Detritus, a Critical Essay

by

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M.S. 1977

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Critical Essay

Definition of Detritus

Detritus plays an important role in the marine ecosystem. It forms a significant fraction of the available food sources (Darnell, 1958, 1961, 1967; Gant et al, 1971; Heald, 1971; Lenz, 1977; E. P. Odum and Dela Cruz, 1967; W. E. Odum, 1971; W. E. Odum and Heald, 1975; Riley, 1970; Seki, 1972; Teal, 1962). Detritus is the chief link between primary and secondary productivity in salt marshes and mangroves. This is because only a small portion of the net production of the marsh grass or mangrove is grazed while it is alive. The major energy flow between autotrophic and heterotrophic levels is by way of the detritus food chain (Gant et al, 1971; Heald, 1971; E. P. Odum and Dela Cruz, 1967; W. E. Odum, 1971; W. E. Odum and Heald, 1975; Teal, 1962).

The word "detritus" originated from the Latin verb deterere which means "to rub away" or "to wear off" (W. E. Odum, 1971). The term was used originally by geologists to denote material resulting from the disintegration of rock. Detritus has been defined in several definitions by biologists according to their own work. As defined by E. P. Odum and Dela Cruz (1967), organic detritus is particulate material that was formerly part of a living organism. This definition includes particles ranging from the freshly dead bodies of plants and animals through finely disintegrated particles of these organisms to fecal pellets and aggregates of colloidal-size particles. It is also considered materials which are sorbed upon the basic particle: bacteria, fungi and protozoans, along with adsorbed dissolved organic and inorganic compounds. Darnell (1967) defines detritus as all types of biogenic material in various stages of microbial decomposition which represent potential energy sources for consumer species. This includes all dead organisms as well as the secretions, regurgitations, excretions and egestions of living organisms, together with all subsequent products of decomposition which still represent potential sources of energy. He divides organic detritus into two categories: particulate organic detritus (material retained by filters with apertures of one micron diameter) and subparticulate organic detritus (material which passes through such filters). Detritus can be defined according to size. During the processes of decomposition and disintegration the component parts of plant materials are subjected to autolysis, hydrolysis, mechanical fragmentation, and grazing, which result in a gradual reduction of particle size. The plant material is fragmented until the individual particle size does not exceed 2 or 3 mm in smallest dimension. Material of this size is referred to as detritus. This includes the particle's associated microflora and fauna. The nature or origin of specific particles is used to categorize detritus into groups; for instance, suspended detritus, mangrove detritus, allochthonous detritus and inorganic detritus. Includes in the last category are shell fragments, fish scales and otoliths, sand grains and precipitate carbonate particles (Heald, 1971). Lenz (1972) also defines detritus in relation to size. Detritus in this sense is the non-living part of suspended particulate matter. Detritus comprises a variety of different compounds which may be classified according to nature, origin and specific weight. The smallest detritus particles are in the range of 0.5-1 μm to separate from dissolved organic material. He divides detritus into two main components: biogenous detritus, which is all kinds of phytoplankton and zooplankton fragments and decaying products of organic and inorganic nature, faecal pellets and excreta of organisms, and terrigenous detritus, which is minerals originating from the continental weathering processes and organic debris discharges by river into the sea. I favor Darnell's and Heald's definition of detritus as all types of biogenic material in various stages of microbial decomposition including all dead organisms as well as associated microflora and fauna, secretions, excretions and egestions of living organisms. The particle sizes range from 3 mm to 1 μm in diameter. Size should be specified in the definition of detritus. If not specified, a dead whale should be considered detritus for it is biogenic material under microbial decomposition stages. Nature and origin of specific particles should also be used to categorize detritus into groups.

Mangrove Ecosystem

Mangroves are trees or bushes growing between the level of high water of spring tides and the mean sea-level (Macnae, 1968). Mangrove swamps dominate the world's coastline between $25^{\circ}N$ and $25^{\circ}S$, extending $10-15^{\circ}$ further south in eastern South Africa, Australia, and New Zealand, and 7° further north in Japan (Mann, 1972). The term "mangrove" may be used in reference to particular species of trees or to the whole swamp association (Kuenzler, 1969). Mangroves are dominated by a few species of plants such as Rhizophora spp., Avicennia spp., Sonneratia spp., Bruguiera spp. and Ceriops spp. Zonation in mangroves in different parts of the world may be different but it is common to find species of Rhizophora and Avicennia as important components. These plants are well adapted to the loose, wet and dominantly saline substrate. The complex prop roots and air-roots serve as a respiratory function and are well adapted to resisting wave action. They also serve to trap sediment and protect the shoreline from erosion. Mangroves exhibit different degrees of viviparity of the fruits and seeds. In contrast to the low diversity of plants, many kinds of animals are found in mangrove swamps. Mangroves provide several distinct microhabitats such as roots, stems and leaves of trees, in or beneath deadwood, in or on soil (Kuenzler, 1969; Macnae & Kalk, 1962; Macnae, 1963, 1968; Mann, 1972).

Mangroves are considered as one of the most productive of all estuarine ecosystem[9]. Mann (1972) summarizes the net production of coastal macrophyte communities, expressed as gram calories per square meter per year (gC/m^2 per year) as in Table 1.

Table 1 - Net production of coastal macrophyte communities, gC/m^2 per year (From Mann, 1972)

Community	Location	Net Production
Subtidal		
Laminaria	Atlantic Coast	1225-1900
Macrocystis	California	400-820
	Indian Ocean	2000*
Thalassia	Caribbean area	590-900
	Indian Ocean	500-1500
Zostera	Denmark and Washington State	58-340
	Alaska	50-1500*
Intertidal		
Fucoids	Atlantic Canada	640-840
Spartina	Atlantic Canada & USA	130-897
Mangrove	Puerto Rico	1,400*
	Florida	352
	Average of lower and higher figures.	440-1100

* Indicates extrapolation from short term measurements.

Mangroves themselves are the dominant producers in the ecosystem, but algae are also important. The algae are composed of blue-green and green algae. Other than the primary production, leaves, twigs and various parts of the trees constitute a substantial portion of the annual production in form of detritus. Golley, et al (1962) made a study of the structure and metabolic rate of a red mangrove forest, Rhizophora mangle in Puerto Rico. The biomass of various parts of the trees, expressed as grams dry weight/m^2, were 778 g of leaves 1274 g of branches, 2796 g of tree trunks, 1437 g of prop roots and about 5000 g of roots. The gross production in May is 8.23 g C/m^2 per day. The amount of organic matter in leaves that fall to the soil surface is 0.65 g C/m^2 per day. The organic matter converted to wood for tree trunks and production by algae in the mud surface are 0.4 and 0.38 g C/m^2 per day respectively. Heald (1971) reported the production of mangrove debris in form of leaves and twigs was estimated to average 2.4 g/m^2/day in red mangrove forest in Florida.

Detritus Particles as a Food Source

Two principal food chains or pathways in estuarine ecosystem are the grazing food chain, in which living plants are the primary energy source for the consumer, and the detrital food chain, in which dead and decaying organic materials are the energy source (E. P. Odum, 1963). In mangrove ecosystem, both principal food chains are present. It is more apparent that detrital food chain is more important in this system comparing to the grazing food chain. Several studies support this. Heald (1971) concluded that red mangrove leaves were not heavily grazed while alive. Only 5.1 percent of the leaf was consumed by terrestrial organisms. The remainder entered the aquatic system as debris. This became an important energy source for the detrital food chain. W. E. Odum (1971) and W. E. Odum and Heald (1972) studied stomach contents of organisms found in the South Florida estuary. Of about 120 species examined, roughly one-third can be classified as detritus consumers. These are defined as organisms whose digestive-tract contents averaged at least 20 percent vascular plant detritus by volume on an annual basis. Their study is in contrast to Darnell (1958, 1961, 1967) for Lake Pontchartrain, Louisiana. Darnell considered a detritus consumer to be any organism which contained more than five percent "detritus" in its digestive tract. His list of detritus consumers was dominated by 21 species of fishes and relatively few invertebrates. He lumped most materials of an organic origin in the category of detritus. Odum argued that in this case well digested organisms may have been classified as detritus. He felt that most of the fish lacked the long digestive tract required for effective utilization of detritus, it was possible that many species picked up 5-10% of detritus incidentally and were unable to derive nourishment from it. It should be noted that in Odum's data, detritus only referred to vascular plant's fragments. In general, both Darnell and Odum agreed that detritus is important to consumers in the estuary.

Sources of Detritus in the Mangroves

According to my conclusion on the definition of detritus, sources of detritus in mangroves can be summarized as follows:

1) Phytoplankton (including algae and autotrophic bacteria)

2) Mud-flat diatoms and filamentous algae (especially blue-greens)

3) Mangrove vegetations - leaves, twigs, seedling and various parts of the trees

4) Dead organisms such as fragments of zooplankton and excretion

Organic debris in order to enter the detrital food chain has gone through the process of biodecomposition or biodegradation. Important mechanisms of biodecomposition include chemical dissolution, autolysis, hydrolysis, oxidation, mechanical fragmentation, enzymatic lysis by bacteria and fungi, and the activities of scavenging organisms (Darnell, 1967; Fell and Master, 1973; Fell, et al, 1975; Golterman, 1972; Heald, 1971; Hann, 1972; Meyers and Hopper, 1966, 1973; Newell, 1973). How detritus from different sources enter the detrital pool in the mangroves will be viewed separately.

Source of Detritus from Phytoplankton, Diatom and Filamentous Algae

Phytoplankton, diatom and filamentous algae are important primary producers in the estuarine ecosystem. They are considered the base of the grazing food chain. It can also be called the phytoplankton food chain. Dead phytoplankton and filamentous algae can add to the detrital pool. Input of detritus from the incoming tides in forms of algae and phytoplankton is also important to the system. Only a few studies deal with the transfer between the two food chains, the phytoplankton and the detrital food chain. Also the transfer between detritus and primary producers such as benthic algae that takes place at the mud and water interface is less known. Golterman (1972) studied the role of phytoplankton in detritus formation. He calculated only 10 percent of the phytoplankton will be converted to detritus by the process of bacterial mineralization.

A rapid mineralization by bacteria takes place when the algal cells are autolysed. The autolysed cells are referred to as leached cells. There is a rapid phosphate liberation. The products of autolysis such as amino acids may induce bacterial attack on algal cells. The attachment of the bacteria is necessary to establish a good contact between the enzyme, proteinase and the substrate. During the bacterial breakdown, intermediate stages occur to have high nutritional value. But the resulting detritus have low nutrient consisting of mainly cell wall (Golterman, 1972).

Saunder (1972) gave another aspect of how phytoplankton can be related to the detrital food chain. He found that the quality of the organic detritus generated in Frains Lake, Michigan was a function of the structure of the phytoplankton community. He tested this by estimating assimilation efficiency for detritus in Daphnia. Early in the study, the phytoplankton community was dominated by cryptomonads. The cryptomonads tended to decrease with time. The community has gone through successions of cryptomonads, green algae, blue-green algae and diatom. The higher assimilation efficiency for detritus observed early in the study was due to the fact that this detritus was derived from highly nutritious, thin walled phytoflagellates. As the phytoplankton community became dominated by green algae with heavy cell walls, the assimilation efficiency decreased as in Table 2.

Table 2. Assimilation efficiency in gravid Daphnia in percentage of food source ingested, Frains Lake, Michigan. (From Saunders, 1972)

Date	Algae	Bacteria	Detritus
27-IV-67	53	-	13
3-V -67	78	52	18
9-V -67	67	23	8
16-V -67	72	12	8
23-V -67	54	16	3
30-V -67	88	14	7
6-VI-67	43	52	7
14-VI-67	32	26	2
20-VI-67	20	24	2
27-VI-67	33	28	2

The aspect of diatom and filamentous algae as a source of detritus has not been studied. The proportion of diatom filamentous algae contributing to the detrital pool should be observed. Biodecomposition processes should also be studied.

Source of Detritus from Mangrove Vegetations

This includes leaves, twigs, seedlings and various parts of the plant going through the process of biodecomposition. Biodecomposition or biodegradation involves both mechanical and chemical processes. Chemical processes in biodecomposition are autolysis, hydrolysis and oxidation. Autolysis is the breakdown of tissues by their own enzymes. It is an initial step in destruction of cell membrane. Bacterial and fungal decomposers play the most important role in chemical breakdown. Mechanical breakdown usually occur through the action of waves and water currents which affect materials that have been structurally weakened through chemical action. The tearing and grinding processes of many consumer species also play a significant role (Darnell, 1967).

Rate of biodeposition of leaf litter depends on several factors. It is not only depends upon where the leaf falls initially, but also on where it may be transported later. Newly shed leaves may fall directly into the water, in which they will float for several days. During this time, they may be carried away and deposited in a different environment. They may be fall onto dry ground and remain there for considerable time before rising water levels carry them elsewhere. Heald (1971) exposed red mangrove leaves in nylon bags of 2.5 mm mesh and found that after 1 year 95% had disappeared in brackish water, 82% in fresh water and only 72% on dry land. Temperature is another important factor on determining biodecomposition rate. It affects the rate of chemical reactions, the activity of enzymes and the metabolism of organisms (Heald, 1971). Process of biodecomposition of leaf litter in mangroves:

1) Autolysis

This is the period when soluble material leachs out. Leaching of water soluble organics as well as inorganic compounds from leaves furnishes nutrients for micro-organisms. The leaves themselves provide substrate for bacteria and fungi, many of which obtain all or a part of their energy requirements from the breakdown of plant proteins, fats and celluloses (Heald, 1971).

2) Colonization of bacteria and fungi

The colonization of bacteria on detrital particles takes place in three stages:

2.1) Reversible phase - Physical and physico-chemical forces play a major role in preventing or assisting settlement of bacteria on the submerged surface. These forces are double layer ionic forces as well as London-Van der Waal's forces. Bacteria are normally negatively charged at the surface at the pH prevailing in natural water. The magnitude of these changes on bacteria and those on the surface of the substrate will determine the bacterial settlement.

2.2) Irreversible phase - Bacteria become cemented into place by adhesive material. Several means of permanent attachment occur in bacteria; for instance, adhesive polysaccharide, typical rosette to hook in place, and hair-like projections known as pili.

2.3) Biological phase - After cells settled, they may grow and divide so that a micro-ecosystem is developed on the surface of the detritus (Floodgate, 1972). In many cases, bacteria produce a heavy slime layer on the leaf during the first week of submergence. This slime acts as a matrix for accumulation of detritus, algae, micro fauna? meiofauna and fungal spores. Fungi develop on and in the leaves within the first week of submergence. Fungi show succession varied in their ability to survive throughout the degradation process. The Phycomycetes are one of the most important fungal groups. Deuteromycetes and Ascomycetes are also associated with the decomposition of the mangrove leaves. (Fell and Master, 1973; Fell, et al, 1975). Fungi species, found associated with the decomposition of mangrove seedlings, do not relate to fungi in the water column and mud. Similar fungal successions take place in both injured and uninjured sets of seedlings. Succession begins with Hyphomycetes to Sphaeropsidales, Ascomycetes and Hyphomycetes. The role of fungi seem to be as invaders of the protective external tissues. In injured seedlings, bacteria and protozoa enter the tissues via the wound and rot them (Newell, 1973).

3) Populations of predators such as ciliates and nematodes begin to build up. Bacteria are a primary food source for many micro-organism. While some animals, such as the amphipods and polychaetes, consume leaf particles and appear to derive their energy from leaf and fungal material, the majority of the animals, particularly the nematodes, are bacterial feeders (Fell, et al, 1975). Nematodes also feed on fungi on detrital particles. Fungi usually associate with cellulose degradation on the leaves. Cellulose degradation site serves as a locus for aggregation of nematodes. This is shown by the growth of Aphelenchoides marinus on fungal mycelia on seagrass. Another species of nematode, Metoncholaimus sp. also heavily settle on mycelial-cellulose mats of marine fungi (Meyers and Hopper, 1966, 1975).

4) Macrobenthic organisms begin to tear off pieces of the plant material with its attached community of micro-organisms. Detritus-feeding invertebrates derive their nourishment mainly by stripping the microorganisms from the plant material as it passes through their guts. The faecal pellets may be recolonized by microorganisms and the process repeats until all the plant material has been utilized. The result of this process is a steady reduction in particle size, with a consequent increase in surface-area-to-volume ratio; an increase in microbial population and a reduction in the C:N ratio of the detritus (Heald, 1971; Mann, 1972). Macrofauna such as amphipods may increase the rate of biodeposition by

decreasing the particle size of the detritus. This will increase the detritus total surface and thus increase the biologically active surface for bacteria. Fenchel (1970) studied the decomposition of organic detritus derived from the Turtle grass, Thalassia testudinum. He found that the detritus-consuming amphipod Parhyallella whelpleyi fed on on detrital particles and on its own fecal pellets. But it only uses the microorganisms colonizing on the surface. The amphipod increased the decomposition rate by decreasing the particle size and thus increasing the microbial activity on detritus.

The breakdown process of leaves, twigs and seedlings probably ends only if the particle is removed from the system by deposition and burial in the sediments, or when it becomes so reduced in size that it can no longer support an abundant microbiota. Even then, very fine (colloidal) particulate matter often remains available in the form of aggregates loosely bonded by bacteria, fungi and molecular forces. E. P. Odum and Dela Cruz (1967) showed that nanno fraction of detritus amounted to 95 percent of detrital content collected from the salt marsh tidal creek. They suggested that the highly decomposed, unrecognizable nanno fraction might be of the greatest importance.

Source of Detritus from dead organisms and excretions

Detrital fraction deriving from dead organisms such as fragments of zooplankton, exoskeleton of crustaceans, has not been thoroughly studied. Most of the works dealing with detritus emphasized mainly on plant material or else undistinguishable detritus. One interesting work by Wheeler (1967) on copepod detritus in the deep sea showed that the concentration of copepod carcasses/m^3 was more than the living. This can be applied to the near shore environment as well so that the copepod detritus or fragments of dead organisms could be important to larger, more mobile predators, suhh as fishes and prawns that are unable to detect and capture smaller particulate matter. Faecal pellets may be recolonized by microorganisms and enter the detrital pool again. Several invertebrates may feed on their own faecal pellets such as the amphipod, Parhyalella whelpleyi (Fenchel, 1970).

Nutritional Aspects of detritus

Changes in the chemical composition of red mangrove leaves during biodecomposition are summarized by Heald (1971). An actively photosynthesizing leaf is found to consist of 6.1 percent protein, 1.2 percent fat, 15.7 percent crude fiber, 9.2 percent ash and 67.8 percent carbohydrate. These are expressed in percentage of ash-free dry weight. Mobilization and withdrawal of proteins and some soluble carbohydrates during the processes leading to abscission results in decreased protein (3.1 percent) and carbohydrate (59.6 percent) immediately before leaf fall. Fats are not mobilized and are increased to 6.3 percent. During the biodecomposition the large apparent increase of protein content appears in the first month. The carbohydrates are lost by 10 percent in the initial leaching process. Fat content is steadily declined as a result from fragmentation of the cuticle and microbial utilization of cellular fats. Changes in the relative chemical composition of mangrove leaves undergoing breakdown in brackish water for a period of twelve months are shown in Figure 1 and Table 3.

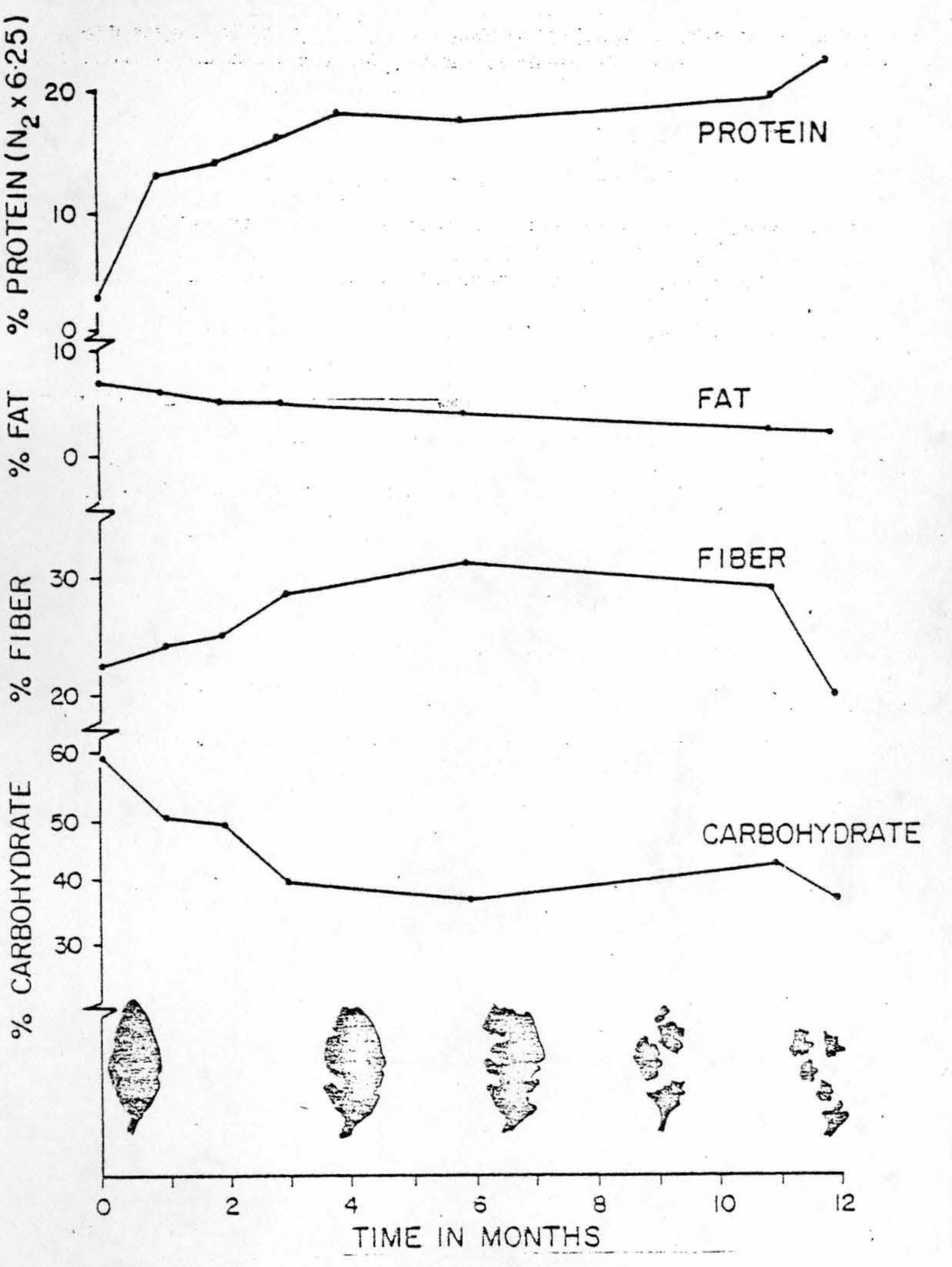


Figure 1. Chemical composition of red mangrove leaves during degradation in brackish conditions. (From Heald, 1971)

Table 3. Chemical composition and caloric content of red mangrove leaves at successive stages of biodecomposition. (Derived from Heald, 1971)

Mangrove leaves	% Nitrogen	% Protein (nitrogen x 6.25)	% Fat	Caloric Value Kcal/gram
Fresh green leaves	1.5	9.4	1.2	9.564
Dead leaves prior to falling from tree	0.9	5.6	6.9	4.818
Submerged 1 month	2.1	13.1	6.2	5.020
2 months	2.3	14.4	5.3	5.085
3 months	2.8	17.5	5.3	4.568
4 months	3.1	19.4	-	4.602
6 months	3.3	20.6	-	4.647
12 months	-	-	1.7	4.433

Protein content increases throughout the twelve month period. If protein content is accepted as an indicator of the nutrient value of a food source, then the value of mangrove leaf increases as the leaf ages. The original plant protein will be lost gradually during the breakdown process, but it will be compensated by increases in the amount of fungal and bacterial protein as microbial colonization continues, as demonstrated in Figure 2.

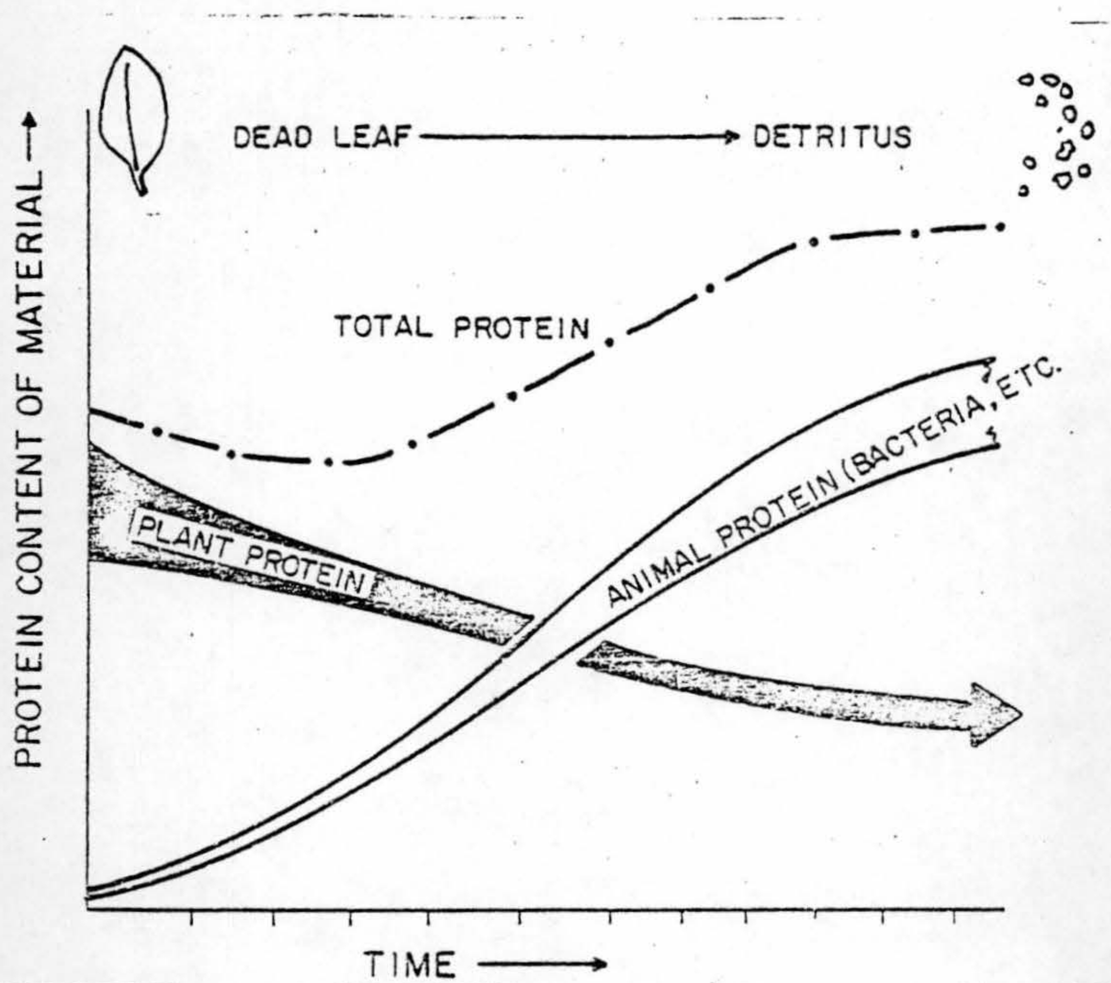


Figure 2
Diagram representing the principle of protein enrichment of red mangrove leaves during biode composition (From Heald, 1971)

The decomposing leaf with its associated micro-organisms are an important energy source for consumer organisms. Many studies showed that consumers gained nutrients from associated microorganisms on the detritus. Baier, as quoted by Heald (1971) and Seki (1972) was one of the first to hypothesize that detritus were resistant to digestion by organisms and that only the microbial fraction of the detritus can be digested. Baier divided bacteria feeders into three categories:

1) Those which feed directly upon bacteria (e.g., rotifers, copepods, ciliates, flagellates and larval stages).

2) Those which swallow the entire substrate, digesting certain portion and ejecting the rest (e.g., nematodes, *Tubifex*, chironomidae, mussel, ciliates, rotifers, flagellates).

3) Those which graze on solid surface (e.g., snails, ostracods, copepods, amoebas).

It has been found that protein content increased in detritus during biodecomposition is related not only to bacteria population but fungi as well (Heald, 1971). The importance of fungi as food is emphasized in relation to nematode colonization (Fell and Master, 1973; Fell, et al 1975; Meyers and Hopper, 1966, 1975).

Detrital Food Webs

There are many considerations in studying the food chain or food web of an ecosystem. First of all, food chains are simple and short-lived. As animals grow, the nature of their diet changes in accordance with the size and availability of prey organisms. Simple linear food chains are infrequently observed in nature. Food webs, in which populations have trophic relationship with a variety of food species and a variety of predators, are common. Moreover, seasonal changes in the composition of the population also change the food chains. So food chains are considered dynamic processes undergoing succession (Wyatt, 1976).

In order to understand the food webs, it is necessary first to understand the trophic relationships of the individual organisms. This is accomplished by analyses of diets and arrangement of the organisms into a trophic sequence. The diet of each species through age should also be considered. Most of the food chain or food web diagrams based upon the actual data sampling at a place at particular time so the changes in diets of individual species is avoided. Seasonal changes in the population which might influence the food webs is also often ignored. In general, the food web diagrams are usually simplified as much as possible. They generally are used to represent the whole ecosystem.

Analyses of diets in organisms are not simple. The most common procedure is stomach-content analysis. Digestive process is involved. If the food is well digested, it might be hard to recognize or be totally absorbed and would not be present in the gut content. If the food is not digested, large fragments remain in the content. But should it be considered as food or diet since it is less usable to organisms. More accurate procedures in analyses of diets in organisms are needed.

In my attempt of looking into the food web diagrams for the mangroves in Southeast Asia, Hawaii and the East Coast of the United States, few studies have been made on the topic. The detritus-based food web diagram has been proposed for a mangrove in Florida (W. E. Odum, 1971; W. E. Odum and Heald, 1973). This is used as the basic frame for my construction of food webs for Hawaii and Southeast Asia. Simplified food web diagrams for each sampling station of Heeia Mangrove Swamp have been given by Walsh (1967). His sampling stations are located in different parts of the mangrove of different physical measurements. In Southeast Asia, food webs in defoliated and non-defoliated mangroves are compared. These are also compared between the dry and the wet season too (de Sylva, 1972).

In diagrams studied, the top predators are fishes. Birds and other mammals in the mangroves have been ignored in their roles within the food webs. The roles of meiofauna are not emphasized. I find this is important for the meiofauna may play three roles in the food webs; as the primary consumers, as top predators, and as detrital regenerators which bring detritus back into the system. Nematodes are good examples. They are considered the dominant meiofaunal representative. They feed selectively to non-selectively on sedimentary deposit. They also feed as epigrowth feeders and predators (Meyers and Hopper, 1973).

Food Webs in Mangroves of the East Coast of the United States

There are at least four ways by which the freshly fallen leaf organic material may be utilized by the heterotrophic community: (1) dissolved organic substances ⟶ microorganisms ⟶ higher consumers, (2) dissolved organic substances ⟶ sorption on sediment particles ⟶ higher consumers either directly or by way of microorganisms, (3) leaf material ⟶ high consumers, (4) leaf material ⟶ bacteria and fungi ⟶ higher consumers. The first two routes are based upon the rapid loss of water-soluble organic substances which occurs during the first few weeks after the leaf enters the water. Soluble organic substances of mangrove leaf origin either may be used by bacteria and other microorganisms directly from the water or may become sorbed upon fine organic and inorganic particles in suspension or in the surface sediments. These particles, in turn, may be ingested by fishes and invertebrates and the sorbed substances removed in the digestive tract and assimilated by the animal. The third route, that of leaf material serving directly as a food source for higher consumers, may be important early in the biodecomposition process when the leaf still retains significant amounts of digestible plant proteins, fats and carbohydrates. The fourth route depends upon the ability of bacteria and fungi to break down the leaf material. Bacteria and fungi serve as the major food source for microorganisms (W. E. Odum, 1971).

The principal flow of energy in the North River food web is summarized by W. E. Odum (1971). The route is mangrove leaf detritus ⟶ bacteria and fungi ⟶ detritus consumers ⟶ lower carnivores ⟶ higher carnivores. A conceptual model of the North River food web is shown in Figure 3. The diagram of the detritus-consuming omnivorous organisms of the North River estuary is given in Figure 4.

North River trophic groups are herbivores, omnivores, lower carnivores, middle carnivores and top carnivores. In his diagram, herbivores include heterotrophic bacteria, meiofauna and macrofauna such as copepods and insect larvae. Herbivores are defined as organisms which are primarily plant eaters but on occasion derive some nourishment from animal tissues such as microorganisms absorbed on the particles surface. Omnivores are those animals that can exist on a diet of either plant and animal materials. These herbivores and omnivores are considered detritus consumers which play the important link between the detrital food source and the secondary consumers such as other omnivores and carnivores. Detritus consumers are defined as organisms whose digestive-tract contents averaged at least 20 percent vascular plant detritus by volume on an annual basis. Table 4 is the list of detritus consumers found in North River estuary.

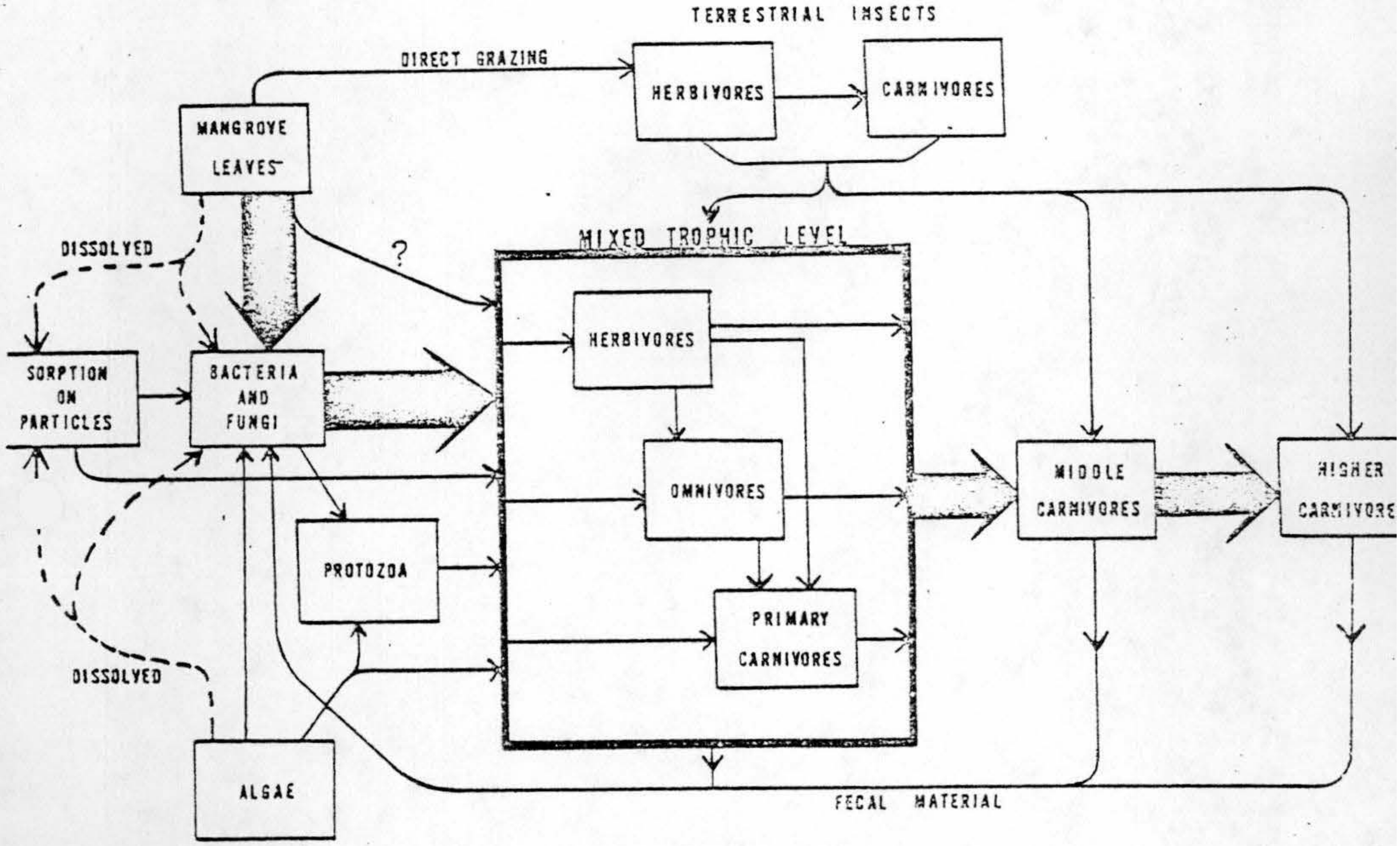


Figure 3. A Conceptual Model of the North River, Florida, food web showing the most important flow of energy as a broad arrow, less important food chains as narrow arrows and the pathway of dissolved leaf material as a dotted line (From W. E. Odum, 1971).

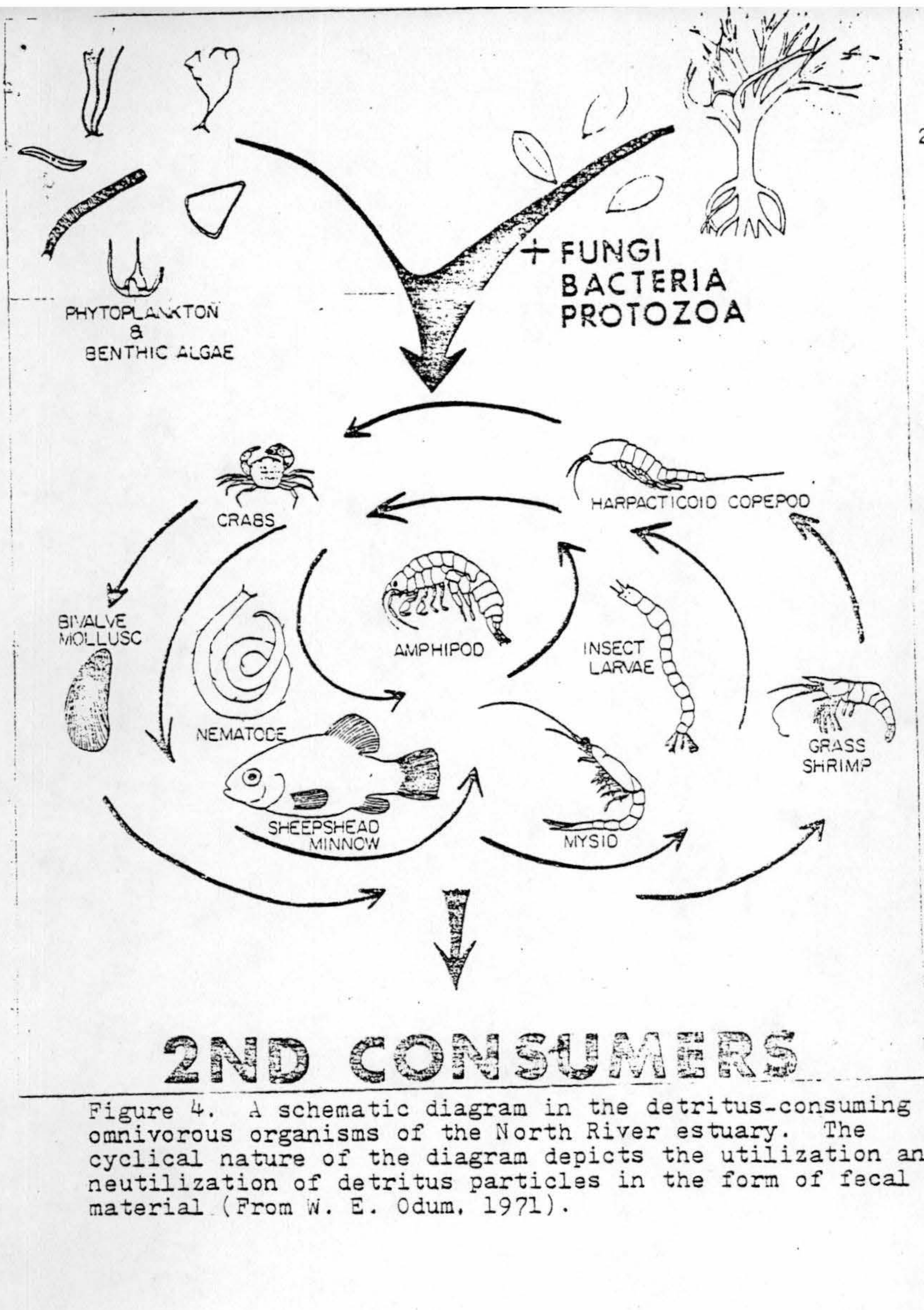


Figure 4. A schematic diagram in the detritus-consuming omnivorous organisms of the North River estuary. The cyclical nature of the diagram depicts the utilization and neutilization of detritus particles in the form of fecal material (From W. E. Odum, 1971).

Table 4. Detritus consumers in North River estuary, Florida. These are organisms whose digestive tracts contained at least 20% vascular plant detritus on average (From W. E. Odum, 1971).

Fish:	Sheepshead killifish	*Cyprinodon variegatus*
	Goldspotted killifish	*Floridichthyes carpio*
	Diamond killifish	*Adinea xenica*
	Sailfin molly	*Poecilia latipinna*
	Crested goby	*Lophogobius cyprinoides*
	Striped mullet	*Mugil cephalus*
Annelids polychaetes		*Nereis pelagica*
		Neanthes succinea
Crustacea	Cumaceans	
	Mysids	
	Harpacticoid and planktonic copepods	
	Amphipods	
	Ostracods	
	Caridean shrimps	
	Snapping shrimp	*Alphaeus heterochaetis*
	Crabs	*Rhithropanopeus harrisii*
Insects	Chironomid midge larvae	

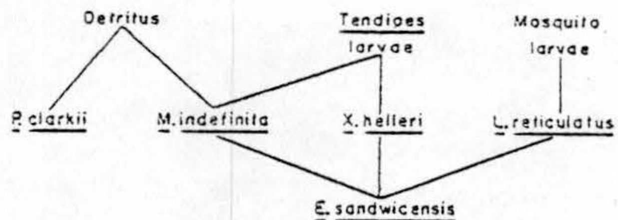
It should be noted that Odum considered mangrove leaves, phytoplankton and benthic algae as the major sources of detritus. He did not consider the source of detritus from dead organisms in his diagram. He also added the meiofaunal group in the herbivores category and emphasized protozoa as a distinct group.

Food Webs in Hawaiian Mangroves

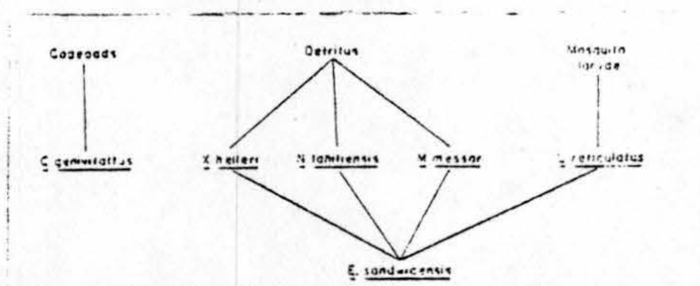
Walsh (1967) conducted an ecological study in Heeia Mangrove Swamp in Hawaii. He constructed simplified food webs for each sampling station based on the qualitative faunal and stomach-content analyses as shown in Figure 5.

Figure 5. Food webs at stations 1, 3, 6 in Heeia Mangrove Swamp. The first trophic level is shown at the top (From Walsh, 1967).

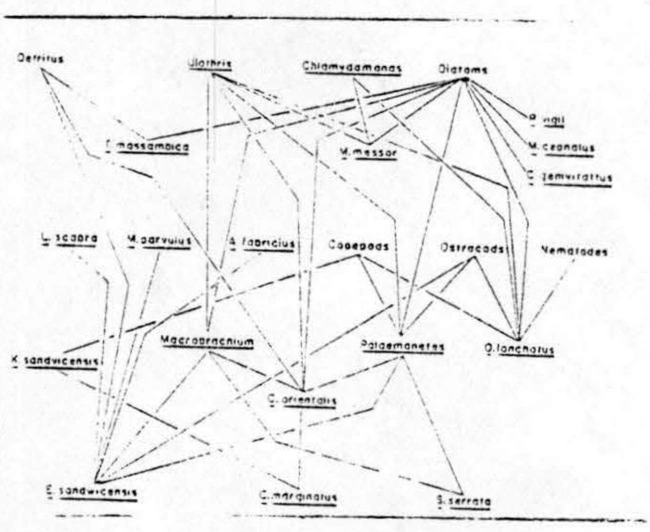
Station 1



Station 3



Station 6



Can't read

From Walsh's data, I divided the organisms into different trophic groups as herbivores, omnivores, lower carnivores and top carnivores as shown in Table 5.

Table 5. Trophic groups of macrofauna in Heeia Mangrove Swamp, Hawaii (Data from Walsh, 1967).

Herbivores

- Pisces
  - Xiphophorous hellerf
  - Tilapia mossambica
  - Mugil cephalus
  - Chonophorous genivittatus
- Mollusca
  - Neritina tahitiensis
  - Littorina scabra
  - Melampus parvulus
- Arthropoda
  - Procambarus clarkii
  - Mosquito larvae
  - Tendipes tentens larvae
  - Copepods
  - Ostracods
  - Metopograpsis messor
  - Macrobrachium sp.
  - Podophthalmus vigil
  - Alpheus fabricius makayii

Omnivores

- Mollusca
  - Melania indefinita
  - Pisidium sp.
- Arthropoda
  - Charybdis orientalis
  - Palaemonetes sp.

Lower carnivores

Pisces

Lebistes reticulatus

Xiphophorous helleri

Kuhlia sandvicensis

Oxyurichthyes lonchotus

Arthropoda

Palaemontes sp.

Top Carnivores

Pisces

Eleotris sandwicensis

Conger marginatus

Arthropoda

Scylla sevrata

* Some macrofauna are left out from the trophic group list.

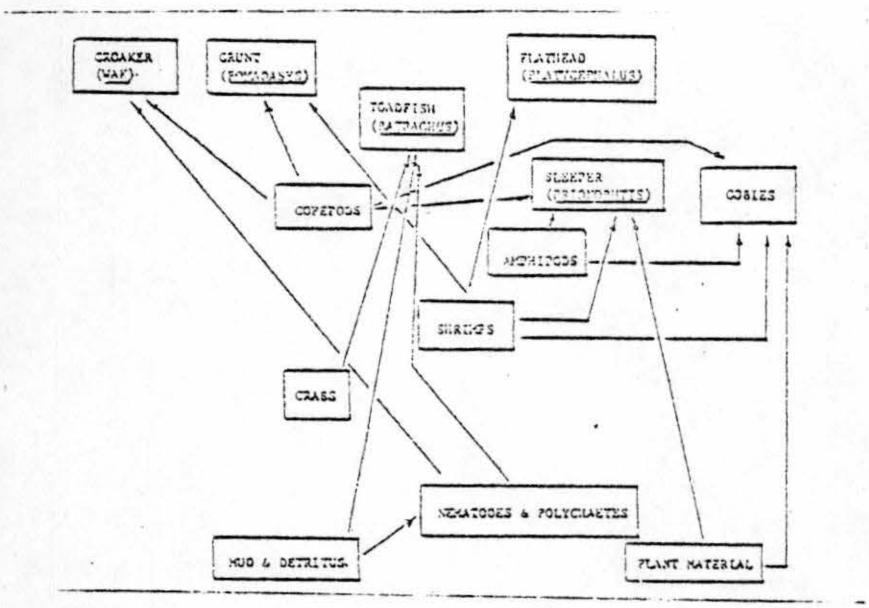
Walsh's food webs are more localized and did not give the picture of the whole mangrove food webs. Microorganisms as well as birds and mammals have not been considered.

Food Webs in Southeast Asian Mangroves

In Southeast Asia, studies of food chains and food webs are scarce. Few trophic relationships, which are the basic for food chain studies, have been analyzed. De Sylva (1972) has studied the effects of military defoliation from various herbicides on the estuarine ecology in South Viet Nam. He found that the food webs in the non-defoliated mangroves are more complex than the defoliated forest. In the defoliated mangrove forest of the Rung Sat Zone, the food web during the wet season is simple. Detritus becomes an important food source in the more complex dry season food web. This is in contrast with the non-defoliated estuary. During the wet season, the complex food web derives energy from detritus food source. Phytoplankton is believed to be the energy source for the dry season. These food webs are shown in Figures 6, 7.

Figure 6. Food webs in a non-defoliated estuary, Vung Tau, South Viet Nam in the dry and wet season (From de Sylva, 1975)

A. Wet season



B. Dry season

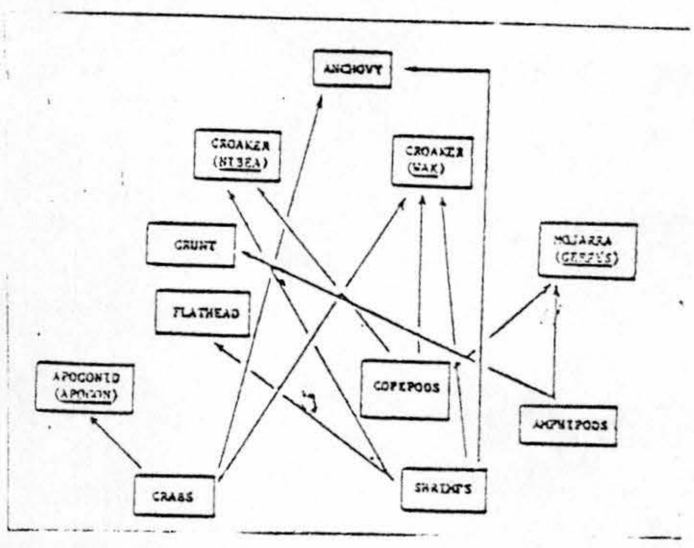
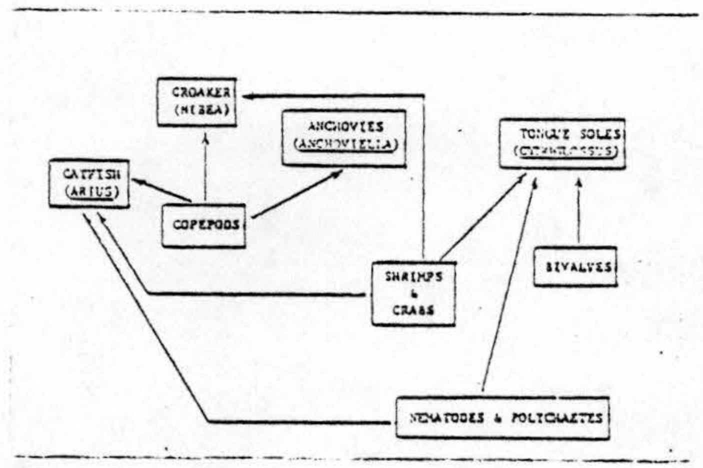
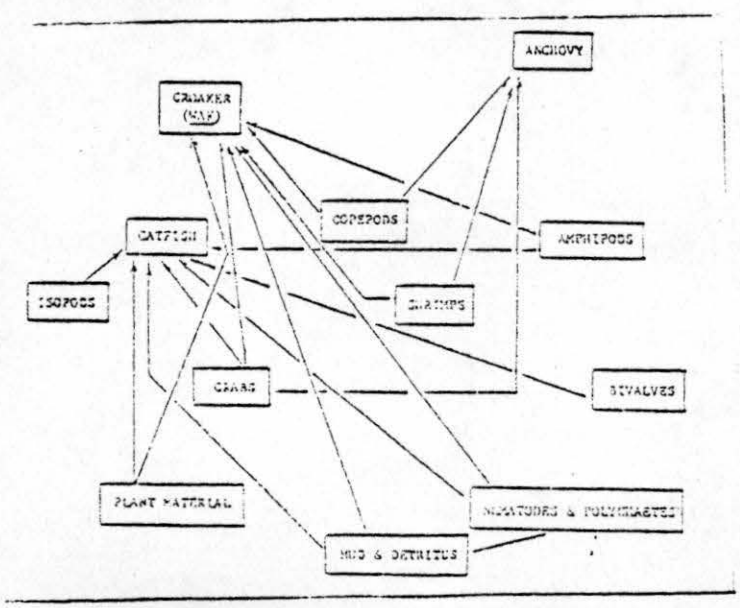


Figure 7. Food webs in a defoliated estuary, Rung Sat Zone, ~~South Viet~~ Nam in the dry and wet season (From de Sylva, 1975)

A. Wet season



B. Dry season



The food webs shown here are oversimplified. In some diagrams, the primary source of energy such as detritus and phytoplankton are left out. Nekton receive more attention. From these food webs, I divided the organisms into different trophic groups as summarized in Table 6.

Table 6. Trophic groups in non-defoliated mangrove, Vung Tau and defoliated mangrove, Rung Sat, South Viet Nam (deroved from de Sylva, 1975)

Herbivores
- Pisces
  - Gobies
- Arthropoda
  - Copepod
  - Amphipod
  - Isopod
- Mollusca
  - Bivalves

Omnivores
- Pisces
  - Sleeper *Prionobutis*
- Arthropoda
  - Crabs
  - Shrimps
- Polychaeta
- Nematoda

Carnivores
- Croaker *Wak*, *Nibea*
- Grunt *Pomadasys*
- Toadfish *Batrachus*
- Mojarra *Gerres*
- Apogonid *Apogon*
- Flathead
- Catfish *Arius*
- Anchovies *Anchoviella*
- Tonguw aolwa *Gynoglossus*

I want to emphasize ~~on~~ the mangroves in Thailand and Malaysia. Macrofaunal studies in the mangrove swamps have been made but none on the food webs or trophic relationships. Macnae (1968) gave an intensive account on the fauna and flora of mangrove swamps in the Indo-West Pacific region. Sasekumar (1974) studied the distribution of macrofauna on a Malayan mangrove shore. Zonation of macrofauna, on a mangrove shore, Phuket Island, Thailand was studied by Frith and et al (1976). From these data I looked for similar organisms in different locality and divided them into various trophic groups as in Table 7.

Proposed Model of the Food Web in the Mangrove Ecosystem

In this model, I want to indicate sources of detritus in the mangroves. Trophic levels are divided into the following:

1) Heterotrophic microorganisms-bacteria, fungi.

2) Meiofauna-protozoa, ciliates, nematodes, rotifers.

3) Herbivores - those that assimilate plant material directly by grazing or consuming microorganisms or neiofauna from detritus.

4) Omnivores - those that assimilate both plant and animal material whenever available. The meiofauna, herbivores and omnivores can be called detritus consumers or detritus feeders.

5) Lower carnivores - those that depend upon animal tissues as food usually small animals.

6) Top carnivores.

The model is shown in Figure 8.

Table 7. Trophic groups in Southeast Asia mangroves with emphasis on Thailand and Malasia (derived from Frith, et al, 1976; Macnae, 1968; Sasekumar, 1974)

Herbivores

Mammalia

Leaf monkey *Presbytis cristatus*

Arthropoda

Mosquitos

Flyflies

Isopods

Cirripedes *Balanus amphitrite*

Chthamalus withersii

Mud-lobsters Family Callianassidae

Ocypodid crabs Family Ocypodidae

Mollusca

Lamillibranch molluscs Family Ostreidae

Polychaeta

Sedentary polychaetes

Sipunculida

Omnivores

Pisces

Mud skipper *Boleophthalmus*

Arthropoda

Amphipods

Isopods

Grapsid crabs Family Grapsidae

Xanthid crabs Family Xanthidae

Fiddler crabs *Uca* spp.

Anomuran crabs Family Paguridae, Coenobitidae

Alpheid prawn *Alpheus* spp.

Mollusca

Gastropods Family Neritidae, Littorinidae

Assimineidae, Ellobiidae

Polychaeta

Errant polychaetes Family Nereidae

Carnivores

Mammalia

Fish cat *Felis viverrima*

Mongooses *Herpestes*

Aves

Cormorants

Heron *Egretta eulophotes*

Sea eagle *Haliastur* sp.

Kingfishers

Woodpeckers *Picus viridanus*

P. vittatus

Amphibia & Reptilia

Hydrophiid snakes

Frogs *Rana* spp.

Crocodiles

Pisces

Mud skipper *Periophthalmus*

Mollusca

Murex Family Muricidae

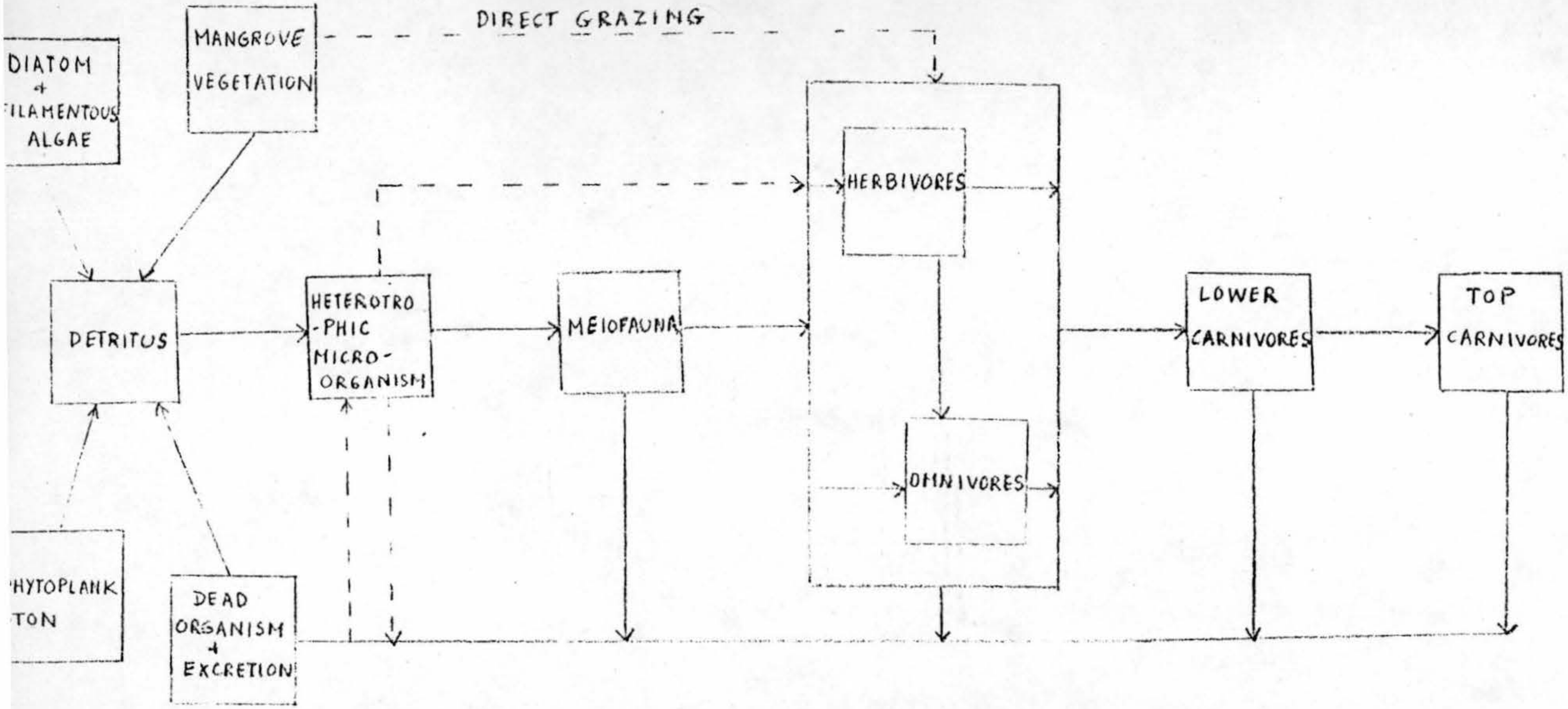


Figure 8. Proposed Model of the food web in the mangrove ecosystem. The dark line indicates the main pathway while the dotted line indicates the alternative pathway.

Roles of Organisms at Each Level of the Food Web

Trophic groups of organisms from various mangroves can be filled in this general model.

1) Heterotrophic microorganisms

Bacteria and fungi play an important role in the breakdown process of detrital particles. Furthermore they enrich the nutritional values of detritus by increasing the protein content. They are the major food sources for meiofauna.

2) Meiofauna

Meiofauna are detrital feeders or indiscriminate feeders on bacteria and benthic diatom. There is a complexity in the meiofauna food web. Each major taxonomic group may have different feeding types, with each species feeding on various material in the sediment. Small turbellarians may be the top of the food chain in some systems. As active predators they will attack larger forms and either swallow their prey whole or suck out the prey with strong jaws and a muscular pharynx, respectively. Many macrofauna may skip the intermediate meiofauna link and feed directly on bacteria and protozoa. They will occupy the same trophic level as their smaller meiofauna counters and they are competing with each other. As dead meiofauna are rapidly broken down by bacteria action, these will assist in the recycling of nutrients at a low trophic level (Coull, 1973).

3) Herbivores

Herbivores are organisms that assimilate plant material directly by grazing or consuming microorganisms or meiofauna from detritus. There are some fishes that feed on both microalgae and decaying detritus. These fishes will shorten the food chains by replacing the zooplankton or other macrofauna as the critical herbivore link. Striped mullet, *Mugil cephalus* studied in Florida mangrove swamp is a good example (W. E. Odum, 1970). Mullets have a pharynageal filtering device which enables them to suck up surface layers of mud and select the very fine particles. The gut contents consistently had higher organic matter content than the deposits on which they were feeding. The fish also feed on microalgae from the surface of the sediment and macrophytes.

4) Omnivores

Omnivores are organisms that assimilate both plant and animal material. They usually ingest more plant material than animal material. Omnivores can either feed on herbivores or be on the same trophic level by competing for the detrital food source.

Meiofauna, herbivores and omnivores are considered as detritus consumers or detritus feeders. There are at least three major types of detritus feeders: (a) grinders, (b) deposit feeders, and (c) filter feeders (W. E. Odum and Heald, 1975). Amphipod and most crabs are grinders which fed on large pieces of leaf material which are masticated into smaller particles. Polychaetes are usually considered deposit feeders. Bivalves are the best example of filter feeders

5) Lower carnivores

These species, predominantly small fishes, feed on the preceding herbivorous and omnivorous groups. In this category might include some wading birds and game fishes.

6) Top carnivores

These species form the top of food chain including predacious fishes, wading birds, mammals, amphibia and reptiles. Their food derives from all the lower trophic levels, but the most common ingested organisms are from the lower carnivores level.

It is hard to assign the trophic level to a certain group of organisms for they have varied diets. Their feeding habit might change through the life cycle. Juvenile forms may be strictly herbivores feeding on microalgae. But adults may be predacious carnivores.

External Factors that alter the Food Webs

Other than the changes in feeding habit in the organisms themselves that might change the whole relationship, external factors mainly seasonal changes and man-made causes such as defoliation, forest clearing or burning are also important. Seasonal changes in the Monsoon area such as Southeast Asia can have a great influence on the structure of the food chain. This is because of the changes in species composition and abundance of both plants and animals. De Sylva (1975) studied the food web during the wet and the dry season in a nondefoliated coastal region near Vung Tau, South Viet Nam. The food web during the wet season is complex with several pathways and trophic levels. During the wet season, the primary source of energy is detritus, while during the dry season it is believed to be phytoplankton. Heavy rainstorms can cause mass mortality of mangrove fauna. Three separate events of mass mortality among sessile marine organisms in Kingston Harbor, Jamaica following heavy rainstorms, have been reported by Goodbody (1961). The river flooding is not necessarily the only cause of the disaster but in an enclosed mangrove lagoon the runoff from the mangroves themselves is also of importance in killing organisms attached to the mangrove roots. This is mainly due to drastic salinity changes.

Effects of defoliation by herbicides on estuarine ecosystem in South Viet Nam are one of the results from the Second Indochina War. An estimated 124×10^3 ha of true mangrove plus 27×10^3 ha of rear mangrove were subjected to military herbicide spraying. A single spraying most often destroys the entire plant community. Both food and cover were eliminated by the U.S. attacks not only for its enemy forces but for most organisms as well. The primary producers are essentially wiped out. Various aquatic animal populations have been depleted as a result of the mangrove destruction. The few remaining survivors were apparently no longer reproducing. An enormous reduction in the number of birds were reported. Population levels of the clam, Polymesoda coaxans (Corbiculiidae) were depleted (de Sylva & Michel, 1974; Tschirley, 1969; Westing, 1971, SIPRI report, 1976). In the defoliated mangrove forests of the Rung Sat Zone, the food web during the wet season is simple. It was expected that the devastation of mangroves would result in large amounts of detritus accumulating at the bottom of the estuaries, but because the strong tidal currents carry them away from the estuaries, very little is available as a food source. The food web during the dry season is more complex deriving from detritus as the major food source (de Sylva, 1975).

Discussion and Conclusion

Several problems are involved in attempting to construct the food chain or food web for an estuarine ecosystem. First of all, there are two basic types of estuarine food webs. The first is based primarily upon detritus but always with a component of phytoplankton and benthic algae. The key organisms in this food web are a group of detritus feeders. This type of food web is characteristic of shallow, muddy estuaries with extensive plant communities of marsh grasses, sea grasses and mangroves. The second type is the grazing food web based upon phytoplankton and dependent upon a key group of zooplankton and zooplankton grazers. This type of food web is found in deeper estuaries with clearer water. Each estuary probably has a tendency to be dominated by one type of food web, tub both types will always be present (W. E. Odum and Heald, 1975). In studying the detritus-based food web, the first problem that we encounter is the definition of the word "detritus." Detritus is an ambiguous word and needs to be defined in each case. Sources of detritus into the system depend upon the definition of detritus. Secondly, it is hard to assign the organisms to different trophic levels. This needs tremendous efforts. Stomach analysis is often the useful tool. It is usually hard to determine the origin of digested fragments in the stomach. Moreover the undigested fragments found might be interpreted as the main food of the organism but in the early stages of digestion. It could also be interpreted that the food eaten is not assimilated by the organism. Procedures for stomach analysis are needed. A technique which has a great promise for identification of food chains in coastal ecosystems is the analysis of bio-chemical pathways. Jeffries (1972) has shown that marsh grasses have a biochemical pattern characterized by fatty acids that are 16 to 18 C-atoms in length, while marine animal tissue tends to be rich in long-chain (C 20-22) polyunsaturated acids. The fatty acid spectrum of detritus in a cove bordered by <u>Spartina</u> was dominated by 16C-atom chains. When the gut contents of the fishes <u>Fundulus majalis</u> and <u>Fundulus heteroclitus</u> were examined, it was found that their fatty acids composition could most reasonably be explained by a diet consisting of 5 parts detritus to 1 part marine invertebrates.

Food web is a dynamic process that undergoes succession. The feeding habit of organisms may change throughout their life cycle. This can alter the food web. Seasonal changes and man-made causes such as defoliation, forest burning and pollution may initiate the changes in the food web.

I proposed a general model for the detrital food web in the mangrove ecosystem. Four sources of detritus in the mangrove are phytoplankton, diatom and filamentous algae, mangrove vegetation and dead organism and excretion. Five important trophic levels are involved: heterotrophic microorganism, meiofauna, herbivores, omnivores, lower carnivores and top carnivores. The main pathway is detritus → heterotrophic microorganism → meiofauna herbivores → omnivores → lower carnivores → top carnivores. In most cases, the taxonomic studies of microorganism and meiofauna have been ignored. Only macrofauna and fishes are emphasized. From the trophic groups for each mangrove ecosystem, we can easily construct the food web simply by filling in the components in each trophic level.

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