NETWORK ANALYSIS OF A BENTHIC FOOD WEB MODEL OF A PARTLY RECLAIMED ISLAND IN THE SUNDARBAN MANGROVE ECOSYSTEM, INDIA

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ABSTRACT

Network analysis is performed on a 14 species food web model of the ecosystem occupying a mudflat on a partly reclaimed island of the Sundarban mangrove ecosystem. The results demonstrate a dramatic difference between this heavily impacted mangrove ecosystem in its modes of primary and secondary production and its diminished role of detritus vis-a-vis its less disturbed counterparts.

Unlike most benthic mangrove systems, the Sundarban bottom community receives a large contribution from the phytoplankton populations. In this system herbivory and detritivory are virtually equal, in contrast to the usual herbivory:detritivory ratio of 1:5. Anthropogenic impacts have changed the physiography of this system so as to increase the relative importance of zooplankton and meiobenthos as herbivores. Although a slight degree of omnivory is exhibited by the populations of larger organisms, all flows of each integer of trophic length into a food chain may be aggregated that represents the underlying trophic status of the starting food web. Only a small number of pathways of recycle can be identified (31), and the Finn cycling index for this system is quite low (8.4%). Litterfall comprises only 16% of the total system input, which is very little in comparison with most mangrove systems. Pathway redundancy is rather high in this ecosystem, indicating that the surviving system is probably highly resilient to further perturbations, as one might expect for a highly impacted system.

Keywords: Network analysis, benthic, foodweb, mangrove, and ascendancy

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1.Introduction

The Gangetic delta of the Hooghly-Brahamaputra 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 4200 sq. km. [3], 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, some of which are partly developed but most of which remain virgin. Sagar Island, particularly reclaimed and the largest island in this deltaic complex and is cris-crossed by twelve tidal creeks of various sizes, fringed with mangrove vegetation, and all connected with the principal estuarine water.

Below we consider a 14 species network of trophic exchanges in the ecosystem of the mud flats on Sagar Island. Earlier, the structure and function of this ecosystem particularly the virgin parts were investigated using deterministic models [15,17,18,23] and disturbed part also studied by some authors [9,21]. The two or three species models these investigators employed were unable to afford them a full understanding of this system. Here, we use network analysis to give further insight into this mangrove ecosystem, which has been reclaimed in places, but over all is gradually diminishing.

Network analysis has been used to quantify the structure of system networks, the degree of cycling, and the magnitudes of interdependency among components [1,8,10,32.35]. We employ it 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 (see below.)

The data used in this model were collected from different sources, including direct field observation by one of the authors (SR), from various Ph.D. theses project reports [1,4,6,7,19,22,33]. 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 [26] and Strickland and Parson [27]. 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.* [16] and also by gravimetric methods [14]. Respirational and metabolic losses were assessed by keeping the animal enclosed in a limited volume of water cut off from the atmosphere [34]. 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} y^{-1} [24], and the standing stocks were reported as kcal m^{-2}.

2. Quantitative Methods

The computer package NETWRK [13] 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. We begin by denoting the magnitude of the transfer of medium from i to j as Tij, 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 the crux of the calculations, however, revolves around the accompanying matrix of dietary coefficients, **G**, where the matrix components are calculated from the T_{ij} as $G_{ij} = T_{ij} / \Sigma_k T_{kj}$. In words, Gij is the fraction of j's diet that is comprised by i. The algebraic powers of the **G** matrix are extremely informative. The reader is invited to test, for example, that the i-jth 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-jth 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 **G** has been normalized by the total input to each column j, the elements G_{ij} are all less than or equal to unity. The elements of successively higher algebraic powers of **G** tend to diminish in magnitude. In fact, one might question whether the infinite series of such powers ($\mathbf{S} = \mathbf{G}^0 + \mathbf{G}^1 + \mathbf{G}^2 + \mathbf{G}^3 + \ldots$) 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 **I** ($= \mathbf{G}^0$) is the identity matrix with ones along the diagonal and zeroes elsewhere. The limit matrix, **S**, is called the "structure matrix", and the i-jth 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 [12,20,31]. 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 [28] 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 [29]. (Simple cycles contain no repeated taxa.) Often the pattern of recycled flows reveals clues to how the system is functioning to process medium [2]. 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 [11].

Finally, Ulanowicz [30] 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 $\Sigma_m T_{im}/T$. According to Boltzmann [5], the indeterminacy associated with this marginal probability is $-k*\log(\Sigma_j T_{ij}/T)$, 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 $T_{ij}/\Sigma_k T_{kj}$. The corresponding indeterminacy, $-k*\log(T_{ij}/\Sigma_k T_{kj})$, 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, $k*\log([T_{ij}*T]/[\Sigma_m T_{im}*\Sigma_k T_{kj}])$.

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-jth 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, $AMI = k*\Sigma_{i,j}(T_{ij}/T)\log([T_{ij}*T]/[\Sigma_m T_{im}*\Sigma_k T_{kj}])$. Like other informational indices, AMI does not have physical dimensions. In order to impart physical extent to AMI, we 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 $A = \Sigma_{i,j}T_{ij}\log([T_{ij}*T]/[\Sigma_m T_{im}*\Sigma_k T_{kj}])$.

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, we 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 $C = \Sigma_{i,j}T_{ij}\log(T_{ij}/T)$. 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 (Fig. 1). 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.
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/macro benthic 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. *Partia* 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.

We discuss first the contribution and dependency coefficients, which are tabulated (Table 1 and Table 2). Each contribution coefficient (Table 1) represents the fraction of a particular component, throughput that is contributed to the diet of another specific component. The results show that the phytoplankton community (compartment – 2) makes a significant contribution to the community production of the mud flat. 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 time these erosions are inundated by tidal water. The relatively elevated areas are covered by benthic algae, some grasses, and by scanty *Phoenix* sp. populations. Because the ditches are constantly inundated by water, phytoplankton are more abundant in these ditches.

It was mentioned earlier how only remnants of *Phoenix* sp. vegetation can be found in the Sundarban. In comparison with other mangrove species *Phoenix* sp. produces less litter, as its leaf fall is scant, and its leaves are small, needle-shaped and narrow [25]. As a result, litterfall makes an unusually small contribution to the Sundarban ecosystem in comparison to other mangrove ecosystems, which are usually dominated by this input.

The total dependency matrix (Table 2), 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 [28]. 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 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.

We have studied the trophic level of each compartment by considering the total number of pathways feeding into that compartment. As described above, 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 (Fig. 2). 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 (Fig. 3).

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 (Fig.3). That is, the Lindeman transformation matrix maps a trophic web, as encountered in nature, into an abstract, but equivalent trophic "chain" of concatenated transfers. One of the most interesting results concerns the ratio of herbivory:detritivory. Herbivory, the 2nd step in the grazing chain, is 13400 kcal m^{-2} y^{-1}, and detritivory is reported as 15700 units. That is they are virtually of the same magnitude. Benthic dominated systems are usually characterized by a ratio of about 1:5 or less. In Chesapeake Bay it is almost 1:10. In virgin mangrove system detritus is a major component, so that mangrove ecosystems are generally referred to as detritus-based ecosystems. Here however 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 5,6 and 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. Bowsers (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.

Counting primary producers and detritus as trophic level 1 results in an effective "trophic pyramid, as shown in Fig.4.

Feedback via recycling is critical in determining overall system structure. Cycles in ecosystems constitute an important factor that contributes to their autonomous behavior [29,30]. Cycle analysis reveals that only a small number of cycles (31) exists in the Sundarban ecosystem. In addition, the Finn cycling index, which represents the fraction to total activity that is devoted to recycling [11,31], indicates that only 8.4% 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 Sundarban as a highly disturbed ecosystem.

The total system throughput (T) measures the size of the system in terms of the aggregate activity of flow through all its components. The value of T in this system is 136,570 kcal m^{-2} y^{-1} Because 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. This proportion is very small in comparison to other mangrove systems, where the corresponding values usually exceeds 95%. The main reason behind the small subsidy 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 35-45% in most ecosystems. The relative ascendancy, in the Sundarban 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. In most other applications to network data, these indices have exhibited very little change in response to impacts. However, in this system the effects are quite dramatic and unmistakable. It is hoped that these unequivocal results will alert other investigators to the utility of network analysis.

Last of all, we acknowledge that what we report here is but the beginning of the network analysis of the Sundarban mangrove ecosystem. We certainly do not claim to have presented a complete picture of this ecosystem, especially of the benthic system. In order to achieve a more complete treatment of the matter, we now turn our attention to the undisturbed, virgin system of Sundarban mangroves.

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Table 1

Donor	Recipient			
	Zooplankton	Browsers	Filter/Deposit Feeders	Meio/Macro Benthic Herbivores
Benthic Algae	0	0.0709	0.124	0.0994
Phytoplankton	0.551	0	0.0180	0
Macrophytes	0	0.0680	0.138	0
Zooplankton	0	0	0.0129	0
Browsers	0	0	0.0311	0
Filter/deposit Feeders.	0	0	0.0175	0
Meio/Macro Benthic herbivores	0	0	0.0292	0
Bacteria	0	0	0.0144	0
Benthic detritivores	0	0	0.0038	0
Pelagic detritivores	0	0	0.0058	0
Macrobenthic	0	0	0.0202	0

carnivores				
Pelagic Carnivores	0	0	0.0227	0
Top Carnivores	0	0	0.0060	0
Detritus	0	0	0.0382	0

contd.........

Donor	Recipient			
	Bacteria	Benthic Detritivores	Pelagic Detritivores	Macrobenthic Carnivores
Benthic Alage	0.153	0.131	0.102	0.0873
Phytoplankton	0.101	0.0868	0.00677	0.0387
Macrophytes	0.146	0.125	0.117	0.0486
Zooplanktons	0.0726	0.0622	0.0590	0.156
Browsers	0.175	0.150	0.190	0.0588
Filter/Deposit Feeders	0.0984	0.115	0.0106	0.0102
Meio/Macro Benthic Herbivores	0.164	0.141	0.241	0.0930
Bacteria	0.0809	0.115	0.0106	0.0102
Benthic Detritivores	0.0214	0.0184	0.0485	0.0121
Pelagic Detritivores	0.0327	0.0280	0.0170	0.1020
Macrobenthic	0.114	0.0974	0.0115	0.0109

Carnivores				
Pelagic Carnivores	0.128	0.110	0.0130	0.0122
Top Carnivores	0.0339	0.0291	0.0034	0.0032
Detritus	0.216	0.185	0.0219	0.0021

contd.................

Donor	Recipient		
	Pelagic Carnivores	Top Carnivores	Detritus
Benthic Alagae	0.0355	0.0348	0.708
Phytoplankton	0.0916	0.0174	0.470
Macrophytes	0.0486	0.0430	0.675
Zooplankton	0.156	0.0195	0.336
Browsers	0.0588	0.0384	0.813
Filter/Deposit Feeders	0.113	0.137	0.456
Meio/Macro Benthic Herbivores	0.0930	0.0626	0.762
Bacteria	0.0102	0.0118	0.375
Benthic Detritivores	0.0121	0.0317	0.0993
Pelagic Detritivores	0.102	0.0901	0.152
Macrobenthic Carnivores	0.0109	0.114	0.527
Pelagic Carnivores	0.0122	0.0564	0.594
Top Carnivores	0.0032	0.0037	0.157
Detritus	0.021	0.023	0.127

Table 2

Donor	Recipient			
	Zooplankton	Browsers	Filter/Deposit Feeders	Meio/Macro Benthic Herbivores
Benthic Alagae	0	0.461	0.376	0.239
Phytoplankton	1.00	0	0.0459	0
Macrophytes	0	0.539	0.509	0.761
Zooplanktons	0	0	0.0181	0
Browsers	0	0	0.0145	0
Filter/Deposit Feeders	0	0	0.0175	0
Meio/Macro Benthic Herbivores	0	0	0.0367	0
Bacteria	0	0	0.0236	0
Benthic Detritivores	0	0	0.0054	0

Pelagic Detritivores	0	0	0.0064	0
Macrobenthic Carnivores	0	0	0.0163	0
Pelagic Carnivores	0	0	0.0127	0
Top Carnivores	0	0	0.0021	0
Detritus	0	0	0.292	0

Contd.........................

Donor	Recipient			
	Bacteria	Benthic Detritivores	Pelagic Detritivores	Macrobenthic Carnivores
Benthic Algae	0.281	0.281	0.281	0.293
Phytoplankton	0.157	0.157	0.157	0.122
Macrophytes	0.327	0.327	0.327	0.536
Zooplanktons	0.0619	0.0619	0.0619	0.103
Browsers	0.0497	0.0497	0.0497	0.110
Filter/Deposit Feeders	0.0598	0.0598	0.0598	0.366
Meio/Macro Benthic Herbivores	0.126	0.126	0.126	0.375
Bacteria	0.0809	0.135	0.110	0.0217
Benthic Detritivores	0.0184	0.0184	0.0184	0.0847
Pelagic	0.0219	0.0219	0.0219	0.0231

Detritivores				
Macrobenthic Carnivores	0.0558	0.0558	0.0558	0.0115
Pelagic Carnivores	0.0434	0.0434	0.0434	0.0090
Top Carnivores	0.0072	0.0072	0.0072	0.015
Detritus	1.0	1.0	1.0	0.207

contd...........

Donor	Recipient		
	Pelagic Carnivores	Top Carnivores	Detritus
Benthic Algae	0.193	0.301	0.281
Phytoplankton	0.419	0.127	0.157
Macrophytes	0.322	0.454	0.327
Zooplanktons	0.392	0.0784	0.0619
Browsers	0.0492	0.0511	0.0497
Filter/Deposit Feeders	0.203	0.391	0.0598
Meio/Macro Benthic Herbivores	0.210	0.225	0.126
Bacteria	0.0301	0.0556	0.0809
Benthic Detritivores	0.0307	0.128	0.0184
Pelagic Detritivores	0.202	0.283	0.0219
Macrobenthic Carnivores	0.0157	0.263	0.0558
Pelagic Carnivores	0.0122	0.0899	0.0434

Top Carnivores	0.0020	0.0037	0.0072
Detritus	0.282	0.506	0.127

Table 3

Total System Throughput	136570
Development Capacity	700300
Ascendency	204250
Overhead of Imports	89349
Overhead of Exports	37615
Dissipative Overhead	134300
Redundency	234790
Finn Cycling Index	0.08375

Legends for figures:

Fig. 1. The diagram of energy flows among 14 compartments of the network of the benthic food web of the Sundarban mangrove ecosystem. All flows are in (kcal m^{-2} y^{-1}) and standing stock densities in (kcal m^{-2}). The ground symbols represent respiratory losses. The arrows connecting one compartment to other represent flows and the arrows from outside to compartment and also from compartments to outside represent inflow and outflow respectively.

Fig. 2 The effective trophic positions of each taxon in 17 compartments food web model of Sundarban mangrove ecosystem.

Fig. 3 The trophic aggregation of the Sundarban mangrove benthic network with the autotrophs and detritus separated and mapped into Lindeman-type trophic levels. The trophic levels are designated by Roman numerals (= I – V, and D – represents the detritus pool).

Fig. 4 The trophic aggregation shown in Fig. 3, except the primary producers and the detritus have been merged (I + D), yielding a true “trophic pyramid”.

Legends for tables:

Table 1 Total contribution coeffcient which represents the fractions a component contributed to the “diets” of other components.

Table 2 Total dependency coefficient which represents the fraction of the total amount of energy leaving one compartment eventually enters another compartment, via both direct food chains and cycling.

Table 3 Showing the information indices (kcal m^{-2} y^{-1})