THE RAFFLES BULLETIN OF ZOOLOGY 2008 Supplement No. **18**: 41–55
Date of Publication: 15 Aug.2008

ECOLOGICAL IMPORTANCE OF CHEMOAUTOTROPHIC LUCINID BIVALVES IN A PERI-MANGROVE COMMUNITY IN EASTERN THAILAND

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ABSTRACT. **–** A quantitative survey of molluscs inhabiting a disturbed, intertidal muddy-sand flat near mangroves in a sheltered bay in southeastern Thailand recorded a high abundance (to 1,380 m^{-2}) of the small, chemosymbiotic lucinid bivalves *Pillucina vietnamica* and *Indoaustriella dalli.* Two other larger lucinids, *Anodontia bullula* and *A. philippiana*, were recorded living near the transects, whereas another, *Ctena delicatula*, inhabited a cobble habitat on a rocky headland at the entrance to the bay. The presence of symbiotic bacteria in the ctenidial filaments was confirmed for each species. Most abundant of the associated molluscan fauna were the epifaunal gastropods *Cerithideopsilla cingulata*, *Cerithium coralium* and *Clithon oualaniensis*, and the infaunal bivalves *Gafrarium tumidum*, *Anomalocardia squamosa*, *Pristis capsoides* and *Anadara troscheli*. Biomass estimates for the lucinids ranged from 0.51 to 3.95 gm^{-2}. The results highlight the ecological importance of chemoautotrophic bivalves in peri-mangrove communities.

KEYWORDS. **–** chemosymbiosis, Lucinidae, abundance, diversity, inventory.

INTRODUCTION

Although chemosymbiotic communities around deep-sea hydrothermal vents and cold seeps have attracted much attention, by far the most widespread sulphidic habitat is the subsurface anoxic zone of shallow-water marine sediments (Fenchel & Riedl, 1970; Ott et al., 2004; Stewart et al., 2005). This habitat supports a high diversity of chemosymbiotic organisms and prominent amongst these are bivalves of the families Lucinidae and Solemyidae (Fisher, 1990; Reid, 1990; Taylor & Glover, 2000, 2006). Lucinidae have attracted much biological interest because of the likely obligate chemosymbiosis with sulphide-oxidising bacteria housed in the gills and from which they derive much of their nutrition (Reid & Brand, 1986; Distel, 1998; Gros et al., 2003). Typically lucinids live at the boundary between oxic and suboxic zones in the sediment from where sulphide-rich interstitial water is channeled into the mantle cavity by probing and tunneling activities of the foot (Stanley, 1970; Dando et al., 1986, 1994). Lucinids are often associated with organic-rich habitats such as seagrass beds (Jackson, 1972; Barnes & Hickman, 1999; Johnson et al., 2002), mangrove fringes (Lebata & Primavera, 2001; Glover et al., 2008), and hydrocarbon rich sites such as cold seeps (Oliver & Holmes, 2006), but many others inhabit intertidal and subtidal, unvegetated sand and mud. Although the biology of a few lucinid species, notably from the northern Atlantic, is known in some detail (e.g., Fisher & Hand, 1984; Frenkiel & Mouëza, 1995; Frenkiel et al., 1996; Johnson & Fernandez, 2001; Gros et al., 2003), for the tropical Indo-West Pacific, most species remain unstudied and lack even basic information of distributional range, habitat preferences or estimates of abundance. Johnson et al. (2002) highlighted the importance of chemoautotrophic symbioses in estimates of the primary production of seagrass beds, but for most areas, information is lacking.

Preliminary sampling of intertidal sediments fronting the mangrove fringe of Kungkrabaen Bay, Thailand, indicated that two small (< 10 mm), poorly known lucinids were abundant. In order to make an assessment of the importance of chemosymbiotic bivalves to this community, we decided to make a more detailed quantitative survey from which to estimate species composition, abundance, biomass, and distribution of the lucinids and associated molluscan fauna.

MATERIALS AND METHODS

Kungkrabaen Bay is a shallow, semi-enclosed bay on the southeastern coast of the Gulf of Thailand, with an area of approximately 640 hectares (6.4 km^2) (Fig. 1). The inner bay is fringed by extensive mangrove stands, but the landward margins of these are heavily disturbed by aquacultural development of prawn and fish ponds. Most of the bay is extremely shallow with a large area of sand and mud flats emersed at low spring tides or covered by just a few centimetres of water.

Faunal sampling. – Sampling took place over eight days between 22 August and 2 September 2005. Two transects for quantitative sampling were selected in the middle part of the bay (Fig. 1); the shorter transect (2) was used to confirm the general uniformity of the fauna. Transect 1 (started at 12°35.4'N 101°54.39'E) extended for 406 m, with 10 stations sampled for molluscs and sediment analysis. The first station (0) was located 0.5 m from the mangrove prop roots, the next 5 m to seaward, with a further eight stations located 50 m apart. Transect 2 (12°35.89'N 101°54.19'E) comprised three stations between 80 m and 400 m from the mangrove fringe. Extremely soft mud, extending to 80 m from the mangrove margin, precluded sampling in that area. At each station, two quadrat samples (23.5 × 32 cm = 752 cm^{-2}) were taken; the sediment was excavated with trowels to a depth of 15 cm and sieved through 2 mm-mesh sieves. All molluscs were collected for examination in the laboratory where they were identified, counted, and the shells of sub-samples measured.

Fig. 1. Aerial view of Kungkrabaen Bay showing location of the transects (T1 and T2). The asterisk indicates location of rocky shore inhabited by *Ctena delicatula*.

Other samples were taken from a wide range of intertidal habitats within the bay, including seagrass patches and amongst prop roots at mangrove margins; samples within the bay contained similar species to those encountered along the transects. Additionally, we sampled the fauna of intertidal cobble substrata at the rocky, exposed headland (Fig. 1) at the northern entrance to the bay (Laem Ban Tha Klaeng, 12°35.26'N 101°53.03'E). Away from Kungkrabaen Bay, a similar cobble and boulder habitat was sampled at Koh Nom Sao, Laem Singha District (12°27.9'N 102°0.14'E).

Biomass. – Estimates of biomass were made from dry weights of the two lucinid species, and for comparison, four of the most abundant infaunal bivalve species. Shells were measured for 15 individuals of each species; the bodies were then removed and placed on pieces of foil, dried in an 80°C oven for 24 hours, and the dry weights obtained. Regressions of shell length versus dry weight, combined with the size/density data, were used to estimate biomass·m^{-2} for each species.

Sediment analysis. – Particle-size analysis was performed by Gardline Environmental Ltd. using nested sieves for larger grains, with particle size distributions below 1.00 mm determined using a Malvern Mastersizer 2000 particle sizer. To determine total organic matter, 1 g of ground sediment was dried at 50°C to constant weight, and then heated in a muffle furnace at 450°C for 4 hours. The cooled sample was then reweighed with the percentage loss on ignition (LOI) calculated.

Gill preparations. – Ctenidial and other tissues were fixed in a cold 2.5% solution of glutaraldehyde in phosphate buffer. Tissue pieces were sliced with a razor blade, dehydrated through an ascending series of acetone solutions, and then critical point dried for examination by scanning electron microscopy (SEM).

Identification of fauna. – Species identifications were made using the reference collections and library at The Natural History Museum, London, with comparison with type specimens when appropriate. Voucher material of all species is deposited in the collections of The Natural History Museum, London.

RESULTS

The two quantitative transects were located in the middle part of the bay on extensive intertidal, gently shelving, muddy sand flats (Fig. 1). Mangroves and their prop roots, largely of *Rhizophora*, form a sharp landward boundary to the mud flat (Fig. 2A), which is emersed at low spring tides to about 450 m from the mangrove fringe. The mud flat is colonized by patchy growths of the seagrass *Halodule pinifolia* (Miki) den Hartog (Fig. 2C), as well as filamentous green algae and *Ulva.* Small patches of the larger seagrass, *Enhalus acoroides* (L.f) Royle, were also present adjacent to seaward parts of the transect. Seagrass growth was generally more luxuriant about 300–400 m from the mangrove fringe.

Sediment. – Results of the sediment analysis are summarized in Table 1. Sediments were relatively uniform across the transect, ranging between sandy mud, muddy sand, and fine sand, with a varying gravel component, mainly of shell fragments. The finest sediments occurred around mangrove prop roots (Station 0) or at Stations 6 and 7, approximately 250–300 m from the mangroves, where growth of the seagrass *Halodule* is more abundant with the leaves, roots, and rhizomes likely stabilising the sediment. In general, sediments across the transect were poorly sorted, reflecting significant components of shells and coarser debris. All sediments were blackened just below surface, but in areas where *Halodule* growth was most dense, the sediment was particularly black and smelled strongly sulphurous. Organic content varied between 0.5 and 2.7% LOI with higher values in the seaward part of the transect, where seagrass was more abundant.

Species composition of the molluscan fauna. – The molluscan fauna recorded from the transects and other Lucinidae located within the bay are listed in Table 2 and the most abundant species illustrated in Fig. 3. Five species of Lucinidae (Fig. 3A–E) were recorded alive; these are briefly discussed below. The presence of symbiotic bacteria contained in bacteriocytes within the ctenidial filaments is confirmed in all species. Additionally, a few worn, dead shells of *Cardiolucina macassari* were found in sieved sediment.

Pillucina vietnamica, a small lucinid (length to 8.3 mm), is widely distributed along continental shores from the Red Sea to eastern Australia (Glover & Taylor, 2001), usually occurring in sediment close to mangroves. Large pink ctenidia are visible through the shell. The ctenidial filaments are thick, with bacteriocytes packed with coccoid to rod-shaped bacteria to 8 µm long and 3 µm wide (Fig. 4A–B).

Indoaustriella dalli, a small species (length to 9.8 mm) first described from the Gulf of Thailand near Kungkrabaen Bay (Lynge, 1909), has a relatively narrow distribution in Southeast Asia. It belongs to a clade of lucinids closely associated with, or peripheral to, mangrove habitats (Glover et al., 2008). The ctenidia are red-brown and composed of thick filaments with the bacteriocytes containing abundant rod-shaped bacteria to 8–10 µm length and 1–2 µm width (Fig. 4C–D). The ctenidial filaments are notable for the abundant, large (8 µm diameter), spherical, probably sulphur-rich granules (Fig. 4D).

Fig. 2. A, Mangrove fringe and intertidal muddy sand flat at site of Transect 1; B, cobble habit of *Ctena delicatula* at the rocky headland at northern entrance to Kungkrabaen Bay; C, surface of sediment on Transect 1 with *Halophila* seagrass and the gastropods *Clithon oualaniensis*, *Cerithideopsilla cingulata*, and *Cerithium coralium*; D, local Thai fisherwomen digging for *Lingula* near Transect 1.

Table 1. Summary of sediment analysis across Transect 1.

Station Number	Distance from mangroves (m)	Mean size (µm)	Mean phi	% Fines (< 63µm)	% Sand	% Coarse (> 2mm)	Sorting Description	Sediment Description	Total Organic Content (% LOI)
0	0.5	13	6.3	44.9	54.0	1.1	very poor	sandy mud	1.0
1	5.5	29	5.1	25.8	71.7	2.5	very poor	muddy sand	0.5
2	56	25	5.3	14.7	75.2	10.1	very poor	fine sand with gravel	1.2
3	106	16	6.0	5.8	88.7	5.5	poor	fine sand with gravel	0.9
4	156	22	5.5	24.5	72.9	2.7	very poor	muddy sand	0.8
5	206	41	4.6	38.5	57.6	3.9	very poor	sandy mud	0.7
6	256	16	6.0	42.2	55.8	2.0	poor	sandy mud	1.4
7	306	16	5.9	46.5	53.2	0.3	very poor	sandy mud	0.8
8	356	23	5.4	34.3	57.6	8.1	very poor	muddy sand with gravel	1.4
9	406	15	6.1	13.3	82.2	4.5	very poor	muddy sand with gravel	2.7

Anodontia (*Cavatidens*) *bullula* (length to 25 mm) is known only from a few records from northern Australia and Southeast Asia (Taylor & Glover, 2005). It burrows to depths of approximately 20 cm. The ctenidia are large and purple-black with bacteriocytes containing abundant, elongate bacteria about 5 µm long and 0.5–0.7 µm wide (Fig. 5B).

Anodontia (*Pegophysema*) *philippiana,* the largest (length to 67 mm) of the lucinids present in the bay, was not recorded in quantitative samples but several individuals were live-collected close to the seaward edge of the mangroves from sediment depths of 25–40 cm. The species is widely distributed across the Indo-West Pacific from East Africa to New Caledonia (Taylor & Glover, 2005), with the usual habitat near the outer fringe of mangroves (Lebata & Primavera, 2001). The ctenidia are large, purple-black in colour, and composed of thick filaments with bacteriocytes containing long, thin bacteria (Taylor & Glover, 2005: Fig. 5D).

Ctena delicatula was not recorded within Kungkrabaen Bay but was common at Laem Ban Tha Klaeng, a rocky headland at the northern entrance (12°35.263'N 101°53.034'E) where it occurred along with *Gafrarium dispar* (Dillwyn, 1817) and *Semele carnicolor* (Hanley, 1847) in an intertidal, wave-washed area of cobbles, pebbles, and gravel accumulated between rocky outcrops (Fig. 2B). *Ctena delicatula* was also abundant in a similar boulder and cobble habitat on the island of Koh Nom Sao, Laem Singha District (12°27.9'N 102°0.143'E; site KKB-21) near to the southeastern point of Kungkrabaen Bay. Compared with the other lucinids of Kungkrabaen Bay, *C. delicatula* has thin, flimsy gills with short abfrontal extensions of the filaments and relatively few bacteriocytes containing small rod-shaped bacteria about 2.0 µm length and 0.7 µm width. Cells containing numerous, rounded granules (5 µm) are concentrated at the proximal ends of the filaments (Fig. 5A).

Distribution and abundance. – The distribution of molluscs across the transects is shown in Tables 3 and 4 and the most abundant species are highlighted in Fig. 6.

For Transect 1, 26 molluscan species totaling 2,673 individuals were recorded, numbering 4–13 (mean 8.8) species and 134 animals per quadrat (Table 3). Nine species accounted for 98% of the total number, and 10 species were represented by only one or two individuals. By far the most abundant mollusc was the epifaunal gastropod *Cerithideopsilla cingulata* that accounted for 47% of individuals and reached densities of 2,220 m^{-2}. Next most abundant were the lucinid *Pillucina vietnamica,* the small neritid gastropod *Clithon oualaniensis*, the cerithiid *Cerithium coralium,* the lucinid *Indoaustriella dalli*, and the tellinid bivalve *Pristis capsoides*. The highest densities of molluscs were recorded between 100 and 200 m from the mangroves (Fig. 6), mainly accounted for by the abundance of *Cerithideopsilla cingulata* and *Pillucina vietnamica*, and declined both seawards and landwards. The deposit-feeding tellinid *Pristis capsoides* was more abundant in the landward part of the transect. Qualitative sampling near the transect showed that *Anodontia philippiana* and *Psammotaena elongata* (Lamarck, 1818) were also more common near the mangroves.

From the shorter Transect 2, 19 molluscan species and 744 individuals were recorded (Table 4), ranging from 9 to 13 (mean 10) species and 141 individuals per quadrat. Seven of the species accounted for 96% of total number and eight of the species were present as one or two individuals only. Again, *Cerithideopsilla cingulata* was the most abundant species with densities to 868 m^{-2}, followed by *Clithon oualaniensis*, *Cerithium coralium*, *Pillucina vietnamica*, and *Indoaustriella dalli*.

The distribution of the two abundant lucinid species is shown in more detail in Fig. 7. Across Transect 1, *Pillucina vietnamica* reached maximum densities of 800–860 m^{-2}

Table 2. Taxonomic list of molluscan species recorded from transects within Kungkrabaen Bay, with additional lucinids recorded from the bay. Average shell height (H) or length (L) of specimens on transect is given following the name.

Bivalvia

Arcidae

Anadara troscheli (Dunker, 1882), H to 30 mm

Ostreidae

Saccostrea sp. (juveniles attached to *Cerithideopsilla*), H to 12 mm

Lucinidae

Anodontia (*Cavatidens*) *bullula* (Reeve, 1850), H to 25 mm

Anodontia (*Pegophysema*) *philippiana* (Reeve, 1850), H to 67 mm. Not recorded on transect but present near mangroves

Pillucina vietnamica Zorina, 1978, H to 8 mm

Indoaustriella dalli (Lynge 1909), H to 9.8 mm

Ctena cf. *delicatula* (Pilsbry, 1904), H to 11.5 mm. Not recorded from transect but at entrance to bay. (Note: A systematic revision of *Ctena* species from the Indo-Pacific and elsewhere is urgently needed. Although superficially similar to the widespread Pacific species *Ctena bella* (Conrad, 1837), the Kungkrabaen Bay species differs in being smaller, more anteriorly extended and with less prominent ribbing and narrower interspaces. These differences are corroborated by molecular analyses (Taylor & Glover, unpubl. data). The syntypes of *Codakia delicatula* Pilsbry, 1904, described from the Ryuku Islands, have similar morphological features to the KKB specimens and we here use this as the provisional name.)

Cardiolucina macassari (Prashad, 1932), H to 5.7 mm, dead shells on transect

Solenidae

Solen sp., L to 26 mm

Mactridae

Meropesta pellucida (Gmelin, 1791), H = 8 mm

Mactra sp. (juvenile), L = 4 mm

Ungulinidae

Cycladicama cumingi (Hanley, 1845), H to 19.5 mm

Veneridae

Anomalocardia squamosa (Linnaeus, 1758), H to 27 mm

Dosinia cretacea (Reeve, 1850), H = 20 mm

Gafrarium tumidum Röding, 1798, H to 40 mm

Costellipitar sp., H = 7 mm

Marcia hiantina (Lamarck, 1818), H to 22 mm

Placamen calophyllum (Philippi, 1836), H to 22 mm

Tellinidae

Pristis capsoides (Lamarck, 1818), H to 34 mm

Nitidotellina nitens (Deshayes, 1855), H to 7 mm

Pinguitellina pinguis (Hanley, 1844), H to 10 mm

Tellinides sp., H to 7 mm

Corbulidae

Corbula sp., H = 7 mm

Laternulidae

Laternula truncata (Lamarck, 1818), H = 10 mm

Gastropoda

Neritidae

Clithon oualaniensis (Lesson, 1831), L to 5.5 mm

Potamididae

Cerithideopsilla cingulata (Gmelin, 1791), L to 20 mm

Cerithidea alata (Philippi, 1849), L to 20 mm

Cerithiidae

Cerithium coralium Kiener, 1841, L to 25 mm

Clypeomorus pellucida (Hombron & Jacquinot, 1852), L to 17 mm

Cerithium sp., L = 12 mm

Nassariidae

Hebra corticata (A. Adams, 1852), L to 13.7 mm

Plicarcularia leptospira (A. Adams, 1852), L to 15.5 mm

Plicarcularia pullus (Linnaeus, 1758), L to 15.5 mm

Conidae

Eucithara sp., L to 12 mm

Fig. 3. Lucinidae and other common molluscs from the transects. A, *Pillucina vietnamica*; B, *Indoaustriella dalli*; C, *Ctena delicatula*; D, *Anodontia* (*Cavatidens*) *bullula*; E, *Anodontia* (*Pegophysema*) *philippiana*; F, *Pristis capsoides*; G, *Nitidotellina nitens*; H, *Anadara troscheli*; I, *Gafrarium tumidum*; J, *Anomalocardia squamosa*; K, *Solen* sp.; L, *Clithon oualaniensis*; M, *Cerithideopsilla cingulata*; N, *Cerithium coralium*; O, *Plicarcularia pullus*.

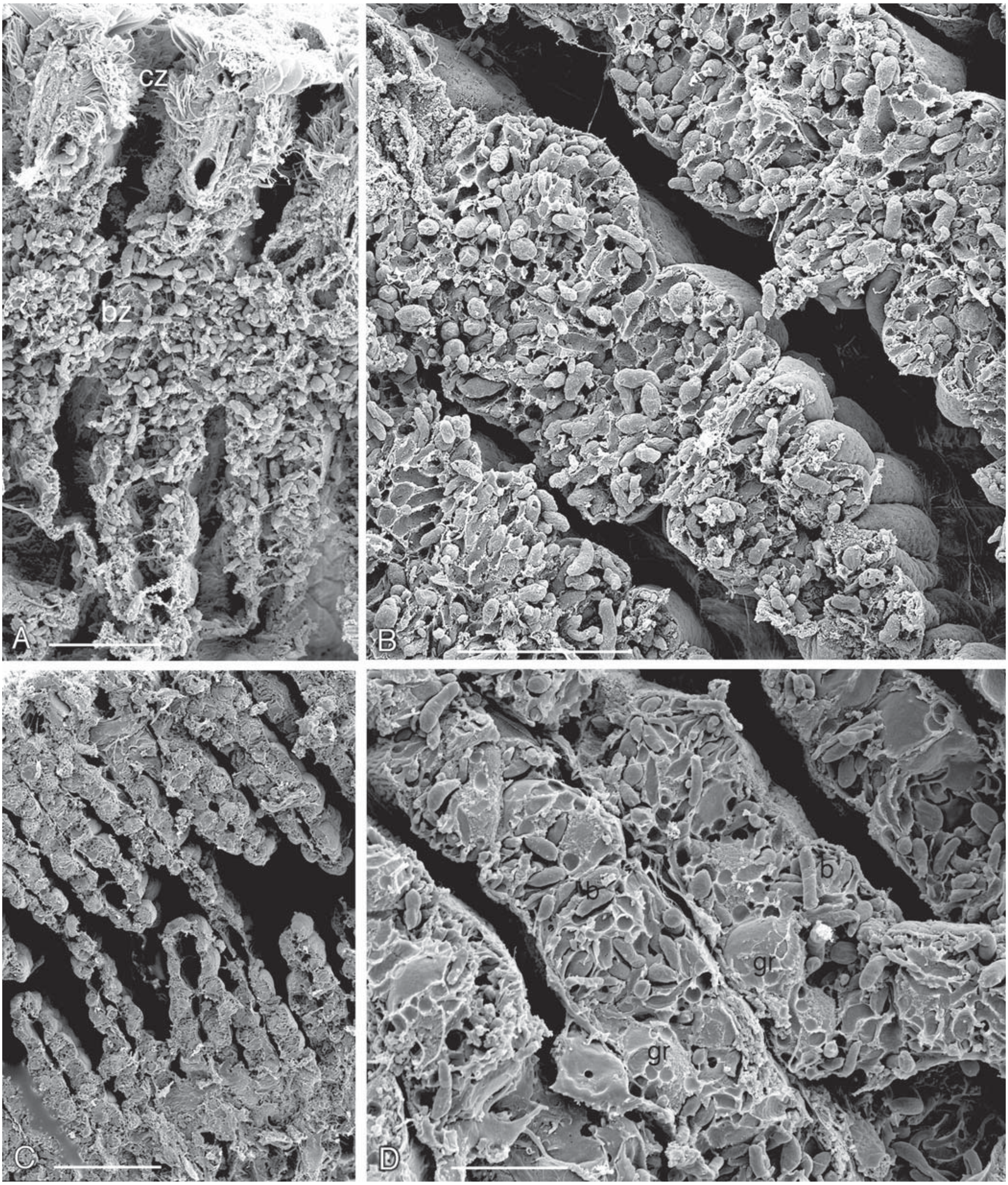

Fig. 4. Sections through ctenidial filaments of Lucinidae: A, *Pillucina vietnamica* gill filament showing distal ciliated zones and broad bacteriocyte zone; B, *P. vietnamica*, detail of filaments with bacteriocytes packed with symbiotic bacteria; C, *Indoaustriella dalli* gill filaments; D, *I. dalli* detail of gill filament showing bacteria and large spherical granules. Scale bars = A, 20 µm; B, D, 10 µm; C, 50 µm. b, bacteria; bz, bacteriocyte zone; cz, ciliated zone; gr, granule.

between 55–155 m from the mangrove fringe, whereas the less abundant *Indoaustriella dalli* attained maximum densities of 100–112 m^{-2} at 200–250 m. Only three individuals of *Anodontia bullula* were recorded in the quadrats. The mean density of all Lucinidae across the transect was 526 m^{-2} (range 126–938 m^{-2}). On Transect 2, *Pillucina vietnamica* reached a maximum density of 692 m^{-2} at 400 m from the mangrove fringe, while *I. dalli* varied between 35–186 m^{-2} with a maximum at 300 m. Total Lucinidae had a mean density of 423 m^{-2} (range 100–771 m^{-2}).

Size. – Both *Pillucina vietnamica* and *Indoaustriella dalli* are small species (< 10 mm). The size distribution for *Pillucina vietnamica* across Transect 1 is shown in Fig. 8A; the median size ranged 4.5–5.7 mm, with the individuals from amongst the mangrove prop roots (0.5 m) slightly larger at 6.5 mm. At all 10 stations, 50% of the individuals fell within a narrow range of sizes, variation 0.7–1.3 mm, with 75% of the individuals within 1.7–3.2 mm of each other (Fig. 8A). A one-way Analysis of Variance (ANOVA) followed by a Tukey Test, with $\alpha = 0.05$, revealed that the means are significantly different between most of the stations, except those for stations 3 and 4 are equal, as are those for stations 8 and 9. However, no clear relationship between distance from the mangrove and size was indicated in these data.

Median sizes of *Indoaustriella dalli* ranged between 4.5–9.0 mm (Fig. 8B), but the sample sizes were smaller. Because the sample sizes were so small (< 17 individuals) compared to those of *Pillucina vietnamica* (typically >> 17 individuals), the ANOVA and Tukey Test, with $\alpha = 0.05$, revealed that the means for eight of the stations were equal. The two exceptions were the station within the mangrove prop roots (0.5 m), which had a sample size of two, and the station at 306 m from the mangrove fringe, which had the largest size range, 4.8 mm (Fig. 8B).

Analysis of size classes for *Pillucina vietnamica* (Fig. 9) shows that the 4.1–6.0 mm size class was dominant at all stations, except within the mangrove prop roots where the 6.1–8.0 mm size class was dominant. However, only 17 individuals were found at station 1 (prop roots), compared to 33–132 individuals collected at the other stations. The 2.1–4.0 mm size class was present between 5.5 and 256 m from the mangroves and completely absent from all other stations. Also, the seaward parts of the transect (206–406 m) had a higher proportion of individuals in the 6.1–8.0 mm size class than shoreward stations, again except for Station 1.

Biomass.– Results of the biomass determinations for the more abundant bivalves are shown in Table 5. Dry weights of the two Lucinidae species were estimated at approximately 1.9 gm dry weight m^{-2}, with *Pillucina vietnamica* accounting for 1.75 gm m^{-2}. By comparison, the larger-bodied, but much less abundant, *Gafrarium tumidum* and *Pristis capsoides* contributed approximately 2.65 gm m^{-2} each, with *Anadara troscheli* and *Anomalocardia squamosa* at 0.98 and 0.65 gm·m^{-2}, respectively.

Feeding guilds of molluscan fauna.– The molluscan community recorded along the transect included species with a variety of feeding strategies including algal grazing, detrivory, suspension feeding, deposit feeding, carnivory, and chemosymbiosis. We have classified the species into these broad categories (Fig. 10). Grazing and surface browsing gastropods, *Clithon oualaniensis, Cerithideopsilla cingulata*, and *Cerithium coralium* were the most abundant epifaunal molluscs and responsible for high levels of bioturbation from their surface grazing trails (Fig. 2C). According to Kamimura & Tsuchiya (2004), *Cerithideopsilla* is an obligate detritivore, ingesting particulate organic material from the sediment surface layer. Apart from the largely chemoautotrophic lucinids, most other common bivalves are shallow-burrowing suspension feeders, except for the

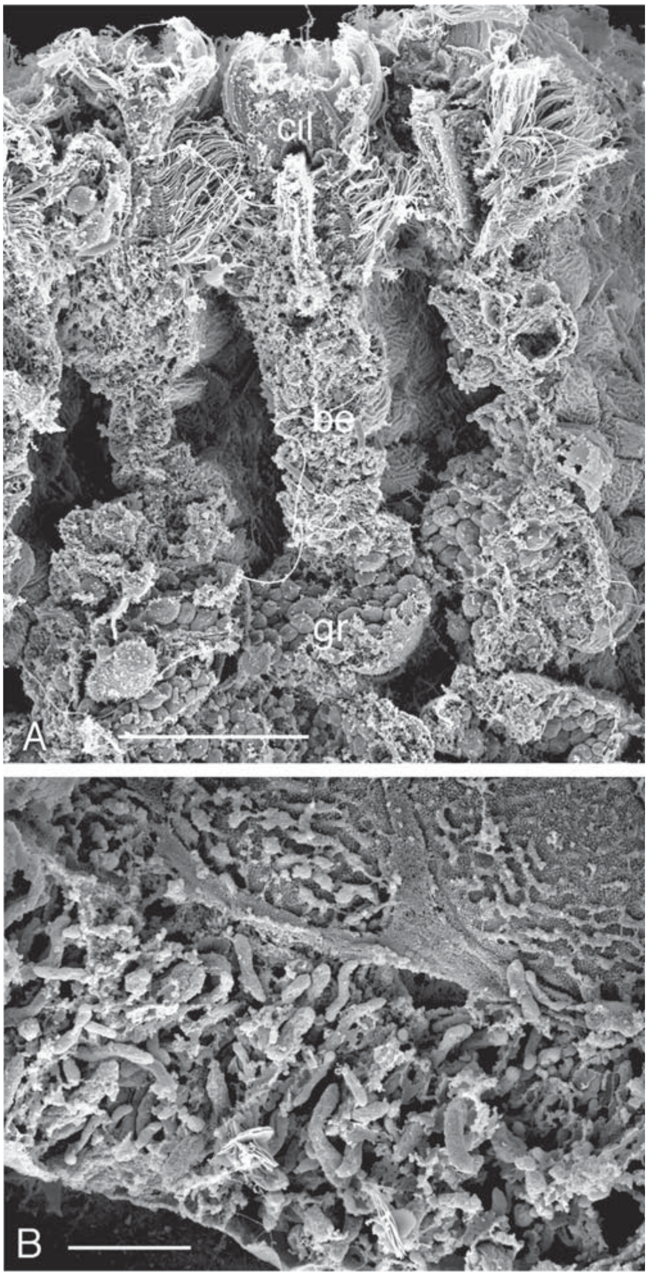

Fig. 5. Sections through gill filaments of Lucinidae: A, *Ctena delicatula,* showing distal ciliated zone, thin bacteriocyte zone, and proximal granule cells; B, *Anodontia bullula*, section through bacteriocytes with long, thin bacteria. Scale bars = A, 20 µm; B, 5 µm. be, bacteriocyte zone; cil, ciliated zone; gr, granules.

Table 3. Ranked abundance of molluscs recorded from Transect 1. Lucinidae species are highlighted.

	Stations																				
Species	**0A**	**0B**	**1A**	**1B**	**2A**	**2B**	**3A**	**3B**	**4A**	**4B**	**5A**	**5B**	**6A**	**6B**	**7A**	**7B**	**8A**	**8B**	**9A**	**9B**	**Total individuals**
Cerithideopsilla cingulata	–	–	–	8	115	22	325	4	255	82	96	88	42	41	12	94	14	12	27	28	1,265
Pillucina vietnamica	12	5	2	34	55	66	16	37	34	96	3	45	63	3	17	16	18	46	27	23	618
Clithon oualaniensis	–	–	3	2	27	58	12	5	16	19	8	6	79	9	4	1	22	16	6	2	295
Cerithium coralium	–	–	–	–	4	7	2	3	–	2	8	8	65	75	3	6	6	3	3	4	199
Indoaustriella dalli	2	–	3	1	6	7	3	2	2	8	4	12	14	3	9	2	4	6	9	1	98
Pristis capsoides	9	8	9	18	5	9	5	–	1	3	1	5	3	3	1	–	–	–	–	1	81
Gafrarium tumidum	–	1	3	7	5	5	4	1	–	1	–	1	–	1	–	–	–	–	–	–	29
Anomalocardia squamosa	1	1	1	3	3	3	3	3	1	1	1	2	1	1	2	–	1	–	–	–	28
Nitidotellina nitens	–	–	–	–	–	–	–	1	–	3	–	2	2	3	–	1	–	3	–	–	15
Solen sp.	–	–	–	–	1	–	–	1	–	–	1	–	1	–	–	–	2	–	1	–	7
Plicarcularia pullus	–	–	–	1	–	–	1	–	–	–	1	–	2	–	–	–	–	1	–	–	6
Tellinides sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	3	–	–	–	1	1	–	5
Anadara troscheli	–	–	–	–	–	–	–	–	–	–	–	–	1	3	–	–	1	–	–	–	5
Anodontia bullula	–	–	–	–	–	1	–	–	1	–	–	–	1	–	–	–	–	–	–	–	3
Dosinia cretacea	–	–	–	–	–	1	1	–	–	–	–	–	–	–	–	–	1	–	–	–	3
Saccostrea sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	–	–	–	–	1	3
Costellipitar sp.	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	1	–	–	2
Cerithidea alata	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2
Eucithara sp.	–	–	–	–	–	–	–	–	–	1	–	–	–	1	–	–	–	–	–	–	2
Pinguitellina pinguis	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Tellinidae sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	1
Meropesta pellucida	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	1
Mactra sp. (juv.)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	1
Laternula truncata	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	1
Cerithium sp.	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Clypeomorus pellucida	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	1
Total species	4	6	6	8	10	10	10	9	7	11	9	11	12	13	8	7	9	9	9	7	26
Total individuals	24	18	21	74	222	179	372	57	310	217	123	171	274	147	49	121	69	89	76	60	2,673

Table 4. Ranked abundance of molluscs recorded from Transect 2. Lucinidae species are highlighted.

	Station						
Species	**1A**	**1B**	**2A**	**2B**	**3A**	**3B**	**Total individuals**
Cerithideopsilla cingulata	122	8	6	1	1	84	222
Clithon oulaniensis	1	28	9	6	4	38	86
Cerithium coralium	1	–	107	33	9	1	151
Pillucina vietnamica	–	2	17	15	74	30	138
Indoaustriella dalli	7	5	11	17	8	4	52
Anomalocardia squamosa	–	1	4	14	4	7	30
Gafrarium tumidum	3	6	12	6	1	1	29
Pristis capsoides	2	3	2	2	2	–	11
Saccostrea sp.	2	–	3	1	2	–	8
Placamen calophyllum	–	–	1	1	1	–	3
Hebra corticata	–	–	3	–	–	–	3
Marcia hiantina	–	–	–	2	–	–	2
Nitidotellina nitens	–	–	–	–	2	–	2
Anadara troscheli	–	–	1	1	–	–	2
Cycladicama cumingi	–	1	–	–	–	–	1
Costellipitar sp.	–	–	–	–	1	–	1
Tellinides sp.	–	–	–	–	–	1	1
Solen sp.	–	–	–	–	–	1	1
Corbula sp.	–	–	–	1	–	–	1
Total species	7	8	12	13	12	9	19
Total individuals	138	54	176	100	109	167	744

deposit-feeding tellinids, *Pristis capsoides* and *Nitidotellina nitens*. The fauna is unusual for the paucity of carnivorous gastropods, including only a few scavenging nassariids and the conoidean *Eucithara*. Although not recorded from the transect quadrats, the molluscivorous muricid gastropod *Chicoreus capucinus* (Lamarck, 1822) is frequent on the inner mudflat and around the mangrove prop roots (Tan, 2008).

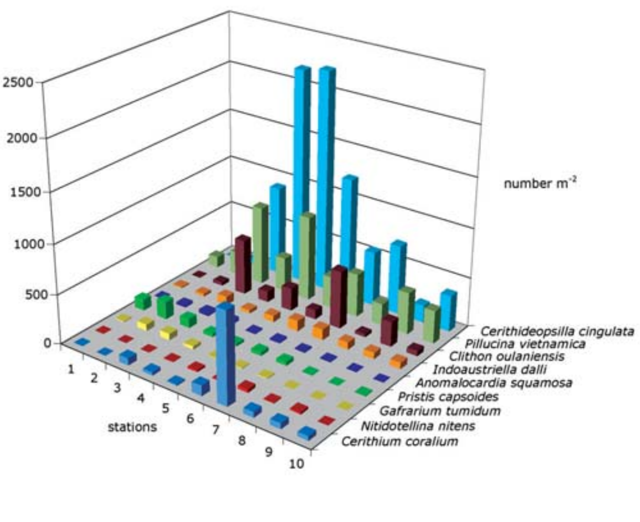

Fig. 6. Distribution and abundance of the most common molluscs along Transect 1.

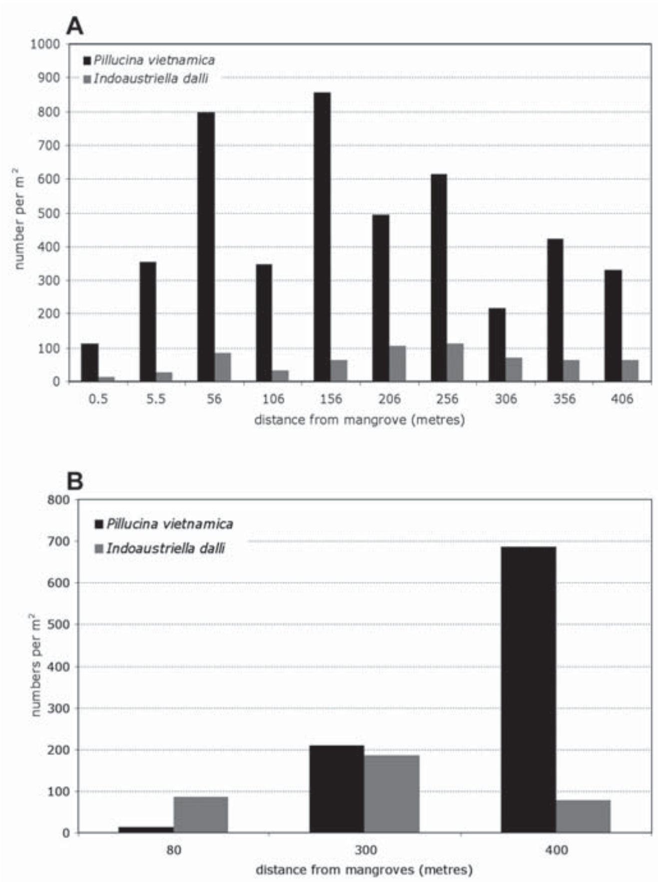

Fig. 7, Distribution of *Pillucina vietnamica* and *Indoaustriella dalli* across: A, Transect 1; B, Transect 2.

Table 5. Biomass estimates for Lucinidae species and other common bivalves.

Species	density (m^{-2} ± SD)	range	mean size	dry wt ($g{\cdot}m^{-2}$)	range
Pillucina vietnamica	408 ± 242	112–858	5.3 ± 0.7	1.75	0.48–3.7
Indoaustriella dalli	65 ± 32	13–112	5.9 ± 1.2	0.14	0.029–0.246
Gafrarium tumidum	19 ± 26	0-66	25.5 ± 9.3	2.66	–
Pristis capsoides	53 ± 57	0–178	16.9 ± 6.4	2.65	–
Anadara troscheli	7 ± 2	0–3	20.1 ± 10.3	0.98	–
Anomalocardia squamosa	18 ± 14	0–178	17.2 ± 7.4	0.65	–

DISCUSSION

This study revealed in the intertidal mud and sand flats of Kungkrabaen Bay a high abundance of two small species of Lucinidae, *Pillucina vietnamica* and *Indoaustriella dalli*. Despite the likely importance of these chemoautotrophic bivalves to the productivity of the mud flat, both of these species are poorly known with only basic taxonomic information available. Indeed *I. dalli* has hardly been mentioned since its original description (Lynge, 1909). The habitat occupied by the lucinids of sheltered muddy bays backed by mangroves, with nutrient input from terrestrial runoff, is widespread in Southeast Asia and similar abundances of small lucinids should occur at other localities in the region but are generally unreported.

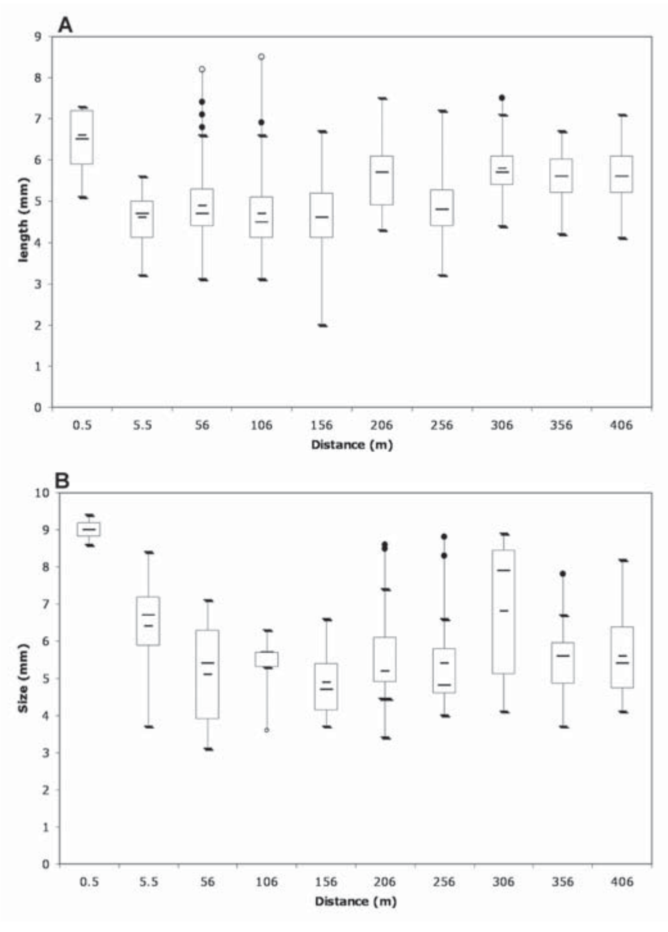

Fig. 8. Box plots of shell lengths of: A, *Pillucina vietnamica*; B, *Indoaustriella dalli*, across Transect 1. Box limits are quartiles, black bars are means, grey bars are medians, whiskers extend 3/2 interquartile range, black circles are outliers and open circles extreme outliers.

Although the abundance of lucinids for Kungkrabaen Bay is high, it is not exceptional as shown by comparison with a few other studies (Table 6). There is little published data for the tropical Indo-Pacific; an exception is the high density (ca. 3,000 m^{-2}) of *Pillucina* sp. (probably *Pillucina vietnamica*) reported from dugong-grazed seagrass beds in a sheltered bay on the Andaman Sea side of southwestern Thailand (Nakaoka et al., 2002). On Lizard Island, Queensland, *Divaricella irpex* (E. A. Smith, 1885), with densities of to 570 m^{-2}, is the most abundant of several lucinids (Glover & Taylor, unpublished data). On an oceanic atoll, Paulay (2000) recorded *Ctena bella* (Conrad, 1834) and *Wallucina fijiensis* (E. A. Smith, 1885) at 40 and 15 m^{-2} respectively. Just outside the tropics, at Rottnest Island, Western Australia, Barnes & Hickman (1999) recorded *W. assimilis* (Angas, 1867), which is of similar size (length 5.5–9.0 mm) to our Thailand species, at densities to 1,000 m^{-2} in shallow, subtidal seagrass beds. Further afield, the highest densities of any lucinid recorded are for the Mediterranean *Loripes lacteus* (Linnaeus, 1758), to 2,600 m^{-2} from *Posidonia* beds of Corsica (Johnson et al., 2002).

Although we recorded four species of lucinids from the muddy sands of Kungkrabaen Bay, *Ctena delicatula* occupied a rather different habitat amongst wave-washed, angular cobbles and gravel on an exposed rocky shore at the entrance to the bay. In our experience, *Ctena* species are often found in sand and gravel pockets on rock platforms. At first sight, this might seem an unsuitable habitat for a chemosymbiotic bivalve, but finer sediments and degrading organic material are often trapped in the quieter environment beneath the cobbles. We observed that *C. delicatula* from Kungkrabaen Bay has thinner gill filaments and smaller, fewer bacteriocytes (Fig. 5A) than the lucinids within the bay, which leads to speculation of perhaps lesser dependence on chemoautotrophy. *Ctena* species are amongst the most abundant and widespread of tropical lucinids but details of biology are known for only one species, *Ctena orbiculata* (Montagu, 1808), from the western Atlantic (Barnes, 1993).

By contrast to the abundant lucinids in sheltered Kungkrabaen Bay, nearby more exposed, intertidal, sandy beaches were sampled for bivalves and no Lucinidae were recorded. The habitat is both more mobile and unvegetated with less accumulation of organic material. The bivalve fauna of these

Table 6. Some population density values for intertidal or shallow subtidal Lucinidae obtained from the literature.

Species	Habitat	Density (/m²)	Locality	Reference
Pillucina sp.	seagrass	3,000+	western Thailand	Nakaoka et al., 2002
Ctena bella (Conrad, 1837)	seagrass	40	Tawara Atoll	Paulay, 2000
Wallucina fijiensis (Smith, 1885) (as *W. haddoni*)	seagrass	15	Tawara Atoll	Paulay, 2000
Divaricella irpex (Smith, 1885)	sand, sparse seagrass	222–570	Lizard Island, Australia	Taylor & Glover, unpublished
Cardiolucina pisiformis (Thiele, 1930)	intertidal sand-mud	41	Dampier,	Glover et al., 2003 W. Australia
Wallucina assimilis (Angas, 1867)	seagrass	718–1,048	Rottnest Is., W. Australia	Barnes & Hickman, 1999
Codakia orbicularis (Linnaeus, 1758)	seagrass	19–52	Jamaica Jackson,	1972
Ctena orbiculata (Montagu, 1808)	seagrass	13	Jamaica	Jackson, 1972
"*Parvilucina*" *costata* (d'Orbigny, 1842)	seagrass	15	Jamaica	Jackson, 1972
Stewartia floridana (Conrad, 1833)	seagrass	84	Florida, USA	Fisher & Hand, 1984
Loripes lacteus (Linnaeus, 1758)	seagrass	242–2,666	Corsica	Johnson et al., 2002
Lucinoma borealis (Linnaeus, 1776)	seagrass	120–1,500	Brittany, France	Monnat, 1970
Lucinoma borealis (Linnaeus, 1776)	sand and seagrass	3.8	Devon, England	Dando et al., 1986
Lucinella divaricata (Linnaeus, 1758)	seagrass	200–300	Brittany, France	Monnat, 1970
Indoaustriella dalli (Lynge, 1909)	sand/mud, seagrass	13–112	Kungkrabaen Bay, Thailand	this study
Pillucina vietnamica Zorina, 1978	sand mud, seagrass	112–858	Kungkrabaen Bay, Thailand	this study

shores included *Meretrix meretrix* (Linnaeus, 1758), together with *Donax*, *Solen* and *Mactra* species.

It should be emphasized that the intertidal habitats of Kungkrabaen Bay are highly disturbed. There is extensive and intensive artisanal shellfish exploitation, notably digging for the burrowing brachiopod *Lingula*, but also the gathering of bivalves including *Anomalocardia*, *Gafrarium*, *Anadara*, and *Psammotaena* (Fig. 2D). This foraging activity has likely taken place for a very long time and has undoubtedly

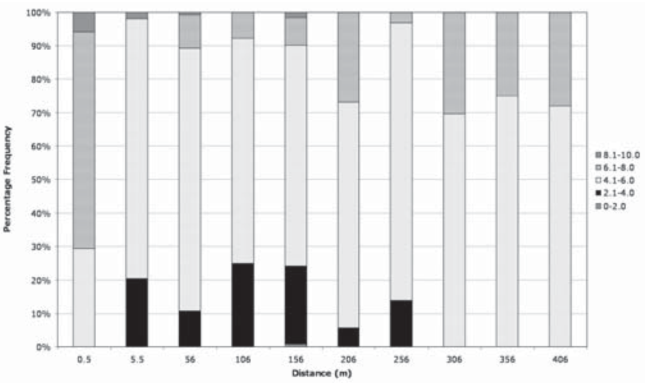

Fig. 9. Size classes of *Pillucina vietnamica* at stations across Transect 1.

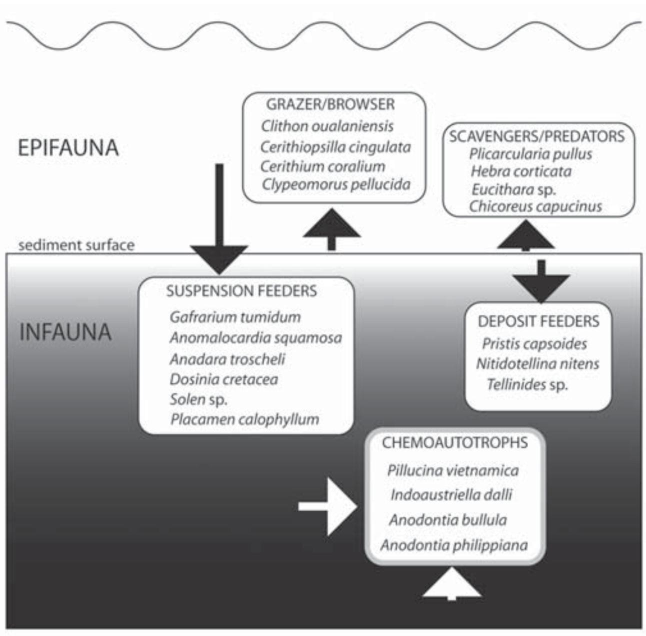

Fig. 10. Feeding guilds of the common molluscs from transects at Kungkrabaen Bay. Origin of the food source is indicated by arrows.

disrupted seagrass growth and influenced the stability of the sediment surface. The lucinids are too small to be of any economic interest but the sediment disturbance and removal of many of the larger bivalves has likely influenced their abundance and distribution. Additionally, the whole bay is influenced by the extensive disturbance and drainage from the massive development of fish and prawn farms (Fig. 1) in the landward parts of the mangrove fringe (Tookwinas, 1998). However, results from isotope studies suggest that effluent nutrients from the prawn farms are largely trapped by the mangroves and in the inner bay sources of particulate organic material are mainly from seagrass, algae, and plankton (Thimdee et al., 2003).

As exemplified by Kungkrabaen Bay, chemoautotrophic lucinid bivalves are often abundant in many tropical shallow-water habitats such as seagrass beds and peri-mangrove habitats. They represent an ecologically important component of these systems in terms of their biomass, production, and cycling of buried organic material via sulphide-oxidising symbiotic bacteria (Johnson et al., 2002). However, details of their role in the productivity of these systems have been little studied or altogether ignored. Past studies have often recognized the abundance of lucinids in seagrass communities (Moore et al., 1968; Taylor & Lewis, 1970; Jackson 1972) but classified the bivalves as particulate suspension feeders and misinterpreted their role in the communities.

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. Our thanks to them all.

We thank Nopadon Kakhai for local advice, along with Graham Oliver, Paul Valentich-Scott, Rüdiger Bieler, Paula Mikkelsen and Tan Koh Siang for valuable discussions in the field and laboratory. Roger Bamber (NHM) is thanked for arranging the sediment analysis, Paul Callomon (Academy of Natural Sciences, Philadelphia) for images of the syntypes of *Ctena delicatula*, and Alex Ball (NHM Electron Microscope Unit) for much advice.

EAG and JDT are indebted to Phil Rainbow and the Department of Zoology, NHM, for continuing support and facilities.

THAI ABSTRACT

จากการสำรวจเชิงปริมาณเกี่ยวกับมอลลัสก์ที่อาศัยอยู่ในพื้นที่ๆ ได้รับผลกระทบจากกิจกรรมของมนุษย์   บริเวณพื้นทรายปนโคลน ในแนวน้ำขึ้นน้ำลงใกล้ป่าชายเลนในอ่าวที่มีคลื่นลมสงบบริเวณ ภาคตะวันออกเฉียงใต้ของประเทศไทย พบว่ามีความหนาแน่นของ หอยสองฝาวงศ์ลูไซนิดีย์ขนาดเล็กที่มีแบคทีเรียอาศัยอยู่ในเหงือก แบบ chemosymbiotic ชนิด *Pillucina vietnamica* และ *Indoaustriella dalli* อยู่สูง (1,380 ตัว/ตารางเมตร) ส่วนหอยสอง ฝาในวงศ์เดียวกันอีกสองชนิดคือ *Anodontia bulla* และ *A. philippiana* ก็มีพบอยู่บ้างในบริเวณใกล้แนวที่ทำการสำรวจ ในขณะที่หอยลูไซนิดอีกชนิดหนึ่งคือ *Ctena delicatula* จะพบ อาศัยอยู่ในพื้นที่ๆ   เป็นกรวดบริเวณปากทางเข้าของอ่าวคุ้งกระเบน จากการศึกษาครั้งนี้พบว่าหอยในวงศ์ลูไซนิดีย์ทุกชนิดที่สำรวจพบ มีแบคทีเรียที่เป็นประโยชน์อาศัยอยู่ในเหงือก ส่วนหอยชนิดอื่นๆ ที่พบว่าอาศัยอยู่ร่วมกับหอยสองฝาชนิดดังกล่าวได้แก่ *Cerithideopsilla cingulata*, *Cerithium coralium* และ *Clithon oualaniensis* ที่เป็นหอยฝาเดียวประเภทที่อาศัยบนพื้นผิว และ พบหอยสองฝาที่ฝังตัวอยู่ในพื้นได้แก่ *Gafrarium tumidum*, *Anomalocardia squamosa*, *Pristis capsoides* และ *Anadara troscheli* จากการประมาณการชีวมวลพบว่าชีวมวลของหอย ลูไซนิดมีค่าระหว่าง 0.51 ถึง 3.95 กรัม/ตารางเมตร ผลของ การศึกษาครั้งนี้ชี้ให้เห็นถึงบทบาททางนิเวศวิทยาที่สำคัญของหอย ที่มีการดำรงชีวิตแบบ chemoautotrophic ที่อาศัยอยู่ในบริเวณ ขอบของป่าชายเลนด้านที่ติดกับทะเล

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