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ABUNDANCE OF SOME SELECTED DETRITUS IN A THAI MANGAL

by

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CONTENTS

ABSTRACT

Zooplankton samples were collected from a mangrove channel over a period of three months. Living and non-living parts of each sample were separated microscopically. The relative abundances of three types of detritus (faecal pellets, plant fragments, sand and mud aggregates) were measured. Filtration, weighing and calcination processes were used succesively to estimate the dry weight and organic content of each part of the samples. Results, related to sampling station position, tidal levels and channel structure, illustrate that detritus constitutes at least 40% of the samples. Samples collected deep inside the mangrove area were the richest in detritus (up to 95%). Faecal pellets and mineral particles and aggregates were the most abundant at neap-tide while plant fragments dominated in the channels at spring-tide. The importance of non-living particles is emphasized by a detrital organic matter content of up to 35.7 mg/m^3 of channel water.

I. INTRODUCTION

Suspended particulate matter in a mangrove environment is probably one of the most characteristic features of this biotope. Planktonic organisms and organic detritus of various origins as well as clays, sand and mud particles are mixed by tidal or estuarine waters. Such detritus and minerals contribute considerably to the amount of suspended matter usually found in the mangrove coastal zone and, thereby, increase the number of particles that deposit on the mud flat bordering the forest. In addition, the mixing process occurring between salt and fresh waters, induce the formation of colloids and biocolloids. All these factors contribute to make mangrove waters turbid as well as making them an important source of detrital food for living organisms (Odum, 1971; Kuentzler, 1974).

Jørgensen (1966) stressed that, whereas in open seas organic detritus is ultimately of phytoplanktonic origin, coastal areas are much richer in various kinds of suspended material. Potential sources of food for suspension feeders can be classified into five distinct groups: (1), phytoplankton; (2), organic detritus; (3), dissolved and colloidal organic matter; (4), heterotrophic micro-organisms and (5), zooplankton. In the particular case of tidal mangroves, the origin of these groups is autochtonous as well as allochtonous. Golley *et al.* (1962) have pointed out

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that phytoplankton, bacteria and vegetation of the mangrove forest, contribute chiefly to increase the amount of biodetritus in mangrove channels while the allochtonous dead material is supplied by the marginal vegetation surrounding the area and by the tidal waters entering the channels during flood-tides. The same authors reported that in Puerto Rico, the biomass of a red mangrove forest can exceed 11,000 g/m^2 of dry weight in addition to 6.4 g/m^2 of dry weight for the associated animal biomass. In a survey of a Malaysian mangrove forest Noakes (1955) reported timber yield of 14 g/m^2/day. It is not, therefore, surprising that, with a gross production of more than 15 g of organic matter/m^2/day (Golley *et al.*, 1962), Odum and Odum (1959) have classified the mangrove ecosystem as one of the most fertile living communities. Due to high productivity, export of dead organic matter which originates in the turn-over processes of the forest is considerable. Golley *et al.* (1962) reported an export of 1.1 g C/m^2/day by tidal waters from Puerto Rico mangroves and in Florida, Heald (1969) recorded an export by tidal waters of 800 g of plants detritus a year from each square metre of mangrove forest.

Macro-detritus generally floats (leaves, pieces of wood, roots) and where it escapes from the labyrinth of trees, reaches the seaward mud flat. Small particles (usually < 1 cm), however, often remain in a suspended state as a part of the leptotel (total suspended matter) and will slowly settle in mangrove channels, on the mud flat beyond or in other coastal areas. This settlement, induced by a decrease in tidal current speed, constitutes the first sediment layer. Analysis of tropical estuarine suspended matter and sediments has already proved that, except for pigments, the composition of the leptotel is almost the same as the composition of the sapropel (Quasim and Sankaranarayanan, 1972).

Although only a few investigations have been made on this subject, the influence of detritus collected with a net during plankton sampling programmes can be very important in estimating the standing stock of planktonic organisms especially in coastal waters. For example, the measurement of biovolume and biomass of collected plankton by the usual methods (dry weight, displacement volume, settling volume) must be interpreted with care as the occurrence of detritus in samples may influence the results of both measurements (Golley *et al.*, 1962; Kenchington, 1970). It is common, however, even in a mangrove environment, to express the amount of particulate matter of samples as a whole, i.e. including plankton and detritus (seston), though the two constituents may not have the same energetic value and of course not the same ecological significance.

Various experiments have been undertaken to quantify the nutritional value of different types of detritus found in coastal and mangrove waters for pelagic and benthic marine animals. Although detritus used in such experiments have sometimes been of artificial origin due to the difficulty of separating the natural detrital matter from living organisms (Jørgensen, 1966), these experiments are very instructive with regard to the information they give about the ability of animals to feed on dead organic matter. Observations of stomach contents of pelagic and benthic animals living in the mangrove waters have also shown that detrital material might be one of the most important foods of certain aquatic organisms (Odum, 1971).

Three groups of detritus feeders can be identified: (1), filtering animals (e.g. sponges, bivalves, barnacles); (2), scraping animals (e.g. limpets, echinoids) and (3), grazing animals including those animals living on the sea floor (e.g. annelids, crabs) and the zooplankton (Fox, 1950; Margalef, 1974).

In a tidal mangrove such as that at Nam Bor Bay, Phuket, Thailand (Fig. 1), the schematic diagram (Fig. 2) illustrates the state of detrital matter between high tide and low tide. With regard to this diagram, the value given by Golley *et al.* (1962) for mangrove productivity (8.23 g

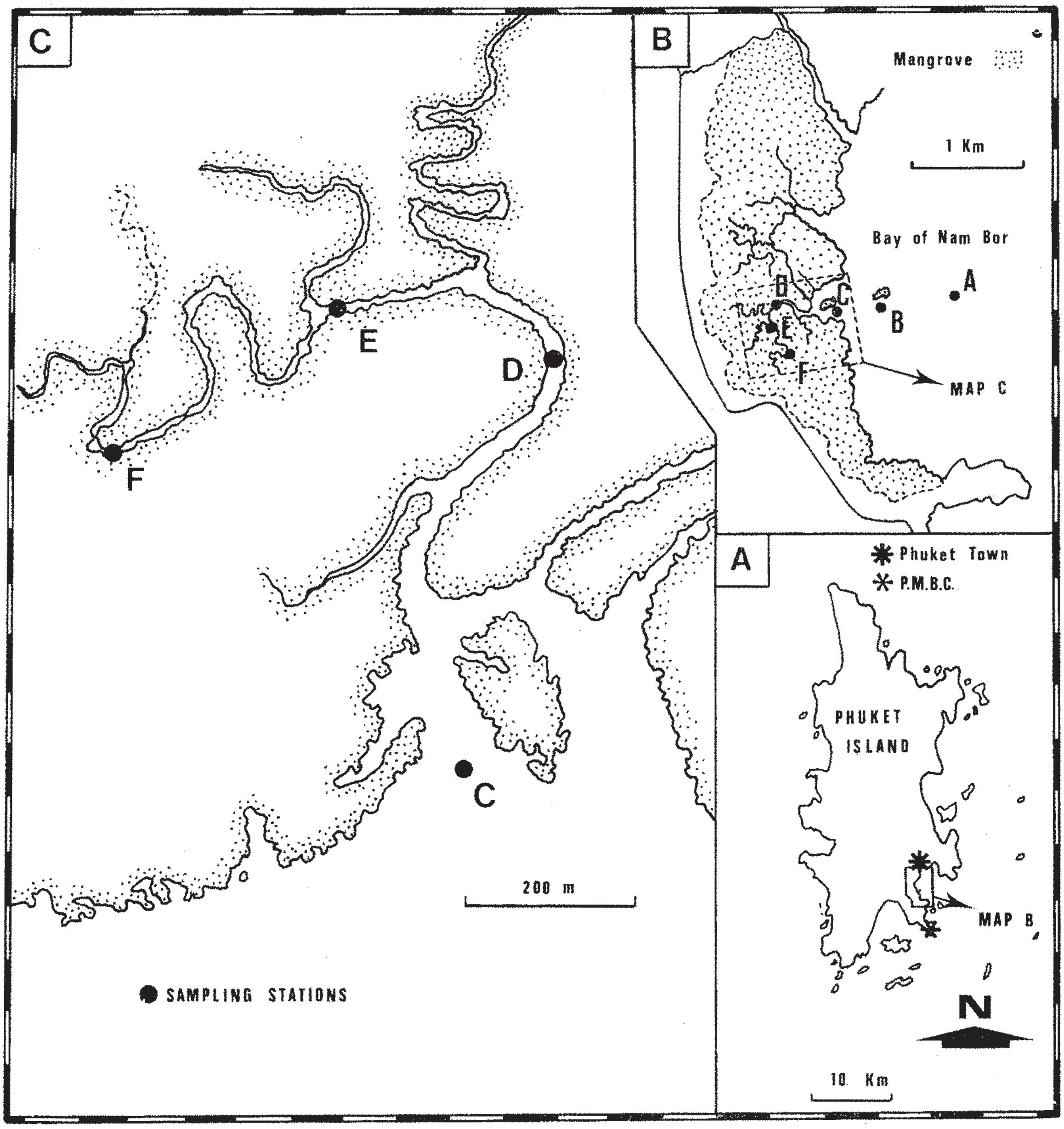

Fig. 1. Maps of the study area. A. Phuket Island. B. Bay of Nam Bor with the location of the six sampling stations and of the mangrove area. C. Main channel.

C/m²/day) should be kept in mind (Fig. 2A). In addition, the importance of dead matter in the formation of mangrove soils (Fig. 2E) has been pointed out by many authors (Stephens, 1962; Golley *et al.*, 1962; Rutzler, 1969; Kuentzler, 1974). The quantity of suspended and floating detritus (Fig. 2D) carried through mangrove channels during ebb-tide (Fig. 2F) is a function of the tidal level (Orr and Morehouse, 1933) which affects current strength and thereby

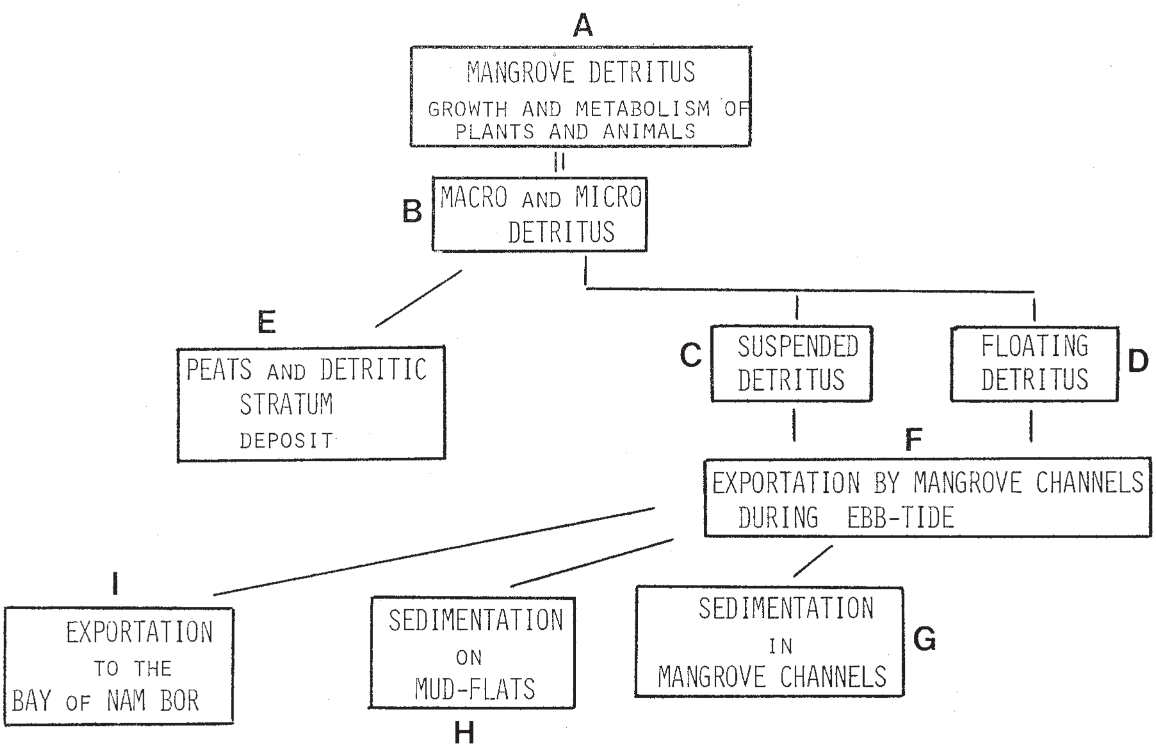

Fig. 2. Diagram of pathways followed by detritic matter during neap-tide.

the amount of particles of any type that are washed by the flowing water from the mangrove soil surface (Orr and Morehouse, 1933; Heald, 1969; Kuentzler, 1974) and also eroded from the banks of channels (Rutzler, 1969). Current strength also influences the sedimentation rate of suspended particles in channels (Fig. 2G) and on the mud flat (Fig. 2H). Particles which do not settle are carried into the open bay (Fig. 2I). Turn-over by living organisms (e.g. bacteria, mycoflora, plankton, crabs, sediment feeders and filter feeders), finally increase the rate of mineralization of organic dead matter (Teal, 1962; Swart, 1963; Jørgensen, 1966; Kuentzler, 1974) and thereby greatly contributes to increase the quantity of micronutrients and of dissolved organic matter in the outflowing waters (unpublished data).

The purpose of this work was to study, over a period of three months, the amount of detrital matter put into suspension at high tide (i.e. during flood-tide) (Fig. 2C) and collected in a net during a zooplankton sampling programme in one of the main channels of the mangrove at Nam Bor Bay.

II. MATERIALS AND METHODS

The investigated site is situated on Phuket Island, Thailand (7°51′N - 98°24′E) (Fig. 1). The mangrove forest, located near Phuket Town (Fig. 1) and bordering Nam Bor Bay, covers an area of about 3.5 km^2 and is dominated by *Rhizophora apiculata* Blume and *R. mucronata* Lamk.

Bordered seawards by a large mud flat covered by seawater during high tide, the forest is dissected by numerous channels of various depth and breadth which are flooded twice a day by tidal water. The mangrove is without river water drainage, except at the northern edge of the forest (Phuket River) (Fig. 1). There is, however, an important fresh water supply during the rainy season (April-May to October-November) due to the run-off of rain water from the surrounding hills. Although clearing of trees for charcoal production has recently commenced, the forest is still relatively undamaged.

Five boat-trips were made to the study area from January to April 1975 during periods of high tide. Six sampling points were fixed along one of the main channels of the area (Fig. 1B): three in the channel across the mangrove (mangrove stations D., E. and F.), one at the junction between the forest and the mud flat (transition station C.), one on the mud flat (B.) and one in the bay (A.), beyond the mud flat. Both the latter are considered to be bay stations. The depth of this channel, measured at the different stations, varied from 4.0 to 1.0 m depending on the tidal height. When measured at other points along the channel, depth ranged from 5.1 m to zero.

Quantitative sub-surface (20 to 50 cm depth layer) plankton samples were taken from each station with a circular net of 30 cm mouth width and a mesh aperture of 0.333 mm that retains almost all zooplanktonic organisms. A flowmeter was used to measure the volume of water filtered during each haul. Samples were preserved in neutralized formalin. A subsample of each sample (1/6.6) was isolated and sorted by hand under the binocular microscope with the purpose of separating planktonic organisms from detrital particles. The dry weights of the two parts obtained were determined by separate filtration through small size ashless filter paper and by oven drying (12 hours at 75°C). Afterwards, organic and mineral fractions of the dry matter was estimated by furnace calcination (6 hours at 450°C). Plankton caloric equivalents were obtaiend by use of a transformation formula based on the organic content of dry plankton (Cal./g of dry weight = $-227+152x\%$ Carbon) (Platt *et al.*, 1969). Carbon content was obtained by multiplying organic matter content by 0.6 (Platt *et al.*, 1969).

Prior to filtration, each detrital subsample was examined microscopically and their approximate composition estimated. This method involved sorting of the detritus into four subgroups (plant detritus, faecal pellets, mineral particles and aggregates, and the remainder), with the purpose of assessing their relative abundance. Groups were arranged in circles and measured with a micrometer (average of two diameters). Precentage composition was then obtained by using transformation coefficients converting measured sizes into dry weight from calibration curves. A further subsample (1/6.6) of each collected sample was filtrated and dessicated as a whole (i.e. without sorting) to test the validity and reliability of the subsampling and sorting methods ($r = 0.890$).

As tidal levels differed from one field-trip to another, a tidal index (I_t) was defined as follows:

$$I_t = \frac{HT + \frac{(HT + LT1) + (HT - LT2)}{2}}{100}$$

This tidal index, depending on the high tide level (HT) and on the mean difference between the preceding low tide level (LT 1) and succeeding low tide level (LT 2), is thus a function of the mass of water that enters the mangrove in approximately six hours (first half of the tidal cycle) and subsequently comes out (second half of the tidal cycle). This can be considered an expression of the maximum flow rate of the water through the channels for a given tidal level.

III. RESULTS

Although this method is time consuming, sorting by hand of the samples is the only way to estimate the exact amount of detrital matter that has been collected simultaneously with living plankton. Results obtained by this method

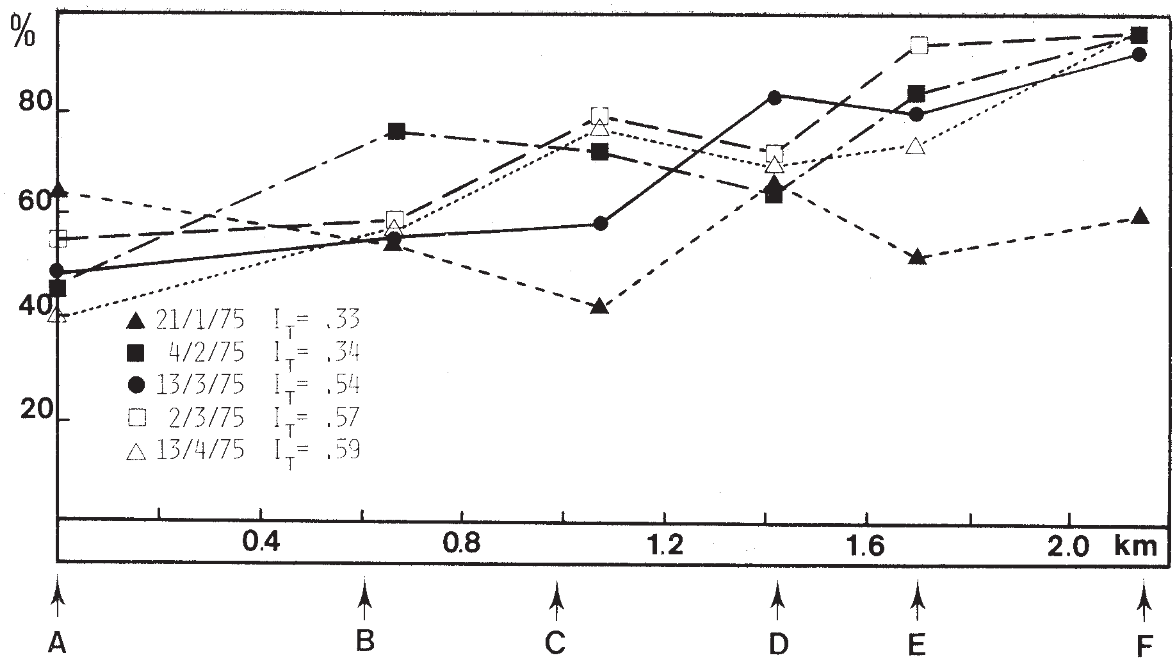

Fig. 3. Relative abundance of detritus in samples collected during five different tidal cycles, expressed as a function of the distance between station A and any other station.

are presented as % relative abundance in Figure 3 where they are related to the distance separating each station from the outer one (station A). Detritus was always very abundant even at station A which is located in the Bay (41 - 66% of total suspended matter). Although samples from station B were usually richer in dead matter (57 - 77%), detrital matter was most abundant at station F with values of up to 95%. The influence of tidal levels (represented by the I_t value corresponding to each field-trip) on detrital levels was also demonstrated, as the highest percentages of detritus occurring at the mangrove stations (D, E, F) gave the highest I_t values (0.54 and 0.59). This is best seen by reference to Table 1, where average values of dry weight of living and non-living particles/m^3 (mg d.w./m^3) have been calculated for the two types of tidal index (0.33 - 0.34 and 0.54 to 0.59) and for each type of site (bay, transition station, mangrove). Values obtained for plankton (Table 1) were very similar. Conversely, it seems that the absolute abundance of suspended detritus in the mangrove area depends on the tidal index. The average value recorded for stations D, E, and F was 3.7 times greater for the highest I_t than for the lowest one (49.1 and 13.1 mg d.w./m^3 respectively). In addition, the average value recorded for station F only, was about twice as high as those calculated for the three mangrove stations and a comparison of mean results obtained for station F for each type of tidal index shows that there is an increase of about 60 mg d.w./m^3 of detritus when the I_t reached high values. At the lowest tidal index, no real difference was noted between the three types of station, while there was a gradual increase in the amount of detrital matter present in the water from the outer to the inner stations when I_t values were high.

The following observations were made with regard to detritus composition: plant detritus predominantly consisted of vascular plant particles usually from 0.4 to 15 mm in total length

Table 1. Dry weights of living and non-living particles (mg/m^3). Extreme values in brackets.

Dry weights (mg/m^3)	Tidal index range	Bay St. A-B	Transition St. C	Mangrove St. D-E-F
Living fraction	0.33–0.34	8.0 (5.4–11.7)	11.4 (7.1–15.7)	4.7 (1.4–15.3)
	0.54–0.59	5.2 (3.1–8.2)	3.7 (2.1–4.6)	6.2 (3.4–14.6)
Non-living fraction	0.33–0.34	12.9 (8.9–17.4)	14.8 (11.1–18.6)	13.1$^+$ (3.7–31.5)
	0.54–0.59	6.1 (4.0–10.3)	10.7 (6.4–17.8)	49.1^{++} (6.7–98.6)

26.5$^+$ and 86.4^{++} for station F.

and with a maximum width of 0.2 mm. Faecal pellets were usually large (0.35 to 1.5 mm) and most probably of benthic origin. Mineral particles comprised sand grains and shell fragments while mineral aggregates comprised fragments of mangrove soil that have been washed into the channel waters. The "remainder" comprised debris of dead plankton, moultings and different types of unidentified fibres and membranes. The relative abundance of each type of detritus in the samples is shown in Figure 4. For stations A and B (Fig. 4, A; B), the remainder was always dominant (72 to 95%) for low and high values of I_t. Mineral particles and faecal pellets were not very numerous at those two stations but with low values of I_t, their abundance increased progressively from station A to station C and in the mangrove channel they become dominant with an average relative abundance of 60 to 83% (Fig. 4, A; B). Conversely, for high I_t, these values never exceeded the maximum of 17% (Fig. 4, D). Plant particles were numerous within the mangrove when the tide level was higher (Fig. 4, C, D, E). Maximum values were obtained for stations D and E (54 and 75% respectively) with an I_t of 0.59 whereas with a smaller index, no value exceeded 21% of the total detrital matter, even at the inner stations. The calculated average values of the total relative abundances of mineral particles and faecal pellets for each type of station and tidal index (Table 2) seems to illustrate more clearly the influence of tidal level on the abundance of those two kinds of detritus. Starting at 6% for outer stations, their average value increases to 17% at the intermediate station and to more than 17% in the mangrove area, while the corresponding values for high tidal index are all lower than 6%.

The organic content of the living part of each sample was found to be relatively constant and the use of the formula of Platt *et al.* (1969) gives an average caloricity of 5.88 Kcal-g of dry weight. To estimate the caloric equivalent of the detrital part of each subsample is impossible without the use of a calorimeter. Thus, no relationship could be found between detrital quantity and caloricity as the nature and composition of the former changes in time and space. Nevertheless, the organic matter content of the samples has been estimated by calcination and mean values have been calculated (Table 4). In addition, results obtained for total organic matter content of non-sorted samples have also been given (Table 3) but show little variation. Conversely, results obtained for organic matter content of the sorted detritus, shows great variation with absolute abundance (mg/m^3) especially if tidal levels were high. An increasing organic matter gradient can be drawn up from the outer stations to the mangrove stations (Table 4), this being especially significant for the highest I_t values.

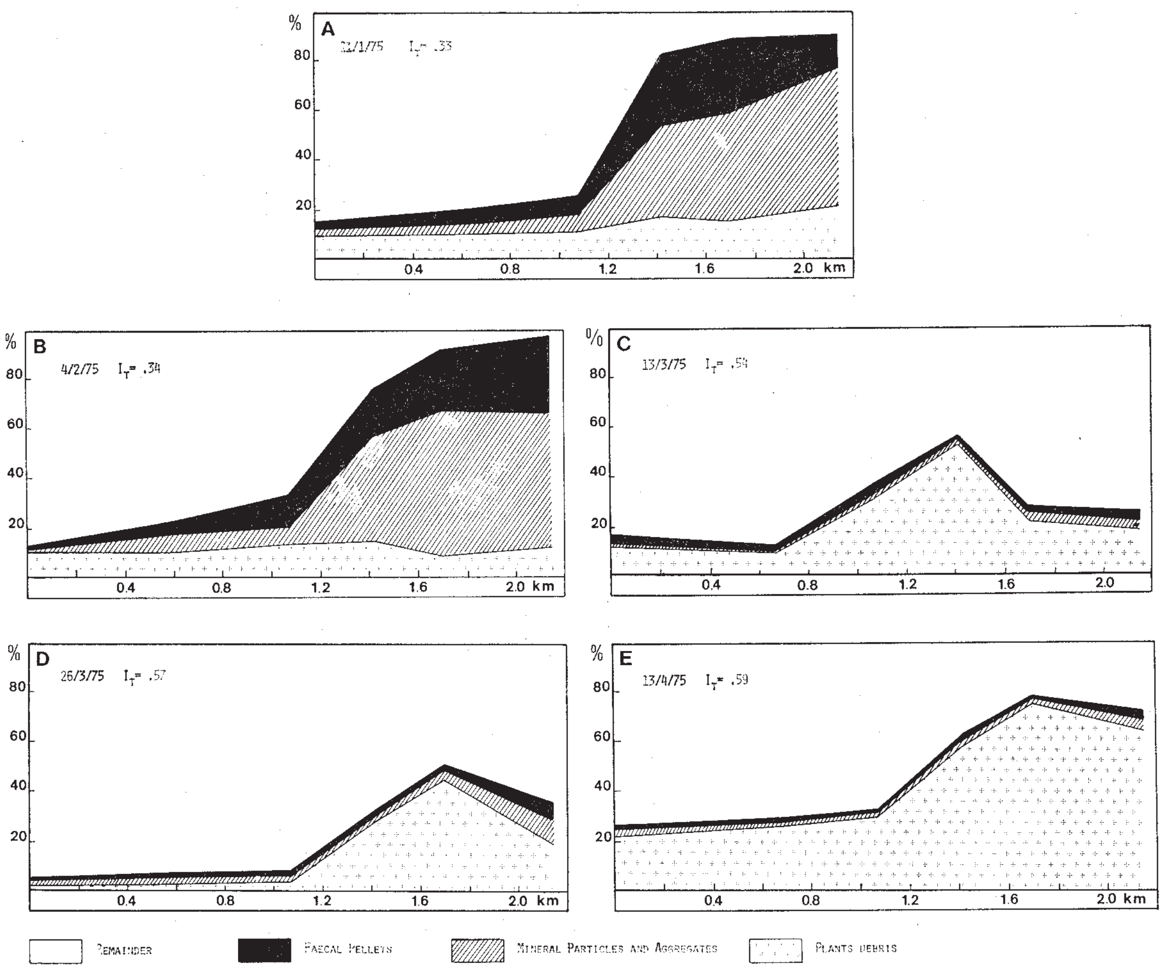

Fig. 4. Composition of the detritic part of each sample expressed as a function of the distance between each station and station ABCDE.

IV. DISCUSSION

Similarly to what has been found in other mangrove systems (Golley *et al.*, 1962), the suspended detritus in the channel of Nam Bor Bay mangrove represents a large amount of the total suspended material and should therefore be taken into account whenever plankton sample biomass or volume are estimated.

Results indicate that both the nature and relative abundance of the detritus are influenced by the tidal index, i.e., the tidal levels, and plant debris were found to be much more abundant with rising values of the tidal index, reflecting the effect of flooding water moving over the mangrove soil during high tides, while faecal pellets and mineral aggregates, both heavier, were dominant in the water column when the tidal index is lower, i.e. when the water level does not overreach the channel banks. A similar method as the one used in this work was used to estimate the net-export of particulate matter by Golley *et al.* (1962), who report values of 24.4 g/m^3 of outgoing water; these authors, however, used a much finer mesh aperture

Table 2. Average relative abundance of faecal pellets and mineral particles (%). Extreme values in brackets.

Tidal index range	Bay St. A-B	Transition St. C	Mangrove St. D-E-F
0.33 – 0.39	6.0	17.0	71.8
	(1.7–10.0)	(13.6–20.5)	(60.4–83.0)
0.54 – 0.59	3.2	3.8	5.9
	(1.7–3.9)	(1.4–5.6)	(2.5–17.3)

Table 3. Average values of organic matter content of total suspended matter (% of dry weight). Extreme values in brackets.

Tidal index range	Bay St. A-B	Transition St. C	Mangrove St. D-E-F
0.33 – 0.39	50.8	57.8	39.4
	(40.3–55.6)	(41.2–74.3)	(21.0–58.7)
0.54 – 0.59	55.7	48.1	43.4
	(47.8–75.4)	(36.3–57.9)	(29.1–60.3)

Table 4. Average values of organic matter content of the non-living fraction (mg/m^3). Extreme values in brackets

Tidal index range	Bay St. A-B	Transition St. C	Mangrove St. D-E-F
0.33 – 0.39	5.1	6.3	7.2
	(3.4–7.6)	(4.4–10.4)	(2.9–9.4)
0.54 – 0.59	2.4	4.6	27.0
	(1.6–3.6)	(3.2–7.5)	(10.9–35.7)

(0.150 mm) and included leptotel plus floating detritus in their estimation.

Kenchington (1970), using a mesh size of 0.190 mm in Menai straits, found that detritus particles may account for 10 to about 90% of the total amount of particles collected by the net (living and non-living), representing from 1 to approximately 19 mg/m^3 dry weight. These values are quite similar to what was obtained in the case of the mangrove waters of Nam Bor (Fig. 3 and Table 1), although these waters proved to be richer in detritus, especially when considering that a more selective filtering gauze was used (0.333 mm). The importance of the tidal range was also emphasized by Kenchington (*op. cit.*) and he found that abundance of detritus increased considerably with rising tidal range; the same conclusion can be drawn from the Nam Bor mangrove experiment, in particular when refering to stations D, E and F (Table 1).

As it was noted previously, an abundance of vascular plant debris (54-75%) has been found to be related to very high tidal indices (Fig. 4). This can be compared with the data obtained by Heald (1966) from a Florida red mangrove area, where 35 to 60% of suspended matter was found

Table 5. Abundance of the different types of detritus in relation with their weight, origin and the current strength in the three parts of the system studied.

Tidal index and Current Strength	Detritus → / Stations ↓	Remainder Light	Faecal Pellets Heavy	Min. Part. Aggr.	Plants Debris
Low I_t	Bay	+ + + +	+ +	+ +	+ +
Weak Current	Transition	+ + +	+ + +	+ +	+ +
	Mangrove	+ + +	+ + +	+ + + +	+ +
High I_t	Bay	+ + + +	+	+	+ + +
Strong Current	Transition	+ + + +	+	+	+ + +
	Mangrove	+ + +	+	+	+ + + +

to be ultimately red mangrove debris. This is of great importance as vascular plant detritus sometimes represents the primary source of food for aquatic animals (Odum, 1971). Information obtained in the present work are summarized in Table 5, the relative abundance of detritus being symbolized by plus (+) symbols.

Although the average relative abundance of organic matter content of detritus is not very different from one type of station to another, absolute abundance in mg/m^3 of water, increases from outer to inner stations (Table 4). This can be related to a disproportionate increase in the amounts of living and non-living particles (Table 1). Consequently, the potential quantity of detrital organic matter available in the mangrove channel waters at high tide is much higher than in the Bay (up to 11.2 times more for the highest I_t value). Conversely and, as indicated in Table 1, the dry weight of living organisms is relatively constant. This could be an indication that an important part of the largest detritus, i.e. larger than 0.333 mm eventually settle down on channel bottom or on the mud flat before reaching the Bay, thus representing a food source for benthic species (Teal, 1962; Odum, 1971).

Discrimination between the two types of tidal index emphasized in this paper seems to be satisfactory with regard to the logical inferences that can be made. The results presented here, however, must be considered only partial for three main reasons. First, the tidal index may vary from about 0.25 to about 0.65 (extreme values calculated for the years 1974-75 for Nam Bor Bay). The range of variation for the amount and composition of the detritus collected at the different stations could therefore be greater than that proposed here for the tidal index examined, i.e. 0.33-0.59. The influence of the tidal level on both composition and abundance of detritus can be assessed, and this fully agrees to what was observed by Kenchington (1970). Second, seasonal factors (dry or rainy) may influence the abundance and nature of the detritus. Third, the sampling system used during this work involved size selection and the amount of particles caught with the plankton net certainly represents only a part of the total suspended matter.

The importance of hand-sorting to evaluate the relative abundance of detritus and living particles has been pointed out previously, especially with regard to results obtained for Tables 1 and 4. Plant detritus, due to its abundance, probably plays an important role as a food resource, as it does in other mangrove systems (Odum, 1971). More studies must be carried out, however, to determine the quantity of detrital matter exported by the ebbing tide (Fig. 2, F) and the amount of detritus settling both in channels and on the mud flat (Fig. 2, G, H). By comparing total mangal productivity (plants and animals) with export of detritus from the channels valuable information will be obtained with regard to nutrient input into the bay beyond (in this case Nam Bor Bay) and the trophic relationships that exist between suspended matter and the pelagic fauna and between detrital deposits and the benthic fauna.

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REFERENCES

FOX, D.L., 1950. Comparative metabolism of organic detritus by inshore animals. Ecology, **31** (1) : 100–108.

GOLLEY, F., ODUM, H.T. & WILSON, R.F., 1962. The structure and metabolism of a Puerto Rico red mangrove in May. Ecology, **43** (1) : 9–19.

HEALD, E.J., 1969. The production of organic detritus in a South Florida estuary. Ph.D. dissertation. University of Miami. 110 p.

JØRGENSEN, C.B., 1966. Biology of suspension feeding. Pergamon Press., N.Y. 357 p.

KENCHINGTON, R.A., 1970. An investigation of the detritus in Menai Straits plankton samples. J. Mar. Biol. Ass. U.K. **50** : 489–498.

KUENTZLER, E.J., 1974. Mangrove swamps system. *In* : Coastal Ecology Systems of the U.S. Vol. I. (Ed. Odum, H.T., B.J. Copeland & E.A. McMahan) : 346–371.

MARGALEF, A.R., 1974. Ecología. Ed. Omega, S.A., Barcelona. 951 p.

NOAKES, P.S.P., 1955. Methods of increasing growth and obtaining natural regeneration of the mangrove type in Malaya. Malayan Forester **18** : 23–30.

ODUM, H.T. & E.P. ODUM, 1959. Principles and concepts pertaining to energy in ecological systems. *In* : Odum, E.P., Fundamentals of Ecology. Saunders, Phila. 546 pp.

ODUM, W.E., 1971. Pathways of energy flow in a South Florida estuary. Univ. of Miami Sea Grant Bull. 7. 162 p.

ORR, A.P. & F.W. MOREHOUSE, 1933. Physical and chemical conditions in mangrove swamps. Great Barrier Reef Exped. 1928–1929. Sci. Rep. **2** : 102–110.

PLATT, T., V.M. BRAWN & B. IRWIN, 1969. Caloric and carbon equivalents of zooplankton biomass. J. Fish. Res. Bd. Can. **26** : 2345–2349.

QUASIM, S.Z. & V.N. SANKARANARAYANAN, 1972. Organic detritus of a tropical estuary. Mar. Biol. **15** : 193–199.

RUTZLER, K., 1969. The mangrove community: aspects of its structure, faunistics and ecology. *In* : Ayala-Castañares & F. Phleger, Eds. Lagunas Costeras: Un Simposio. UNAM-UNESCO: 515–536.

STEPHENS, W.M., 1962. Mangroves: trees that make land. Rep. Smithson. Inst. 491–496.

SWART, H.J., 1963. An investigation of the mycoflora in the soil of some mangrove swamps. Acta Bol. neerl. **12** : 98–111.

TEAL, J.M., 1962. Energy flow in the salt marsh ecosystem of Georgia. Ecology **42** (4) : 614–624.

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