

CHAPTER 3

Role of network analysis in comparative ecosystem ecology of estuaries

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Introduction

Assessments of trophic structure through ecological network analysis (ENA) have been done in a wide variety of estuarine and coastal environments. For example, some have used it to compare trophic structures within ecosystems focusing on temporal conditions (Baird and Ulanowicz 1989; Baird et al. 1998) and among ecosystems focusing on spatial conditions (e.g. Baird and Ulanowicz 1993; Christensen 1995). These comparisons have used carbon or energy as the currency with which to trace the interactions of the food webs, although other key elements such as nitrogen and phosphorus have also been used in ENA (Baird et al. 1995; Ulanowicz and Baird 1999; Christian and Thomas 2003). One of the primary features of ENA is that the interactions are weighted. That is, they represent rates of flow of energy or matter and not simply their existence. Other kinds of comparisons have been attempted less frequently. Effects of currency used to track trophic dynamics has received little attention (Christian et al. 1996; Ulanowicz and Baird 1999), and comparisons of ENA with other modeling approaches are quite rare (Kremer 1989; Lin et al. 2001). There is a need to expand the applications of network analysis (NA) to address specific questions in food-web ecology, and to use it more frequently to explain and resolve specific management issues. The NA approach must be combined with other existing methods of identifying ecosystem performance to validate and

improve our inferences on trophic structure and dynamics.

Estuaries are excellent ecosystems to test the veracity of the inferences of ENA for three reasons. First, more NAs have been conducted on estuaries than on any other kind of ecosystem. Second, estuarine environments are often stressed by natural and anthropogenic forcing functions. This affords opportunities for evaluating controls on trophic structure. Third, sampling of estuaries has often been extensive, such that reasonable food webs can be constructed under different conditions of stress. Finally, other modeling approaches have been used in numerous estuarine ecosystems. Results of these alternate modeling approaches can be compared to those of ENA to test the coherence of inferences across perspectives of ecosystem structure and function. These conditions set the stage for an evaluation of the status of ENA as a tool for comparative ecosystem ecology.

Comparative ecosystem ecology makes valuable contributions to both basic ecology and its application to environmental management. Given the critical position of estuaries as conduits for materials to the oceans and often as sites of intense human activities in close proximity to important natural resources, ENA has been used frequently for the assessment of the effects of environmental conditions within estuaries related to management. Early in the use of ENA in ecology, Finn and Leschine (1980) examined the link between fertilization of saltmarsh grasses and shellfish production.

Baird and Ulanowicz (1989) expanded the detail accessible in food webs and the consequences of this increased detail in their seminal paper of seasonal changes within the Chesapeake Bay. In 1992, Ulanowicz and Tuttle determined through ENA and field data that the overharvesting of oysters may have had significant effects on a variety of aspects of the food web in Chesapeake Bay. Baird and Heymans (1996) studied the reduction of freshwater inflow into an estuary in South Africa and noted changes in food-web structure and trophic dynamics. More recently, Brando et al. (2004) and Baird et al. (2004) evaluated effects of eutrophication and its symptoms on Orbetello Lagoon, Italy, and Neuse River Estuary, USA, respectively. All of these studies involved comparisons of conditions linked to human impacts.

The first comprehensive review of the methodologies and use of ENA, an associated software NETWRK4, and application in marine ecology was published in 1989 (Wulff et al. 1989). Other approaches to ENA have been developed and applied to food webs. The software programs ECOPATH and ECOSIM have been used throughout the world to address various aspects of aquatic resources management (see www.ecopath.org/ for summary of activities; Christensen and Pauly 1993). In parallel with NETWRK4, ECOPATH was developed by Christensen and Pauly (1992, 1995) and Christensen et al. (2000), based on the original work of Polovina (1984). The dynamic simulation module, ECOSIM, was developed to facilitate the simulation of fishing effects on ecosystems (Walters et al. 1997). NETWRK4 and ECOPATH include, to various extents, similar analytical techniques, such as input–output analysis, Lindeman trophic analysis, a biogeochemical cycle analysis, and the calculation of information-theoretical indices to characterize organization and development. However, some analyses are unique to each. There are several differences in the input methodology between the NETWRK4 and ECOPATH software, which lead to differences in their outputs. Heymans and Baird (2000) assessed these differences in a case study of the northern Benguela upwelling system. Environs analysis, developed by Patten and colleagues (reviewed by

Fath and Patten 1999), provides some of the same analyses found in NETWRK4 but includes others based on the theoretical considerations of how systems interact with their environment. Lastly, social NA is beginning to be applied to ecological systems. A software package so used is UCINET (www.analytictech.com/ucinet.htm; Johnson et al. 2001; Borgatti et al. 2002). Although several methods and software packages exist for evaluating weighted food webs, none has been developed and validated to an extent to give a good understanding of the full implications of the variety of results.

We have organized this chapter to address the use of ENA associated with estuarine food webs in the context of comparative ecosystem ecology. Comparisons within and among estuaries are first considered. ENA provides numerous output variables, but we focus largely on five ecosystem-level variables that index ecosystem activity and organization. We address the ability of recognizing ecosystem-level change and patterns of change through the use of these indices. Then we compare several estuarine food webs to budgets of biogeochemical cycling to assess the correspondence of these two facets of ecosystems. Again we use these same indices and relate them to indices from the biogeochemical budgeting approach of the Land–Ocean Interaction in the Coastal Zone (LOICZ) program. How do the two modeling approaches compare in assessing ecosystems? Finally, comparisons of food-web diagrams are problematic if the food webs are at all complex. Recently, visualization tools from biochemistry and social networks have been used to portray food webs. We explore this new approach in the context of intrasystem comparisons.

Estuarine food-web comparisons

We highlight how food webs are perceived to change or remain stable across a variety of conditions. First, we compare systems temporally from intra and interseasonal to longer-term changes. Within a relatively unimpacted ecosystem, food webs may tend to be relatively stable with differences among times related to altered,

weather-related metabolism and differential growth, migrations and ontogenetic changes in populations (Baird and Ulanowicz 1989). Human impacts may alter these drivers of change and add new ones. Multiple food-web networks for an ecosystem tend to be constructed under common sets of rules, facilitating temporal comparisons. Then we compare food webs among ecosystems where major differences may exist in the very nature of the food webs. Interpreting such differences is more difficult than intrasystem comparisons and must be viewed with more caution. We have used studies of intersystem comparisons where effort was made by the authors to minimize differences in rulemaking and network structure. Should networks be constructed under different constraints, such as inconsistent rules for aggregation, the interpretation of differences in the NA results is difficult and should be viewed with more caution.

Ecological network analysis provides a myriad of output variables and indices. Each has its own sensitivity to differences in network structure. Generally, indices of population (i.e. at compartment-level) and cycling structure are more sensitive than ecosystem-level indices in terms of responsiveness to flow structure and magnitude of flows (Baird et al. 1998; Christian et al. 2004). Also, because currency and timescale may differ among networks, direct comparisons using different flow currencies are difficult. We focus on five ecosystem-level output variables of ENA, four of which are ratios. These are described in greater detail elsewhere (Kay et al. 1989; Christian and Ulanowicz 2001; Baird et al. 2004). The first adds all flows within a network, total system throughput (TST), and reflects the size, through activity, of the food web. Combinations of flows may be interpreted as occurring in cycles, and the percentage of TST involved in cycling is called the Finn Cycling Index (FCI; Finn 1976). The turnover rate of biomass of the entire ecosystem can be calculated as the sum of compartment production values divided by the sum of biomass (P/B). Networks can be collapsed, mathematically into a food chain, or Lindeman Spine, with the processing of energy or matter by each trophic level identified (Ulanowicz 1995). The trophic efficiency (TE)

of each level represents the ingestion of the next level as a percentage of the ingestion of the focal level. The geometric mean of individual level efficiencies is the system's TE. Ulanowicz has characterized the degree of organization and maturity of an ecosystem through a group of information-based indices (Ulanowicz 1986). Ascendency/developmental capacity (A/C) is a ratio of how organized, or mature, systems are, where ecosystems with higher values reflect relatively higher levels of organization. Thus, these five indices can be used to describe both extensive and intensive aspects of food webs. While our focus is on these indices, we incorporate others as appropriate to interpret comparisons.

Temporal comparisons

There are surprisingly few estuarine ecosystems for which food-web networks have been examined during different times. Most networks represent annual mean food webs. We provide a brief review of some for which we have direct experience and can readily assess the focal ecosystem-level indices. These are ecosystems for which NETWRK4 was applied rather than ECOPATH, because of some differences in model construction and analysis (e.g. general use of gross primary production in NETWRK4 and net primary production in ECOPATH). The shortest timescale examined has been for a winter's *Halodule wrightii* ecosystem in Florida, USA (Baird et al. 1998) where two sequential months were sampled and networks analyzed. Seasonal differences between food webs were a central part of the Baird and Ulanowicz (1989) analysis of the food web in Chesapeake Bay. Almunia et al. (1999) analyzed seasonal differences in Maspalomas Lagoon, Gran Canaria, following the cycle of domination by benthic versus pelagic primary producers. Florida Bay, which constitutes the most detailed quantified network to date, has been analyzed for seasonal differences (Ulanowicz et al. 1999). Finally, inter-decadal changes, associated with hydrological modifications, were assessed for the Kromme Estuary, South Africa (Baird and Heymans 1996). Table 3.1 shows the five indices for each temporal condition for these ecosystems.

Table 3.1 Temporal changes in ecosystem-level attributes for different estuarine ecosystems

Time period	TST (mg C m ⁻² per day)	FCI (%)	P/B (day ⁻¹)	TE (%)	A/C (%)
<i>St Marks, intraseasonal</i>					
January 1994	1,900	16	0.037	4.9	36
February 1994	2,300	20	0.041	3.3	32
<i>Neuse, intraseasonal</i>					
Early summer 1997	18,200	14	0.15	5.0	47
Late summer 1997	17,700	16	0.30	4.7	47
Early summer 1998	18,600	16	0.24	3.3	47
Late summer 1998	20,700	16	0.33	4.9	46
<i>Chesapeake, interseasonal</i>					
Spring	1,300,000	24	n.a.	9.6	45
Summer	1,700,000	23	n.a.	8.1	44
Fall	800,000	22	n.a.	10.9	48
Winter	600,000	23	n.a.	8.6	49
<i>Maspalomas Lagoon, interseasonal</i>					
Benthic-producer-dominated system	13,600	18	n.a.	11.4	40
Transitional	12,300	23	n.a.	12.8	38
Pelagic-producer-dominated system	51,500	42	n.a.	8.7	45
<i>Florida Bay, interseasonal</i>					
Wet	3,460	26	n.a.	n.a.	38
Dry	2,330	n.a.	n.a.	n.a.	38
<i>Kromme, interdecadal</i>					
1981–84	42,830	12	0.012	4.5	48
1992–94	45,784	10	0.011	2.8	46

Note: Flow currency of networks is carbon; n.a. means not available.

Ecological network analysis was applied to a winter's *H. wrightii* ecosystem, St Marks National Wildlife Refuge, Florida, USA (Baird et al. 1998; Christian and Luczkovich 1999; Luczkovich et al. 2003). Unlike most applications of ENA, the field sampling design was specific for network construction. From these data and from literature values, the authors constructed and analyzed one of the most complex, highly articulated, time- and site-specific food-web networks to date. Two sequential months within the winter of 1994 were sampled with the temperature increase of 5°C from January to February. Metabolic rates, calculated for the different temperatures and migrations of fish and waterfowl affected numerous attributes of the food webs (Baird et al. 1998). The changes in the focal indices are shown in Table 3.1. Activity estimated by the three indices was higher during the warmer period with >20% more TST, and FCI,

and a 12% increase in P/B. However, organization of the food web (A/C) decreased, and dissipation of energy increased lowering the TE. Although statistical analysis of these changes was not done, it would appear that the indices do reflect perceived effects of increased metabolism.

The food web of the Neuse River Estuary, NC, was assessed during summer conditions over two years (Baird et al. 2004; Christian et al. 2004). The Neuse River Estuary is a highly eutrophic estuary with high primary production and long residence times of water. Temperature was not considered to differ as dramatically from early to late summer, but two major differences distinguished early and late summer food webs. First was the immigration and growth of animals to the estuary during summer, which greatly increased the biomass of several nekton compartments. Second, hypoxia commonly occurs during summer, stressing both

nekton and benthos. Hypoxia was more dramatic in 1997 (Baird et al. 2004). Benthic biomass decreased during both summers, but the decrease was far more dramatic during the year of more severe hypoxia. Changes in the ecosystem-level indices were mostly either small or failed to show the same pattern for both years (Table 3.1). A/C changed little over summers or across years. TST, FCI, and TE had different trends from early to late summer for the two years. Only P/B showed relatively large increases from early to late summer. Thus, inferences regarding both activity and organization across the summer are not readily discerned. We have interpreted the results to indicate that the severe hypoxia of 1997 reduced the overall activity (TST) by reducing benthos and their ability to serve as a food resource for nekton. But these ecosystem-level indices do not demonstrate a stress response as effectively as others considered by Baird et al. (2004).

The food web in Chesapeake Bay was analyzed for four seasons (Baird and Ulanowicz 1989). Many of the changes linked to temperature noted for the within-season changes of the food web in St Marks hold here (Table 3.1). TST and P/B are highest in summer and lowest in winter, although the other measure of activity, FCI, does not follow this pattern. However, FCI is a percentage of TST. The actual amount of cycled flow ($TST \times FCI$) does follow the temperature-linked pattern. TE failed to show a pattern of increased dissipation with higher temperatures, although it was lowest during summer. Organization, as indexed by A/C, showed the greatest organization in winter and least in summer. Hence, in both of the aforementioned examples, times of higher temperature and therefore, higher rates of activity and dissipation of energy were linked to transient conditions of decreased organization. These findings are corroborated for spring—summer comparisons of these food webs are discussed later in the chapter.

Maspalomas Lagoon, Gran Canaria, shows, over the year, three successive stages of predominance of primary producers (Almunia et al. 1999). The system moves from a benthic-producer-dominated system via an intermediate stage to a pelagic-producer-dominated system. The analysis of system-level indices revealed that TST and A/C

increased during the pelagic phase (Table 3.1). The proportional increase in TST could be interpreted as eutrophication, but the system has no big sources of material input from outside the system. Almunia et al. (1999) explained the increase in A/C as a shift in resources from one subsystem (benthic) to another (pelagic). The FCI was lowest during the benthic-dominated stage and highest during the pelagic-dominated stage, and matter was cycled mainly over short fast loops. The pelagic-dominated stage was interpreted as being in an immature state, but this interpretation is counter to the highest A/C during the pelagic stage. The average TE dropped from the benthic-dominated stage to the pelagic-dominated stage, and the ratio of detritivory to herbivory increased accordingly. Highest values of detritivory coincided with lowest values of TE.

Florida Bay showed remarkably little change in whole-system indices between wet and dry seasons (Ulanowicz et al. 1999; www.cbl.umces.edu/~bonda/FBay701.html). Although system-level indices during the wet season were about 37% greater than the same indices during the dry season, it became apparent that this difference was almost exclusively caused by the change in system activity (measured as TST), which was used to scale the system-level indices to the size of the system. The fractions of A/C and the distribution of the different components of the overhead were almost identical during both seasons. Ulanowicz et al. (1999) concluded that the Florida Bay ecosystem structure is remarkably stable between the two seasons. (FCI was high during the wet season (>26%) but could not be calculated for the dry season since the computer capacity was exceeded by the amount of cycles (>10 billion).)

Lastly, we consider a larger timescale of a decade for the Kromme Estuary, South Africa. Freshwater discharge to this estuary was greatly reduced by 1983 due to water diversion and damming projects, greatly lessening nutrient additions, salinity gradients, and pulsing (i.e. flooding; Baird and Heymans 1996). Can ecosystem-level indices identify resultant changes to the food web? Although there was a slight increase in TST, the trend was for a decrease in all other measures (Table 3.1). However, all of these were decreases of

less than 20%, with the exception of TE. This general, albeit slight, decline has been attributed to the stress of the reduced flow regime (Baird and Heymans 1996). The TE decreased during the decade to less than half the original amount. Thus, much less of the primary production was inferred to pass to higher, commercially important, trophic levels. Further, TE of the Kromme under a reduced flow regime was among the smallest for ecosystems reviewed here.

In summary, most temporal comparisons considered were intra-annual, either within or among seasons. Seasons did not have comparable meaning among ecosystems. The Chesapeake Bay networks were based on solar seasons, but Maspalomas Lagoon and Florida Bay networks were not. All indices demonstrated intra-annual change, although the least was associated with A/C. This is to be expected as both A and C are logarithmically based indices. Summer or warmer seasons tend to have higher activity (TST and FCI or $FCI \times TST$), as expected. In some cases this was linked to lower organization, but this was not consistent across systems. We only include one interannual, actually interdecadal, comparison, but differences within a year for several systems were as great as those between decades for the Kromme Estuary. Interannual differences in these indices for other coastal ecosystems have been calculated but with different currencies and software (Brando et al. 2004; others). Elmgren (1989) has successfully used trophic relationships and production estimates to assess how eutrophication of the Baltic Sea over decades of enhanced nutrient loading has modified production at higher trophic levels. Even though the sample size remains small, it appears that intra-annual changes in food-web structure and trophic dynamics can equal or exceed those across years and across different management regimes. Obviously, more examples and more thorough exploration of different indices are needed to establish the sensitivities of ecosystem-level indices to uncertainties in ecosystem condition.

Interecosystem comparisons

Ecological network analysis has been used in inter-system comparisons to investigate the structure

and processes among systems of different geographic locations, ranging from studies on estuaries in relatively close proximity (Monaco and Ulanowicz, 1997; Scharler and Baird, in press) to those of estuarine/marine systems spanning three continents (Baird et al. 1991). Perhaps the most extensive comparison has been done by Christensen (1995) on ecosystems using ECOPATH to evaluate indices of maturity. These comparisons are limited, as discussed previously, because of differences in rules for constructing and analyzing networks. We review here some of the estuarine and coastal marine comparisons that have taken into account these issues, beginning with our focal indices.

The geographically close Kromme, Swartkops, and Sundays Estuaries, differ in the amount of freshwater they receive, and consequently in the amount of nutrients and their habitat structure (Scharler and Baird 2003). Input-output analysis highlighted the differences in the dependencies (or extended diets) of exploited fish and invertebrate bait species. Microalgae were found to play an important role in the Sundays Estuary (high freshwater and nutrient input) as a food source to exploited fish and invertebrate bait species, whereas detritus and detritus producers were of comparatively greater importance in the Kromme (low nutrients) and Swartkops (pristine freshwater inflow, high nutrients) Estuaries (Scharler and Baird, in press).

When comparing some indicators of system performance such as TST, FCI, A/C, and TE of the Kromme, Swartkops, and Sundays Estuaries, it revealed an interplay between the various degrees of physical and chemical forcings. The Kromme Estuary is severely freshwater starved and so lacks a frequent renewal of the nutrient pool. Freshets have largely disappeared as a physical disturbance. The Sundays system features increased freshwater input due to an interbasin transfer, and the Swartkops Estuary has a relatively pristine state of the amount of freshwater inflow but some degree of anthropogenic pollution (Scharler and Baird, in press). NA results showed that the Swartkops was more impacted due to a low TST and a high average residence time (ART, as total system biomass divided by

total outputs) of material and least efficient to pass on material to higher trophic levels. The Kromme was more self-reliant (higher FCI) than the Sundays (lowest FCI). The Sundays was also the most active featuring a comparatively high TST and low ART. However, a comparatively high ascendancy in the Sundays Estuary was not only a result of the high TST, which could have implicated the consequences of eutrophication (Ulanowicz 1995a), but it also featured the highest AMI (the information-based component of ascendancy) (Scharler and Baird, in press). The Kromme Estuary had the comparatively lowest A/C, and lowest AMI, and Baird and Heymans (1996) showed that since the severe freshwater inflow restrictions, a decline of the internal organization and maturity was apparent.

Intercomparisons of estuaries and coastal aquatic ecosystems have often focused on other issues in addition to the focal indices of this chapter. One important issue has been the secondary production of ecosystems, which is of special interest in terms of commercially exploited species. As Monaco and Ulanowicz (1997) stated, there can be differences in the efficiency of the transformation of energy or carbon from primary production to the commercial species of interest. By relating the output of planktivorous and carnivorous fish, and that of suspension feeders to primary production, it became apparent that in Narragansett Bay twice as many planktivorous fish and 4.6–7.4 as many carnivorous fish were produced per unit primary production than in Delaware or Chesapeake Bay, respectively. The latter, on the other hand, produced 1.3 and 3.5 as much suspension feeding biomass than Narragansett and Delaware Bay from one unit of phytoplankton production (Monaco and Ulanowicz 1997). This analysis was performed on the diet matrix to quantify a contribution from a compartment (in this case the primary producers) in the network to any other, over all direct and indirect feeding pathways, and is described as part of an input–output analysis in Szyrmer and Ulanowicz (1987).

This approach of tracing the fate of a unit of primary production through the system was also applied by Baird et al. (1991) who calculated the fish yield per unit of primary production in

estuarine and marine upwelling systems. They used a slightly different approach, in that only the residual flow matrices (i.e. the straight through flows) were used for this calculation, since the cycled flows were believed to inflate the inputs to the various end compartments. In this study, the most productive systems in terms of producing planktivorous fish from a unit of primary production were the upwelling systems (Benguela and Peruvian) and the Swartkops Estuary, compared to the Baltic, Ems, and Chesapeake (Baird et al. 1991). In terms of carnivorous fish, the Benguela upwelling system was the most efficient, followed by the Peruvian and Baltic (Baird et al. 1991).

Trophic efficiencies have also been used to make assumptions about the productivity of a system. In perhaps the first intersystem comparison using NA, Ulanowicz (1984) considered the efficiencies with which primary production reached the top predators in two marsh gut ecosystems in Crystal River, Florida. Monaco and Ulanowicz (1997) identified that fish and macroinvertebrate catches in the Chesapeake Bay were higher compared to the Narragansett and Delaware Bay, despite its lower system biomass, because the transfer efficiencies between trophic levels were higher. Similarly, transfer efficiencies calculated from material flow networks were used to estimate the primary production required to sustain global fisheries (Pauly and Christensen 1995). Based on a mean energy transfer efficiency between trophic levels of 48 ecosystems of 10%, the primary production required to sustain reported catches and bycatch was adjusted to 8% from a previous estimate of 2.2%.

In the context of the direct and indirect diet of exploited and other species, it can be of interest to investigate the role of benthic and pelagic compartments. The importance of benthic processes in the indirect diet of various age groups of harvestable fish was determined with input–output analysis by Monaco and Ulanowicz (1997). The indirect diet is the quantified total consumption by species *j* that has passed through species *i* along its way to *j* (Kay et al. 1989). They found that benthic processes in the Chesapeake Bay was highly important to particular populations of juvenile and adult piscivores. Indirect material

transfer effects revealed that the Chesapeake Bay relied more heavily on its benthic compartments compared to the Narragansett and Delaware Bays and that disturbances to benthic compartments may have a comparatively greater impact on the system (Monaco and Ulanowicz 1997). The pattern changes somewhat with season, as discussed in the section, "visualization of network dynamics" of this chapter.

The shallow Kromme, Swartkops, and Sundays Estuaries were found to rely more on their benthic biota in terms of compartmental throughput and the total contribution coefficients in terms of compartmental input (Scharler and Baird, in press). In terms of carbon requirements, the Kromme and Swartkops Estuaries depended two-thirds on the benthic components and one-third on the pelagic components, whereas the Sundays Estuary depended to just over half on its benthic components. The Sundays Estuary was always perceived to be "pelagic driven," probably due to the high phyto and zooplankton standing stocks, which are a result of the regular freshwater and nutrient input. By considering not only direct effects, but also all indirect effects between the compartments, the regular freshwater input suppressed somewhat the dependence on benthic compartments, but has not switched the system to a predominantly pelagic dependence (Scharler and Baird, in press).

Indicators of stress, as derived from ENA, have been discussed in several comparative studies. Baird et al. (1991) proposed a distinction between physical stress and chemical stress. The former has in general been influencing ecosystems, such as upwelling systems, for a time long enough so that the systems themselves could evolve under the influence of this type of physical forcing. Freshwater inflow into estuaries similarly determines the frequency of physical disturbance, due to frequent flooding in pristine systems and restrictions thereof in impounded systems. On the other hand, chemical influences are in general more recent through anthropogenic pollution, and the systems are in the process of changing from one response type (unpolluted) to another (polluted) that adjusts to the chemical type of forcing (Baird et al. 1991). With this perspective, Baird et al. (1991)

pointed out that the system P/B ratio is not necessarily a reflection of the maturity of the system, but due to NA results reinterpreted maturity in the context of physical forcing (e.g. the upwelling systems (Peruvian, Benguela) are considered to be mature under their relatively extreme physical forcings, although they have a higher system P/B ratio than the estuarine systems (Chesapeake, Ems, Baltic, Swartkops)).

Comparison of whole-system indices between the Chesapeake and Baltic ecosystems provided managers with a surprise (Wulff and Ulanowicz 1989). The conventional wisdom was that the Baltic, being more oligohaline than the Chesapeake, would be less resilient to stress. The organizational status of the Baltic, as reflected in the relative ascendancy (A/C) was greater (55.6%) than that of the Chesapeake (49.5%) by a significant amount. The relative redundancy (R/C) of the Chesapeake (28.1%) was correspondingly greater than that of the Baltic (22.0%), indicating that the Chesapeake might be more stressed than the Baltic. The FCI in the Chesapeake was higher (30%) than in the Baltic (23%). As greater cycling is indicative of more mature ecosystems (Odum 1969), this result seemed at first to be a counter-indication that the Chesapeake was more stressed, but Ulanowicz (1984) had earlier remarked that a high FCI could actually be a sign of stress, especially if most of the cycling occurs over short cycles near the base of the trophic ladder. This was also the case in this comparison, as a decomposition of cycled flow according to cycle length revealed that indeed most of the cycling in the Chesapeake occurred over very short cycles (one or two components in length), whereas recycle over loops that were three or four units long was significantly greater in the Baltic. The overall picture indicated that managerial wisdom had been mistaken in this comparison, as the saltier Chesapeake was definitely more disrupted than the Baltic.

Intermodel and technique comparisons

Another modeling protocol was developed under the auspices of the International Geosphere-Biosphere Program (IGBP), an outcome of the 1992

Rio Earth Summit and established in 1993. The aims of the IGBP are “to describe and understand the physical, chemical and biological processes that regulate the earth system, the environment provided for life, the changes occurring in the system, and the influence of human actions.” In this context, the Land Ocean Interactions in the Coastal Zone (LOICZ) core project of the IGBP was established. LOICZ focuses specifically on the functioning of coastal zone ecosystems and their role in the fluxes of materials among land, sea, and atmosphere; the capacity of the coastal ecosystems to transform and store particulate and dissolved matter; and the effects of changes in external forcing conditions on the structure and functioning of coastal ecosystems (Holligan and de Boois 1993; Pernetta and Milliman 1995).

The LOICZ biogeochemical budgeting procedure was subsequently developed that essentially consists of three parts: budgets for water and salt movement through coastal systems, calculation of rates of material delivery (or inputs) to and removal from the system, and calculations of rate of change of material mass within the system (particularly C, N, and P). Water and salt are considered to behave conservatively, as opposed to the nonconservative behavior of C, N, and P. Assuming a constant stoichiometric relationship (e.g. the Redfield ratio) among the nonconservative nutrient budgets, deviations of the fluxes from the expected C:N:P composition ratios can thus be assigned to other processes in a quantitative fashion. Using the flux of P (particularly dissolved

inorganic P), one can derive whether (1) an estuary is a sink or a source of C, N, and P, that is $\Delta Y = \text{flux}_{\text{out}} - \text{flux}_{\text{in}}$, where $Y = \text{C, N, or P}$; (2) the system’s metabolism is predominantly autotrophic or heterotrophic, that is, $(p - r) = \Delta \text{DIP}(\text{C:P})_{\text{part}}$, where $(p - r)$ is photosynthesis minus respiration; and (3) nitrogen fixation (nfix) or denitrification (denit) predominates in the system, where $(\text{nfix} - \text{denit}) = \Delta \text{DIN} - \Delta \text{DIP}(\text{N:P})_{\text{part}}$ (Gordon et al. 1996). A summary of attributes for this modeling approach is shown in Table 3.2.

This section explores the possibility of linkages between the two different methodologies of ENA and LOICZ biogeochemical budgeting protocol. The rationale for this hypothesis is:

The magnitude and frequency of N and P loadings and the transformation of these elements within the system, ultimately affect the system’s function. Since we postulate that system function is reflected in network analysis outputs, we infer that there should exist correspondence in the biogeochemical processing, as indexed by the LOICZ approach, and trophic dynamics, as indexed by network analysis outputs.

To do this, we used ENA and LOICZ variables and output results from six estuarine or brackish ecosystems based on input data with a high level of confidence (Table 3.3). We first performed Spearman’s and Kendall’s correlation analyses between the ENA and LOICZ output results of a number of system indices of the six ecosystems. From the correlation matrices we selected those variables which showed correlation values of 80%

Table 3.2 System properties and variables derived from NA and the LOICZ biogeochemical budgeting protocol used in factor analysis

LOICZ variables	Description of variable/system property
<i>Nutrient loading</i>	<i>From land to ocean, two macronutrients and their possible origins</i>
Dissolved inorganic nitrogen (DIN) (mol m^{-2} per year)	Products of landscape biogeochemical reactions
Dissolved inorganic phosphorus (DIP) (mol m^{-2} per year)	Materials responding to human production, that is, domestic (animal, human) and industrial waste, and sewage, fertilizer, atmospheric fallout from vehicular and industrial emissions
ΔDIN (mol m^{-2} per year)	$\text{Flux}_{\text{out}} - \text{Flux}_{\text{in}}$
ΔDIP (mol m^{-2} per year)	$\text{Flux}_{\text{out}} - \text{Flux}_{\text{in}}$
Net ecosystem metabolism (NEM) (mol m^{-2} per year)	Assumed that the nonconservative flux of DIP is an approximation of net metabolism: $(p - r) = -\Delta \text{DIP}(\text{C:P})$
NFIXDNIT (mol m^{-2} per year)	Assumed that the nonconservative flux of DIN approximates N fixation minus denitrification: $(\text{nfix} - \text{denit}) = \Delta \text{DIN} - \Delta \text{DIP}(\text{N:P})$

Table 3.3 Ecosystem-level attributes used for comparison of NA results of estuarine food webs with biogeochemical budgeting models

System	Morphology		ENA				
	Volume (m ³)	Area (m ²)	A/C (%)	TST (mgCm ⁻² per day)	FCI (%)	P/B (day ⁻¹)	TE (%)
Kromme	9.00E+06	3.00E+06	33.7	13,641	26	0.73	6.2
Swartkops	1.20E+07	4.00E+06	28	11,809	44	3.65	4
Sundays	1.40E+07	3.00E+06	43	16,385	20	10.95	2.6
Baltic Sea	1.74E+13	3.70E+11	55.6	2,577	23	29.2	16.2
Cheasapeake	3.63E+10	5.90E+09	49.5	11,224	23	51.1	9
Neuse	1.60E+09	4.60E+08	46.8	11,222	15.4	94.9	4.5
LOICZ models (mol m⁻² per year)							
	Δ DIP	Δ DIN	(nfix–denit)	(p–r) NEM	DIN loading	DIP loading	GPP ^a
Kromme	6.80E–03	1.59E–01	4.93E–01	–7.27E–01	3.01E–02	7.30E–04	2.15E+02
Swartkops	–6.25E–02	–1.01E+01	–9.13E+00	6.65E+00	1.40E+00	6.85E–02	1.10E+02
Sundays	4.70E–03	–2.26E–01	–3.02E–01	–5.03E–01	1.43E+00	1.18E–02	8.53E+03
Baltic Sea	–9.41E–03	–1.52E–01	–1.17E–01	5.12E–01	1.33E–01	1.25E–03	2.50E+03
Cheasapeake	–1.42E–02	–5.95E–01	2.78E–01	1.51E+00	4.82E–01	1.00E–02	6.27E+03
Neuse	–1.69E–04	–1.64E–03	4.02E+01	6.55E+00	1.77E–01	1.56E–02	5.04E+03

^a GPP is in C and was also calculated through stoichiometry for N and P. These values are not included here.

and higher, on which we subsequently performed factor analysis. The system properties and the values of the ecosystem properties on which the factor analysis was based are given in Table 3.3.

The output from factor analysis yielded eigen values of six principal components, of which the first four principal components account for 98.4% of the variance between the system properties. The factor loadings for each of the LOICZ and NA variables are given in Table 3.4, and taking +0.7 and –0.7 as the cutoff values, certain variables are correlated with one another and can be interpreted as varying together on these principal factors. The first three principal components explain 87.7% of the variance and none of the factor loadings of the fourth principal component exceeded the cut-off value, so this factor was not considered further. A number of inferences can be made:

1. The first principal component explains 46% of the variance and which includes three LOICZ and three ENA variables. Table 3.4 (under the first principal component) shows that of the LOICZ-derived variables Δ DIN and Δ DIP correlate negatively with DIP loading, which means that the magnitude of DIP loading will somehow affect the flux of DIN and DIP between the estuary and the coastal sea.

Table 3.4 Unrotated factor loadings of the selected system variables listed in Table 3.1

Variables/property	Principal component			
	1	2	3	4
<i>Network variables</i>				
A/C	0.79	0.31	0.13	0.51
FCI(%)	–0.94	0.04	–0.10	0.19
TST	–0.08	–0.81	–0.25	–0.49
P/B(day ⁻¹)	0.55	–0.02	0.81	0.03
Trophic Efficiency (%)	0.23	0.85	–0.07	0.46
GPP-C	0.70	–0.61	–0.05	0.35
GPP-N	0.69	–0.65	–0.04	0.30
GPP-P	0.70	–0.65	–0.03	0.29
<i>LOICZ variables</i>				
DIN loading	–0.47	–0.76	–0.20	0.37
DIP loading	–0.87	–0.34	0.32	0.17
Δ DIP	0.89	0.03	–0.26	–0.37
Δ DIP	0.94	0.17	–0.19	–0.20
(nfix–denit)	0.55	–0.10	0.75	–0.34
(p–r) NEM	–0.44	–0.19	0.88	0.02

Note: Four principal components are extracted (columns 1–4).

The FCI correlates negatively with the A/C and carbon GPP (gross primary productivity) of the ENA-derived properties, and one can thus expect lower FCI values in systems with high A/C.

This inverse relationship has in fact been reported in the literature (cf. Baird et al. 1991; Baird 1998). From the linkage between the ENA and the LOICZ modeling procedure, we can infer from these results that there appears to be a positive correlation among DIN and DIP flux, GPP, and ascendancy. Systems acting as nutrient sinks may thus well be positively associated with GPP and ascendancy, and such systems are thus more productive (higher GPP) and organized (higher A/C). The data given in Table 3.3 show to some degree that the Baltic Sea, the Chesapeake Bay and the Neuse River Estuary have high A/C associated with their performance as nutrient sinks.

2. Of the variance, 25% is explained by the second principal component, which had high factors scores for one LOICZ-and two ENA-derived variables (Table 3.4). The results would indicate some positive correlation between DIN loading and TST, but both are negatively associated with the TE index (Table 3.3).

3. The third principal component, which accounts for 17% of the variance (Table 3.4) shows positive correlations between two LOICZ variables ((nfix-denit), net ecosystem metabolism ($p - r$)), and one ENA system-level property, the P/B. We can construe from these relationships that the P/B is influenced by the magnitude and nature of one or both of the two LOICZ-derived properties.

The underlying associations are summarized in a scatter plot of the ecosystem positions relative to the first two principal components (Figure 3.1) and a cluster tree (Figure 3.2), which essentially reflects the results from factor analysis presented above. The three systems in the middle of Figure 3.1 occupy a relatively “neutral domain” in the context of their responses to the variability of the NA and LOICZ parameters given on the x- and y-axes, and appears to relate to the analyses of Smith et al. (2003) that a large proportion of the estuaries for which biogeochemical results are available cluster

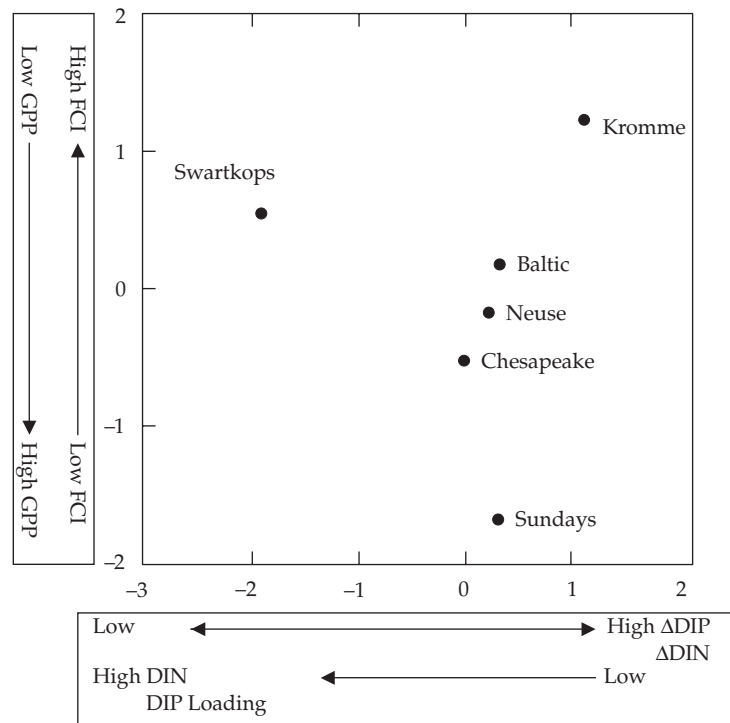


Figure 3.1 System position within the plane of the first two principal components.

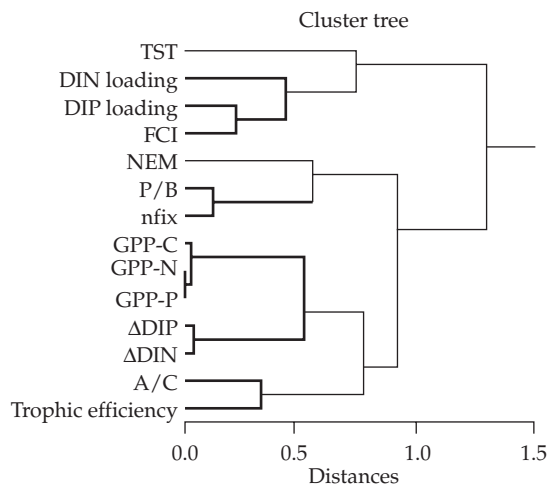


Figure 3.2 Cluster tree of ENA and LOICZ variables.

around neutral values of $(p-r)$ (or NEM) and $(nfix - denit)$. These three systems, namely the Baltic Sea, the Chesapeake Bay, and the Neuse River Estuaries are large in terms of aerial size and volume compared to the three smaller systems (namely the Swartkops, Kromme, and Sundays Estuaries), which are scattered at the extreme ranges of the variables. Table 3.3 shows that the larger systems are bigger in volume and size by 3–5 orders of magnitude, but that the DIN and DIP loadings on a per meter square basis of all six systems fall within in the same range. Other noticeable differences are the shorter residence times of material, the small volume and low rate of fresh water inflows compared with the three bigger systems. Although the scales of the axes in Figure 3.1 are nondimensional, the positions of the various systems reflect the relative order of the four variables plotted on the x- and y-axis, respectively, and corresponds largely with the empirical outputs from ENA and the LOICZ budgeting protocol. Finally, a cluster tree (Figure 3.2), which shows the similarity of the variables using an average clustering of the Pearson correlation r (as a distance measure $= 1 - r$), groups the NA and LOICZ variables in a hierarchical manner. Using a distance of <0.2 as a cutoff, the P/B ratio from NA is closely grouped with the $[nfix - denit]$ of LOICZ, which suggests that overall production and nitrogen balance is linked in these estuaries.

In addition, the FCI from NA and DIP loading from LOICZ vary together as well, which suggests that overall cycling is linked to phosphorous in some way. This result is similar in many ways to the factor analysis above, especially the variables that score highly on principal factors 1 and 3 (Table 3.4).

The fundamental differences between the net flux methodology of LOICZ modeling and the gross flows of material inherent in food-web networks must be kept in mind, but the correlation between the methodologies is encouraging in our search for better understanding of ecosystems function. We should thus emphasize the possible linkages and the complimentary results derived from these methodologies. ENA results have rarely been related to other approaches. Comparisons, such as this, are essential to broaden our understanding of how ecosystems function and are structured in a holistic way.

Visualization of network dynamics

The display of dynamic, complex food webs has been problematic in past, due to the multiple species and linkages that must be rendered. This display limitation has prevented the visualization of changes that occur at the level of the whole food web. Seasonal changes, changes over longer periods of time, impacts due to fishing or hunting, and pollution impacts can all affect food-web structure, but unless this can be quantified and visualized, it is difficult for most to appreciate. Most current approaches involve either simplifying the food web by aggregating species into trophic species and by displaying “wiring diagrams” of the underlying structure. We use network statistical modeling software to analyze the similarities in the food webs and display the results using three-dimensional network modeling and visualization software.

We used the visualization technique described in Johnson et al. (2001, 2003) and Luczkovich et al. (2003) to display a series of food webs of the Chesapeake Bay, originally described by Baird and Ulanowicz (1989). This technique involves arranging the nodes (species or carbon storage compartments) of the food-web network in a

three-dimensional space according to their similarity in feeding and predator relationships, as measured by a model called regular equivalence. In the regular equivalence model, two nodes in close position in the three-dimensional graph have linkages to predator and prey nodes that themselves occupy the same trophic role, but not necessarily to the exact same other nodes. Thus, here we visualize the change in trophic role of the compartments in Chesapeake Bay as they change from spring to summer.

In the example we display here, Baird and Ulanowicz (1989) modeled the carbon flow in a 36-compartment food web of the Chesapeake Bay. The model was adjusted seasonally to reflect the measured changes in carbon flow among the compartments. This model was originally constructed using the program NETWRK4. We obtained the input data from the NETWRK4 model from the original study and converted them to text data using a conversion utility from Scientific Committee on Oceanographic Research (SCOR) format (Ulanowicz, personal communication). The carbon flow data in a square matrix for each season was imported into UCINET (Borgatti et al. 2002) to compute the regular equivalence coefficients for each compartment (or node). Due to migrations and seasonal fluctuations in abundance, the model had 33 compartments in spring, 36 in summer, 32 in fall, and 28 in winter. They are listed in Table 3.5 along with their identification codes and seasonal presence and absences. The algorithm for computing regular equivalence (REGE), initially places all nodes into the same class and then iteratively groups those that have similar type of connections to predators and prey. Finally, a coefficient ranging from 0 to 1.00 is assigned to each node, which reflects their similarity in food-web role. These coefficients have been found to have a relationship with trophic level, as well as differentiate the benthos and plankton based food webs (Johnson et al. 2001; Luczkovich et al. 2003). After the REGE coefficients were computed, the matrices for each season were concatenated so that a 144×36 rectangular matrix of the coefficients was created. The combined four-season REGE coefficient matrix was analyzed using a stacked correspondence analysis

Table 3.5 The compartments in the four seasonal models of Chesapeake Bay and their identification numbers

	Compartment name	Spring	Summer	Fall	Winter	Trophic level
1	Phytoplankton	x	x	x	x	1.00
2	Bacteria in suspended POC	x	x	x	x	2.00
3	Bacteria in sediment POC	x	x	x	x	2.00
4	Benthic diatoms	x	x	x	x	1.00
5	Free bacteria	x	x	x	x	2.00
6	Heterotrophic microflagellates	x	x	x	x	3.00
7	Ciliates	x	x	x	x	2.75
8	Zooplankton	x	x	x	x	2.16
9	Ctenophores	x	x	x	x	2.08
10	Sea Nettle		x			3.44
11	Other suspension feeders	x	x	x	x	2.09
12	<i>Mya arenaria</i>	x	x	x	x	2.09
13	Oysters	x	x	x	x	2.08
14	Other polychaetes	x	x	x	x	3.00
15	<i>Nereis sp.</i>	x	x	x	x	3.00
16	<i>Macoma spp.</i>	x	x	x	x	3.00
17	Meiofauna	x	x	x	x	2.67
18	Crustacean deposit feeders	x	x	x	x	3.00
19	Blue crab	x	x	x	x	3.51
20	Fish larvae		x			3.16
21	Alewife and blue herring	x	x	x	x	3.16
22	Bay anchovy	x	x	x	x	2.84
23	Menhaden	x	x	x	x	2.77
24	Shad	x	x			3.16
25	Croaker		x	x	x	4.00
26	Hogchoker	x	x	x	x	3.91
27	Spot	x	x	x		4.00
28	White perch	x	x	x	x	3.98
29	Catfish	x	x	x	x	4.00
30	Bluefish	x	x	x		4.59
31	Weakfish	x	x	x		3.84
32	Summer flounder	x	x	x		3.99
33	Striped bass	x	x	x		3.87
34	Dissolved organic carbon	x	x	x	x	1.00
35	Suspended POC	x	x	x	x	1.00
36	Sediment POC	x	x	x	x	1.00

Source: From Baird and Ulanowicz (1989).

(Johnson et al. 2003), which makes a singular value decomposition of the rows and column data in a multivariate space. We used the row scores (the 36 compartments in each of the 4 seasons) to plot all 144 points in the same multivariate space. The network and correspondence analysis coordinate data were exported from UCINET to a coordinate file so that the food web could be viewed in Pajek (Batagelj and Mrvar 2002). (Note: we have also used real time interactive molecular modeling software Mage for this purpose; see Richardson and Richardson (1992)). Pajek was used to create the printed versions of this visualization.

The three dimensional display of the spring (gray nodes with labels beginning "SP" and end-

ing with the node number) and summer (black nodes with labels beginning with "SU" and ending with the node number) food web of the Chesapeake network shows groupings of nodes that have similar predator and prey relationships, so that they form two side groups at the base of the web, and a linear chain of nodes stretching upwards (Figure 3.3). The arrows show the shift in coordinate position from spring to summer (we omit the arrows showing carbon flow here for clarity). The vertical axis in this view (note: normally axis 1 is plotted along the horizontal, but we rotated it here to have high trophic levels at the top) is correspondence analysis axis 1, which is significantly correlated ($r=0.72$) with the trophic

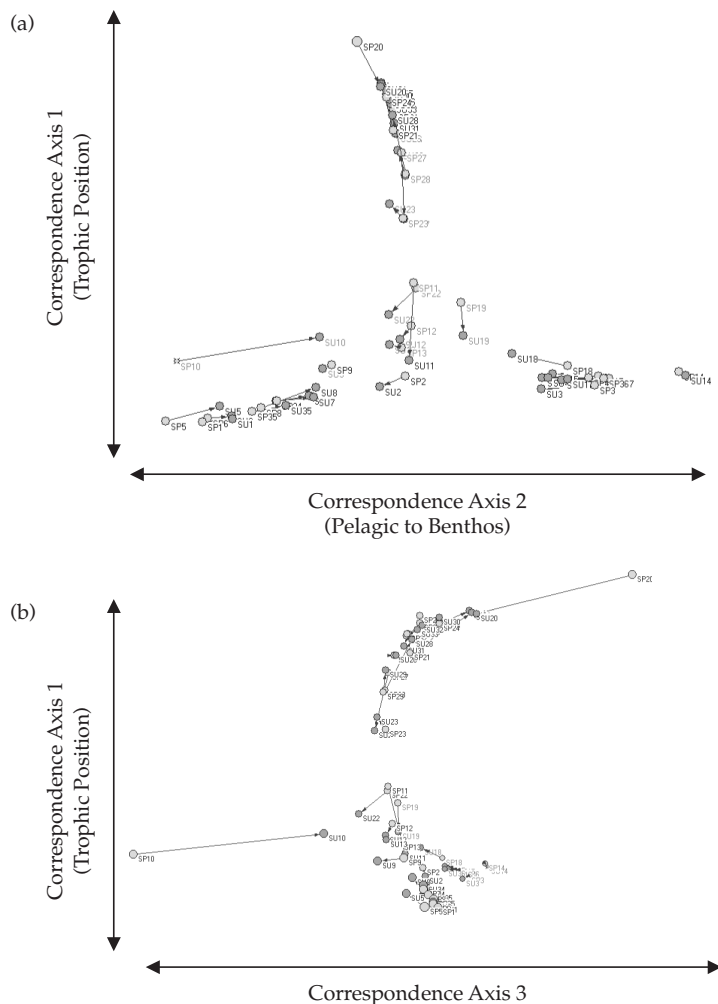


Figure 3.3 (a) The food-web network of the Chesapeake Bay in spring (gray "SP" node labels) and summer (black, "SU" node labels), displayed using Pajek. The arrows show the shift in coordinate position from spring to summer. The stacked correspondence analysis row scores were used to plot the positions in three-dimensional space. (b) Another view showing the shift along the first and third axes, which represent trophic position as before and degree of connectedness to the network. The two compartments that were absent from the summer network: sea nettles (10) and other suspension feeders (11) are shown as moving into the center in the summer and becoming connected to the network.

levels (Table 3.5) that were calculated based on annualized carbon flows for each compartment by Baird and Ulanowicz (1989). In Figure 3.3 (a), there is a group at the right side of the base of the web, which is composed of compartments that are associated with detritus or the benthos, including bacteria in the sediment particular organic material (POC; 3), benthic diatoms (4), *Nereis* (15), other polychaetes (14), crustacean deposit feeders (18), and sediment POC (36) (note: the number in the parenthesis is the serial number of each compartment in Table 5). On the left side of the base of this web, there are plankton-associated groups, including phytoplankton (1), free bacteria (5), heterotrophic microflagellates (6), zooplankton (8), and dissolved organic carbon (34), and suspended POC (35). In the center at the base of the web, we find the bacteria in the suspended POC (2), which is midway between the benthic group and the plankton group, due to the fact that these bacteria are important as food of consumers in both groups. Stretching in a near-linear chain above the base are various consumers that are higher trophic levels. Compartments with low effective trophic levels (TL) include oysters (13; TL = 2.08), soft-shelled clams *Mya arenaria* (12; TL = 2.09), bay anchovies (22; TL = 2.77), other suspension feeders (11; TL = 2.09), and menhaden (23; TL = 2.77). Higher on the correspondence analysis vertical axis are compartments catfish (29), white perch (28), spot (27), hogchoker (26), alewife and blueback herrings (21), summer flounder (32), striped bass (33), bluefish (30), shad (24), and larval fish (20).

One way to interpret these visualizations is that those compartments that move the most in the coordinate space show the greatest seasonal change in trophic roles. Species that move downward along axis 1 are consuming more of the primary production or consuming more prey at low trophic levels. This is also shown for the whole system as higher TST and P/B ratios in the summer (Table 3.1), but our visualization shows the contribution of individual compartments to the system-wide changes. Some good examples are other suspension feeders (11), which move downward on the trophic position axis, because they feed more on the phytoplankton

in the summer. This can also be seen in the case of bay anchovy (22), which takes in more zooplankton (8), and spot (27) which increase consumption of "other polychaetes" (14) in the summer (Baird and Ulanowicz 1989). In all of these cases, an increase in consumption of species with lower trophic positions is driving this change in the visualization.

Another interpretation of the coordinate movements is that the species which derive energy from the pelagic zone in the summer are moving toward the center on axis 2. For example, free bacteria (5) and zooplankton (8) move toward the center of the diagram from spring to summer as they increase their consumption of dissolved organic carbon (34) and ciliates (7), respectively, while crustacean deposit feeders (18) move toward the center since they consume less sediment POC (36) in the summer. Thus, the degree to which the whole ecosystem shifts from benthic to pelagic primary production can be easily visualized. This also can be visualized dynamically across multiple seasons. We do not show the other seasons here, but interactively, one can turn off and on a similar display for each season and show that the nodes in the fall and winter move back towards the springtime positions. This can also be done over multiple years, if the data were available, or in varying salinities, temperatures, and under different management schemes.

Conclusions

Estuarine and coastal ecosystems have been locations where numerous studies have incorporated ENA to assess food-web structure and trophic dynamics. ENA also affords a valuable approach to comparative ecosystem ecology. Numerous ecosystem-level indices are calculated and complement indices at lower level of hierarchy. Comparisons of five ecosystem-level indices of food webs over various temporal and spatial scales appeared to correspond with our understanding of levels of development and stress within several estuarine systems. Intra-annual variations in these indices within an ecosystem were equal to or exceeded that for the limited number of cases of interannual comparisons. Interecosystem comparisons are more difficult because of differences in

rules for network construction used for different ecosystems, but patterns in calculated indices were consistent with expectations. Finally, two relatively new approaches to understanding estuarine ecosystems, namely models of biogeochemical budgets and visualization tools were compared to the focal indices. The biogeochemical modeling complemented the ecosystem-level network indices, providing an extended assessment of the limited number of ecosystems evaluated. Visualization of food webs is problematic when those food webs are complex. This problem is exacerbated when one wants to compare food-web structures. We demonstrated a relatively new approach to visualizing food webs that enhances one's ability to identify distinctions between

multiple conditions. Thus, we evaluated how ENA can be used in comparative ecosystem ecology and offer two new approaches to the discipline.

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