# PHYSICAL AND CHEMICAL CHARACTERISTICS OF MANGROVE CRAB (NEOEPISESARMA VERSICOLOR) BURROWS IN THE BANGRONG MANGROVE FOREST, PHUKET, THAILAND; WITH EMPHASIS ON BEHAVIOURAL RESPONSE TO CHANGING ENVIRONMENTAL CONDITIONS

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# PHYSICAL AND CHEMICAL CHARACTERISTICS OF MANGROVE CRAB (*NEOEPISESARMA VERSICOLOR*) BURROWS IN THE BANGRONG MANGROVE FOREST, PHUKET, THAILAND; WITH EMPHASIS ON BEHAVIOURAL RESPONSE TO CHANGING ENVIRONMENTAL CONDITIONS

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*NEOEPISESARMA VERSICOLOR*
SESARMID CRAB
BURROW MORPHOLOGY
BURROW WATER CHEMISTRY
BEHAVIOURAL RESPONSE
TEMPERATURE
SALINITY

ABSTRACT. – Morphology of burrows made by the leaf-eating sesarmid crab, *Neoepisesarma versicolor* at the Bangrong mangrove forest, Phuket, Thailand, was investigated using *in situ* resin casts. In addition, the temporal variation in temperature and salinity of crab burrow water was compared with the behavioural response of crabs to changes in these environmental parameters. Burrows in the high intertidal zone typically have 2-5 openings and vary in basic morphology. The openings are associated with vertically oriented shafts of 5 to 25 cm depth. The remaining part of burrows usually comprises smooth walled horizontal tunnels of 1.8 to 5.2 cm diameter with several dead-ends and small chambers in an unpredictable pattern. The depth of burrows in Bangrong varies from 55 to 110 cm. Burrow morphology is affected by factors such as sediment characteristic and age of burrows as well as type and abundance of associated fauna. The average burrow has a volume of about 11 × $10^3$ $cm^3$ and a wall surface area of about 17 × $10^3$ $cm^2$. At a normal crab density of 0.2 $m^{-2}$, *N. versicolor* burrows displace 0.3% of the sediment volume to a depth of 84 cm and the sediment-water (air) interface is increased by 33.6%. The constantly cool (around 28 ºC) water in the extended and tidally irrigated crab burrows is high in salinity (30-38‰), but remains oxic and very low in sulfide most of the time. *N. versicolor* is not affected severely by salinity fluctuations, but prefers salinities between 10 and 30‰, which is below the normal burrow water salinity. Most crabs avoid temperatures above 29 ºC, indicating that the cool burrows are ideal shelters during hot days. Burrows therefore provide crabs with protection from particularly high temperature, desiccation and predators while maintaining tolerable conditions with respect to other essential parameters.

*NEOEPISESARMA VERSICOLOR*
CRABE SÉSARMIDÉ
MORPHOLOGIE DES GALERIES
CHIMIE DE L'EAU DES GALERIES
RÉPONSE COMPORTEMENTALE
TEMPÉRATURE
SALINITÉ

RÉSUMÉ. – La morphologie des galeries du Crabe Sésarmidé *Neoepisesarma versicolor*, qui se nourrit de feuilles dans la mangrove de Bangrong, Phuket, Thaïlande, a été étudiée *in situ* à l'aide de moulages en résine. En outre, la variation temporelle de la température et de la salinité de l'eau des galeries de Crabes a été comparée avec la réponse comportementale des Crabes aux changements de ces facteurs environnementaux. Les galeries de la zone intertidale élevée offrent 2-5 ouvertures et leur morphologie est variable. Les ouvertures sont associées à des souches orientées verticalement entre 5 et 25 cm de profondeur. La partie restante des galeries comprend généralement des tunnels horizontaux à parois lisses de 1,8 à 5,2 cm de diamètre dont plusieurs sont sans issue, et de petites chambres disposées de manière aléatoire. La profondeur des galeries de Bangrong varie entre 55 et 110 cm. La morphologie de ces galeries de Crabes est influencée par des facteurs tels que les caractéristiques des sédiments, par leur âge, ainsi que par le type et l'abondance de la faune associée. Les galeries ont un volume moyen d'environ 11 × $10^3$ $cm^3$ et une surface pariétale d'environ 17 × $10^3$ $cm^2$. A une densité normale des Crabes de 0,2 $m^{-2}$, *N. versicolor* déplace 0,3 % du volume sédimentaire lors du creusement à une profondeur de 84 cm, et l'interface sédiment-eau (air) s'accroît de 33,6 %. L'eau, dont la fraîcheur est maintenue constante (environ 28 °C) dans les galeries entières et irriguées par les marées, offre une salinité élevée (30-38 ‰), mais demeure oxygénée et avec un faible taux de sulfide la plupart du temps. *N. versicolor* n'est pas affecté sévèrement par les fluctuations de salinité entre 10 et 30 ‰, valeur qui est inférieure à la salinité normale de l'eau de la galerie. La plupart des Crabes évitent les températures supérieures à 29 °C, ce qui indique que les galeries fraîches sont des abris idéaux pendant les jours chauds. Les galeries assurent ainsi aux Crabes protection contre les températures très élevées, la dessication et les prédateurs, tout en maintenant des conditions de vie tolérables en ce qui concerne les autres facteurs du milieu essentiels.

## INTRODUCTION

Sesarmid crabs are among the dominant crustaceans in intertidal mangrove ecosystems of Southeast Asia. Their habit of eating mangrove leaves and processing plant materials make them important mediators of organic matter transformation and nutrient dynamics (Robertson 1986, Robertson & Daniel 1989, Lee 1989, N Thongtham pers obs). They actively dig and maintain burrows in the sediment (Gherardi *et al*. 1999). The burrow has a variety of functions, such as providing a refuge from disturbance, predation (Warren 1990) and environmental extremes (Dittmann 1996), as well as forming a food storage (Giddins *et al.* 1986).

Burrows of crabs and other invertebrates affect sediment topography and biogeochemistry, by modifying particle size distribution, drainage, redox conditions, and organic matter decomposition within the sediment (Warren & Underwood 1986, Mouton & Felder 1996, Botto & Iribarne 2000). The burrows also act as conduits of organic matter transport, either passively by gravity and tidal action or actively when crabs pull leaves into their burrows, and thus supplying the associated communities of microorganisms and animals with substrates (Lee 1998, Smith III *et al*. 1991). In contrast to other crustaceans i.e. fiddler crabs (*Uca* spp.) and thalassinidean shrimps, only few studies have examined the morphology of sesarmid crab burrows and their effects on sediment structure (Nickell & Atkinson 1995, Rowden & Jones 1995, Bird & Poore 1999, Kinoshita 2002). Many species of sesarmid crabs construct deep burrows in hard, dry mud between dense roots of mangrove trees making excavation extremely difficult (Emmerson 2001).

Sesarmid crabs are known to remove and ingest most of the daily leaf litter fall in Asian, Australian and African mangrove forests (Robertson 1986, Micheli 1993, Olafsson *et al*. 2002, N. Thongtham pers obs.). *N. versicolor* is one of the most conspicuous sesarmid crab species in mangrove forests of Thailand. This particular species is a delicacy in the Thai cuisine and consequently of economic importance for and intensively harvested by local people in coastal areas. However, little attention has been paid to the impact of its burrowing and deposit feeding activities on mangrove communities and sediment dynamics. The objective of this study was therefore to identify and characterize the physical structure (burrow morphology), chemical environment (e.g. salinity, oxygen and sulfide) and temperature conditions of *N. versicolor* burrows in the Bangrong mangrove forest, Thailand. The results are supplemented with and related to observations of the behavioural response of *N. versicolor* to changes in temperature and salinity.

## MATERIALS AND METHODS

*Study site*: The study was conducted in the Bangrong mangrove forest, Phuket, Thailand (8º 03' N, 98º 25' E). For a detailed description of the basic geomorphology, hydrology and biogeochemistry of the area, consult Kristensen *et al*. 2000, Holmer *et al*. 2001, Suraswadi & Kristensen 2002. The physical characteristics of *N. versicolor* burrows were studied at 4 stations from the high intertidal to the mid intertidal zone of the forest (Fig. 1). The dominant trees in this area were *Rhizophora apiculata*, *R. mucronata, Acanthus* sp., and *Ceriops tagal*.

Station 1 was located in the innermost part of the mangrove forest, close to the main creek. This station was the primary study site where most measurements were performed. Stations 2 and 3 were located at the forest floor between few trees, mostly saplings of *C. tagal*. Station 4 was located in the outermost part of the forest near a boat pier where most trees were cut, except for a few remaining *R. apiculata*.

*Sediment characteristics*: Three replicate sediment cores were sampled from each station by hand at low tide using 8 cm. i.d. transparent acrylic core tubes. After sectioning into the chosen depth intervals (0–1, 2–3, 6–8 and 14–16 cm), subsamples from each slice were taken to determine density, water content, organic content and grain size. Density was determined as the weight of a known volume of wet sediment. Water content was obtained as weight loss upon drying the sediment at 95 ºC for 24 h. The dried sediment was subsequently used for determination of organic matter as the loss of weight after ignition at 520 ºC for 5 h. Other subsamples of wet sediment were sieved through a Wentworth series of sieves to determine the grain size distribution.

*Morphology of N. versicolor burrows*: Burrow morphology was examined from resin casts in areas with few trees present to prevent interference from roots and to minimize destruction of trees during excavation. Two to three casts were randomly excavated from each station.

The number and diameter of burrow openings in the area were determined. Polyester resin (manufactured by Thai polyset, marketed as polylight PF 042TP by Pongpana Co., Thailand) was mixed thoroughly with pe-

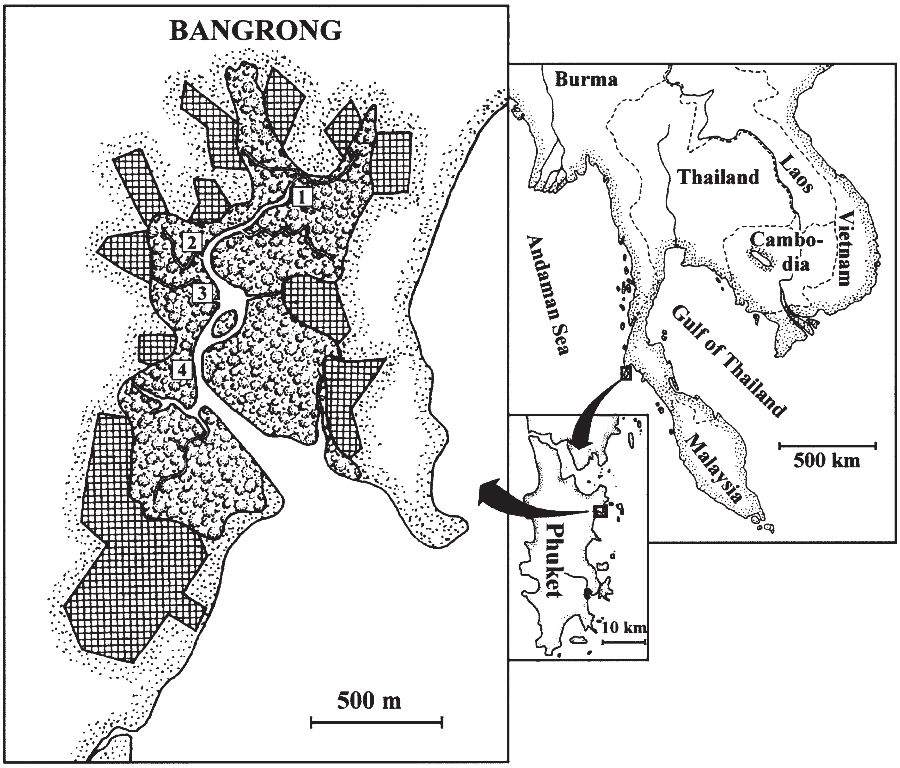

Fig. 1. – Map of the Bangrong mangrove forest, with indication of sampling stations. The cross-hatched areas represent shrimp ponds.

roxide catalyst (36% Methyl ethyl ketone peroxide in dimethyl phthalate) at a ratio of 1% v/v in a 2-litre plastic can. The mixture was poured slowly into one average-sized burrow opening until this and all connected openings were completely filled with resin. The resin was left to harden for at least one day. Subsequently, the casts were excavated by hand and shovel. The depth of burrows into the sediment was noted during excavation.

After careful cleaning, the resin casts were photographed. A qualitative description of burrows was made from photos, describing the overall structure and branching type. The burrows were subsequently described quantitatively by measuring the diameter of burrow shafts and galleries for every 10 cm using a sliding caliper (±0.1 mm). Burrow volume (v, $cm^3$) was calculated using the weight of casts and the specific density of the resin (1.2 $g\ cm^{-3}$). From the average burrow diameter (d, cm) and the burrow volume, burrow length (L, cm) and surface area (s, $cm^2$) can be calculated using the following equations:

$$L = 4v(\pi d^2)^{-1}$$
$$s = \pi dL$$

*Chemistry and temperature of water in N. versicolor burrows*: A narrow silicone tube was carefully inserted as deep as possible (about 25 cm) into 3 crab burrows at station 1. Water within the burrows was collected using a 60 ml syringe every hour for 12-hour periods at both spring and neap tide. Control samples of creek water from the main creek were obtained similarly. The samples were analyzed for $O_2$ by the standard Winkler technique (Parsons *et al.* 1984), $CO_2$ by the flow injection/diffusion cell technique (Hall & Aller 1992), and salinity using a hand refractometer. A separate water sample was transferred to 20 µl of 20% zinc acetate and subsequently analyzed for hydrogen sulfide by the methylene blue method (Cline 1969).

The water level in the main creek was continuously monitored from a level pole placed in the creek. Simultaneously, temperatures inside and around air-exposed crab burrows were measured using liquid-in-glass thermometers. The thermometer was inserted 15 to 30 cm (depending on complexity) into burrows during receding tide in the morning (6:30). Temperature was monitored every hour during the following low tide period and terminated during rising tide in the evening (18:30). Three replicates were done for burrows exposed to the sun and in the shade of mangrove trees, respectively. Temperatures were also obtained from surrounding surface sediment exposed to the sun and in the shade, as well as water in the adjacent creek.

*Behavioural response of N. versicolor to changing environmental conditions*: Observations of behavioral response were made with *N. versicolor* in an aquarium (30×125×30 cm), which was divided into three compartments by 7 cm high Plexiglas separators. The middle and largest compartment (55 cm wide) was filled with mangrove sediment to 7 cm depth, while the two lateral compartments were filled with water. Crabs released to the middle compartment were allowed to move freely into either of the two lateral compartments. One of these acted as a control and contained 25‰ seawater at a temperature of 29 °C, while the other contained water of variable salinity or temperature. In one experiment the salinity was gradually increased from 0 to 40‰ in steps of 5‰ every 24 h while the temperature remained at 29 °C. In another experiment, the temperature was increased from 29 to 36 °C in steps of 2–3 °C every 24 h while the salinity was maintained at 25‰. At the start of each experiment, 14 crabs were released to the middle sediment compartment. A video camera was mounted to observe the number of crabs entering each of the water-filled compartments at hourly intervals during 24-hour periods as well as the average duration each crab spent in the compartments.

Observations from the two compartments during different treatments were compared using paired Students t-test, where each pair was the hourly mean of data obtained from each experiment.

## RESULTS

### *Sediment characteristics*

The sediment at the study sites consisted of impermeable silt and fine sand with a median particle size between 66 and 152 µm and 35-48% of particle less than 63 µm (Table I). The porosity was high (0.4-0.75) and generally decreased with depth in the sediment except at station 4 (Table II). Organic matter content ranged between 7 and 14% dw and did not vary much among stations or with depth in the sediment, except for station 4 and to a lesser extent station 2 where the organic content increased linearly by 83 and 30%, respectively, from the surface to 14–16 cm depth (Table II).

### *Morphology of* **N. versicolor** *burrows*

Burrows of *N. versicolor* were most frequent in the high intertidal zone between roots and trunks of mangrove trees, where 4-5 openings $m^{-2}$ (station 1) were observed compared with 2 openings $m^{-2}$ in the mid intertidal zone (station 4). The openings of fully developed *N. versicolor* burrows were easily distinguishable from those of other species due to their larger size (diameter between 3 and 9 cm). Occupied burrows had traces of crab activity on the recently excavated sediment around burrow openings and occasional remains of partly eaten leaves as well as deposited faeces. Since crabs inhabiting specific burrows were difficult to catch as they disappeared between roots, in crevices or deep down in their burrows, no relationship was obtained between carapace width and burrow diameter.

Table I. – Characteristics of sediment surrounding burrows at the selected stations in the Bangrong mangrove forest.

| Station | sediment type | Silt (< 63 µm) % d.w. | Median grain size µm |
|---|---|---|---|
| 1 | muddy sand | 48 | 66 |
| 2 | fine sand | 35 | 152 |
| 3 | very fine sand | 35 | 103 |
| 4 | very fine sand | 37 | 114 |

Table II. – Organic matter content and porosity of sediment surrounding burrows at the selected stations in the Bangrong mangrove forest. Values are given as mean ± S.E.

| Station | Depth cm | Organic content % d.w. | Porosity vol/vol |
|---|---|---|---|
| 1 | 0-1 | 13.5 ± 1.0 | 0.75 ± 0.02 |
| | 2-3 | 10.5 ± 1.8 | 0.65 ± 0.05 |
| | 6-8 | 11.5 ± 1.4 | 0.69 ± 0.06 |
| | 14-16 | 10.8 ± 0.9 | 0.65 ± 0.05 |
| 2 | 0-1 | 8.7 ± 0.5 | 0.68 ± 0.02 |
| | 2-3 | 8.6 ± 0.1 | 0.62 ± 0.02 |
| | 6-8 | 10.0 ± 0.3 | 0.63 ± 0.02 |
| | 14-16 | 11.3 ± 1.5 | 0.64 ± 0.01 |
| 3 | 0-1 | 9.3 ± 0.4 | 0.65 ± 0.02 |
| | 2-3 | 8.0 ± 0.6 | 0.57 ± 0.02 |
| | 6-8 | 8.2 ± 0.2 | 0.59 ± 0.01 |
| | 14-16 | 9.4 ± 0.4 | 0.63 ± 0.00 |
| 4 | 0-1 | 6.6 ± 1.1 | 0.41 ± 0.16 |
| | 2-3 | 7.3 ± 1.2 | 0.51 ± 0.03 |
| | 6-8 | 8.8 ± 1.5 | 0.53 ± 0.04 |
| | 14-16 | 12.1 ± 2.5 | 0.50 ± 0.09 |

The shape and morphology of crab burrows varied considerably, and no two burrows were similar. Their shapes ranged from very simple, straight burrow with few branches as shown in Fig. 2 D from station 4, to the complex, labyrinthine structures with up to 5 openings, as found at the other stations (Fig. 2A-C). The surface opening of burrows was always associated with a more or less vertically oriented shaft. The length of the shaft varied from 5 to 25 cm among casts. Small burrows protruding as side branches to the large burrow shafts were evident in all examined *N. versicolor* burrows and belong to an associated fauna of small crustaceans and juvenile sesarmids. The remaining part of burrows usually comprised smooth walled horizontal tunnels with several dead-ends and small chambers in an unpredictable pattern. Transverse shape of the burrows was circular to oval with a diameter ranging from 1.8 to 5.2 cm. The depth of burrows varied from ca. 55 to 105 cm (Table III). Most burrows reached the low tide water table, although two burrows in the innermost high-intertidal area were dry at the bottom at low tide. The volume of the examined burrows ranged from 5 to 19 × $10^3$ $cm^3$. The total length of individual burrows was 5-45 m and the walls had an area of 8–33 × $10^3$ $cm^2$.

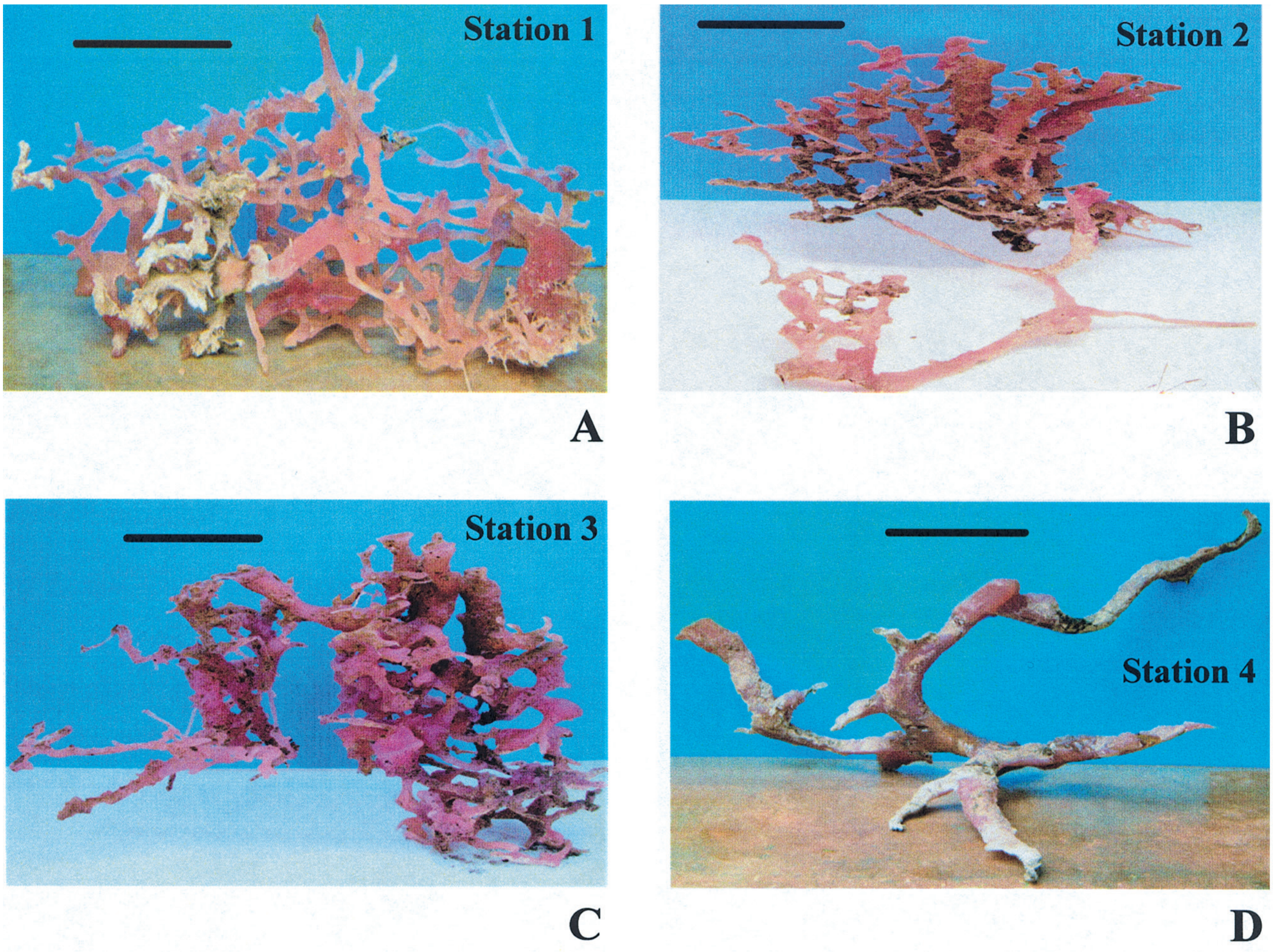

Fig. 2. – Resin casts of *N. versicolor* burrows from the examined stations in the Bangrong mangrove forest (scale = 30 cm).

Table III.– Morphometric characteristics of *N. versicolor* burrows based on resin casts. The average values are given ± S.E. The station origin of casts is given with reference to those shown in Fig. 2 by letters in brackets.

| Station (cast) | surface openings (#) | depth (cm) | mean diameter (d, cm) | volume (v, x10$^3$ cm$^3$) | total length (L, cm) | surface area (s, x10$^3$ cm$^2$) |
|---|---|---|---|---|---|---|
| 1 (A) | 4 | 70 | 1.8 | 7.02 | 2,757 | 15.59 |
| 2 (B) | 4 | 95 | 2.5 | 12.67 | 2,582 | 20.27 |
| 2 | 2 | 65 | 2.3 | 18.85 | 4,537 | 32.78 |
| 3 (C) | 5 | 106 | 2.4 | 8.39 | 1,855 | 13.98 |
| 3 | 4 | 87 | 2.4 | 12.76 | 2,820 | 21.26 |
| 4 (D) | 1 | 105 | 5.2 | 10.51 | 495 | 8.09 |
| 4 | 2 | 85 | 4.1 | 12.56 | 952 | 12.26 |
| 4 | 2 | 55 | 2.1 | 5.00 | 1,444 | 9.53 |
| average | 3.0 ± 0.5 | 84 ± 7 | 2.9 ± 0.4 | 10.97 ± 1.51 | 2,180 ± 452 | 16.72 ± 2.82 |

### ***Burrow water chemistry and temperature***

The salinity in crab burrows (30–38‰) at station 1 was generally higher than water in the main creek (30–35‰), but exhibited a similar tidal variation (Fig. 3A, B). Salinity generally decreased during falling tides and increased during rising tides. Carbon dioxide in the crab burrow water (2.6–4.4 mM) was always higher than in creek water (1.9–2.9 mM) with only limited tidal changes (Fig. 3C, D). Oxygen in burrow water was gener-

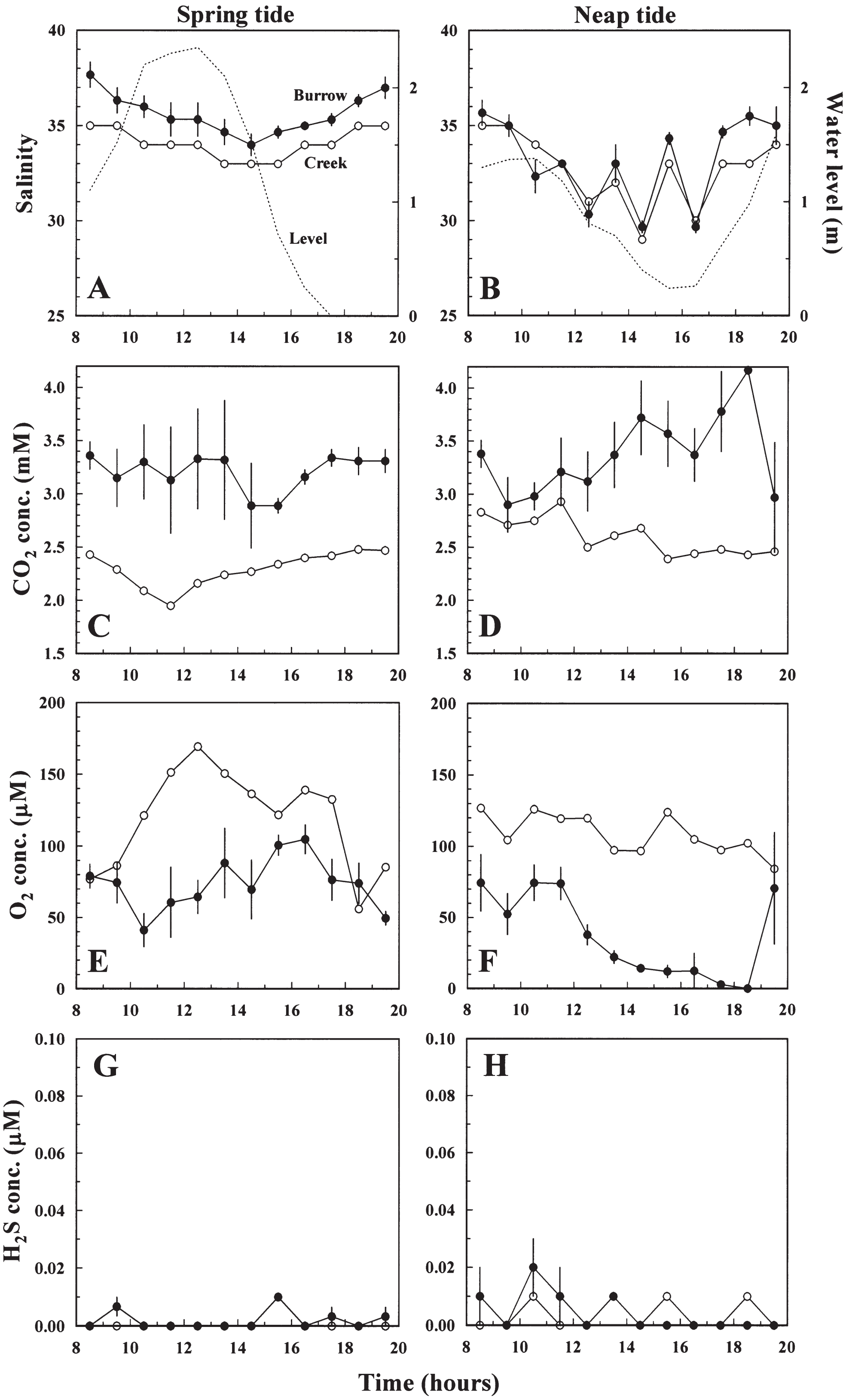

Fig. 3. – Temporal variations of salinity, carbon dioxide and oxygen concentrations in crab burrow water throughout tidal cycles during spring and neap tide. The results are compared with variations in creek water (● burrow water, ○ creek water, -----– water level).

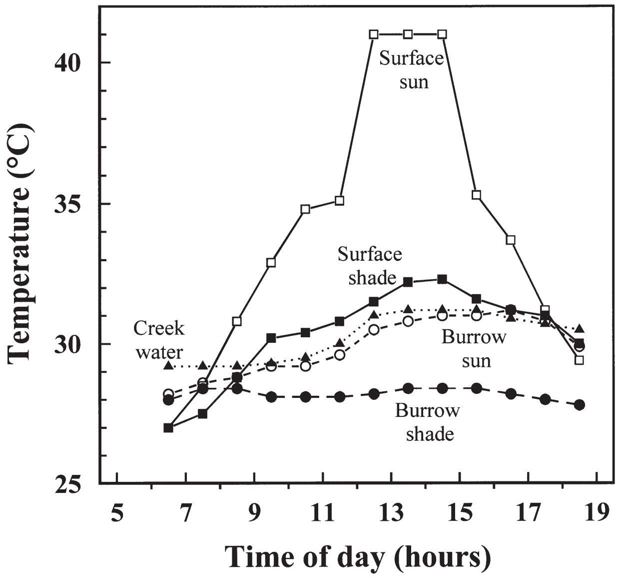

Fig. 4. – Temperatures at different locations within and around crab burrows at the Bangrong mangrove forest. Values for burrows are mean of temperatures from 3 burrows. All other values are based on single measurements.

ally lower than in the main creek, but fluctuated more with tides in an inverse pattern to that of carbon dioxide (Fig. 3E, F). Oxygen was similar in creek and burrow water at low water at spring tide, but increased more in creek than burrow water during rising tide. At neap tide, the difference in oxygen was least at high water and largest at low water. Sulfide in crab burrow was generally low and almost undetectable in both burrow and creek water, except for low concentrations at high water during neap tide (Fig. 3G, H).

Temperature at the various microhabitats in Bangrong fluctuated depending on location and time of the day (Fig. 4). Temperature of surface sediment exposed to the sun exhibited the largest variation. Heating by the sun increased temperature from a morning level of 27 °C to 41 °C during early afternoon, while a cooling to about 29 °C occurred in the late afternoon. Surface sediment shaded by trees was also exposed to fluctuating temperatures, but with a much lower amplitude; warming from 27 °C in the morning to 32 °C during the early afternoon and a subsequent cooling to 30 °C in the late afternoon. Temperatures within crab burrows in the shade was 1 °C higher than surface sediment in the morning, but remained almost constant throughout the day, while those exposed to the sun fluctuated 3 °C, from 28 °C in the morning to 31 °C in the afternoon. Creek water temperature was 2 °C warmer than surface sediment in the morning, but only increased to a maximum of 31 °C during the afternoon.

### *Behavioural response of* **N. versicolor**

Each crab released in the middle sediment compartment of the aquarium moved to the two lateral water compartments once or twice every hour. Some individuals were in the water only for 10 sec before returning to the sediment compartment, while others remained immersed for hours, indicating that this species has a well-adapted and versatile respiratory system. Most of the crabs left the water immediately when the temperature was higher than 29 °C, or when the salinity was lower than 10‰ or higher than 30‰. The average number of immersed crabs and the time they spent in the test compartment at 29 °C and within the salinity range of 10 and 30‰ (Fig. 5) were not significantly different from those in control compartments. Outside these limits, the number of visits and time spent in the test compartment was significantly lower ($p < 0.01$) than in the control compartment. The mean immersion time at 32 °C and 15 ‰ was much longer than at the control temperature because one crab in each case remained immersed at this temperature and salinity for extended time.

## DISCUSSION

### *Burrow morphology and environmental conditions*

Burrows of *N. versicolor* are found mostly among roots of trees in mid to high intertidal zones of mangrove forests. Casts demonstrate that the burrow morphology varies considerably between but also within locations, and differs in appearance from other burrowing crab species. However, the dimensions of *N. versicolor* burrows are comparable to those previously reported for *Sesarma messa* burrows in Australian mangrove forests (Stieglitz *et al.* 2000a). The structure and general characteristics of the sediment appears to be an important factor determining the distribution and morphology of crab burrows (Morrisey *et al.* 1999, Frusher *et al.* 1994, Frith *et al.* 1976). Other factors affecting the appearance *of N. versicolor* burrows include age of burrows, number of occupants, intensity of predators and burrowing activity of associated fauna (Stieglitz *et al.* 2000a, Candisani *et al.* 2001, Kinoshita 2002).

The simple burrow structure with few branches and just one opening as found in the compact (low porosity) sediments at station 4 suggests that crabs create simple burrow structures when the sediment is of a relatively hard nature (Fig. 2). Softer (high porosity) sediment, on the other hand, allows more complex structure of burrows because the crabs can

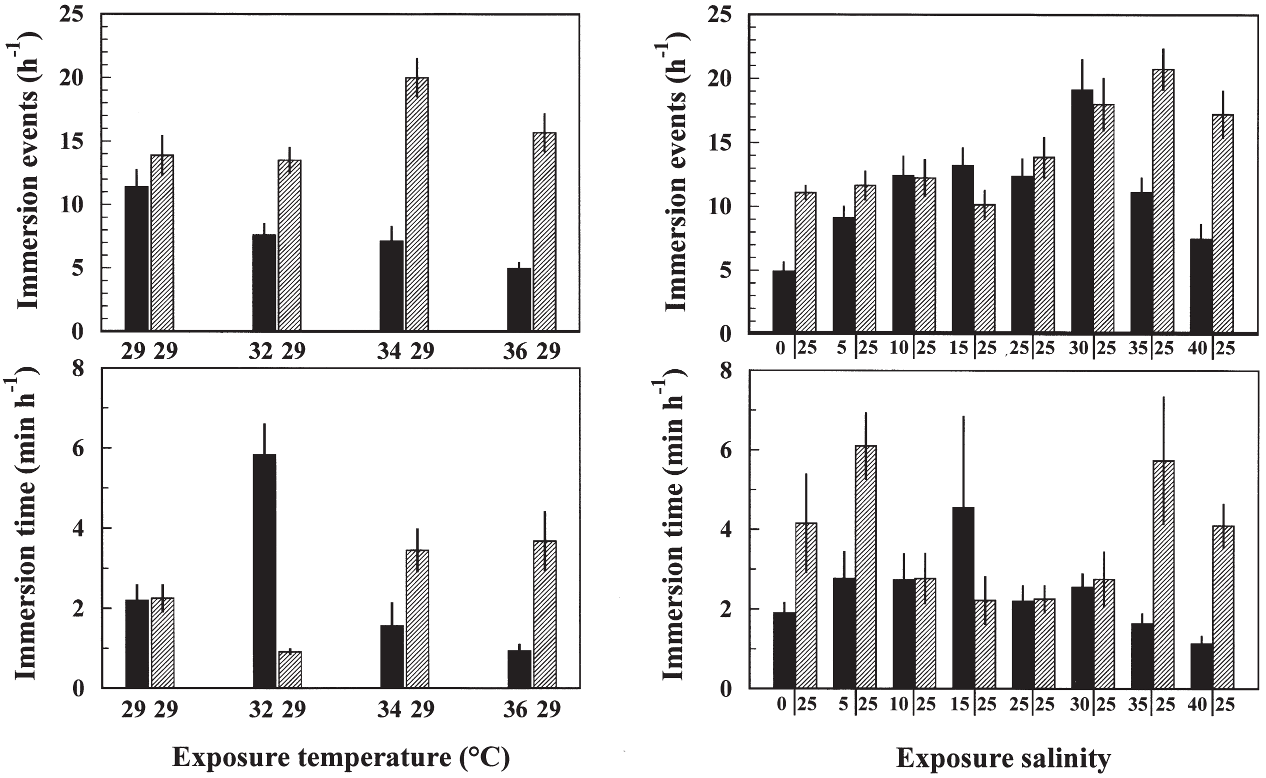

Fig. 5. – On the left, upper panel: number of immersion events per hour (mean ± SE); lower panel: Total time immersed in minutes per hour (mean ± SE) by crabs allowed to choose between water of various experimental temperatures and a fixed control (29 °C) temperature. The experiment lasted 24 hours. On the right, upper panel: number of immersion events per hour (mean ± SE); lower panel: Total time immersed in minutes per hour (mean ± SE) by crabs allowed to choose between water of various experimental salinities and a fixed control (25‰) salinity. The experiment lasted 24 hours.

easily change direction by purpose or avoid obstructions when digging. The depth of burrows also varies considerably, but most of them penetrate to the low tide water table and only few burrows in the uppermost high intertidal area actually dry out during low tide. The multiple entrances to the burrow systems presumably provide easy access to shelter from predators as threatened crabs rapidly retreat into the nearest available burrow opening.

Continued maintenance and number of generations of crabs that occupy the burrows will add complexity to the morphology through time. Each adult *N. versicolor* normally occupies its own burrow, except for temporary visits of neighbouring crabs while seeking refuge. These unwanted visitors are usually rapidly expelled again as *N. versicolor* is territorial and willing to fight for burrows (N. Thongtham, pers obs). More than 75% of the burrows under study were observed to have occupants continuously for more than a year, which is considerably longer than for other grapsid species such as *Sesarma meinertii* and *Cardisoma carnifex* (Micheli *et al.* 1991). Neighbouring burrows may accidentally become fused despite the territorial behavior and add to the variation and complexity of burrow morphology, which greatly exceeds that of other decapod crustaceans such as thalassinidean mud shrimps and fiddler crabs (*Uca* spp.) (Rowden & Jones 1995, Botto & Iribarne 2000, Kinoshita 2002). The complex structure of *N. versicolor* burrows may also be the result of continued digging efforts by several generations of occupants as well as burrowing of associated fauna such as alpheid shrimps, fiddler crabs and juvenile sesarmids (Emmerson 2001). The associated fauna is particularly important in the shallow parts where their burrows protrude as small side branches to the large burrow shafts. However, resin casts may not retrieve all the laterally extended branches due to the viscous nature of the resin. Furthermore, breakage of narrow branches during excavation may have resulted in incomplete recovery of burrows.

The complexity of burrows prevents collection of water from the deepest parts by the presently applied technique. The flexible tube used could only be inserted to a depth of about 25 cm into burrows. The sampled burrow water may therefore be contaminated with creek water especially during high tide when burrows were completely flooded. Thus, by the use of a newly developed conductivity and sampling probe, Stieglitz *et al.* (2000a, b) found that tidal mixing of water in burrows of *Sesarma messa* and *Alpheus macklay* caused complete flushing within one hour during high tide. Consequently burrow water composition in the present study is only slightly different from water in the main creek when currents are strong and tidal irrigation of burrows extensive during spring tide periods (Ridd 1996), whereas large differences may develop during neap tide periods, particularly at low tide (Stieglitz *et al.* 2000a). The lower salinity of water in the creek than burrow water (Fig. 3A, B) is consistent with results of Suraswadi (2002). Salinity in Bangrong creeks is highly variable and can be as low as 26.0‰, while the salinity of porewater remains high at 37–39‰ due to evaporation during air exposure and exclusion of salt by tree roots (Passioura *et al.* 1992, Suraswadi 2002). Average temperature of the crab burrows under the shade of mangrove trees and those exposed to the sun are generally lower and certainly more constant than in the open air at the sediment surface (Fig. 4), especially when the sediment surface is exposed to the sun (may reach 41°C).

The higher carbon dioxide and lower oxygen concentrations in burrow water compared with creek water (Fig. 3C, D, E, F) is caused by the vicinity of burrows to respiring organisms (crabs, associated fauna and microorganisms) as well as chemical reoxidation processes and diffusion across the burrow wall (Kristensen 2000). When crabs stay inside their burrows e.g. during high tide oxygen in burrow water is depressed (to about 50% of the level in creek water). Anyway, oxygen remains present at sufficient levels for the inhabitants (Hagerman 1998, McMahon 2001) and is replenished from entrapped air and by tidal irrigation. As burrows emerge during low spring tide, and crabs leave their burrows, rapid percolation of oxygen-rich water from the creek increases oxygen in burrow water to a level approaching that of creek water. However, less water percolates into burrows at the more sluggish current and lower tidal amplitude during neap tides causing a decrease in oxygen to very low levels. As the crabs mostly are out of burrows or remain near the opening at this time, they are not affected by the noxious conditions deeper in burrows. The renewal of oxygen in burrow water during high tide not only serves respiratory purposes for the inhabitants, but also oxidizes and thus removes potentially toxic metabolites (e.g. sulfide and ammonium) (Kristensen 2000). Accordingly, sulfide is rarely detected in burrow water at high tide during both spring and neap periods (Fig. 3G, H).

*N. versicolor* is an active burrower particularly in the upper intertidal area of the Bangrong mangrove forest. Its abundance at the primary study site (station 1) has been found to be 0.2 ind. $m^{-2}$ (N Thongtham pers obs). Accordingly, *N. versicolor* burrows displace 0.3% of the sediment volume down to average depth of 84 cm and can extend the area of potentially oxic sediment-water (air) interfaces by 33.6%. If all burrowing grapsid crab species present at the study areas with a total abundance of up to 5 $m^{-2}$ (N Thongtham pers obs) are considered, the area of sediment-water (air) interfaces in the form of burrow walls may exceed that of the surface sediment several times. For comparison, populations of thalassinidean shrimp burrows are estimated to add 1 to 9 $m^2$ of wall surface area for every $m^2$ of the sediment surface (Griffis & Suchanek 1991). Accordingly, crab burrows evidently provide a steady and massive supply of oxygen into deeper sediment layers. The presence of oxygen not only support the burrow inhabitants, but is also very important for microbial processes and is considered to accelerate microbial processes, including organic carbon and nitrogen mineralization as well as nitrification and denitrification, whereas sulfate reduction is hampered and potentially toxic sulfide is oxidized (Kristensen *et al.* 1985, Andersen & Kristensen 1991, Morrisey *et al.* 1999).

### *Crab behaviour and the role of burrows*

Semi-terrestrial grapsid crabs are capable of withstanding long periods of air-exposure as substantiated by an average of 5–8 min spent in water per hour for *N. versicolor*. They only need a film of water beneath their body to maintain circulation and reoxidation of water over the brachial surfaces (Alexander & Ewer 1969, Kofoed *et al.* 1985). This permits them to breathe air and thus to be active during low tide periods and colonize high intertidal areas (Frith *et al.* 1976).

Most studies on preference and tolerance of grapsid crabs to environmental extremes have primarily been done on larvae or juveniles (Anger 1996, Spivak 1999), and not on adults. In the present study, adult crabs were exposed to different environmental conditions and allowed freely to choose their favorable environment. Our salinity preference experiment revealed that *N. versicolor* is an euryhaline organism with capacity to tolerate and survive in a wide range of salinities (Fig. 5). The range of salinities that occur within burrows of this species is somewhat higher than its optimum salinity choice (10–30‰), but appears to be within tolerable limits.

*N. versicolor* avoids water temperatures above the average (29 °C) recorded from tidal creeks of the Bangrong mangrove forest (Fig. 4 & 5). Crabs are usually resting quietly in the cool shade among root crevices on the forest floor or near their burrow openings at low tide when the temperature on exposed mud surfaces exceeds the tolerable level during hot and sunny days. Moreover, air in burrows is moister than at the sediment surface (Eshky *et al.* 1995), and they usually contain open water during low tide. Thus, burrows provide cool and moist refuges that protect crabs from overheating and desiccation. The need for protection against extreme temperatures appears to be so strong that crabs choose to ignore suboptimal conditions in burrows with respect to e.g. salinity. Accordingly they are most active outside burrows between dusk and dawn or after periods of rain when the surrounding temperature is relatively low (N Thongtham pers obs). Sesarmid crabs are very sensitive to disturbances and exhibit a rapid evasive dispersal among crevices or down into their burrows, which provides an essential protection against predators such as crab-eating macaque monkeys. Recovery time after disturbance of these crabs is at least 20 minutes (pers obs). Most individuals of *N. versicolor* stay in their burrow during high tide, but at night they occasionally climb proproots or trunks of mangrove trees to forage. Under these circumstances they always remain no more than 2–3 cm above the water level.

In conclusion, burrows of *N. versicolor* are complex and extended structures remain inhabited by generations of crabs for very long periods. They are important extensions of the sediment surface that are irrigated with creek water, and thus maintain low saline, cool and oxic conditions up to 1 m below the sediment surface. Burrows not only provide crabs with protection from high temperatures, desiccation and predators while maintaining tolerable conditions with respect to other essential parameters, but also support associated fauna and highly active microbial communities.

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