Sri Lanka J. Aquat. Sci. 4 (1999): 69-81

Mangrove Vegetation Structure and the Abundance of Shrimps in Chilaw Lagoon, Sri Lanka

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Abstract

The mangrove vegetation structure and its relationship to abundance of shrimps around Pambala area in Chilaw lagoon, Sri Lanka were investigated. Belt transects of 10 m width were laid across mangrove stands with apparent variation in their vegetation structure. Data on floristic composition, stand density, basal area, mean stand diameter, tree height, stand above-ground biomass were collected and relative density, dominance, frequency and importance value of constituent species as well as complexity index and Shannon-Wiener diversity index were calculated with the data.

Abundance of shrimps in the lagoon adjacent to these transects were obtained using a cast net of 1 cm stretched mesh size. Cast net was operated from a canoe by an experienced cast net fisher and samples were taken from locations at the distances of 50m, 100m, 150m and 200m from the shoreline. Samples were taken from these sites during four times of a day, i.e. 08.00 – 09.00 h, 09.00 – 10.00 h, 10.00 – 11.00 h and 11.00 – 12.00 h.

Structural properties of the mangrove stands in the three localities were different from each other. Stand density (2,487 – 12,400 plants/ ha) was related negatively to mean stand diameter (6.82 cm – 3.24 cm) and Shannon-Weiner diversity index (1.242 – 0.304). Average above ground biomass for *Rhizophora mucronata* (23.69 kg – 2.26 kg) also showed a negative trend with increasing density, indicating more disturbed the stand due to cutting etc., higher the density of small stems and lower the species diversity in the stand.

The highest abundance (53.2%) of shrimps (*Penaeus indicus, P. semisulcatus, P. monodon* and *Metapenaeus dobsoni* together) was observed close to the mangrove stands (at 50m from the shoreline), which showed a gradual decline towards the middle of the lagoon. The highest shrimp abundance was (68.6%) at the site adjacent to the structurally richest mangrove stand (diversity index 1.242; complexity index 42.36) and the lowest (10.3%) around the sparse mangrove stand (diversity index 0.304; complexity index 46.06). The effects of structural complexity and the distance from the shore on the abundance of shrimps in this part of Chilaw lagoon and their interactions were found to be significant ($p<0.05$).

The results of the present study indicate that the abundance of shrimps in the Pambala area of Chilaw lagoon shows a positive relationship with the structural complexity and maturity of mangrove stands.

Introduction

Mangals are considered to be among the most productive ecosystems on Earth. Net primary productivity of mangrove ecosystems has been measured to be in the range of 300 – 2,000 g carbon fixed per m^2 per year (Mann 1982). Decomposition of mangrove litter eventually produces particulate and dissolved organic matter which in turn become the food energy for most of the aquatic organisms. Besides, mangrove vegetation may potentially provide habitats and refuge to the juvenile fish and shellfish.

It is documented that shrimp production in coastal waters is positively influenced by the presence of mangrove vegetation in the adjacent coastal areas (Macnae 1974; Martosubroto & Naamin 1977; Turner 1977). Kathiresan *et al.* (1994) through their studies at the Pichavaran mangals in Tamilnadu, India, have revealed that the shrimp seed resources in mangrove waters depend on the vegetation and its structural attributes. The ecology of mangroves however is poorly understood, particularly the significance of these ecosystems to the secondary productivity of the adjacent coastal waters. It is therefore imperative that the functioning of these inter-tidal ecosystems is investigated with a view to augmenting their conservation and management. This is particularly important in a developing tropical country like Sri Lanka where mangroves are generally found to occur, nevertheless are subjected to severe pressures of destruction under the current forces of the market economy.

Present study was carried out as a preliminary investigation to ascertain whether the abundance of shrimps in the Pambala area of Chilaw lagoon (southern part) is related to the structure of the mangrove vegetation that fringes the lagoon.

Materials and Methods

Study area

Chilaw lagoon ($7^0$28' N - $7^0$35' N and $79^0$47' E – $79^0$50' E) is located in the intermediate climatic zone on the western coast of Sri Lanka. The total extent of the lagoon and the associated aquatic environment is about 1,800 ha and two thirds of the lagoon shore is fringed with mangals which account for approximately 150 ha.

Study sites

In order to eliminate the effect of proximity to sea that has a bearing on the level of recruitment of marine organisms to the lagoon and thus their abundance in it, the study sites were selected from the southern part of Chilaw lagoon, around Pambala. This part of the lagoon has a distant connection to the sea (Fig. 1). Three belt transects of 10m wide were laid across the mangrove vegetation, perpendicular to the shoreline in three mangrove stands which were considered to be representative of the mangrove vegetation in the area. Auxiliary information on physiognomy such as species composition, average height and vigor of the stands as well as the plant densities were used to determine the approximate differences in vegetation structure of the mangals. Thus three transects, i.e. A, B and C (Fig. 1) were laid across three apparently different (structurally) mangrove stands inPambala area.

Vegetation structure

Each transect was sub-divided into 10m x 10m plots and data on structural parameters, i.e. floristic composition, plant density, frequency of occurrence of constituent species, basal area, mean stand diameter and tree height according to the method described by Shaefer-Novelli & Cintron (1984). Trees/stems with diameters of 2.5 cm or above at breast height (1.2 m above ground) were measured for the purpose.

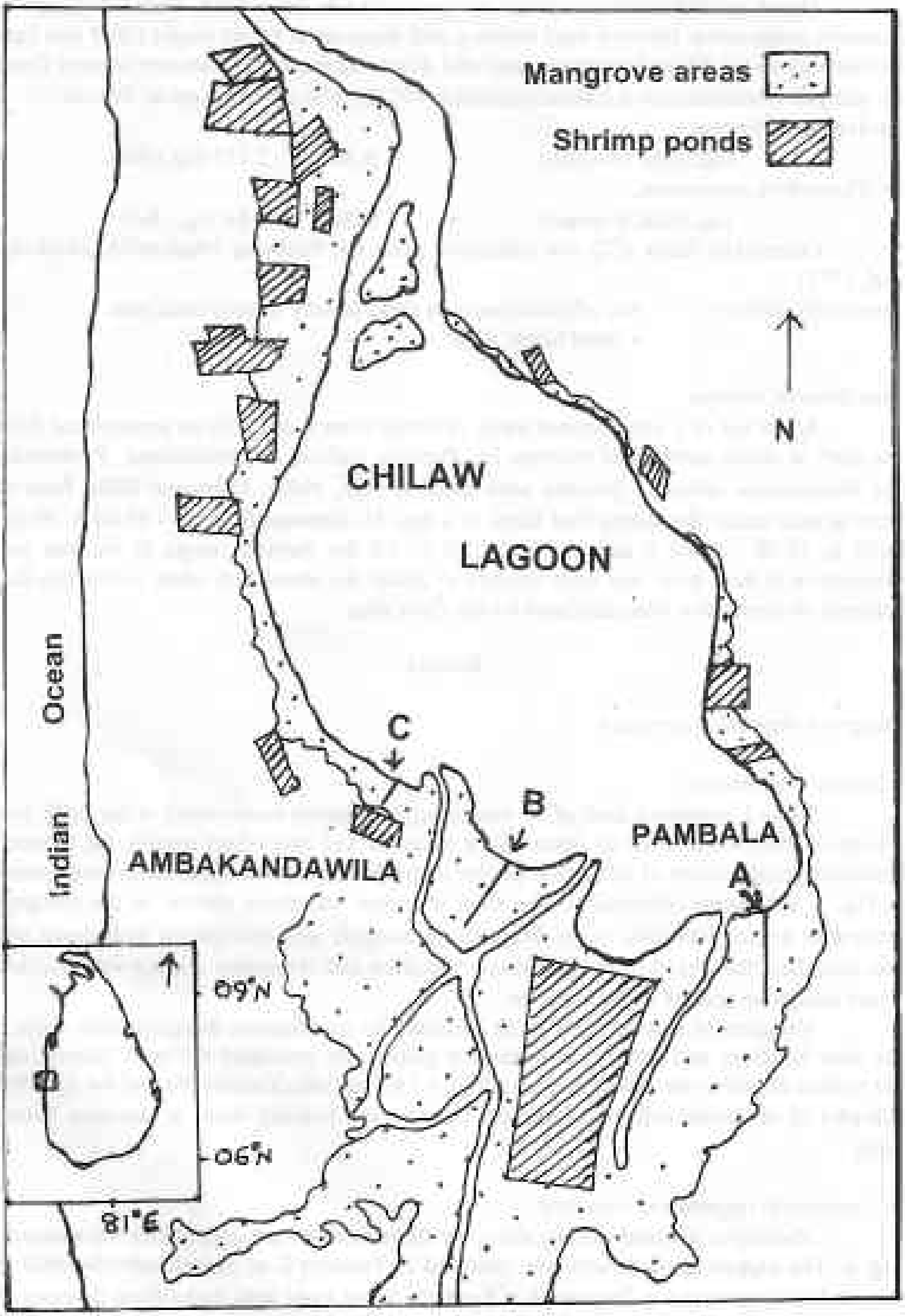

Fig. 1. Map of the study area and locations of transects (A, B and C). Inset shows the location of Chilaw lagoon in Sri Lanka.

Above ground biomass of the mangrove stands have been obtained using the allometric relationship between total biomass and diameter at breast height (dbh) that have been developed for *Rhizophora mucronata* and *Avicennia marina* in Puttalam lagoon/ Dutch bay mangals (Amarasinghe & Balasubramaniam 1992a). The equations are as follows:

For *Avicennia marina,*

$$\log_e(\text{total biomass}) = 5.551 + 2.153 \log_e(\text{dbh})$$

For *Rhizophora mucronata,*

$$\log_e(\text{total biomass}) = 6.247 + 2.64 \log_e(\text{dbh})$$

Complexity index (CI) was calculated using the following relationship (Holdridge *et al.* 1971).

Complexity Index = No. of plant species x stand density x stand basal area x stand height x 10^{-5}

Abundance of shrimps

A cast net of 1 cm stretched mesh, operated from a canoe by an experienced fisher was used to obtain samples of shrimps, i.e. *Penaeus indicus, P. semisulcatus, P. monodon* and *Metapenaeus dobsoni*. Samples were taken at 50m, 100m, 150m and 200m from the shore at each study site during four times of a day, i.e. between 08.00 h – 09.00 h, 09.00 - 10.00 h, 10.00 - 11.00 h and 11.00 - 12.00 h. All the shrimps caught in the cast nets, irrespective of their body size were counted to obtain the abundance value. Using this data, Shannon-Wiener index was calculated for the three sites.

Results

Mangrove vegetation structure

i. Species composition

Table 1 presents a total of 13 true mangrove species encountered at the study sites. Eleven of them were found to occur in the transects and two others outside the transects. Percentage composition of mangrove species in the three study sites (transects) are presented in Fig. 2. *Avicennia officinalis* is the most abundant mangrove species in the mangrove ecosystem around Pambala, while *Bruguiera sexangula* and *Rhizophora mucronata were* less abundant than the former. *Bruguiera cylindrica* and *Avicennia marina* were the least found mangrove species in the transects.

Variation of species diversity as indicated by the Shannon diversity index value, in the three locations and along each transect is graphically presented in Fig. 3. Accordingly, the highest diversity was recorded from sub plot I at Pambala (Transect **B**) and the least from sub plot III at Ambakandawila (Transect **C**). Species diversity tends to decrease towards land.

ii. Community (vegetation) structure

Variations of stand density along the three transects are graphically represented in Fig. 4. The highest stand density was observed in Transect **C** at Ambakandawila while the lowest density occurred in Transect **A** at Pambala. Stand basal area, mean stand diameter and average stand height are depicted in Figs 5, 6 and 7 respectively.

The standing above-ground biomass values of *Avicennia marina* and *Rhizophora mucronata* in the water-front plots of each transect are presented in Table 2.

The highest relative density value was recorded for *Avicennia officinalis* in Transect **C** (93.53) indicating that this mangrove stand is a monospecific, of *A. officinalis*. *Bruguiera sexangula* in Transect **B** records the second highest value (among the three sites) of relative density (59.93).

Shannon-Wiener diversity index values for the stands **A**, **B** and **C** were 1.242, 0.8151 and 0.3037 respectively. Comparison of the values among the three sites has shown that they are significantly different from each other ($p<0.05$). The complexity indices for the Transects **A, B** and **C** have been calculated to be 42.36, 41.70 and 46.06 respectively.

iii. Shrimp abundance

Four species of shrimps were encountered in the samples and they are, *Penaeus indicus, P. semisulcatus, P. monodon* and *Metapenaeus dobsonii*. Percentage occurrence of shrimps in the samples obtained from the lagoon waters near the three trnasects, are presented in Table 3. Table 4 presents the percentage abundance of shrimps at various distances from the show (at all three sites). Contingency tests (Chi-square tests) indicate that shrimp abundance is significantly different between the sites as well as at various distances from the shore ($P<0.05$).

Table 5 presents the percentage occurrence of shrimps in the samples obtained at different times of the day from the three sampling sites.

Table 1. List of true mangrove species and mangrove associated species encountered in the mangrove ecosystem at Pambala (* - True mangrove species that occurred outside the transects).

True mangrove species

1.	*Acanthus ilicifolius*
2.	*Acrostichum aureum*
3.	*Aegiceras corniculatum*
4.	*Avicennia officinalis*
5.	*Avicennia marina*
6.	*Bruguiera cylindrica**
7.	*Bruguiera sexangula*
8.	*Excoecaria agallocha*
9.	*Lumnitzera racemosa*
10.	*Rhizophora apiculata*
11.	*Rhizophora mucronata*
12.	*Xylocarpus granatum* *
13.	*Sonneratia alba**

Mangrove associated species

1.	*Dolochandrone spathacea*
2.	*Hibiscus tiliaceus*
3.	*Heritiera littoralis*

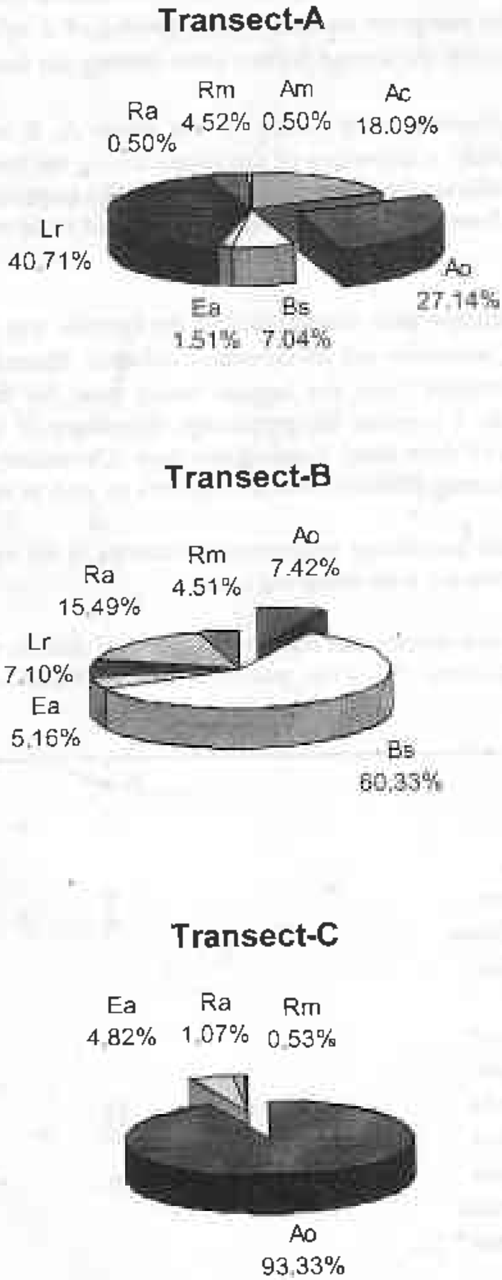

Fig. 2. Percentage composition of constituent species of the three mangals (A, B and C) sampled in Chilaw lagoon. (Ac - *Aegiceras corniculatum*; Ao - *Avicennia officinalis*; Bs - *Bruguiera sexangula*; Ea - *Excoecaria agallocha*; Lr *Lumnitzera racemosa*; Ra - *Rhizophora apiculata*; Rm - *Rhizophora mucronata*)

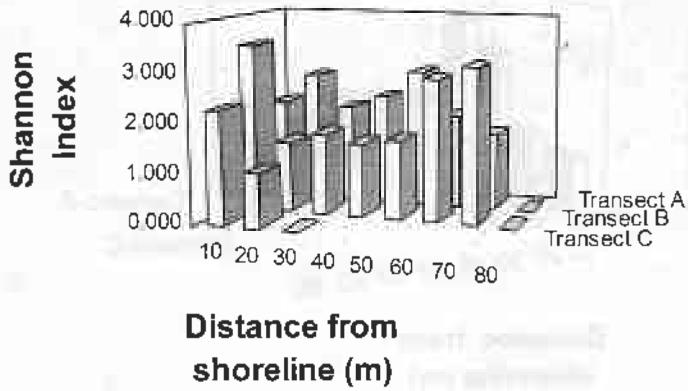

Fig. 3. Shannon - Wiener Index values along the transects (A, B and C) in the three mangals sampled in Chilaw lagoon.

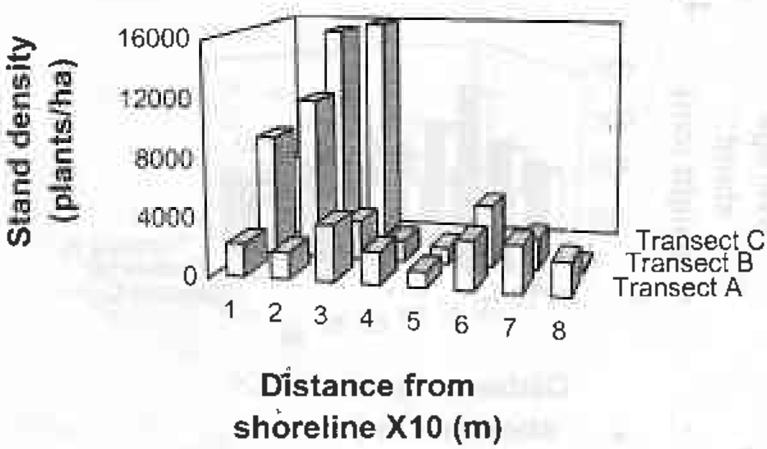

Fig. 4. Density of mangrove plants along transects (A, B and C) at the three sampling sites in Chilaw lagoon.

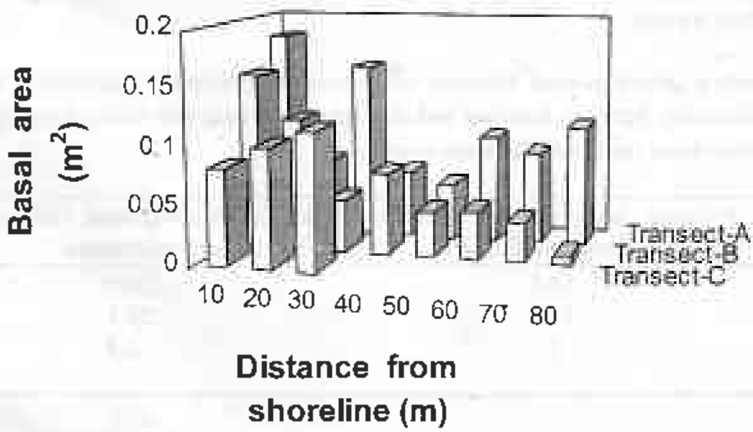

Fig. 5. Basal area of mangrove stands along the transects (A, B and C) in Chilaw lagoon.

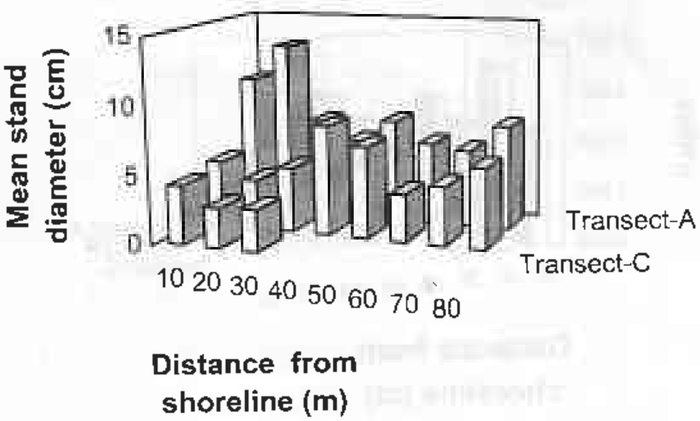

Fig. 6. Mean stand diameter of the sub plots along the transects in the three sampling sites (A, B and C) in Chilaw lagoon.

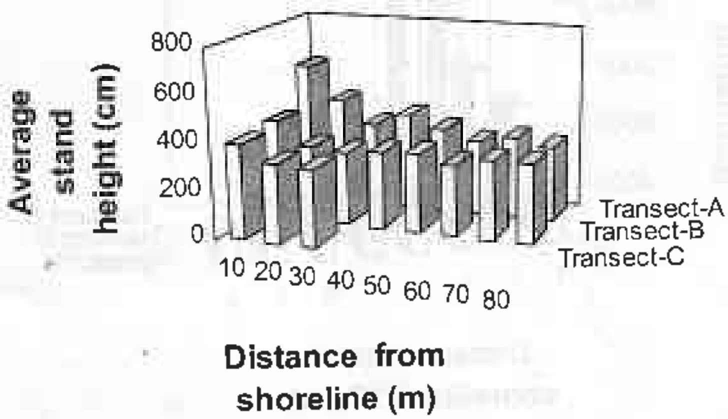

Fig. 7. Average mangrove stand height along the transects at the three sampling sites (A, B and C) in Chilaw lagoon.

Table 2. Standing above-ground biomass of *Avicennia officinalis* (calculated using the allometric relationship between biomass and dbh for *A. marina*) and *Rhizophora mucronata* in the water-front areas (plots) of the three study sites.

Study site	Average above-ground biomass (kg) of *Avicennia officinalis*	Average above-ground biomass (kg) of *Rhizophora mucronata*
A	12.4	236.9
B	11.6	23.1
C	2.1	2.3

Table 3. Percentage occurrence of shrimps at the three sites.

Study site	% Occurrence of Shrimps
A	68.59
B	21.15
C	10.26

n = 1154, $\chi^2 = 31.73$, $P < 0.05$

Table 4. Percentage shrimp abundance at different distances from the shoreline.

Distance from shoreline (m)	% abundance of shrimps
50	53.21
100	24.79
150	11.97
200	10.04

n = 1154, $\chi^2 = 10.01$, $P < 0.05$

Table 5: Percentage abundance of shrimps at different times of the day in the three sampling sites.

Time of the day	08.00 - 09.00h	09.00 - 10.00h	10.00 - 11.00h	11.00 - 12.00h
% Shrimp abundance	28.42	30.56	23.29	17.74

Discussion

The mangrove stands at the three sampling sites were different from each other structurally. The floristic diversity was the highest at site **A** (Pambala), where 8 out of the 11 true mangrove species that were observed to occur in these mangals were encountered. Site **C** (Ambakandawila) was the poorest in species diversity as 93% of the vegetation was comprised of a single species, *Avicennia officinalis*. Mangrove species diversity along the three transects (sampling sites) too is a noteworthy feature, as it reveals that the water-front areas of these mangals support a greater species diversity than the inland parts of the same mangal (Fig. 3). Apart from the edaphic factors such as soil salinity and availability of nutrients for growth, the diversity of the seed bank and rate of its replenishment too may contribute to the variation in diversity of plant communities. Areas located at the edge of the water are with better opportunities to receive a diverse supply of seeds/propagules that can be brought in by tides. Furthermore, this is the area that is flushed with tide more frequently than the inland areas and hence are supplied constantly with nutrients while toxic waste materials such as ammonia are removed regularly from the root environ, thus providing relatively a favourable micro-environment for mangrove growth.

Mangrove stem densities are significantly different among the three stands and Transect **C** is the most dense (Fig. 4) due to the presence of a large number of small stems. Hence, the stand basal area, mean stand diameter and the average height of this mangal is relatively low. This indicates that this mangrove stand is subjected to human pressure due to constant cutting, which has been observed to take place, mainly for light timber requirements to construct temporary dwellings and firewood. It is also evident (Fig. 5) that the water-front areas of the mangal at Ambakandawila, which is more readily accessible, is subjected to this effect more than the inland parts of it. Although the plant density in Transect **A** is relatively low, the basal area, mean stand diameter and the average height of the stand are greater than those of the other two stands, indicating that it is the least disturbed among the three stands. Unlike other two mangrove stands, this mangal is guarded by the neighbouring fisher community and they extract only the dried branches of mangroves as firewood and seldom cut branches for poles.

The complexity index values however, did not reflect this trend as the tree density in the mangal at Ambakandawila was relatively high compared to that of the other two mangals, and hence it contributed to yield a high complexity index value for this stand which composed of a large number of small trees mainly of one species, i.e. *Avicennia officinalis*. As such, complexity index that is calculated as in this study is of low efficacy in explaining the state of maturity of a mangrove stand.

When considered the spatial parameters pertaining to each constituent species of these mangrove stands, it is evident that Transect **C** constitutes predominantly with species of *Rhizophora, Lumnitzera racemosa* and *Bruguiera sexangula,* on contrary to Transect **C**, where *Avicennia offiinalis* is the dominant species. The standing above ground biomass values for the dominant species in the water-front areas (Table 3) show that unlike at Site **C** which is covered mainly by *Avicennia officinalis,* the lagoonward end of the mangrove stand at Site **A** supports mature plants of *Rhizophora* sp., that possess an extensive prop/stilt root system which extends to the shallow waters of the lagoon edge. On the contrary, lagoon edge of Site **C** is fringed with pneumatophores of *A. officinalis*. Because of the low tidal amplitude prevailing, the daily tides do not reach most of the inner parts of the mangal but the water-front areas. Besides other factors, the physical structures of mangrove plants such as prop/stilt roots, pneumatophores and stems that occur at the edge of the mangal may play a crucial role in creating the physical structure and quality of the micro-environment that provide refuge for the aquatic organisms. Greater diversity of a community therefore will render an array of habitats, which in turn could support a large diverse community of aquatic organisms. Moreover, diverse communities of mangroves may also perform a better function in producing organic material which finally contribute to the carbon pool or the primary source of food/ energy of these ecosystems, both as dissolved and particulate organic matter (Boto & Bunt 1981; Odum 1982; Boto *et al.* 1984; Ridd *et al.* 1988; Robertson *et al.* 1988).

The abundance of shrimps in the lagoon adjacent to the three mangrove stands was significantly different from each other, indicating a possible influence of the neighbouring mangrove stand on it. The greatest abundance, i.e. 68.5% of the total number of fish present in the samples, was observed close to Transect **A** at Pambala, which recorded the highest mangrove plant diversity, stand basal area and mean stand diameter. The least percentage abundance (10.26%) on the other hand, was observed near the mangrove stand at Ambakandawila (Transect **C**) which also recorded the lowest stand basal area, mean stand diameter and species diversity. Shrimp abundance near Site **B** that showed intermediate values for the key structural parameters, also recorded an intermediate value (21.15%) for shrimp abundance.

The structure of the mangal can possibly affect the shrimp abundance either directly or indirectly. Relatively high net above ground primary productivity values have been reported from mangals in Dutch bay (Sri Lanka) which also have shown greater diversity

(Amarasinghe & Balasubramaniam 1992b), indicating that more developed and structurally diverse mangrove communities possess a greater ability to trap solar energy through photosynthesis part of which is stored in the plant parts that contribute to form the structure of the mangal. Organic matter in decomposing mangrove plant tissues can enter the organic pool in the estuary/lagoon either as detritus (partially decomposed, bacteria laden organic particles) or as soluble organic compounds that leach from the plant parts and subsequently be transformed into particulate form by bacteria or through adsorption onto suspended particles (Mathias 1974). Since most of these bacteria reside on the surface of large particles (Darnell 1967) or tend to clump as their populations grow in numbers, organic particles can be formed of a spectrum of sizes which are suitable for consumption by the filter feeders, from zooplankton to bivalves (Snedaker 1978). Estuarine organisms which depend on this source of food can therefore be expected to occur abundantly in locations that produce/receive organic matter.

Larvae and juveniles that are abundant in mangrove areas, select their food by the size of the food particles. Shrimps are reported to feed directly on mangrove detritus and an assimilation efficiency of 92% has been shown by *Metapenaeus monoceras* fed with a diet composed of *Rhizophora* leaves (Macintosh 1984). Besides, benthic and epiphytic assemblages of algae, feacal matter of aquatic organisms, larvae and other invertebrates too can become food for shrimps and other organisms such as crabs that occupy the inter-tidal areas. All the shrimp species encountered in this study are omnivorous and hence may feed on detritus matter depending on its availability. Although no quantitative measurements were made, examination of the guts of adult shrimps showed that largest proportion of the gut contents was detritus. Shrimp post larvae are almost exclusively planktivorous, nevertheless juveniles and sub-adults depend on benthic food sources. Large shrimps such *as Penaeus monodon, P. semisulcatus and P. indicus* tend to be more carnivorous (Hall 1962). Inshore penaeid species collected from Selangor (Malaysia) waters were found to have consumed 64% to 88% of animal material (by volume) and 12% to 36% of plant matter of which 11% to 59% to be of mangrove origin (Leh & Sasekumar 1980). Availability of particulate organic matter may enhance not only the shrimp populations but also the other aquatic organisms that shrimps predate on. This also in turn, will contribute to the greater occurrence of shrimps near mangrove areas where the pool of organic matter is expected to be rich. The low tidal amplitude and the resultant weak tidal currents in Sri Lankan waters may restrict the distribution of organic matter and hence could be expected to be in abundance near its place of origin.

Shrimp abundance has also shown a negative relationship with the distance from the mangrove stand (towards the lagoon). When considered the abundance of shrimps at different distances from the shore near all three transects, 53.2% were found to occur within 50m from the mangrove shore while the least proportion, i.e. 10.04% was between 150-200m from the mangal (Table 5). These observations further substantiate the positive effect of mangroves on shrimp occurrence in the lagoon.

Furthermore, presence of creeks, water holes etc. within the mangal may enhance the quality of mangals as nursery grounds as they contribute to widen the types of suitable habitats available for the shrimp larvae and sub-adults which are reported to spend about 8 months in sheltered intertidal areas such as mangals (Macnae 1974; Twilley 1985). Apart from the availability of organic food material and physical habitat structures (adventitious roots that grow above ground and stems), occurrence of such protective habitats too may contribute to enhance the suitability of mangrove areas for shrimps.

Results of this preliminary study thus provide evidence to corroborate the contention that mangals support greater abundance of shrimps in their associated waters. Moreover, they reveal that this ecological role is better performed by structurally diverse and mature mangrove stands.

Acknowledgements

Authors extend their sincere gratitude to Mr. Douglas Tissera of Pambala for his untiring assistance in the field for data collection and also pay respect to his courageous efforts to protect the mangroves at Pambala in Chilaw lagoon.

References

Amarasinghe M.D. & S. Balasubramaniam 1992a.
Structural properties of two types of mangrove stands on the north western coast of Sri Lanka. Hydrobiologia 247: 7-27.

Amarasinghe M.D. & S. Balasubramaniam 1992b.
Net primary productivity of two mangrove forest stands of the north western coast of Sri Lanka. Hydrobiologia 247: 37-47.

Boto K.G. & J.S. Bunt 1981.
Tidal export of particulate organic matter from a northern Australian mangrove system. Estuarine, Coastal and Shelf Sciences 13: 247-255.

Boto K.G., J.S. Bunt & J. Wellington 1984.
Variation in mangrove forest productivity in northern Australia and Papua New Guinea. Estuarine, Coastal and Shelf Sciences 19: 321-329.

Darnell R.M. 1967.
Organic detritus in relation to the estuarine ecosystems. Estuaries 83: 376-382.

Hall D.N.F. 1962.
Observations on the taxonomy and biology of some Indo West Pacific Penaeidae (Crustacea, Decapoda). Colonial Office Fishery Publications, No.17, London:229

Holdridge L.R., W.C. Grenko, W.H. Hathe, T. Liang & J. Joshi 1971.
Forest environment in tropical life zones: A pilot study. New York: 247

Kathiresan K., M. Xavier Ramesh & V. Venkatesan 1994.
Forest structure and prawn seeds in Pichavaram mangroves. Environment and Ecology 12(2): 465-468.

Leh C. & A. Sasekumar 1980.
Feeding ecology of prawns in shallow waters adjoining mangrove shores. Proceedings of Asian Symposium on Mangrove Environment, Research and Management, University of Malaysia, Kuala Lumpur.

Macintosh D.J. 1984.
Ecology and productivity of Malaysian mangrove crab populations. Proceedings of the Asian Symposium on Mangrove Environment: Research and Management, University of Malaysia, Kuala Lumpur. 347-377 pp.

Macnae W. 1974.
Mangrove forests and fisheries. IOFC/DEV/74/34, FAO, Rome. 1-35 pp.

Mann K.H. 1982.
Ecology of coastal waters: A systems approach. University of California Press, Berkeley, California. 322 p.

Martosubroto P. & N. Naamin 1977.
Relationship between tidal forests (mangroves) and commercial shrimp production in Indonesia. Marine Research Bulletin of Indonesia 18: 81-86.

Mathias J.A. 1974.
The possible significance of leaf litter fall and decomposition in Malaysian mangrove swamps. A paper presented at the I.B.P. Synthesis meeting, Kuala Lumpur (unpublished).

Odum W.E., 1982.
The ecology of the mangroves of south Florida: A community profile. FWS/OBS-81/24, Bureau of Land Management, Fish and Wildlife Service, U.S. Department of Interior. 50-60 pp.

Ridd P.V., M.W. Sandstrom & E. Wolanski 1988.
Outwelling from tropical tidal salt flats. Estuarine, Coastal and Shelf Sciences 26: 243-253.

Robertson A.I., D.M. Alongi P. Daniel & K.G. Boto 1988.
How much mangrove detritus reaches the Great Barrier Reef Lagoon. In: Proceedings of the Sixth International Coral Reef Committee (J.H. Choat ed.), Volume 12. 601-606 pp. Vol.2. Sydney.

Sheaffer Novelli, Y. & G. Cintron 1984.
Methods for studying mangrove structure. In: The mangrove ecosystem: research methods (S.C. Snedaker & J.G. Snedaker eds). 91-113 pp. UNESCO, Paris.

Snedaker S.C. 1978.
Mangroves: Their value and perpetuation. Nature and Resources 16(3): 6-13.

Turner R.E. 1977.
Intertidal vegetation and commercial yields of penaeid shrimp. Transactions of the American Fisheries Society 106(5): 411-416.

Twilley R.R. 1985.
An analysis of mangrove forests along the Gambia river estuary. Implications for the management of estuarine resources. Report No. 6 of the University of Michigan, Great Lakes and Marine Waters Centre International programmes. 74-75 pp.