowicz, 1989);

iv. The biogeochemical cycle routine of NETWRK assesses the structure and magnitude of the cycling of material in the system (Finn, 1976). The cycle distribution gives the amount of material that flows through cycles of various lengths, where a cycle represents a series of transfers between compartments beginning and ending in the same compartment without going through the same compartment twice (Baird et al., 2004a). The Finn Cycling Index (or FCI), is derived from the fraction of the sum of flows that is devoted to cycling, and is equal to Tc/TST, where Tc is the amount recycled and TST the sum of all flows in the ecosystem. The FCI is an index of the retentiveness of the system (Baird and Ulanowicz, 1989; Baird et al., 2004a,b);

v. Various global system indices, based on information theory, describe the developmental and organizational state of the ecosystem (Ulanowicz, 1986, 2004). The TST measures the extent of the total activity of the system, and is calculated as the sum of all the flows through all compartments. The system Ascendency (A), which is a single measure of the magnitude and diversity of flows between compartments, reflects on the functional attributes of the system. It

Table 3
C, N and P biomass and energetics of all compartments in flow networks

Comp #	Compartment	Carbon		Nitrogen		Phosphorus	
		Parameter	Value	Parameter	Value	Parameter	Value
1	Phytoplankton	Bc (1.00)	1040	Bn (2.00)	167.7	Bp (2.00)	25.4
		GPP	159 661.95	N uptake	14 558.1	P uptake	2201.5
		NPP	90 260.85	N prod	14 558.1	P prod	2201.5
		Rc	69 401.1				
2	Microphytobenthos	Bc (1.00)	136.2	Bn (2.00)	22.0	Bp (2.00)	3.2
		GPP	356 732.75	N uptake	37 577.3	P uptake	5682.4
		NPP	232 979.5	N prod	37 577.3	P prod	5682.4
		Rc	123 753.25				
3	Macrophytes	Bc (1.00)	2960	Bn (2.00)	477.4	Bp (2.00)	72.2
		GPP	29 630.7	N uptake	2102.9	P uptake	318.0
		NPP	13 037.8	N prod	2102.9	P prod	318.0
		Rc	16 592.9				
4	Free-living bacteria	Bc (2.00)	9.79	Bn (2.00)	1.9	Bp (2.00)	0.6
		Pc	27 776.5	Pn	5446.4	Pp	964.8
		Rc	25 717.9				
		Ec	2054.95	Un	170.3	Up	578.8
		Cc	55 549.35	Cn	5616.7	Cp	1543.6
5	Zooplankton	Bc (2.00)	11.19	Bn (3.00)	2.5	Bp (3.00)	0.2
		Pc	540.2	Pn	123.1	Pp	10.8
		Rc	149.65	Un	40.4	Up	6.3
		Ec	978.2	Fn	105.6	Fp	11.1
		Cc	1668.05	Cn	269.0	Cp	28.2
6	Hydrobia ulva	Bc (2.13)	1888	Bn (2.88)	401.7	Bp (2.79)	64.4
		Pc	2693.7	Pn	572.8	Pp	91.9
		Rc	4150.05	Un	1109.3	Up	90.0
		Ec	20 075	Fn	2769.0	Fp	532.5
		Cc	26 918.75	Cn	4451.0	Cp	714.3
7	*Littorina littorea*	Bc (2.13)	67.9	Bn (2.88)	14.4	Bp (2.79)	2.3
		Pc	51.1	Pn	10.9	Pp	1.7
		Rc	153.3	Un	32.1	Up	3.8
		Ec	306.6	Fn	42.3	Fp	8.1
		Cc	511	Cn	85.2	Cp	13.7
8	*Arenicola marina*	Bc (2.45)	5913	Bn (2.59)	1765.1	Bp (2.38)	203.9
		Pc	15 465.05	Pn	4616.1	Pp	533.2
		Rc	14 388.3	Un	8711.9	Up	997.9
		Ec	73 240.9	Fn	4882.7	Fp	1795.1
		Cc	103 094.25	Cn	18 210.8	Cp	3326.2
9	*Scoloplos armiger*	Bc (2.45)	1030.23	Bn 2.59)	307.5	Bp (2.38)	35.5
		Pc	357.7	Pn	106.8	Pp	12.3
		Rc	2730.2	Un	1219.6	Up	98.8
		Ec	7121.15	Fn	474.7	Fp	218.2
		Cc	10 209.05	Cn	1801.1	Cp	329.3
10	Capitellidae	Bc (2.50)	25.7	Bn (2.43)	7.7	Bp (2.23)	0.9
		Pc	51.1	Pn	15.2	Pp	1.8
		Rc	215.35	Un	132.4	Up	11.4
		Ec	532.9	Fn	35.5	Fp	24.8
		Cc	799.35	Cn	183.1	Cp	37.9
11	Oligochaeta	Bc (2.50)	84	Bn (2.55)	25.1	Bp (2.33)	3.0
		Pc	83.95	Pn	25.1	Pp	3.6
		Rc	817.6	Un	181.4	Up	13.0
		Ec	412.45	Fn	27.5	Fp	26.7
		Cc	1314	Cn	233.9	Cp	43.3
12	*Heteromastus filiformes*	Bc (2.50)	72	Bn (2.55)	21.5	Bp (2.33)	2.5
		Pc	142.35	Pn	43.0	Pp	5.0
		Rc	273.75	Un	235.6	Up	22.4
		Ec	1835.95	Fn	122.3	Fp	47.3
		Cc	2252.05	Cn	400.9	Cp	74.6

Table 3 (continued)

Comp #	Compartment	Carbon		Nitrogen		Phosphorus	
		Parameter	Value	Parameter	Value	Parameter	Value
13	*Lanice conchilega* Polychaete	Bc (2.01)	63.45	Bn (2.86)	13.5	Bp (2.88)	0.8
		Pc	120.45	Pn	25.6	Pp	4.2
		Rc	233.6	Un	34.2	Up	3.3
		Ec	105.85	Fn	14.6	Fp	1.7
		Cc		Cn	74.4	Cp	9.1
14	Nereis diversicolor Polychaete	Bc (2.26)	193.48	Bn (2.57)	57.8	Bp (2.43)	6.7
		Pc	204.4	Pn	61.0	Pp	7.1
		Rc	828.55	Un	326.8	Up	31.6
		Ec	2164.45	Fn	144.3	Fp	66.6
		Cc	3197.4	Cn	532.2	Cp	105.2
15	*Pygospio elegans*	Bc (2.01)	127.71	Bn (2.86)	27.2	Bp (2.90)	1.5
		Pc	171.55	Pn	36.5	Pp	2.0
		Rc	795.7	Un	128.2	Up	11.0
		Ec	339.45	Fn	46.8	Fp	17.6
		Cc	1306.7	Cn	211.6	Cp	30.6
16	*Corophium arenarium* Amphipod	Bc (2.13)	52.05	Bn (2.89)	11.6	Bp (2.81)	1.8
		Pc	51.1	Pn	11.4	Pp	1.7
		Rc	120.45	Un	18.4	Up	2.9
		Ec	18.25	Fn	1.8	Fp	0.4
		Cc	189.8	Cn	31.5	Cp	5.0
17	*Corophium volutator* Amphipod	Bc (2.13)	257.15	Bn (2.88)	57.1	Bp (2.80)	8.8
		Pc	390.55	Pn	86.8	Pp	13.3
		Rc	1835.95	Un	312.6	Up	48.6
		Ec	445.3	Fn	42.8	Fp	9.1
		Cc	2671.8	Cn	442.2	Cp	71.0
18	*Gammarus* species Amphipod	Bc (2.21)	2.24	Bn (2.86)	0.5	Bp (2.93)	0.1
		Pc	3.65	Pn	1.0	Pp	0.2
		Rc	21.9	Un	2.8	Up	0.4
		Ec	7.3	Fn	0.7	Fp	0.4
		Cc	32.85	Cn	4.4	Cp	1.0
19	*Mytilus edulis*	Bc (2.01)	2030	Bn (2.86)	431.9	Bp (2.90)	23.3
		Pc	730	Pn	155.3	Pp	8.4
		Rc	4018.65	Un	629.6	Up	45.7
		Ec	671.6	Fn	92.4	Fp	72.8
		Cc	5420.25	Cn	877.3	Cp	126.9
20	*Cerastoderma edule*	Bc (2.01)	11 400	Bn (2.86)	2425.5	Bp (2.90)	131.0
		Pc	20 732	Pn	4410.9	Pp	238.3
		Rc	6500.65	Un	1825.7	Up	861.4
		Ec	76 427.35	Fn	10 541.7	Fp	1293.1
		Cc	103 660	Cn	16 778.3	Cp	23 992.8
21	*Mya arenaria*	Bc (2.01)	2076.81	Bn (2.86)	441.9	Bp (2.90)	23.9
		Pc	1657.1	Pn	352.6	Pp	19.1
		Rc	3854.4	Un	605.9	Up	69.9
		Ec	2774	Fn	382.6	Fp	105.1
		Cc	8285.5	Cn	1341.1	Cp	194.0
22	Small polychaetes	Bc (2.51)	199	Bn (2.99)	59.4	Bp (2.85)	6.9
		Pc	332.15	Pn	99.1	Pp	11.5
		Rc	1149.75	Un	228.9	Up	18.9
		Ec	584	Fn	38.9	Fp	32.7
		Cc	2065.9	Cn	367.0	Cp	63.1
23	*Tharyx killariensis*	Bc (2.50)	24	Bn (2.55)	5.1	Bp (2.33)	0.3
		Pc	47.45	Pn	10.0	Pp	0.5
		Rc	91.25	Un	18.2	Up	2.3
		Ec	94.9	Fn	13.3	Fp	4.9
		Cc	233.6	Cn	41.5	Cp	7.7
24	*Macoma baltica*	Bc (2.13)	2652	Bn (2.81)	564.3	Bp (2.74)	30.5
		Pc	797 890	Pn	1697.6	Pp	91.7
		Rc	1485.55	Un	1028.4	Up	483.3
		Ec	42 121	Fn	5809.8	Fp	767.5
		Cc	841 496.55	Cn	8535.9	Cp	1324.5

Table 3 (continued)

Comp #	Compartment	Carbon		Nitrogen		Phosphorus	
		Parameter	Value	Parameter	Value	Parameter	Value
25	Phyllodocidae	Bc (3.13)	10	Bn (3.88)	3.0	Bp (3.79)	0.3
		Pc	10.95	Pn	3.0	Pp	0.3
		Rc	109.5	Un	24.7	Up	1.4
		Ec	14.6	Fn	1.0	Fp	2.9
		Cc	135.05	Cn	28.7	Cp	4.6
26	Small Crustacea	Bc (2.24)	333	Bn (2.78)	74.0	Bp (2.63)	11.4
		Pc	489.1	Pn	108.7	Pp	16.7
		Rc	2058.6	Un	370.2	Up	57.6
		Ec	657	Fn	63.2	Fp	16.8
		Cc	3204.7	Cn	542.1	Cp	91.0
27	Carcinus maenas Shore crab	Bc (2.37)	34.15	Bn (3.20)	7.6	Bp (3.10)	1.2
		Pc	51.1	Pn	11.4	Pp	2.3
		Rc	80.3	Un	6.2	Up	1.0
		Ec	175.2	Fn	39.3	Fp	5.6
		Cc	306.6	Cn	56.9	Cp	8.8
28	Crangon crangon	Bc (3.01)	30.96	Bn (3.45)	6.9	Bp (3.18)	1.1
		Pc	124.1	Pn	27.6	Pp	4.2
		Rc	620.5	Un	88.6	Up	13.8
		Ec	124.1	Fn	27.8	Fp	0.5
		Cc	868.7	Cn	144.0	Cp	18.5
29	Nepthys spp.	Bc (3.22)	484.28	Bn (2.37)	144.6	Bp (2.35)	16.7
		Pc	1949.1	Pn	581.8	Pp	67.2
		Rc	1850.55	Un	558.5	Up	130.0
		Ec	6712.35	Fn	447.5	Fp	236.0
		Cc	10 512	Cn	1587.8	Cp	433.2
30	Pomatoshistus microps (goby)	Bc (3.32)	3.17	Bn (3.73)	1.1	Bp (3.57)	0.2
		Pc	10.95	Pn	3.9	Pp	0.6
		Rc	25.55	Un	18.88	Up	7.1
		Ec	222.65	Fn	30.5	Fp	0.8
		Cc	259.15	Cn	53.32	Cp	8.5
31	P. minutus (goby)	Bc (3.11)	0.47	Bn (3.84)	0.2	Bp (3.83)	0.03
		Pc	3.65	Pn	0.66	Pp	0.10
		Rc	3.65	Un	6.81	Up	1.71
		Ec	58.4	Fn	8.0	Fp	0.19
		Cc	65.7	Cn	15.47	Cp	2.00
32	Pleuronectes platessa (plaice)	Bc (3.16)	0.03	Bn (3.75)	0.01	Bp (3.59)	0.002
		Pc	0.07	Pn	0.02	Pp	0.003
		Rc	0.11	Un	35.46	Up	0.005
		Ec	0.33	Fn	0.03	Fp	0.001
		Cc	0.51	Cn	35.51	Cp	0.009
33	P. flesus (flounder)	Bc (3.37)	0.004	Bn (4.14)	0.001	Bp (4.10)	0.003
		Pc	0.75	Pn	0.26	Pp	0.003
		Rc	1.57	Un	3.26	Up	0.336
		Ec	8.81	Fn	0.79	Fp	0.037
		Cc	11.13	Cn	4.3	Cp	0.376
34	Clupea harengus (herrings)	Bc (3.00)	0.0073	Bn (4.00)	0.002	Bp (4.00)	0.0003
		Pc	0.02	Pn	0.007	Pp	0.002
		Rc	0.04	Un	0.010	Up	0.0009
		Ec	0.02	Fn	0.003	Fp	0.0001
		Cc	0.08	Cn	0.020	Cp	0.003
35	M. merlangus (whiting)	Bc (3.74)	0.53	Bn (4.42)	0.21	Bp (4.18)	0.032
		Pc	1.09	Pn	0.43	Pp	0.0031
		Rc	2.92	Un	1.44	Up	0.285
		Ec	5.11	Fn	0.46	Fp	0.032
		Cc	9.12	Cn	2.33	Cp	0.32
36	Gadus morhua (cob)	Bc (3.07)	0.02	Bn (4.37)	0.01	Bp (4.14)	0.0011
		Pc	0.04	Pn	0.01	Pp	0.003
		Rc	0.11	Un	0.02	Up	0.004
		Ec	0.06	Fn	0.01	Fp	0.001
		Cc	0.21	Cn	0.04	Cp	0.008

Table 3 (*continued*)

Comp #	Compartment	Carbon		Nitrogen		Phosphorus	
		Parameter	Value	Parameter	Value	Parameter	Value
37	*Myoxocephalus scorpio*	Bc (3.07)	0.02	Bn (4.26)	0.01	Bp (4.14)	0.0011
		Pc	0.04	Pn	0.01	Pp	0.003
		Rc	0.08	Un	0.02	Up	0.002
		Ec	0.06	Fn	0.01	Fp	0.001
		Cc	0.18	Cn	0.04	Cp	0.006
38	Shelduck	Bc (3.14)	18.6	Bn (3.85)	5.3	Bp (3.71)	1.3
	Tadorna tadorna	Pc	18.25	Pn	5.1	Pp	1.3
		Rc	700.8	Un	96.6	Up	4.6
		Ec	178.85	Fn	96.6	Fp	4.6
		Cc	897.9	Cn	198.3	Cp	10.6
39	Eider	Bc (3.03)	48	Bn (3.86)	13.7	Bp (3.89)	3.4
	Somateria mollissima	Pc	47.45	Pn	13.6	Pp	3.4
		Rc	1857.85	Un	270.1	Up	14.0
		Ec	474.5	Fn	270.1	Fp	14.0
		Cc	2379.8	Cn	553.8	Cp	31.4
40	Oystercatcher	Bc (3.13)	10.9	Bn (3.77)	3.1	Bp (3.63)	0.8
	Haematopus ostralegus	Pc	14.6	Pn	3.9	Pp	1.0
		Rc	532.9	Un	77.4	Up	5.4
		Ec	135.05	Fn	77.4	Fp	5.4
		Cc	682.55	Cn	158.6	Cp	11.8
41	Avocet	Bc (3.14)	0.9	Bn (3.71)	0.3	Bp (3.76)	0.7
	Recurvirostra avosetta	Pc	3.65	Pn	1.0	Pp	0.3
		Rc	54.75	Un	15.2	Up	1.1
		Ec	14.6	Fn	15.2	Fp	1.1
		Cc	73	Cn	31.4	Cp	2.5
42	Golden plover	Bc (3.28)	3.2	Bn (3.85)	0.9	Bp (3.75)	0.2
	Pluvialis apricaria	Pc	3.65	Pn	0.7	Pp	0.2
		Rc	102.2	Un	16.2	Up	2.2
		Ec	25.55	Fn	16.2	Fp	2.2
		Cc	131.4	Cn	33.1	Cp	4.5
43	Knot	Bc (3.03)	2.7	Bn (3.85)	0.8	Bp (3.87)	0.2
	Calidris canutus	Pc	3.65	Pn	1.4	Pp	0.7
		Rc	193.45	Un	25.7	Up	1.1
		Ec	51.1	Fn	25.7	Fp	1.1
		Cc	248.2	Cn	52.8	Cp	2.9
44	Dunlin	Bc (3.13)	4.6	Bn (3.87)	1.3	Bp (3.78)	0.3
	Calidris alpina	Pc	3.65	Pn	1.6	Pp	0.4
		Rc	211.7	Un	29.1	Up	4.3
		Ec	54.75	Fn	29.1	Fp	4.3
		Cc	270.1	Cn	59.7	Cp	9.1
45	Bar-tailed Godwit	Bc (3.17)	2.7	Bn (3.67)	0.8	Bp (3.47)	0.2
	Limosa lapponica	Pc	3.65	Pn	1.1	Pp	0.3
		Rc	156.95	Un	29.1	Up	3.9
		Ec	40.15	Fn	29.1	Fp	3.9
		Cc	200.75	Cn	59.4	Cp	8.0
46	Curlew	Bc (3.18)	4.9	Bn (3.78)	1.4	Bp (3.60)	0.4
	Numenius arquata	Pc	3.65	Pn	0.8	Pp	0.2
		Rc	109.5	Un	35.5	Up	1.2
		Ec	29.2	Fn	35.5	Fp	1.2
		Cc	142.35	Cn	71.7	Cp	2.6
47	Black-headed gull	Bc (3.28)	2.1	Bn (3.66)	0.6	Bp (3.3.47)	0.2
	Larus ridibundus	Pc	3.65	Pn	0.6	Pp	0.2
		Rc	83.95	Un	16.2	Up	1.5
		Ec	21.9	Fn	16.2	Fp	1.5
		Cc	109.5	Cn	33.0	Cp	5.2
48	Common gull	Bc (3.08)	2.2	Bn (3.81)	0.6	Bp (3.80)	0.2
	Larus canus	Pc	3.65	Pn	0.6	Pp	0.1
		Rc	80.3	Un	11.3	Up	0.6
		Ec	21.9	Fn	11.3	Fp	0.6
		Cc	105.85	Cn	23.1	Cp	1.3

Table 3 (continued)

Comp #	Compartment	Carbon		Nitrogen		Phosphorus	
		Parameter	Value	Parameter	Value	Parameter	Value
49	Herring gull	Bc (3.11)	7.7	Bn (3.84)	2.2	Bp (3.75)	0.6
	Larus argentatus	Pc	7.3	Pn	1.6	Pp	0.4
		Rc	219	Un	31.1	Up	1.6
		Ec	58.4	Fn	31.1	Fp	1.6
		Cc	284.7	Cn	63.8	Cp	3.6
50	Other birds	Bc (3.15)	6.2	Bn (3.78)	1.8	Bp (3.64)	0.4
		Pc	3.65	Pn	1.2	Pp	0.3
		Rc	167.9	Un	22.9	Up	2.3
		Ec	47.45	Fn	22.9	Fp	2.3
		Cc	219	Cn	47.0	Cp	4.9
51	Mallard	Bc (3.37)	8.8	Bn (3.57)	2.5	Bp (3.41)	0.6
	Anas platyrhynchos	Pc	3.65	Pn	1.2	Pp	0.3
		Rc	135.05	Un	31.4	Up	3.6
		Ec	80.3	Fn	31.4	Fp	3.6
		Cc	219	Cn	64.0	Cp	7.6
52	Pintail	Bc (2.00)	2.6	Bn (3.00)	0.7	Bp (3.00)	0.2
	Anas acuta	Pc	3.65	Pn	0.7	Pp	0.2
		Rc	76.65	Un	9.7	Up	1.4
		Ec	43.8	Fn	9.7	Fp	1.4
		Cc	124.1	Cn	20.0	Cp	3.0
53	Widgeon	Bc (2.00)	38	Bn (3.00)	10.9	Bp (3.00)	2.7
	Anas penelpe	Pc	29.2	Pn	8.3	Pp	2.1
		Rc	919.8	Un	113.6	Up	16.8
		Ec	511	Fn	113.6	Fp	16.8
		Cc	1460	Cn	235.5	Cp	35.6
54	Brent goose	Bc (2.00)	10	Bn (3.00)	2.9	Bp (3.00)	0.7
	Branta bernicla	Pc	7.3	Pn	1.7	Pp	0.4
		Rc	182.5	Un	22.7	Up	3.4
		Ec	102.2	Fn	22.7	Fp	3.4
		Cc	292	Cn	47.1	Cp	7.1
55	Sediment bacteria	Bc (2.00)	625	Bn (2.00)	122.5	Bp (2.00)	35.7
		Pc	35 806.5	Pn	7020.9	Pp	1424.3
		Rc	39 785	Un	10 869.5	Up	8116.9
		Ec	13 924.75	Fn	0	Fp	0.0
		Cc	89 516.25	Cn	17 890.4	Cp	9541.2
56	Meiobenthos	Bc (2.00)	944.52	Bn (2.33)	103.8	Bp (2.35)	32.6
		Pc	7555.5	Pn	830.3	Pp	260.5
		Rc	28 751.05	Un	6149.8	Up	991.7
		Ec	13092.55	Fn	872.8	Fp	451.5
		Cc	49 399.1	Cn	7852.9	Cp	1703.4
57	Suspended particulates [mg m^{-2}]	POC (1)	167.44	PON (1)	25.4	POP (1)	3.0
58	Sediment Particulate C, N & P [mg m^{-2}]	POC (1)	19 000	PON (1)	3021.0	POP (1)	433.0
59	Dissolved C, N & P [mg m^{-2}]	DOC (1)	62.02	DN (1)	18.5	DP (1)	0.4

Biomass (Bc, Bn, Bp) in mg m^{-2}; GPP & NPP in mg C m^{-2} year^{-1}, Cc = Pc + Rc + Ec where C = consumption, Pc = Secondary Production, Rc = Respiration, Ec = Egesta and c = Carbon; Consumption Cn,p = Production Pn,p, Un,p = Dissolved excretory products, Fn,p = Particulate excretory products, and where n = Nitrogen, p = phosphorous given in mg m^{-2} year^{-1}. The trophic level of each component is given in brackets after the B(iomass) parameter.

incorporates both the size and organization of flows into a single index, and is formally expressed as the product of TST and the average mutual information (AMI) inherent in the flow network. Complex trophic structure and high system productivity enhance ascendency. The AMI index, or normalized ascendency, is indicative of the developmental status of the ecosystem and thus of its inherent organization, i.e. the degree of specialization of flows in the network (Ulanowicz, 2004). The Development Capacity (DC) is the product of TST and the flow diversity. It measures the potential for a system to develop and is the natural upper limit of A. The total system overheads (i.e. overheads on imports, exports and dissipation) and redundancy (i.e.

a measure of the uncertainty associated with the presence of multiple or parallel pathways among the components of the network (Kay et al., 1989; Ulanowicz and Norden, 1990) is numerically represented by the difference DC − A, and represents that fraction of the DC that does not appear to be as organized structure (Bondini and Bondavalli, 2002). The magnitudes of the imports and exports reflect the self-reliance of a system, i.e. the higher these values, the more dependent the system becomes on external exchanges. A system with low redundancy is considered to be susceptible to external perturbations, which may impact on the trophic interactions between system components. Parallel pathways of energy and material transfers on the other hand, however,

can act as a buffer or reserve should external perturbations or changes in biodiversity occur. It is postulated that a sustainable system requires a balance between ascendancy and redundancy, for should a perturbation occur, the system can draw from the overhead to keep it in operation, but then in a less organized state (Ulanowicz, 1986; Baird et al., 1991; Scharler and Baird, 2005).

Ascendency measures the efficiency and definitiveness by which energy transfers are made, whereas the overhead quantifies how inefficient and ambiguous the system performs on average. A higher index of A reflects increased ecological succession characterized by, e.g. species richness, decreased cost of overheads to the system, greater internalisation of resources, and finer trophic specialization (Scharler and Baird, 2005). Internal Ascendency (A_i) and internal developmental capacity (DC_i) are functions of internal exchanges alone, and thus exclude exogenous transfers. The ratios A/DC and A_i/DC_i have been used to compare the organizational status of ecosystems on temporal (Baird and Ulanowicz, 1989; Baird and Heymans, 1996; Baird et al., 1998, 2004b) and spatial (Baird et al., 1991, 2004a, 2007; Baird and Ulanowicz, 1993; Baird, 1998b, 1999) scales. The magnitude of various attributes, particularly the DC, A, overheads and redundancy, are strongly influenced by the TST (cf. Ulanowicz, 2004). By dividing theses capacities (DC, A, and overheads) by TST, the resultant normalized values, given in Table 4, are scaled to eliminate the singular effect of TST (cf. Baird and Ulanowicz, 1989; Baird et al., 1998).

Flow diversity, defined as DC/TST (or normalized DC), measures both the number of interactions and the evenness of flows in the food web, and is thus a much more dynamic concept than species diversity (Mann et al., 1989; Baird et al., 1998). Comparatively higher values of this index indicate an increase in interactions and a lower degree of unevenness and variability in the flow structure (Baird et al., 2004b). The effective number of connections between compartments is given by three connectance indices, and is derived from the log-averaged number of links calculated from the systems overhead (Baird et al., 2004b). The Overall Connectance includes the effect of external transfers; the internal connectance index characterizes only internal exchanges, whereas the food web connectance index refers only to transfers among the living compartments in the system (Ulanowicz, 2004). Standings stocks of all the compartments and flows in C, N and P between them, imports and exports, essential input information for the construction of the flow models for network analysis, are given as Appendix A in the electronic store of the journal.

3. Results

3.1. Network analysis

The C, N and P networks have been mapped into the simplified Lindeman Spine consisting of discrete trophic levels (cf. Ulanowicz and Kemp, 1979; Baird and Ulanowicz, 1989; Kay et al., 1989; Baird et al., 2004a), and are illustrated in Fig. 3. The primary producers, detrital and dissolved C, N and P were combined in the three Spines which show the inputs into the first trophic level, returns to the detrital pool (RDP in Fig. 3), transfer from one level to the next higher one, imports to and exports from specific levels, and respiration in the carbon Spine (Fig. 3a). External detrital imports (DI, 32 897 mg C m^{-2} year^{-1}) and returns to the detrital pool (RDP, 362 991 mg C m^{-2} year^{-1}) to level I of the C spine comprise entirely of particulate material (Fig. 3a) while the gross production of autotrophs in the system amounts to 604 000 mg C m^{-2} year^{-1}. In the case of nitrogen, the input of 99 613 mg N m^{-2} year^{-1} at level I consists of 62 952 mg N m^{-2} year^{-1} externally imported dissolved N (or "new" N), 36 661 mg N m^{-2} year^{-1} of regenerated DN within

Table 4
Global system attributes derived from network analysis for Carbon, Nitrogen and Phosphoros in the Sylt-Rømø Bight.

Sytstem Attributes	Carbon	Nitrogen	Phosphorous
Trophic efficiency (logarithmic mean, %)	3.1	6.0	16.8
Number of cycles	1197	414 744	538 800
Finn Cycling Index (%)	17.2	43.3	80.8
Average Path Lenght (APL=TST-Z/Z)	2.8	3.65	9.81
Average Residence Time (ART; days)	26	29	201
Total System Throughput (TST)(gCm^{-2}year-1)	2430.6	463.3	60.2
Development Capacity (DC)(gCm^{-2}year-1bits)	11803.0	2043.8	283.6
Ascendency (A) (gCm^{-2}year-1bits)	4689.5	876.03	122.09
Relative Ascendency (A/DC, %)	39.7	42.9	43.1
Average Mutual Information (A/TST) (normalized A)	1.93	1.89	2.03
Average Internal Mutual Information (Ai/TST)	0.98	1.26	1.84
Overheads on imports (gCm^{-2}year-1bits)	1165.0	45.0	6.1
Overheads on exports (gCm^{-2}year-1bits)	386.3	213.3	8.5
Dissipative Overheads (gCm^{-2}year-1bits)	1664.2	0	0
Redundancy (R) (gCm^{-2}year-1bits)	3897.8	909.5	146.9
Relative Redundancy (R/DC, %)	33.0	44.5	51.8
Normalized Redundancy (R/TST)	1.60	1.96	2.44
Internal Development Capacity (DCi) (gCm^{-2}year-1bits)	62291.6	1494.4	257.4
Internal Ascendency (Ai) (gCm^{-2}d-1bits)	2393.8	584.9	110.5
Relative Internal Ascendency (Ai/DCi, %)	38.0	39.1	42.9
Internal Redundancy (Ri)(gCm^{-2}year-1bits)	3897.8	909.5	146.9
Normalized Internal Redundancy (Ri/TST)	1.6	2.0	2.4
Flow Diversity (DC/TST, %)(normalized DC)	4.86	4.41	4.71
Φ (sum of overheads/TST)	1.24	0.56	0.24
Overall connectance	2.242	2.474	2.657
Intercompartmental connectance	2.754	2.638	2.421
Foodweb connectance (living compartments only)	2.199	2.221	2.193

the system (see Table 2), and 107 840 mg m^{-2} year^{-1} particulate N from the detrital pool. The external input of P (2512 mg P m^{-2} year^{-1}) at level 1 comprise only of particulate P. It would appear that sufficient DP is regenerated in the system to satisfy consumer demand (see Table 2b).

From the trophic analyses up to eight integer trophic levels have been identified for the C, N and P networks, but with minuscule
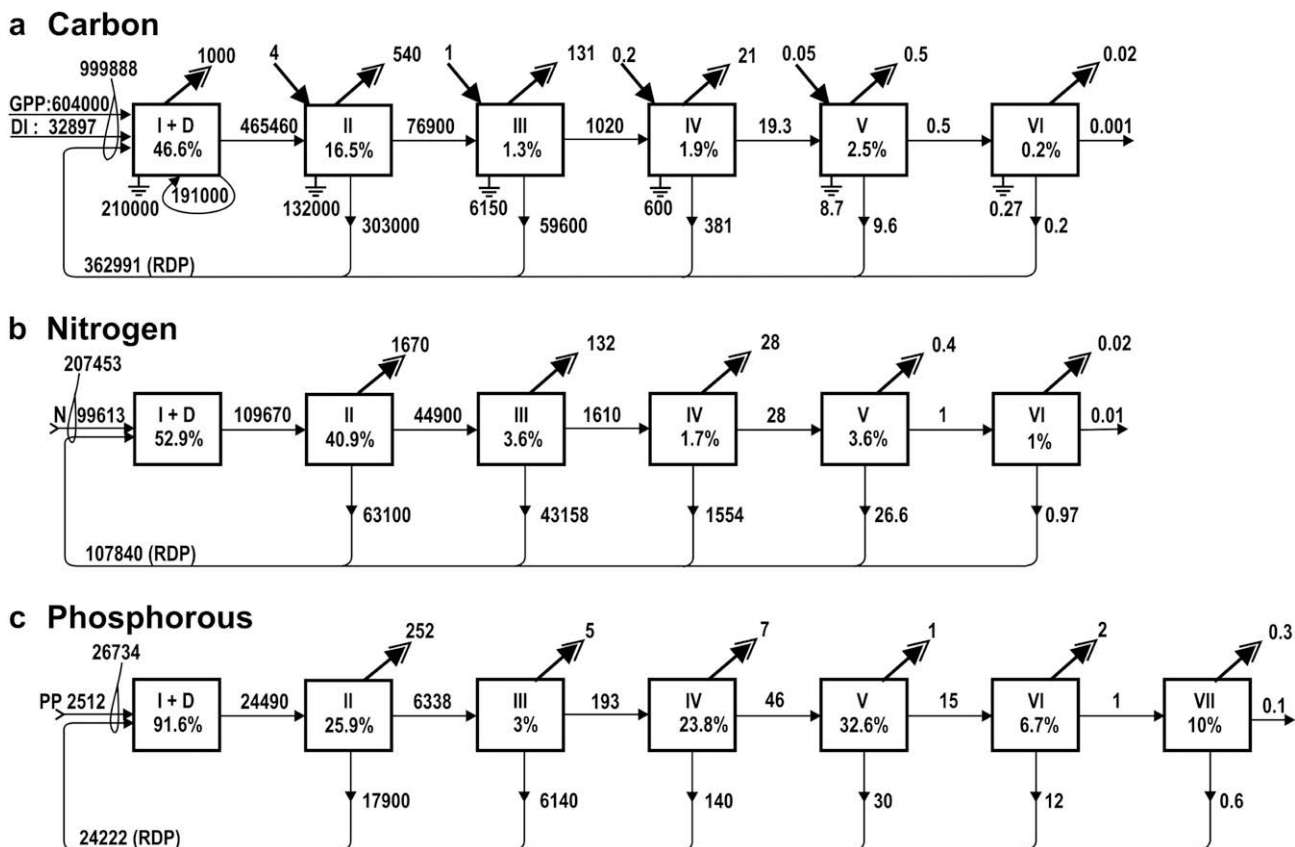
Fig. 3. The Lindeman Spines of carbon, nitrogen and phosphorus. All values given in mg m^{-2} year^{-1}. Percent value in integer trophic level indicates the fraction of input in a level passed on to the next higher one. Solid arrows indicate imports, capped arrows exports from integer trophic levels.

amounts transferred beyond level VI, with the exception of P at levels VI and VII. All primary producers, particulate and dissolved nutrient pools were assigned to the level I, from where C, N and P are transferred to the higher trophic levels. The trophic position of each compartment (given in Table 3) is derived from the trophic analysis routine of NETWRK4.2a and based on the dietary composition of each and the distribution of the trophic levels of its prey (Ulanowicz and Kemp, 1979; Levine, 1980; Baird and Ulanowicz, 1989). Of interest is that autotrophs occupy the first trophic level when C is the currency, whereas the dissolved and particulate pools of N and P form the first level when they are used as currencies with autotrophs shifted to the second level as consumers of dissolved N and P. Solar energy and dissolved nutrients are the main driving forces as input energy for plants and are thus conventionally assigned to the first trophic level. When using N or P as currencies, the dissolved and particulate fractions form the basis of the food web as plants are dependent on the dissolved fractions of N and P (and of other elements such as silica) generated within the system or imported, and thus constitute the first trophic level, with autotrophs at the second level. This implies that the same species, or community, may not occupy exactly the same trophic level for different currencies, as indicated in Table 3. The assignment of each trophic unit is calculated based on the percent of uptake of prey, in terms of C, N or P, by consumers from an integer trophic level as given by the Lindeman Trophic Aggregation routine of NETWRK4.2a. For example, the shellduck (#38) population would obtain 86.5% of its carbon energy at integer trophic level III, 13.4% at level IV, and 0.12% at level V, and feed on average at the non-integer level 3.14 ($= (0.865 \times 3) + (0.134 \times 4) + (0.0012 \times 5)$). With N as currency shellduck derives 16.5% of its uptake from level III, 82.5% from IV, 0.86% form V, and 0.1% from VI ($= (0.165 \times 3) +$

$(0.825 \times 4) + (0.0086 \times 5) + (0.001 \times 6)$), placing it at trophic position 3.85. Similarly, this population obtains 31.1% of its P uptake from level III, 67.2% from IV, 1.61% from V, and 0.133% from VI, thus occupying a trophic position at level 3.71. Shellduck thus feeds mainly at the lower end of level III with C as currency, but at the higher end of III when N or P are used as currencies. However, this pattern is not consistent as can be seen from the apportionments of species and communities in Table 3 which shows the trophic position of species in the Bight for the three different currencies.

The percent value in the discrete level boxes indicates the efficiency of transfer from the lower to the next higher level. The trophic efficiencies decline in all spines from level 1, but all also show some increase at level V, but is notably higher at IV and V in the P spine (Fig. 3c). P is particularly effectively transported to and utilised by consumers at the higher trophic levels, and so is N in comparison with C. It would also appear from the Lindeman Spines that little energy and material is transferred from level III to higher levels. This level includes fish (#30–37) and birds (#38–54) in the C network, with crabs (#27 and #28), fish and birds in the N model, all with relatively few predators. The low efficiency of transfer from level III in the P food web includes the Phyllodocidae (#25), which prey extensively on *Hydrobia* (#6 at trophic position 2.75, Table 3), whilst it forms only small fractions of the food of other predators such as crabs, plaice (#32), and birds. The logarithmic mean trophic efficiencies for C, N and P are, respectively, 3.1, 6.0 and 16.8 (see Table 4), implying that P is more efficiently transferred between trophic levels and their respective components than either N or C.

The greatest differences in the behaviour of C, N and P can be observed in the structure and magnitude of the recycling and retention of the three elements in the Bight. The number of cycles increase from 1185 for C, to 414 744 for N and to 538 800 for P. The
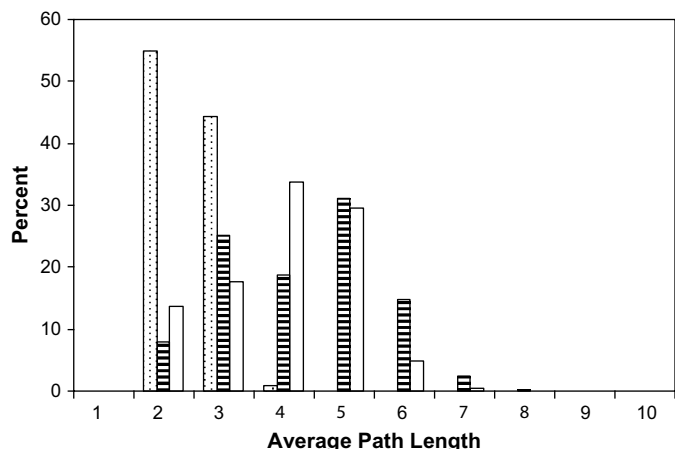
Fig. 4. Percentage of total carbon, nitrogen, and phosphorus activity involved in recycling over cycles with different path lengths. Stippled bar = carbon, horizontal striped bar = nitrogen, blank bar = phosphorus.

FCI indices (or the amount of the total system activity devoted to cycling) increase from 17.5% for C, to 43.3% for N and to 80.8% for the P networks on an annual basis (see Table 4). Of further interest is how the amounts recycled are distributed amongst the path length by which these elements are, respectively, cycled. About 99% of C is cycled over short path lengths involving 2–3 model compartments, and although path lengths of up to 9 were identified, the amount involved over longer ones is miniscule. Nitrogen shows a clear bimodal distribution showing one peak of activity over cycles of three transfers, followed by a drop at path length 4, and a strong second peak at loops of 5. A possible explanation for the bimodality is bacterial activity during the nitrification–denitrification processes which involve shorter path lengths (as with carbon), while N is transferred over longer loops involving organisms at higher trophic levels. About 52% of N is cycled over path lengths of between 2 and 4, and about 48% over longer loops. P on the other hand shows a peak of recycling at path lengths 3, 4 and 5, over which about 81% of P is recycled. Both N and P appear to be cycled over longer path lengths than C (Fig. 4).

These patterns of recycling is reflected in the APL (or average path length), which quantifies the average number of transfers a unit of an element will undergo from the time it enters the food web until it leaves the system, and the ART (or average residence time) of an element in the system; both indices reflect on the trophic function of an ecosystem (Kay et al., 1989). The APLs calculated were 2.8 for C, 3.7 for N, and 9.8 for P (see Table 4). The APL is a measure of the retention of energy or an element within a system, and the APL values calculated for C, N and P illustrate that P flows through many more compartments before it leaves the ecosystem than either C or N. The ART calculated for P was also much longer (201 days) than the 26 and 29 days derived for C and N, respectively. P is thus retained for a longer time in the system, and participates in longer cycles than N or C (see Table 4). Furthermore, the FCIs also show that 80.8% of P is recycled, to a far greater extent than C (17.2%) and N (43.3%). The cycling structures of both N and P are complex, and although the residence time of N appears to be the shortest, more than 40% of the systems N throughput is recycled. Little C is recycled, whilst it is transferred over short cycles with much of the C energy dissipated through respiration of the biota.

Various system level indices were derived from network analysis (see Table 4). Actual values for TST, DC, A, the Overheads, and Redundancy (R) are not comparable due to the atomic ratios between the elements. However, dimensionless ratios, such as the Relative Ascendency and Relative Internal Ascendency (A/DC and

A_i/DC_i, respectively), Average Mutual Information (AMI, A/TST), Relative and Normalized Redundancy (R/DC and R/TST, respectively), Flow Diversity (DC/TST), and the connectance indices, are. The A/DC, and A_i/DC_i ratios show an increase from carbon to phosphorus, indicating that the behaviour of P takes place in a more organized way than the other two elements, with C showing the lowest degree of organization. The same trend can be observed for the Internal AMI (when only internal exchanges are considered), pointing to an increasing degree of the specialization of flows from C to N to P in the Bight ecosystem. Further evidence of this trend is the increase in the Flow Diversity index which reflects on the number of interactions and the evenness of flows in the networks and thus on the dynamics of the system. Higher indices of Flow Diversity indicate a larger number of interactions and a greater evenness in the flow structure. This index is the highest for C, followed by P and N, indicating that there is a greater degree of variability and unevenness in the nitrogen flow structure than in those of C and P (see Table 4).

Values calculated for the Relative Redundancy (R/DC), the Normalized redundancy (R/TST), and the Normalized Internal Redundancy (R_i/TST) ratios, are measures of system stability (Rutledge et al., 1976; Baird et al., 2007), increase from C to N to P, reflecting on an increase in parallel pathways from C to N to P. The overall connectance index points to an increase in internal and external connections from C to N to P.

4. Discussion

Ecological network analysis is mostly used on networks of food webs with energy (or carbon as a surrogate for energy), and many examples exist examining trophic structures on spatial and temporal scales with carbon as the currency (see references given in Table 1). It (ENA) has had limited application to biogeochemical networks and cycling, although nitrogen cycling in coastal ecosystems has received considerable attention by, for example, Christian et al. (1992, and the references therein), Forès et al. (1994), Baird et al. (1995), Christian et al. (1996), Hinrichsen and Wulff (1998), Thomas and Christian (2001), Christian and Thomas (2003), and Borrett et al. (2006). The processes of nitrogen transformation, inputs, transport, and fate in coastal systems have been elegantly described by, e.g. Stanley and Hobbie (1981), Carpenter and Capone (1983 and references therein), Boynton et al. (1995), Nixon et al. (1996), and Boynton and Kemp (in press). The behaviour of phosphorus in the marine and coastal environment has similarly been described by, for example, Sundby et al. (1992), Boynton et al. (1995) and Nixon et al. (1996).

Biogeochemical networks and cycling of P in coastal zones have received scant attention, with only Baird (1998a) and Ulanowicz and Baird (1999) attempting to describe P dynamics in the Chesapeake Bay by means of ENA.

It is necessary to point out the fundamental differences between networks constructed to examine the biogeochemical (or nutrient) dynamics and recycling, and those based on food webs and trophodynamics. In trophic models where energy (or carbon) is used as currency, cycling is between living and dead organic forms and where organic detritus plays a major role in the cycling of material. Ecological systems are open with respect to energy, while energy sources and dissipated energy (respiration) are treated as external to the ecosystem (DeAngelis et al., 1989; Borrett et al., 2006). The energy influx in these models is usually in the form of some external source (principally solar light), and as energy passes through successive trophic levels it becomes degraded toward low thermal energy less capable to perform any work (DeAngelis, 1980). Biogeochemical networks and cycling differ fundamentally from trophic ones in that they are minimally dissipative, include both particulate and dissolved inorganic compounds, and focus strongly

on bacterial processes for the remineralization on nutrients. Borrett et al. (2006) postulated that these characteristics enhance cycling and the resultant indirect flows in biogeochemical networks. In these most of the nutrients required by the biota are internally generated through mineralization processes, and depend to a lesser extent on external inputs. In this context nutrient models can be considered as relatively "closed" systems in which the total stock of nutrients, along with the magnitude and rate of recycling, impose limits on the standing stock of biomass and on primary production (De Angelis et al., 1989). Of course, biomass production is not limited in systems open to nutrient loading, although the rate of recycling of nutrients may impose limits on the rate of production.

In this paper, we employ ENA to comment on the dynamics of C in a trophic model, and on N and P in biogeochemical networks, each consisting of 59 compartments. Previous studies on biogeochemical networks are mainly concerned with N in highly aggregated models consisting of 4–8 compartments, while only a few models contain a larger number of compartments, e.g. 36 in the Chesapeake Bay, 16 in the Baltic Sea, and 18 in three different marsh models of the Great Sippewissett Marsh in Falmouth, MA, US (cf. Thomas and Christian, 2001). The phosphorus network of the Chesapeake Bay consists of 36 compartments (Ulanowicz and Baird, 1999).

All the system level indices such as the A/DC, A_i/DC$_i$, Internal AMI, R/DC, normalized and normalized internal redundancy ratios, and the overall connectance index, show an increase from C to N to P (see Table 4), indicating the development of more structured and organized networks from the trophic based C network to the biogeochemical networks of N and P. When the Development Capacity is decomposed into two components, namely ascendency and the systems overhead, the fraction of the Development Capacity comprised of ascendency is 39.7% for C, and slightly higher for N and P at 42.9% and 43.1% in the Bight, respectively. The same small differences were observed between these elements in the Chesapeake Bay where the relative ascendency was calculated at 43.7%, 42.7% and 42.2% for the C, N and P networks, respectively (Baird et al., 1995; Baird, 1998a). The relative and the normalized redundancy, reflecting the degree of parallel pathways in a system, increase substantially in the flow networks from C (33% and 1.6) to N (44.5% and 2.0) to P (51.8% and 2.4) (see Table 4). The relative and normalized redundancy in the Chesapeake Bay for C was 33.9% and 1.39, 42.2% and 2.03 for N, and 44.7% and 2.10 for P, marginally lower than those derived for the Bight. The consistency in trends and the remarkable similarity of these indices across two large coastal ecosystems is noteworthy and calls for more comparative data from other coastal ecosystems.

Of interest is the trend in and magnitude of cycling in the trophic and biogeochemical networks. The FCI (the proportion of cycled flows to the TST) were calculated at 17.2%, 43.3% and 80.8% in the C, N and P networks respectively. The APL indices also correlate with the FCI trend of the Bight for the three elements (see Table 4), whilst a corresponding increase in FCI with APL has been observed for a large number of trophic models (Baird et al., 1991; Christensen, 1995). Although nitrogen is more tightly cycled than C in the Bight, its intermediate FCI value of 43% (much lower than the FCI of 80% for P), is most probably due to the dissipation of N_2 and N_2O through denitrification, whereas no gaseous products are produced in the recycling of P (Sundby et al., 1992; Boynton et al., 1995).

A similar trend in the FCI indices for C, N and P networks was also observed in Chesapeake Bay where they ranged, respectively, from 21%, 52.6% and 72% (Baird, 1998a,b; Ulanowicz and Baird, 1999). Baird et al. (1991) and Baird and Ulanowicz (1993) associated higher FCI values with chemical "stress". However, here we show that the increase in cycling indices in biogeochemical networks where "stress" is not an issue in the Bight emphasise the

fundamental difference between trophic based food webs and biogeochemical networks as postulated by Christian et al. (1996).

The enumeration of cycle distributions of C, N and P (Fig. 4) shows a steep decline in the amount of C cycled over short pathways. Nitrogen, however, shows a distinct bimodal distribution with one peak of activity centred over cycles of 2 and 3, followed by a drop at four transfers, and a strong second peak of activity at pathway lengths of 5 and 6. Such a bimodal cycle structure was also observed by Baird et al. (1995) for N in the Chesapeake Bay. The cycle distribution of phosphorus has a unimodal distribution with most of the activity taking place over four and five pathway lengths, as also observed in the Chesapeake Bay where the activity is centred over higher pathway lengths of 5 and 6 (Baird, 1998a).

Although the FCIs and the cycle distributions of Chesapeake Bay and the Bight cannot be directly compared because of the differences in the topology (number of compartments) of the models used, they nevertheless serve as a rough basis for comparison.

The postulated differences between the behaviour of energy (or carbon) and nutrient fluxes in coastal ecosystems are clearly articulated in the results derived from ENA for the Sylt-Rømø Bight. The carbon or trophic model shows a relatively low cycling index with most of the energy transferred over short path lengths. Both biogeochemical networks have longer residence times, show higher FCIs, and that N and P are highly retentive, where nutrients are passed along over longer pathways and over a progressively increasing number of cycles from C to N to P networks. P is particularly tightly recycled and exhibits the longest residence time in the system. These characteristics have been considered by DeAngelis (1980) and DeAngelis et al. (1989) to reflect on the resilience of food web and biogeochemical models, respectively. They argued that the magnitude of flux, or the investment in biomass per unit standing stock, is positively correlated with the resilience of energy models, whereas the basic factor determining the resilience of nutrient models seems to be the degree of recycling, but that the resilience of a model decreases as the degree of recycling increases. Resilience refers to the rapidity by which a perturbed system returns to its original equilibrium state and the shorter the recovery time, the greater the resilience. Pomeroy (1970) and Jordan et al. (1972) observed the recovery time of systems with tight nutrient cycling when disturbed is slower because of the limited external influx of nutrients. From this follows that since N and, particularly, P, are tightly recycled with high FCIs over longer path lengths and a large number of cycles in the Bight, the biogeochemical networks of these two elements will take longer to recover from a perturbation. The long ART and very high FCI (81%) of phosphorus would then suggest that the P network would take longer to recover following a perturbation than N and particularly C. Under these circumstances P could then become the limiting nutrient for biological productivity in the Bight. On the other hand, the higher redundancy values of P (see Table 4) suggest a larger number of parallel pathways of transfer between the components in the system which could buffer perturbations, implying that should a perturbation occur, the system then has the capacity to use the remaining pathways to function the way it does, contributing to its stability (Rutledge et al., 1976; Ulanowicz, 2004). Stability and resilience are related in the ecological sense, yet the arguments raised above are somewhat contradictory. This may well be because ENA methodologies (network analysis, Ecopath, network environ analysis) are predominantly based on energy food web models, and that the fundamental differences between trophic and biogeochemical networks are not fully encapsulated in these.

5. Conclusion

The results obtained from ENA presented here reflect on the system properties derived from the flow networks of C, N, and P,

and are thus based on the nature and framework of the networks. The behaviour of three essential macro elements in the Bight derived from the analysis of complex flow networks illustrated an increase in the system properties that reflect on the organization and specialization of the ecosystem from C to N to P. The structure and magnitude of recycling increase dramatically from C to N to P, emphasising not only the complexity of this process, but also the differences between elemental cycling in aquatic ecosystems.

Acknowledgements

Appendix A. Supplemental material

Supplementary information for this manuscript can be downloaded at doi: 10.1016/j.ecss.2008.08.012.

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