Assessment of ecosystem changes in response to freshwater inflow of the Kromme River Estuary, St. Francis Bay, South Africa: A network analysis approach

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Abstract

We present results on changes which occurred at the ecosystem level over a period of 10 years in the relatively pristine Kromme River estuary, St. Francis Bay, South Africa. Carbon flow models were constructed for the estuary based on data collected before 1984 and again during the period 1988 to 1992. The first data set was collected during a period of regular and substantial freshwater inflow (average of about 117×10^6 m^3·a^{-1}), and the second set after the impoundment of the river in 1984 and the resultant decrease in freshwater inflow to less than 2×10^6 m^3 per annum. The salinity regime changed from one with gradient (35 to 15) to a homogenous one where the salinity remained virtually constant at 35 and higher since the construction of the dam in 1984. The flow models were analysed and global system properties, such as the total system throughput, the magnitude and structure of cycling, development capacity, ascendancy and relative ascendancy, were used to assess whether the system has undergone change due to reduced freshwater inflow rates since 1984. Results showed that while some of the biotic compartments increased in biomass and abundance, others declined. Based on the results we conclude that the estuary has changed from a plankton-dominated system to one dominated by submerged benthic vegetation and macrobenthic invertebrates in response to reduced freshwater inflows.

Introduction

The measurement and quantification of energy and material flows in natural ecosystems have received considerable attention (cf. Fasham, 1985; Longhurst, 1984; Baird and Ulanowicz, 1989). The description of the rate of flux between the living and non-living components of an ecosystem requires information on biomass, feeding ecology, energy relationships, predator-prey interactions, and primary and secondary production rates, which is necessary if the system is to be studied from a holistic, or ecosystem, point of view.

Detailed energy flow models have been described for a number of systems such as the Chesapeake Bay (Baird and Ulanowicz, 1989), the Baltic Sea (Wulff and Ulanowicz, 1989), and a salt marsh ecosystem (Asmus and McKellar, 1989). Flow models of South African estuaries and other marine ecosystems are limited to those of the Swartkops estuary (Baird, 1988; Baird et al., 1991), the Kromme estuary (Heymans, 1992; Heymans and Baird, 1995), and the Benguela upwelling system (Baird et al., 1991). In addition to the construction of flow models, the analysis of complex food web matrices by means of network analysis is receiving more and more attention (cf. Wulff et al., 1989, Baird and Ulanowicz, 1989, 1993). The application of network analysis allows not only an insight of the properties of the ecosystem, but also the comparison of different ecosystems (e.g. Baird et al., 1991; Baird and Ulanowicz, 1993), and the comparison of the same system on a temporal scale (Field et al., 1989; Baird and Ulanowicz, 1989).

Network analysis includes input-output, trophic and cycling analysis and the calculation of ecosystem indices such as total system throughput, development capacity, ascendancy and system overhead. Detailed reference to the basic concepts, theory and methodology of network analysis is given by Ulanowicz (1986) and Kay et al. (1989), while Wulff et al. (1989) reviewed the methods and applications of network analysis in marine ecology.

As mentioned above, a very useful application of network analysis lies in the field of comparative ecosystem ecology. A particular ecosystem can thus be assessed at different times, say on a daily, seasonal, annual, or longer time scales. For example, Field et al. (1989) examined the succession of a planktonic community following an upwelling event, Warwick and Radford (1989) assessed seasonal changes in an estuarine benthic community, Baird and Ulanowicz (1989) and Baird et al. (1995) reported on the seasonal dynamics of carbon and nitrogen of the Chesapeake Bay respectively, all using network analysis techniques. The objective of this paper is to assess changes in biomass, in the rates of flow between the various living and non-living components, and in the system properties that may have occurred in the Kromme estuary, St. Francis Bay, during the past 15 years. In the years prior to 1984 a substantial amount of information was collected on the plant and animal communities. During 1984 a second large impoundment (the Impofu Dam) was completed in the catchment area about 16 km from the mouth of the estuary, substantially reducing the freshwater inflow into the estuary. Hypersaline conditions in the upper reaches and the virtual absence of a typical estuarine salinity gradient have been observed since then (Heymans, 1992). In order to assess possible changes in the abundance, productivity and diversity of the system in response to reduced freshwater inputs, an intensive quantitative sampling programme was conducted in the estuary during the period 1988 to 1992. We have compared the results from this period with those collected prior to 1984, using network analysis techniques in an attempt to illustrate changes that may have occurred at the ecosystem level.

Study site

The Kromme estuary (34:08'S, 24:51'E) discharges through a permanently open inlet into St Francis Bay, approximately 55 km
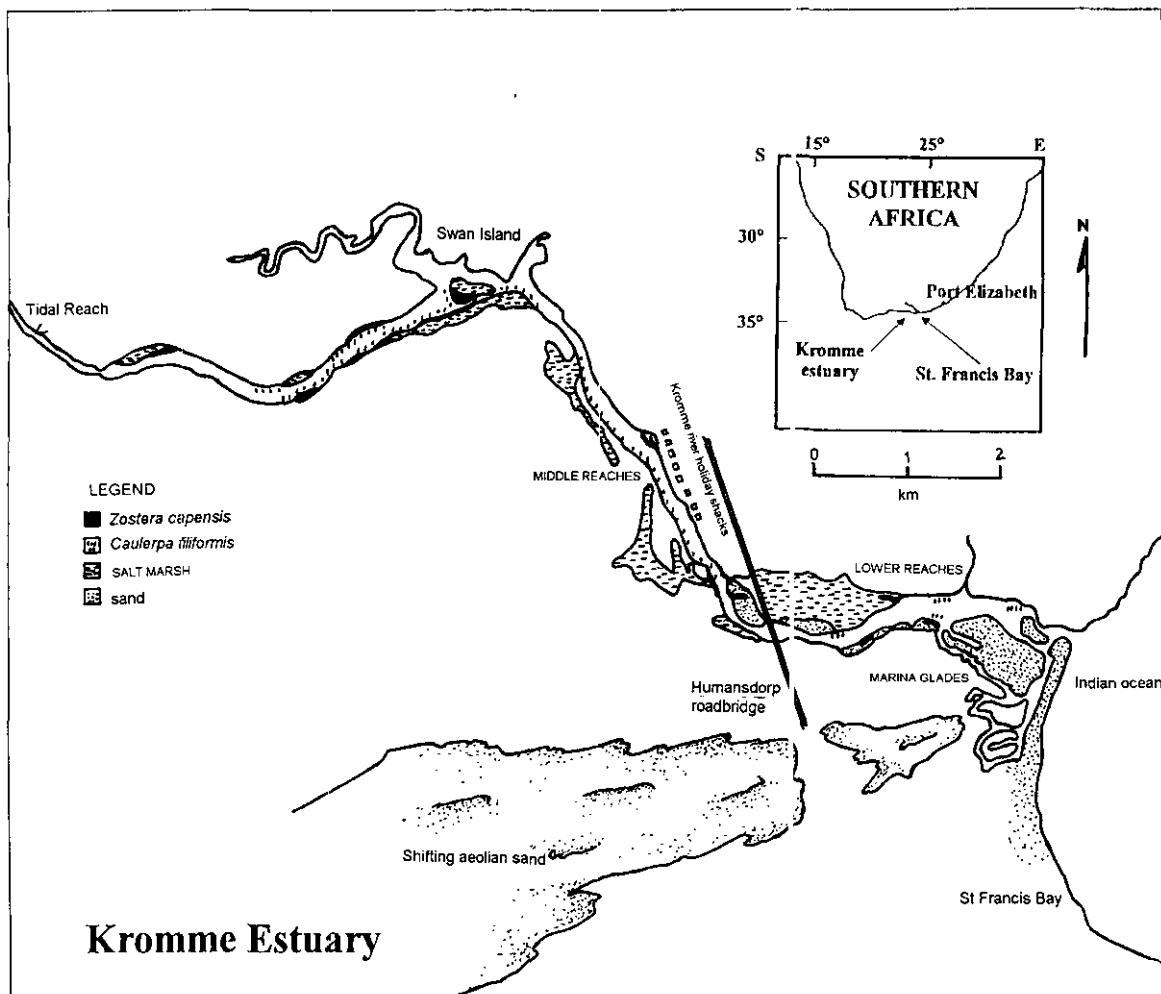

Figure 1
Map showing the location of the Kromme River estuary along the eastern coast of South Africa

west of Port Elizabeth (see Fig. 1). The total length of the river is about 95 km and meanders through relatively undisturbed rural areas with virtually no agricultural activity, nor is there any urban or industrial development in the catchment of approximately 936 km² (Reddering and Esterhuizen, 1983). The mean annual runoff from the catchment into the estuary for the period 1924 to 1980 (prior to the construction of the second dam) was about 116.8 x 10⁶ m³ (Bickerton and Pierce, 1988), whereas the annual runoff since 1984 (after the construction of the dam) averaged at about 1.3 x 10⁶ m³ (Baird et al., 1992). The estuary is about 13.7 km long with a surface area of ca. 3 km². The intertidal areas are narrow in the upper reaches, but wide sandy and muddy flats occur in the lower 4.5 km of the estuary. Saltmarshes occupy about 100 ha, with about 90% occurring on the north bank 1.8 km from the tidal inlet (see Fig. 1); rice grass (*Spartina maritima*) is the dominant halophyte on the marshes. Dense beds of eelgrass (*Zostera capensis*) occur inter- and subtidally along the length of the estuary.

The estuary is shallow (average depth at low-water spring-tide of 2.5 m), with a tidal amplitude of 1.6 m during spring-tide at the tidal inlet but which decreases upstream. The tidal prism during spring tides is on average 1.87 x 10⁶ m³ and during neap-tide 0.661 x 10⁶ m³ in volume. The average flushing time at spring-tide is approximately 27 h (Baird et al., 1992), and the

water temperature fluctuates between 17.7°C in winter and 28.0°C in summer The salinity has rarely dropped below 30 during the past decade, whereas prior to the completion of the Impofu Dam in 1984 the mean annual salinity ranged from 35 in the mouth to less than 20 in the upper reaches (Baird et al., 1992).

Materials and methods

Two carbon flow models were constructed for the Kromme estuary; one representing the pre-1984 period and the other the post-1984 years (data for the post 1984 period were collected during the years 1938 to 1992). Each model consists of 25 living and 3 non-living components, and illustrates the standing stocks (in mgC·m⁻²) of all compartments as well as the fluxes between them (in mgC·m⁻²·d⁻¹). The data used in the construction of the annually averaged models were collected during the course of many research projects conducted by the staff and students of the Departments of Botany and Zoology of the University of Port Elizabeth since the early seventies. Most of this information was published in the scientific literature, incorporated into a large number of unpublished master and doctoral theses, under-graduate student projects, and reports, whilst some data are yet to be published. Data have also been obtained from present on-going studies. The relevant data and information sources are listed in

TABLE 1
**REFERENCES TO DATA SOURCES AND INFORMATION ON BIOMASS AND ENERGETICS, INCLUDING DIET
COMPOSITION AND ECOLOGICAL COEFFICIENTS OF BIOTIC COMPONENTS IN THE KROMME RIVER ESTUARY
(MODEL COMPARTMENT NUMBER IN PARENTHESES)**

Model compartment	Parameter	Reference
Phytoplankton (1)	Biomass C:Chlorophyll-a ratio P:B, P:R ratios DOC exudate	Hilmer (1990) unpublished data, Dept. of Zoology, UPE. Cuff et al. (1983); Shannon and Field (1985) Baird (1988); Baird and Ulanowicz (1989); Baird et al. (1991) Wiebe and Smith (1977); Larson and Hagström (1979); Fenchel (1982); Wolter (1982); Vegter and De Visscher (1984); Laanbroek et al. (1985)

Macrophytes
   Halophytes (2)
   Macrophytes (3)
	Biomass
	Energetics
		Adams and Talbot (1992); Adams (1991)
		Pierce (1983); Hanekom (1982); Hanekom and Baird (1988); Baird (1988);
		Knoop (1988)

Benthic micro-algae (4)	Biomass and production	Dye (1978 a & b); Cuff et al. (1983), unpublished data, Dept. of Zoology, UPE.
Free-living bacteria (5)	Biomass Energetics	Hilmer (1990), unpublished data, Dept. of Zoology, UPE. Findlay et al. (1986); Baird et al. (1991)
Microzooplankton (7)	Biomass	Baird et al. (1981); Jerling and Wooldridge (1991, 1994); Jerling (1993)
Zooplankton Copepods (8)	Biomass Energetics	Jerling and Wooldridge (1994); Jerling (1993); Baird et al. (1981); Baird (1988) Siegfried and Kopache (1980); Wooldridge and Webb (1988); Wooldridge (1986); Jerling and Wooldridge (1991); Baird et al. (1991)
	Feeding	Wooldridge and Bailey (1982); Siegfried and Kopache (1980); Wooldridge and Webb (1988)
Fish larvae (10)	Biomass Energetics and ecological ratios	Melville-Smith (1981); Marais and Erasmus (1977) Baird (1988)
Marsh suspension feeders (11)	Biomass, consumption, production, respiration	Matthewson (1989); Hecht (1973) Els (1982)
Marsh detritivores (12)	Biomass, consumption, production, respiration	Matthewson (1989); Hecht (1973)
Marsh grazers (13)	Biomass, consumption, production, respiration	Matthewson (1989); Hecht (1973)
Non-marsh estuarine macrofauna (14, 15 and 16)	Biomass Energetics and ecological ratios	Hanekom (1982); Hanekom (1980); Els (1982), unpublished data, Dept. of Zoology, UPE. Baird (1988); Baird and Ulanowicz (1989); Palmer (1980); Hanekom and Baird (1992); McLusky (1981); Banse and Mosher (1980)
Meiofauna: Marsh (17) Estuary (18)	Ash-free dry mass Biomass	Dye (1977) Dye (1977); Baird (1988); Groeneveld (1990); Dye and Furstenberg (1978); Baird et al. (1981)
Fish (19, 20, 21, 22)	Biomass Energetics	Cloete (1990); Marais (1983b, 1988, 1990); Hay (1985); Hanekom and Baird (1984) Baird (1988); Ratte (1989); Talbot and Baird (1985a); Banse and Mosher (1980)
	Feeding	Marais (1984); Whitfield and Blaber (1978); Bennett (1989); Whitfield (1988); Christensen (1978); Coetzee (1986); Bennett et al. (1983); Smale and Kok (1983); Joubert and Hanekom (1980); De Wet and Marais (1990); Talbot and Baird (1985b); Masson and Marais (1975)

Table 1 which include, for example, reference to standing stocks, rates of growth, respiration and consumption (in the case of heterotrophs), and diet composition of various fish species.

Not all the data necessary to complete the pre-1984 network were available and in those cases we assumed that the post-1984 information (on standing stocks) represents the pre-1984 condition. These compartments are the benthic micro-algae, sediment and attached bacteria, heterotrophic microflagellates, sediment and suspended particulate organic carbon (POC), and dissolved organic carbon (DOC) concentrations. Similarly, the larval fish component was not assessed since the late seventies, and the same values reported by Melville-Smith (1981) were used for the 1988 to 1992 period.

The seasonal variation in most of the biotic components is relatively small, considering the temparate climate regime of the region. Episodic floods seem to have a greater effect on the abundance of plant and animal life than, for example, seasonal variations in temperature (cf. Hanekom and Baird, 1988; Marais, 1983a, 1988; Wooldridge, 1986).

Information on the flux of energy and material between the various compartments was obtained from the sources listed in Table 1, or based on ecological ratios (e.g. P:B, P:C and P:R ratios) from relevant literature on similar species or communities from similar environmental regimes. We acknowledge that not all the compartments in the models are equally well studied. This is, however, a universal problem in ecosystem studies. We are nevertheless confident that the results presented here provide an adequate assessment of the behaviour of this ecosystem over a period of about 20 years.

For heterotrophs, carbon uptake (C) by each living compartment was balanced by respiration (R), production (P) and egesta (E). For primary producers (phytoplankton, macrophytes and benthic algae) gross primary production (GPP) was assumed equal to the sum of net primary production (NPP) and respiration (R). Exudation by primary producers is considered to be the main source of DOC (Valiela, 1984), although DOC can also be released from the breakdown of dead organic matter, and from messy feeding by zooplankton (Copping and Lorenzen, 1980). Estimates of the release of DOC from phytoplankton cells range from 2% to 50% of the photosynthate production (Fogg et al., 1965), and we have assumed a constant loss of 25% of the net phytoplankton production (Baird and Ulanowicz, 1989; 1993) and about 2% from macrophytes (Brylinski, 1977). The DOC which is in turn taken up by free-living bacteria (Wiebe and Smith, 1977; Azam et al., 1983; Ducklow, 1983; Finlay et al., 1986). The production of compartments not recycled or used in the foodweb was assumed to be exported from the system. The system was also assumed to be in a steady state during the two periods; thus the annually averaged inputs to each compartment were balanced by corresponding outputs. The values for GPP were considered to be the inputs into the system.

In this comparative study of the same system during two time periods, we focus specifically on those system properties derived from the network analysis of the food webs and which illustrate changes that may have occurred over the intervening period since 1984. These are:

- The trophic efficiencies of the estuary during the pre-1982 and post-1982 period. This is accomplished by the mapping of the complex network of trophic transfers into a linear chain, the Lindeman Spine (Ulanowicz, 1995), with discrete trophic levels. The Lindeman Spine illustrates the net amount each trophic level receives from the previous one as well as the

amounts it generates through exports, respiration, detritus for recycling and the net production for transport to the next level.

- The Finn cycling ndex (FCI), which gives the proportion of the flow in a system that is recycled compared to the total system throughpu. (Finn, 1976). The FCI is equal to T_c/TST where T_c is the amount of system activity devoted to cycling, and measures the retentiveness of a system; the higher the FCI, the greater the proportion recycled and the more mature or less stressed the system (Odum, 1969);

- The average path ength (APL) measures the average number of transfers a unit of flux will experience from its entry into the system until it leaves the system. This index is derived from APL = (TST-Z)/Z where Z equals the sum of all exogenous inputs (Baird and Ulanowicz, 1993).

- Global measurements of ecosystem organisation such as:
  - Total system throughput (TST), which measures the total activity and s ze of the system and the sum of all flows occurring with in the system and between the system and its environment. These latter flows include all imports, exports and dissipation. The bigger the value of TST, the more material flows through the systems. Individual compartments may be characterised by estimating the throughflow (T) through each compartment, and is a useful indication of the relative rates at which the flow medium enters and leaves each compartment. The value of T for each compartment thus gives the rate of energy flow through the compartment in relation to its standing stock (Kay et al. 1989). We have used this index (T) to compare the relative si ze and activity of individual compartments during each o the two study periods.
  - Network ascendancy (A), a measure which incorporates both the size and organisation of flows. It is formally expressed as the product of TST and the mutual information inherent in the network. Ulanowicz (1986) proposed ascendancy as a measure of the maturity of the system, i.e. A increases as an ecosystem evolves through a series of developmental stages towards maturity.
  - Development capacity (C) which measures the potential for a system to develop. C is considered to be the upper limit of A, and thus both C and A will decrease if a system is affected by disturbance or pollution stress.
  - System overheads (ø), given numerically as the difference C-A and which represents the cost to the system to operate the way it does.
  - Internal ascendancy (A$_i$) and internal development capacity (C$_i$), which are functions of internal exchanges alone (and thus excludes exogenous transfers into and out of the system). The ratio A$_i$:C$_i$ is considered to be most representative of the system's development status (Field et al., 1989; Baird et al., 1991).

Results

Ecosystem flow networks and trophic structures

Some of the general properties of the Kromme estuary are given in Table 2. Of importance is the difference in the salinity regime of the system which showed a much wider range and variability prior to 1984 (see Table 2 and Fig. 2a and b). Since the reduction in freshwater inflow, the salinity of the estuary became homogenous throughout and varied narrowly around a mean of 35 ppt (see Fig. 2b). A salinity gradient, a typical characteristic of an

TABLE 2
PROPERTIES OF THE KROMME ESTUARY PRIOR TO 1984 AND FOR THE PERIOD 1988 TO 1992

Attribute	< 1984	1988-1992
Temperature range (°C)	12.2-27.8	12.0-28.0
Annual mean salinity range	18.1-35.0	35.00
Net primary production (gC·m^{-2}·d^{-1})	5.20	5.52
Total standing stock of primary producers (gC·m^{-2})	540.00	602.60
Total standing stock of heterotrophs (gC·m^{-2})	22.60	45.80
Total standing stock of system (gC·m^{-2})	562.60	648.40
Total production (primary and secondary) (gC·m^{-2}·d^{-1})	6.87	6.79
NPP consumption efficiency (%)	8.60	4.10
Detritivory:herbivory ratio	8.0:1	15.5:1
P:B ratio (annual)	4.46	3.82

estuary, does not exist, and has not existed since 1984 (Bickerton and Pierce, 1988; Baird et al., 1992).

The total standing biomass of the estuary increased from about 563 gC·m^{-2} in 1984, to 648 gC.m^{-2} in 1992; an increase of 85 gC·m^{-2} (or about 15%). Results in Table 2 also show that although the rate of primary production has remained virtually the same, significant changes took place in the standing stocks of the primary producers. Whereas phytoplankton biomass decreased from 3.7 gC·m^{-2} prior to 1984 to 0.4 gC.m^{-2} in 1992 (see Figs. 2 and 3) the biomass of submerged macrophytes (particularly *Zostera capensis* and *Caulerpa falciformis*) increased from 59.9 gC·m^{-2} to 125.7 gC·m^{-2} (Adams, 1991; Adams and Talbot, 1992) (see Figs. 2 and 3). Reasons for these changes are that phytoplankton production in estuaries is usually positively correlated with freshwater inflow (Flint, 1985; Paerl et al., 1990; Hilmer and Bate, 1990; 1991), whereas a decrease in turbitity and water velocities, a more stable sediment and salinity environment, and reduced freshwater inputs, favour submerged macrophyte production (Adams, 1994; Adams and Talbot, 1992). These conditions have prevailed in the Kromme estuary since 1984.

The total standing stock of all heterotrophic components (compartments 5 to 24 in Figs. 3 and 4) doubled from 22.6 gC·m^{-2} to 45.8 gC·m^{-2} during the two periods of study respectively (see Table 2). The increase in biomass, however, did not occur in all the components; in fact, some showed a noticeable decrease. The standing stocks of water column compartments (5 to 9) decreased, which is most obvious in the mesozooplankton (copepods and mysids, compartments 8 and 9 in Figs. 3 and 4). Increases in biomass occurred in compartments 11, 12 and 16. These include the marsh suspension feeders (mainly *Upogebia africana*: Crustacea) (11), marsh detritivores (mainly *Paratylodipax algoensis*, *P. edwardsii* and *Sesarma catenata*: Crustacea) (12), and suspension feeders occurring in the non-marsh region of the estuary (mainly *Lamya capensis*, *Loripes clausus*, *Macoma litoralis*: Mollusca, and *Upogebia africana*: Crustacea) (16). There was also a notable increase in two species of carnivorous gastropods namely *Hydatina physis* and *Natica genuana* (14), and in the standing stocks of several fish components. Zooplanktivorous fish (mainly *Gilchristella aestuarius* and *Antherina breviceps*) (19) increased since 1984 from 270 mgC·m^{-2} to 715 mgC·m^{-2}, benthic feeding fish (mainly *Lithognathus lighognathus*, *Rhabdosargus globiceps*, *R. holubi*, and species of the fam. Gobiidae) (21) increased from 935 mgC·m^{-2} to 2 249 mgC·m^{-2}, and species of the fam.
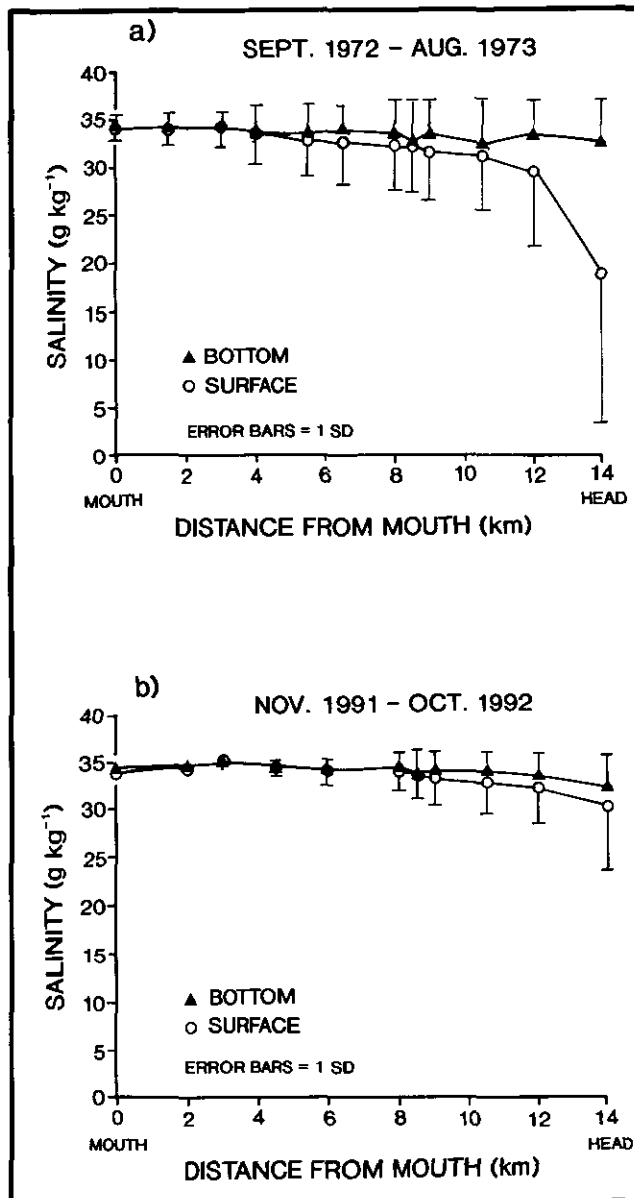

Figure 2
Mean annual salinity ranges from the mouth to the head of the estuary for two different time periods:
(a) September 1972 to August 1973, and
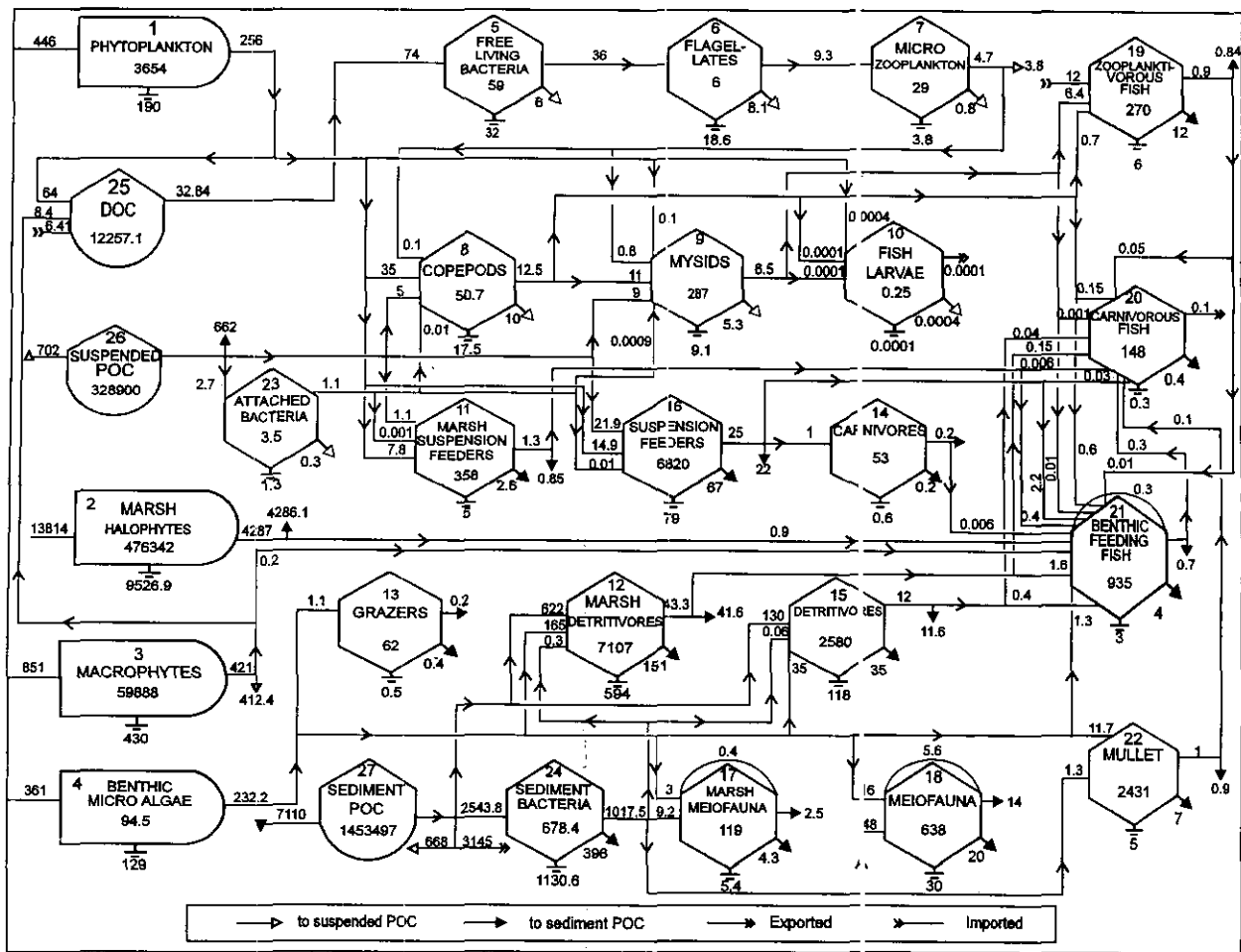(b) November 1991 to October 1992

Figure 3
Carbon flow model of the Kromme estuary representing the pre-1984 period. Biomass given in $mgC \cdot m^{-2}$ and flows in $mgC \cdot m^{-2} \cdot d^{-1}$

| TABLE 3 |
| THROUGHPUTS (IN $mgC \cdot m^{-2} \cdot d^{-1}$) OF EACH MODEL COMPARTMENT IN THE KROMME ESTUARY FOR THE PERIODS PRIOR TO 1984 AND 1988-1992 RESPECTIVELY |

| Compartment	< 1984	1988-1992	Compartment	< 1984	1988-1992
1. Phytoplankton	446.00	49.00	14. Carnivorous macrofauna	1.00	11.70
2. Halophytes	13 800	13 800	15. Detritivores	165.00	936.00
3. Macrophytes	851.00	1 960	16. Suspension feeders	171.00	412.00
4. Benthic micro-algae	361.00	361.00	17. Marsh meiofauna	12.70	13.00
5. Free-living bacteria	74.00	33.00	18. Meiofauna	70.00	30.00
6. Heterotrophic micro-zooflagellates	36.00	16.40	19. Zooplanktivorous fish	19.00	48.00
			20. Carnivorous fish	0.80	0.60
7. Microzooplankton	9.30	4.10	21. Benthic feeding fish	8.00	20.00
8. Copepods	40.00	16.00	22. Mullet	13.00	17.00
9. Mysids	21.00	0.40	23. Attached bacteria	2.70	2.70
10. Fish larvae	0.01	0.01	24. Sediment bacteria	2 546	2 540
11. Marsh suspension feeders	9.00	95.00	25. DOC	74.00	39.00
12. Marsh detritivores	788.00	1 150	26. Suspended POC	702.00	679.00
13. Marsh grazers	1.10	1.10	27. Sediment POC	7 110	7 310
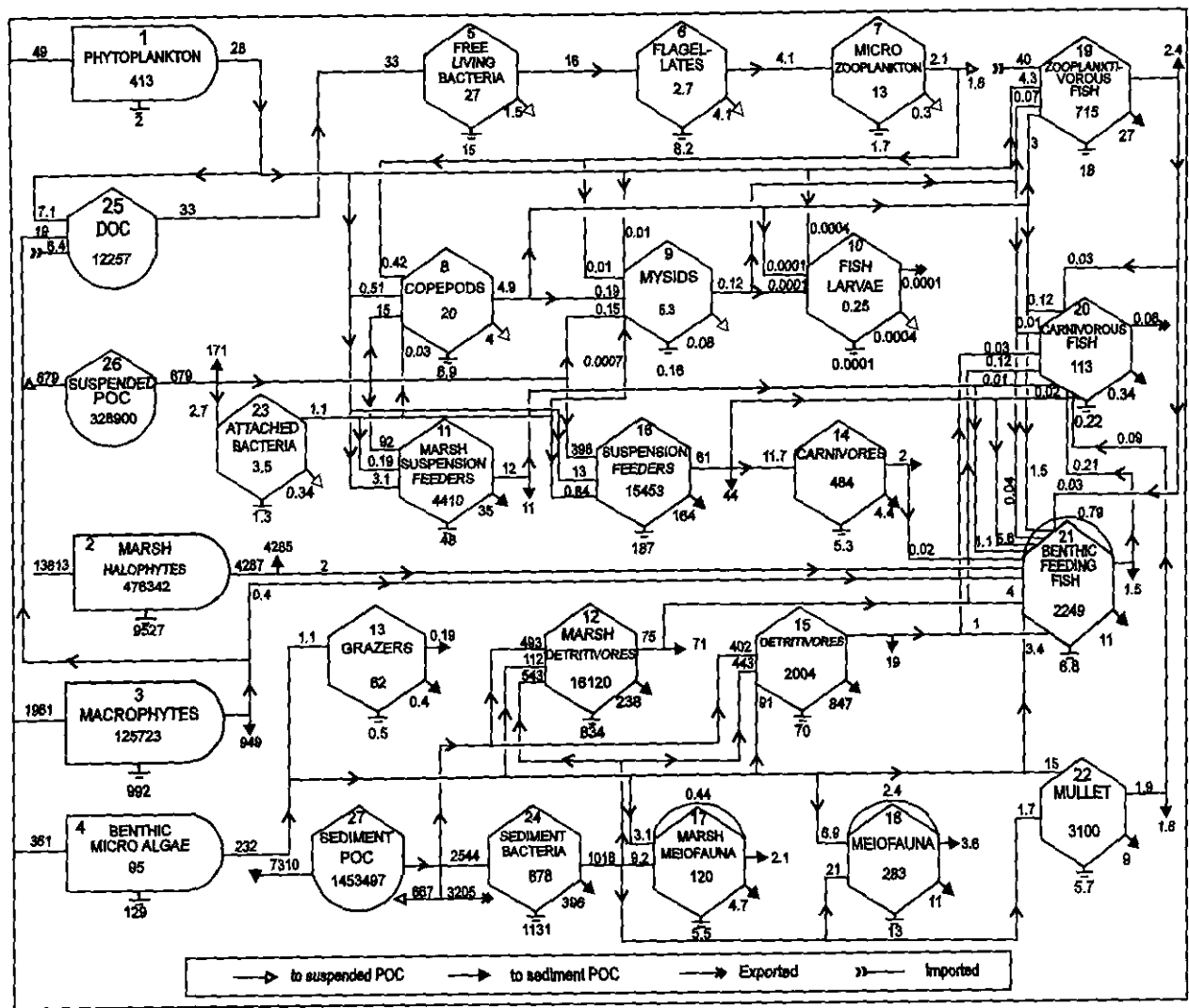
Figure 4

Carbon flow model of the Kromme estuary representing the period 1988 to 1992. Units as in Fig. 3
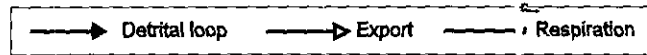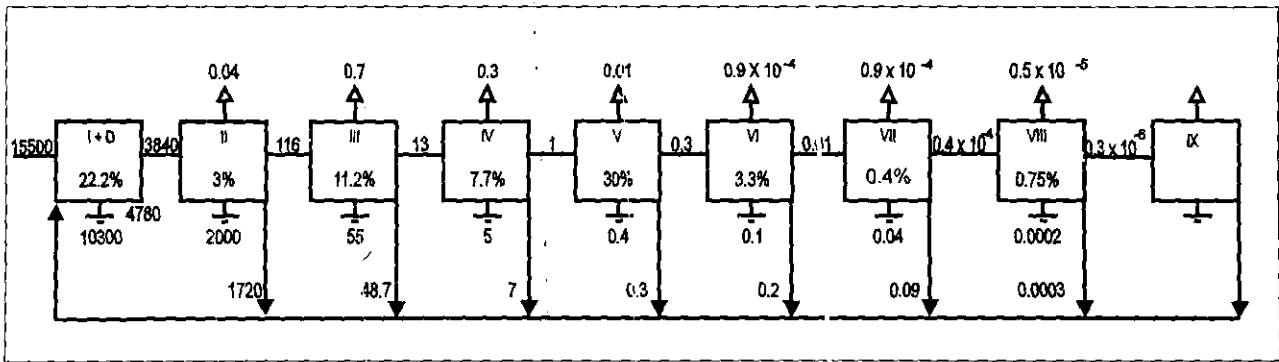
Mugilidae (22) from 2 431 mgC·m⁻² to 3 100 mgC·m⁻².

The production rate of all living components, however, remained virtually constant at about 6.85 gC·m⁻²·d⁻¹, although the annual P:B ratio also decreased by about 14% from 4.46 to 3.82 (see Table 2). Of interest is the decrease in the direct consumption by heterotrophs of primary production products (plants). During the pre-1984 years, about 8.6% of the NPP was consumed by herbivores, whereas only 4.1% was utilised by 1992. This decrease in the consumption efficiency refers mainly to phytoplankton production and utilisation; its production, as well as phytoplankton consumption by zooplankton, declined (see Figs. 3 and 4). The consumption of halo- and macrophytes by estuarine invertebrates and fish is low (Marais, 1984; De Wet and Marais, 1990), and thus little of their production is directly utilised. It would appear that a large proportion of macrophyte production is reduced to detritus, and channelled into the detritus food web (Hanekom and Baird, 1988), a common process in coastal and estuarine systems (Mann, 1972). There was indeed an increase in suspension feeders and detritivores and thus an increase in detritus consumption. This observation is reflected in the detrivory:herbivory ratio, i.e. the ratio between detritus consumption (uptake of suspended and sediment POC) and direct grazing on primary producers, which increased from 8:1 to 15.5:1 (see Table 2).

The configuration of the flow structure of the carbon flow networks of the Kromme estuary, representing the pre-1984 period and the post-1984 period has remained essentially the same (Figs. 3 and 4) respectively. This is expected since no large changes in the species composition of the various communities have been observed, nor has any the "new" species been encountered during the 1988 to 1992 surveys. A measure of the changes in the activity of the individual compartments (depicted in Figs. 3 and 4) is given in Table 3 which lists the throughput (T) of each compartment in mgC·m⁻²·d⁻¹. These results show that the T of some compartments decreased whilst that of others increased since 1984. The compartments that decreased in T consist mainly of the planktonic component of the ecosystem, including phytoplankton, which declined dramatically in T from 446 to 49 mgC·m⁻²·d⁻¹ (i.e. by 89%), free-living bacteria, heterotrophic microflagellates and microzooplankton decreased each by about 55%, copepods by 60%, mysids by 98%, and carnivorous fish by about 25%.

Compartments which increased noticeably in throughput include the benthic components of the ecosystem, such as the submerged benthic macrophytes (mainly *Z. capensis* and *C. falciformes* (Adams and Talbot, 1992) by about 130%, salt marsh suspension feeders and detritivores by 955% and 46% respectively, other estuarine suspension feeders and detritivores by
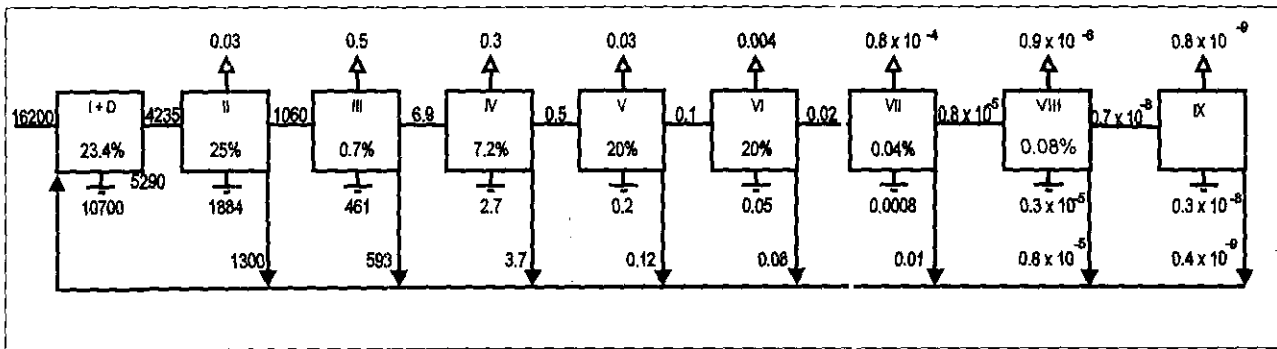
a.

0.04   0.7   0.3   0.01 0.9×10^{-4} 0.9×10^{-4} 0.5×10^{-5}

| 15500 | I+D 22.2% | 3840 | II 3% | 116 | III 11.2% | 13 | IV 7.7% | 1 | V 30% | 0.3 | VI 3.3% | 0.01 | VII 0.4% | 0.4×10^{-4} | VIII 0.75% | 0.3×10^{-6} | IX |

4780
10300   2000   55   5   0.4   0.1   0.04   0.0002

1720   48.7   7   0.3   0.2   0.09   0.0003

⟶ Detrital loop   ⟶▷ Export   ⟶ Respiration

b.

0.03   0.5   0.3   0.03   0.004 0.8×10^{-4} 0.9×10^{-6} 0.8×10^{-9}

| 16200 | I+D 23.4% | 4235 | II 25% | 1060 | III 0.7% | 6.9 | IV 7.2% | 0.5 | V 20% | 0.1 | VI 20% | 0.02 | VII 0.04% | 0.8×10^{-5} | VIII 0.08% | 0.7×10^{-8} | IX |

5290
10700   1884   461   2.7   0.2   0.05   0.0008 0.3×10^{-5} 0.3×10^{-8}

1300   593   3.7   0.12   0.06   0.01 0.8×10^{-5} 0.4×10^{-9}

Figure 5

The Lindeman Spine for (a) the pre-1984 period and (b) 1988 to 1992. The aggregation of the flow networks in Figs. 3 and 4 into a concatenated chain of transfers through the system for the two periods respectively. Primary producers and detritus compartments are merged in the first trophic level (I+D). Per cent values in boxes represent the daily trophic efficiencies. Inputs and outputs from each level given in $mgC \cdot m^{-2} \cdot d^{-1}$

TABLE 4
CYCLE DISTRIBUTION
A: DISTRIBUTION OF CYCLES PER NEXUS (%)

Cycles per Nexus	< 1984	1988-1992
1.00	23.00	18.00
2.00	13.00	21.00
3.00	9.00	9.00
4.00	12.00	12.00
5.00	0.00	5.00
6.00	12.00	0.00
7.00	7.00	0.00
8.00	8.00	16.00
9.00	0.00	9.00
10.00	0.00	10.00
16.00	16.00	0.00

B: PERCENTAGE OF CYCLED FLOW THROUGH LOOPS OF VARIOUS PATH LENGTHS

Path length	< 1984	1988-1992
1.00	0.00	0.00
2.00	45.00	95.00
3.00	53.00	4.00
4.00	2.00	0.70
5.00	0.02	0.02
Total cycled flow ($mgC \cdot m^{-2} \cdot d^{-1}$)	4 973	4 713

TABLE 5
INDICES OF SYSTEM ORGANISATION DERIVED FROM NETWORK ANALYSIS

Index	< 1984	1988-1992
Total systems throughput (T, $mgC \cdot m^{-2} \cdot d^{-1}$)	42 831	45 784
Average path length (APL)	1.77	1.82
Finn cycling index (FCI, %)	11.00	10.80
Number of cycles	100.00	99.00
Trophic efficiency (geometric mean, %)	4.50	2.80
Development capacity (C, $mgC \cdot m^{-2} \cdot d^{-1}$)	141 930	160 940
Ascendency (A, $mgC \cdot m^{-2} \cdot d^{-1}$)	68 587	74 367
Redundancy (R, $mgC \cdot m^{-2} \cdot d^{-1}$)	34 754	42 787
Relative ascendency (A:C, %)	48.30	46.20
Internal capacity (C_i, $mgC \cdot m^{-2} \cdot d^{-1}$)	58 150	69 429
Internal ascendency (A_i, $mgC \cdot m^{-2} \cdot d^{-1}$)	23 397	26 641
Internal relative ascendency ($A_i:C_i$, %)	40.20	38.40

141% and 467% respectively, zooplanktivorous and benthic feeding fish by 153% each, and mullet species by 31%. The only benthic component which showed evidences of decrease was the meiofaunal community in the non-marsh areas. The other living compartments remained at approximately the same activity levels as before the dams' construction (see Table 2). The TST has, however, increased only by about 7% over the intervening period (see Table 5), despite large shifts in some individual compartmental throughputs. It would thus appear that the increase in the system's activity, measured as TST, is mainly due to an increase in benthic biomass and production (i.e. of compartments 3, 11, 12, 15, 16, 21 and 22).

The carbon flow networks were mapped into simplified Lindeman Spines, together with their associated routes of recycling (Fig. 5) (Ulanowicz, 1995; Baird and Ulanowicz, 1989; 1993). The primary producers (1) and the detrital pool (D) are merged to represent the first trophic level. Detrital returns from all the other trophic levels are shown as well as the loop of detritus contribution from plants. The flow of energy (in mgC·m⁻²·d⁻¹) from the one level to the next is shown whilst the trophic efficiencies, defined as that fraction of the total carbon input a level received that is passed on to the next one, are given as percentages in the boxes. Respiration and exports from each level are also shown in Fig. 5. Each spine contains 9 trophic levels, but negligible transfers occur at those higher than the sixth. The trophic efficiencies generally decrease with ascending levels, although the efficiencies at the fifth trophic levels in the pre-1984 and post-1984 Kromme estuary are unexpectedly higher than the preceding ones, which means that the system is quite effective in delivering resources to the higher trophic components, despite the relatively low efficiencies over the first few transfers (Baird and Ulanowicz, 1993).

Results from the Lindeman Spine analysis show that the sum of efficiencies (48%) of the first two trophic levels during the 1988 to 1992 period is much higher than during the pre-1984 period of 25%. This difference is mainly due to the increased efficiency at the second level in the 1988 to 1992 period (up from 3% to 25%); the efficiency at the first level remained constant at about 23% (see Fig. 5) which means that the increase in the trophic efficiency at the second level is attributed to an increased uptake of detrital material. This observation is also reflected in the increase in the detritivory:herbivory ratio over the study period (see Table 2). The geometric mean of the trophic efficiencies in the pre-1984 period (4.5) was nearly double that of the 1988 to 1992 period (2.8) (see Table 5), indicating a drastic decrease in the overall efficiency of energy transfer in the system.

Cycling of material

The cycling of material is recognised as an important and universal characteristic of natural ecosystems (Odum, 1969) and contributes to their autonomous behaviour (Ulanowicz, 1986). Material in ecosystems is cycled through a number of cycles of different path lengths. Short cycles with short path lengths are usually indicative of fast cycling rates, whereas longer cycles (and path lengths) are associated with slow rates (Baird and Ulanowicz, 1989). In this paper three aspects of cycling are discussed, namely the number of cycles and their distribution against cycle length, the FCI, and the APL for the system.

The number of cycles per nexus and the total number of cycles for the two periods are given in Table 4A, and the amount of cycled flow over various path lengths in Table 4B. A nexus is defined as a collection of cycles in which each cycle shares the same unique

"weak arc", which represents the slowest flow between two connecting compartments in the cycling structure. The number of cycles remained constant with 100 in the pre-1984 period and 99 during the 1988 to 1992 years (see Table 2). Table 4A shows a fairly even distribution of cycles per nexus during both periods, although there was a shift to fewer cycles (<5) per nexus in the latter period, and a slight rearrangement of the larger nexuses with seven or more cycles. A surprisingly large nexus, consisting of 16 cycles, was present in the pre-1984 period in which the weak arc existed between attached bacteria (compartment 23) and copepods (8). This nexus was not present in the 1988 to 1992 cycle structure, pointing to a less complicated cycling structure during this period which could possibly be due to the much reduced abundance of copepods and their subsequent diminished role in the dynamics of the food web.

A shift in the amount of flow cycled through various path lengths also occurred during the intervening period. During the pre-1984 period more than 99% of cycled flows occurred via shorter and faster loops of path lengths of 3 and less. By 1992 the recycling of material was more evenly distributed over path lengths of 2 and 3 loops (see Table 4B). The reason for this shift is not clear, but it could be due to the increase in the development of longer pathways involving a greater amount of detritus. The FCI and APL remained relatively constant during the two periods of study (see Table 5).

System properties

The global measures of the systems' organisation for the two study periods are given in Table 5. There was a slight increase in the TST, an index of the systems' activity, of about 7% from pre-1984 to 1992. The development capacity (C), ascendancy (A) and redundancy (R) also increased since 1984 by about 13%, 8% and 23% respectively. The relative ascendancy (A:C), a dimensionless ratio that excludes the influence of TST (the growth component) on A and C decreased marginally by about 2% (Table 5). The difference in the normalised internal ascendancy ratio (A$_i$:C$_i$) is approximately the same as for the A:C ratio (about 2%), but is much lower, by about 8% for both periods, than the A:C ratio per cent values (Table 5).

Discussion

Comparison of ecosystems of different size and geographical position using system attributes derived from network analysis has been reported by Baird et al. (1991) and Baird and Ulanowicz (1993). The successional development of a system over time can also be assessed using network analysis, or, changes in a system can be evaluated if it had been impacted by some external influence. In this study the consequences of reduced freshwater inflow in an estuary were examined from a holistic point of view. The most obvious difference in the system between 1984 and the succeeding years was the disappearance of the salinity gradient and the development of a homogeneous body of estuarine water with a salinity virtually the same as that of sea water. Although no large changes in species composition or topology of the system were observed, the biomass of many components decreased or increased significantly. In the absence of any other physical and/or chemical disturbances or impacts (cf. Baird and Pereyra-Lago, 1992; Baird et al., 1992; Anon, 1991) we postulate that the observed changes could be ascribed to the altered salinity regime of the Kromme estuary. The most significant changes took place in the biomass and production of phyto- and zooplankton in the water

column, and in benthic macrophytes and some invertebrate species. There was a substantial increase in detritivory and a decrease in direct grazing over the intervening period, and coupled with the lowered NPP efficiency (see Table 2) points to an increased reliance of the system on detritus and the recycling of interally produced organic material.

Analysis of the structure and magnitude of cycling in the Kromme estuary showed that although the APL, FCI and numbers of cycles remained virtually the same during the intervening period (see Table 5), more material is now (1988 to 1992) cycled through slightly longer loops (Table 4B). The cycle distribution nevertheless still shows a diversity of nexuses containing long cycles (Table 4A) and seen in conjunction with the low FCI and APL values for both study periods, stress on the system has not necessarily increased since 1984 (Ulanowicz, 1986). Baird and Ulanowicz (1993) compared the Kromme estuary with other estuaries on a worldwide basis and concluded that this estuary is less stressed than the others they examined.

The global indices of system organisation are listed in Table 5 and show that there was an increase in the development capacity (C), the total activity (or size) of the system (TST) and in ascendancy (A). Both the A:C and the A_i:C_i ratios declined in the Kromme estuary, and considering the observed changes in biomass and production of some compartments, it can be inferred that the system as a whole declined in terms of its internal organisation and maturity. This is also reflected in the decline in the P:B ratio (from 4.46 to 3.82) which is considered to be an index of the functional status of an ecosystem. There are also noticeable differences between the A:C and A_i:C_i ratios for the two study periods, but the order of difference (7% to 8%) remained approximately the same. It has been speculated that a large decrease in the A_i:C_i ratio in relation to the A:C ratio could indicate a strong dependency of such systems on external connections (Baird and Ulanowicz, 1993). The decrease in the A_i:C_i ratios for the Kromme estuary does point to some dependence on external connection, as expected from an estuarine system: these differences are, however, not as large (>15%), as those observed for the Chesapeake Bay and Baltic Sea (Baird et al., 1991).

Baird et al. (1991) observed that the development status of an ecosystem, or a change in its status, can only be assessed from a suite of indices. It has also become clear that dimensionless indices, such as the A:C, A_i:C_i and FCI, can be used for this purpose (Mann et al., 1989; Field et al., 1989), and that the correlation between the FCI and the A_i:C_i ratio could be most revealing (Baird et al., 1991). Furthermore, Ulanowicz (1986) has argued and Baird et al. (1991) and Baird and Ulanowicz (1993) have shown that stressed systems are associated with high FCI values. The inverse relationship between the FCI and the A_i:C_i ratio existed and still exists in the Kromme estuary, which implies that the system is less stressed than others (cf. Baird and Ulanowicz, 1993). This analysis has shown, however, that the Kromme estuary has indeed undergone changes at the system level as indicated by decreases, particularly in the A:C and P:B ratios, and increases in TST, C and A. Of interest, however, is the decrease in the A_i:C_i ratios which suggests that the level of organisation and the maturity of the system has declined somewhat since the flow of freshwater into the system was reduced. An important conclusion from this study is that although large changes in individual components of the network (e.g. phytoplankton, zooplankton, some vertebrate and fish components) were observed, only marginal changes were apparent at the whole-system scale. Fluctuations in individual components are more likely to be observed, whilst changes at the systems level may be subtle and

not easily detected. This study has shown that some of the global properties of the estuary have changed, most probably due to reduced freshwater inflows, and that it now functions somehow differently than 15 years ago, and is gradually, and possibly irreversibly, shifting away from a typically estuarine ecosystem. It is clear that there was a decline in water column biomass and productivity, and an increase in benthic macrophytes and some macrobenthic invertebrates (particularly filter- and detritus feeders). Freshwater input, or the lack of it, seems to influence the activity, properties, and functions of estuaries.

Acknowledgements

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