

## DISTRIBUTION OF MOLLUSCS IN MANGROVES AT SIX SITES IN THE UPPER GULF OF THAILAND

**Cheewarat Printrakoon**

*Department of Biology, Faculty of Science, Mahidol University, Rama VI Road, Phayathai, Bangkok 10400, Thailand.*

*Email: cheewarat040@yahoo.com*

**Fred E. Wells**

*Research Associate, Department of Zoology (Invertebrates), Field Museum of Natural History,*

*1400 South Lake Shore Drive, Chicago, Illinois 60605 U. S. A.*

*Present address: Western Australian Department of Fisheries, Level 3, 168 St. Georges Terrace, Perth,*

*Western Australia 6000, Australia.*

*Email: Fred.Wells@fish.wa.gov.au*

**Yaowaluk Chitramvong**

*Department of Biology, Faculty of Science, Mahidol University, Rama VI Road, Bangkok 10400, Thailand.*

*Email: scyct@mahidol.ac.th*

*(Corresponding author)*

**ABSTRACT.** – Molluscs were studied in mangroves at six sites in the upper Gulf of Thailand from March to June 2004. At each site, density, diversity, and biomass of molluscs were measured in replicate samples made in four habitats: *Avicennia* and *Rhizophora* tree zones, and the unvegetated mudflat and channel. There is no *Rhizophora* zone at the site at Ang Sila. A moderate diversity of 47 species (31 gastropods and 16 bivalves) was collected. There was considerable variation in population characteristics between sites and between habitats at a site. Mangrove tree habitats tended to have greater diversity than unvegetated habitats. Mean density varied from 9.4/m<sup>2</sup> at Ban Num Chieo to 841.5/m<sup>2</sup> at Bangpoo, a difference of almost two orders of magnitude. There was no clear pattern of density in the different habitats. Three habitats (mudflat, *Avicennia* and *Rhizophora* tree zones) each had one site where there were no molluscs found. The greatest densities were recorded in three different habitats: 1,120.6/m<sup>2</sup> in the channel at Laem Chabang; 1,235.8/m<sup>2</sup> in *Rhizophora* at Khlong Khon; and 3,289.6/m<sup>2</sup> in *Avicennia* at Bangpoo. The high densities in these three habitats were contributed entirely by three different species, one at each of the habitats. The greatest biomass was found at different sites from the greatest density. A single species of bivalve was responsible for the high biomass at the three sites with the greatest biomass; the dominant species differed at the three habitats. Three assemblage groupings were found. The largest comprised molluscs from all *Avicennia* and *Rhizophora* habitats and the channel habitats at Bangpoo and Bang Ya Phreak. All five mudflat and two channel habitats formed a second group, and the Laem Chabang channel formed an isolated group. Gastropods were mostly epifaunal (24 species) or arboreal (7 species); most bivalves were infaunal. All 16 bivalves were filter feeders, and 23 gastropods were herbivores. In general, filter feeders and detritivores dominated density and biomass. This is consistent with the ecological role of molluscs being intermediate between the mangroves as primary producers and the higher trophic levels in the food web. Marine species dominated the salinity preference.

**KEYWORDS.** – Trophic levels, habitat, salinity, density, diversity, biomass.

---

### INTRODUCTION

Mangrove forests are comprised of taxonomically diverse, salt-tolerant species of trees and shrubs that thrive in intertidal zones of sheltered tropical and warm-temperate shores and estuaries throughout the world (Macnae, 1968; Tomlinson, 1986; Yamada, 1998). Mangroves are key contributors of primary production to coastal marine ecosystems, either

within the mangrove community itself or through export of trunks, branches, and leaves of the mangroves to other areas by waves and currents. Few animal species feed directly on living mangroves. Instead, dead and decaying parts of the plants are broken down into progressively smaller pieces by a combination of physical, chemical and biological actions to form a rich detritus-based foodweb (Hutchings & Saenger, 1987). The Indo-West Pacific region has both the highest

diversity of mangrove plant species and the largest areas of mangroves (Duke, 1992; Duke et al., 1998; Ellison, 1999). Southeast Asian mangroves comprise a third of the world's total (Macnae, 1968; Yamada, 1998), with Thailand having some of the most diverse mangrove forests in Southeast Asia. Mangrove areas of 120,536 km<sup>2</sup> and 328,093 km<sup>2</sup> are reported in the central and eastern parts of the Gulf of Thailand, respectively (UNEP, 2005). Mangroves are valuable resources for Thailand. The forests have both ecological and economic functions, providing both physical environment and a source of nutrients (Tomlinson, 1986; Field, 1996; Ng & Sivasothi, 1999). The forests are nursery grounds or habitat for a wide variety of commercial species, including fish, prawns, crabs, oysters and other shellfish (Sasekumar & Chong, 1998; Hogarth, 1999; Ng & Sivasothi, 1999). Despite their importance, mangroves in Thailand have been substantially reduced in area because the trees have been cut down to provide firewood and the land has been reclaimed for use for shrimp farms, etc., or damaged by pollution. Although they have provided different figures, Aksornkoae et al. (1993), Khemnark (1995), Menasveta (1997) and many others have reported substantial declines in the areas covered by Thai mangroves. The threat is continuing (Aksornkoae & Tokrisna, 2004), although there have been some areas of active replanting (Macintosh et al., 2002). Because of their importance, it is critical that more investigations are undertaken to understand the functioning of Thai mangrove ecosystems.

Mangrove invertebrates are important links in energy flow between the initial detritus at the bottom of food webs to higher-order predators such as birds and fish (Berry, 1963). Molluscs are one of the dominant invertebrate groups in the mangrove community and are thought to play a significant ecological role in the structure and function of mangrove systems (Lee, 1999; Ng & Sivasothi, 1999; Tan & Chou, 2000; Macintosh et al., 2002; Ashton et al., 2003). Despite their importance, there are few quantitative data on the diversity, density, and biomass of molluscs in mangroves (Wells, 1983, 1984, 1986a), and little is known of the molluscs in Thai mangroves (Brandt, 1974; Frith et al., 1976; Tantanasiwong, 1978, 1979; Macintosh et al., 2002; Wells et al., 2001; Sanpanich et al., 2004, 2006). To help fill this gap in our knowledge, the present paper investigates the molluscs found in six mangrove systems in the upper Gulf of Thailand.

## MATERIALS AND METHODS

Molluscs were studied in mangroves at six sites in the upper Gulf of Thailand from March to June 2004 (Fig. 1): Khlong Khon (13°38'50.8"N 100°35'63.3"E), Bang Ya Phreak (13°30'15.7"N 100°16'22.8"E), Bangpoo Industrial Estate (13°31'08.7"N 100°38'72.7"E), Ang Sila (13°20'79.8"N 100°57'32.1"E), Leam Chabang Industrial Estate (13°04'98.4"N 100°52'84.6"E) and Ban Nam Chieo (12°12'25.7"N 102°33'50.7"E). Four habitats were examined at each sampling site: unvegetated seaward mudflat, unvegetated channel, and *Avicennia* and *Rhizophora* tree

zones (except that no *Rhizophora* zone was present at Ang Sila). In each habitat, six replicate stations were sampled within a randomly chosen 10 × 10 m<sup>2</sup> quadrat. In each replicate, three sampling strategies were employed and the data pooled. Visible molluscs were collected by hand within a 0.5 m<sup>2</sup> steel ring randomly placed on the sediment. A 0.1 m<sup>2</sup> cylinder was then placed in the center of the ring. The sediment was removed to a depth of 20 cm and sieved through a 1-mm mesh. Living molluscs remaining on the sieve were collected. Arboreal species in each quadrat were hand picked from six trees closest to the ring. All collected molluscs were placed separately in labeled plastic bags.

In the laboratory, molluscs were sorted to species, counted and identified using Brandt (1974), Reid (1986), Lamprell & Whitehead (1992), Lamprell & Healy (1998) and Swennen et al. (2001) as references. Specimens of uncertain identification were compared with specimens in the Western Australian Museum. Voucher specimens are deposited in the Malacology Laboratory and Museum of Mahidol University, Thailand. The feeding strategy and salinity preferences of each species were determined using information from Beesley et al. (1998). Dry weight, shell-free biomass was determined using the techniques of Wells (1983). The dendrogram, based on species presence and absence, was constructed using the Bray-Curtis similarity index and the Primer 5 software package (Clarke & Warwick, 1994).

## RESULTS

**Population characteristics.** – A total of 47 species of molluscs, 31 gastropods and 16 bivalves, were found at the six sites (Table 1). Ten molluscan species were found in each of the unvegetated habitats of the channel and the mudflat; another 19 species were found in *Rhizophora* and 28 species in *Avicennia*. Diversity at individual sites was low, ranging from 11 species at Ban Num Chieo to 24 species at Khlong Khon (Table 2). Mangrove tree habitats tended to have higher diversity (0–16 species) than unvegetated habitats (0–4 species). Molluscs were not found in either unvegetated habitat at Ban Num Chieo, whereas the maximum number of



Fig. 1. Six study sites in the upper Gulf of Thailand.

Table 1. Biological characteristics of molluscs found at six sites in mangroves in the upper Gulf of Thailand. Habitat: Arb, arboreal; Epi, epifaunal; Inf, infaunal. Salinity tolerance (Sal.): Est, estuarine; Fw, freshwater; Mar, marine. Feeding strategy (FS): Carn, carnivore; Detr, detritivore; Herb, herbivore; Filt, filter feeder; Sca, scavenger.

Family	Species	Habitat	Sal.	FS
<b>Gastropods</b>				
Assimineidae	<i>Assiminea brevicula</i> (Pfeiffer, 1854)	Epi	Est	Herb
Amphibolidae	<i>Salinator burmana</i> Blanford, 1867	Epi	Mar	Herb
Ellobiidae	<i>Ellobium aurisjudae</i> (Linnaeus, 1758)	Epi	Mar	Herb
	<i>Cassidula aurisfelis</i> (Bruguère, 1789)	Epi	Mar	Herb
	<i>Cassidula multiplicata</i> (Deshayes, 1830)	Epi	Mar	Herb
	<i>Lemodonta siamensis</i> (Morelet, 1875)	Epi	Mar	Herb
	<i>Melanopus siamensis</i> (Martens, 1865)	Epi	Mar	Herb
	<i>Pythia scarabaeus</i> (Linnaeus, 1758)	Epi	Mar	Herb
	<i>Haminoea</i> sp.	Epi	Mar	Herb
Iravadiidae	<i>Fairbankia cochinchinensis</i> Bavay & Dautzenberg, 1910	Epi	Fw	Det
	<i>Iravadia ornata</i> Blanford, 1867	Epi	Fw	Det
Littorinidae	<i>Littoraria articulata</i> (Philippi, 1846)	Arb	Mar	Herb
	<i>Littoraria carinifera</i> (Menke, 1830)	Arb	Mar	Herb
	<i>Littoraria intermedia</i> (Philippi, 1846)	Arb	Mar	Herb
	<i>Littoraria melanostoma</i> (Gray, 1839)	Arb	Mar	Herb
	<i>Littoraria pallescens</i> (Philippi, 1846)	Arb	Mar	Herb
	<i>Littoraria strigata</i> (Philippi, 1846)	Arb	Mar	Herb
Muricidae	<i>Chicoreus capucinus</i> (Lamarck, 1822)	Epi	Mar	Carn
	<i>Thais gradata</i> (Jonas, 1846)	Epi	Mar	Carn
Nassariidae	<i>Nassarius foveolatus</i> (Dunker, 1847)	Epi	Mar	Sca
	<i>Nassarius stolatus</i> (Gmelin, 1791)	Epi	Mar	Sca
Neritidae	<i>Clithon oualaniensis</i> (Lesson, 1831)	Epi	Est	Herb
	<i>Neritina violacea</i> (Gmelin, 1791)	Epi	Est	Herb
	<i>Neritodryas dubia</i> (Gmelin, 1791)	Epi	Est	Herb
Onchidiidae	<i>Onchidium</i> sp.	Epi	Mar	Herb
Potamididae	<i>Cerithidea cingulata</i> (Gmelin, 1791)	Epi	Mar	Herb
	<i>Cerithidea obtusa</i> (Lamarck, 1822)	Epi	Mar	Herb
	<i>Cerithidea quadrata</i> Sowerby, 1866	Arb	Mar	Herb
	<i>Telescopium telescopium</i> (Linnaeus, 1758)	Epi	Mar	Herb
Stenothyridae	<i>Stenothyra</i> sp.	Epi	Fw	Det
Thiaridae	<i>Sermyla riqueti</i> (Grateloup, 1840)	Epi	Fw	Det
<b>Bivalves</b>				
Arcidae	<i>Anadara granosa</i> (Linnaeus, 1758)	Inf	Mar	Filt
Anomiidae	<i>Enigmonia aenigmatica</i> (Holten, 1802)	Arb	Mar	Filt
Corbiculidae	<i>Gelonia erosa</i> (Lightfoot, 1786)	Inf	Mar	Filt
	<i>Gelonia expansa</i> (Mousson, 1849)	Inf	Mar	Filt
Glauconomidae	<i>Glauconome virens</i> (Linnaeus, 1767)	Inf	Mar	Filt
Isognomonidae	<i>Isognomon ephippium</i> (Linnaeus, 1758)	Arb	Mar	Filt
Lucinidae	<i>Austriella</i> sp.	Inf	Mar	Filt
Mactridae	<i>Mactra cumingii</i> (Reeve, 1854)	Inf	Mar	Filt
	<i>Mactra iridescens</i> (Kuroda & Habe, in Habe, 1958)	Inf	Mar	Filt
Mytilidae	<i>Modiolus</i> sp.	Arb	Mar	Filt
Noetiidae	<i>Striarca olivacea</i> (Reeve, 1844)	Inf	Mar	Filt
Ostreidae	<i>Crassostrea gigas</i> (Thunberg, 1793)	Arb	Mar	Filt
	<i>Saccostrea cucullata</i> (Born, 1778)	Arb	Mar	Filt
Tellinidae	<i>Macoma</i> sp.	Inf	Mar	Filt
Veneridae	<i>Anomalocardia squamosa</i> (Linnaeus, 1758)	Inf	Mar	Filt
	<i>Marcia hiantina</i> (Lamarck, 1818)	Inf	Mar	Filt

Table 2. Comparison of habitats occupied by molluscs in four habitats at six sites in mangroves in the upper Gulf of Thailand.

Habitat	Diversity		Density ± SE (N/m²)	Biomass ± SE (g/m²)
	No. of species	Mean ± SE		
Khlong Khon				
Mudflat	4	1.6 ± 0.4	37.0 ± 11.8	9.6 ± 3.2
Channel	4	3.0 ± 0.2	98.3 ± 20.4	14.2 ± 2.0
<i>Avicennia</i>	10	5.0 ± 0.5	65.2 ± 11.0	2.8 ± 0.9
<i>Rhizophora</i>	6	4.6 ± 0.2	1235.8 ± 311.4	15.9 ± 8.2
Total/Means	24	3.5 ± 0.3	359.1 ± 128.3	10.6 ± 2.3
Bang Ya Phreak				
Mudflat	3	1.0 ± 0.4	23.3 ± 13.4	2.1 ± 1.0
Channel	3	1.1 ± 0.4	10.3 ± 3.4	0.3 ± 0.1
<i>Avicennia</i>	7	1.8 ± 1.1	18.3 ± 11.2	1.9 ± 0.9
<i>Rhizophora</i>	5	1.6 ± 0.6	7.6 ± 4.2	1.2 ± 0.9
Total/Means	18	1.4 ± 0.3	14.9 ± 4.4	1.4 ± 0.4
Bangpoo				
Mudflat	3	1.6 ± 0.2	59.6 ± 13.8	0.7 ± 0.2
Channel	2	1.1 ± 0.1	17.0 ± 5.5	0.1 ± 0.1
<i>Avicennia</i>	16	7.0 ± 1.1	3289.6 ± 1919.3	2.8 ± 0.8
<i>Rhizophora</i>	0	-	-	-
Total/Means	21	2.4 ± 0.6	841.5 ± 535.8	0.9 ± 0.3
Ang Sila				
Mudflat	2	0.3 ± 0.2	2.3 ± 1.6	1.7 ± 1.6
Channel	1	0.6 ± 0.2	7.0 ± 3.3	0.2 ± 0.0
<i>Avicennia</i>	9	4.0 ± 0.6	43.2 ± 8.2	0.4 ± 0.2
Total/Means	12	1.6 ± 0.4	17.5 ± 5.2	0.7 ± 0.5
Leam Chabang				
Mudflat	3	2.3 ± 0.2	172.0 ± 35.6	6.7 ± 2.6
Channel	2	1.6 ± 0.2	1120.6 ± 434.2	0.1 ± 0.0
<i>Avicennia</i>	3	2.1 ± 0.3	6.9 ± 1.1	7.0 ± 3.0
<i>Rhizophora</i>	9	3.3 ± 0.8	13.9 ± 4.5	6.9 ± 2.8
Total/Means	17	2.3 ± 0.2	328.3 ± 140.0	5.1 ± 1.2
Ban Num Chieo				
Mudflat	0	-	-	-
Channel	0	-	-	-
<i>Avicennia</i>	6	2.0 ± 0.3	7.5 ± 3.3	3.7 ± 2.6
<i>Rhizophora</i>	5	1.8 ± 0.4	30.36 ± 10.5	27.0 ± 15.5
Total/Means	11	0.9 ± 0.2	9.4 ± 3.6	7.7 ± 4.3

species (4) was found on the mudflat and channel at Khlong Khon. *Avicennia* tended to have the most diversity, with 3–17 species, whereas *Rhizophora* varied from 0–9 species.

Density varied considerably, both between sites and between habitats at each site. Mean density varied from 9.4/m<sup>2</sup> at Ban Num Chiao to 841.5/m<sup>2</sup> at Bangpoo, a difference of almost two orders of magnitude. Although there was considerable variation between habitats at a site, all habitats at Khlong Khon, Bangpoo and Leam Chabang tended to have higher molluscan densities than the same habitat types at Bang Ya Phreak, Ang Sila and Ban Num Chiao. There was no clear pattern of density in the different habitats. Three habitats

(mudflat, *Avicennia* and *Rhizophora* tree zones) each had one site where there were no molluscs found; the lowest density in the channel was 7.0/m<sup>2</sup> at Ang Sila. Similarly, the greatest densities were recorded in three different habitats of three different sites: 1,120.6/m<sup>2</sup> in the channel at Laem Chabang, 1,235.8/m<sup>2</sup> in *Rhizophora* at Khlong Khon, and 3,289.6/m<sup>2</sup> in *Avicennia* at Bangpoo. The high densities in these three habitats were contributed entirely by three different species: the oyster *Crassostrea gigas* was 87.0% of total density in *Rhizophora* at Khlong Kong, the bivalve *Glaucanome virens* was 79.4% of total density in *Avicennia* at Bangpoo, and the thiarid gastropod *Sermyla riqueti* was 99.2% of total density in the channel at Leam Chabang.

Because large animals have a disproportionate amount of biomass, the sites where biomass was highest did not match those with the greatest density (Table 2). The greatest mean biomasses, ranging from 5.1 to 10.6g/m<sup>2</sup>, were found at Khlong Khon, Laem Chabang, and Ban Num Chieo. The greatest biomasses in a particular habitat were both in *Rhizophora*: 15.9g/m<sup>2</sup> at Khlong Khon and 27.0g/m<sup>2</sup> at Ban Num Chieo. The channel zone at Khlong Khon had a total biomass of 14.3g/m<sup>2</sup>. As with density, biomass was concentrated in one species in each habitat, and the dominant species was different in each of the three habitats with high biomass: *Crassostrea gigas* was 91.4% of total biomass in *Rhizophora* at Khlong Khon, *Anadara granosa* was 64.9% of total biomass in the channel at Khlong Khon, and *Geloina expansa* was 91.4% of total biomass in *Rhizophora* at Ban Num Chieo.

The dendrogram (Fig. 2) shows the relationships between species present at 21 sites. No *Rhizophora* habitat was available at Ang Sila, and no molluscs were collected in the mud and channel habitats at Ban Num Chieo. There are three groupings on the dendrogram. The largest is comprised of all the *Avicennia* and *Rhizophora* habitats and the channel habitats at Bangpoo and Bang Ya Phreak. All other channel and mudflat habitats are separated from the main grouping, indicating a clear differentiation between the molluscs that

live in the mangrove tree zones and those in the unvegetated areas of the mudflat and the channel. All five mudflat and two channel habitats form a second group on the dendrogram and the Leam Chabang channel forms an isolated group of its own.

**Habitats occupied.** – Gastropods were mostly epifaunal species (24), with seven, primarily *Littoraria*, being arboreal. In contrast, 11 of the bivalve species were infaunal. In the cumulative data for the six sites, epifaunal species dominated density in channel habitats (1,188.3/m<sup>2</sup>), but large infaunal bivalves dominated biomass (13.7g/m<sup>2</sup>) (Fig. 3). In contrast, infaunal species dominated both density (263.3/m<sup>2</sup>) and biomass (20.2g/m<sup>2</sup>) on the mudflat. Infaunal species dominated density in *Avicennia* (2,620.0/m<sup>2</sup>) and large epifaunal species dominated biomass (12.6 g/m<sup>2</sup>). Arboreal species dominated density in *Rhizophora* (1,212.4/m<sup>2</sup>) and infaunal species dominated biomass (24.7g/m<sup>2</sup>). There was considerable variation in the relative proportions of infaunal, epifaunal, and arboreal species at the six sites. Density was dominated by epifaunal species at Leam Chabang (1,146.4/m<sup>2</sup>), by infaunal species at Bangpoo (2,668.3/m<sup>2</sup>), and by arboreal species at Khlong Khon (1,231.3/m<sup>2</sup>). In terms of biomass, epifaunal species dominated at Leam Chabang (13.2 g/m<sup>2</sup>), and infaunal species at Khlong Khon (23.3 g/m<sup>2</sup>) and Ban Num Chieo (27.6 g/m<sup>2</sup>).

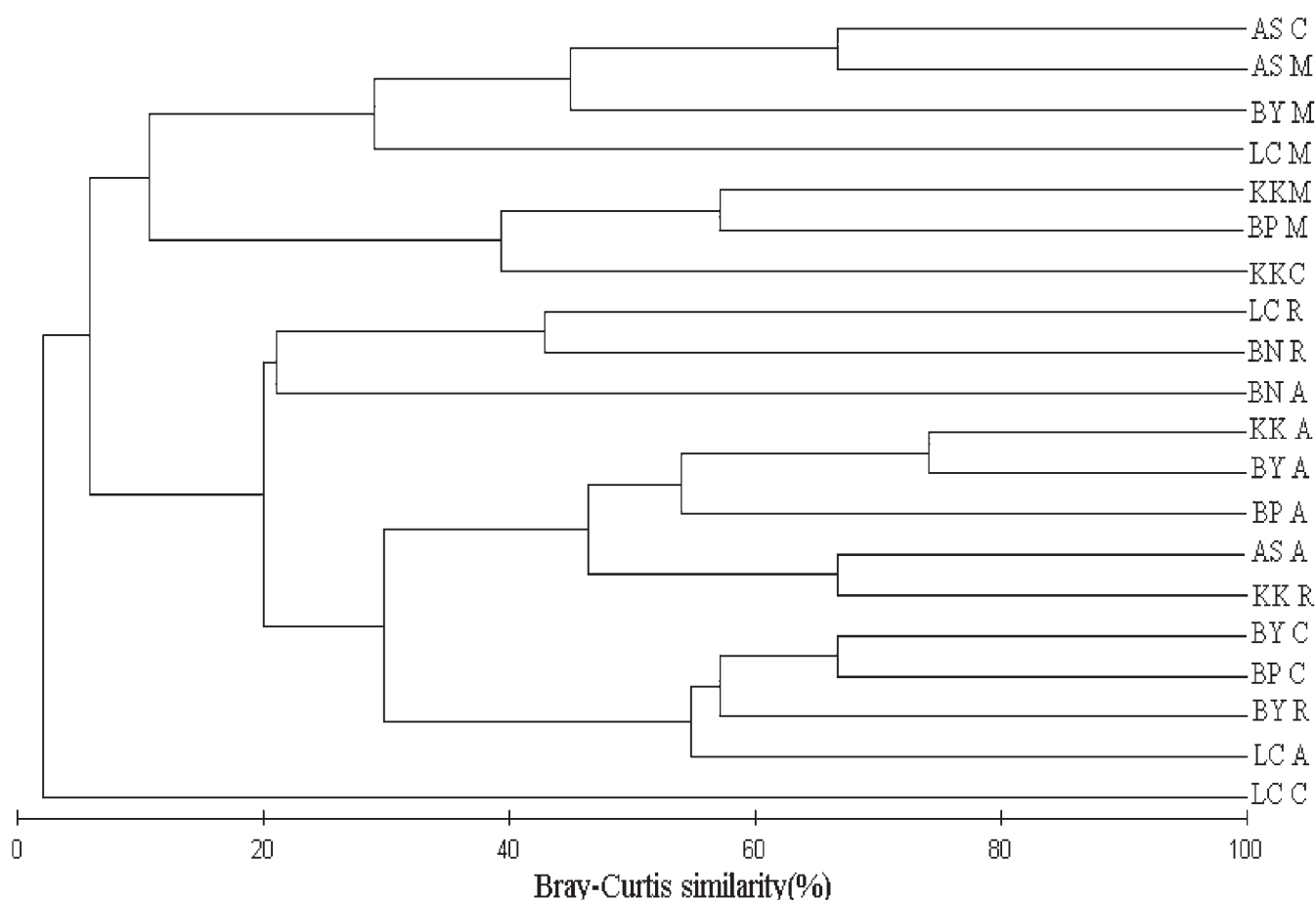


Fig. 2. Dendrogram of Bray-Curtis similarity based on presence and absence of molluscan species in four habitats at six study sites in the upper Gulf of Thailand: A, *Avicennia*; AS, Ang Sila; BN, Ban Nam Chieo; BP, Bangpoo; BY, Bang Ya Phreak; C, channel; KK, Khlong Khon; LC, Leam Chabang; M, mudflat; R, *Rhizophora*.



**Feeding strategies.** – Molluscs collected at the six sites were divided into five feeding strategies: filter feeders, herbivores, detritivores, scavengers, and carnivores (Table 1). All 16 of the bivalves were classified as filter feeders. Twenty-three of the gastropods were classified as herbivores, with four being classified as detritivores and two each as scavengers and carnivores (Table 1). Filter feeders were the dominant feeding strategy in terms of density and biomass in the mudflat and in *Rhizophora*. Detritivores dominated density in channel habitats, but filter feeders dominated biomass. In *Avicennia*, filter feeders dominated density, but herbivores dominated biomass (Fig. 4). The dominance of filter feeders breaks down when individual sites are examined, with density and biomass being clumped at particular sites. Over 95% of the mean density of filter feeders was contributed by the sites at Khlong Kong and Bangpoo; over 84% of the biomass was contributed by Khlong Kong and Ban Num Chieo.

**Salinity preferences.** – All 16 of the bivalves and 23 of the gastropods were classified as marine species; 4 gastropods were classified as estuarine and 4 as freshwater (Table 1). As would be expected from the dominance of diversity by marine species, they dominated mean density and biomass in the cumulative data for the six sites (Fig. 5), except that freshwater species dominated diversity in the channel and estuarine species dominated biomass in *Rhizophora*. The high

diversity of freshwater species was contributed entirely by the site at Leam Chabang and the high biomass of estuarine species occurred only at Ban Num Chieo.

## DISCUSSION

**Population characteristics.** – The general picture presented by the data from the six sites in mangroves in the upper Gulf of Thailand is that diversity is moderate. This is particularly true when it is considered that the six sites were spread over a wide geographical area in a region known for high biodiversity. In this extensive study, only 47 species of molluscs were collected and all were gastropods and bivalves; there were no chitons or scaphopods. Brandt (1974) recorded 56 species of estuarine molluscs in the same geographic region, compared to only four species in the present study. However, Brandt's study was a taxonomic one that would be expected to generate a larger species list. Frith et al. (1976) examined the zonation and abundance of molluscs in mangroves and on the sand and mudflat at Ao Nam Bor, on the Andaman Sea coastline near Phuket and found 43 species. Thirty-four species of molluscs were found in the Ranong Biosphere Reserve by Macintosh et al. (2002), who concluded that molluscan diversity in the upper Gulf of Thailand is less than in the Andaman mangroves.

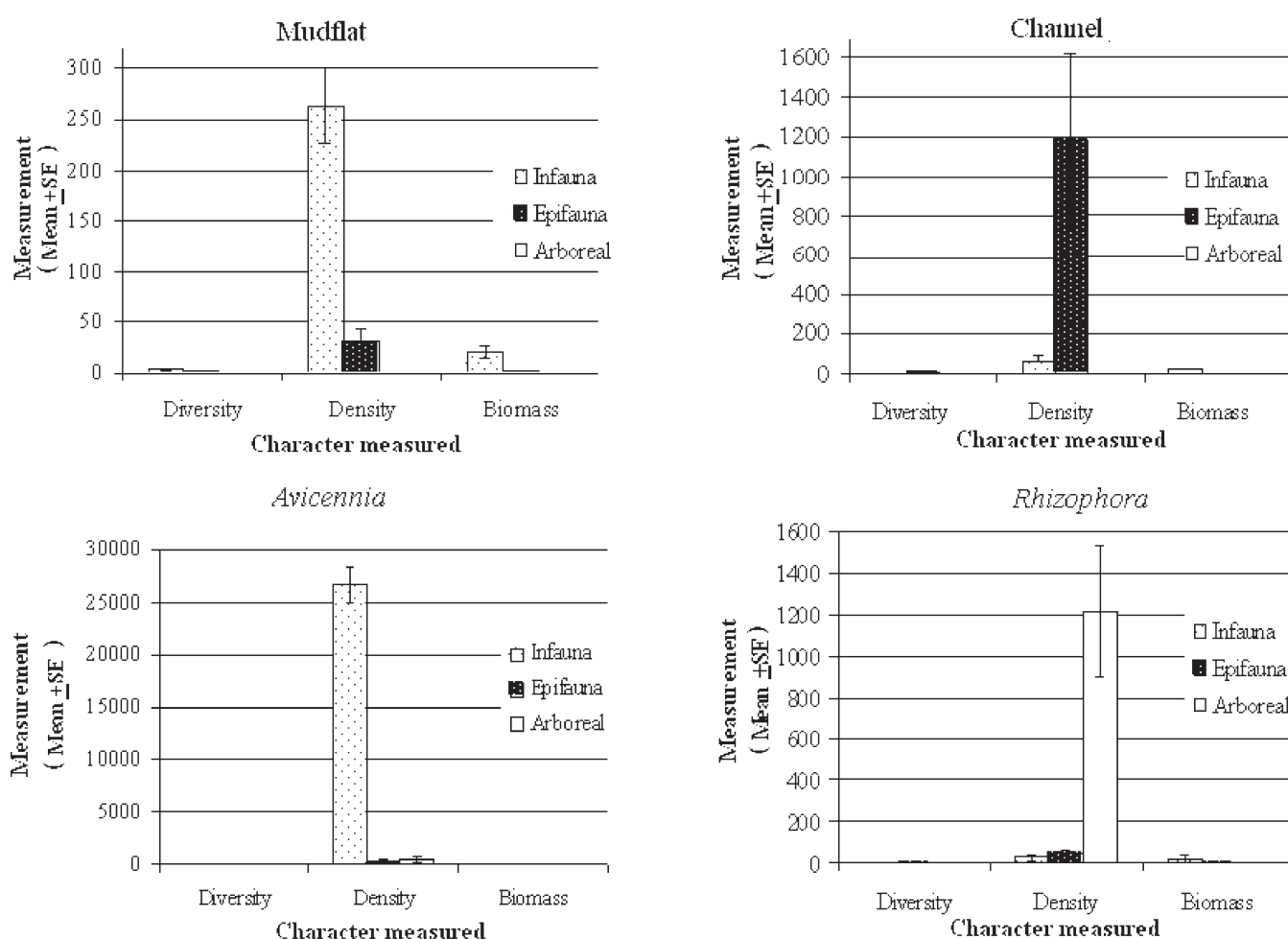


Fig. 3. Comparison of microhabitats occupied by molluscs in four habitats at six sites in mangroves in the upper Gulf of Thailand.

Wells (1983, 1984, 1986a) recorded 58 species in the Bay of Rest, northwestern Australia and 24 species in Hong Kong mangroves (Wells, 1986b, 1986c). Jiang & Li (1995) found 52 species in the Jiulong River estuary, China.

In the present study, the vegetated habitats (*Avicennia* and *Rhizophora*) had greater diversity than the unvegetated mudflat and channel zones. Similar findings were made by Sasekumar (1974), Frith et al. (1976); Wells & Slack-Smith (1981); Henriques (1980); Sheriden (1997) and Sasekumar & Chong (1998). The Thai mangrove areas studied here had greater diversity (28 species) in the vegetated zones than the 8 species recorded in the Kimberley, Western Australia (Wells & Slack Smith, 1981), the 6 species found at Klong Nga, Ranong, Thailand (Macintosh et al., 2002), and the 21 species in the Bay of Rest, Western Australia (Wells, 1983, 1984, 1986a) and was close in diversity to Sai Keng, Hong Kong, where 23 species were found (Wells, 1986b, 1986c). Molluscan diversity in *Rhizophora* (19 species) was lower than in *Avicennia*, but was still higher than in other *Rhizophora* areas: 7 species each in the Kimberley, Western Australia (Wells & Slack-Smith, 1981) and in the Bay of Rest (Wells, 1983, 1984), 11 species in a Malaysian mangrove (Sasekumar & Chong, 1998) and 6 species at Ranong (Macintosh et al., 2002). However, the pattern of greater diversity in the vegetated zones was the opposite of that found by Wells (1983, 1984) in the Bay of Rest, where the mudflat had the greatest diversity. As with density,

biomass of molluscs in the present study was greater in the vegetated tree zones than on the mudflat or in the channel. The same trend was reported by Macintosh et al. (2002) but a somewhat opposite result was reported by Wells (1983, 1984), who showed that molluscs in *Avicennia* had a slightly higher biomass than on the mudflat; biomass in *Rhizophora* was very low.

Perhaps the key finding of the present study is that there is considerable variation in the diversity, density and biomass of molluscs at the six sites in the upper Gulf of Thailand. No generalizations can be made that any of the four habitats examined (mudflat, channel, *Avicennia* and *Rhizophora*) dominated in any of the three characteristics measured. Instead there was considerable variation between sites and habitats within and between sites. Where a high density or biomass was present in a given habitat, it was due to the presence of a single species. The other studies cited above all referred to one site in a geographic region, with the implicit assumption being made that the pattern at that site is a general pattern for the region. The present study throws this generalization into question, and suggests the need for multiple sites to be examined in other geographic regions.

**Habitats occupied.** – Overall, molluscan diversity comprised about half epifaunal species (24), with infaunal (11) and arboreal species (12 species) each being approximately one quarter of the total diversity. As with the population

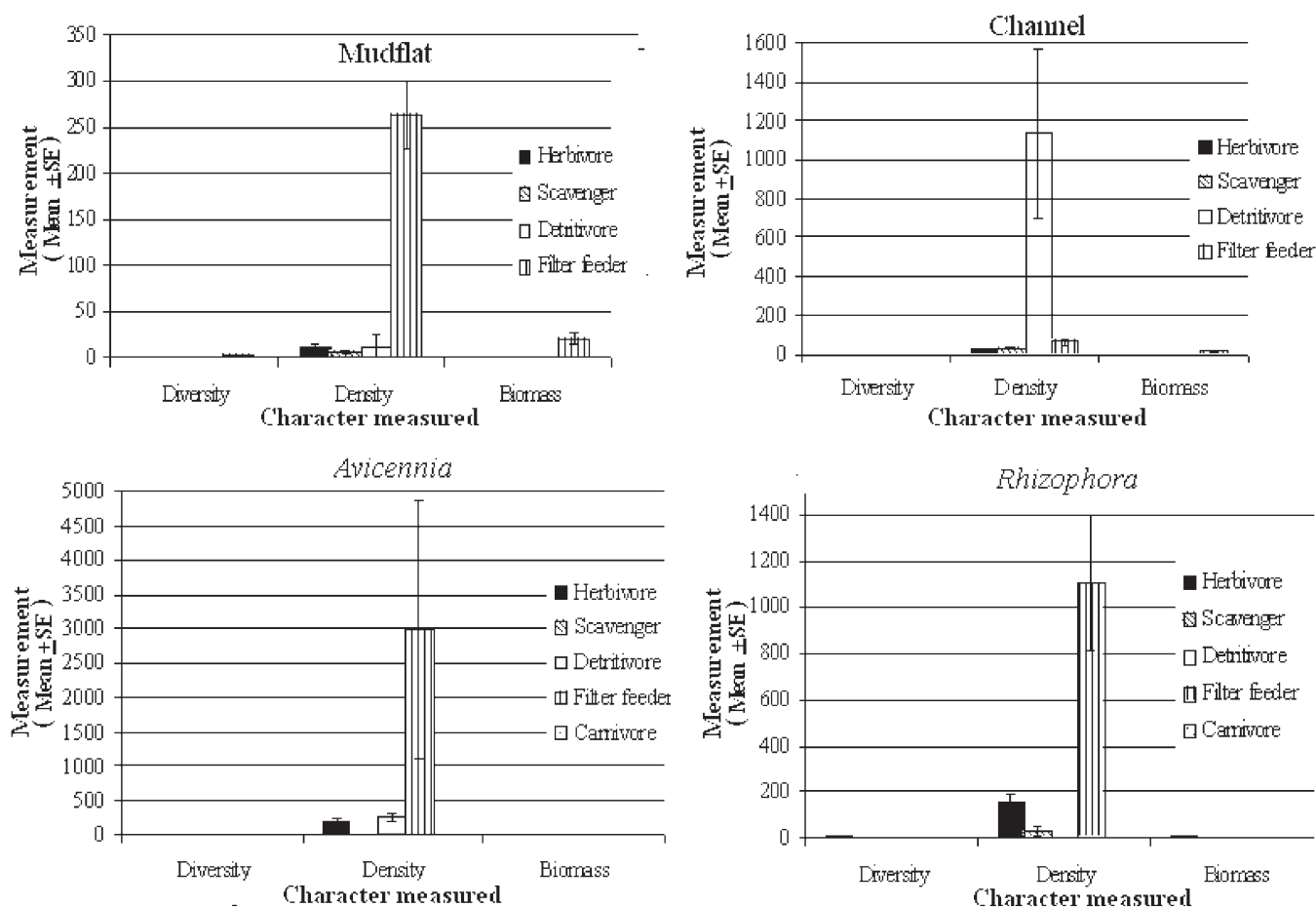


Fig. 4. Comparison of feeding strategies of molluscs in four habitats at six sites in mangroves in the upper Gulf of Thailand.

characters, it is difficult to generalize about the relative importance of molluscs in the three different microhabitats examined: infaunal, epifaunal and arboreal. This is because of the clumped nature of populations of individual species at some sites, where their considerable abundance or biomass skewed the overall results for the habitat type. Wells (1983, 1984) reported very low densities and biomasses of infaunal molluscs in both *Rhizophora* and *Avicennia* zones, a feature also found for density by Wells & Slack-Smith (1981). However, the present study showed that, at least at some sites, high densities or biomasses could be found in the sediment in mangroves in the upper Gulf of Thailand.

**Feeding strategies.** – Overall in the present study, filter feeders dominated at three of the habitats: mudflat, *Avicennia*, and *Rhizophora*. Detritivores dominated at the channel zone. As would be expected, filter feeders dominated in those sites with high densities (Khlong Khon and Bangpoo), except at Leam Chabang where detritivores dominated. Again, this is a reflection of the clumping of high density of a single species in a particular habitat. Despite the fact that 23 of the gastropod species were classified as herbivores, the density and biomass of surface-rasping herbivores was very low. Scavengers and carnivores were found in very low

numbers. There are few comparative data on feeding types of molluscs in mangroves, but similar results were obtained by Wells (1983, 1984). The importance of filter feeders and detritivores is consistent with the mangrove ecosystem being a detritus-based system dependent on the breakdown of mangrove products by a combination of physical, chemical, and biological activities (Hutchings & Saenger, 1987). The high density and biomass of molluscs in the sites examined is evidence of their ecological importance in converting primary production from the trees into animal tissue available to higher trophic levels.

**Salinity preferences.** – An estuary is simply defined as the region of interaction between inland freshwater sources and the salt waters of the open ocean, and can have both vegetated (mangrove) and unvegetated (mudflat) habitats (Macnae, 1968; Levin et al., 2001; Williams, 2003). Thirty-nine of the 47 species (83%) collected in the present study were classified as marine. Aside from the channel at Leam Chabang, marine species dominated in the sites examined in the present study. The results are somewhat surprising considered that mangroves are found in estuarine areas. However, they occur along the seaward margins of the estuaries, where salinities are higher.

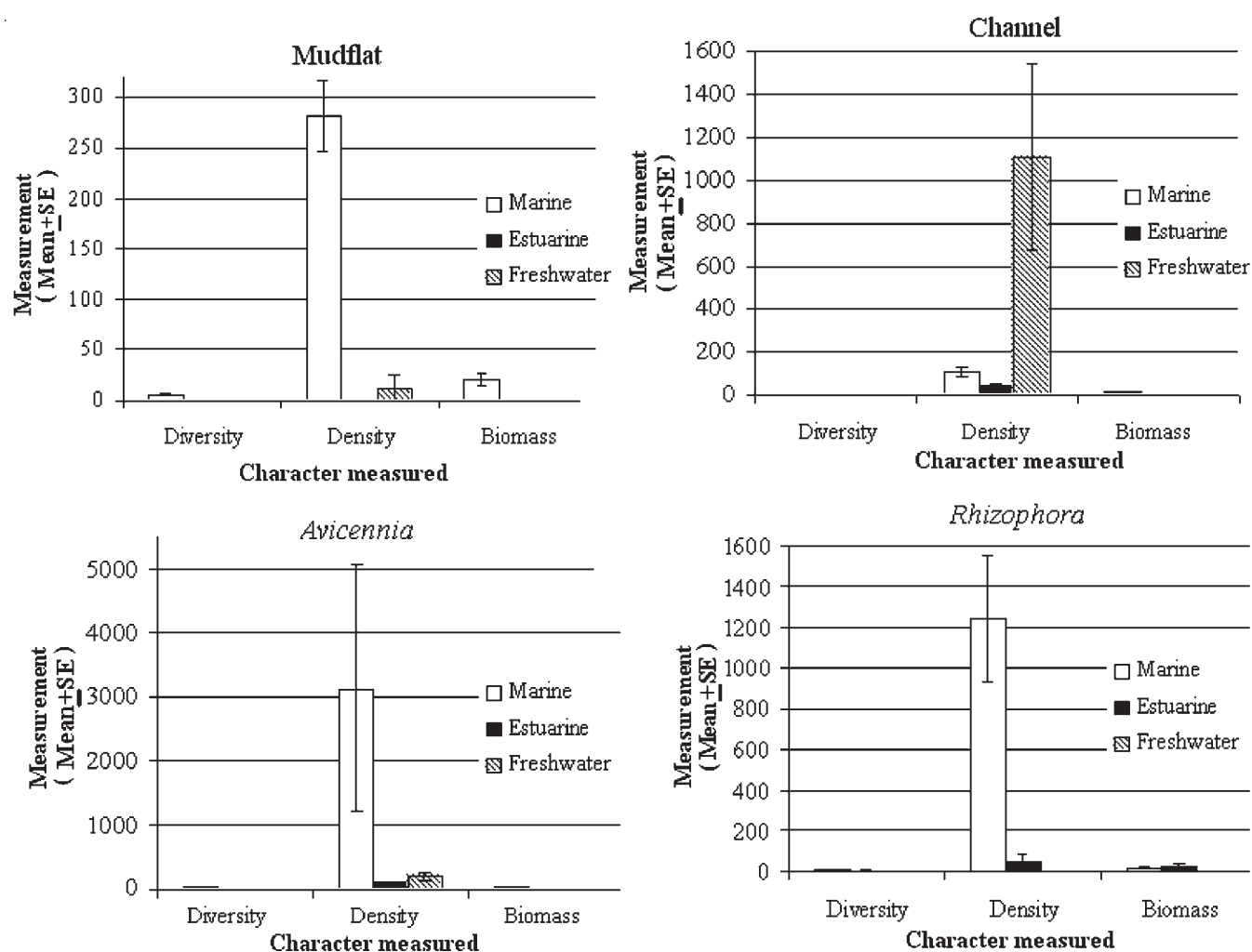


Fig. 5. Comparison of salinity tolerances of molluscs in four habitats at six sites in mangroves in the upper Gulf of Thailand.



## ACKNOWLEDGMENTS

The International Marine Bivalve Workshop (with contributions on other molluscan groups) in Chantaburi, Thailand, was organized by Kashane Chalermwat (Burapha University), Fred Wells (Western Australian Department of Fisheries), Rüdiger Bieler (Field Museum of Natural History, Chicago) and Paula M. Mikkelsen (American Museum of Natural History), and supported by U.S. National Science Foundation grant PEET DEB-9978119 (to RB and PMM). Field transportation in Thailand and chemicals were provided by the Faculty of Science, Burapha University. The study was support by The Royal Golden Jubilee Ph. D. Program of the Thailand Research Fund (4 B MU/44/M.1.). We thank Acharaporn Doungkaew, Siriporn Sriaram, Siriya Saneewong Na Ayathaya, and Dr. Kitithorn Sanpanich who kindly provided field assistance. Staff from the Research and Development Station No. 4 (Trat Province), No. 5 (Samut Sakhon Province), and No. 7 (Samut Songkhram Province), Department of Marine and Coastal Resources, provided information on all study sites and assistance with field surveys. We also thank the Department of Soil Science, Faculty of Science, Faculty of Agriculture, Kasetsart University, for sediment texture analysis and S. M. Slack-Smith, Western Australian Museum, for advice on the identification of bivalves.

## THAI ABSTRACT

คณะผู้วิจัยได้ศึกษาหอยในป่าชายเลนหกแห่งในอ่าวไทยตอนบน จากเดือนมีนาคม ถึง มิถุนายน พุทธศักราช 2547 โดยการวัดความหนาแน่น ความหลากหลายและชีวมวลของหอยในสิ่งแวดล้อม 4 ลักษณะ คือ ในเขตดิน *Avicennia* และ *Rhizophora* ในเขตหาดโคลน และภายในร่องน้ำในบริเวณอ่างศิลาที่ไม่มีดิน *Rhizophora* จากการศึกษาพบหอยทั้งสิ้น 47 ชนิด (หอยฝาเดียว 31 ชนิด หอยสองฝา 16 ชนิด) และมีความแตกต่างกันระหว่างลักษณะของประชากรกับสถานที่เก็บตัวอย่าง รวมทั้งสิ่งแวดล้อมภายในแต่ละสถานที่ เขตป่าชายเลนมักมีความหลากหลายของหอยสูงกว่าเขตไม่มีพรรณไม้ โดยความหนาแน่นของหอยมีค่าตั้งแต่ 9.4/ตรม ที่บ้านน้ำเขียวถึง 841.5/ตรม ที่บางปู โดยไม่มีรูปแบบความหนาแน่นที่ชัดเจนในสิ่งแวดล้อมที่ต่างกัน ในสภาพแวดล้อมหาดโคลน *Avicennia* และ *Rhizophora* มีแห่งละ 1 ที่ ๆ ไม่พบหอยเลยและความหนาแน่นสูงสุดพบในสภาพแวดล้อมดังนี้คือ ร่องน้ำแหลมฉะบับ (1,120.6/ตรม) *Rhizophora* ที่คลองโชน (1,235.8/ตรม) และ *Avicennia* ที่บางปู (3,289.6/ตรม) ความหนาแน่นดังกล่าวมาจากจำนวนหอย 1 ชนิด (ทั้ง 3 สถานที่) ส่วนชีวมวลสูงสุดพบในสถานที่ที่ต่างจากสถานที่ที่มีความหนาแน่นสูงสุด ทั้งนี้มีหอยสองฝาเพียง 1 ชนิด ที่ทำให้ชีวมวลสูง ในทั้ง 3 สถานที่ คณะผู้วิจัยพบกลุ่มประชากรหอยที่มีลักษณะเฉพาะ โดยกลุ่มใหญ่ที่สุดมาจากดิน *Avicennia* และ *Rhizophora* และร่องน้ำบริเวณบางปู และบางหญ้าแพรก หาดโคลนทั้ง 5 แห่ง และร่องน้ำอีก 2 แห่งเป็นกลุ่มที่สอง ส่วนร่องน้ำบริเวณแหลมฉะบับเป็นกลุ่มสุดท้ายที่ไม่เหมือนกลุ่มอื่น หอยฝาเดียวที่พบส่วนมากอยู่บนพื้นผิว (24 ชนิด) หรืออยู่บน

ต้นไม้ (7 ชนิด) หอยสองฝาส่วนมากเป็นพวกฝังตัวและกินอาหารโดยการกรอง หอยฝาเดียว 23 ชนิด เป็นหอยกินพืช โดยทั่วไปหอยที่กินอาหารโดยการกรองและหอยที่กินตะกอนมีลักษณะเด่นที่สุดในด้านความหนาแน่นและชีวมวล ซึ่งตรงกับบทบาททางนิเวศวิทยาของหอยที่เป็นตัวเชื่อมระหว่างผู้ผลิตในป่าโกงกางและผู้บริโภคในลำดับที่สูงขึ้น

## LITERATURE CITED

- Aksornkoae, S. N., N. Paphavasit & G. Wattayakorn, 1993. Mangroves of Thailand. Present status of conservation, use and management. In: Clough, B. F. (ed.), *The Economic and Environmental Values of Mangrove Forests and Their Present State of Conservation in the South-East Asia/Pacific Region*. International Society for Mangrove Ecosystems, Okinawa, Japan. Pp. 83–133.
- Aksornkoae, S. & R. Tokrisna, 2004. Overview of shrimp farming and mangrove loss in Thailand. In: Barbier, E. B. & S. Sathirathai (eds.), *Shrimp Farming and Mangrove Loss in Thailand*. Edward Elgar, London. Pp. 37–51.
- Ashton, E. C., D. J. Macintosh & P. J. Hogarth, 2003. A base line study of the diversity and community ecology of crab and molluscan macrofauna in the Sematan mangrove forest, Sarawak, Malaysia. *Journal of Tropical Ecology*, **19**: 127–142.
- Bavay, A. & P. Dautzenberg, 1910. Contribution a la faune fluviatile de l'Extrême-Orient (Chine et Indo-Chine). *Journal de Conchyliologie*, **58**: 1–21, pl. 1.
- Beesley, P. L., G. J. B. Ross & A. Wells (eds.), 1998. *Molluscs: The Southern Synthesis. Fauna of Australia, Volume 5*. CSIRO Publishing, Melbourne. 1234 pp.
- Berry, A. J., 1963. Faunal zonation in mangrove swamps. *Bulletin of the National Museum, State of Singapore*, **32**: 90–98.
- Blanford, W. T., 1867. Contributions to Indian malacology, no. 8. List of estuary shells collected in the Irawadi (sic) in Pegu, with descriptions of new species. *Journal of the Asiatic Society of Bengal*, **36**: 51–72.
- Born, I. 1778. *Index Rerum Naturalium Musei Caesarei Vindobonensis. Pars I. Testacea*. Officina Krausuana, Vindobonae (= Kraus, Vienna). Pp. [xI] + 458 + [82], 1 pl.
- Brandt, R. A. M., 1974. The non-marine aquatic Mollusca of Thailand. *Archiv für Molluskenkunde*, **105**: i–iv, 1–423.
- Bruguère, J. B., 1789. *Encyclopédie Méthodique ou par Ordre des Matières. Histoire Naturelle des Vers, des Mollusques ... Volume 1*. Panckoucke, Paris. 344 pp.
- Clark, K. R. & R. M. Warwick, 1994. *Change in Marine Communities and Interpretation*. Plymouth Marine Laboratory, Plymouth, United Kingdom. 144 pp.
- Deshayes, G. P., 1830. *Encyclopédie Méthodique ou par Ordre des Matières. Histoire Naturelle des Vers, des Mollusques ... Volume 2*. Mme. V. Angasse, Paris. 594 pp.
- Duke, N. C., 1992. Mangrove floristics and biogeography. In: Robertson, A. I. & D. M. Alongi (eds.), *Tropical Mangrove Ecosystems*. Coastal and Estuarine Studies 41. Pp. 63–100.
- Duke, N. C., M. C. Ball & J. C. Ellison, 1998. Factors influencing biodiversity and distributional gradients in mangroves. *Global Ecology and Biogeography Letters*, **7** (1, Biodiversity and Function of Mangrove Ecosystems): 27–47.

- Dunker, W. [G.] B. R. H., 1847. Diagnoses Buccinorum quorundam novorum. *Zeitschrift für Malakozoologie*, **1847**: 59–64.
- Ellison, A. M., 1999. Origins of mangrove ecosystems and the mangrove biodiversity anomaly. *Global Ecology and Biogeography*, **8**: 95–115.
- Field, C. D. 1996. *Restoration of Mangrove Ecosystems*. International Society for Mangrove Ecosystems, Okinawa, and International Tropical Timber Organization, Yokohama. 250 pp.
- Frith, D. W., R. Tantasiriwong & O. Bhatia, 1976. Zonation of macrofauna on a mangrove shore, Phuket Island. *Phuket Marine Biological Center Research Bulletin*, **10**: 1–37.
- Gmelin, J. F., 1791. *Caroli a Linné ... Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis . . . Editio decima tertia, aucta, reformata. Volume 1, Part 6*. G. E. Beer, Lipsiae [Leipzig]. Pp. 3021–4120.
- Grateloup, J.-P. S. de, 1840. Mémoire descriptif sur plusieurs espèces de coquilles nouvelles ou peu connues de mollusques exotiques vivants, terrestres, fluviatiles et marins. *Actes de la Société Linnéenne de Bordeaux*, **11**: 389–455.
- Gray, J. E., 1839. Molluscos animals and their shells. In: Beechey, F. W. (ed.), *The Zoology of Captain Beechey's Voyage; Comp. from the Collections and Notes Made by Captain Beechey, the Officers and Naturalist of the Expedition to the Pacific and Behring's Straits Performed in His Majesty's ship "Blossom", Under the Command of Captain F. W. Beechey ... in the Years 1825, 26, 27 and 28*. H. G. Bohn, London. Pp. 103–155.
- Habe, T., 1958. Report on the Mollusca chiefly collected by the S. S. Soyo-Maru of the Imperial Fisheries Experimental Station on the continental shelf bordering Japan during the years 1922–1930. Part 4. Lamellibranchia (2). *Publications of the Seto Marine Biological Laboratory*, **7**(1):19–52, pls. 1–2.
- Henriques, P. R., 1980. Faunal community structure of eight soft shore, intertidal habitats in the Manukau Harbour. *New Zealand Journal of Ecology*, **3**: 97–103.
- Hogarth, P. J., 1999. *The Biology of Mangroves*. Oxford University Press, Oxford, United Kingdom. 228 pp.
- Holtén, H. S., 1802. *Enumeratio Systematica Conchyliarum Beat. J. H. Chemnitzii Quondam Ecclesiae Zebaothu Havniae Pastoris, Plurium Societatum Sodalis p.p. quae Publica Auctione Venduntur...* K. H. Seidelini, Copenhagen. [vii] + 88 pp.
- Hutchings, P. A. & P. Saenger, 1987. *Ecology of Mangroves*. University of Queensland Press, St. Lucia, Queensland. 388 pp.
- Jiang, J. X. & R. G. Li, 1995. An ecological study on the Mollusca in mangrove areas in the estuary of the Jiulong River. *Hydrobiologia*, **295**: 213–220.
- Jonas, J. H., 1846. Ueber die Gattung *Proserpina*, und Beschreibungen neuer Conchylien. *Zeitschrift für Malakozoologie*, 1846: 10–16.
- Khemnark, C., 1995. *Ecology and Management of Mangrove Restoration and Regeneration in East and Southeast Asia. Proceedings of the Ecotone IV. 18–22 January 1995. Surat Thani, Thailand*. Amarín Co., Ltd., Bangkok, Thailand. 339 pp.
- Lamarck, J. B. P. A. de M. de, 1818. *Histoire Naturelle des Animaux sans Vertèbres, Présentant les Caractères Généraux et Particuliers de ces Animaux, leur Distribution, leurs Classes, leurs Familles, leurs Genres, et la Citation des Principales Espèces qui s'y Rapportent...* Volume 5. Deterville, Verdier, Paris. [iii] + 612 pp.
- Lamarck, J. B. P. A. de M. de, 1822. *Histoire Naturelle des Animaux sans Vertèbres, Volume 7*. J. B. Lamarck, Paris. [iii] + 711 pp.
- Lamprell, K. & J. Healy, 1998. *Bivalves of Australia, Volume 2*. Backhuys Publishers, Leiden. 288 pp.
- Lamprell, K. & T. Whitehead, 1992. *Bivalves of Australia, Volume 1*. Crawford House, Bathurst, New South Wales. 182 pp.
- Lee, S. Y., 1999. The effect of mangrove leaf litter enrichment on macrobenthic colonization of defaunated sandy substrates. *Estuarine, Coastal and Shelf Science*, **49**: 703–712.
- Lesson, R. P., 1831. *Voyage Autour du Monde sur la Coquille, Pendant 1822–1825 par M. L. J. Duperey. Volume 2, Zoophytes*. Paris. 128 pp.
- Levin, L. A., D. F. Boesch, A. Covich, C. Daham, C. Erséus, K. C. Ewel, R. T. Kneib, A. Moldenke, M. A. Palmer, P. Snelgrove, D. Strayer & J. M. Weslawski, 2001. The function of marine critical transition zones and the importance of sediment biodiversity. *Ecosystems*, **4**: 430–451.
- Lightfoot, J., in D. C. Solander, 1786. *A Catalogue of the Portland Museum, Lately the Property of the Duchess Dowager of Portland, Deceased: which will be Sold by Auction, by Mr. Skinner & Co. on Monday the 24th of April, 1786, and the Thirty-seven Following Days, at Twelve O'clock, Sundays, and the 5th of June, (the Day his Majesty's Birth-Day is Kept) Excepted, at her Late Dwelling-house, in Privy-garden, Whitehall by Order of the Acting Executrix*. Skinner, London. i–viii + [3] + 194 pp., 1 pl.
- Linnaeus, C., 1758. *Systema Naturae per Regna Tria Naturae. Tomus I. Editio Decima, Reformata*. Laurentii Salvii, Stockholm. [ii] + 824 pp.
- Linnaeus, 1767, *Systema naturae, Tomus I. Pars II. Editio Duodecima, Reformata*. Holmiae. (Laurentii Salvii). Pp. 533–1327.
- Macintosh, D. J., E. C. Ashton & S. Havanon, 2002. Mangrove rehabilitation and intertidal biodiversity: a study in the Ranong mangrove ecosystem, Thailand. *Estuarine, Coastal and Shelf Science*, **55**: 331–345.
- Macnae, W., 1968. A general account of the fauna and flora of mangrove forests in the Indo-West Pacific region. *Advances in Marine Biology*, **6**: 73–270.
- Martens, E. von, 1865. [Über neue Landschnecken aus Ost-Indien und über zwei Seesterne von Costa Rica.] *Monatsberichte der Königlich Preussischen Akademie der Wissenschaften zu Berlin*, **1865**: 51–59.
- Menasveta, P., 1997. Mangrove destruction and shrimp culture systems. *World Aquaculture*, **28**: 36–42.
- Menke, C. T., 1830. *Synopsis Methodica Molluscorum, 2nd edition*. C. T. Menke, Pyrmont. xvi + 169 pp.
- Morelet, A., 1875. *Séries Conchyliologiques comprenant l'énumération de Mollusques ... Livraison 4*. Paris.
- Mousson, J. R. A., 1849. *Die Land- und Süßwasser-Mollusken von Java*. Friedrich Schulthess, Zürich. 126 pp., 22 pls.
- Ng, P. K. L. & N. Sivasothi (eds.), 1999. *A Guide to Mangroves of Singapore, 2 Volumes*. Science Centre Singapore, Singapore. 328 pp.
- Pfeiffer, L., 1854. A monograph of the genera *Realia* and *Hydrocena*. *Proceedings of the Zoological Society of London*, **1854**: 304–309.
- Philippi, R. A., 1846. Descriptions of a new species of *Trochus*, and of eighteen new species of *Littorina*, in the collection of

- H. Cuming, Esq. *Proceedings of the Zoological Society of London*, **1845**: 138–143.
- Reeve, L. A., 1844. Monograph of the genus *Arca*. *Conchologica Iconica; or, Illustrations of the Shells of Molluscos Animals*, **2**: 17 pls. and captions.
- Reeve, L. A., 1854. Monograph of the genus *Mactra*. *Conchologica Iconica; or, Illustrations of the Shells of Molluscos Animals*, **8**: 21 pls. and captions.
- Reid, D. G., 1986. *The Littorinid Molluscs of Mangrove Forests in the Indo-Pacific Region: the Genus Littoraria*. British Museum (Natural History), London. 227 pp.
- Sanpanich, K., F. E. Wells & Y. Chitramvong, 2004. Distribution of the family Littorinidae (Mollusca: Gastropoda) in Thailand. *Records of the Western Australian Museum*, **22**: 241–251.
- Sanpanich, K., F. E. Wells & Y. Chitramvong, 2006. Effects of the 26 December 2004 tsunami on littorinid molluscs near Phuket, Thailand. *Journal of Molluscan Studies*, **72**: 311–313.
- Sasekumar, A., 1974. Distribution of macrofauna on a Malayan mangrove shore. *Journal of Animal Ecology*, **43**: 51–69.
- Sasekumar, A. & V. C. Chong, 1998. Faunal diversity in Malaysian mangroves. *Global Ecology and Biogeography Letters*, **7**: 57–60.
- Sasekumar, A. & C. R. Wilkinson. 1994. Compatible and incompatible uses of mangroves in ASEAN. In: Wilkinson, C. R. (ed.), *Living Coastal Resources of Southeast Asia: Status and Management. Report of the Consultative Forum, Third ASEAN-Australia Symposium on Living Coastal Resources, Chulalongkorn University, Bangkok, Thailand, May 1994*. Australian Institute of Marine Science, Townsville. Pp. 77–83.
- Sheriden, P., 1997. Benthos of adjacent mangroves, seagrass and non vegetated habitats in Rockery Bay, Florida, U. S. A. *Estuarine Coastal Shelf Science*, **44**: 455–469.
- Sowerby, G.B. II, 1866. Monograph of the genus *Cerithidea*. *Conchologica Iconica; or, Illustrations of the Shells of Molluscos Animals*, **15**: 4 pls. and captions.
- Swennen, C., R. G. Moolenbeek, N. Ruttanadukul, H. Hobbelink, H. Dekker & S. Hajisamae, 2001. The molluscs of the southern Gulf of Thailand. *Thai Studies in Biodiversity [The Biodiversity Research and Training Program, Bangkok]*, **4**: 1–210.
- Tan, K. S. & L. M. Chou, 2000. *A Guide to the Common Seashells of Singapore*. Science Centre Singapore, Singapore. 160 pp.
- Tantanasiriwong, R., 1978. An illustrated checklist of marine shelled gastropods from Phuket Island, adjacent mainland and offshore islands, western peninsular Thailand. *Phuket Marine Biological Center Research Bulletin*, **21**: 1–22.
- Tantanasiriwong, R., 1979. An illustrated checklist of marine shelled bivalves from Phuket Island, adjacent mainland and offshore islands, western peninsular Thailand. *Phuket Marine Biological Center Research Bulletin*, **27**: 1–15.
- Thunberg, C. P., 1793. Tekning och beskrifning på en stor ostronsort ifrån Japan. *Kongliga Vetenskaps Akademiens Nya Handlingar*, **14**(2): 140–142.
- Tomlinson, P. B., 1986. *The Botany of Mangroves*. Cambridge University Press, Cambridge, United Kingdom. 413 pp.
- UNEP [United Nations Environment Programme], 2005. [Mangrove distribution in Thailand]. *Report of Natural Resources and Environment Status: Mangrove*. UNEP GEF SCS Project on “Reversing Environmental Degradation Trends in the South China Sea and Gulf of Thailand,” Bangkok. 60 pp. [in Thai]
- Wells, F. E., 1983. An analysis of marine invertebrate distributions in a mangrove swamp in northwestern Australia. *Bulletin of Marine Science*, **33**: 736–744.
- Wells, F. E., 1984. Comparative distribution of macromolluscs and macrocrustaceans in a north-Western Australian mangrove system. *Australian Journal of Marine and Freshwater Research*, **35**: 591–596.
- Wells, F. E., 1986a. Distribution of molluscs across a pneumatophore boundary in a small bay in northwestern Australia. *Journal of Molluscan Studies*, **52**: 83–90.
- Wells, F. E., 1986b. Distribution of marine invertebrates in a Hong Kong mangrove, with emphasis on molluscs. In: Morton, B. (ed.), *Proceedings of the Second International Workshop on the Malacofauna of Hong Kong and Southern China, Hong Kong, 1983*. Hong Kong University Press, Hong Kong. Pp. 783–793.
- Wells, F. E., 1986c. The Potamididae (Mollusca: Gastropoda) of Hong Kong, with an examination of habitat segregation in a small mangrove system. In: Morton, B. & D. Dudgeon (eds.), *Proceedings of the Second International Workshop on the Malacofauna of Hong Kong and Southern China, Hong Kong, 1983*. Hong Kong University Press, Hong Kong. Pp. 139–154.
- Wells, F. E., K. Chalermwat, N. Kakhai & P. Rangubpit, 2001. Population characteristics and feeding of the snail *Chicoreus capucinus* at Ang-Sila, Chonburi Province, Thailand. [Proceedings of the 11th Congress and Workshop, Tropical Marine Mollusc Programme (TMMP).] *Phuket Marine Biological Center Special Publication*, **25**(1): 31–39.
- Wells, F. E. & S. M. Slack-Smith, 1981. Zonation of molluscs in a mangrove swamp in northwestern Australia. In: Wilson, B. R. (ed.), *Biological Survey of Mitchell Plateau and Admiralty Gulf, Kimberley, Western Australia*. Western Australian Museum, Perth. Pp. 265–274.
- Williams, D. D., 2003. The brackish water hyporheic zones: invertebrate community structure across a novel ecotone. *Hydrobiologia*, **510**: 153–173.
- Yamada, I. 1998. *Tropical Rain Forests of Southeast Asia*. University of Hawaii Press, Honolulu. Pp. 117–120.