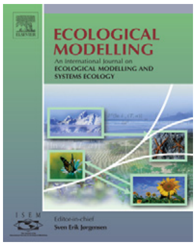
ECOLOGICAL MODELLING 215 (2008) 207–216

available at www.sciencedirect.com

journal homepage: www.elsevier.com/locate/ecolmodel



Comparative study of virgin and reclaimed islands of Sundarban mangrove ecosystem through network analysis

*Santanu Ray**

Ecological Modelling Laboratory, Department of Zoology, Visva-Bharati University, Santiniketan 731235, India

ARTICLE INFO

Article history:
Published on line 9 April 2008

Keywords:
Mangrove ecosystem
Virgin
Reclaimed
Network analysis
Island

ABSTRACT

Sundarban mangrove estuarine ecosystem is one of the best-known detritus-based ecosystems of the world. Mangroves are very specialized ecosystems found at the interface between land and sea. Litterfall of mangroves supplies the detritus, nutrients and regulates the productivity of adjacent Hooghly–Brahmaputra estuarine complex and act as an important nursery ground for many commercially important shell and fin fishes. Presently the mangrove ecosystem of Sundarban is under serious threat for different anthropogenic activities. Many islands of this ecosystem are either totally reclaimed, or partially reclaimed, but about 30% of the islands are still virgin. Two islands are selected, one is from virgin forest and another is from reclaimed part for comparative study of benthic food webs of these two islands by using network analysis for possible human impacts. Selected island with virgin forest is almost free from human interference however the island with reclaimed forest fully disturbed due to almost all sorts of anthropogenic stresses. The results demonstrate a dramatic difference between these two islands. Virgin ecosystem is dominantly controlled by detritus, supplied from the litterfall of mangroves. Unlike the most benthic system the bottom community of reclaimed island receives a large contribution from the phytoplankton populations. Detritivory and herbivory ratio is markedly varied in these two systems, about 1:12 in virgin ecosystem and almost 1:1 in reclaimed system. The number of pathways of recycle can be identified much higher in undisturbed system in comparison with that of the reclaimed. Finn cycling is also very low in disturbed part. Litterfall comprises only 16% in reclaimed island where as in virgin island it is about 70%. Pathway redundancy is rather high in disturbed system, indicating the surviving system is probably highly resilient to further perturbation, as one might expect for highly impacted system. However, in virgin forest the ascendancy value is much higher than the redundancy, showing the system is healthy and almost free from any anthropogenic stress.

1. Introduction

Sundarban mangrove estuarine ecosystem is one of the largest detritus-based ecosystems of the world (Pillay, 1958). The Gangetic delta of the Hooghly–Brahmaputra estuarine complex, by dint of its exciting mangrove ecosystem, has achieved a notable place on the global map. This complex is approximately 170 km in length and at some places exceeds 60 km in width, making it the greatest halophytic formation in the world. It extends over two countries: India (West Bengal) and Bangladesh. The entire region is divided by a dense network of rivers, canals and creeks. The mangrove forest, comprising

---

* Tel.: +91 3463 261 268.
E-mail address: sray@visva-bharati.ac.in.

0304-3800/$ – see front matter © 2008 Elsevier B.V. All rights reserved.
doi:10.1016/j.ecolmodel.2008.02.021

4200 km^2 (Banerjee, 1964), is called “Sundarban”—a name thought to be derived either from beautiful forest (Bengal: “Sundara” = beautiful) or from forest of “Sundari” (local name of *Heritiera fomes*). In addition to sheltering some of the worlds, most graceful game, the ecosystem also supports a luxuriant flora and fauna: plankton, nekton, benthos, salt marshes, in sand and mud flats. The mangrove system covers several islands, most of which (about 70%) are partly reclaimed but some of which (about 30%) remain virgin. Two islands are selected, one is from virgin forest and another is from reclaimed part for comparative study of benthic food webs of these two islands by using network analysis. For the present study selected islands with virgin forest and reclaimed forest are Prentice island and Sagar island, respectively. Prentice island is almost free from both direct and indirect human interferences, surrounded by Thakuran and Saptamukhi rivers. The island is fully covered by different mangrove vegetations but the forest dominated by *Avecinia alba* and *A. officinalis*. The island is criss crossed by many tidal creeks and the vegetations are comparatively denser on either side of the creeks. The soil of this island is typically muddy, alluvial in nature and full of detritus coming from huge litterfall of the mangroves. Sagar island, the largest in the deltaic system fully disturbed due to almost all sorts of direct and indirect anthropogenic stresses. Most part of the island is occupied by human habitation. This island is also cris-crossed by many tidal creeks of various sizes, and all connected with the principal estuarine water. On either side of the creeks instead of mangrove vegetation, cultivated lands are created by inhabitants of this island. Only scanty growth of mangroves particularly grasses and stunted *Phoenix* sp. is noticed at the fringe of the creeks where these meet with the principal estuarine water. Both muddy and sandy types of soil are noticed in this island and the litterfall is much less than its virgin counterpart.

To facilitate cross system comparisons, both the islands are divided into the same 14 compartments comprising similar functional components in the planktonic, benthic and nektonic compartments. The resulting networks of virgin and reclaimed islands are depicted in Figs. 1 and 2, respectively.

Here, the network analysis is used to give comparative insight of both virgin and reclaimed mangrove ecosystems. This analysis has been used to quantify the structure of system networks, the degree of cycling, and the magnitudes of interdependency among components (Asmus and McKellar, 1989; Ducklow et al., 1989; Field et al., 1989; Warwick and Radford, 1989; Wulff and Ulanowicz, 1989). It is employed here to calculate the number of trophic levels, the underlying trophic dynamics, the degree of trophic specialization, the relative dependence of each compartment on a range of energy sources, the effective trophic position of each component, the interdependency among compartments, the overall system ascendancy and the redundancy.

The data used in this model were collected from different sources, including direct field observation by the author, from various Ph.D. theses, project reports (Asmus and McKellar, 1989; Bhunia, 1979; Choudhury, 1984, 1987; Nandi, 1986; Ray, 1987; Ray et al., 2000). In most cases the organisms were sampled fortnightly at different stations. Gross primary productivity (for phytoplankton) was estimated using “light and dark bottle method” of Strickland (1960) and Strickland and Parsons (1968). Biomasses are initially measured as dry weight: A known number of animals/plants were dried until their weight becomes constant. The energy content of the material was determined by “bomb calorimetry”. Feeding rates were measured using the radiometric technique of Moore et al. (1974) and also by gravimetric methods (Lawton, 1970). Respirational and metabolic losses were assessed by keeping the animal enclosed in a limited volume of water cut off from the atmosphere (Wohlschlag, 1957). In some cases it was difficult to determine the rate of respiration in the field, but values for ingestion, consumption, egestion and excretion were available, so that respiration could be determined by difference. All values for the flows of energy were converted into kcal m^{-2} year^{-1} (Southwood, 1978) and the standing stocks were reported as kcal m^{-2}.

2. Quantitative methods

The computer package NETWRK (Kay et al., 1989) was used to perform standardized matrix manipulations that constitute the backbone of what has come to be known as network analysis. There are four major tasks performed by NETWRK: (1) the evaluation of all direct and indirect bilateral relationships in a network of trophic exchanges, (2) the elucidation of the trophic structure immanent in the network, (3) the identification and quantification of all pathways for recycling medium extant in the network, and (4) the quantification of the overall status of the network’s structure.

The fundamental data used in network analysis are the exchanges between the system components. I begin by denoting the magnitude of the transfer of medium from i to j as T_{ij}, where both i and j run from 1 to n, the number of components in the system. (To denote exogenous transfers to and from the system, one may identify 0 as the source of external inputs and $n+1$ as the destination of external outputs.) The activity level of the entire network is characterized by the sum of all T_{ij}, and is called the total system throughput. The crux of the calculations, however, revolves around the accompanying matrix of dietary coefficients, $\mathbf{G}$, where the matrix components are calculated from the T_{ij} as $G_{ij} = T_{ij}/\sum_k T_{kj}$. In words, G_{ij} is the fraction of j’s diet that is comprised by i. The algebraic powers of the $\mathbf{G}$ matrix are extremely informative. The reader is invited to test, for example, that the $i-j$th element of $\mathbf{G}^2$, quantifies exactly what fraction of the input to j travels from i across all pathways of length 2. Similarly, the $i-j$th element of $\mathbf{G}^m$ describes the fraction of all input to j that travels from i to j along all trophic pathways of length m.

Because $\mathbf{G}$ has been normalized by the total input to each column j, the elements $\mathbf{G}_{ij}$ are all less than or equal to unity. The elements of successively higher algebraic powers of $\mathbf{G}$ tend to diminish in magnitude. In fact, one might question whether the infinite series of such powers ($\mathbf{S} = \mathbf{G}^0 + \mathbf{G}^1 + \mathbf{G}^2 + \mathbf{G}^3 + \cdots$) converges to any finite limit? It may indeed be demonstrated that the series does converge to the finite limit, $\mathbf{S} = [\mathbf{I} - \mathbf{G}]^{-1}$, where $\mathbf{I}\,(= \mathbf{G}^0)$ is the identity matrix with ones along the diagonal and zeroes elsewhere. The limit matrix, $\mathbf{S}$, is called the “structure matrix” (also called “integral

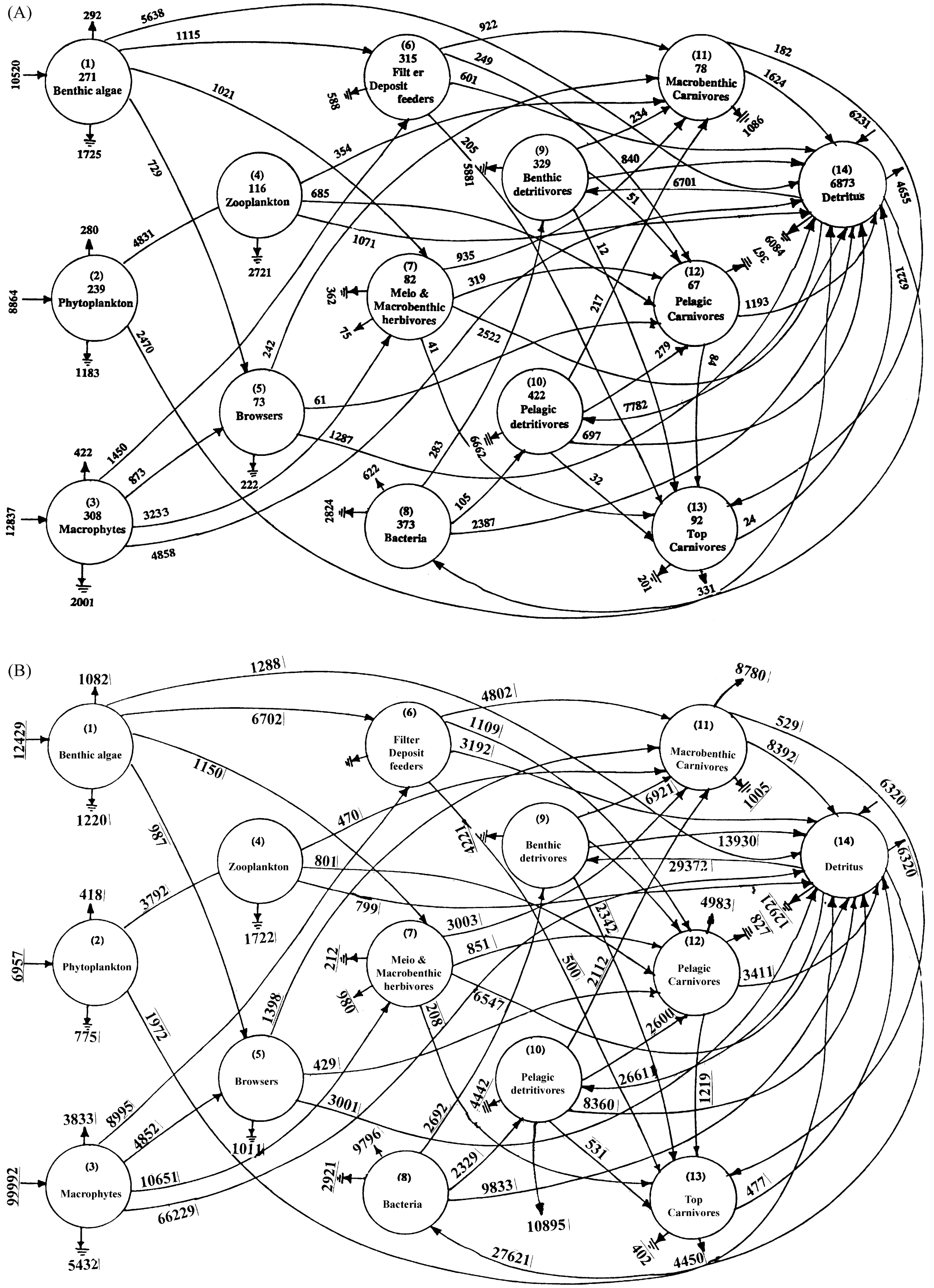


Fig. 1 – (A) Reclaimed island and (B) virgin island. The diagram of energy flow among 14 compartments of the network of the benthic food web of Sundarban mangrove ecosystem. All flows are in (kcal m^{-2} year^{-1}) and standing stock densities in (kcal m^{-2}). The ground symbol represents respiratory losses. The arrows connecting one compartment to other represent flows and the arrows from outside to compartment and also from compartment to outside represent outflow and inflow, respectively.

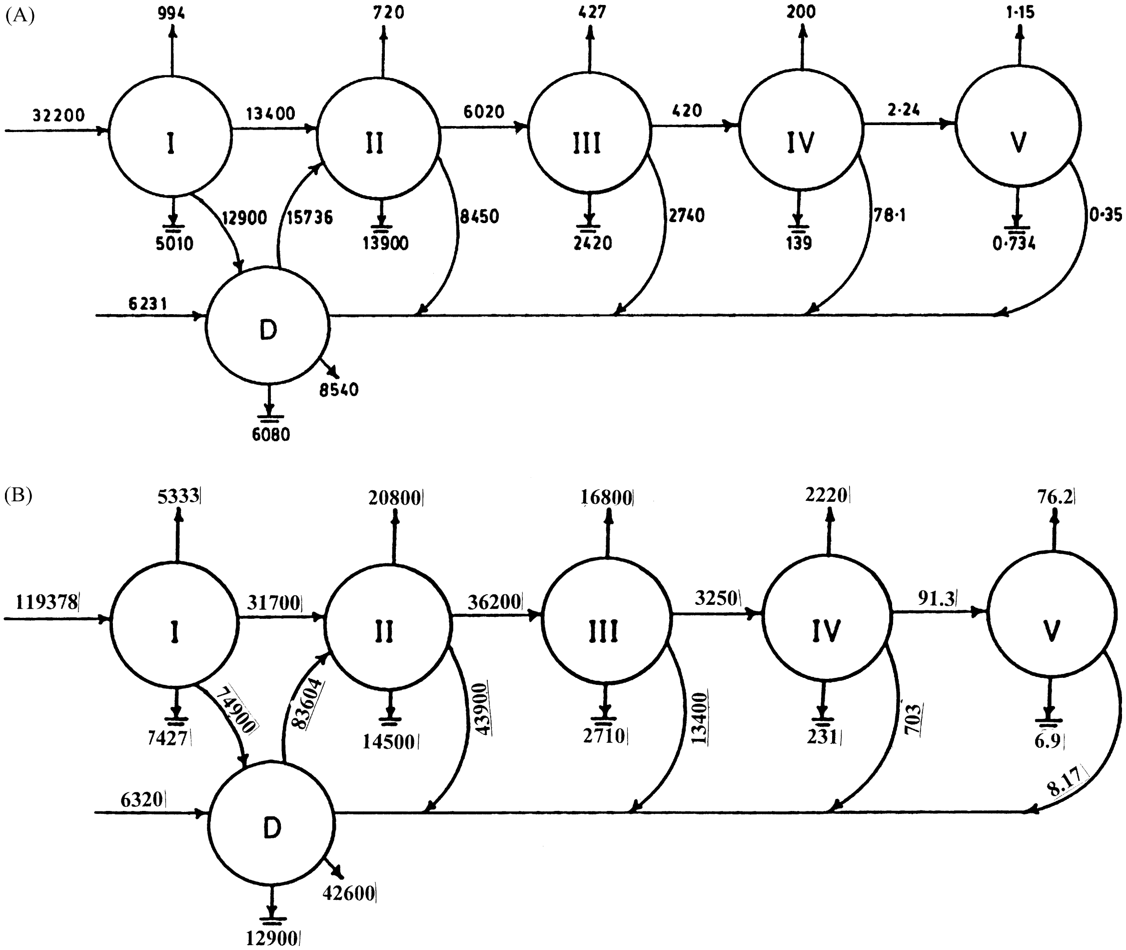


Fig. 2 – Reclaimed island: (A) and Virgin island: (B) – the trophic aggregation of Sundarban mangrove benthic network with the autotrophs and detritus separated and mapped into Lindeman type trophic level. The trophic levels are designated as roman numerals (I–V and D represents the detrital pool).

flow matrix", or "throughflow matrix" both denoted also by **N** in literature (Fath and Patten, 1999; Fath et al., 2001), and the $i-j$th element represents the fraction of total input to j that flows both directly and indirectly from i along all pathways of all lengths.

The powers of **G** can be used to calculate how much of what a species ingests arrives over pathways of various integer lengths (Hannon, 1973; Patten et al., 1976; Ulanowicz and Kemp, 1979). This information allows one to apportion the activity of that taxon to the successive links of a chain of virtual integer trophic levels, or *equivalent trophic chain*, or *trophic pyramid*. The matrix created from the powers of **G** that maps the food web into the virtual chain is called the *Lindeman transformation matrix*. The sum of each column of this latter matrix yields a decimal figure >1 that characterizes the *effective trophic level* of the corresponding taxon. Finally, Szyrmer and Ulanowicz (1987) showed how best to normalize the structure matrix, **S**, so that the ith element of the jth column reveals how much the jth taxon depends both directly and indirectly upon taxon i. The normalized matrix is referred to as the *total dependency matrix* and its elements are sometimes referred to as *dependency coefficients*. They also derived a corresponding normalization that allows one to trace the overall contributions from any one taxon to any other in terms of a *total contribution matrix*.

The matrix of transfers, **T**, by virtue of its pattern of zero and nonzero elements, describes the network connection topology. It is possible to perform a depth-first search on **T** (otherwise known as a backtracking algorithm) to identify all the simple cycles extant in the network (Ulanowicz, 1983). (Simple cycles contain no repeated taxa.) Often the pattern of recycled flows reveals clues to how the system is functioning to process medium (Baird and Ulanowicz, 1989). In any event, the fraction of the total activity, **T**, comprised by the recycled flow is called the Finn Cycling Index, and has been used to gauge the degree of maturity of some systems (Finn, 1976).

Finally, Ulanowicz (1986) demonstrates how one may characterize both the activity level and the degree of organization of a network by an informational index called the system *ascendency*. Organization is evidence of constraint acting in a structure. To quantify the average degree of constraint at work in a system, one begins in information theory by quantifying the opposite notion, the degree of indeterminacy. One estimates that the probability that any quantum of medium leaves taxon i, as estimated by the frequency $\sum_m T_{im}/T$. According to Boltzmann (1872), the indeterminacy associated with this marginal probability is $-k\log(\sum_j T_{ij}/T)$, where k is a scalar constant. In order to gauge the constraint that is necessary to guide this quantum into taxon j in particular, one estimates the conditional probability that, having left i, the quantum arrives at j as the quotient $T_{ij}/\sum_k T_{kj}$. The corresponding indeterminacy, $-k\log(T_{ij}/\sum_k T_{kj})$, should in most cases be less than the unconditional indeterminacy quoted above. The difference between the apriori and aposteriori indeterminacy's should, therefore, measure the amount of constraint guiding the flow from i to j. This difference takes the form, $k\log([T_{ij}T]/[\sum_m T_{im}\sum_k T_{kj}])$.

In order to estimate the average amount of constraint operative in the network, it is necessary simply to weight each such $i-j$ term by the joint probability of the $i-j$th flow occurring (as estimated by the frequency T_{ij}/T) and sum over all possible combinations of i and j. The result is what is called the average mutual information of the flow network, AMI, and takes the explicit form, $\mathrm{AMI}=k\sum_{i,j}(T_{ij}/T)\log([T_{ij}T]/[\sum_m T_{im}\sum_k T_{kj}])$. Like other informational indices, AMI does not have physical dimensions. In order to impart physical extent to AMI, I elect to set the scalar constant, k, equal to the total system throughput, T and call the result the system ascendency, A. It follows that $A=\sum_{i,j}T_{ij}\log([T_{ij}T]/[\sum_m T_{im}\sum_k T_{kj}])$.

The problem with the full ascendency often is that it is heavily dominated by the scale of system activity, T. In order to focus on the organizational aspect of A, I note that an upper bound on A exists in the diversity of system processes as scaled by T. This limit is called the system's *development capacity*, C, where $C=\sum_{i,j}T_{ij}\log(T_{ij}/T)$. Because the difference $\Phi=C-A$ is always non-negative, one may speak of Φ as the system *overhead*. It is usually dominated by the *redundancy* of parallel pathways in the network. It follows that the organizational status of the network is related to the fraction of the capacity that appears as constrained flow, or what is called the *relative ascendency*, A/C. In similar fashion, the relative overhead becomes F/C, which is dominated by the *relative redundancy*.

3. Results and discussion

Experiments with various levels of aggregation culminated in the energy flow diagram are depicted both in virgin and reclaimed islands (Fig. 1A and B, respectively). Only those individual species that are both taxonomically and functionally similar have been aggregated. There are total of 14 compartments:

1. Benthic algae—Various algal species (viz., *Ulva* sp., *Enteromorpha* sp., *Vaucheria* sp., *Oscillatoria* sp., *Lyngbya* sp., *Catenella* sp., *Chaetomorpha* sp., and *Xenococcus* sp.) are found on the mud surface as a green mat, exposed during low tide, but submerged during extreme high tide.
2. Phytoplankton—Minute, photosynthetically active plants floating in the water columns, more than 30 species are recorded.
3. Macrophytes—Mainly grasses in salt marshes, e.g., *Spartina* sp., *Saueda* sp., and *Salicornia* sp., and also a few stunted *Phoenix* sp. are noticed in reclaimed island whereas almost all mangrove plants particularly *A. alba* and *A. officinalis* are dominant in virgin island.
4. Zooplankton—More than 18 species of small animal plankton are recorded.
5. Browsers—Mainly mollusks (*Littorina* spp.), benthic amphipods, etc. are noticed.
6. Deposit/filter feeders—In particular, Calms, mollusks, siphunculid and echurids, crabs (*Uca* spp.), etc. are recorded.
7. Meio/macrobenthic herbivores—Mainly annelids (polychaetes), soil nematodes and insect larvae (*Chironomid* spp.) are found.
8. Bacteria—Numerous bacterial species are also recorded in the litter and detritus (bacterioplankton, where applicable, are lumped with the phytoplankton).
9. Benthic detritivores—Including unicellular protozoa, insect larvae, nematodes, mollusks, etc. are recorded.
10. Pelagic detritivores—Mainly the mullet group of fishes, are recorded, e.g. *Mugil* spp.
11. Macrobenthic carnivores—Nematodes, some insect larvae (*Culicoides* spp.), sea anemone, holothuroids, etc. are found.
12. Pelagic carnivores—Small catfishes and other small invertebrates such as *Chaetognaths* sp., etc. are recorded.
13. Top carnivores—Large fish such *Lates* sp., etc. is noticed.
14. Detritus—The nonliving compartment is formed mostly within the food web but also with some input from upper zone of *Phoenix* sp. patches in reclaimed island and huge input from different mangrove plants in virgin island.

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 Fig. 1A and B). The large difference in the magnitude of the inputs to both systems is obvious. Exports from some additional compartments are also noticed in the virgin system (see Fig. 1A and B).

Two major important aspects of input output analyses are contribution and dependency coefficients. Each contribution coefficient represents the fraction of a particular component, throughput that is contributed to the diet of another specific component. Percentage of contribution of one compartment estimates how much of the various inputs actually reach those compartments that provide "useful commercial products" from the systems. In Table 1 are listed the percentage of inputs from primary producers and detritus. It is clear that virgin forest is more "efficient" in producing commercially valuable resources. The results also show that the phytoplankton community (compartment 2) makes a significant contribution to the community production of the mud flat in reclaimed island. This result is in marked contrast to the situation in other mudflat communities. Previously, this mud flat had been dominated by *Phoenix* sp.—an important mangrove plant; but due to heavy infiltration and deforestation by humans, this species is currently faces extirpation. Only a few patches of this plant (and in some areas, dead roots) are to be found. Once this mangrove species is disappeared, erosion by the wave action no longer is prevented, and many ditches form in the mud flat. Most of the times these eroded areas are inundated by tidal water. The relatively elevated areas are covered by benthic algae, some grasses, and by scanty *Phoenix* sp. populations.

Table 1 – Percentage of input from primary producers and detritus that reaches the commercially important compartments

	Primary producers (%)		Detritus (%)	
	Virgin	Reclaimed	Virgin	Reclaimed
Benthic filter feeders	19.4	28.0	0	3.8
Macrobenthic carnivores	40.2	33.1	8.7	0.02
Pelagic detritivores	52.3	27.6	26.2	2.3
Pelagic carnivores	29.6	17.5	7.1	2.1
Top carnivores	11.7	9.5	4.0	2.3

Because the ditches are constantly inundated by water, phytoplankton are more abundant in these ditches. However, in virgin island in addition to the primary productions detritus makes major contribution to almost all the commercially important compartments. Virgin island is totally covered by mangrove forest dominated by *A. alba* and *A. officinalis* and it is reported by Ray and Straskraba (2001) that the litter and in turn detritus production is very high by these mangrove plants. It was mentioned earlier how only remnants of *Phoenix* sp. vegetation can be found in the reclaimed island. In comparison with other mangrove species *Phoenix* sp. produces less litter, as its leaf fall is scanty, and leaves are small, needle-shaped and narrow (Steinke and Ward, 1988). As a result, litterfall makes an unusually small contribution to the reclaimed system in comparison to virgin ecosystem.

Network analysis can be modified to focus on transfers occurring within the system (Szyrmer and Ulanowicz, 1987; Kay et al., 1989). 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 effect” for that component (Wulff and Ulanowicz, 1989). The indirect effect can be assessed through the total dependency matrix, as defined above, conveys the fractions of the total input to a compartment that flow from the various other taxa. Because energy may pass through several intermediate compartments in getting from a given particular taxon to another, the columns of dependency coefficients usually add up to more than 1.0. In fact, the amount by which the column sum exceeds 1.0 is related to the average trophic position of that taxon (Szyrmer and Ulanowicz, 1987). Table 2 shows the percentage of dependency of four most important commercially compartments on other compartments in both virgin and reclaimed systems. Again, the predominance of pelagic productions (both primary and secondary productions) is obvious in the indirect diet of all commercially important compartments in reclaimed forest. But in virgin counterpart macrobenthic carnivore, pelagic carnivore, pelagic detritivore compartments) are more heavily dependent upon the detritus and detrital food sources whereas benthic filter feeders and top carnivores are mainly rely on planktonic chain. One is struck by the relative scarcity of any large dependencies (i.e., those near 1.0). The result helps to strengthen the anecdotal observation that the reclaimed system seems to possess a large redundancy of trophic pathways (parallel routes), and therefore is probably highly resilient to subsequent perturbations, as one might expect from a heavily impacted system.

In both virgin and reclaimed systems trophic levels of each compartment are studied by considering the total number of pathways feeding into that compartment. The “Lindeman transformation matrix” partitions the energy flowing into each consumer into discrete trophic fractions. The elements of the column of the Lindeman matrix can be weighted by its corresponding trophic level to yield an effective trophic level for each consumer compartment (Figs. 2A and 2B for reclaimed and virgin systems, respectively) (counting primary producers and detritus as trophic level 1 results in an effective “trophic pyramid, as shown in Fig. 3A for reclaimed island and Fig. 3B for virgin island). This exercise reveals that, although a slight degree of omnivory is exhibited by compartments 9–13, alternatively, one may aggregate all flows of each integer trophic length into a food chain that represents the underlying trophic status of the starting food web. That is, the Lindeman transformation matrix maps a trophic web, as encountered in nature, into an abstract, but equivalent trophic “chain” of concatenated transfers. In reclaimed island one of the most interesting results concerns the ratio of herbivory:detritivory. Herbivory, the 2nd step in the grazing chain is 13,400 kcal m^{-2} $year^{-1}$ and detritivory reported as 15,700 units. That is they are virtually of the same magnitude. Here in reclaimed forest the production of detritus and its input from external source are very low, due to deforestation. Therefore, this system contains fewer detritivores. The pelagic detritivores that remain consist mainly of the mullet group of fishes, and were recorded in this system only during new moon and full moon, when tidal heights are greatest. In this mud flat, the benthic algae sustain a high rate of herbivory, but their contributions to compartments 5–7 seem unexceptional. Herbivory appears to consist largely of zooplankton grazing on phytoplankton and meiobenthos on macrophytes. The prominence of these processes is highly unexpected in any type of mud flat. Three distinctly different zones are noted in this system: ditches, flat areas, and some comparatively elevated areas. Zooplankton are confined mainly to the ditches, macrophytes (particularly grasses and scanty *Phoenix* sp.) occupy the flat areas, and benthic algae are confined to elevated areas. Browsers (compartment 5), deposit/filter feeders and particularly macrobenthos are restricted mainly to the grass beds. Only meiobenthos and a few macrobenthic fauna are found in the algal bed. This distribution probably contributes to the dominance of these two modes of secondary production.

In virgin system detritivory (from D to II) strongly predominates over herbivory (from I to II), it is about 1:3 (31,700 kcal m^{-2} $year^{-1}$: 83,604 kcal m^{-2} $year^{-1}$). Benthic dominated systems are usually characterized by a ratio of about 1:3 or less and in Chesapeake Bay it is almost 1:10 (Baird and Ulanowicz, 1989). In virgin mangrove system detritus is a major component, so that mangrove ecosystems are generally referred to as detritus-based ecosystems. As already

Table 2 – Percentage of dependency of the commercially important compartments on other compartments (V, virgin island and R, reclaimed island)

	Benthic filter feeders		Macrobenthic carnivore		Pelagic detritivore		Pelagic carnivore		Top carnivore	
	V	R	V	R	V	R	V	R	V	R
Benthic algae	12.5	37.6	10.3	29.3	8.8	28.1	9.0	19.3	8.8	13.1
Phytoplankton	0	4.6	4.1	12.2	3.2	15.7	9.9	41.9	3.2	12.7
Macrophytes	87.5	50.9	82.6	53.6	81.6	32.7	76.7	32.2	81.6	45.4
Zooplankton	0	1.8	3.1	10.3	1.3	6.2	8.6	39.2	1.3	7.8
Browsers	0	1.4	9.3	11.0	3.8	5.0	6.7	4.9	3.8	5.1
Filter and deposit feeders	0	1.7	28.5	36.6	5.8	6.0	14.6	20.3	5.8	39.1
Meio and macrobenthic herbivores	0	3.7	20.0	37.5	8.2	12.6	13.8	21.0	8.2	22.5
Bacteria	0	2.4	8.9	2.2	18.1	11.0	12.7	3.0	10.9	5.6
Benthic detritivore	0	0.5	38.8	8.5	15.8	1.8	48.5	3.1	15.8	12.8
Pelagic detritivore	0	0.6	14.7	2.3	9.3	2.2	29.0	20.2	9.3	28.3
Macrobenthic carnivore	0	1.6	4.0	1.2	8.1	5.6	5.6	1.6	8.1	26.3
Pelagic carnivore	0	1.3	1.7	0.9	3.4	4.3	2.4	1.2	3.4	9.0
Top carnivore	0	0.2	0.2	1.5	0.4	0.8	0.3	0.2	0.5	0.4
Detritus	0	2.9	48.3	20.7	100.0	100.0	69.4	28.2	28.0	50.6

mentioned the selected virgin island in this present study is fully covered with mangroves dominated by *Avecennia* spp. The litterfall of these mangroves are high and in turn the detritus (Ray, 1987) and so the inputs and flow in any trophic level is much higher in comparison to the reclaimed counterpart. Exports from all the commercially important compartments as human catch for food are much more pronounced in virgin system.

Feedback via recycling is critical in determining overall system structure. Cycles in ecosystems constitute an important factor that contributes to their autonomous behavior (Ulanowicz, 1983, 1986). Cycle analysis reveals that only a small number of cycles (31) exist in the reclaimed ecosystem and in addition, the Finn cycling index, which represents the fraction to total activity that is devoted to recycling (Finn, 1976; Ulanowicz and Kemp, 1979), indicates that only 8.4%

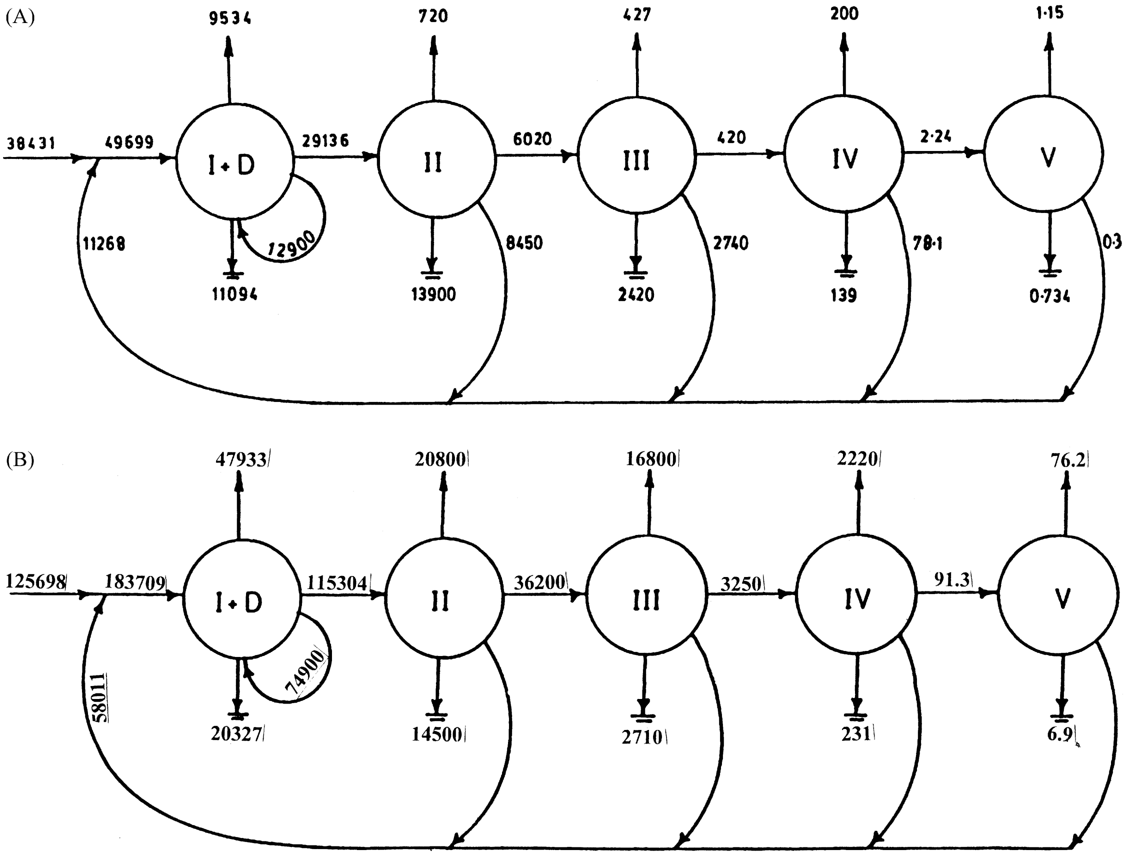


Fig. 3 – Reclaimed island: (A) and Virgin island: (B) – the trophic aggregation of Sundarban mangrove benthic network with the autotrophs and detritus merged (I + D), yielding a true tropic "trophic pyramid".

of the total energy flow travels over cyclical pathways. The low Finn cycling index and the small number of cycles in the system reinforce the picture of the reclaimed system as a highly disturbed ecosystem. In virgin ecosystem 21.3% of the total flow moves over cyclical pathways and the number of cycles is slightly higher than reclaimed island (38). The two systems possess a comparable number of cycles however, most of the recirculation in reclaimed system occurs over cycles of very short lengths, whereas the virgin system cycles are generally longer and hence distributed among more trophic levels. Ulanowicz (1983) proposed that the more intense cycling appears to occur in shorter, faster and trophically lower loops. Set against this observation, the reclaimed system appears to be stressed.

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 (Kay et al., 1989). The average trophic pathways for the living species in the two systems are plotted as bar diagrams in Fig. 4. In both the systems the compartments from 5 to 10 feed chiefly at the second trophic level. Clear differences between the systems exist in the macrobenthic carnivore (11) and pelagic carnivore (12), which feed roughly one step higher in virgin island. There appears to be a real biological difference between the feeding habits of the carnivores (both macrobenthic and pelagic) in the two systems. In the virgin system these two compartments feed more to trophically higher compartments like filter deposit feeders (6) and meio and macrobenthic herbivores (7).

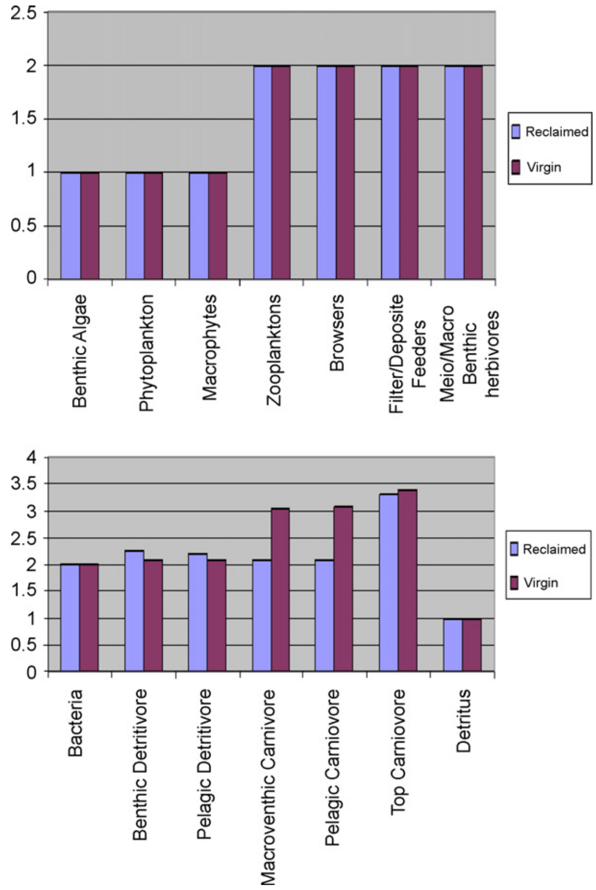


Fig. 4 – The effective trophic position of each taxon of 14 compartments food web model of both reclaimed and virgin Sundarban mangrove ecosystem.

Table 3 – Different information indices in both reclaimed and virgin islands

Total system throughput (kcal m^{-2} $year^{-1}$)	539,040	136,570
Development capacity (kcal m^{-2} $year^{-1}$)	2,571,000	700,300
Relative ascendency (%)	37	29
Imports (%)	13.8	12.75
Exports (%)	12.2	5.37
Respiration (%)	17.3	19.2
Redundancy (%)	19.6	33.5
Finn cycling index (%)	21.3	8.3

The total system throughput (*T*) measures the size of the system in terms of the aggregate activity of flow through all its components. The values of *T* in this present study are 136,570 kcal m^{-2} $year^{-1}$ and 539,040 kcal m^{-2} $year^{-1}$ in reclaimed and virgin systems, respectively. As the mangrove biome is usually considered to be a detritus-based system, it is of utmost importance to calculate the fraction of total system throughput that is subsidized by the mangrove litterfall. That fraction is very small: only 16% of the total system input is comprised of litterfall in reclaimed system whereas it is about 78% in virgin island. The proportion is very small in reclaimed island in comparison to virgin mangrove systems. In other undisturbed mangrove system where the corresponding value sometimes exceeds 95% (Ray et al., 2000). The main reason behind the small subsidy in reclaimed system is the near total destruction of major mangrove plants by human impacts.

Finally network analysis provides several information indices that characterize overall system status (Table 3). One of the most revealing of these indices is the relative ascendancy, which gauges how much of the trophic complexity appears in organized or constrained form. This index commonly runs from 35 to 45% in most ecosystems. The relative ascendancy, in the reclaimed mangrove ecosystem is significantly lower (29%), however, and the relative redundancy (unorganized complexity) is high (34%). These proportions reveal the extent of human impact upon this ecosystem, which is fast disappearing. The relative ascendancy is normal (37%) in virgin system like other any undisturbed systems.

4. Conclusion

Out of about 450 islands in Sundarban mangrove ecosystem, Sagar island is the largest island but this island in poor shape since 50 years. However, that the Prentice island is not the actual virgin representative of this mangrove ecosystem. Both Sagar and Prentice islands are situated in western part of the Sundarban mangrove ecosystem. The freshwater runoff is contributed in the western sector of this forest by Hooghly river (in Indian part) and eastern part by Padma river (in Bangladesh part). Fresh water runoff is much higher in Padma than Hooghly and so freshwater influence is much greater in eastern part than western part. Many important mangrove plants including largest and most important plant *Hereteria fomes* grow well in less saline environment. It is reported by many authors that the eastern part represents more dense mangrove forest and litterfall and overall productivity in the adjacent estuary are much higher in this part than western counterpart (Bhunia, 1979; Nandi, 1986; Ray, 1987). The eastern part is not properly accessible to the researchers due to improper convenience and most of the part is under the jurisdiction of project tiger. Therefore, the collected data of the eastern part of Sundarban mangrove ecosystem for running the network analysis are not adequate and certainly do not claim to have presented a complete comparative picture of reclaimed and virgin ecosystems, especially of the benthic system. In order to achieve more complete treatments such as the comparative study and actual assessment of the virgin mangrove system, have to turn the attention to the eastern part to select for virgin system of Sundarban mangroves.

Acknowledgements

I gratefully acknowledge the support from the CSIR, New Delhi (Project Ref. No. 37/1185/04/EMR-II). I am also thankful to the Department of Zoology, Visva Bharati University for laboratory and computer facilities. I also sincerely acknowledge Prof. B.C. Patten, University of Georgia, USA and Prof. R.E. Ulanowicz, University of Maryland, USA from whom I have developed my ideas on Network Analysis. Thanks are due to my Ph.D. students Madhumita Roy and Sudipto Mandal for their helps for preparing the graphs and tables for this manuscript. Last of all I also thank the anonymous reviewer for his suggestions for improving the paper.

REFERENCES

Asmus, M.L., McKellar Jr., H.N., 1989. Network analysis of the north inlet saltmarsh ecosystem. In: Wulff, F., Field, J.G., Mann, K.H. (Eds.), Network Analysis in Marine Ecology, Methods and Applications. Springer-Verlag, NY, pp. 206–219.

Baird, D., Ulanowicz, R.E., 1989. The seasonal dynamics of the Chesapeake Bay ecosystem. Ecol. Monogr. 59, 329–364.

Banerjee, A.K., 1964. Forests of Sundarban, Centenary Commemoration Volume, West Bengal Forests. DFO, Planning and Statistical Cell, Writer's Building, Calcutta, India, p. 188.

Bhunia, A., 1979. Ecology of the tidal creeks and mudflats of Sagar Island (Sundarban) West Bengal. Ph.D. Thesis. Calcutta University.

Boltzmann, L., 1872. Weitere studien uber das Waermegleichtgewicht unter Gasmolekuelen. Wien. Ber. 66, 270–275.

Choudhury, A., 1984. Productivity of Sundarban Mangrove Ecosystem in Both Reclaimed and Virgin Island. DST, Govt. of India.

Choudhury, A., 1987. Productivity of Sundarban Mangrove Ecosystem in Both Reclaimed and Virgin Island. DST, Govt. of India.

Ducklow, H.W., Fasham, M.J., Vezina, A.F., 1989. Derivation and analysis of flow networks for open ocean plankton systems. In: Wulff, F., Field, J.G., Mann, K.H. (Eds.), Network Analysis in Marine Ecology, Methods and Applications. Springer-Verlag, NY, pp. 159–205.

Fath, B.D., Patten, B.C., 1999. Review of the foundations of network environ analysis. Ecosystems 2, 167–179.

Fath, B.D., Patten, B.C., Choi, J.S., 2001. Complementarity of ecological goal functions. J. Theor. Biol. 208, 493–506.

Field, J.G., Moloney, C.L., Attwood, C.G., 1989. Network analysis of simulated succession after an upwelling event. In: Wulff, F., Field, J.G., Mann, K.H. (Eds.), Network Analysis in Marine Ecology, Methods and Applications. Springer-Verlag, NY, pp. 132–158.

Finn, J.T., 1976. Measures of ecosystem structure and function derived from analysis of flows. J. Theor. Biol. 56, 363–380.

Hannon, J.T., 1973. The structure of ecosystems. J. Theor. Biol. 41, 535–546.

Kay, J.J., Graham, L.A., Ulanowicz, R.E., 1989. A detailed guide to network analysis. In: Wulff, F., Field, J.G., Mann, K.H. (Eds.), Network Analysis in Marine Ecology, Methods and Applications. Springer-Verlag, NY, pp. 15–61.

Lawton, J.H., 1970. Feeding and food energy assimilation in larvae of the damselfly *Pyrrhosoma nymphula* (Sulz.) (Odonata:Zygoptera). J. Anim. Ecol. 39, 669–689.

Moore, S.T., Schuster, M.F., Harris, F.A., 1974. Radioisotope technique for estimating lady beetle consumption of tobacco budworm eggs and larvae. J. Econ. Ent. 67, 703–705.

Nandi, S., 1986. Ecology of benthic gastropods in the littoral mudflats and Hooghly estuary, India. Ph.D. Thesis. Calcutta University.

Patten, B.C., Bosserman, R.W., Finn, J.T., Cale, W.J., 1976. Propagation of cause in ecosystems. In: Patten, B.C. (Ed.), System Analysis and Simulation in Ecology, vol. 4. Academic Press, NY, pp. 457–579.

Pillay, T.V.R., 1958. Biology of the *Hilsa* sp. Ind. J. Fish 5, 201–207.

Ray, S., 1987. Ecology of littoral larval dipterans (Arthropoda:Insecta) of the mangrove ecosystem of Sundarbans, India. Ph.D. Thesis. Calcutta University.

Ray, S., Straskraba, M., 2001. The impact of detritivorous fishes on a mangrove estuarine system. Ecol. Model. 140, 207–218.

Ray, S., Ulanowicz, R.E., Majee, N.C., Roy, A.B., 2000. Network analysis of a benthic food web model of a partly reclaimed island in the Sundarban mangrove ecosystem. Indian J. Biol. Syst. 8, 263–278.

Southwood, T.R.E., 1978. Ecological Methods with Particular reference to the Study of Insect Populations. Chapman and Hall, NY.

Steinke, T.D., Ward, C.J., 1988. Litter production by mangroves. II. St. Lucia (Estuary) and Richards Bay (South Africa). S. Afr. J. Bot. 54, 445–454.

Strickland, J.D.H., 1960. Measuring the production of marine phytoplanktons. Bull. Fish. Res. Bd., Canada.

Strickland, J.D.H., Parsons, T.R., 1968. A practical handbook of seawater analysis. Bull. Fish. Res. Bd., Canada.

Szyrmer, J., Ulanowicz, R.E., 1987. Total flows in ecosystems. Ecol. Model. 35, 123–136.

Ulanowicz, R.E., 1983. Identifying the structure of cycling in ecosystems. Math. Biosci. 65, 219–237.

Ulanowicz, R.E., 1986. Growth and Development: Ecosystem Phenomenology. Springer-Verlag, NY.

Ulanowicz, R.E., Kemp, W.M., 1979. Towards canonical trophic aggregations. Am. Nat. 114, 871–883.

Warwick, R.M.S., Radford, P.J., 1989. Analysis of the flow network in an estuarine benthic community. In: Wulff, F., Field, J.G., Mann, K.H. (Eds.), Network Analysis in Marine Ecology, Methods and Applications. Springer-Verlag, NY, pp. 220–231.

Wohlschlag, D.E., 1957. Difference in metabolic rates of migratory and resident freshwater forms of an arctic whitefish. Ecology 38, 502–510.

Wulff, F., Ulanowicz, R.E., 1989. A comparative anatomy of the Baltic Sea and Chesapeake Bay ecosystems. In: Wulff, F., Field, J.G., Mann, K.H. (Eds.), Network Analysis in Marine Ecology, Methods and Applications. Springer-Verlag, NY, pp. 232–256.