

DISTRIBUTION AND ABUNDANCE OF *CHICOREUS CAPUCINUS*
(LAMARCK, 1822) (PROSOBRANCHIA: MURICIDAE) IN THE MANGROVE
AT AO NAM BOR, PHUKET, THAILAND

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ABSTRACT

Chicoreus capucinus was studied, using stratified random sampling technique, in addition to potential prey species, the topographic level of the study area, and the characteristics of the tide. A simple method for determining the mean water velocity during tidal inundation was developed. *C. capucinus* was distributed throughout the entire study area, even in areas emersed for more than 85 % of the time. The species was usually found on the prop roots of the mangrove trees. The vertical distribution was limited by tidal factors. A clear zonation of potential prey existed, with high abundances in the seaward regions, and low densities in the middle and landward parts. *C. capucinus* principally preyed on oysters, *Saccostrea cucullata* (Born, 1778) (emend. Born 1780), but was not limited by the distribution of this species. The abundance depended on a combination of food availability and tidal factors. In the more landward regions *C. capucinus* feed on *Teredo* sp.

INTRODUCTION

Mangrove ecosystems are the main vegetation type in protected intertidal areas along tropical and subtropical coastlines. During this century, large areas of mangrove forests have been destroyed by over-exploitation and conversion to other uses, and the total world coverage has been greatly reduced (Chapman 1977; English *et al.* 1994). Mangroves cover an area of about 20 million hectares world-wide (English *et al.* 1994).

Mangrove ecosystems play an essential role on many tropical coasts. Not only do they form highly productive ecosystems capable of exporting energy and materials to adjacent, relatively deprived communities, but they also support a diverse heterotrophic food chain, including fish, crustaceans, birds, small mammals and numerous invertebrates (Carter 1991).

Frith *et al.* (1976) studied macrofauna of the mangrove and adjacent habitats in Ao Nam Bor, Phuket Island, Thailand, and compared it to other studies of mangrove macrofauna. They concluded that there is a distinct and characteristic mangrove macrofauna which is not just simply dependant upon the same

conditions on which the trees depend but on the environment produced by the presence of the trees. Despite their importance the functioning of mangrove ecosystems has received little attention (Wells 1983), and the knowledge of the invertebrate fauna depending on this habitat is limited.

The Muricidae (Prosobranchia: Gastropoda) constitutes one of the best-known and most distinctive families of molluscs (Radwin & D'Attilio 1976). They are voracious predators, occupying important niches in many food webs and taking on economic importance wherever shell fisheries exist. In spite of this, little is known of the muricid *Chicoreus capucinus* (Lamarck, 1822). The species' geographical distribution, as described by Houart (1992), did not include the regions around the Andaman Sea. It is, however, found in many locations on Phuket Island, Thailand, on muddy substrate and on prop roots of mangrove trees. In Ao Nam Bor it is found exclusively in the mangrove and not on the adjacent sand and mud flat biotopes (Frith *et al.* 1976).

The aim of this study was to investigate the distribution and abundance of *C. capucinus*

in the mangrove at Ao Nam Bor and to analyse some of the factors limiting the spatial distribution of the species.

The most important features of the physical environment of the mangrove is the tide (Whitten *et al.* 1987). Tidal regime is a major factor influencing species distribution, abundance and growth. Hence an attempt to quantify the frequency and duration of tidal inundation as well as the water velocity when inundated through the mangrove was made.

It is hypothesised that the distribution and abundance of *C. capucinus* is related to the distribution of its prey, the oyster *Saccostrea cucullata* (Born, 1778) (emend. Born 1780). To test this hypothesis an investigation of the spatial distribution and abundance of *C. capucinus* as well as its potential prey was conducted.

MATERIALS AND METHODS

Description of the study area

The field study was carried out at Ao Nam Bor mangrove shore on the east coast of Phuket Island, Southern Thailand (98°25'E, 7°51'N) (Fig. 1). Field sampling was carried out at low tide during May to November 1995.

The study site was a 50 m wide band of mangrove forest approximately 300 m north of a klong (channel) in the southern end of the bay. This channel forms an accessible

path through the mangrove to the seaward intertidal mudflat, making the area immediately adjacent highly disturbed by man. Further north, where the study site was chosen, no apparent disturbance occurred during the study period.

The mangrove forest consisted predominantly of *Rhizophora apiculata* (Blume) 5 to 10 m high, making a dense canopy over the entire study area. The forest floor was covered with prop roots, old tree stumps and branches, as well as leaf litter. The surface of the substrate was smooth, in the sense that it was relatively free of small channels and depressions. There was no freshwater outflow near the mangrove, other than drainage water from the adjacent mainland during rains, and the study site was completely drained during low tide. The landward edge of the study site, 80 m from the seaward edge, was bordered by an approximately 10 m wide very dense band of young tree shoots. This was extremely inaccessible and was not included in the study. Past this fringe the mangrove had been cut down, the area being utilised mainly for shrimp farming.

Tidal inundation

In order to determine the frequency and duration of tidal inundation along transects through the study area, an attempt to describe the local topography was made. The method was modified after English *et al.* (1994). One and a half meter lengths of canvas pre-dyed with a water-soluble food dye was attached to 2 m long half inch aluminium pipes. Three transects, 10 m apart, were established through the study area of the mangrove forest from the seaward edge to the landward margin. Pipes were placed at 20 m intervals along the transects at low tide on November 11, 1995, and left for one tidal flooding. Immediately after the high tide period the height of the watermark above the soil surface was measured.

Topographic level. Using the tidal predictions from tide tables for Thai waters at Ko

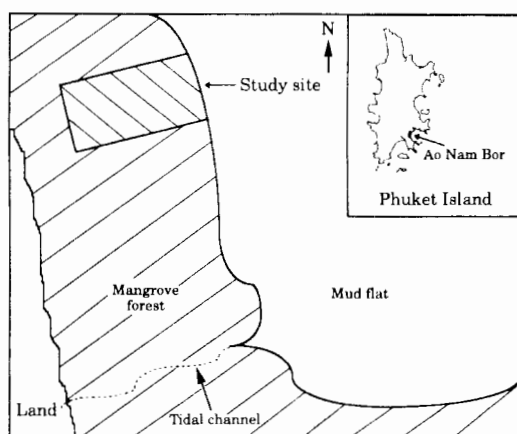


Figure 1. Location of the study site.

Taphao Noi, Phuket (Royal Thai Navy 1995), the topographic level of the study area was calculated. The topographic level (Ht) is given by the difference between the predicted height of high tide (Hp) and the measured water level (Hm), ($Ht = Hp - Hm$).

Tidal inundation. The water level at the different stations as a function of time was calculated using the tide table, with the predicted water level each hour of the high tide cycle investigated, and the calculated topographic level. The duration of the inundation (of the particular day) at each station was determined graphically to the nearest 1/2 hour. The pattern of tidal inundation at the different stations for the entire month of November, 1995, was calculated in the same manner.

Water velocity

No equipment for hydrographic measurement was available, so a simple inexpensive method for measuring the mean water velocity was applied. When placed in flowing water, chalk disintegrates, and the rate of chalk disintegration can be used to estimate the volume of water that flowed past the chalk.

Laboratory experiment. The relation between chalk disintegration (wash-off) and water volume that flowed past was experimentally determined in the laboratory. Pieces of chalk were attached to 1/2" aluminium pipes, 10 cm long, using cotton. The total length of chalk above the tube was 3 cm. Chalk diameter 1.5 cm above the pipe edge was measured with callipers to the nearest 0.1 mm. Pipes with chalk were placed in an experimental flume tank in Phuket Marine Biological Center, the edges of the pipes extending 1.5 cm above the sandy sediment. The flume tank was an 8 m vertical recirculated flume with a canal width of 60 cm (Steenfeldt 1995b). Chalk was exposed to a constant water flow of $7.82 \pm 0.44 \text{ cm s}^{-1}$, for 6 different periods of time, and the difference in chalk diameter before

and after the experiment calculated. The flux, 3 cm above the sediment, was determined by S. Steenfeldt on the basis of flow profiles made in the flume tank (Steenfeldt 1995a).

Chalk was left to dry overnight before measurement. The chalk was not disintegrated evenly around the cylinder, so the maximum and minimum diameters were measured, and the average of these used as the final measurement for chalk wash-off. Three replicates for each of the six different periods of time were carried out, and the relationship between the chalk wash-off and the water volume flown past was determined using linear regression.

Field experiment. Pieces of chalk placed in 1/2" aluminium pipes as described in the laboratory experimental set-up were placed in the field next to the dyed canvas used to estimate the tidal inundation. Three pipes were placed at each station at low tide, left for one high tide cycle and recovered. The chalk was left to dry overnight, and the diameter 1.5 cm above the pipe edge was subsequently measured in the laboratory. The same procedure as in the laboratory experiment was adapted. The difference in chalk diameter measured in the field after the tidal inundation was calculated and converted into water volume passed per area (m^3/m^2) using the relation estimated in the laboratory. Using the calculated period of tidal inundation in each station, the mean water velocity was estimated.

Distribution and abundance of C. capucinus

Sampling technique. A preliminary survey of the distribution and abundance of *C. capucinus* along 3 transects perpendicular to the coastline, showed great variation in abundance and distribution of the species between the different transects, as well as along each transect, indicating a clumped distribution. In light of this a more thorough investigation of abundance and distribution of *C. capucinus* was carried out.

Stratified random sampling. The study area was initially divided into four strata of equal size (50 x 20 m), parallel to the coastline, the first being the most seaward and the last the most landward stratum. Each stratum was separately sampled randomly with 2.0 x 2.0 m quadrates. Ten percent of the area was sampled, and samples were chosen using a random number table. The randomly pre-selected sites were located using measuring tapes and a compass. The number of individuals of *C. capucinus* per sample was recorded, with a note on the substrate to which the snail was attached, the height above the ground, feeding activity and presence of egg capsules. Feeding activity was determined by slowly tilting the snails, and observing whether the proboscis was contracted or extended into a prey specimen or the substrate.

Data analysis. The distribution and abundance of *C. capucinus* in the 4 equally sized strata were analysed. The variance for all 4 strata was much greater than the mean, and statistical tests did not reveal any significant difference in mean abundance between the 4 strata (Kruskal-Wallis test, $P < 0.01$). The original division into strata, was done without consideration of habitat characteristics other than distance from the seaward edge of the mangrove. A closer look at the data, however, suggested that a better resolution in the most seaward regions of the study site was needed to reveal differences in abundance. The study site was subsequently divided into 4 new strata of unequal size (stratum 1 - 4) (Fig. 2), the boundaries of these were determined on the basis of the observed distribution, and on the habitat characteristics described below.

Stratum 1: 0-10 m from the seaward edge. Three large specimens of *Rhizophora apiculata* with extensive systems of thick prop roots densely covered with sedentary lamellibranch molluscs and barnacles. A "gap" of 1/2-1 m of bare mudflat under the canopy existed between stratum 1 and 2.

Stratum 2: 10-20 m from the seaward edge.

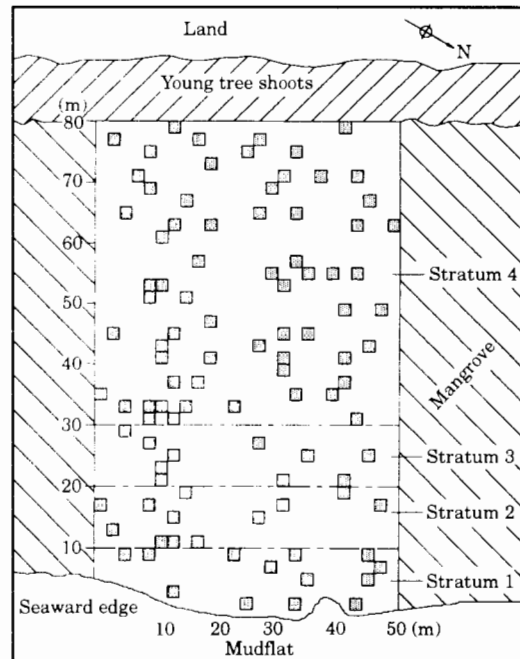


Figure 2. Map of the study area in relation to the seaward mud flat and landward edge. Division into strata in relation to distance from the seaward edge is indicated with broken lines. Dotted squares = sampling quadrats (2.0 x 2.0 m).

Forest floor mostly covered by prop roots densely covered with sedentary lamellibranch molluscs and barnacles. However, in some areas, the roots were thinner young roots, with little epifauna.

Stratum 3: 20-30 m from the seaward edge. Prop roots not as high as in stratum 1 and 2, and there was a patchy distribution of lamellibranch molluscs and barnacles.

Stratum 4: 30-80 m from the seaward edge. Prop roots relatively thin. No sedentary lamellibranch molluscs and barnacles. The forest floor gets progressively more and more covered with leaf litter, old logs and branches.

Further analysis of the data is based on this stratification.

The overall mean per sampling unit for the entire population \bar{Y}_{st} was estimated according to Cochran (1977),

$$\bar{y}_{st} = \sum_{h=1}^L W_h y_h$$

and the variance of the stratified mean $V(\bar{y}_{st})$ (Cochran 1977) was given by

$$V(\bar{y}_{st}) = \sum_{h=1}^L \left[\frac{W_h^2 s_h^2}{n_h} (1 - f_h) \right]$$

where W_h = stratum weight (the size of the stratum N_h / the size of the entire statistical population N); y_h = sample mean, s_h^2 = observed variance, n_h = sample size and f_h = sampling fraction; the suffix h denotes the stratum.

Departure of *C. capucinus* densities from random dispersion patterns were tested by comparing the ratio of sample variance to mean abundance in quadrates. Calculated index of dispersion was tested in two tailed Chi-square test.

Distribution of potential prey

Each stratum was separately sampled using a 0.25 m² quadrat. Samples were preselected using a random table. Within each quadrat all sedentary lamellibranch molluscs and barnacles were counted up to a height of 1 m above the sediment. No estimation of vertical stratification of the faunal distribution was attempted. All molluscan epifauna within each quadrat, also up to 1 m above the sediment, was collected, and subsequently identified in the laboratory. All scientific names are in accordance with Goto & Poppe (1996). Besides barnacles only the molluscan fauna was identified, and only the epifauna. Other fauna encountered was, however, noted. The mean densities for each species was calculated for each stratum, and subsequently multiplied by four so that the density values could be expressed as the number of individuals per m².

RESULTS

Topographic level

The topographic level as a function of the distance from the seaward edge of the mangrove is shown in Fig. 3. The surface of the substrate in the study area was smooth in the sense that it was relatively free of small

channels and depressions. There was no significant difference in the topographic level between the 3 transects. The ground was elevated approximately 1 m from the seaward edge to the landward edge of the study site. It had a gentle slope, gradually increasing with distance from the seaward edge, from 0.54° in the 20 most seaward m up to 0.89° in the 20 most landward m of the study site. The mean slope was 0.72°.

The maximum tidal level for the four different moon phases is indicated in the figure. It should be noted, that these levels vary between months, and the figure only represents the month of November, 1995. The minimum tidal levels are not indicated, since the entire study site was above these. The site was completely drained during low tide.

Tidal inundation

The water level as a function of time during one tidal inundation on November 11, 1995 is illustrated in Fig. 4. All stations, i.e., the entire study area, was wetted by this par-

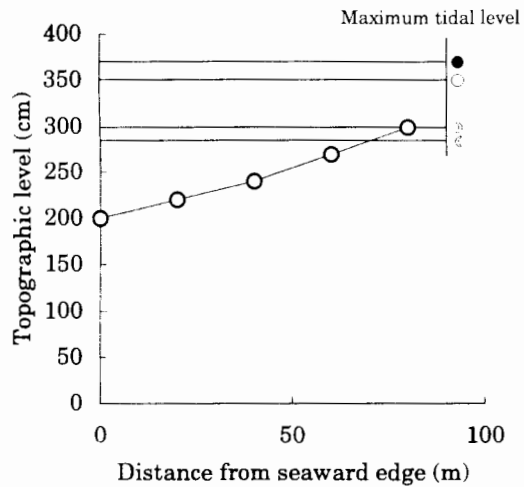


Figure 3. Topographic level through the study area. Water level (0.0) is defined as the lowest low water, i.e. the low water plane which the tide does not fall below (Royal Thai Navy 1995). Maximum water levels in relation to the different phases of the Moon are marked with lines; ○ = full moon (Nov.7); ☾ = wane (Nov.15); ● = new moon (Nov. 22); ☽ = wax (Nov. 29).

ticular high tide period. The period inundated varied a great deal, however, from approximately 7.0 hours along the seaward edge, to 6.0, 5.0, 3.5 hours in station 2, 3, and 4 respectively, to only one hour at the most landward edge of the study site. The roots and stems of the mangrove trees were wetted only up to 10 cm above ground at station 5, while the water level was approximately 105 cm at station 1. Fig. 4 shows that the prop roots 95-105 cm above the ground at the seaward edge were wetted for the same period of time as the first 10 cm above ground at the landward edge.

The tidal record for the month of November, 1995 at the five stations are shown in Fig. 5. The tide is semidiurnal, with 58 tidal inundations over the 30 day period. The figure also shows a periodicity of the tide in relation to the lunar cycle. There exists a regular spring-neap tide inequality, the maximum water level at high tide being 1.20 m

lower at neap tide than at spring tide.

At spring tide the entire study site is inundated, even if only for a short period of time and only up to 1/2 m above ground, while at neap tide the more landward regions of the mangrove is not inundated at all, for consecutive days.

Only 91 and 59 % of the tidal inundations reached station 4 and 5, respectively in November 1995. Station 4 was not wetted for 2.5 days in a row, while station 5 was dry for more than 6.5 consecutive days during neap tide. The most seaward fringe of the mangrove was under water more than 4 times as long as the landward regions. Data is summarised in Tab. 1.

Water velocity

Laboratory experiment. There is a linear relationship between chalk wash-off and the volume of water that flowed past the chalk (Fig. 6).

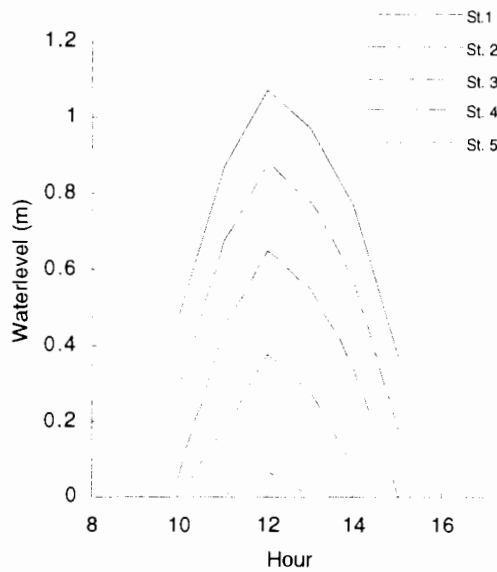


Figure 4. Waterlevel as a function of time during one tidal inundation on November 11, 1995. Each curve represents the tidal level at one station. Distance from seaward edge: St. 1 = 0 m, St. 2 = 20 m, St. 3 = 40 m, St. 4 = 60 m and St. 5 = 80 m.

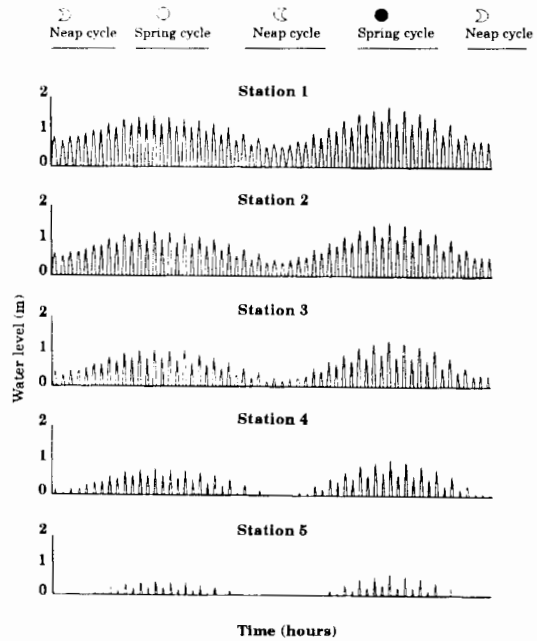


Figure 5. Pattern of tidal inundation for the month of November 1995 at the 5 different stations in the mangrove forest, in relation to the phases of the moon: full ☽, wane ☾, new ● and wax ☽. Tidal level above ground level.

Table 1. Components of the tidal cover at the five different stations during the month of November, 1995.

	Station 1	Station 2	Station 3	Station 4	Station 5
Distance from seaward edge (m)	0	20	40	60	80
Tidal inundations that reach station	58	58	58	53	34
% inundations that reach station	100	100	100	91	59
Hours inundated	439	372	316	201	104
% time inundated	61.0	57.7	43.9	27.9	14.6
Average length of each tidal cover (hour)	7.6 ± 0.9	6.4 ± 0.6	5.4 ± 0.7	3.5 ± 1.6	1.8 ± 1.6
Minimum length of each tidal cover (hour)	6	5	4	0	0
Maximum length of each tidal cover (hour)	10	8	6	5	5
Average length of each of dry period (hour)	4.9 ± 1.0	6.0 ± 0.5	6.9 ± 0.6	9.7 ± 7.7	14.6 ± 26.5
Minimum length of each dry period (hour)	1	5	6	7	8
Maximum length of each dry period (hour)	6	7	8	62	161

Field experiment. The mean water volume that flowed past and the mean water velocity in relation to distance from seaward edge of the mangrove forest on November 11, 1995 is shown in Fig. 7. The amount of water flowing past is a decreasing function of the distance from the seaward edge. The amount of water that passes station 5 is only 1/6 of the amount that flows past station 1. The variances on the mean velocities are significantly heterogeneous (Hartley's 1950 F_{max} -test (Sokal & Rohlf 1981), also after logarithmic transformation. Since the data does not meet the assumptions for an Anova,

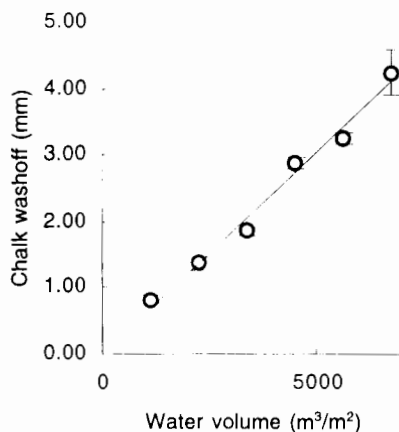


Figure 6. Relation between chalk washoff and volume water that flowed past. (Mean standard deviation). Regression line: $y = 0.0006 x + 0.0267$; $r^2 = 0.97$.

the equality of means were systematically tested pairwise using *t*-tests.

There is no significant difference in the water velocity at stations 2, 3, and 4 (20-60 m from the landward edge). However, the water velocity is significantly larger in the most seaward station, at the edge of the mangrove ($P < 0.01$), and especially at the most landward station, 80 m from the seaward edge ($P < 0.001$), and the mean velocity is also significantly different between the two (stations 1 and 5) ($P < 0.05$). The mean velocity in the seaward edge is not much, (though significantly) larger than inside the mangrove (Fig. 7), while at station 5 the mean velocity is more than 50 % larger than in the rest of the study area.

As a whole, the figure indicates that the conditions in relation to water currents and velocity are similar throughout most of the mangrove when under water. The factor that is variable, is the time inundated, and thereby the amount of water passing a certain point. The results are summarised in Tab. 2.

Distribution and abundance of C. capucinus

Mean density standard deviation for each of the four strata is shown in Fig. 8. The data was tested for homogeneity of variance using Hartley's (1950) F_{max} -test (Sokal & Rohlf 1981). The variances are significantly het-

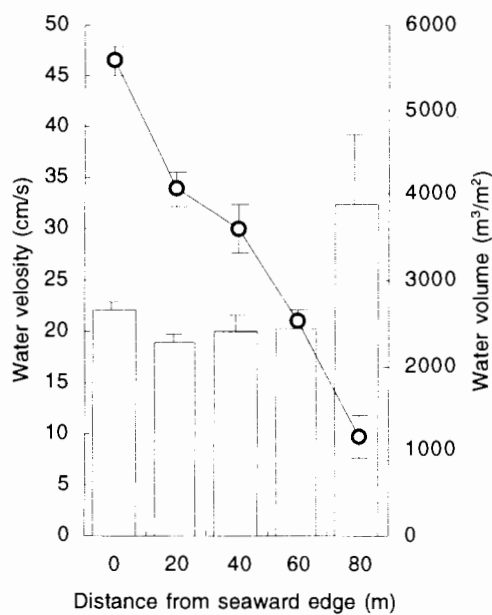


Figure 7. Mean water volume that flowed past (line) and mean water velocity (bars) through the study area during the tidal cycle on November 11, 1995. Small bars represents standard deviations.

erogeneous, so the data was subsequently transformed using $\log(x+1)$ transformation (Sokal & Rohlf 1981). The data does still not meet the assumptions of an Anova, i.e., the data are inherently heteroscedastic. Therefore the equality of means were systematically tested pairwise using *t*-tests. There is no significant difference in mean abundance between stratum 1 and 4, and no significant difference in means between stratum 2 and 3, but the means of stratum 2 and 3 com-

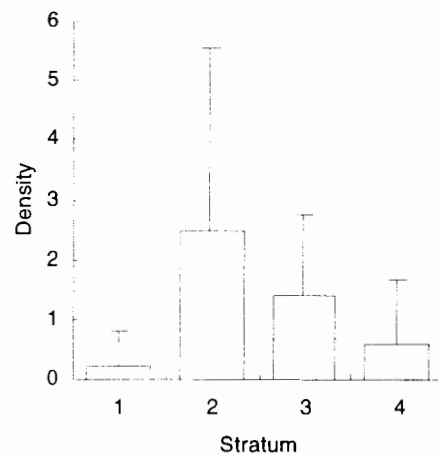


Figure 8. Mean density of *C. capucinus* per 4 m² sample. Horizontal bars represents the standard deviation of the mean.

pared to 1 and 4 are significantly different at 95 % experiment level of significance (Tab. 3). *C. capucinus* is more abundant in stratum 2 and 3 than in stratum 1 and 4.

The mean density in the population was 0.23 ± 0.08 snails per m² which corresponds to a population total of 861 ± 143 specimens in the study area.

Dispersion pattern. Ratios of sample variances to mean abundance's indicated that dispersion patterns were aggregated in stratum 2 and 4 ($P < 0.001$), while no significant departure from randomness was detected in the spatial pattern in stratum 1 and 3 ($P < 0.001$). The distribution was effectively random, but undetectable clump-

Table 2. Hours inundated, water volume passed and mean water velocity at the 5 different stations during one tidal cycle on November 11, 1995.

Station	Distance from seaward edge (m)	Hours inundated (hw)	Chalk washoff (mm)	Water volume (m ³ /m ²)	Flux/hours inundated (m ³ /m ² x hw)	Mean water velocity (cm/s)
1	0	7.0	3.4±0.10	5582±174	797±25	22.0±0.7
2	20	6.0	2.5±0.13	4065±207	678±41	18.8±1.0
3	40	5.0	2.2±0.17	3597±286	719±57	20.0±1.6
4	60	3.5	1.6±0.07	2539±115	725±33	20.2±0.9
5	80	1.0	0.7±0.21	1169±241	1169±241	32.5±6.7

Table 3. Pairwise *t*-tests for equality of mean densities between strata. Significant differences ($P < 0.05$) is indicated by an asterisk.

	Stratum 1	Stratum 2	Stratum 3	Stratum 4
Stratum 1	0			
Stratum 2	*	0		
Stratum 3	*	<i>ns.</i>	0	
Stratum 4	<i>ns.</i>	*	*	0

ing may have been present.

The maximum number of snails found in one sample was 10 individuals. Of these, 7 individuals were found in one breeding cluster. A total of 5 breeding clusters were encountered, 2 in stratum 2 and 3 in stratum 4. The maximum number in one aggregation was 7 individuals. Two snails found in the same cluster, were actively ovipositing. Egg capsules were exclusively found on or in crevices of old decomposing logs and tree stumps.

Feeding activity. 66, 47, and 70 % of the snails in stratum 1, 2 and 3 respectively, were actively feeding, and all were feeding on *S. cucullata*. Those not feeding were principally found in breeding clusters, a few on the mud. In stratum 4 only two snails (5 %) were found feeding on *S. cucullata*, while two were preying on *Cultellus* sp. The two snails were partly buried in the mud, having bored their characteristic hole through the prey shell near the umbo. This was the only instance where this prey species was observed in the study area (due to the fact that infauna was not investigated). Many specimens of *C. capucinus* were found on old decomposing roots and tree stumps, often with their proboscis extended into the wood, possibly feeding on wood boring molluscs (*Teredo* sp.).

Vertical distribution. The vertical distribution of the sampled snails from stratum 2 - 4 is illustrated in Fig. 9. Stratum 1 is omitted, due to the low number of snails found here. More snails are found on prop roots climbing to a higher level in the more sea-

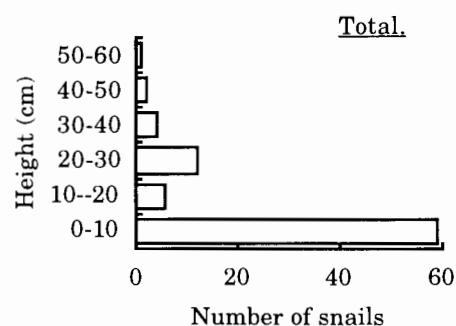
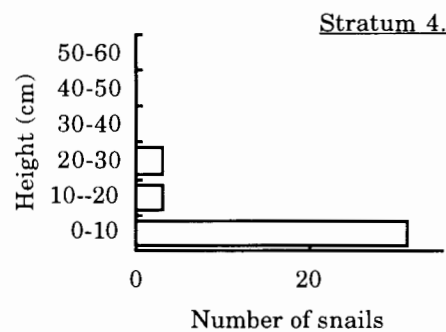
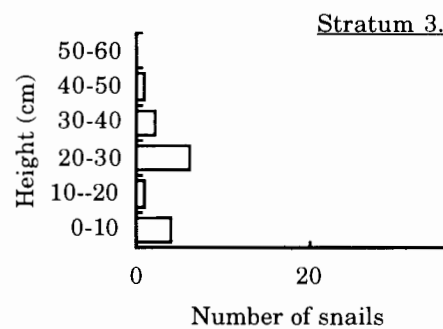
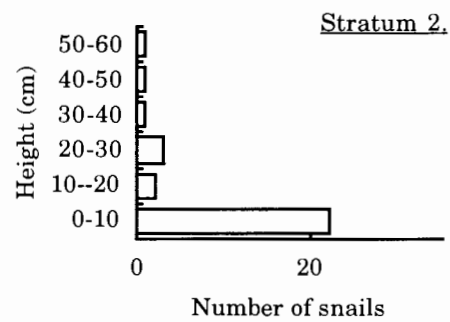


Figure 9. Vertical distribution of *C. capucinus*. Number of snails pr. 10 cm intervals in stratum 2 - 4, and total for the entire study area.

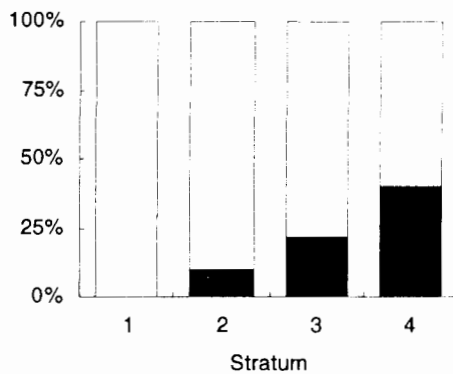


Figure 10. Substrate to which the snails were attached. White part of bar indicates snails on prop roots, black part indicates snails directly on the mud.

ward regions. In stratum 4, a high proportion (65 %) was found on the ground, approximately half of them attached to a root, the other half on the mud between roots (Fig. 10).

Distribution of potential prey

The most abundant sedentary tree-dwellers were the lamellibranch molluscs *S. cucullata* and *Isognomon ehippium* (Linné) and one species of unidentified acorn barnacle. All of these were very abundant in the 3 most seaward strata (Fig. 11), the most abundant being *S. cucullata*. Although no attempt was made to quantify the vertical distribution of the potential prey, a few observations of the zonation of the most abundant species were made. *I. ehippium* typically occur as bunched masses between the clefts of prop roots, often close to the mud. *S. cucullata* are mainly found cemented to the trunk and prop roots of the mangrove trees, from the mud up to approximately half a metre above the forest floor, but some are also found in clumps lying on the forest floor and some cemented to *I. ehippium*. Barnacles share the trunk and roots with the oysters, but extend their distribution higher up above the oysters, where they appear to be more numerous.

Barnacles were also found in stratum 4, but no sedentary lamellibranch molluscs were found here. The variation is much greater

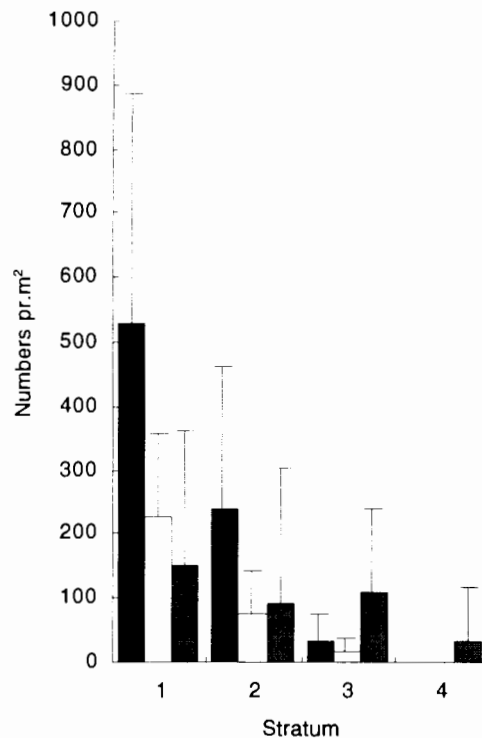


Figure 11. Distribution and abundance of the three most abundant potential prey species. Horizontal bars represents the standard deviation. Black = *S. cucullata*, white = *I. ehippium* and grey = barnacles.

than the mean indicating that the distribution of all three species is aggregated. The density and distribution of the observed species are summarised in Tab. 4.

Besides the fauna listed in Tab. 4, wood boring molluscs (*Teredo* sp.), were frequently encountered. The infauna was not investigated.

DISCUSSION

The mangrove environment is unique among sea shores in providing a sheltered muddy substratum with most of the vegetation growing above the level of high water of neap tides (Sasekumar 1974). In the present study some of the area was exposed to the air for 85 % of the time and covered by high tide only briefly, at varying and often long intervals. However, the leaf canopy provides a cool, stable and humid environment and

Table 4. Density and distribution of potential prey. Mean density values per metre square in each of the four strata.

	Stratum 1	Stratum 2	Stratum 3	Stratum 4
Distance from seaward edge (m)	0-10	10-20	20-30	30-80
Samples (n)	8	8	8	20
<i>Saccostrea cucullata</i> (Born)	531.5±355.1	239.0±223.5	33.0±41.4	
<i>Isognomon ephippium</i> (Linné)	228.5±127.0	75.5±67.1	15.5±22.9	
Acorn barnacle (<i>Thalamus</i> or <i>Balanus</i>)	150.0±211.4	93.5±207.6	107.5±133.9	35.0±84.0
<i>Semiricinula turbinoides</i> (Blainville)	2.5±3.0			
<i>Orania livida</i> (Reeve)	1.5±3.0	2.5±3.0		
<i>Littoraria</i> sp.		0.5±1.4		
<i>Nerita cf. albicilla</i> (Linné)	3.0±3.5	2.5±4.2	4.5±4.0	2.5±4.2
<i>Cerithidea cingulata</i> (Gmelin)	13.0±22.7	14.0±12.5		
<i>Monodonta labio</i> (Linné)	0.5±1.4			

the stems and roots provide a firm substratum. The strong wave action and extremes of temperature and evaporation which characterise rocky and sandy shores are considerably reduced on mangrove shores (Sasekumar 1974). Inside the mangrove forest the temperature is lower than on the mudflat, and the forest area represents a more equitable environment for the mangrove biota than the mudflat (Whitten *et al.* 1987).

Of all hydrographic measurements, current velocity is the most difficult to determine (Kjerfve 1990). Estuarine currents can be highly variable from one tidal cycle to another, and also vary strongly both in direction and in intensity with the stage of the tide, ebb tidal currents being stronger than flood tidal currents (Wolanski *et al.* 1980; Kjerfve 1990). In mangroves, accurate measurements of currents are often not possible because the density of vegetation precludes the use of current meters with fins, and because of low velocities.

The method used in the present study for measuring water flow and velocity only gives a crude measure of the mean water velocity during one particular tidal cycle. It ignores the variable directionality of the flow, with the rising and falling of the tide, and the ef-

fects on velocity created by the habitat. The flow of water does not take place through well defined channels, since these do not exist, but occur through a dense growth of trees and roots. In determining the relationship between chalk disintegration and water volume flown past in the laboratory, the flow was unidirectional and constant, and the water velocity generated in the flume was smaller than those observed in the field. This could also have an effect on the results. The estimates of mean velocity in Ao Nam Bor are high compared to the values reported by others (Wolanski *et al.* 1980). Despite its limitations, the method is sufficient to offer a comparison between the different stations of the physical conditions in regard to water velocity and turbulence.

The mean velocity is higher in the seaward edge of the mangrove than inside the mangrove, probably because the momentum of the water entering the mangrove is dissipated by friction around vegetation in the first few metre (Wolanski *et al.* 1980). However, the mean velocity inside the mangrove is only slightly smaller than along the edge. The mean velocity is high along the most landward edge of the study site. In this area the vegetation density was high and the forest floor was covered with leaf litter,

branches and rubbish. This may cause the water flow to be more constricted, resulting in more turbid water and a higher flow rate. In general the results indicate that the physical conditions inside the mangrove are fairly similar throughout the study site, when inundated by the tide. Water velocity and turbulence when inundated can, as single factor, and speaking in very broad terms, be excluded as a limiting factor on the distribution of the macrofauna within the mangrove. The interesting, and perhaps obvious, physical factor influencing the distribution of the macrofauna is time inundated, or perhaps more importantly the maximum time interval emerged. However, the extreme emersion period of over six days during neap tide along the landward edge of the study site did not exclude *C. capucinus* from extending its distribution to this area.

Even though the elevation of the land is low, the effect on the community structure is evident. Zonation patterns are clearly distinguished, especially in the most seaward regions. The most striking changes with distance from the edge is the rapid decrease of encrusting animals on the roots and trunks of the trees. This is commonly accepted to be due to the fact that they rely on frequent inundation for feeding (Sasekumar 1974; Whitten *et al.* 1987). Where tidal factors and food are not limiting the distribution of the sessile animals, the major limiting resource for the sessile species is the primary space for settling (Hunter 1970). In Ao Nam Bor these species are found only on the roots and tree trunks as there are no other substrates for settlement. Consequently the variability in the abundance of the encrusting animals within each of the three most seawards strata, is to a large extent accounted for by the heterogeneity in the habitat with respect to root cover, and comparable quantitative measurements of the tree-dwelling populations are impossible to obtain unless the surface area of the roots and tree trunks are calculated (Frith *et al.* 1976).

A sharp decline in the species diversity of benthic molluscan epifauna exists with in-

creasing distance from the seaward edge of the mangrove and hardly any benthic epifauna was encountered in stratum 4. Wells (1983) also found that benthic invertebrates are almost absent from the centre of the mangrove in the Bay of Rest, Western Australia, and reported this to be consistent with findings of others.

The difference in the vertical distribution of *C. capucinus* between strata, reflects the difference in tidal cover. In the more seaward regions the water level is high when inundated, and snails can crawl high up the roots and still be inundated for a certain period of time, while at higher levels of the shore, the vertical range is limited. The distribution of *C. capucinus* is three-dimensional and the space available for the snails to colonise within a certain tidal limit is effectively larger per unit surface area in the more seaward regions. Decreasing density per unit area with distance from the seaward edge may be a result of this.

Snails are principally found attached to the roots, but progressively more snails are found on the mud, with increasing distance from the seaward edge. This could, in conjunction with the constraints placed by the tide, be a reflection of the distribution of the prey, but may also reflect a specific preference for a hard substratum. The snails may be more protected from predation by crabs and fish during high tide, when attached to the roots. In the more landward regions the snails may also have a refugium from predation, since more snails are found directly on the mud here. An investigation of the potential predators of *C. capucinus* and their distribution and behaviour during high tide is needed to test this hypothesis. No predation of *C. capucinus* was observed during low tide.

Food does not appear to limit the distribution of *C. capucinus* within the mangrove. In the most seaward regions of the mangrove, *C. capucinus* principally prey on oysters, the most important occupant of the space supplied by the mangrove roots. The snail extends its distribution past the dis-

tribution of the oysters, into stratum 4, where it appears mainly to feed on the wood boring mollusc *Teredo* sp. However, food does have a significant effect on the abundance of the snail. In stratum 2 and 3 where oysters are abundant, the density of *C. capucinus* is much higher than in the more landward regions (stratum 4) where no oysters occur. In stratum 1 where food is very abundant, the snails are rare.

Desiccation is considered to be one of the primary factors influencing the distribution and habitat of the littoral fauna (Gibson 1970). Resistance to desiccation is dependent on temperature and humidity (Gibson 1970). The snails may be more exposed to desiccation at the seaward edge of the mangrove forest where there is no shelter from solar radiation, and the temperature gets high when exposed during the day. Low tide during the spring portions of the tidal cycle occur about dawn and dusk, with high tides during the midday and this may alleviate somewhat the effect of physical extremes encountered by the animals at the edge of the mangrove.

The density of *C. capucinus* in stratum 1 is surprisingly low, since food is abundant, the exposure time relatively short and the species was observed to be relatively abundant in other areas under seemingly similar environmental conditions. Outside the study area, *C. capucinus* was often observed on roots directly exposed to the sun in the seaward fringe of the mangrove, and in the mangrove at Ao Yon, Phuket, the species was found on the muddy substrate directly under the sun, where the mangrove canopy had been cut down. Therefore desiccation did not generally appear to be a deciding factor in determining the distribution of the species. The low number of snails in stratum 1, could possibly be caused by an "island effect", due to the nature of the habitat, and the patchy

distribution of the prop. roots in this area. Snails may not readily cross the relatively open area between the roots in stratum 1 and 2.

The aggregated distribution of *C. capucinus* in stratum 2 and 4 can be accounted for by the breeding clusters found here. Except for the breeding clusters, more than 3 snails were never observed in one place, and in stratum 1 and 3 where *C. capucinus* was randomly dispersed no breeding clusters were encountered. It appears that the snails are randomly distributed when feeding, but aggregate to breed.

C. capucinus is only found inside the mangrove biotope, and is never observed on the adjacent mud flat. One could speculate that this is because of lack of food, since neither oysters nor *Teredo* is found here. A dense population of cerithids (*Cerithium cingulata* (Gmelin, 1791) is, however, found abundantly on the mud flat bordering the mangrove forest. In the laboratory *C. capucinus* from Ao Nam Bor readily attacks this species, and show a strong preference for the small gastropod over oysters (Gribsholt, in prep.). On the mud flat there is no firm substrates, and snails may be more exposed to predation and dislodgement, and the risk of desiccation may be higher. The mudflat constitute an environment of an altogether different and more variable character than the environment provided by the mangrove forest.

ACKNOWLEDGEMENTS

Thanks are due to the staff at Phuket Marine Biological Center, particularly the Reference Collection Unit, for their assistance during my stay in Thailand. I thank Professor Jorgen Hylleberg for the opportunity to participate in the TMMP, and Dr. Peter Middelfart and Svend Steinfeldt for supervision, advice, and general support.

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