Wulff, F. and R.E. Ulanowicz. 1989. A comparativ
anatomy of the Baltic Sea and Chesapeake Bay.
pp. 232-256. In: F. Wulff, J.G. Field, and
K.H. Mann (eds.) Network Analysis in Marine
Ecology. Springer-Verlag, Berlin.

Chapter 11

A COMPARATIVE ANATOMY OF THE BALTIC SEA AND CHESAPEAKE BAY ECOSYSTEMS

Fredrik Wulff
Askö Laboratory
University of Stockholm
S-10691 Stockholm
SWEDEN

Robert E. Ulanowicz
Chesapeake Biological Laboratory
University of Maryland
Solomons, Maryland 20688-0038
USA

INTRODUCTION

The theoretical basis for describing and explaining ecological processes has been historically deficient at higher hierarchical levels, such as at the level of whole ecosystems. The manifest tendency for modern technological society to perturb large natural systems has, to a large extent, motivated studies at the ecosystem level, because experience has shown that we cannot explain these changes by studying organisms and populations in isolation (Mann 1982).

The development of ecosystem theory has been hampered by the difficulties in collecting data at this higher level. However, exploited ecosystems have recently begun to offer unique opportunities for testing ecosystem level hypotheses (Leggett *et al.* 1985). The ever increasing availability of data from these systems is beginning to make comparative studies attractive. At the same time analytical tools have emerged that now make it possible to describe system-level structural and functional relationships using these new data sets. In this exercise we apply a suite of the techniques that were described earlier in this book (Kay *et al.* 1989, Chapter 2, this volume) to two exploited marine systems, the Baltic Sea and Chesapeake Bay.

DESCRIPTION OF THE SYSTEMS

The Baltic Sea

The Baltic Sea is a large non-tidal estuary (373,000 km^2) with narrow and shallow connections to the Kattegat and the North Sea (Fig. 11.1). The system is composed of three major basins: the Baltic proper,

south of the Åland archipelago (257,000 km^2), the Bothnian Sea (80,000 km^2) and the Bothnian Bay (36,000 km^2). The salinity of the upper layer of the Baltic proper is about 7 ‰, due to the positive freshwater balance and the narrow and shallow connections to the ocean limiting salt water inflow. The salinity below the permanent halocline, situated at about 65 meters, is between 10 and 15 ‰. The deep water is replenished by dense water from the Kattegatt. The intermittent inflows are driven primarily by barotropic flows due to the level differences between the Baltic and the Kattegatt. A seasonal thermocline develops in May and is reinforced to a depth of about 20 meters during summer. Surface water cooling and wind driven entrainment deepens the thermocline to the depth of the halocline in the fall. The upper part of the deep water (about 10 meters) is then mixed into the surface layer by the fall-winter storms counteracting the freshwater inputs and brackish surface water outflows through the Danish sounds, keeping the salinity constant. Maximum summer temperature is about 20°C above the thermocline and 2.5 - 6°C below. Ice is regularly formed in the coastal zones during late winter but rarely in the open Baltic proper.

The Baltic ecosystem is comprised of a low diversity assemblage of euryhaline marine and brackish estuarine species, fresh water species and glacial marine or fresh water relicts (Segerstråle 1957). Many species tend to occupy broader ecological niches than in their original habitats.

The original oligotrophic Baltic proper has undergone measurable eutrophication during the last 50 years, due to increased nutrient inputs (Larsson *et al.* 1985). Primary production is nitrogen limited in the Baltic proper, as in most coastal marine systems, whereas the Bothnian Bay is phosphorus limited and still ultra-oligotrophic. Basin-wide nutrient budgets (Larsson *et al.* 1985) indicate that nitrogen inputs from land and precipitation and by bluegreen algal blooms are to a large extent counteracted by denitrification. Phosphorus inputs are accumulating in bottom sediments. There is much evidence that the biogeochemical state of the Baltic has changed. Anoxic conditions in the deep water are more common and the concentrations of both nitrogen and phosphorus in the water have increased during the last several decades (Nehring *et al.* 1987). Increased production and sedimentation of organic matter has resulted in anoxia and an almost complete elimination of the benthic macrofauna in the deep basins but a considerable biomass increase above the halocline (Cederwall & Elmgren 1980). Fish catches have also increased (Ojaveer *et al.* 1981).

This study covers conditions in the Baltic proper. The peripheral northern subsystems have lower salinities and a less pronounced stratification.

Chesapeake Bay

Chesapeake Bay, the largest drowned river valley estuary in the United States (12,500 km^2) is situated along the Atlantic Ocean coast from latitude 35°50'N at its mouth to 39°40'N at its head (Fig.11.1). About 50 % of freshwater input to the system enters via the Susquehanna River, with most of the balance coming from the Potomac River. The tidal range throughout the estuary is small, averaging about 0.6 meters. The resultant flow structure is that of a moderately mixed estuary with residual flows seaward near the surface and landward at depth. The bay is shallow with an average depth of about 9 m and exceeding 60 m only in a very few locations along the channel. The input of fresh water to the bay from the Susquehanna is seasonal, peaking at about 5,700 m^3sec^{-1} in late February and early March. During the summer months there is moderately strong stratification with the combined halocline-thermocline residing at about 8 - 10 m depth. There are frequent periods of anoxia below the halocline during summer, and winds and storms will occasionally drive the anoxic waters onto the littoral shelf. Stratification tends to diminish in late September. The region of the Chesapeake covered in this study is the mesohaline middle portion from about 6 ‰ to 18 ‰. This domain covers almost half the total area of the estuary. The flushing time of the mesohaline zone is about 42 days. The mesohaline zone remains relatively ice-free during most years. Summer temperatures in this region average 25-28°C.

The mesohaline Chesapeake is characterized by a small number of species which are euryhaline but the Baltic has an even smaller number, especially of marine species.

As far as can be determined, the Chesapeake has always been slightly eutrophic, typical of the natural state of most east coast estuaries of the United States. Sediment loads increased with the clearing of land in the watershed during the late 17th century and continued until the 1970's when sediment controls were put in place. Over the past half century, nutrient loads from domestic sewage and non-point source agricultural runoff have increased appreciably. Three significant changes in the mesohaline system evidence the increased loadings: (1) The increased frequency and duration of dinoflagellate blooms (primarily *Gymnodynium splendens*) beginning in late spring and extending into the fall (2) The virtual disappearance of submerged aquatic grasses, apparently due to suffocation by heavy periphyton overgrowth (3) The increased frequency and duration of anoxia below the thermocline. The mesohaline region is nitrogen-limited during the summer. Although there is reason to believe that the oligohaline region is occasionally phosphorus-limited during the cooler months, such limitation probably does not appreciably impinge upon the mesohaline region.

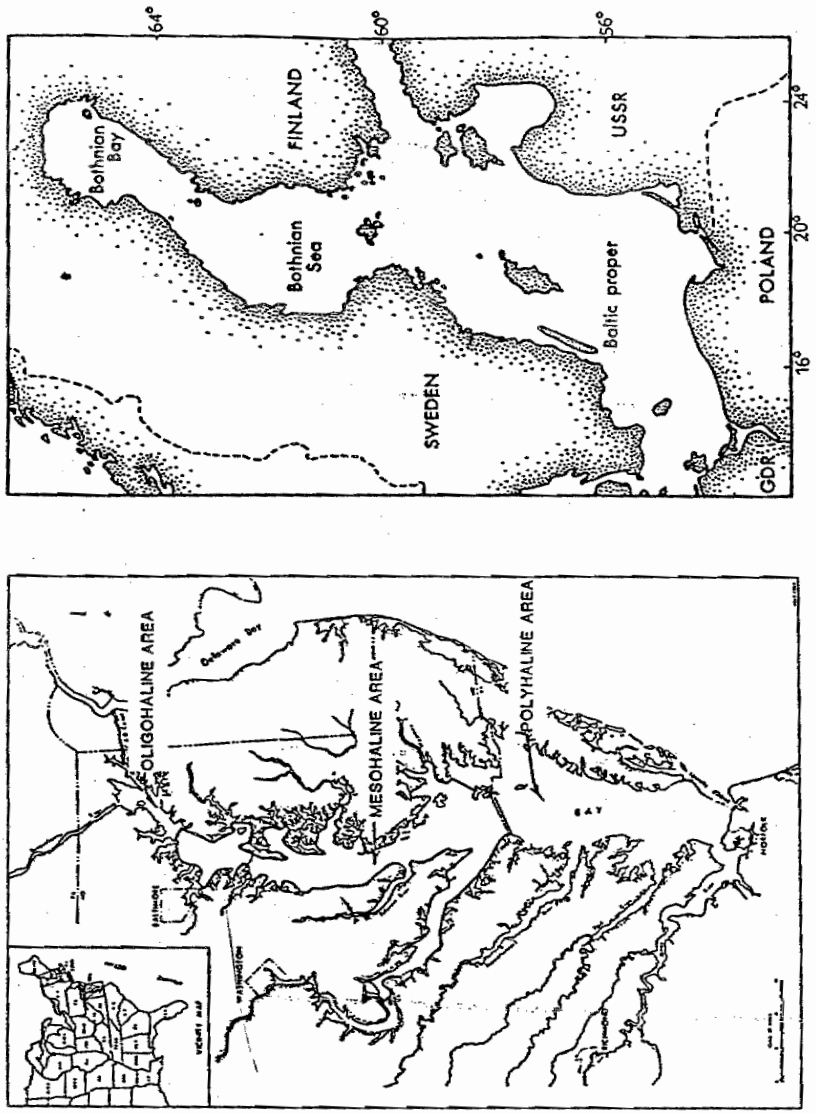

Figure 11.1. Maps of the Baltic Sea and the Chesapeake Bay.

THE NETWORKS

To facilitate cross-system comparisons, we have divided both ecosystems into the same 13 compartments comprising similar functional components in the planktonic, benthic and nektonic subsystems. The resulting networks are depicted in Fig 11.2 using the energy symbols developed by Odum (1971). All arrows in the figure represent carbon flows and are expressed in mg C m^{-2} d^{-1}, as averaged over an annual cycle. For each heterotrophic compartment (the hexagon symbols) we have balanced the inputs (feeding) with the exports by adjusting either the respiratory losses (arrows ending in an electric grounding symbol), the faeces production or the feeding by organisms in other compartments. The overall inputs into the system are the gross primary production by the autotrophic compartments (the bullet symbols) and the advection of allochotonous organic matter into the system. The systems are assumed to be in steady state, i.e., annually averaged inputs and outputs are balanced for each compartment. The 15 member representation of the Chesapeake ecosystem is an aggregated version of a 36 compartment network of flows among the ecosystem of the mesohaline reach of the Bay. Those readers desiring more details about how this system was estimated are referred to Baird & Ulanowicz (1986).

All estimates of annual net production in the Baltic have been taken from an extensive review by Elmgren (1984) and supplemented by estimates of consumption, assimilation efficiency, and respiration in order to obtain complete carbon budgets for each compartment. Annual rates of production in the Chesapeake have been aggregated from seasonal studies conducted by Sellner *et al.* (1985). The biomass of primary producers was estimated by Tuttle *et al.* (1985, 1986), the respiration by Flemer & Olman (1971) and the DOC exudates (25% of net production) by Wiebe & Smith (1977).

The Planktonic Subsystems

Phytoplankton

The *Baltic* pelagic system (see Hällfors *et al.* 1981, and Wulff *et al.* 1986 for reviews) is subject to large seasonal production pulses, starting with the spring diatom bloom in March-April, then followed by a minimum in June and a second pulse during July-August that is dominated by small flagellates. Sometimes, very conspicuous blooms of nitrogen- fixing bluegreen algae occur during late summer. Autumn blooms are sporadic, except in the southern parts, where they occur with regularity. The annual net primary production has been estimated at 160 g C m^{-2} y^{-1} by Elmgren (1984). (Gross production was derived from this figure by assuming a 30 % respiratory loss). Phytoplankton biomass in the *Chesapeake* is dominated by flagellates and small centric diatoms during the warm season and by larger

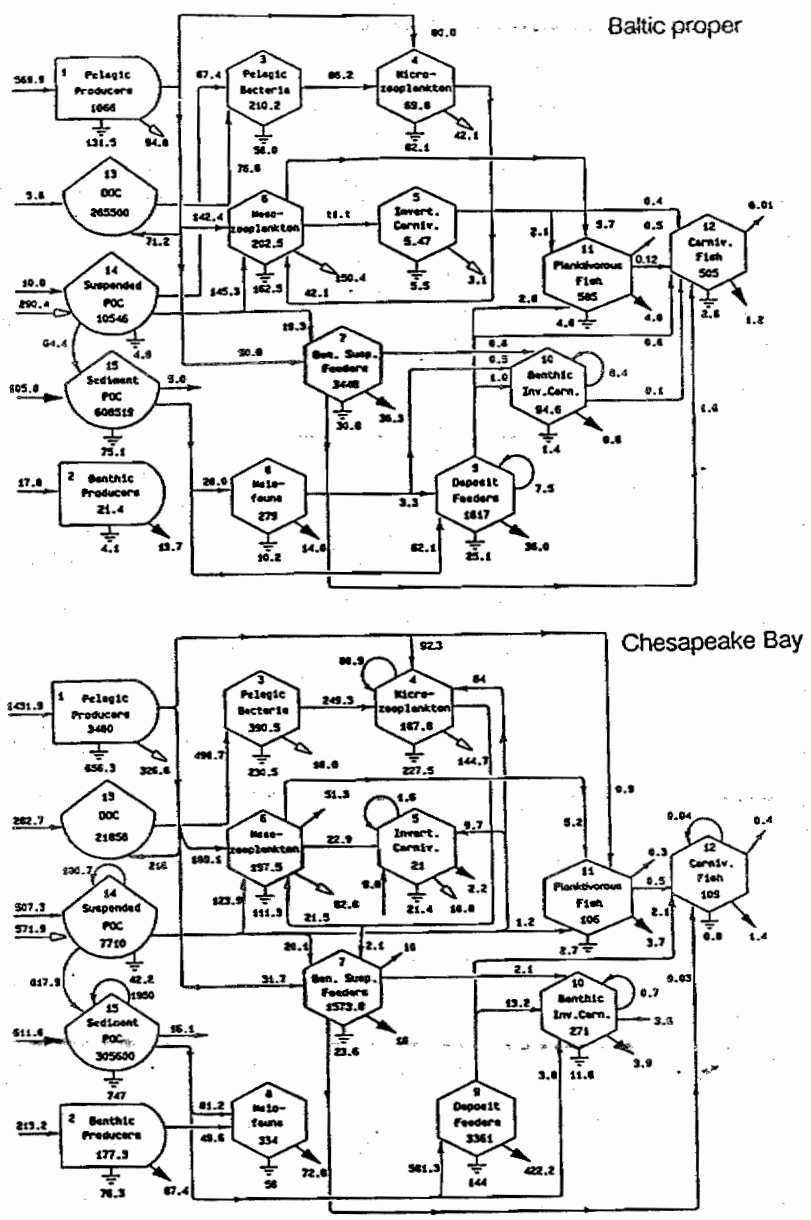

Figure 11.2. Carbon flow diagrams of the Baltic proper and the Chesapeake Bay , units are in mg C m^{-2} (biomasses) and mg C m^{-2} day^{-1} (flows). For simplicity, POC flows between compartments are not connected. Instead, open arrows indicate flows to suspended POC, filled arrows flows to sediment POC.

diatoms during the winter (Sellner *et al.* 1985). On a seasonal basis the greatest productivity occurs throughout the summer (39% of annual production), followed in order of magnitude by the spring (27%), fall (20%) and winter (14%) seasons.

Microbial loop

The importance of the microbial food chain, wherein phytoplankton exudate is utilized by bacteria and then channeled into the flagellate-ciliate-mesozooplankton food chain (Azam *et al.* 1982) has been established for the *Baltic*. To arrive at the figures shown we began with measurements of phytoplankton exudate and bacterial production (Larsson & Hagström 1979). We then assumed that bacteria grow with an carbon conversion efficiency of 60% and that the remaining requirements of the bacteria are met by the suspended POC (14). All bacteria are considered to be eaten by heterotrophic flagellates and ciliates, lumped here into the microzooplankton compartment (4). An annual biomass production of 15 g C m^{-2} and an assimilation efficiency of 50 % have been assigned to the microzooplankton. All net production by this compartment is consumed by mesozooplankton. The levels and role of bacterioplankton in *Chesapeake Bay* have been the subject of much research (Tuttle *et al.* 1985, 1986; Ducklow 1983, 1986) and some controversy (Sherr *et al.* 1987), so that a sufficient amount of actual data was available. It is worth noting that stocks of free living bacteria in the Chesapeake are generally higher than those observed in any comparable estuary. At times the pelagic bacterial production exceeds primary production (Malone *et al.* 1986).

Mesozooplankton

The overwintering mesozooplankton population (6) is very small in the *Baltic*, and maximum biomasses are observed during late summer. This compartment is dominated by the copepods (*Acartia*, *Temora*, *Pseudocalanus*), but rapidly reproducing (parthenogenetic) populations of rotifers (*Synchaeta*) and cladocerans (*Bosmina*, *Podon*, *Evadne*) are sometimes important during the late spring and summer. The carbon flows relating to the mesozooplankton are calculated by applying a C/P ratio of 4 and a P/R ratio of 0.5 to an estimated annual biomass production of 15 g C m^{-2}. The mesozooplankton community in the *Chesapeake* is dominated by the calanoid copepod, *Acartia tonsa*, during the summer and fall and by *Eurytemora affinis* in the late winter and spring (Heinle, 1966). They feed mainly on phytoplankton and suspended detrital particles (14) (Heinle & Flemer 1975; Roman 1984 a,b), but recent evidence suggests they also garner substantial sustenance from microzooplankton, such as tintinnid ciliates (Stoecker & Saunders 1985). A most interesting aspect of the Chesapeake ecosystem is that these important grazers are least abundant during that time of the year (summer) when primary production is greatest.

Carnivores

Planktonic invertebrate carnivores (5) in the *Baltic* consist primarily of medusae (*Aurelia aurita*) in the southern parts and mysids in coastal areas. A C/P ratio of 0.22 and a R/B ratio of 1 are used in conjunction with an annual biomass production of 2.4 g C m^{-2} to estimate the flows associated with this element. Their only food source is mesozooplankton and all their net production is consumed by fish. In the *Chesapeake* this compartment is dominated by the ctenophore, *Mnemiopsis leidyi*, which becomes very abundant during summer and fall. It feeds mostly on mesozooplankton and to a lesser extent upon suspended detritus and microzooplankton (Kremer 1979). Their high stocks during the summer exert heavy grazing pressure upon the mesozooplankton, and this consumption is thought to be the reason for the depressed levels of copepods during the summer (Baird & Ulanowicz 1986).

Allochtonous inputs

Regarding allochtonous organic carbon input to the *Baltic* (taken from Larsson *et al.* 1985), one third is channeled into the pool of dissolved organic matter, DOC (13), and the rest to the pool of suspended organic matter, POC (14). The POC pool receives additional inputs issuing from the faeces of pelagic organisms and from phytoplankton, however we have disregarded as insignificant any excretion of DOC by heterotrophs. Small fractions of these two pools are lost in the flow of water out of the Baltic. The concentrations of suspended detrital carbon in the *Chesapeake* waters and the rates of its deposition on to the sediment have been measured by Boynton *et al.* (1985, 1986). The input to this compartment has been calculated by difference and is one of the least reliable values appearing in the network.

The Benthic Subsystems

Shallow sandy littorals are typical in the eastern and southern parts of the *Baltic*. The shallow soft bottom vegetation is dominated by fresh water plants (*Phragmites, Potamogeton, Chara, Ruppia*), although dense beds of the marine eel grass (*Zostera*) may occur in some of the southern parts. Dense algal vegetation covers the shallow rocky shores of the barren archipelagos found in the western and northern parts of the sea. The typical zonation starts with a filamentous green algal belt (*Cladophora*) occupying the first meter, followed by a brown algae (*Fucus*) down to about 8 meters. Below that depth one finds a scattering of red algae (see Jansson & Kautsky 1977, Hällfors & Niemi 1981). Although this benthic vegetation plays an important role as a spawning and nursery ground, few herbivores utilize these plants directly, and the net production (5 g C m^{-2} y^{-1} as an average for the whole Baltic proper) is channeled into the sediment detrital pool (15).

In the Baltic, two bivalves (*Mytilus edulis, Macoma balthica*) overwhelmingly dominate the benthic filter feeding community (7), and two amphipods (*Pontoporeia affinis* and *P. femorata*) comprise the

deposit feeding community (9). The polychaete, *Harmothoe sarsi*, the isopod, *Mesidotea entomon*, and the priapuloid, *Halicryptus spinulosus*, are the important benthic invertebrate carnivores (10) (see Ankar 1977 and Elmgren 1978). Echinoderms and decapod crustaceans are totally absent, except in the southernmost part. One compartment defined entirely by the size of its member organisms is the meiofauna (8), a heterogeneous mixture of predominantly deposit feeders, but including some carnivores. In this network we assumed that their food sources are primarily bacteria and sediment POC and that they are consumed by deposit feeders and by benthic invertebrate carnivores.

Rooted aquatic vegetation (*Potamogeton, Ruppia, Myriophyllum*) in the *Chesapeake* has declined drastically over the past 10-12 years and now accounts for a very small fraction of overall production. However, the biomass of subtidal, benthic diatoms is not negligible and has been estimated from live chlorophyll *a* measurements on the sediment surface (Boynton *et al.* 1986). Biomass and production are highest in the summer and lowest in winter. About 35% of the benthic microflora production is consumed by the meiofauna and the remainder becomes sediment POC.

The Chesapeake benthic community is somewhat more diverse than that of the Baltic. There are three main categories of benthic invertebrates: the suspension feeders, (including *Crassostrea virginica* and *Mya arenaria*), the deposit feeders (polychaetes such as *Nereis succinea*, bivalves like *Macoma balthica* and various amphipod crustaceans), and the commercially important predator/scavenger, *Callinectes sapidus*. The benthic-feeding carnivores are dominated by the fish *Leiostomeus xanthurus*.

The Nektonic Subsystems

Like the rest of the fauna, the fishes found in the *Baltic* are a mixture of fresh and salt water species especially in the littoral communities. The fishery is however totally dominated by three marine species; the sprat (*Sprattus sprattus*), herring (*Clupea harengus*) and cod (*Gadus morhua*). The two former species constitute the filter feeding fish compartment (11) and cod dominate the carnivorous fish compartment (12) of the Baltic network. The only other fishes for which data are available are also exploited fishes (species like flounder, turbot, salmon, pike and perch) and are lumped into carnivorous fishes. Again, the synthesis by Elmgren (1984) on available data on fish stocks and food composition has been used. Very little quantitative information on smaller and abundant species like gobiids and sticklebacks are available except in some coastal regions (Jansson *et al.* 1985) .

In the *Chesapeake Bay*, filter feeders (11) like Bay anchovy (*Anchoea mitchelli*, a major forage fish) and Atlantic menhaden (*Brevoortia tyrannus*) comprise over half the finfish biomass, and they constitute a significant forage base for the nektonic carnivores (12). The carnivorous fishes are of two types: (1) the benthic predators Atlantic croaker, hogchoker, spot, white perch and white catfish

(*Micropogonias undulatus, Trinectes maculata, Leiostomus xanthurus, Morone americana*, and *Ictalurus catus*) and (2) the pelagic feeders bluefish, weakfish, summer flounder and striped bass (*Pomatomus saltatrix, Cynoscion regalis, Paralichthys dentatus*, and *Morone saxatilis*). The latter group reaches its maximum biomass during the summer and its members emigrate from the mesohaline area during the winter. There is a notable lack of hard data on the stocks of Chesapeake fishes, although reasonable quantitative information on their diets does exist (Homer & Boynton 1978). The standing stocks of the commercial species were estimated approximately from the annual catch, divided by the published P/B ratios for each species (Winberg 1956) .

RESULTS

Given the description of the two systems discussed earlier, it is not surprising that certain differences in the key features of the networks are obvious (from figures 11.2a and b). The large difference in the magnitude of the inputs to both systems is immediately obvious. Primary productivity of the Chesapeake is almost threefold greater than that of the Baltic. Furthermore, allochtonous inflows to the Chesapeake are almost 50% of the magnitude of its primary production, while such inputs to the Baltic are less than 3% of its primary production. There are natural factors which contribute to these contrasting figures: The mean temperature in the Chesapeake is considerably higher and the ratio of its drainage basin to water area is much larger (20:1) than in the Baltic (4:1).

One other structural difference obvious from Figure 11.2 is that in the Baltic the activities of the pelagic components strongly dominate those associated with the benthos. This becomes even more obvious when one calculates the throughput of each compartment, i.e., the amounts flowing through them, as shown below in Table 11.1.

One of the purposes of the "input-output" analysis (see Kay *et al.* 1989, Chapter 2, this volume) is to trace the fate of inputs through the system. For example, Figure 11.3 depicts the percentage of primary production that leaves the system at each compartment. It is immediately obvious that the most important "sinks" for net primary production differ in the two systems. The respiration of the mesozooplankton (6) dominates the Baltic sinks, whereas bacterial respiration in the sediments (15) eventually removes most of the autochthonous production from the Chesapeake. This observation serves to underscore the predominance of the pelagic system in the Baltic versus the key role of the benthos in the more shallow Chesapeake. The picture for the eventual fates of the allochtonous inputs is similar to that for the in situ production.

Table 11.1. Total carbon throughput (mg C m^{-2} day^{-1}) for each compartment in the networks.

Compartment	Baltic	Chesapeake
Pelagic Producers (1)	570	1430
Benthic Producers (2)	178	213
Pelagic Bacteria (3)	144	499
Microzooplankton (4)	166	495
Inv. Carnivores (5)	11.1	44
Mesozooplankton (6)	330	253
Benthic Susp. Feeders (7)	69.3	53.9
Meiofauna (8)	28	131
Deposit Feeders (9)	73	581
Benthic Inv. Carnivores (10)	2.5	19.8
Planktivorous Fish (11)	10.5	7.3
Carnivorous Fish (12)	3.8	2.6
Dissolved Org. Matter, DOC (13)	76.8	499
Suspended POC (14)	300	1180
Sediment POC (15)	170	3380

Another purpose to which input-output analysis can be put is to estimate how much of the various inputs actually reaches those compartments that provide **"useful commercial products"** from the systems. In Table 11.2 are listed the percentages of inputs from the three major sources reaching four of the commercially important compartments.

It is clear that the Baltic is more "efficient" in producing commercially valuable resources. For example, a unit of phytoplankton production produces about four times as much planktivorous fish as does its counterpart in the Chesapeake.

Input-output analysis can be modified to focus on transfers occurring within the system (Szyrmer & Ulanowicz, 1987; Kay *et al.* 1989, Chapter 2, this volume). More specifically, it is possible to calculate the fraction of the total intake by a given compartment that at one time or another passed through each of the other compartments. The list of such fractions pertaining to a given species can legitimately be called the **"indirect diet"** for that component. Because the same material will have passed through several compartments on its way to the target species, the sum of such fractions will exceed unity, and in fact will be related to the trophic status of that particular compartment. Table 11.3 lists indirect diets (in %) of the carnivorous and the plankton-feeding fish in both systems.

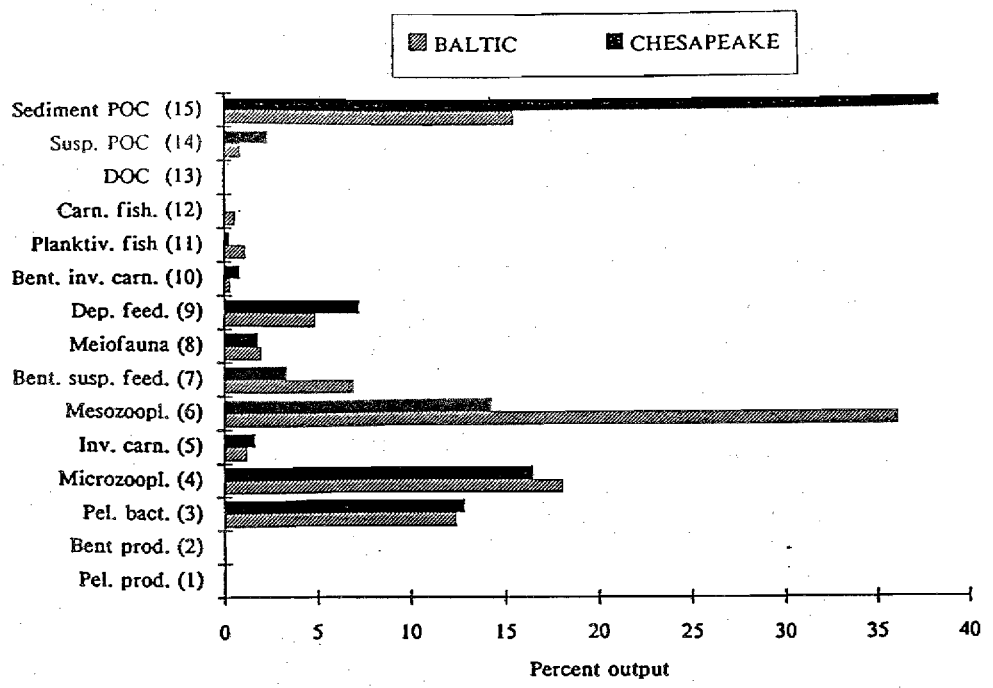

Figure 11.3. Results from the input/output analysis showing where net primary production leave the system.

Table 11.2. The percentage of input from three major sources that reaches the four commercially important compartments.

Source	System	Benthic filterf.	Benthic carn.	Planktiv. fish	Carn. fish
Phytoplankton production	Baltic	11.9	0.4	1.7	0.6
	Chesapeake	2.9	0.6	0.4	0.1
Benthic production	Baltic	0	1.2	1.8	0.6
	Chesapeake	0	1.0	0	0.1
Allochtonous input	Baltic	8.9	0.6	2.5	0.8
	Chesapeake	2.0	1.6	0.4	0.2

Table 11.3. Indirect diets (in % of total intake) of the carnivorous and the filter-feeding fishes in both systems.

	Carnivorous fish		Planktivorous fish	
Compartment	Baltic	Chesapeake	Baltic	Chesapeake
Pelagic Producers (1)	94.8	41.5	94.1	68.3
Benthic Producers (2)	2.9	9.6	3.0	0
Pelagic Bacteria (3)	8.0	9.8	11.7	9.6
Microzooplankton (4)	15.5	13.2	22.6	13.8
Invertebrate Carnivores (5)	16.4	1.6	20.7	1.0
Mesozooplankton (6)	48.2	19.0	83.2	72.5
Benthic Susp. Feeders (7)	49.8	2.6	8.2	0
Meiofauna (8)	4.6	5.8	4.3	0
Deposit Feeders (9)	24.5	79.8	26.3	0
Benthic Inv. Carnivores (10)	2.9	0.5	0.1	0
Planktivorous Fish (11)	32.7	19.5	1.0	0
Carnivorous Fish (12)	0.2	1.5	0.3	0
Dissolved Org. Matter, DOC (13)	4.6	9.8	6.7	9.6
Suspended POC (14)	43.4	79.5	51.7	52.6
Sediment POC (15)	25.0	79.8	26.3	0

Again, the predominance of the Baltic pelagic production (1) is obvious in the indirect diet of the carnivorous fish (95 %), while less than half (42 %) of the diet of Chesapeake carnivorous fishes was once phytoplankton. Other items in the indirect diets underscore this difference. The Baltic fishes are more heavily dependent upon the mesozooplankton (6), benthic suspension feeders (7) and benthic invertebrate carnivores (10), whereas the benthic deposit feeders (9) and detrital material (15) are the primary resources for the Chesapeake carnivores. The surprisingly heavy reliance of Chesapeake carnivores upon the deposit feeders is illuminating. In the Baltic the suspension feeders that are actively removing materials from the water column play a vital link in the food chain to the carnivores. In the Chesapeake the benthic deposit feeders take over the corresponding role. This difference between emphasis on suspension and deposit feeding probably reflects the fact that much of the primary production in the Chesapeake is not grazed and winds up being passively deposited on the sediments and respired or buried.

In the Chesapeake there is a sharp demarcation between the carnivorous fish (12), which depend on detrital food sources, and the plankton-feeding (11) fish which rely mostly on the grazing food chain. In the Baltic this difference is much less pronounced. This is mainly because primary and secondary

Table 11.4. The average path lengths (APL) in the two networks.

Compartment	Baltic	Chesapeake
Pelagic Producers (1)	3.28	3.14
Benthic Producers (2)	2.80	3.52
Pelagic Bacteria (3)	2.55	2.78
Microzooplankton (4)	2.59	3.19
Invertebrate Carnivores (5)	2.45	3.42
Mesozooplankton (6)	2.73	2.59
Benthic Susp. Feeders (7)	2.28	2.50
Meiofauna (8)	2.50	3.36
Deposit feeders (9)	2.53	4.14
Benthic Inv. Carnivores (10)	1.93	1.91
Planktivorous Fish (11)	2.09	3.40
Carnivorous Fish (12)	1.72	3.26
Dissolved Organic Matter, DOC (13)	3.55	3.78
Suspended POC (14)	3.54	4.88
Sediment POC (15)	2.34	4.24

A measure that bears a loose inverse correlation to trophic position is the **average path length (APL)**, which measures the average number of compartments that a particle starting at one particular compartment will pass through before leaving the system (Table 11.4). In contrast to the trophic index, the average path length includes the effects of recycling within the system. In systems without recycling (food chains or tree-like webs) the average path length and the trophic position would be tightly correlated in an inverse fashion.

One does perceive a decrease in the APL for higher members of the Baltic food chain. However, any such correlation in the Chesapeake is confounded by more intensive recycling. The small APL of the benthic invertebrate carnivores (10) reflects both the large metabolic losses and the large exports (i.e., harvesting of blue crab in the Chesapeake or predation by Baltic carnivores [cod], which in turn are heavily exploited.) The big APL for Chesapeake fishes (11, 12) can be attributed to their high production of fecal matter and natural mortality, both of which contribute to the intensive benthic recycling. Exploitation of and respiratory losses by the Baltic fishes give them a reduced APL.

As indicated in Kay *et al.* (1989, Chapter 2, this volume) any arbitrary network can be mapped into a **Lindeman-like trophic chain with accompanying routes of recycling.** The "trophic foundations" of the

two ecosystems are presented in Figures 11.5a and b. It should be repeated here that the trophic compartments (as indicated by the roman numerals) are not discrete aggregations of the components shown in Figure 11.2. Any one real compartment may have its activity distributed among several of the trophic compartments in accordance with the trophic structure of its diet. In comparing the two chains in Figure 11.5 one is struck by three significant differences: (a) The food chain in the Baltic possesses one more level than does the Chesapeake chain. (b) The larger chain in the Baltic is probably due to the generally higher trophic efficiencies inherent in that system. (c) Detritivory (the flow from D to II) strongly predominates over herbivory (the flow from I to II) in the Chesapeake (by a ratio of more than 4:1). The corresponding ratio in the Baltic is only 1.5:1.

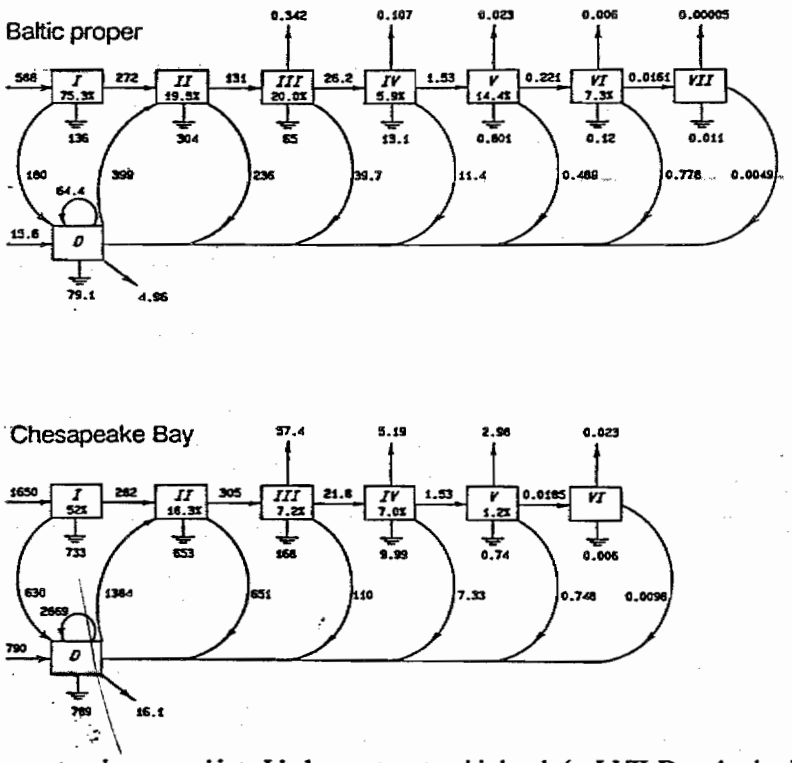

Figure 11.5. The two networks mapped into Lindeman-type trophic levels (=I-VII, D = detritus) with recycling included. Percentages inside boxes refers to overall trophic efficiencies.

The pathways of recycling in an ecosystem may correspond to the system-level means of control in the system (see Kay *et al.* 1989, Chapter 2, this volume). Therefore, much information about the system functioning can be obtained from an **enumeration of the individual cycles in a system** along with some relative weighing of those circuits (Ulanowicz 1983). The two systems possess a comparable number of cycles (22 in the Baltic vs. 20 in the Chesapeake), however, most of the recirculation in the Chesapeake occurs over cycles of very short lengths, whereas the Baltic cycles are generally longer

(and hence distributed among more trophic levels) as shown in Figure 11.6. When an ecosystem is stressed, the relative amount of cycling that occurs usually rises. However, the more intense cycling appears to occur in shorter, faster and trophically lower loops (Ulanowicz 1984). Set against this observation, the Chesapeake Bay appears to be more stressed than the Baltic.

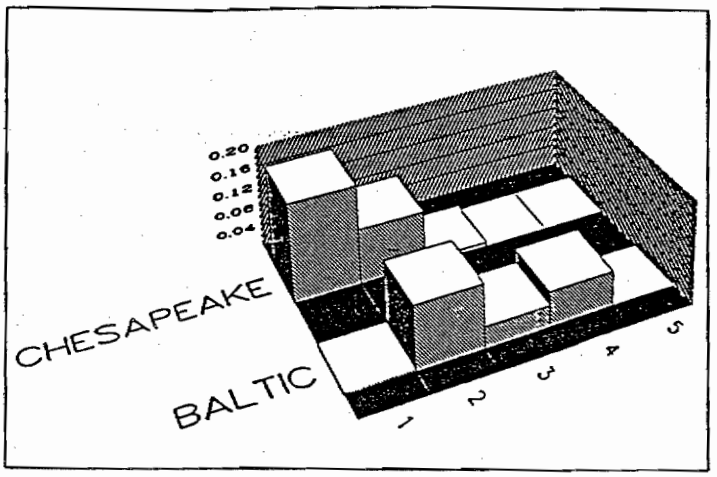

Figure 11.6. Cycle distributions against cycle lengths (1-5) in the two systems, weighted for total activities.

One may actually separate the cycled flow from the network and study its structure, as shown in Fig. 11.7. Visually and topologically the two structures are quite similar. They both possess a bipartite structure, with the cycles among the plankton remaining separated from those occurring in the benthos and nekton. The primary cycling route in the Baltic is in the water column between the zooplankton and the suspended POC (6-14-6). In the Chesapeake the dominant loop lies in the benthos between the deposit feeders and the sediment bacteria-POC (9-15-9). The pelagic bacteria in Chesapeake Bay do not participate in any recycling. They function as a sink for excess productivity instead (Ducklow *et al.* 1986). Filter-feeding fish and benthos are likewise absent from Chesapeake cycling, but their apparent function is to shunt material and energy from the planktonic domain of control into the benthic-nektonic subsystem. The function of the benthic filter feeders in the Baltic appears to parallel its Chesapeake counterpart. The separation of both systems into distinct domains of cycling appears to be due to the absence of any significant route for carbonaceous material deposited on the bottom

to return to the plankton and thereafter be consumed by suspension feeders. The importance of resuspension and feeding on previously deposited POC is not taken into account in the networks and is an obvious area for further research. Before drawing any conclusions comparing the two systems as wholes, it is useful to consider the magnitudes of various whole-system indices as listed in Table 11.5.

Table 11.5. Indices of total system behaviour.

Index	Chesapeake	Baltic
Finn cycling index (%)	29.7	22.8
Average path length (APL, trophic links)	3.61	3.27
Total system throughput (T, mg C-bits)	11224	2577
Development capacity (C, mg C-bits	33000	8007
Ascendancy (A, mg C-bits)	16335	4452
Relative Ascendancy (A/C, %)	49.5	55.6
Overhead on inputs (O_o/C, %)	2.6	0.9
Overhead on exports (O_e/C, %)	0.4	0.0
Overhead on respirations (O_s/C, %)	19.4	21.4
Redundancy (O_r/C, %)	28.1	22.0
Flow diversity (bits)	2.94	3.10

The percentage of total system activity involved in recycling is called the Finn cycling index (Finn 1976). It was originally proposed to test Odum's (1969) conjecture that a greater degree of cycling is an indicator of a more mature system. However, as mentioned above, the sheer magnitude of cycling may actually be more indicative of a stressed system. In the Chesapeake considerably more activity (30 %) consists of recycling than in the Baltic (23 %). In the Chesapeake cycling is confined mostly to short and fast cycles. The Baltic, in contrast, possesses longer and slower loops. Hence, it is necessary to qualify a Finn cycling index with a more thorough study of the cycling structure before drawing any conclusions concerning the state of a system's development.

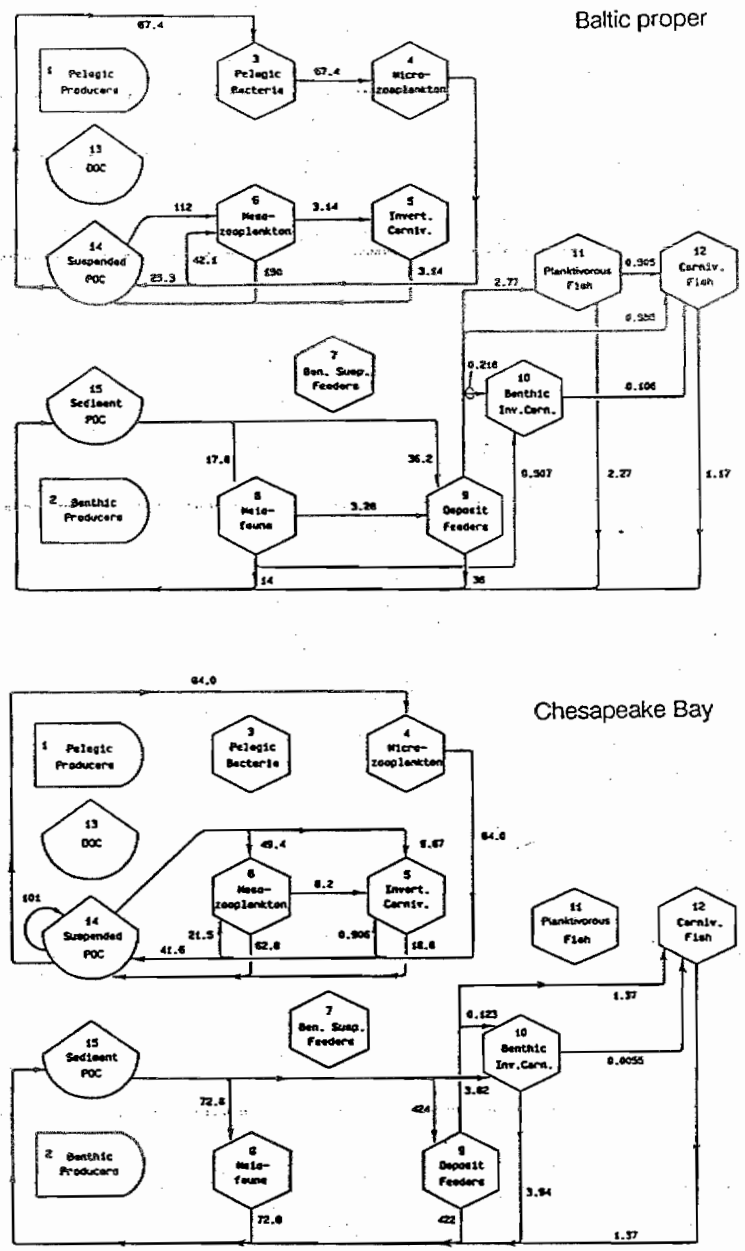

Figure 11.7. The networks for the Baltic and the Chesapeake showing only the cycled flows.

That the Baltic is more highly developed than the Chesapeake is underscored by the differences in the whole system APL. As the APL is correlated in inverse fashion to the average trophic positions of a system, the lower value of this index for the Baltic shows that relatively more activity is taking place at higher trophic positions in this estuary.

That the total system throughput (T) and development capacity (C) of the Chesapeake are both about fourfold higher than in the Baltic is a consequence of the markedly higher mean temperature and productivity of the more temperate estuary. When the development capacities are decomposed into their five components (ascendancy, three overhead terms and the redundancy) one notices only minor differences in their relative magnitudes (as indicated by the percentages of their respective development capacities.) To a certain extent these similarities may be attributed to the procrustean aggregation scheme used to make the systems comparable, but it is probably also due to a true underlying similarity between these systems.

CONCLUSIONS

The classical idea that a higher species diversity imparts stability to the ecosystem (e.g. Hurd *et al.* 1971) has commonly been used as an argument that the Baltic is more sensitive to pollution than are the more diverse marine systems. Jernelöv & Rosenberg (1976) and Rosenberg (1976) have challenged this hypothesis and proposed instead that low species diversity leads to a high genetic diversity, which would make the Baltic communities more adaptive than their marine counterparts. On the other hand, species exposed to the osmotic stress imposed by the low salinities might be more sensitive to additional stresses from pollution (Tendengren & Kautsky 1987). A reduction of species diversity does not necessarily mean that the number of functional units has decreased nor that the major pathways in the food web have been altered (Pimm 1984). Elmgren (1984) has shown that the food webs of the Baltic subareas are strikingly similar to those of other marine areas. Only in the Bothnian Bay, where the low salinity has eliminated the marine bivalves, do the foodwebs decrease in functional diversity. Nixon *et al.* (1986) showed that the yield of fish per unit of primary production for all the Baltic subareas accords well with those observed in most other marine areas. The various techniques used here to analyze networks make it possible to take these comparative studies of the structure and function of ecosystems one step further. It must be remembered that the networks, although fairly complicated, themselves represent gross simplifications of the real systems. Applying network analysis techniques certainly highlighted some real differences between the two estuaries, but some of the differences could be consequences of how the networks were constructed.

According to most of the "classical" theories (Odum 1969), brackish systems should be less developed with fewer feedback control loops and lower transfer efficiencies than their marine and freshwater

production in the Chesapeake is sufficiently high during the winter to continue to support the plankton-feeding habits of fish in that category, but the pelagic production in the Baltic drops so low in the cold months that most zooplankton (6) are forced to overwinter in diapause, thereby forcing the planktivorous fish to go to the bottom and utilize the benthic deposit-feeders (9) (Aneer, 1980).

An important index of how a particular component of an ecosystem is performing is its average trophic level. This index is the average trophic level at which a species feeds as weighted by the amounts arriving at that species over all actual pathways (see Kay *et al.* 1989, Chapter 2, this volume). The average trophic pathways for the living species in the two systems are plotted as bar graphs in Figure 11.4. In both systems compartments 3, 6, 7, 8 and 9 feed chiefly at the second trophic level, while 4, 5, 10 and 12 function at higher, but similar, trophic positions. Clear differences between the systems exist in the plankton-feeding fish (11), which feed roughly one step higher in the Baltic. There appears to be a real biological difference between the feeding habits of the planktivorous fishes in the two systems. In the Chesapeake the menhaden (*Brevoortia tyrannus*) do act in large part as herbivores consuming phytoplankton, whereas their Baltic counterparts feed exclusively on trophically higher zooplankton during the warmer months and on benthic invertebrates during the winter.

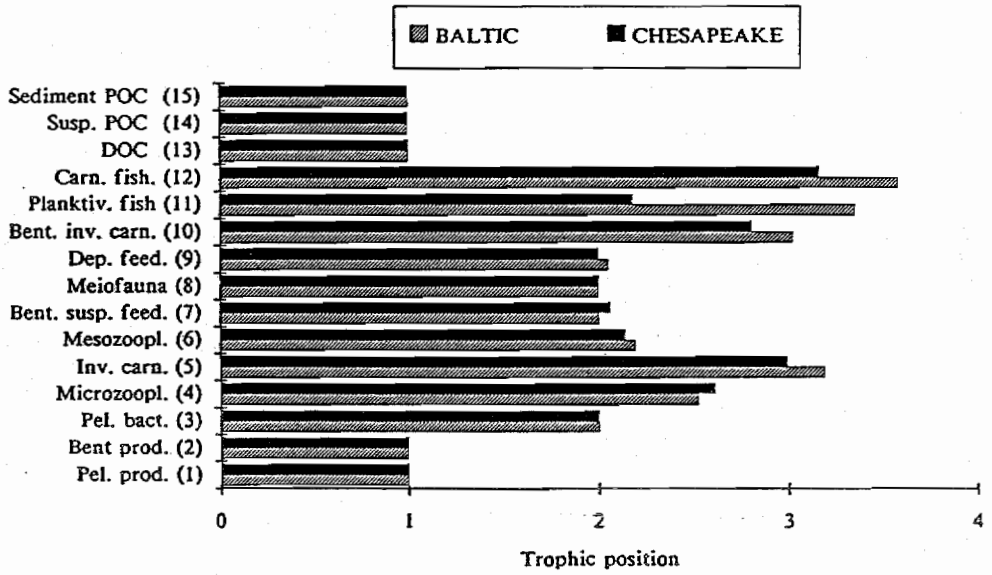

Figure 11.4. Average trophic levels in the two systems.

counterparts. Our analyses show quite the opposite on all counts. The Baltic, in spite of its lower species diversity compared to the Chesapeake Bay, has a higher relative ascendancy and diversity of flows (development capacity divided by T). Furthermore, we showed earlier that the Baltic was trophically more efficient and possesses a more highly structured array of recycling loops than does the Chesapeake. Following the reasoning of Ulanowicz (1986) these characteristics suggests that the Chesapeake is subject to a more intense set of stresses that the Baltic.

This view is also supported by other evidence. Empirical regressions between the areal nutrient input and mean depth/water retention time have been useful in predicting the trophic state in lakes (Vollenweider 1982; Peters 1986). It is interesting to place the present condition of the Baltic and the Chesapeake Bay on such a diagram and compare them with Vollenweider's lines separating permissable from excessive phosphorus loading in lakes (Fig 11.8). The diagram should be used with caution since it was developed for phosphate limited lakes, and the Baltic and Chesapeake are believed to be primarily nitrogen limited.

This is not to say that the Baltic is a pristine body of water. It, too, is the recipient of significant anthropogenic enrichment. However, either such enrichment still serves to increase productivity at all trophic levels (as occurs when oligotrophic waters receive modest increases in nutrient inputs), or else the upper trophic levels have not begun to decline in productivity to anywhere near the extent they have in the Chesapeake. The Chesapeake seems well past the point of diminishing returns, and one has every reason to expect that marginal increases in inputs will not be reflected in greater levels of useful outputs. The reverse seems more likely.

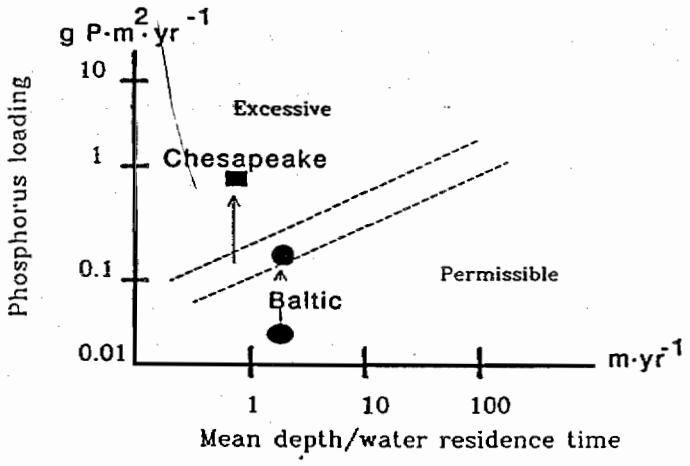

Figure 11.8. A Vollenweider diagram relating permissable-excessive status of lakes to phosphorus loading and mean depth/water retention time, applied to the Baltic and the Chesapeake Bay. Modified from Larsson *et al.* (1985) with data from Smullen *et al.* (1982)

That the Chesapeake Bay ecosystem is in poor shape is hardly news these days. However, that the Baltic appears not to be ecologically as degraded as had been thought is a new viewpoint that might not have appeared were it not for the network analyses performed here. Of course, the semblance of "health" persisting in the Baltic ecosystem should under no circumstances be used as an excuse to relax efforts to protect its biological resources. Rather, the observation should stimulate greater action to preserve the valuable assets that have survived the insults to date. Large mammals, particularity seals were important top predators in the Baltic food web at the beginning of this century (Elmgren 1987). Hunting and biomagnified toxic substances have now reduced the populations to the verge of extinction (Bergman & Olsson 1985). Although the seven Baltic countries have started to take joint action against the increasing pollution, efforts to limit inputs of nutrients and toxic substances have had limited success so far.

Finally, from an academic standpoint, we hope that what we have presented here will stand as a first example of what we hope will become a very fruitful discipline of the "comparative anatomy" of ecosystems.

REFERENCES

Azam, F., T. Fenchel, J. G. Field, J. S. Gray, L. A. Meyer-Reil & F.Thingstad 1983. The ecological role of water-column microbes in the sea, Mar. Ecol. Prog. Ser. 10: 257-263.

Aneer, G. 1980. Estimates of feeding pressure on pelagic and benthic organisms by Baltic herring (*Clupea harengus v: membras* L.), Ophelia, Suppl. 1: 265-275.

Ankar, S. 1977. The soft bottom ecosystem of the Northern Baltic Proper with special reference to the macrofauna, Contrib. Askö Lab., Univ. Stockholm, 19: 1-62.

Baird, D. and R.E. Ulanowicz. 1986. A network analysis of the Chesapeake Bay ecosystem, Ref. No. UMCEES-CBL 87-77, Center for Environmental and Estuarine Sciences, Solomons, MD.

Bergman, A. & M. Olsson 1985. Pathology of Baltic Grey Seal and Ringed Seal females with special reference to adrenocorrtial hyperplasmia: Is environmental pollution the cause of a widely distributed disease? Finnish Game Res. 44: 47-62.

Boynton, W.R., W.M. Kemp & J.M. Barnes 1985. Report to: Maryland Office of Environmental Programs. Chesapeake Bay Water Quality Monitoring Program. Ecosystems Processes Component (EPC). July 1984-June 1985, University of Maryland [UMCEES] CBL 85-21:1-42.

Boynton, W.R., W.M. Kemp, J.H. Garber & J.M. Barnes 1986. Report to: Maryland Office of Environmental Programs. Chesapeake Bay Water Quality Monitoring Program. Ecosystems Processes Component (EPC), July 1985-May 1986, University of Maryland [UMCEES] CBL 86-56: 1-52.

Cederwall, H., & R. Elmgren 1980. Biomass increase of benthic macrofauna demonstrates eutrophication of the Baltic Sea, Ophelia, Suppl. 1: 287-304.

Ducklow, H.W. 1983. Production and fate of bacteria in the oceans, Bioscience 33: 494-501.

Ducklow, H.W., D. A. Purdie, P. J. L. Williams & J. M. Davies 1986. Bacterioplankton: A sink for carbon in a coastal marine plankton community, Science. 232: 865-867.

Elmgren, R. 1978. Structure and dynamics of Baltic benthos communities, with particular reference to the relationship between macro- and meiofauna, Kieler Meeresforsch., Sonderh. 4: 1-22.

Elmgren, R. 1984. Trophic dynamics in the enclosed, brackish Baltic Sea, - Rapp. P.-v. Réun. Cons. int. Explor. Mer 183: 149-166.

Elmgren, R. 1987. Effects of increased nutrient loading on marine ecosystems: the Baltic, Background paper GESAMP WG "Nutrients and Eutrophication in the Marine Environment", Paris, 22 pp.

Flemer, D.A. & J. Olman. 1971. Daylight incubator estimates of primary production in the mouth of the Patuxent River, Maryland, Chesapeake. Sci.12: 105-110.

Finn, J. 1976. The cycling index, J. Theor. Biol., 56: 363-73.

Goodman, D. 1975. The theory of diversity-stability relationships in ecology, Quarterly Review of Biology, 50: 237-266.

Hällfors, G. & Å. Niemi 1981. Vegetation and primary production, pp. 220-238. In: Voipio, A. (ed.) *The Baltic Sea*, Elsevier, Amsterdam, 418 pp.

Heinle, D.R. 1966. Production of a calanoid copepod, *Acartia tonsa* in the Patuxent River estuary, Chesapeake. Sci. 7: 59-74.

Heinle, D.R. & D.A. Flemer. 1975. Carbon requirements of a population of the estuarine copepod *Eurytemora affinis*, Mar. Biol. 31: 235-247.

Homer, M. & W.R. Boynton 1978. Stomach analysis of fish collected in the Calvert Cliffs region, Chesapeake Bay-1977, University of Maryland. UMCEES 78-154-CBL, 1-363.

Hurd, L.E., M.V. Mellinger, L.L. Wolf & S.J. McNaughton 1971. Stability and diversity at three trophic levels in terrestrial ecosystems, Science 173: 1134-1136.

Jansson, B.-O., G. Aneer & S. Nellbring 1985. Spatial and temporal distribution of the demersal fish fauna in a Baltic archipelago as determined by SCUBA census, Mar. Ecol. Prog. Ser., 23: 31-43.

Jansson, A.-M. & N. Kautsky 1977. Quantitative survey of hard bottom communities in a Baltic archipelago, pp 359-366. In: Keegan, B. F., P. O. O'Ceidigh, and P. S. J. Boaden (eds) *Biology of benthic organisms*, Pergamon Press, Oxford. 630 pp.

Jernelöv, A. & R. Rosenberg, 1976. Stress tolerance of ecosystems, Environ. Cons. 3: 43-46.

Kay, J.J., L. Graham & R. E. Ulanowicz 1989. A detailed guide to network analysis, In: Wulff, F., J.G. Field & K. H. Mann (eds) *Network Analysis in Marine Ecology. Methods and Applications.* Lecture Notes in Coastal and Estuarine Studies, Springer-Verlag, New York.

Kautsky, N. 1981. On the trophic role of the blue mussel (*Mytilus edulis* L.) in a Baltic coastal ecosystem and the fate of the organic matter produced by the mussels, Kieler Meeresforsch., Sonderh. 5: 454-461.

Kremer, P. 1979. Predation by the ctenophore *Mnemiopsis leidyi* in Narranganset Bay, Rhode Island, Estuaries 2: 97-105.

Larsson, U., R. Elmgren & F. Wulff 1985. Eutrophication and the Baltic sea: causes and consequences, Ambio, 14: 9-14.

Larsson, U. & Å. Hagström 1979. Phytoplankton exudate release as an energy source for the growth of pelagic bacteria, Mar. Biol. 52: 199-206.

Leggett, W.C., W.R. Boynton, V. F. Gallucci, L. Johnson, R. Margalef, J. McGlade, D. Mikelecky, R. Rosen, R. O. Ulloa & J. Watson 1985. Hypothesis testing and sampling design in exploited ecosystems, pp 237-240. In: Ulanowicz, R.E. & T. Platt (eds) *Ecosystem theory for biological oceanography*. Can. Bull. Fish. Aquat. Sci. 213

Malone, T.C., W.M. Kemp, H.W. Ducklow, W.R. Boynton, J.H. Tuttle & R.B. Jonas 1986. Lateral variation in the production and fate of phytoplankton in a partially stratified estuary, Mar. Ecol. Prog. Ser. 32: 149-160.

Mann, K. H. 1982. *Ecology of Coastal Waters. A Systems Approach*, Studies in Ecology, Volume 8. Blackwell Scientific Publications, Oxford, 322 pp.

Nehring, D., G. Aertebjerg, P. Alenius, V. Astok, S. Fonselius, M. Hannus, V. Tervo, A. Troszinska, P. Tulkki & A.K. Yurkovskis, 1987. Nutrients, pp 35-81. In: Lassig, J. (ed). *First periodic assessment of the state of the marine environment of the Baltic Sea area, 1980-1985; Background document*. Baltic Sea Environm. Proc. 17B.

Nixon, S. W., C.A. Oviatt, J. Frithsen & B. Sullivan 1986. Nutrients and the productivity of estuarine and coastal marine ecosystems, J. Limnol. Soc. sth. Afr. 12 : 43-71.

Odum, E.P. 1969. The strategy of ecosystem development, Science 164: 262-270.

Odum, H.T. 1971. *Environment, Power and Society*, Wiley-Interscience, New York, 331 pp.

Ojaveer, E. 1981. Marine pelagic fishes , pp. 276-292, In: A. Voipio (ed) *The Baltic Sea*. Elsevier, Amsterdam, 418 pp.

Peters, R. H. 1986. The role of prediction in limnology, Limnol. Oceanogr. 31: 1143-1159.

Pimm, S. L. 1984. The complexity and stability of ecosystems, Nature, Vol. 307: 321-326.

Roman, M.R. 1984a. Utilization of detritus by the copepod, *Acartia tonsa*, Limnol. Oceanogr. 25: 949-959.

Roman, M.R. 1984b. Ingestion of detritus and microheterotrophs by pelagic marine zooplankton, Bulletin of Marine Science 35: 477-494.

Rosenberg, R.1976. The relation of treatment and ecological effects in brackish water regions, Pure and Appl. Chem. 45: 199-203.

Segerstråle, S.G. 1957. Baltic Sea, Mem. Geol. Soc. America 67: 751-800.

Sellner, K. G., R.V. Lacouture, D. C. Brownlee & C. R. Parrish 1985. Report to: Maryland Office of Environmental Programs (OEP), Chesapeake Bay Water Quality Monitoring Program. Phytoplankton and microzooplankton; data summary. The Academy of Natural Sciences, Benedict Estuarine Research Laboratory, Benedict, MD

Sherr, E. B., B. F. Sherr & L. J. Albright 1987. Bacteria: Link or sink? Science. 235: 88-89.

Smullen, J. T., J. Taft. & J. Macknis 1982. Nutrient and sediment loads to the tidal Chesapeake Bay system, pp. 147-262, In: E.G. Macalaster, D., D.A.Barker. and M. Kasper (eds.), Chesapeake Bay Program Technical Studies: a Synthesis. U.S. Environmental Protection Agency, Washington, DC.

Stoecker, D. K. & N. K. Sanders. 1985. Differential grazing by *Acartia tonsa* on a dinoflagellate and a tintinnid, J. Plankton Res. 7: 85-100.

Szymer, J. & R.E. Ulanowicz 1987. Total flows in ecosystems, Ecol. Mod. 35: 123-136.

Tuttle, J.H., T. Malone, R. Jonas, H. Ducklow & D. Cargo. 1985. Nutrient-dissolved oxygen dynamics: Roles of phytoplankton and microheterotrophs under summer conditions, Report to U.S. Environmental Protection Agency. University of Maryland [UMCEES] CBL 85-39:1-50.

Tuttle, J.H., T. Malone, R. Jonas, H. Ducklow & D. Cargo. 1986. Nutrient-dissolved oxygen dynamics: Roles of phytoplankton and microheterotrophs under summer conditions, Report to U.S. Environmental Protection Agency. University of Maryland [UMCEES] CBL 86-125:1-153.

Ulanowicz, R. E. 1983. Identifying the structure of cycling in ecosystems, Mathematical Biosciences 65: 219-237.

Ulanowicz, R. E. 1986. *Growth and Development: Ecosystems Phenology*. Springer-Verlag, New York, 203 pp.

Vollenwieder, R. A. (ed) 1982. *Eutrophication of Waters. Monitoring, Assessment and Control.* OECD, Paris, France, 154 pp.

Wiebe, W. J. & D. F. Smith 1977. Direct measurement of dissolved organic carbon release by phytoplankton and incorporation by micro-heterotrophs, Mar. Biol. 42: 213-223.

Winberg, G. G. 1956. *Rate of Metabolism and Food Requirements of Fish*, Fisheries Research Board, Canada Translation Series, No. 194.

Wulff, F., G. Aertebjerg, G. Nicolaus, Å. Niemi, P. Ciszevski, S. Schulz & W. Kaiser, 1986. The changing pelagic ecosystem of the Baltic Sea, Ophelia, Suppl. 4: 299-319.

To obtain a diskette containing the software for the techniques used in this book, (for IBM or compatible computers on a MS DOS 360 kB diskette, for a Macintosh computer on a 3.5" diskette) send a money order or bank draft for US $ 10.00 payable to SCOR to:

Excecutive Secretary, SCOR
Department of Oceanography
Dalhousie University
Halifax, N. S. CANADA
B3H 4JI,

requesting Network Analysis Software.