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# The comparative ecology of six marine ecosystems

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## SUMMARY

We compare six marine ecosystems worldwide, using a network analysis of carbon flows for the Swartkops and Ems estuaries, Chesapeake Bay, the Baltic Sea and the Peruvian and Benguela upwelling regions. We find that there is an inverse correlation between the Finn Cycling Index (FCI) and the normalized internal ascendancy or system maturity ($A_i:C_i$). We also show that there is a clear distinction between system maturity ($A_i:C_i$) and the production : biomass ($P:B$) ratio; in upwelling systems the $P:B$ and $A_i:C_i$ ratios are both high, whereas in estuarine systems the $P:B$ ratio is low. The $P:B$ ratio thus cannot be used as an indicator of marine ecosystem evolution. Contrary to current views on ecosystems, the aggregate amount of cycling of materials, such as carbon, is not seen as an indication of system maturity but rather of stress. The reason that higher stressed systems are associated with a higher throughput or FCI could be because perturbations frequently impact higher-level species to a greater extent than the lower trophic components. Any release of standing biomass from these higher levels could therefore be taken up through increased recycling via short intense loops. Overall, we conclude that a network representation is a suitable methodology for inter-ecosystem comparisons.

## 1. INTRODUCTION

Biological throughput and the physical scales over which individuals and populations interact are key factors in determining the spatial and temporal variability of ecosystems. Ecologists have attempted to simulate such changes in whole ecosystems by using sets of coupled differential equations of physical, behavioural and physiological processes. But although this approach has had some success in describing interactions between levels, deeper insights into the dynamics of whole ecosystems may result from more recently developed approaches.

One reason is that many of the biological parameters used in these models are highly variable, because they are derived from systems that are spatially extended, hierarchical (O'Neill *et al.* 1986) and self-organizing (Mann *et al.* 1989). So far, most ecosystem comparisons have generally examined only temporal changes in a single system, e.g. days (Field *et al.* 1989) and seasons (Baird & Ulanowicz 1989; Kremer 1989; Warwick & Radford 1989). Using mean-field, nonlinear systems or cellular automata approaches can improve such intra-system modelling (Huston *et al.* 1988; Rand 1990), but finding a suitable methodology for inter-ecosystem comparison is still a major challenge.

Recent work on the measurement of material and energy flows between the various ecosystem components has shown that the efficiency with which material is transferred, assimilated and dissipated conveys significant information about the fundamental structure of the whole system (Longhurst 1984; Ulanowicz & Platt 1985; Ulanowicz 1986; Wulff *et al.* 1989; Mann *et al.* 1989). The algorithms used, known collectively as network analysis, are derived from input–output, trophic and cycle analysis, and the calculation of total system properties such as ascendancy, throughput and development capacity (Kay *et al.* 1989). Although some parts of network analysis are strictly linear, weighted flow networks have been useful in exploring the spatial and temporal patterns of the interconnections and foodwebs of ecosystems, either at the level of individual elements, intra-level interactions or the whole ecosystem (Mann *et al.* 1989; Baird & Ulanowicz 1989). An example of this approach can be found in a comparison of the Baltic Sea and the Chesapeake Bay (Wulff & Ulanowicz 1989).

The primary purpose of this paper is thus to determine whether a network representation adequately encapsulates the variability within an ecosystem, thereby creating a methodology for inter-ecosystem comparison. Six marine ecosystems differing in size, geographical location, complexity, characteristic time, degree of perturbation and representing different ecotypes were selected (table 1); they included biologically productive and heavily exploited systems, and several which have experienced a large degree of anthropological disturbance. This variability was seen as a good test for the robustness of our approach. Two of the systems examined, the Swartkops and Ems estuaries, are driven by strong tides, dominated by tidal flats and exhibit strong and complete salinity gradients from their mouths to the upper

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Table 1. *Key attributes of the six marine ecosystems analysed*

(Attributes: (1) Area (km$^{-2}$); (2) temperature range (°C); (3) salinity (p.p.t.); (4) components (no.); (5) total standing stock (TSS) (gC m$^{-2}$); (6) net primary production (NPP) (mgC m$^{-2}$ day$^{-1}$); (7) NPP efficiency (%); (8) average path length (APL) (trophic links); (9) Finn cycling index (FCI) (%); (10) production:biomass (day$^{-1}$); (11) number of cycles; (12) trophic efficiency (log mean) (%); (13) total systems throughput (T) (mgC × bits); (14) development capacity (C) (mgC-bits); (15) ascendancy (A) (mgC-bits); (16) A:T; (17) relative ascendancy (A:C) (%); (18) overhead on imports ($\phi$i:C) (%); (19) overhead on exports ($\phi$e:C) (%); (20) overhead on respiration ($\phi$e:C) (%); (21) redundancy ($\phi$r:C) (%); (22) internal capacity (Ci) (mg(-bits)); (23) internal ascendancy (Ai) (mg(-bits)); (24) internal relative ascendancy (Ai:Ci) (%); (25) internal redundancy ($\phi$ri:Ci) (%); (26) flow diversity (C:T); (27) gross primary production (GPP:T) (%); (28) detritivory: T (%); (29) detritivory:herbivory ratio; (30) food web connectance).

| attribute | Swartkops | Ems | Chesapeake | Baltic | Benguela | Peruvian |
|---|---|---|---|---|---|---|
| 1 | 4 | 500 | 5980 | 257 000 | 220 000 | 82 000 |
| 2 | 13–26 | 4–20 | 2–29 | 2–20 | 8–22 | 16–35 |
| 3 | 10–35 | 14–35 | 6–18 | 7–15 | 35 | 35 |
| 4 | 15 | 15 | 15 | 15 | 16 | 16 |
| 5 | 398.1 | 6.7 | 10.1 | 7.8 | 4.3 | 54.4 |
| 6 | 1859 | 202 | 950 | 452 | 548 | 8608 |
| 7 | 38 | 98 | 42 | 87 | 39 | 82 |
| 8 | 3.95 | 3.42 | 3.61 | 3.27 | 2.54 | 2.24 |
| 9 | 43.8 | 28.0 | 29.7 | 22.8 | 0.01 | 3.2 |
| 10 | 0.01 | 0.04 | 0.14 | 0.08 | 0.202 | 0.201 |
| 11 | 14 | 25 | 20 | 22 | 1 | 15 |
| 12 | 4.0 | 12.5 | 9.0 | 16.2 | 12.1 | 3.7 |
| 13 | 17 541 | 1283 | 11 224 | 2577 | 2977 | 48 430 |
| 14 | 62 652 | 5971 | 33 000 | 8007 | 11 046 | 189 730 |
| 15 | 17 565 | 2307 | 16 335 | 4452 | 5593 | 90 789 |
| 16 | 1.00 | 1.8 | 1.46 | 1.73 | 1.88 | 1.86 |
| 17 | 28.0 | 38.6 | 49.5 | 55.6 | 50.6 | 47.6 |
| 18 | 14.1 | 4.8 | 2.6 | 0.9 | 7.6 | 4.4 |
| 19 | 0.4 | 2.5 | 0.4 | 0 | 0.8 | 4.1 |
| 20 | 21.6 | 19.2 | 19.4 | 21.4 | 12.9 | 17.0 |
| 21 | 36.0 | 35.0 | 28.1 | 22.0 | 28.0 | 26.7 |
| 22 | 32 359 | 3430 | 28 508 | 7007 | 5601 | 92 523 |
| 23 | 9842 | 1353 | 9969 | 2810 | 2506 | 41 828 |
| 24 | 30.4 | 39.4 | 35.0 | 39.7 | 45.0 | 45.2 |
| 25 | 69.6 | 60.1 | 65.0 | 60.3 | 55.3 | 54.8 |
| 26 | 3.6 | 4.6 | 2.9 | 3.1 | 3.7 | 3.9 |
| 27 | 14.0 | 22.6 | 14.7 | 30.4 | 20.0 | 30.8 |
| 28 | 6.2 | 6.1 | 12.3 | 15.5 | 0 | 4.1 |
| 29 | 1.5:1 | 0.5:1 | 4.8:1 | 1.5:1 | 0.01:1 | 0.3:1 |
| 30 | 1.46 | 2.2 | 1.87 | 1.85 | 1.55 | 1.75 |

reaches; two have régimes of intermediate salinity: the mesohaline region of the Chesapeake Bay, with salinities from 6–18 p.p.t., and the Baltic Sea proper, with a salinity range of 7–15 p.p.t.; and two are open sea, eastern boundary upwelling regions: the Peruvian and Benguela systems. All six ecosystems are aquatic and either euryhaline or fully saline. The productivity of these aquatic systems, at least within the primary producers, is dominated by an annual cycle. This is in contrast to terrestrial systems, in which long time delays are an innate feature, and in which many biotic elements are either periodically absent or in abeyance.

To compare our results with those from terrestrial systems, we propose that three important criteria must be satisfied: first, the topology, or number of components, together with flow structure and the degree of aggregation among the living components be essentially the same; second, the same medium or currency must be used for all systems (i.e. carbon flows cannot yet be compared with nitrogen transfers); and third an appropriate dimensionless attribute must be identified for comparison. Given these, we were able to examine whether or not the most commonly used whole system properties, such as community productivity or the production biomass ratio, are indeed the best indicators of the evolutionary status of a system.

We chose the degree of network development, measured by specific information-theoretic concepts, as our basis for system intercomparison. Ulanowicz (1980, 1986) has argued that both the amount of species richness and the extent of trophic specificity (the relative lack of trophic niche and overlap) are embodied in the average mutual information of the flow connections (as calculated by Rutledge *et al.* 1976). To have a high network mutual information, a system should have many nodes (species or functional groups) of comparable size that are unambiguously connected with each other. That is, each component exchanges medium with only a very few other compartments. Ulanowicz (1980) scaled the mutual information of the network by its activity or total system throughput ($T$), and named the result the system ascendancy ($A$). This represents the combined attributes of system size and trophic organization.

According to information theory, a natural limit to the ascendancy would be what Ulanowicz called the development capacity ($C$): the joint uncertainty of the flow connections according to the Shannon–Weaver formula, scaled by the total system throughput. In this lexicon, the degree of system development quite naturally becomes the fraction of possible organization that is actually realized, i.e. $A:C$ (Ulanowicz & Mann 1981; Ulanowicz 1986). One final aspect of a highly organized system is its tendency to internalize most of its activity, so that it is relatively indifferent to outside supplies and demands. It is possible to recast $A$ and $C$ as internal indices, $A_i$ and $C_i$ that are functions of the internal exchanges alone (Ulanowicz & Norden 1990). Field *et al.* (1989) cite the ratio $A_i:C_i$ as the quantity most representative of the system's development status, and we elect to use it in the comparisons that follow as our principal index of development.

Systems with a high value of $A_i:C_i$ are by our definition well organized and thereby unlikely to disintegrate spontaneously in the way described by Gardner & Ashby (1970). That is, they possess significant internal stability that makes it difficult for some new influence to change its configuration; this characteristic is known as resistance. On the other hand, the lack of redundancy in an ecosystem's trophic pathways could make it very difficult for a highly developed system to reestablish broken pathways; in this sense it lacks resilience. Many authors have pointed to a complementary relation between ecosystem resilience and resistance.

## 2. MATERIALS AND METHODS

### (*a*) *Brief description of the ecosystems* (*see table 1*)

#### (i) *Swartkops estuary* (*32° 52′ S 25° 39′ E*)

The Swartkops is a small, temperate, turbid, well-mixed estuary which has been studied in some detail during the past ten years (Baird & Winter 1989). The most dominant spatial and temporal scales are those associated with turbulence and which act over periods of hours. Most of the results relevant to this paper are found in Baird *et al.* (1988), Martin & Baird (1987) and Baird *et al.* (1986). The estuary is located on the southeast coast of southern Africa, near Port Elizabeth, and discharges into the Indian Ocean. The river and its estuary flow through heavily populated urban areas, and are thus subject to agricultural and industrial pollution. The estuary attracts many migrating Palearctic birds and is a popular recreational area for boating, sailing, angling and swimming. The salinity ranges from 35 p.p.t. at the mouth to about 10 p.p.t. at the head, and the water temperature varies from 28 to 13.5 °C.

#### (ii) *Ems estuary* (*53° 26′ N 6° 54′ E*)

The Ems is a shallow, semi-diurnal tidal estuary draining into the Wadden Sea. Like the Swartkops, it is a system dominated by turbulence effects; the chemical, physical and biological properties of the Ems estuary have been documented in detail by Baretta & Ruardij (1988). The estuary contains large tidal flats rich in benthic and pelagic life, but there is little evidence of eutrophication and pollution, even though relatively large amounts of nutrients are introduced annually both from the catchment and from the sea (De Jonge 1988). The water temperature ranges from 4 to 20 °C and the salinity from 34 p.p.t. in the Wadden Sea to 14 p.p.t. in the upper reaches.

#### (iii) *Chesapeake Bay* (*Atlantic coast of U.S.A. 36° 50′–39° 40′ N*)

Chesapeake Bay is the largest drowned river valley estuary in the U.S.A. The estuary is tidally mixed, with a characteristic flushing time of 22 days. This analysis concentrates on the mesohaline region, which encompasses about 48% of the total area of the Bay and in which the salinity ranges from 6 to 18 p.p.t. The water temperature varies from 2.3 to 29 °C (Baird & Ulanowicz 1989). The data required for this paper were obtained mainly from Baird & Ulanowicz (1989) and Wulff & Ulanowicz (1989). The Chesapeake Bay is rich in natural resources, such as finfish, blue crab, oysters and clams, which have been heavily exploited for commercial purposes. The Bay also receives large amounts of pollutants and nutrients in the runoff from its catchment area.

#### (iv) *Baltic Sea* (*54° 50′–60° 4′ N and 16°–22° 45′ E*)

The Baltic Sea is a large, enclosed, non-tidal estuary with a total area of about 373000 km$^2$; it is the largest brackish water area in the world (Jansson 1972). It is poorly flushed, and has a mixing time of the order of years. In this analysis we refer only to the Baltic proper, one of three major basins that constitute the Baltic Sea. Owing to increasing inputs of nutrients over the past 50 years, the originally oligotrophic Baltic proper has become slightly eutrophic, and anoxic conditions now occur with greater frequency and duration in the deep water basins (Stigebrandt & Wulff 1987). There has been an increase in benthic biomass in the littoral areas above the halocline, but massive mortalities in benthic populations have occurred in those areas subject to anoxia (Stigebrandt & Wulff 1987; Wulff & Ulanowicz 1989). Fish catches have increased since the 1930s to about 900000 t in 1984, but have subsequently decreased to 730000 t in 1987 (Sparholdt 1989).

#### (v) *Southern Benguela upwelling system* (*eastern Atlantic Ocean 31°–35° S*)

The Benguela ecosystem in the southeast Atlantic Ocean is one of four boundary current regions in the world. The Benguela system is bounded by the Aghulas Current retroflection area to the south of Cape Aghulas (35° S) and the warm Angola Current to the north (18° S), and its physical, chemical and biological properties are described in Shannon (1985), Chapman & Shannon (1985), Shannon & Pillar (1986) and Crawford *et al.* (1987). Upwelling occurs as a result of wind forcing alongshore, which creates an Ekman transport spiral of water offshore that in turn produces a coastal upwelling within one Rosby radius of coastal deformation. The presence of coastal upwelling occurs episodically on the timescale of years commensurate to the NSOI (Northern–Southern Oscillation Index) throughout the Atlantic. The Benguela system is divided into two ecological subsystems separated by a zone of semi-permanent upwelling between 23° S and 31° S off southern Namibia, which effectively prevents the movement of biota between the northern and southern subsystems (Shannon 1985; Shannon & Field 1985; Crawford *et al.* 1987). This analysis refers to the southern Benguela (ICSEAF areas 1.6 and 2.1), an area of about 220000 km$^2$. The system supports significant purse-seine and demersal fisheries, having a total annual catch of 527000 t (David 1987). The data used in this paper also come from Bergh *et al.* (1985), Bergh (1986), Field *et al.* (1989), Lucas *et al.* (1987) and Duffy *et al.* (1987).

### (vi) *Peruvian upwelling system (between 4° S and 14° S)*

The Peruvian upwelling system supports one of the most productive fisheries in the world (Ryther 1969) and for some time the largest single-species fishery (anchoveta, *Engraulis ringens*) anywhere (Pauly & Tsukayama 1987). This eastern boundary current is part of the larger Humbolt Current System in the southwestern Pacific, extends for 2100 km along the coast of Peru, and has an offshore extension of about 370 km. As with the Benguela system, the effects of upwelling occur over a multi-year timescale, known as the ENSO (El Niño Southern Oscillation) Index, the effects of which extend throughout the Pacific. This paper deals with an area of about 82000 km$^2$ in the northern and north-central region of the system that covers the majority of the anchovetas range. Stocks of anchoveta peaked during the 1960s but have declined dramatically since the early 1970s. In contrast, catches of the sardine, *Sarda chiliensis*, have increased since the decline of the anchoveta (Jarre *et al.* 1989).

## (*b*) **Data**

Carbon flow networks were constructed for each of the systems described above, and given as the standing stocks of the various living and non-living components in milligrams of carbon per square metre with the flows between compartments in milligrams of carbon per square metre per day. Although carbon can be represented within a cycle, the solar-driven ecosystem does not require carbon cycling as a critical ingredient in system structure. However, simple calculations of C:N or C:P ratios generally reveal that element cycles are critical to ecosystem function. The carbon uptake ($C$) by each living compartment was balanced by production ($P$) and respiration ($R$) in primary producers, and by an additional term, excreta ($E$), for heterotrophs. The gross primary production in the autotrophic compartments (phytoplankton and benthic algae) was assumed to equal the sum of the net primary production plus algal respiration; these figures were used as the inputs into each system. A comparison of euryhaline and haline systems can be made because the absorption and uptake of $CO_2$ within the top 5–10 mm during photosynthesis is likely to be highly consistent, compared with terrestrial and even some freshwater systems, where processes such as sunfleck production responses (Woodward 1990) may confound inter-system comparisons. System outputs consisted of respiration, exports in the form of suspended material, commercial catches and the emigration of birds and mammals. Because detailed information on the seasonal flows were not generally available, the systems were assumed to be in a steady state. Thus the annually averaged inputs were balanced by the corresponding outputs from each compartment. Biomass, the dietary composition of the various consumers, rates of consumption, respiration and production of the different species or trophic groups were obtained from the literature or calculated using published conversion ratios.

It is argued that ecosystem comparisons are confounded by having compartments with different degrees of aggregation (Kremer 1989; Mann *et al.* 1989). To overcome this, a preliminary trophic analysis was made of each of the original networks. One of the outputs from this analysis was the assignment of an overall trophic position to each species according to its diet (Levine (1980) and see below). The aggregation of species into trophic guilds, for example planktivorous or predatory fish, was based on the average trophic position of those species having approximately the same overall trophic position, diet or feeding pattern, as say detritivores or suspension feeders. For example, the trophic position of the Peruvian anchoveta was determined as follows: the fish derives 57.1% of the time from trophic level 2, 40.5% from level 3 and 1.5% from level 3. It thus feeds on average from the non-integer level 2.423 ($= 0.571 \times 2 + 0.405 \times 3 + 0.0164 \times 4$). Fish species feeding at trophic level 2.0–2.9 were aggregated into one model compartment. The same method was applied throughout for each ecosystem.

A second constraint is that the compartments used to represent each ecosystem should be consistent from one ecosystem to another. We therefore chose a structure consisting of 15–16 compartments, including two or three non-living components, namely suspended particulate organic carbon (POC), sediment POC (bacteria are included in both) and dissolved organic carbon (DOC). All networks had two primary producer compartments, namely pelagic and benthic producers, as well as compartments for pelagic bacteria, micro-zooplankton (2–200 μm), mesozooplankton ($\geqslant$ 200 μm), suspension feeders, meiofauna, benthic detritivores and several fish groups, birds and mammals. One danger in this might be the fact that all the systems do not contain all components. For example, meiofauna were absent from the Benguela system, and the picoplankton would only have been included in the estimate of production, if they had been surveyed in the field. However, we did not attempt to introduce artificially compartments that were not naturally present or which have been shown to play a minimal role in the flow dynamics of a system. Despite these differences, the basic model of system components remained essentially the same for all six examples. We also used the same flow currency, $C$, for each flow model.

Each network was analysed by using computer algorithms described by Ulanowicz (1986) and Kay *et al.* (1989). The following system properties and indices were obtained from our analyses.

1. The effective trophic position of each species, or the weighted average number of trophic steps that separate a living component from the primary producers or non-living components of the system (see calculation above). This index allows one to compare the trophic positions of similar species in different systems.

2. The Lindeman Spine, or the result of mapping the complex network of trophic transfers into a linear food chain with discrete trophic levels. Each level receives a net amount from the preceding trophic level and creates exports, respiration, detritus for recycling, and net production for transfer to the next level. Autotrophs and the non-living organic material pool are assigned to the first trophic level. The trophic efficiency of each level and for the foodweb as a whole can be calculated from the Lindeman Spine. One drawback of this measure is that it depends on a consistent definition of non-utilizable and utilizable components.

3. The Finn Cycling Index (FCI), which gives the proportion of total system activity ($T$) that is devoted to the recycling of media (Finn 1976). Thus FCI = $T_c/T$, where $T_c$ is the amount of system activity involved in cycling. The cycling index measures the retentiveness of a system; the higher the index, the greater the proportion recycled and, possibly, the more mature or less stressed the system (Odum 1969). An individual cycle is a unique pathway which ends and begins in the same compartment: a collection of all such cycles having the same smallest transfer is called a nexus.

4. The average path length (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 = $((T-Z)/Z)$, where $Z$ is the sum of all exogenous inputs.

5. Several global measurements of ecosystem organization including: total system throughput ($T$), which depicts the sum of all the flows occurring in a system; network ascendancy ($A$), the degree of system development; development capacity ($C$), which measures the potential for a particular system to develop; internal ascendancy ($A_i$) and internal developmental capacity ($C_i$) as described above at the end of § 1; system overheads ($\phi$), given numerically by the difference $A$–$C$, which represents the amount of the development capacity that does not appear as organized structure or constraints. On the downside, the overhead represents the cost to the system to operate the way it does. The magnitudes of and uncertainties in the imports, exports and respirations contribute to the overheads, as do the redundancies or parallelisms in the pathways between various components. Collectively, the overhead comprises what are usually regarded as inefficiencies in operation or ambiguities in structure. On the positive side, the overhead represents the degree of freedom, or pool of novelty, that the system has as its disposal to reconfigure itself for any reencounter with a new type of disturbance; internal redundancy ($\phi_{ri}$) is that component of the overhead that derives from the parallelisms in the internal pathways among the components (see Ulanowicz and Norden 1990).

## 3. RESULTS

### (*a*) *Flow Networks*

The carbon flow networks for each of the systems are illustrated in figures 1–6. The Swartkops estuary (figure 1), Ems estuary (figure 2), Chesapeake Bay (figure 3) and the Baltic Sea (figure 4) all consist of 15 compartments. The Benguela (figure 5) and the Peruvian (figure 6) upwelling systems are composed of 16 compartments each. The reason for the difference between these two groups is that the two major planktivorous fish species in the two upwelling systems (compartments 5 and 6 in figure 5, and 8 and 9 in figure 6) were not aggregated. The species in these compartments are heavily exploited in both systems and so their role should be individually assessed; however, it was noted that when aggregated into one compartment, their effect on the system parameters $T$, $A$ and $C$ is minimal. Benthic components are present in all the systems with the exception of the Benguela upwelling system, where there is little evidence that the benthic communities in the deeper, offshore waters have a noticeable effect on the pelagic communities above. The absence of any significant pathway between the pelagic and benthic communities in the Benguela system could be due to the export of slowly sinking detrital material by rapid currents (Chapman & Shannon 1985).

### (*b*) *Trophic structures of the ecosystems*

The results from the network analysis are summarized in table 1. The rate of primary production varies considerably between the systems, with the highest found undoubtedly in the Peruvian upwelling system (table 1), but this reflects the fact that the ratio of phytoplankton to benthic algal production varies between systems. Of interest is the range of net primary production (NPP) consumption efficiencies. This ratio is relatively high for the Ems, Baltic and the Peruvian systems, reflecting an effective utilization of primary production, but relatively low in the Swartkops, Chesapeake and (surprisingly) the Benguela systems. The relatively low use of phytoplankton in the Benguela system can be attributed to the fact that the temporal and spatial distribution of phytoplankton consumers (meso-zooplankton and fish) do not always coincide with areas of high phytoplankton productivity (Brown & Hutchings 1985; Shannon & Field 1985; Bergh 1986). This, together with the export of phytoplankton by currents will contribute to a reduction in herbivory.

The low utilization of primary production in the Swartkops & Chesapeake Bay is offset by their much higher detritivory: herbivory ratios. The Baltic on the other hand is the only system with high detritivory: herbivory ratios, detritivory: $T$ ratios, gross primary

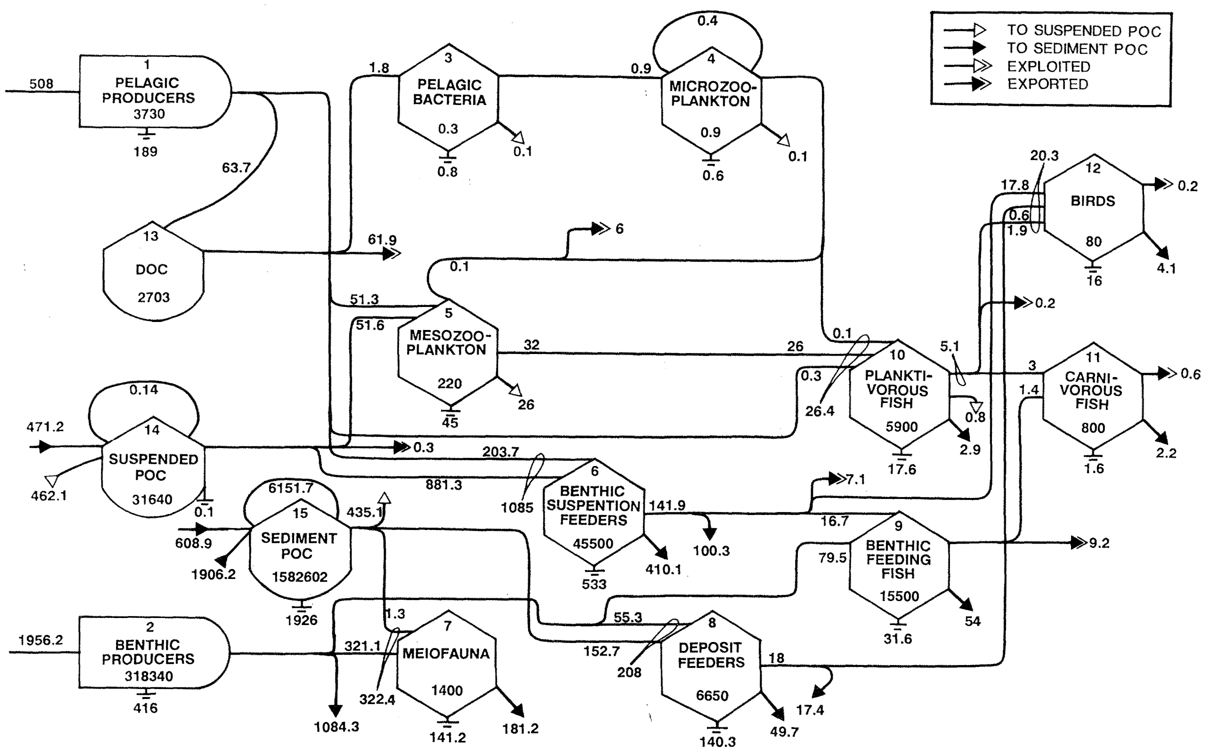

Figure 1. Energy flow network of the Swartkops Estuary (milligrams of carbon per square metre for biomass, milligrams of carbon per square metre per day for flows).

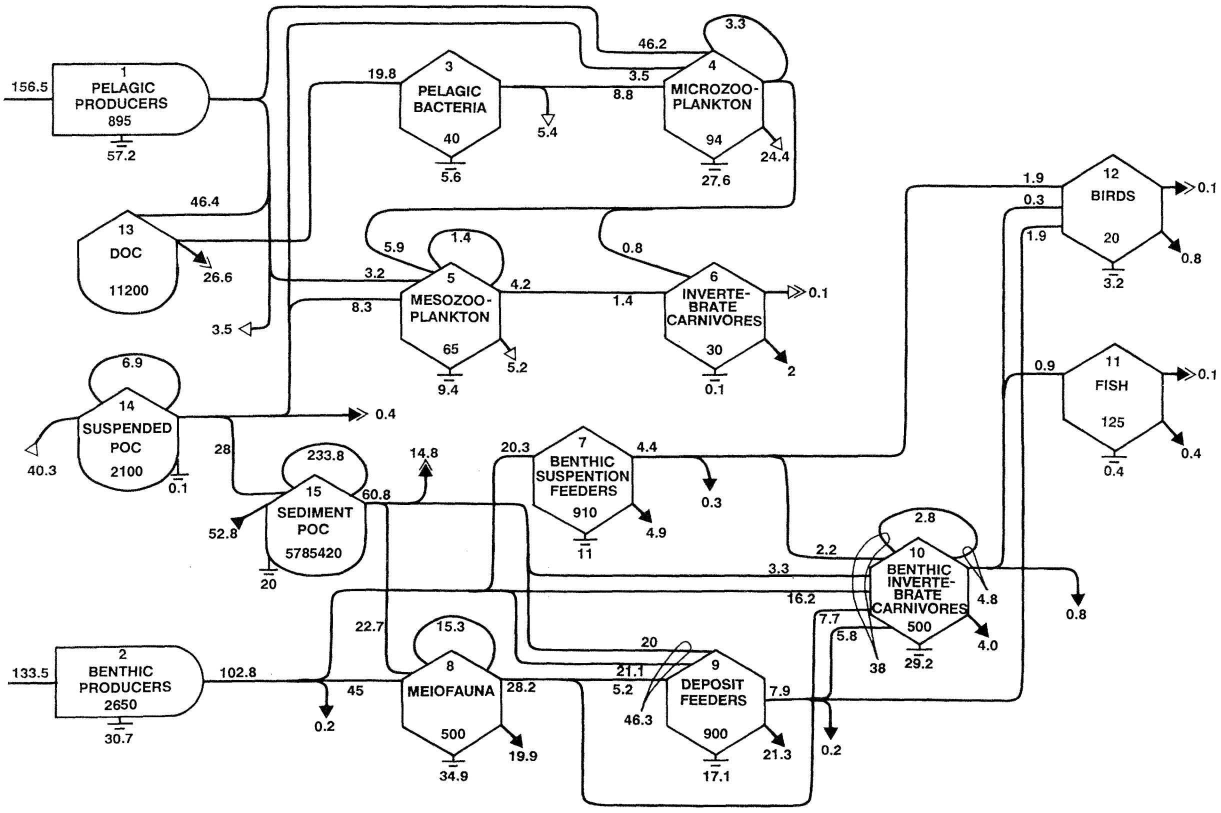

Figure 2. Energy flow network of the Ems Estuary (milligrams of carbon per square metre for biomass, milligrams of carbon per square metre per day for flows).

production (GPP):$T$ ratios and NPP consumption efficiency. If detritivory $T$ and GPP/$T$ are added together then it would appear that about 46% of the total throughput is utilized within the Baltic system, about 11% higher than the next system, the Peruvian upwelling. In the two estuarine systems, these proportions are much lower, about 20% for the Swartkops and 29% for the Ems. Thus one obvious qualitative difference between upwelling systems and the others lies in the detritivory:herbivory ratio. As expected,

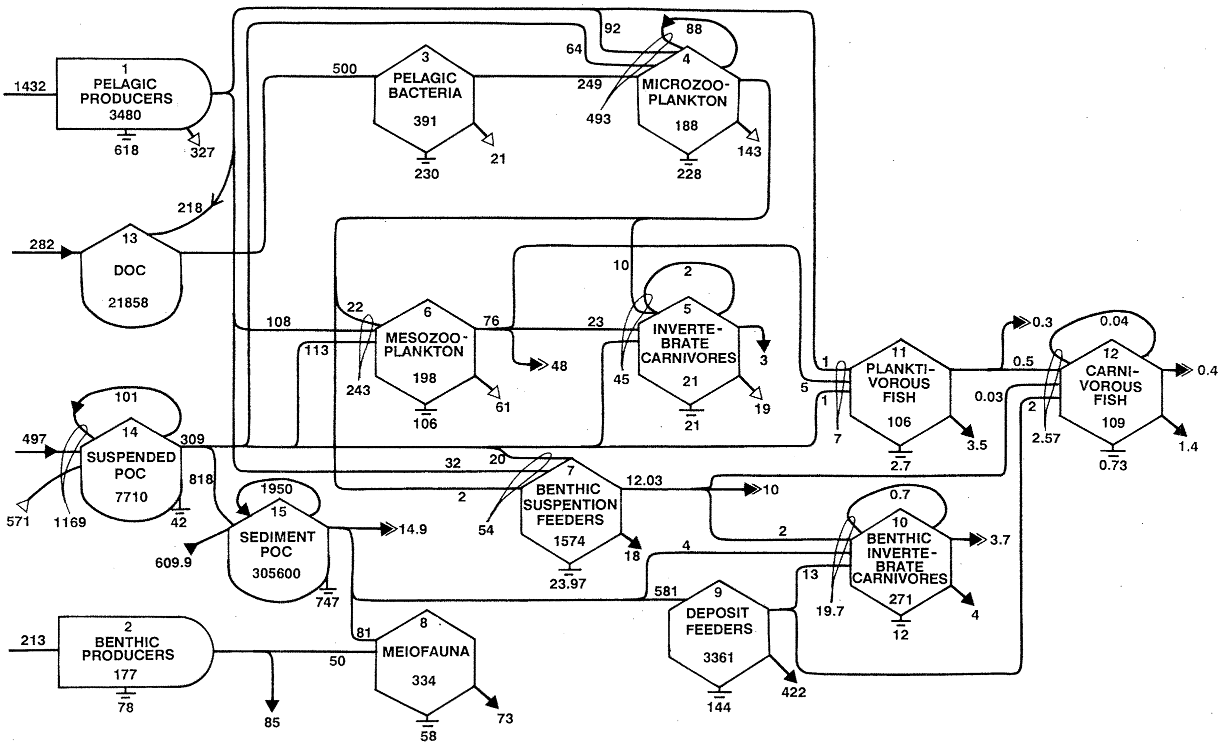

Figure 3. Energy flow network of the Chesapeake Bay (milligrams of carbon per square metre for biomass, milligrams of carbon per square metre per day for flows).

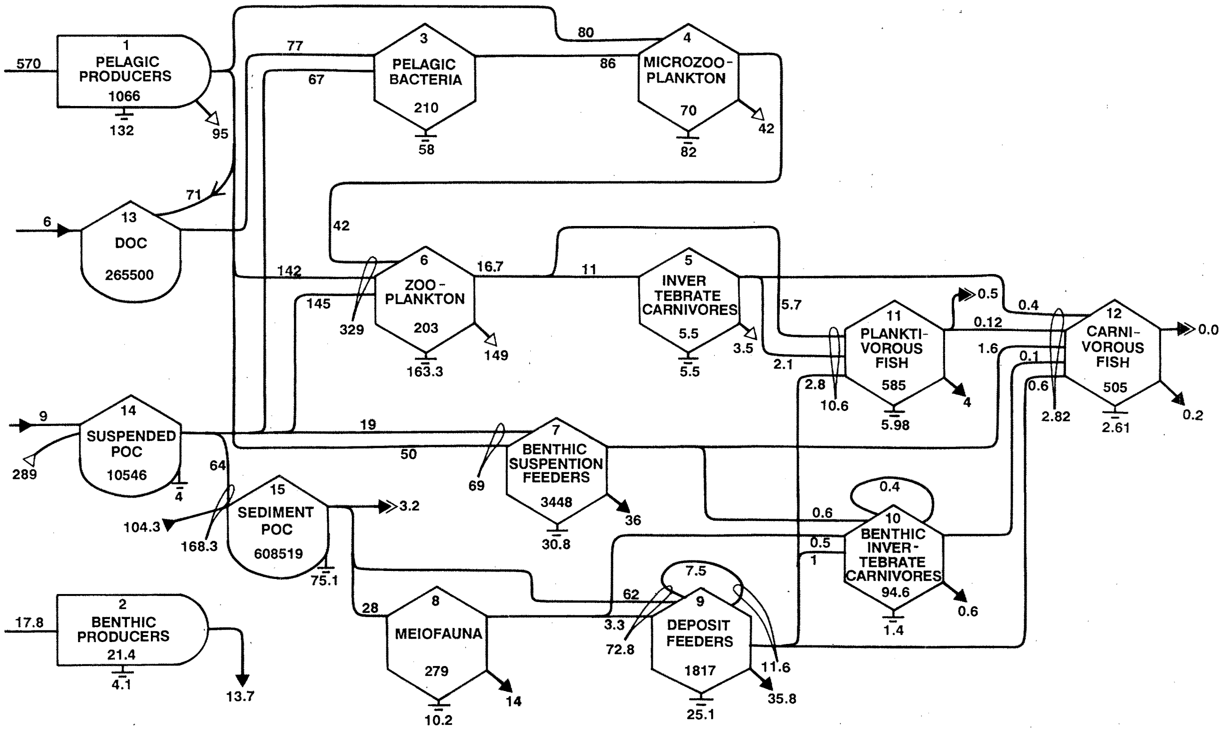

Figure 4. Energy flow network of the Baltic Sea (milligrams of carbon per square metre for biomass, milligrams of carbon per square metre per day for flows).

herbivory exceeds detritivory in the upwelling systems, whereas in the other four systems an inverse observation illustrates a reliance on detritus and its recycling.

Table 2 illustrates the effective trophic position of living components in the six systems. In all the systems, with the exception of the Benguela, consumer species occupy the second and third trophic levels. In the Benguela system the carnivorous fish *Thyrsites atun* (Snoek), birds and mammals feed at one trophic level higher than their counterparts (the hakes, birds and mammals) in the Peruvian system. The differences between the actual trophic positions are, however, small (see table 2). One possible reason for the slightly

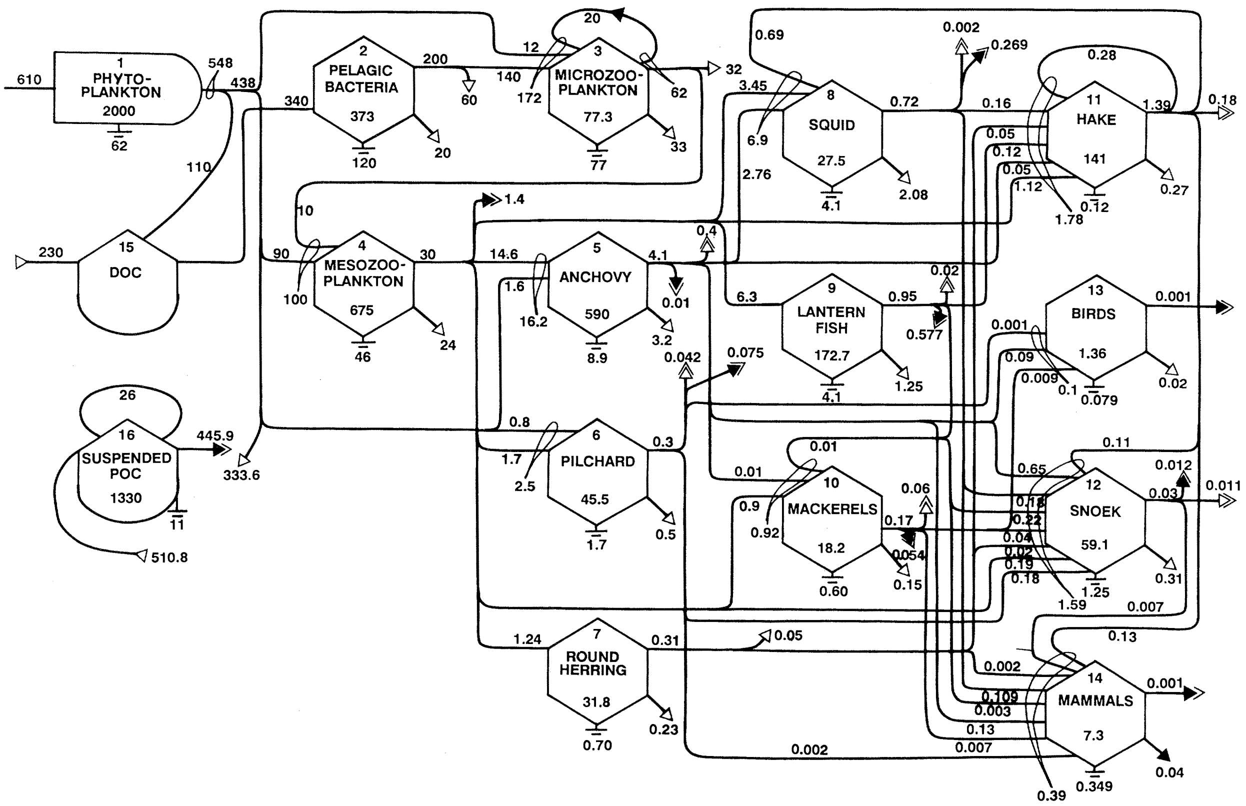

Figure 5. Energy flow network of the Benguela upwelling system (milligrams of carbon per square metre for biomass, milligrams of carbon per square metre per day for flows).

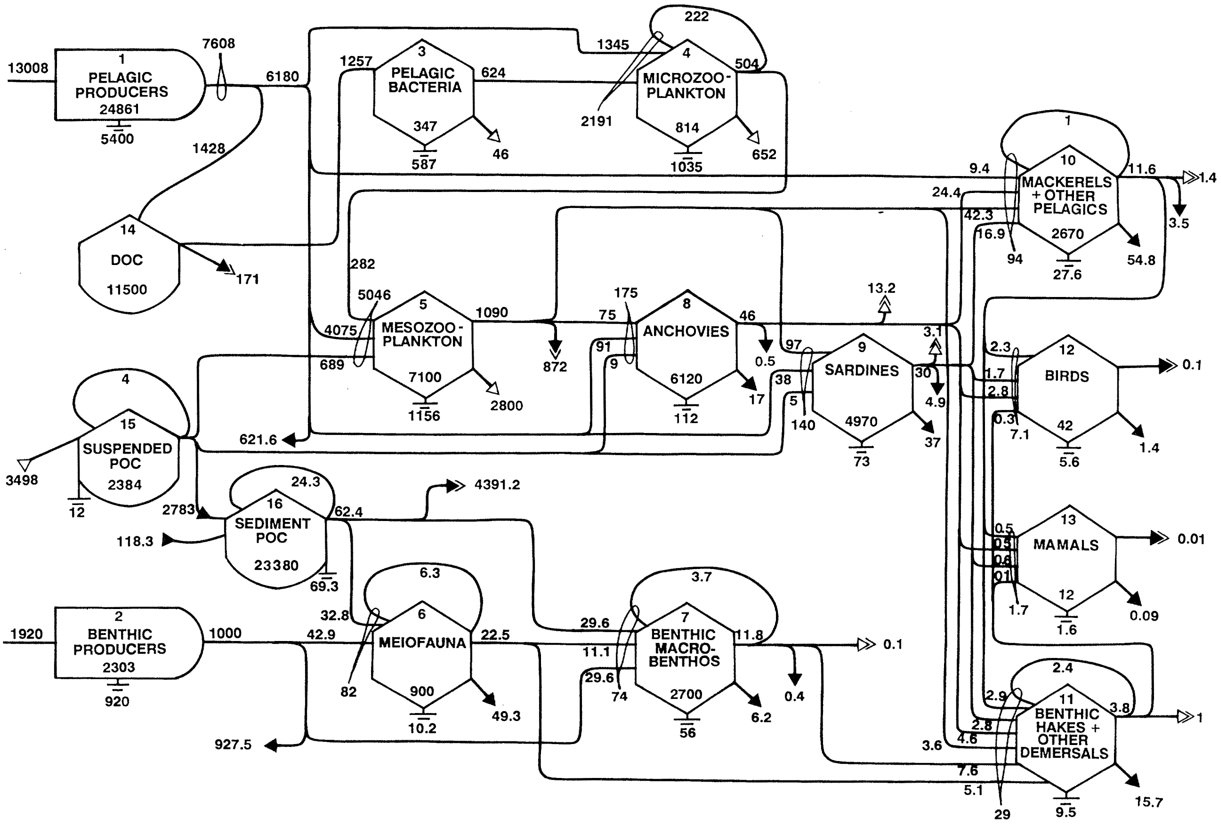

Figure 6. Energy flow network of the Peruvian upwelling (milligrams of carbon per square metre for biomass, milligrams of carbon per square metre per day for flows).

lower trophic position of the Peruvian components can be deduced from the total dependency coefficients, which quantify the degree to which any particular consumer species depends directly and indirectly on any other member of the ecosystem (see Szyrmer & Ulanowicz 1987; Baird & Ulanowicz 1989). It would

Table 2. *Trophic positions* (*TP*) *of species/groups in each ecosystem*

(Numbers refer to compartment numbers in figures 1–6.)

| TP | Swartkops | Ems | Chesapeake | Baltic | Benguela | Peruvian |
|---|---|---|---|---|---|---|
| 2.0–2.19 | 3, 5, 6, 7, 8 | 3, 4, 7, 8, 9 | 3, 6, 7, 8, 9 | 3, 6, 7, 8, 9 | 2, 4 | 3, 5, 6, 7 |
| 2.2–2.39 | — | 5 | — | — | — | 4 |
| 2.4–2.59 | — | 10 | — | 4 | — | 8 |
| 2.6–2.79 | 4, 9 | — | 4 | — | 5 | 9 |
| 2.8–2.99 | 10 | — | 5, 10, 11 | — | 3, 6 | — |
| 3.0–3.19 | 12 | 12 | 12 | 5, 10 | 7, 9 | 10 |
| 3.2–3.39 | — | 6 | — | 11 | 10, 11 | 11 |
| 3.4–3.59 | — | 11 | — | 12 | — | — |
| 3.6–3.79 | 11 | — | — | — | 8 | — |
| 3.8–3.99 | — | — | — | — | — | 12, 13 |
| 4.0–4.19 | — | — | — | — | 12, 13 | — |
| 4.2–4.39 | — | — | — | — | 14 | — |

appear that the Peruvian components obtain some of their sustenance indirectly through suspended and sedimentary organic material which are both at trophic level 1, and, in the case of the hakes (compartment 11 in figure 5) also from the benthos, whereas the snoek, birds and mammals in the Benguela system do not.

The energy flow networks, mapped into simplified Lindeman Spines or trophic aggregations, together with their associated routes of recycling, are given in figure 7 (Ulanowicz 1986; Baird & Ulanowicz 1989; Kay *et al.* 1989). The detrital pool (*D*) is merged with the primary producers (*I*) to represent the first trophic level. Returns from all the other levels are indicated as well as the loop of detritus contribution from plants and the utilization of the organic material by microorganisms. Trophic efficiencies, given as percentages in the boxes, are defined as that fraction of the total carbon into a trophic level which is transmitted to the next higher one. Respiration and exports from each level are also shown.

The number of trophic levels range from five for the Ems estuary to eight for the two upwelling systems. The trophic efficiencies generally decrease with ascending levels (see the logarithmic mean efficiencies in table 1). Of particular interest are the efficiencies at the higher trophic levels: the Benguela and the Baltic systems are quite effective at delivering resources to the higher trophic components, whereas the Swartkops appears to perform relatively poorly in the first four transfers, but unexpectedly well at the final step as a result of the feeding activities of birds on planktivorous fishes. The Ems and the Chesapeake are intermediate in their trophic profiles.

The log-mean efficiencies range from a low value of 3.7% for the Peruvian system to a high of 16.2% for the Baltic Sea. The Benguela system has a threefold, higher efficiency than the Peruvian upwelling system (12.1%); a similar difference can be observed between the two estuarine systems (4% for the Swartkops and 12.5% for the Ems). Thus supposedly similar systems (e.g. upwelling systems or estuaries) appear to have large differences in their trophic efficiencies. In some instances these differences can be traced back to anomalous trophic performance by key species. For example, the high transfer efficiencies at levels IV and V in the Benguela system seem to be related to the ubiquity and assimability of hake. In the Baltic the upper trophic levels are sustained by the dense populations of mysids, which maintain the trophic efficiencies into levels II and III at about 20%.

### (*c*) *Structure of ecosystem cycling*

The cycling of material and energy traditionally has been considered an important process in ecosystem function (Odum 1969). Not only are the number of cycles within a system of importance, but also whether cycling occurs over short and fast routes or over longer and slower loops. Three aspects of cycling are considered in this paper, namely: (i) the number of cycles and their distribution against cycle lengths; (ii) the FCI; and (iii) the whole system (APL).

The number of cycles in each system (table 3*a*) range from 1 in the Benguela to 25 in the Ems estuary. Of interest is the frequency of cycles per nexus and the amount of cycled flow over various path lengths (table 3*b*). The results show that in 3 of the systems (Swartkops, Chesapeake and Benguela) most of the cycling occurs through short and fast loops. This is emphasized in the Swartkops estuary where virtually all the cycling occurs over single cycle nexuses with short path lengths involving species at the lower end of the trophic spectrum (the high ratio of cycle activity in loops of length $\geqslant 3$ to cycles of $\leqslant 2$ is mainly because of a single three-component cycle from sedimentary POC to suspended POC to benthic suspension feeder, the result of physical resuspension of sedimentary POC rather than any biotic process). In the Ems and Chesapeake material is cycled over slightly longer pathways, and becomes more evenly distributed in the Baltic (table 3*b*). Ulanowicz (1984) suggests that a greater diversity of nexuses containing longer cycles implies that there is less stress on a system, and that the relative amount of cycling rises as an ecosystem becomes more stressed. In the Baltic and Chesapeake, where the number of cycles are the same (20), most of the recirculation in the Chesapeake occurs in cycles over very short lengths, compared with the Baltic where the cycles are longer; by this reasoning the Chesapeake is more stressed than the Baltic. We would conclude from these results that the Benguela, Peruvian and Swartkops are all stressed systems, but that the

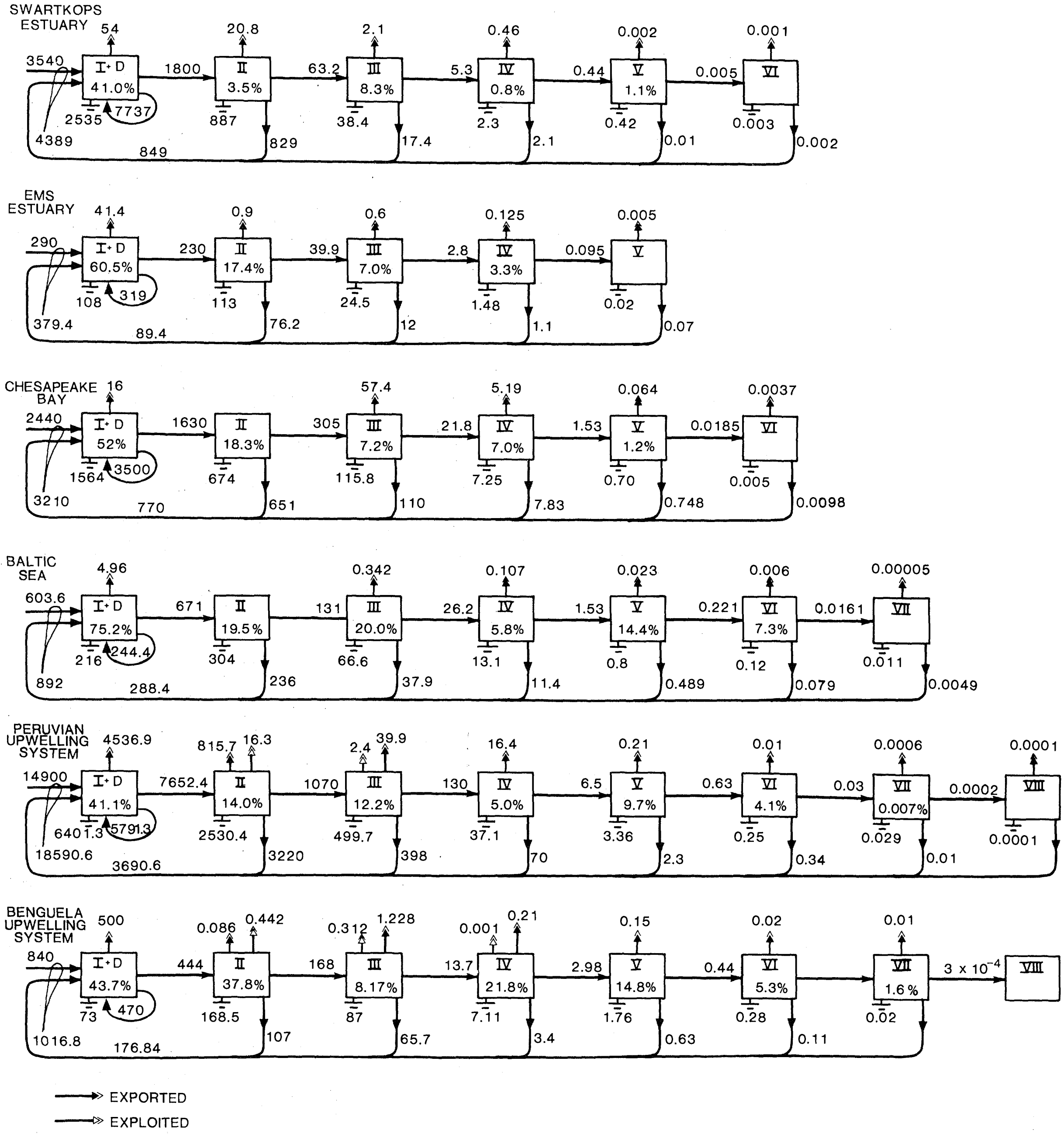

Figure 7. The trophic aggregation in each ecosystem, with the autotrophs merged with the detrital pool ($I+D$); the trophic levels are designated by Roman numerals, and flows given in milligrams of carbon per square metre per day.

nature of the stress is very different: the two upwelling systems are affected by the transitory nature of their physical environments, whereas the Swartkops is impacted by anthropogenic agents.

The Finn Cycling indices (see table 1 and figure 8) range from 0.01 % in the Benguela system to 43.8 % in the Swartkops estuary. The FCI is also low for the Peruvian system (3.2 %) and thus low cycling indices may be characteristic of upwelling systems, where only a small amount of material is cycled through short, fast cycles. The FCIs for the Ems, Chesapeake and Baltic systems, range from 22.8 to 29.7 %, and are intermediate between the upwelling systems and the Swartkops estuary.

The APLs for the two upwelling systems are much lower than those of the other systems (see table 1), meaning that a unit of carbon will only be transferred a few times from when it enters until it leaves these systems. In most other systems the APLs involve at least one more transfer. A unit of flux, carbon in this case, has a shorter residency time in upwelling systems than in estuaries. From the results in tables 1 and 3*a*, *b*, it would appear that both low and high system APL values can be associated with intense activity at lower trophic positions, as illustrated by the Swartkops and by the upwelling systems.

The Swartkops estuary makes an interesting study in the sense that it is a very productive system (it has a high $T$ value), recycles a relatively large proportion (43.8 %) of its total flows over short cycles and has a high system APL value (3.95). The estuary, although not severely polluted, suffers from anthropogenic inputs. Although a large proportion of material is retained within the system, retention takes place over

Table 3. (*a*) *Frequency* (%) *of cycles per nexus*

| Cycles per nexus | Swartkops | Ems | Chesapeake | Baltic | Benguela | Peruvian |
|---|---|---|---|---|---|---|
| 1 | 100 | 32 | 80 | 35 | 100 | 33 |
| 2 | 0 | 24 | 7 | 50 | 0 | 27 |
| 3 | 0 | 12 | 5 | 15 | 0 | 36 |
| 4 | 0 | 32 | 8 | 0 | 0 | 0 |
| number of cycles | 14 | 25 | 20 | 20 | 1 | 15 |

(*b*) *Percentage of cycled flows through loops of various path lengths*

| Path length | Swartkops | Ems | Chesapeake | Baltic | Benguela | Peruvian |
|---|---|---|---|---|---|---|
| 1 | 80.0 | 67.0 | 51.7 | 3.4 | 100 | 1.9 |
| 2 | 2.2 | 24.1 | 34.6 | 44.8 | 0 | 95.2 |
| 3 | 16.1 | 8.2 | 6.9 | 20.8 | 0 | 2.4 |
| 4 | 1.0 | 0.6 | 3.4 | 27.6 | 0 | 0.4 |
| 5 | 0.3 | 0.1 | 3.4 | 3.4 | 0 | 0.1 |
| Total flow ($\mathrm{mgC\ m^{-2}\ d^{-1}}$) | 7679 | 359 | 3334 | 588 | 30 | 1550 |

Table 4. *The percentage of phytoplankton sources that reaches planktivorous and carnivorous fish*

(Commercially exploited species are indicated by an asterisk; compartment numbers in brackets; +, percentage output from one unit of benthic algae)

| | output from 1 unit of phytoplankton | |
|---|---|---|
| ecosystem | planktivorous fish | carnivorous fish |
| Swartkops | 2.88 (10) | 0.32 (11) |
| Ems | — | 0.6 (11) |
| | | [0.6 (11)] + |
| Chesapeake | 0.35 (11)* | 0.08 (12)* |
| | | [0.12 (12)] + |
| Baltic | 1.74 (11)* | 0.63 (12)* |
| | | [0.62 (12)] + |
| Benguela | 2.5 (5)* | 0.19 (7)* |
| | 0.39 (6)* | 1.06 (8)* |
| | 2.89 | 0.97 (9)* |
| | — | 0.14 (10)* |
| | — | 0.27 (11)* |
| | — | 0.25 (12)* |
| | — | 2.88 |
| Peruvian | 1.34 (8)* | 0.72 (10)* |
| | 1.07 (8)* | 0.15 (11)* |
| | 2.41 | 0.05 (12)* |
| | — | 0.93 |

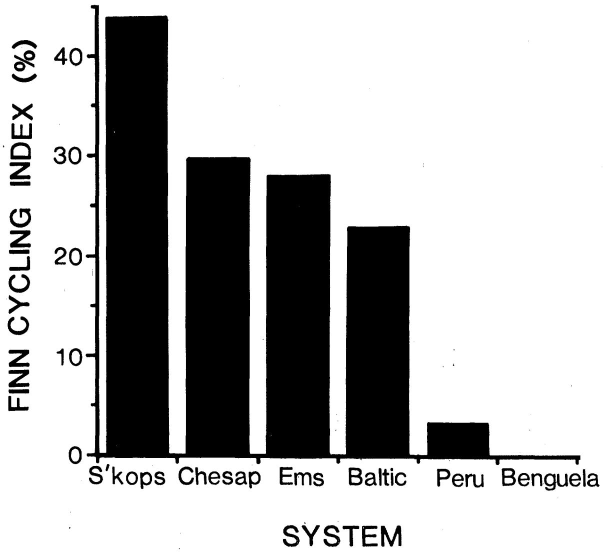

Figure 8. The Finn Cycling Indices (percent).

short circuits within the system; thus the high FCI belies a relatively simplistic cycling structure. At the other extreme, the upwelling systems have very small FCIs, although they resemble the Swartkops in exhibiting simplistic cycle structure. Upwelling systems may be stressed physically by continuous upwelling perturbations, but are not generally subject to anthropogenic pollution. FCI can only be assessed as an indicator of stress in conjunction with other whole system indicators, such as the relative ascendancy (see above).

A final result from the analysis of the trophic structure of these ecosystems is the calculation of fish yield per unit of primary production, using an input–output approach of each system (see Kay *et al.* 1989), in which one can trace the fate of a unit of primary production through the system. In table 4 are listed the percentage of inputs from phytoplankton and benthic algal sources reaching planktivorous and carnivorous fish, which feed mainly at the second and third trophic levels, respectively; some of these species are also of commercial importance. Only the residual flow matrices were used because the cycled flows tend to inflate the inputs into the various end compartments.

The results in table 4 show that the Benguela, Swartkops and Peruvian systems are more than twice as efficient as the Baltic and more than seven times as efficient as the Chesapeake in producing planktivorous fish. In particular, the Benguela system appears to be extremely efficient in the production of commercially exploited carnivorous fish. It is also interesting to note that benthic primary production is more efficiently transported than phytoplankton through the Ems (by an order of magnitude) and Chesapeake to carnivorous fish. In the Peruvian system, just over 1% of primary production reaches the anchoveta, whereas about 2.5% reaches its counterpart, the anchovy, in the Benguela system.

### (*d*) *Global measures of system organization*

The global indices for each of the systems under discussion are given in table 1. The development capacity ($C$) represents the maximum potential evenness and diversity of flows and the total system throughput ($T$) measures the size (or activity) of the system in terms of all its flows (Ulanowicz 1980, 1986; Kay *et al.* 1989). The greater the amount of material flowing through the system, the greater the value of $T$ and thus the activity of the system. When these measures are considered it is clear that the Peruvian system has the largest $C$ and $T$ values. The Benguela system has surprisingly low indices, whereas those of the Swartkops are extremely high compared with the other estuarine systems.

Ascendancy ($A$), represents both the size ($T$) and the organization of flows, and hence the maturity of a system. The relative ascendancy ($A$:$C$) is a dimensionless ratio that excludes the influence of $T$ (the growth component) on $A$ and $C$ and it thus might be considered the most suitable index for comparing different ecosystems (Kremer 1989; Mann *et al.* 1989). The $A$:$C$ ratios for the various systems are listed in table 1. $A$:$C$ is highest for the Baltic (55.6%) and declines for the other estuarine systems (Chesapeake 49.5%, Ems 38.6% and Swartkops, 28%.) The $A$:$C$ ratios for the upwelling systems are also quite high (50.6% in the Benguela and 47.6% in the Peruvian ecosystem). Also given in table 1 are values for the internal capacity ($C_i$), ascendancy ($A_i$) and redundancy ($R_i$). Of particular interest is the normalised internal ascendancy, $A_i$:$C_i$ ratio; this remains approximately the same as the overall $A$:$C$ ratio for all the systems, except for the Chesapeake and Baltic. The internal ratio decreases by 14.5% and 15.9% in the Chesapeake and Baltic systems, respectively, whereas it only decreases by between 0.8 and 5.6% in all the others. This would indicate a strong dependency of these two systems on a few dominant exogenous connections to adjacent ecological and physical systems.

## 4. DISCUSSION

Ecosystem analysis was originally concerned with questions of stability, resistence–resilience, nutrient cycling as key constraints, functions determining structure, energy and available water as explanatory controls on system function, foodchain and foodweb structure. More recently, ideas about maturity and succession through the work of E. P. Odum and others (Odum 1969, Odum, H. T. 1983) have become synonymous with an understanding of the evolutionary processes that work within ecosystems. However, there is some confusion between evolution and succession. For example, Odum (1969) states that 'Ecological succession...culminates in a stabilized ecosystem in which maximum biomass...and symbiotic function between organisms are maintained per unit of available energy flow.' This implies that short-term succession, on the order of decades, is a reflection of long-term evolution in terms of geological time. But if biological turnover and succession can be considered as short-term processes, and hence only a local expression of the much larger evolutionary dynamics of the whole system, then system attributes such as the extant $P$:$B$ ratio may be highly ephemeral.

Many of the current concepts about ecosystems have arisen primarily from the study of freshwater and terrestrial communities, where much of the biomass is locked up and open to view, and the $P$:$B$ ratio appears to decrease in the course of development. What emerges from this analysis of marine ecosystems is an almost opposite picture. That is, the $P$:$B$ ratio increases with the measure of maturity, defined here as $A_i$:$C_i$. Thus the episodic nature of production giving rise to a high $P$:$B$ ratio in upwelling systems cannot be taken as an indication of system immaturity, but rather as a highly adaptive response to the physical nature of the oceanographic regime. We also conclude the maturity of a system can be assessed from its set of topological indices.

Let us now go through the details that support this argument. Qualitative differences among systems or groups of systems usually appear as significant discontinuities in system properties. Here, for example, our attention is drawn to the radical contrast in recycling that exists between the upwelling systems on one hand, and the estuaries on the other. The FCI displays a significant change that might give a clue to the physical differences that discriminate these systems one from another (see figure 8). For example, the two upwelling systems have values of FCI less than 5%, whereas the remaining coastal systems are all in excess of 20%.

Quantitative indices of ecosystem status often appear as correlations among measured system attributes. The one that stands out in this analysis is the inverse rank-order correlation between the FCI and the normalized internal ascendancy, $A_i$:$C_i$ (see table 1). The suggestion was made above that FCI may be an indicator of the stress on a system; in the absence of stress the system is assumed to develop along the lines of greater efficiency. We are suggesting that the normalized internal ascendancy, $A_i$:$C_i$, be taken as the measure of such system efficiency or maturity (Mann *et al.* 1989), and so we should expect to see the inverse relation between FCI and $A_i$:$C_i$ that indeed occurs. When we ordinate the six ecosystems according to their degrees of maturity ($A_i$:$C_i$), starting with the Peruvian system and moving downscale through the Benguela community, to the Baltic, the Ems, the Chesapeake and finally the Swartkops, then we can in fact see that this order also reflects the geological age of the ecosystem (McGlade 1990). This calls into question the more traditional view that maturity is linked specifically to succession and the degree of niche-separation and species diversity. Rather, we consider maturity to be a reflection of a longer-term adaptation to abiotic and biotic conditions, which will not necessarily result in the consistent decrease in the $P:B$ ratio with time as suggested by Odum (1969).

Given that we wish to separate those processes that ecologists can usefully measure from those that have occurred over geological time, let us present the argument in two parts. First, if we consider the short term dynamics, it is possible to apply Odum's premise about the ratio of gross production to standing crop biomass ($P:B$ ratio) to the ecosystems of the world. For example, we can see from this analysis that in going from an open ocean system to an estuarine marsh the $P:B$ ratio goes down dramatically (table 1), and from then on into terrestrial systems the $P:B$ ratios are observed to be lower. This is not a reflection of system maturity, but rather an adaptation to the physical environment and the degree to which biomass is retained within the system. The concept of physical retention as a determinant of biomass and production is not a new one; in oceanography a significant, positive correlation is observed between the biomass of herring populations and the temporal and spatial extent of the retention area used for spawning (Iles & Sinclair 1982). We therefore suggest that an ecological equivalence potentially exists across terrestrial and aquatic biotas, when biomass is retained for approximately the same characteristic time. If true this would allow ecosystems of radically different outward appearances to be considered under a more general theory.

Secondly, along a spectrum of biomass retention and production we will be able to find a range of ecosystems which are evolving under a variety of constraints. Evolutionary advancement or maturity is a measure of where a system lies along this trajectory. Some of the confusion that exists between maturity and the concept of a climax configuration has arisen from a lack of analyses in which the same system attributes have been consistently applied to different ecosystems. This study, by examining a wide range of marine systems, has shown that evolutionary advancement (as measured by increasing $A_i:C_i$) has to do with the ability of an ecosystem to develop a topological network that can mobilize resources and put them into production. On the other hand, the development of a climax ecosystem refers to efficiency and refinements of the underlying topology. Thus some of the qualitative changes we might expect to see as a system matures are (i) increasing numbers of cycles; (ii) longer cycles; (iii) greater specificity of predator-prey interactions, and finally, but perhaps most important; (iv) a topological structure that can withstand large perturbations in available resources through time. On the other hand, the development of a climax ecosystem will result in intensification of existing parts of the network.

It may at first seem strange that such ephermeral communities as those occurring within upwelling regions should be considered mature. But given the results of this analysis, we can say that maturity refers to the configuration of trophic interactions rather than to the individual components present at one particular time. For example, in the Peruvian system, the essential elements are always present, but to an extent that is determined largely by El Niño events that have occurred in the Pacific Ocean for at least a millenium (McGlade 1990). In the two upwelling systems, the $P:B$ and $A_i:C_i$ ratios are both high, whereas among the estuaries, the correlation between these two attributes is less well defined. In fact, Wulff & Ulanowicz (1989) make the important point that the Baltic remains a mesotrophic system despite radical changes in environmental conditions. This suggests that evolution and adaptation to local conditions is still largely an ongoing process, but that physical constraints could eventually create distinctions. More important is the fact that although a system is evolving and maturing there will not necessarily be a linear response between the $P:B$ and $A_i:C_i$ indices.

From this broad picture, some key observations can be made. First, the developmental status of a system can be assessed only from a suite of indices. It is also clear that only dimensionless indices, such as $A_i:C_i$ and FCI, can be used for comparative purposes. Real system values, such as the development capacity, total systems throughput, etc., are usually not useful for inter-system comparisons, although they may be applicable when the same system is compared through time.

Secondly, an assessment combining the magnitude of cycling, the cycling structure and the normalised relative ascendancy values can give a clear yardstick for comparison, but the most revealing correlation lies between FCI and $A_i:C_i$.

Thirdly, a definite distinction must be made between the assessment of system maturity ($A_i:C_i$) and the current functional status of an ecosystem (its $P:B$ ratio). As we have shown here, there is a direct relation between these two indices, which contradicts conventional wisdom about system evolution.

Finally, as Ulanowicz (1984) has argued, contrary to what Odum (1969) has suggested, the aggregate amount of cycling is not an indication of system maturity, but rather of stress within an ecosystem. The results of this analysis support this idea by showing that stressed systems are associated with a higher FCI. How this comes about is unclear, but one possibility is that perturbations often impact higher-level species to a greater extent, thereby releasing resources bound up in standing biomass. The homeostatic response of the less-disturbed lower trophic components is to retain those resources as best they can, usually by recycling the materials among themselves in short, intense loops. Thus, should FCI be inversely correlated with system maturity, as we observed here, it would imply that the Swartkops is the most severely impacted system of those considered, and the Benguela, the least so. However, care should be taken when systems are tagged as stressed. It is known that the Baltic Sea, the Chesapeake Bay and the Swartkops estuary have been, and still are, subject to anthropogenic inputs, and yet large differences exist between the FCIs and $A_i:C_i$ ratios of the Swartkops and the other two. Stress is thus manifested in these system indices in different ways. On the other hand, the two upwelling systems exhibit low FCIs and simple recycling structures, low trophic efficiencies and short system average path lengths but high $A_i:C_i$ ratios. Is stress not implicit in these values?

The distinction lies probably in the interpretation of stress in the sense that upwelling systems are physically stressed as opposed to chemically stressed. Thus the difference could simply lie in the time that the various systems have had to adjust to their applied stresses or forcing functions. Epochs have passed during which the upwelling ecosystems have evolved, whereas many of the chemical perturbations observed in the ecosystems studied here have been generally of more recent origin, and in some cases entirely exotic in nature. In comparing ecosystems, not only is it critical to understand the difference between long-term evolution and short-term functioning, but also to recognize the characteristic scaling or nature of any key perturbations.

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