CHAPTER 4

DISCUSSION

1. Environmental conditions

The mangrove forest is a characteristic feature of tropical coasts. It usually provides a muddy environment with the mangrove vegetation growing well in seawater of the inundated muddy soil. Mangrove plants support themselves above the mud by means of either prop roots (e.g. in *Rhizophora spp.)* or pneumatophores (e.g. in *Avicennia spp.)*. These root systems would obstruct tidal water movement and entrap the fine sediment of silt-clay. The mangrove canopy serves as a sun shade providing underneath cool, humid environment for those tree fauna and mud dwellers. The tree trunks and prop roots provide secure substrates for barnacles, oysters and many other mollusc fauna; whereas the soft mud substrate provides a habitat suitable for both surface and burrowing fauna. The problems of water loss, wave action and extreme high temperature, which are generally characteristic of sandy and rocky shores (Eltingham, 1971; Brasfield, 1978) are reduced in the mangrove biotope.

The mangrove stations of the present study were covered by a variable number of tides in a year. Most of the mangrove areas were wetted by more than 40% of the tides. Tidal inundation, or in the other hand exposure to the air, would partly limit the distribution and abundance of mangrove animals; since many mangrove fauna are tide dependent, especially in relation to the modes of feeding.

Soil factors, including the particle size, organic and moisture content and the consolidation, differed significantly from station to station (Table 2). These factors also played an important role in regulating the pattern of animal distribution and abundance. In the landward innermost station of the mangrove forest, the substrate was comparatively coarse, and it became finer towards the sea and the mud flat. High organic content was found in the mangrove forest. Probably it might be due to a great amount of deposited organic detritus, resulting from the breakdown of mangrove plant material. Soil water pH tended to be more acidic in the mangrove forest and alkaline in the mud flat. The activities of sulfur reducing bacteria might cause the acidity of mangrove soil by production of hydrogen sulfide (Hart, 1959, cited from Sasekumar, 1974), but in itself rapid bacterial decomposition of organic matter will increase the concentration of carbon dioxide, resulting in slightly acidic soils. The mud flat soil showed slightly alkaline condition (see Table 2, compared to Station 1 where the organic content was almost the same. It might be due to photosynthesis by soil microalgae which in the brightly illuminated mud flat can raise the oxygen content. At the same time withdrawal of carbon dioxide during photosynthesis raises pH of the pore water.

2. Species composition and density

The result has shown that the mangrove macrofauna at Ko Maphrao is dominated by polychaetes, crustaceans and molluscs. Species composition within these groups is more or less similar to the composition studied by Berry (1963) and Chuang (1961) in Singapore; Berry (1972) and Sasekumar (1974) in West Malaysia; Wong et al. (1980) in East Malaysia: Frith et al. (1976) and Nateewathana and Tantichodok (1980) in Southern Thailand; Isarankura (1976a, 1976b) in the upper Gulf of Thailand. The predominance of crustaceans and molluscs is also a common feature of mangrove macrofauna found in the other mangrove forests elsewhere (Macnae and Kalk, 1958 in Mozambique; Hutchings and Recher, 1974, in Australia).

Many polychaete species were found in the Ko Maphrao mangrove forest. The result supports the view of Frith et al. (1976) and Sasekumar (1974) that very few polychaete species have been found in the Indo-West Pacific region and other regions, except in localities of Southeast Asia. Morover, more new species have been found from the mangrove forests in Southern Thailand and they have never been recorded, perhaps never been described (Hylleberg and Nateewathana, pers. comm.). The reason why polychaetes have not been commonly recorded outside Southeast Asia is not fully understood. However, Sasekumar (1974) suggested that the abundance of polychaetes might be due to the less acidic soil condition and more constantly moisture.

Little is known about the biology, especially the feeding types, of mangrove dwelling polychaetes. Table 9 summarizes the expected feeding modes of mangrove polychaetes in families, based on the information from Day (1967); Fauchald and Jumars (1979). Most of the polychaetes

Table 9. Type of feeders of polychaetes found in Ko Maphrao mangrove (compiled from Fauchald and Jumars, 1979 and Day, 1967)

Family	Type of feeder
Orbiniidae	Detritus feeder
Capitellidae	Detritus feeder
Maldnidae	Detritus feeder
Ophelidae	Detritus feeder
Phyllodocidae	Detritus feeder and carnivore
Polynoidae	Detritus feeder and carnivore
Polyodontidae	Scavenger and omnivore
Nereidae	Omnivore and detritus feeder
Goniadidae	Carnivore
Onuphidae	Detritus feeder, omnivore
Eunicidae (*Marphysa sp.*)	Detritus feeder and herbivore
Lumbrinereidae	Detritus feeder and carnivore

in the mangrove forest are believed to be detritus feeders. All polychaetes studied so far are capable of absorbing dissolved organic matter (amino acids) from seawater (Southward and Southward, 1972; Hylleberg, pers. comm.).

The crustaceans were represented predominantly by two families of decapodid Crustacea, Ocypodidae and Grapsidae. The crustacean fauna is a very diverse group and a major component of macrofauna in the mangrove forest. It was numerically abundant, and it contributed with a high biomass as well. The crustaceans make burrows which protect them from temperature and salinity stress, predators, and aggression from other crabs (Macintosh, 1977). The crabs also possess special biological adaptations which appear to suit the life in the mangrove forest (Berry, 1972; Malley, 1977). The crabs have to withstand considerable periods of time out of the water (being exposed to air) during low tides; therefore they manage to breathe in air by specialized mechanisms described by Macnae (1968) and Newell (1970). At low tides, they were seen scraping mud on the surface soil. The majority of crustaceans in the mangroves are detritus feeders. Ronhave and Tantichodok (pers. obs.), in a study on seven species of mangrove crabs at Ao Yon, Phuket, found that the stomach of three grapsid species and the fiddler crabs, *Uca lactea* and *U. vocans*, contained a lot of sediment grains, pieces of vascular plants and diatoms. Only a hermit crab *Diogenes avarus* contained some blue green algae indicating herbivory, while small crustacean appendages were dominating in *Thalamita crenata* indicating carnivory. Malley (1978) found that the stomach content of *Chiromanthes onychophorum* (Grapsidae) consisted almost entirely of mangrove leaf material, suggesting that the crabs play a role in mangrove litter decomposition.

Fiddler crabs, *Uca spp.*, constitute one of the most abundant and characteristic groups of crabs. Their ecology and population structure have been extensively investigated in Southeast Asian region (Frith and Brunenmeister, 1980; Frith and Frith, 1977; Macintosh, 1977, 1978). Macintosh (1977, 1980) considered *Uca spp.* as one group of the crabs which play andimportant role in the mangrove food chain. Other crabs which also play a significant role are *Metaplax, Macrophthalmus, Ilyoplax,* and *Sesarma*. However, the ecology and population studies of many dominant groups are still lacking; for example, *Upogebia sp., Tylodiplax tetratylophora* (common in Ko Maphrao mangrove forest) *Ilyoplax spp.* and many grapsid species. They should merit further investigation of their ecological importance.

Of all the molluscs collected, gastropods were the most numerous (27 species), followed by pelecypods (16 species). The pelecypods, often referred to as bivalves, were found in very few numbers, except the small mussel *Musculista senhousia* in the mud flat. The molluscs in the mangrove biotope were dominated by gastropod fauna, whereas in the mud flat they were dominated by pelecypods. Molluscs can be divided into four main feeding categories, filter feeders, deposit feeders, grazers and carnivores. The bivalves, such as cementing oysters, byssus attached mussels, and most burrowing clams, are filter feeders. These species of pelecypods were found more common in the seaward station, the mud flat station and the channel mud banks, where there would be richer supplies of planktonic diet brought in by the tides. *Tellina capsoides* and *T. opalina* represent deposit feeding bivalves found in the study area. The grazers and carnivores carnivores were represented by gastropods, which feed on microalgae, detritus and detritus-associated microorganisms. In addition, the gastropod species, *Naquetia (= Murex) capucina*, and *Polinices flemingiana* are carnivorous. Nielsen (1976) reported *N. capucina* feeding on *Saccostrea cucullata* through small holes bored in oysters, and also on barnacles, *Balanus amphitrite*.

The gastropods that live in mangroves also experience long periods out of water. They are structurally adapted to breathe in air (Macnae, 1968; Berry, 1972) by means of mantle cavity modified into an air-breathing lung. Houlihan (1979) showed that three species of mangrove snails, *Nerita articulata, Cerithidae obtusa* and *Cassidula aurisfelis* are essentially air breathing fauna. Many species, e.g. *Littorina scabra*, always crawl high up the trunk during high tides in order to avoid being submerged (Nielsen, 1976). According to Macnae and Kalk (1958), many tree dwelling gastropods feed on the microflora on the tree trunks, leaves and branches.

Some phyla have only few representatives found in the study area, but the species present can be abundant. A sipunculan *Phascolosoma arcuatum* was the most abundant in the mangrove biotope and was not found elsewhere. They were very common even in an anoxic soil. Little is known about the biology of this sipunculan species. It is believed to feed on detrutus and also play a role in bioturbation of the sediment.

The common fishes at the Ko Maphrao mangrove forest were *Periophthalmus vulgaris*, *Boleophthalmus boddaerti*, *Scartelaos viridis*, and *Ctenogobius vexillifer*, the former three species being the mud-skippers in Periohthalmidae, the latter representing the family Gobiidae. According to literature, *P. vulgaris* is carnivorous; while the other two species are deposit feeders, ingesting diatoms, blue-green algae and sediments containing meiofauna (Khoo, 1966; Lim, 1967, both cited from Macintosh, 1978). Macintosh (1978) also found that *P. vulgaris* is one of the major predators of small fiddler crabs. The other gobiid fishes are little known regarding the feeding habit, but they serve as a food item for the higher trophic level (Sasekumar and Thong, 1980).

3. Biomass and productivity of mangrove macrofauna

The macrofauna biomass (Table 8) shows that the highest value of 11.51 g dry weight m^{-2} was obtained in the middle mangrove forest (Station 2) and the lowest value of 4.62 g dry weight m^{-2} in the seaward mangrove forest (Station 3). The mud flat also provided a high biomass value of 11.17 g dry weight m^{-2}.

In comparison with other mangrove forests, Nateewathana and Tantichodok (1980) obtained biomass values ranging from 3.06-10.23 g dry weight m^{-2} in Ko Yao Yai mangrove forest and 9.84 g dry weight m^{-2} from the mud flat. The biomass values from both mangrove forests are in the same order of magnitude. A further comparison can be made between the Ko Maphrao mangrove forest and the Southern Puerto Rican mangrove forest. Golley et al. (1962) gave the biomass estimate of 6.4 g dry weight m^{-2} which was within the range of the present study.

The dry weight values were converted to calorific values by using a conversion factor of 4.23 kcal per g dry weight (Cummins and Wuycheck, 1971). Since no direct measurements of macrofauna production were made, in attempt to estimate the animal production from the mangrove forest, the P/B (productivity/biomass) ratio from the literature was used to convert the biomass into production. The mean P/B ratio of 1.76 was obtained from Moore (1972), in his study of macrofauna of a muddy sand environment in Florida. This ratio was also employed by Hughes and Gamble (1977) in a study of macrofauna of intertidal soft substratum in Aldabra Atoll, Indian Ocean. The highest animal productivity of 85.7 kcal $m^{-2} yr^{-1}$ was calculated for the middle mangrove station (Station 2) and the lowest in Station 3 of 34.6 kcal $m^{-2} yr^{-1}$ (see Table 10). The mud flat provided an annual production of 83.2 kcal $m^{-2} yr^{-1}$. The figures are high when compared to the value of about 15 kcal $m^{-2} yr^{-1}$ calculated for subtidal benthic production of Phuket area (Petersen and Curtis, 1980). This production of tropical mangrove animals is low compared to the production in the temperate zone, and it presents a puzzle since the turnover rates of animal production might be expected to be faster in the tropics. However, studies on direct measurements of animal production are needed to elucidate this problem.

On the average 20% of food intake would be utilized for secondary

Table 10. Estimates of total biomass, total productivity, productivity of detritus feeders and energy intake of macrofauna.

STATION	Total biomass (g dry wt. m^{-2})	Total biomass ($kcal\ m^{-2}$)	Total productivity ($kcal\ m^{-2}\ yr^{-1}$)	Productivity of detritus feeders ($kcal\ m^{-2}\ yr^{-1}$)	Energy intake by detritus feeders ($kcal\ m^{-2}\ yr^{-1}$)
1	7.07	29.91	52.64	47.38	236.9
2	11.51	48.69	85.69	77.12	385.6
3	4.64	19.63	34.55	31.09	155.5
4	11.17	47.25	83.16	74.84	374.2

production in the detrital food chain, according to Tait, 1972' He calls this a Gross Conversion Efficiency (G.C.E.) of 0.2, where

$$G.C.E. = \frac{\text{Calorific value of new tissue formed}}{\text{Calorific value of ingested food}}$$

Assuming 90% of total production of animals feeding on detritus and associated microorganisms, the productivity estimates of detritus feeders from the mangrove area were estimated (see Table 10). These estimates were then divided by G.C.E. of 0.2 to get the energy intakes to produce the new tissue of the detritus feeders annually. The result (Table 10) shows that the energy intakes of animals in the mangrove forest range from 155 - 385 kcal $m^{-2}yr^{-1}$ with a mean value of 259 kcal $m^{-2}yr^{-1}$ and of the fauna on the mud flat is 374 kcal $m^{-2}yr^{-1}$.

The total primary production of mangrove in Phuket was estimated to be 2700 g dry weight $m^{-2}yr^{-1}$ (roughly equivalent to 11,000 kcal $m^{-2}yr^{-1}$) by Christensen (1978), and leaf production is about 25% of total production (see Discussion : Section 4, Compartment 2). Odum et al. (1972) considered that the major export of mangrove production was leaf litters and half of the annual leaf production in a Florida mangrove swamp was exported into coast water. With these figures, the mangrove primary production of 9600 kcal $m^{-2}yr^{-1}$ would be in the mangrove forest for utilization. This amount of energy is 37 times of the mean energy intake estimate of mangrove macrofauna (259 kcal $m^{-2}yr^{-1}$). This indicates that the energy intake estimate is obviously out of proportion, compared to the energy produced by the mangroves. It might be explained by three reasons : firstly, the P/B ratio used is too low ; secondly, a certain amount of energy produced by mangroves is used up by bacteria and fungi, which are in turn fed on by meiofauna and macrofauna; and thirdly, the production of mangrove macrofauna is regulated by some marine predators which come into the mangrove by tides (see more details in Discussion : Section 4).

4. Considerations towards a conceptual model of a mangrove food web, with emphasis on the food sources.

A conceptual model of a mangrove food web is proposed in Fig. 6. The purpose of this constructed model is to describe briefly the significance of various food sources involving in energy transfer to higher trophic levels in the mangrove ecosystem, and also to speculate the role of the mangrove ecosystem in contribution (export) of organic enrichment to the nearby marine environment.

Sources of primary production

The input of primary production to the mangrove ecosystem is from six basic sources : 1. allochtonous particulate matter, 2. mangrove, 3. phytoplankton, 4. epiphytic microflora, 5. benthic microalgae, and 6. macroalgae.

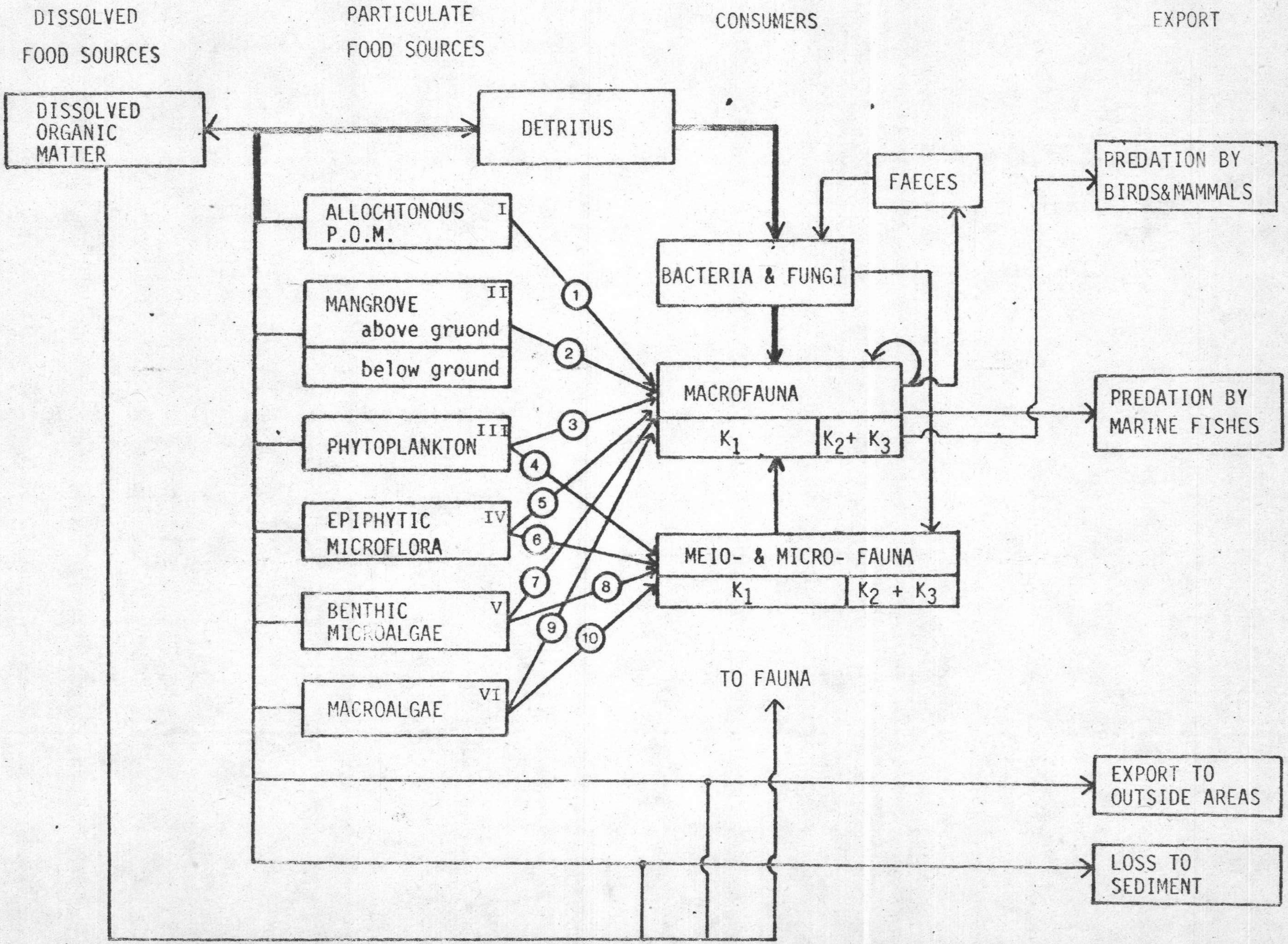
Allochtonous particulate matter (Compartment I)

It originates mostly from terrestrial plants, and includes organic matter in sediments carried by rivers into the mangrove forest. Some terrestrial leaves, e.g. coconut leaves, palm leaves etc., were seen floating in the water channels during high tides. These leaves were found to be chewed up by a polychaete *Marphysa sp.* (Hylleberg,

Figure 6. A conceptual model of a mangrove ecosystem with emphasis on food sources.

I-VI = Autotrophic compartments

1-10 = Routes or pathways from autotrophic compartments to heterotrophic compartments.


DISSOLVED FOOD SOURCES
PARTICULATE FOOD SOURCES
CONSUMERS
EXPORT
DISSOLVED ORGANIC MATTER
DETRITUS
FAECES
PREDATION BY BIRDS&MAMMALS
ALLOCHTONOUS P.O.M. I
MANGROVE above gruond below ground II
PHYTOPLANKTON III
EPIPHYTIC MICROFLORA IV
BENTHIC MICROALGAE V
MACROALGAE VI
BACTERIA & FUNGI
MACROFAUNA
K_1
$K_2 + K_3$
PREDATION BY MARINE FISHES
MEIO- & MICRO- FAUNA
K_1
$K_2 + K_3$
1
2
3
4
5
6
7
8
9
10
TO FAUNA
EXPORT TO OUTSIDE AREAS
LOSS TO SEDIMENT

pers. comm.). The energy transfer from Compartment I enters the heterotrophic macrofauna compartment via Route no. 1.

Mangrove (Compartment II)

It is believed that mangrove production is the most important source of energy, even though we do not know the exact proportion of mangrove production to the total production within the mangrove biotope. The role of mangroves as a detritus source to the adjacent coastal water has been well documented by Odum (1969), Heald and Odum (1970), Heald (1971), Heald et al. (1974) and Odum and Heald (1975). Mangrove production contributes principally in the form of leaf material, which is decomposed more rapidly than the wood and roots. A certain amount of the dead leaves falling from mangrove trees are carried away by tides, but some leaves accumulate on the forest floor where they are decomposed. Some freshly fallen leaves are ingested by a crab *Chiromanthes sp.* (Malley, 1978) and a polychaete *Marphysa sp.* (Hylleberg, pers. comm.). The mangrove plantation unit in Trang Province reported the seedlings damaged by grapsid crabs. Macnae (1966) also found *Sesarma sp.* gnawing seedlings in Australian mangroves. The fallen mangrove stumps are ingested by termites, isopods, a boring bivalve, *Teredo sp.*.

Mangrove leaf production and total net mangrove production of 670 and 2,700 g dry wight $M^{-2}yr^{-1}$ respectively in Phuket mangrove were estimated by Christensen (1978). The total net production has excluded underground production, because of difficulty of estimation. The underground production should not be neglected. Golley et al. (1962) found subterranean roots to be 44% of the total biomass, indicating that the underground production makes a significant contribution to the production.

Phytoplankton (Compartment III)

In the mangrove forest, there are a number of small and large channels which are the habitat for fishes and prawns. Phytoplankton in these waterways and adjacent water also contribute the production to the mangrove ecosystem. Wium-Andersen (1979) measured phytoplankton productivity in a bay adjacent to mangrove areas in Phuket and he obtained a high estimate of 468 g C m^{-2} yr^{-1}, equivalent to about 930 g dry organic matter m^{-2} yr^{-1}. Zooplankton productivity in the mangrove might be expected to be high. Some filter feeders, e.g. barnacles, oysters and other bivalves, derive their nourishment from phytoplankton (via Route no. 3). Meiofauna, such as copepods, are also believed to feed on phytoplankton (Route no.4).

Epiphytic microflora (Compartment IV)

Epiphytic microflora encompasses diatoms and blue green algae, which attach to the surface of mangrove trees, including prop roots and pneumatophores. Some snails (for example : *Littorina spp.)* graze on the microflora on leaf surface (via Route no. 5). Nematodes and other meiofauna are believed to feed on epiphytic microalgae (Route no. 6).

Benthic microalgae (Compartment V)

Benthic diatoms, flagellates and blue green algae are important benthic microalgae associated with sediments. The stomach contents of many macrofauna (e.g. crabs) contain benthic diatoms, blue green algae

(Route no. 7). Nematodes ingest significantly the benthic diatoms (Route no. 8).

Macroalgae (Compartment VI)

Macroalgae include many species of red algae, green algae and brown algae (Lewmanomont, 1976) in the sutdy of algae in mangroves. She recongnized two major groups : those attached to tree trunks or roots and those that grew on the mud flat. Macroalgae are diets for both macrofauna and meiofauna (Route nos. 9 and 10).

All the autotrophic compartments mentioned above would be canalized in two directions, i.e. export from the mangrove ecosystem or remain in the mangrove forest in other forms of organic matter.

The export to the outside mangrove areas is always facilitated by tidal actions. Dead leaf material, particulated organic matter of tissues are transported during high tides. There is also an import from the sea, but it seems small compared to the export. Heald (1971) showed that the net export of fine particulate organic matter was about 50% of the total annual production of particulate organic matter. Leaf export estimate from the studied mangrove is not available at present, but it should be expected to be a high magnitude. The export also includes dissolved organic matter resulting from degradation of dead plants and animal tissues and photosynthesis process. Soluble organic compounds (simple sugars, starchs, organic acids) are liberated into the water; some components are utilized by the animals (through active uptake mechanism) and heterotrophic diatoms (Hellebust and Lewin, 1977; Poovachiranon and Chansang, 1980).

Another export pathway is the loss of organic matter to the sediments. Zobell (1946) believed that 99% of organic matter is minieralized in the ocean and the rest 1% is lost to the bottom sediments. This may be applicable to mangroves also. The organic matter is lost to the sediments in the form of humic acids which are not potentially a food source for the organisms. The humic acids have a turnover time as long as 3,400 years (Williams et al., 1969, cited from Hylleberg and Riis-Vestergaard, in press) The fate and function of humic fractions are unknown (Hylleberg and Riis-Vestergaard, in press).

All the production of autotrophic compartments undergo the process of decomposition, if not transported out at once. Mangrove plants do not appeal much to the macrofauna as food sources, since they contain a lot of resistant components dominated by cellulose and lignin in the tissues. Moreover, tannins which are toxic compounds are also present in mangrove tissues. Few potential herbivores are able to feed on mangrove plants directly.

Plant litters will pass through several steps during the decomposition process. First, the dissolved organic matter is give off from the litters, and then the microbial colonization would initiate. Bacteria and fungi will be important microorganisms colonizing the particulate matter. At the same time the disintegration or reduction in size of particulate material occurs by means of mechanical fragmentation and chewing by some animals. Bacteria and fungi are capable of utilizing the resistant plant compounds and the biomass of these microorganisms will increase the total protein level on the detritus particles. The detritus is ingested by detritus feeders which are the majority of mangrove macrofauna. These animals ingest organic detritus in one form of another, from mangrove leaves to fine particulate materials, decomposed animal detritus, excretion products and microorganisms associated with detritus. This indicates the significance of the detrital food chain in the mangrove ecosystem (see Fig. 6, the thick line indicating the main pathway of detritus formation).

Principally the nourishment the fauna gets from the detritus may be bacteria and fungi which are easily digestible. No studies provide information on the availability and the actual nutritive value of detritus to macrofauna in the mangrove ecosystem. The detritus may be ingested so many times by macrofauna that new surface of the detritus particle is exposed for new microbial attacks. Faeces which is another form excreted from animals is then invaded by bacteria and fungi, recycling back again in the food chain, when faeces is ingested by detritus feeders.

The detritus feeders are in turn fed on by the predatory macrofauna (K_2 & K_3). The macrofauna are then preyed on by the marine fishes that come into the mangrove forest at high tides (Sasekumar and Thong, 1980). This is another way of export of organic matter from the mangrove ecosystem.

The macrofauna is also preyed on by birds and mammals, either residing or visiting mangrove forests. Some fishes are diets of certain mangrove bird species, while sipunculans and crabs are eaten by macaque monkeys. This pathway is also considered as an export pathway.

In order to fully understand an energy flow diagram based on the proposed model, the production of different compartments should be quantified. The contributions of many autotrophs are by and large unknown. Therefore it is not possible to quantify the pathways shown, even though some information has been compiled. However, one interesting aspect awaiting further studies would be to estimate the proportional magnitude of contributions of the mangrove ecosystem to the adjacent areas which support the fisheries productivity and to the mangrove macrofauna itself.