

**POPULATION STUDY OF *LATERNULA TRUNCATA* (BIVALVIA: ANOMALODESMATA: LATERNULIDAE) IN THE MANGROVE SAND FLAT OF KUNGKRABAEN BAY, THAILAND, WITH NOTES ON *LATERNULA* CF. *CORRUGATA***

**Robert S. Prezant**

College of Science and Mathematics, Montclair State University, Montclair, New Jersey 07043, U. S. A.  
Email: prezantr@mail.montclair.edu

**Chirasak Sutcharit**

Animal Systematic Research Unit, Department of Biology, Chulalongkorn University, Bangkok 10330, Thailand.  
Email: jirasak4@yahoo.com

**Kashane Chalermwat**

Department of Aquatic Science, Faculty of Science, Burapha University, Chonburi 20131, Thailand.  
Email: k\_chalermwat@hotmail.com

**Nopadon Kakhai**

Kungkrabaen Bay Royal Development Study Centre, Chantaburi 22120, Thailand.

**Teerapong Duangdee**

Department of Fishery Biology, Faculty of Fisheries, Kasetsart University, Bangkok, Bangkok 10400, Thailand.

**Pongrat Dumrongrojwattana**

Department of Biology, Faculty of Science, Burapha University, Chonburi 20131, Thailand.

**ABSTRACT.** – A population of the anomalodesmatan bivalve *Laternula truncata* (Lamarck, 1818) was examined in a mangrove sand flat in Kungkrabaen Bay, Thailand, to determine population size, cohort distribution, and basic relationships with sediment and infaunal macroinvertebrate biodiversity. Relatively high densities of *L. truncata* were found in muddy sands, often deeply buried in or close to tangled rootlet mats of the mangrove trees *Avicennia alba* Blume, 1827, and *A. marina* (Forsskål) Vierhapper, 1907, along isolated mangrove hummocks. They were less common in open areas of the mangrove flat. This population of *L. truncata* was relatively evenly distributed across size classes, minus the smallest sizes, suggesting continuous recruitment with a possible loss of recent recruits or recruitment. Overall benthic macroinvertebrate biodiversity, along with laternulid density, was higher closer to mangroves but relative infaunal invertebrate dominance increased along a transect that transcended a hummock closer to the mangrove forest, across an open sand flat, and terminated in another isolated hummock farther from the fringing forest. A nearby population of *L. cf. corrugata* (Reeve, 1863) inhabited a distinctly different habitat. *Laternula cf. corrugata* was shallowly buried and dwelt in the mangrove forest proper among different species of mangroves and in sandier sediments. Behavioural observations of both laternulids indicated that both were capable of reburying, with smaller specimens more rapidly, albeit still slowly, succeeding in full re-entry into the sediment. Larger specimens of *L. truncata* were incapable of reburial. Morphological, ecological, and behavioural distinctions between *L. truncata* and *L. cf. corrugata* are considered in light of their habitat differences, confusion within laternulid systematics, and difficulty in resolving the taxonomy of the latter species.

**KEYWORDS.** – *Laternula*, abundance, diversity, recruitment, taxonomy.

---

## INTRODUCTION

Human encroachment through housing and road development, agriculture, salt farms, charcoal production, tin mining and

aquaculture have seriously impinged upon mangroves and mangrove ecosystems of Thailand. Menasveta (1997) calculated as much as a 68% loss of mangrove forests in Thailand as a result of urban development with another

32% impacted by shrimp farming. Khemnark (1995) noted a decrease of approximately 54% of mangrove forests in Thailand between 1961 and 1993. Aksornkoae et al. (1993) suggested that shrimp pond aquaculture was responsible for 64% of this loss. Regardless of the differences in reported numbers, it is clear that the mangals of Thailand have undergone significant human-induced change. With ongoing threats to this ecosystem (Aksornkoae & Tokrisna, 2004) and with recent attempts to restore ecosystems, with some presumed localised successes (Macintosh et al., 2002), it remains imperative that there be a continued and expanded effort to understand the systems and their associated biota. Kathiresan & Bingham (2001) offered a general overview of some of the major taxa found in mangals. Mangrove habitats of the southeastern Gulf of Thailand, although they offer a rich biota and an important fishing habitat, remain biologically poorly known with little information available about even some of the more common taxa. One such group includes laternulid bivalves.

Most of what we know about bivalves in the family Laternulidae comes from a number of papers on the Antarctic bivalve *Laternula elliptica* (King & Broderip, 1831) (for example, see Ansell & Harvey, 1997; Ahn & Shim, 1998; Urban & Mercuri, 1998; Jonkers, 1999; Ahn et al., 2001; Bigatti et al., 2001; Brockington, 2001; Lohan et al., 2001; Momo et al., 2002; Peck et al., 2002, 2004; Ahn et al., 2003; Kang et al., 2003). Various studies on morphology of laternulids are available (Adal & Morton, 1973; Morton, 1973, 1976; Aller, 1974; Savazzi, 1990; Sartori et al., 2006). However, field studies of laternulids from Asia are uncommon. Two species of laternulids, *L. anatina* (Linnaeus, 1758) and *L. cf. corrugata* (Reeve, 1863), were reported from the southern Gulf of Thailand by Swennen et al. (2001). Valves of *L. anatina* were reported as common, washed up on sandy beaches of Pattani Bay and nearby estuaries after heavy winds. *Laternula cf. corrugata* was considered common with numerous living specimens found in muddy substrata in Pattani Bay. The taxonomy of *L. cf. corrugata* is in question with very little in the literature to verify the specific epithet and some confusion with possible synonymies with *L. navicula* (Reeve, 1863). For purposes of this paper, we will refer to it as *L. cf. corrugata* although the taxonomy is not resolved and it is possible that future efforts will synonymise these two taxa with *L. navicula* taking preference. In addition, our survey of Kungkrabaen Bay in the southeastern Gulf of Thailand recovered not *L. anatina* but a large population of *L. truncata* (Lamarck, 1818). These two species, although similar in general shell form, are easily separated by morphological characters including the obvious truncate posterior shell margin and the presence of a lithodesma in the latter.

To better understand *Laternula truncata* we examined population sizes, cohort distribution, burrowing behaviour, general ecology, and relationship to infaunal biodiversity of this bivalve along a transect in Kungkrabaen Bay (Fig. 1A, B). Preliminary comparative ecological, behavioural, and morphological studies of a nearby population of *L. cf. corrugata* were also performed in an preliminary effort to help distinguish these taxa and their requisite habitats.

## MATERIALS AND METHODS

**Sample collections.** – Quantitative and qualitative sampling of a population of *Laternula truncata* was carried out at low tides in late August and early September 2005 on an expansive sand flat in Kungkrabaen Bay, Chantaburi Province, in the southeastern Gulf of Thailand, using standard sampling techniques. A transect was taken between two mangrove hummocks that were otherwise isolated within the flat. The transect was approximately 200 m long between hummocks with the first site approximately 100 m from the edge of the primary fringing mangrove forest and angling out to the last site approximately 150 m from the forest edge (Fig. 1B, C). Five stations (KBAY1 to KBAY5) were sampled along this transect, spaced 50 m apart from each other. A square-meter quadrat was subdivided into four sectors (0.5 × 0.5 m) by

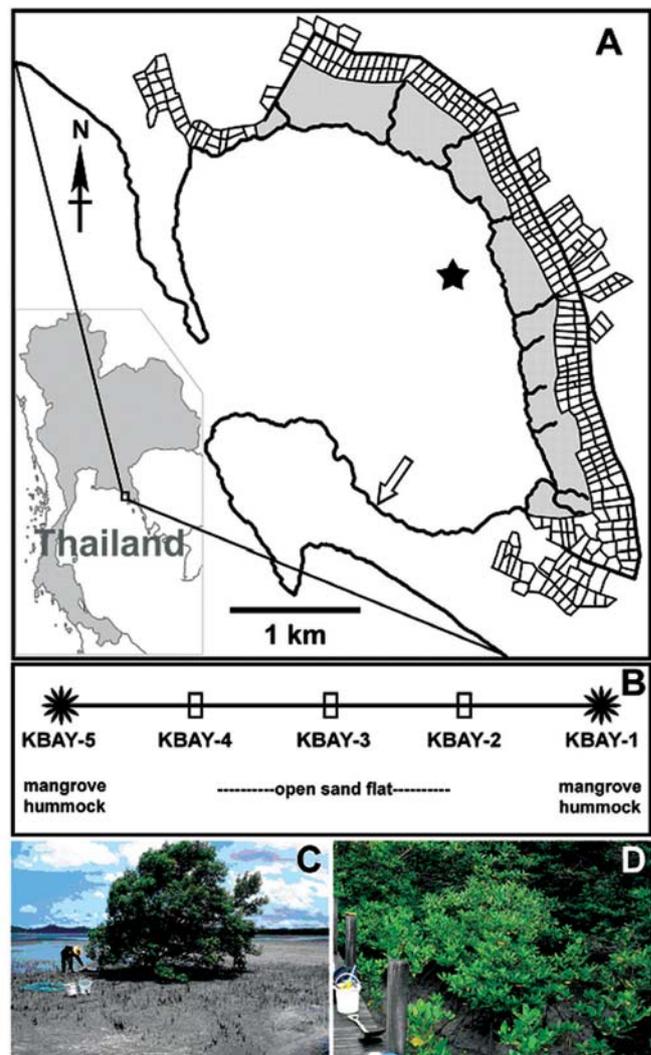


Fig. 1. A, Map of Kungkrabaen Bay surrounded by mangrove forest (grey background) and shrimp farms (blocks). The solid star indicates the site of the transect along the open mangrove sand flat between hummocks (sites of collection of *Laternula truncata*). *Laternula cf. corrugata* was found deeper in the mangrove forest at the site indicated by the white arrow; B, Representation of the transect taken at Kungkrabaen Bay in the study of the *L. truncata* population; C, *Laternula truncata* habitat at KBAY1 site; D, *Laternula cf. corrugata* habitat at site at Kungkrabaen Bay Natural Study Center next to boardwalk.

nylon monofilament. The quadrat was randomly placed just adjacent to the transect line at 50 m intervals including the terminal nodes. Sediment to 20 cm depth was excavated from one quartile of the quadrat and processed through 1.0 and 0.5 mm mesh sieves. Triplicate samples were taken at each station. All living fauna were removed from the sieves. Laternulids were kept alive in buckets of seawater and returned to the laboratory for behavioural observations. All other organisms were preserved in 70% ethanol in the field. Diversity was measured using the Shannon-Wiener Diversity Index [ $H = -\sum(P_i \ln[P_i])$ ] and species evenness was determined using the Simpson Index  $\{D_s = 1 - \sum_i [n_i^*(n_i-1)] \div [N \times (N-1)]\}$ .

A sampling site off the sand flat and within the mangrove forest proper was qualitatively sampled for *Laternula cf. corrugata*. This site was located just off a boardwalk in Kungkrabaen Bay Natural Study Center adjacent to Klong Ta-Sook Canal (Fig. 1A, D). Specimens of *L. cf. corrugata* were collected by hand from this site and brought back to the laboratory as well. Final preservation of all specimens was in 70% ethanol.

The maximum length (L), height, and breadth of each individual laternulid were measured to the nearest 0.1 mm. In total, 187 specimens of *Laternula truncata* were measured. In addition, in a subsample of specimens, the maximum pallial sinus depth and length of umbonal slit were measured. Because the predatory boring muricid snail *Chicoreus capucinus* (Lamarck, 1822) was regularly found on the mangrove flats as well as deeper into the mangrove forest, any indications of bore holes in laternulid shells were also noted.

Sediment samples were taken for granulometric and organic content analyses. Replicate sediment cores to 15 cm depth were taken within an adjacent quartile of the sampling quadrat. The cores were divided into the top 5 cm and next 10 cm. Sediment samples were dried at 100°C for 24 hours and dry-sieved through standard granulometry sieves with particles measured according to the Wentworth scale. The organic content of the sediment was measured by the difference between the dry weight (100°C dried sediments) of the sample and the weight after 1 hour of combustion at 510°C.

Representatives of laternulids from this study have been deposited in the invertebrate collections of Montclair State University, New Jersey, U.S.A., Chulalongkorn University Museum of Zoology, Bangkok, Thailand, and the mollusk collection in the Academy of Natural Sciences, Philadelphia, Pennsylvania, U.S.A. [catalogue numbers at the latter: ANSP 413584 for shells only and A21000 for preserved *Laternula truncata* and ANSP A21001 for *L. cf. corrugata* preserved with soft tissues intact].

**Behaviour.** – Burrowing behaviour was examined in the laboratory using recently collected specimens of *Laternula truncata* and *L. cf. corrugata*. In late August 2005, larger sized specimens of *L. truncata* were placed in a small

aquarium that held 8 cm of field-collected sediment covered with 6 cm of field-collected water. Similarly, a number of medium-sized and smaller clams were placed in separate, similar aquaria to monitor burrowing behaviour and/or differences in rate of burial between size classes. Specific behavioural landmarks were monitored: (1) first foot probe of sediment, (2) movement of valves to upright position, and (3) fully burrowed with only siphons exposed. Similar experiments were performed using mixed sizes of *L. cf. corrugata* placed on sediment in large glass beakers.

## RESULTS

**General description of study sites.** – Kungkrabaen Bay (KBAY) is an extensive shallow mudflat with soft muddy to sandy sediments dotted with small mangrove hummocks along its inner margin and fringed by extensive natural and planted mangroves (Fig. 1A, C). The flats are heavily fished by hand by local residents for edible bivalves (including *Laternula truncata*), crabs, and brachiopods. The bay encompasses an area of approximately 9 km<sup>2</sup> with an average depth of 1.0–2.0 m. The maximum width of KBAY is approximately 5 km from north to south and 2 km wide from east to west. The western side of the bay opens into the Gulf of Thailand and the mouth of the bay is approximately 1 km wide. The northern, southern, and eastern sides are bounded by dense primary mangrove forest and shrimp farms surround the margins of the mangal. The majority of trees are species of *Sonneratia* and *Avicennia* (Fig. 1C, D). There are four major channels carrying nutrients into the bay. The bay is well drained, oxygenated, and the salinity can be brackish ranging down to 4.10 ppt in a typical rainy season (N. Kakhai, unpubl. data). During August 2005, a relatively dry rainy season, we recorded salinities up to 30 ppt.

Our transect (Fig. 1B), designed to determine general distribution and population sizes of *Laternula truncata*, crossed a portion of the open mangrove sand flat with an origin located within an isolated mangrove hummock (site KBAY1) at 12°35'31"N 101°54'29"E. During our short sampling period, salinity at this site ranged from 25–30 ppt during low tide in shallow waters. The transect ran from mangrove hummock (KBAY1) to hummock (KBAY5), the latter two isolated islands of trees being dominated by *Avicennia marina* (Forsskål) Vierhapper, 1907, and *A. alba* Blume, 1827.

Specimens of *Laternula cf. corrugata* were found in sediments within the mangrove forest proper at the Kungkrabaen Bay Natural Study Center (Fig. 1A, D). Our collection site was dominated by the mangrove tree *Sonneratia alba* J. E. Smith in Rees, 1819 (Fig. 1D). The site is located at 12°34'15"N 101°54'25"E. A boardwalk runs along the park in this region and specimens of *L. cf. corrugata* were found just off this pathway in firmly packed sands.

**Population structure.** – Size measurements of all living *Laternula truncata* (Fig. 2A) collected during August 2005 revealed no distinct size cohorts (Fig. 3). Gradations of

sizes showed mostly very small differences spread across the specimens measured from the smallest specimen (just under 15 mm L) to the largest (close to 68 mm L). There was some indication of an age-related die-off in the largest size range because the number of clams decreased rapidly. The majority of clams collected (49 of 73 specimens) were 30–50 mm and only a few smaller than 20 mm or larger than 60 mm were found. Prominent low and tightly positioned rings were present on the shells of *L. truncata* (Fig. 2A–C). These regular concentric rings were interspersed with concentric, irregularly placed but more prominent growth stoppage rings. All such rings seamlessly traversed across the umbonal slit typical of the valves (Fig. 2B).

Each quadrat in the Kungkrabaen Bay transect held specimens of *Laternula truncata* except for KBAY2. The highest densities were found at the mangrove hummocks, sites KBAY1 and KBAY5 (Fig. 4). There was also a seeming relationship between population density and average size. Site KBAY 5 held not just the highest density of bivalves but also the smallest average size (Fig. 4). Larger average bivalve sizes were found in quadrats with lower densities.

Specimens of *Laternula truncata* were often found buried 5–12 cm deep in highly compacted sands beneath mangrove pneumatophores and sometimes tightly enmeshed in rootlets of *Avicennia alba* and/or *A. marina*. The open sand sites between these mangrove islands held few (KBAY3) or no (KBAY2) specimens.

Although no quantitative sampling for *Laternula cf. corrugata* was done, this species was clearly not as common as *L. truncata*. Kungkrabaen Bay Natural Study center is located in the mangrove forest proper. A tourist boardwalk that winds through the forest offers relatively easy access to collection sites. Specimens were often located just beneath the sandy sediment surface, often close to the pneumatophores of *Sonneratia alba* and less commonly in small open patches of moist sand. Specimens of *Chicoreus capucinus* were relatively common on the sediment surface and drilled valves of *L. cf. corrugata* were occasionally found on the sediment surface.

**Remnant population.** – Over some spans of the bay at low tide and usually closer to the mangrove forest, large

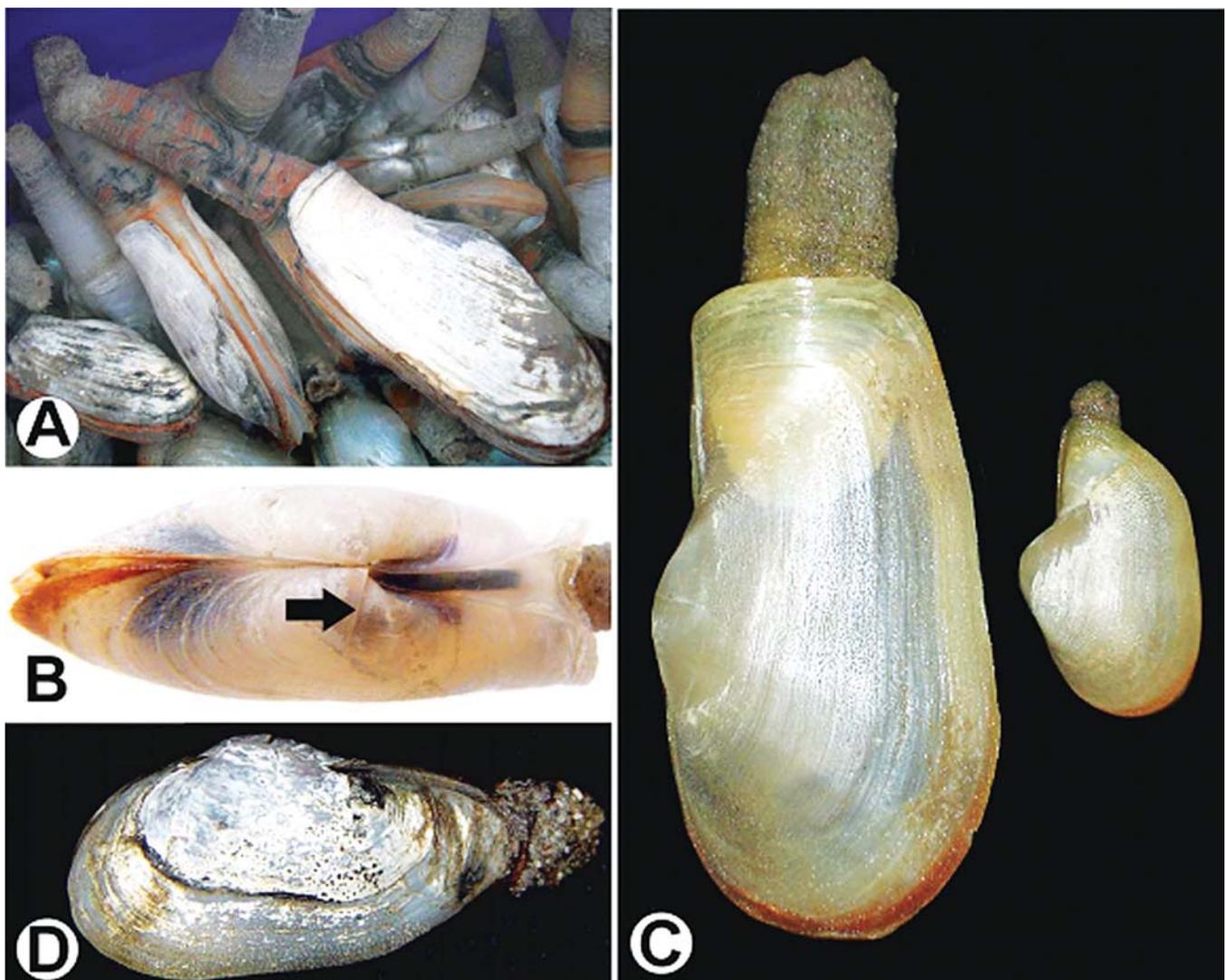


Fig. 2. A, Living specimens of *Laternula truncata* from Kungkrabaen Bay; B, The umbonal slit (black arrow) in the valves of *L. truncata*; C, Ethanol preserved *L. truncata* (left, 58 mm shell length) and *L. cf. corrugata* (23 mm shell length); D, Ethanol preserved *L. cf. corrugata* (19 mm shell length) showing typical shell erosion.

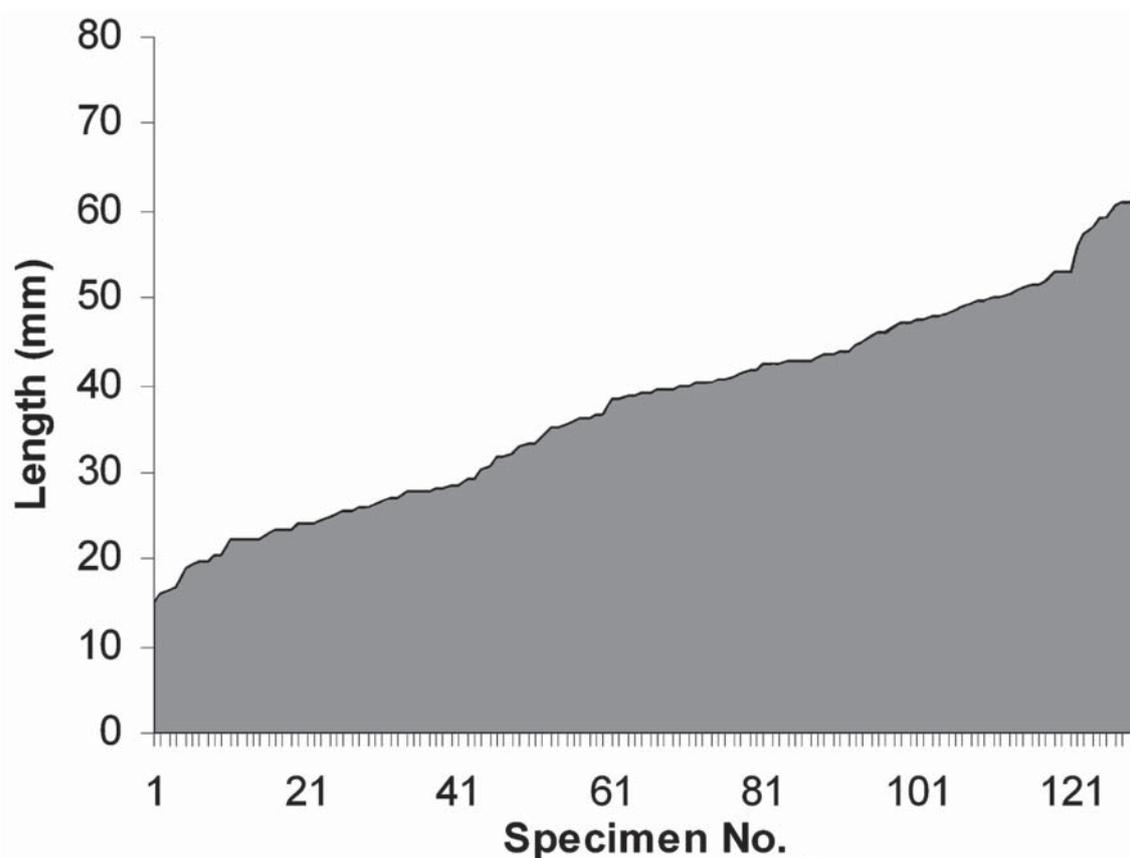


Fig. 3. Cohort distribution by maximum shell length of *Laterula truncata* collected from Kungkrabaen Bay. These specimens represent all living *L. truncata* collected from all quadrats (including samples taken for sediment analyses) along the transect.

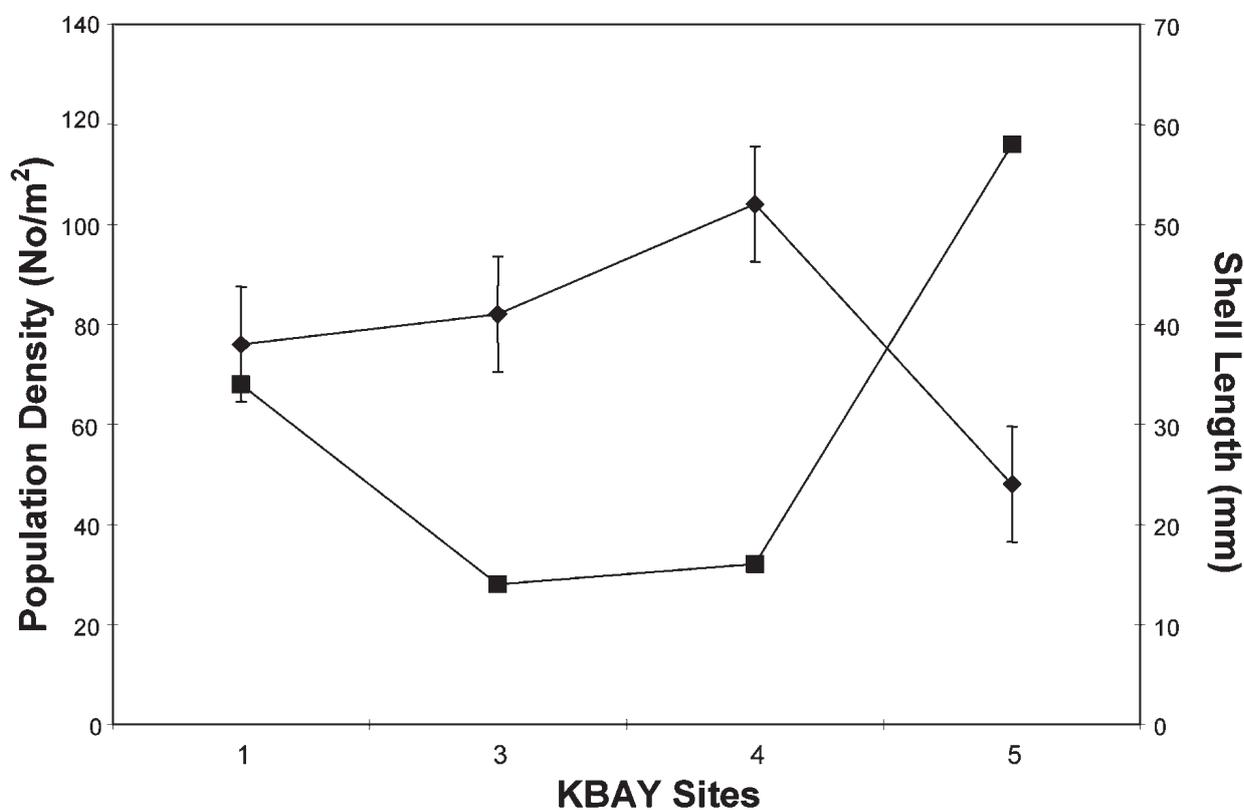


Fig. 4. Comparison between population density and average shell length (SL) for *Laterula truncata* from individual transect sites. SL with Standard Error indicated. Site KBAY2 had no specimens of *L. truncata* and is thus absent from this Fig.. Smallest specimens were found in the highest concentrations (site 5). Solid diamonds = average SL (mm); solid squares number of *L. truncata* m<sup>-2</sup>. SL ranged 22.4–60.8 mm at KBAY1, 24.2–58.0 mm at KBAY3, 51.5–54.2 mm at KBAY4 and 19.7–57.2 mm at KBAY5.

historic populations of *Laternula truncata*, with valves in life position, were exposed. These mostly buried paired valves had approximately the anteriormost 20% portion of the shell protruding above the sand flat surface. The valves usually were sun-bleached white and were not easily removed from their buried positions. These valves, although brittle, remained mostly unbroken prior to removal from the dried sediments. The number of paired valves, in part, likely reflected the fairly large and relatively stable but locally ephemeral populations of *L. truncata* in Kungkrabaen Bay. Almost no small specimens of these relic valves were evident. These sites had a sandy substratum often heavily perforated by fiddler crab burrows. No living specimens of *L. truncata* were found among these remnant shells.

**Sediments and *Laternula truncata* distribution.** – Sediments in Kungkrabaen Bay along our transect were dominated by fine sand and silt/clay (Figs. 5–6) often with a greater proportion of finer sediments in the lower 5–15 cm sampled. The latter probably reflects the lower erosion capacity and higher adhesive qualities of some finer sediments. Quadrat sites KBAY1, KBAY4, and KBAY5 had proportionally less silt/clay in surface sediments than sites KBAY2 and KBAY3. Similarly, site KBAY5 had the lowest silt/clay proportion in the 5–15 cm depth samples, whereas sites KBAY 2 and KBAY3 had the highest silt/clay levels. Over 50% of the top 5 cm of sediments at sites KBAY1 and KBAY5 were fine sands. Approximately 40% and 50% of the sediments from the 5–15 cm depth cores for sites KBAY1 and KBAY5, respectively, were also composed of fine sands. The low energetics of Kungkrabaen Bay are reflected in the low proportion of larger granules and coarse- and medium-sized sand particles.

Organic content of Kungkrabaen Bay sediments along the transect was relatively low, averaging 1.0% (Fig. 7). The lowest levels of sediment organics were found at KBAY1 and KBAY5, averaging less than 1.0%. An exceptionally high organic content was found in the 5–15 cm depth sample at KBAY3, however, this is a suspected localised artefact, most likely created by a compact organic contaminant. For all sites except KBAY5, the deeper sediment sample averaged lower organic content than the surface 5 cm.

The highest concentrations of *Laternula truncata* along the transect were found within quadrats 1 and 5 (Fig. 8). These quadrats also had the lowest percent sediment organics, lowest proportion of silt/clay component and the highest proportion of fine sands. Sites KBAY2, KBAY3, and KBAY4, all with zero to few specimens of *L. truncata*, had higher levels of sediment organics and a lower proportion of fine sands.

**Biodiversity.** – Over 40 species of infaunal macroinvertebrates were found along the transect in Kungkrabaen Bay. In general, overall biodiversity declined as distance increased away from the first mangrove hummock (KBAY1), which was located closer to the primary mangrove forest than the rest of the transect quadrats. There was a linear decrease in the Shannon-Wiener Diversity Index between KBAY1 and KBAY5. As diversity decreased, dominance increased and

evenness decreased (Table 1, Fig. 9). Thus, site KBAY5, close to an isolated hummock, had high dominance (the venerid bivalve *Gafrarium tumidum* Röding, 1798, and the capitellid polychaete *Dasybranchus lumbricoides* Grube, 1878, were abundant) and low evenness (Table 1). Site KBAY1 was fairly even (Index = 0.893) and had relatively low dominance although *G. tumidum* was also common in that quadrat along with the penaeid shrimp *Metapenaeus lysianassa* (De Man, 1888). The highest concentrations of *Laternula truncata* were found within these two hummock sites and so there appears to be no strong relationship between the abundance of this bivalve and overall dominance and evenness. *Gafrarium tumidum* also was dominant in quadrat KBAY2, a site totally lacking *L. truncata*. The relatively small bivalve *Glauconome chinensis* (Gray, 1828) was exceptionally abundant entangled in the muddy sands around mangrove roots at KBAY5 and buried in the sediments to 5 cm deep at KBAY4. The venerid *Anomalocardia squamosa* (Linnaeus, 1758) dominated at KBAY2, the only quadrat sampled that lacked *L. truncata*. The capitellid *D. lumbricoides* was common along most of the quadrats as was the onuphid polychaete *Onuphis branchiata* Treadwell, 1931, a maldanid polychaete (*Isocirrus* sp.), and the large eunicid *Marphysa sanguinea* (Montagu, 1813). In no quadrat along the transect was *L. truncata* the singlemost dominant organism.

**Burrowing behaviour.** – Smaller specimens of *Laternula truncata*, when removed from sediment, more readily probed the sediment with their foot in efforts to regain a foothold and reburrow (Fig. 10). Of the 58 specimens tested, 22 reburied. These averaged 30.77 mm L. The remaining 36 clams did not fully reburrow. The latter animals averaged 43.56 mm L. No specimens larger than 47 mm were able to successfully reburrow in 24 h of observation although many specimens smaller than this size also failed to reburrow. With one exception, all specimens between 15 and 30 mm L reburied within 24 h.

Burrowing behaviour proper is straightforward. After lying on one valve, sometimes for an extended period of time, the foot emerges and immediately probes the sediment, toe down. After some additional time, the foot is thrust into the sediment and in a series of short and slow moves the valves are brought upright. It can then take considerable time again to gain full access into the sediment. Some specimens arched their siphons over to contact the sediment surface and so lifted the shell. This type of behaviour was occasionally redundant and often included rapid adduction of the valves, jetting the bivalve considerable distances within the aquarium. Similar behaviour was also noted in *L. cf. corrugata*.

On the average, smaller clams burrowed more quickly than larger clams but still took up to 2 h to completely burrow beneath the sediment surface. Depth of burial was usually related to siphonal length, which in turn was reflected by the depth of the pallial sinus. In this population of *Laternula truncata*, the pallial sinus averaged 38.5% of the shell length. In *L. cf. corrugata* the pallial sinus averaged 28.7% of the shell length.

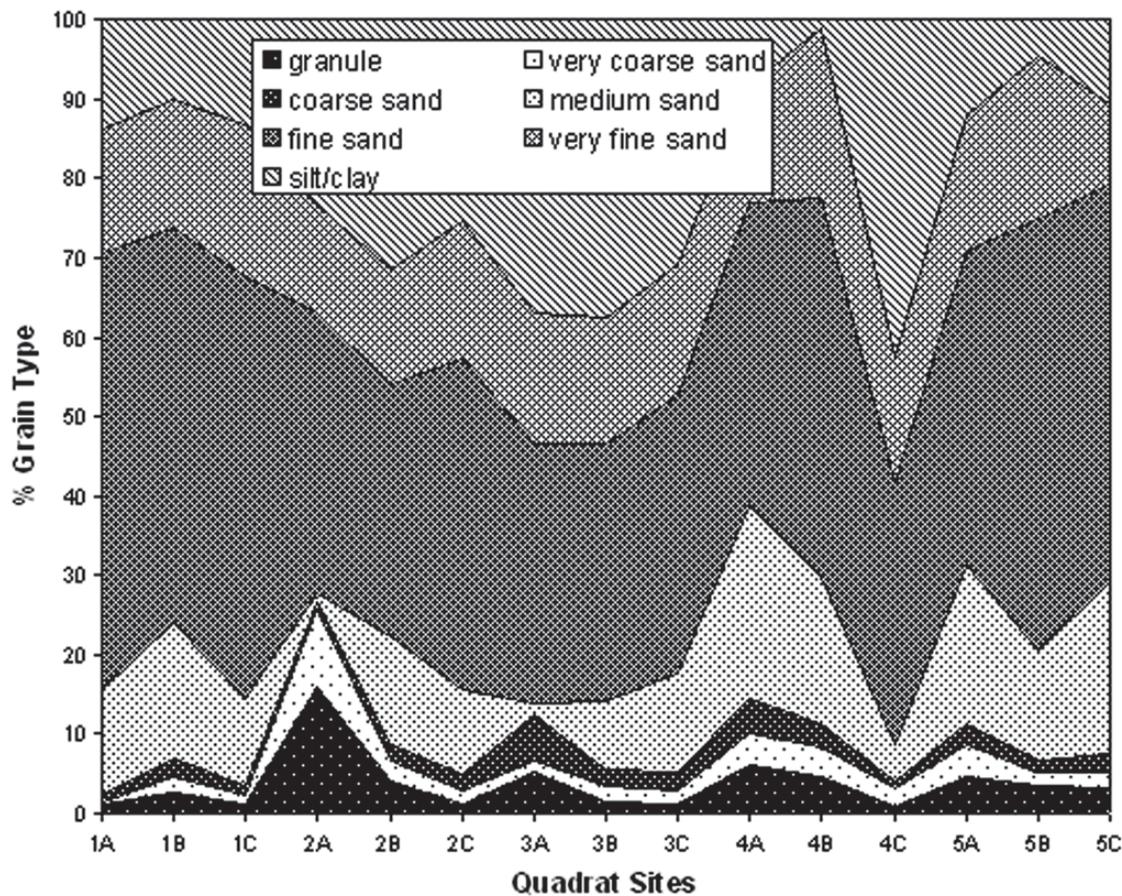


Fig. 5. Granulometric comparisons of top (0-5 cm) core depths of sediments from transect sites in Kungkrabaen Bay.

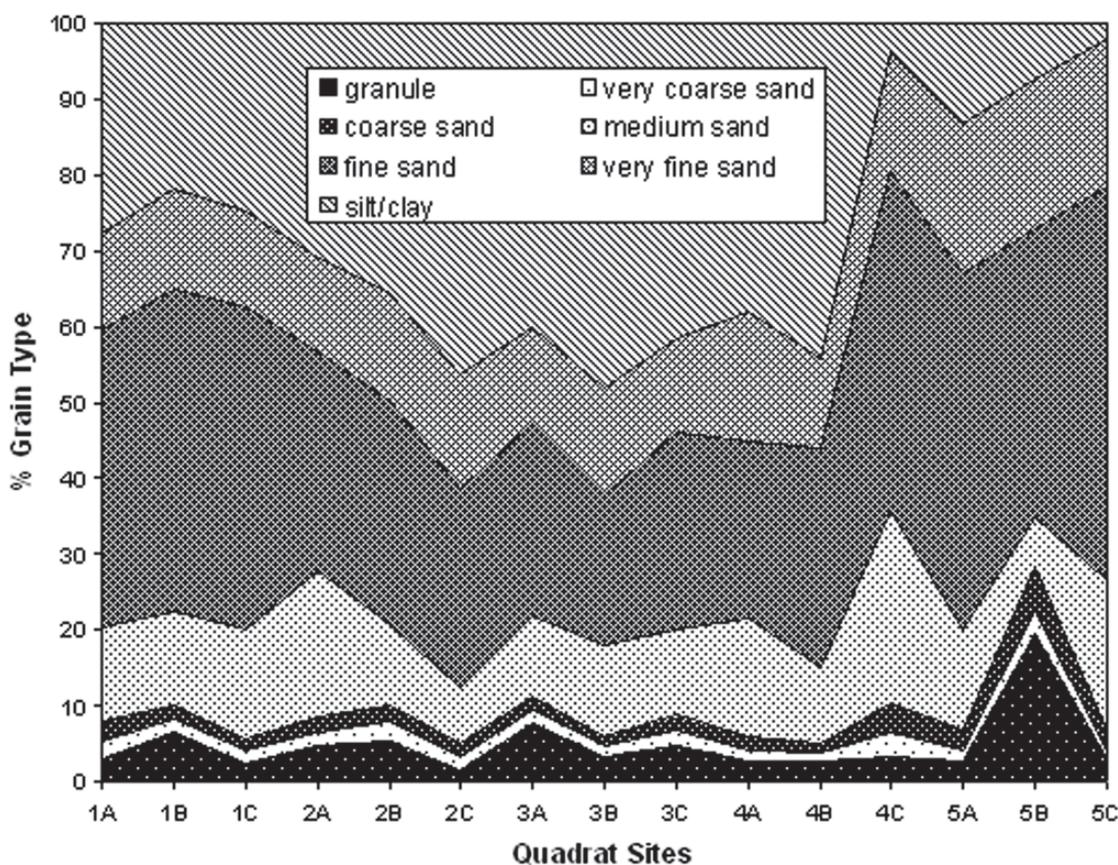


Fig. 6. Granulometric comparisons of lower (5-15 cm) core depths of sediments from transect sites in Kungkrabaen Bay.

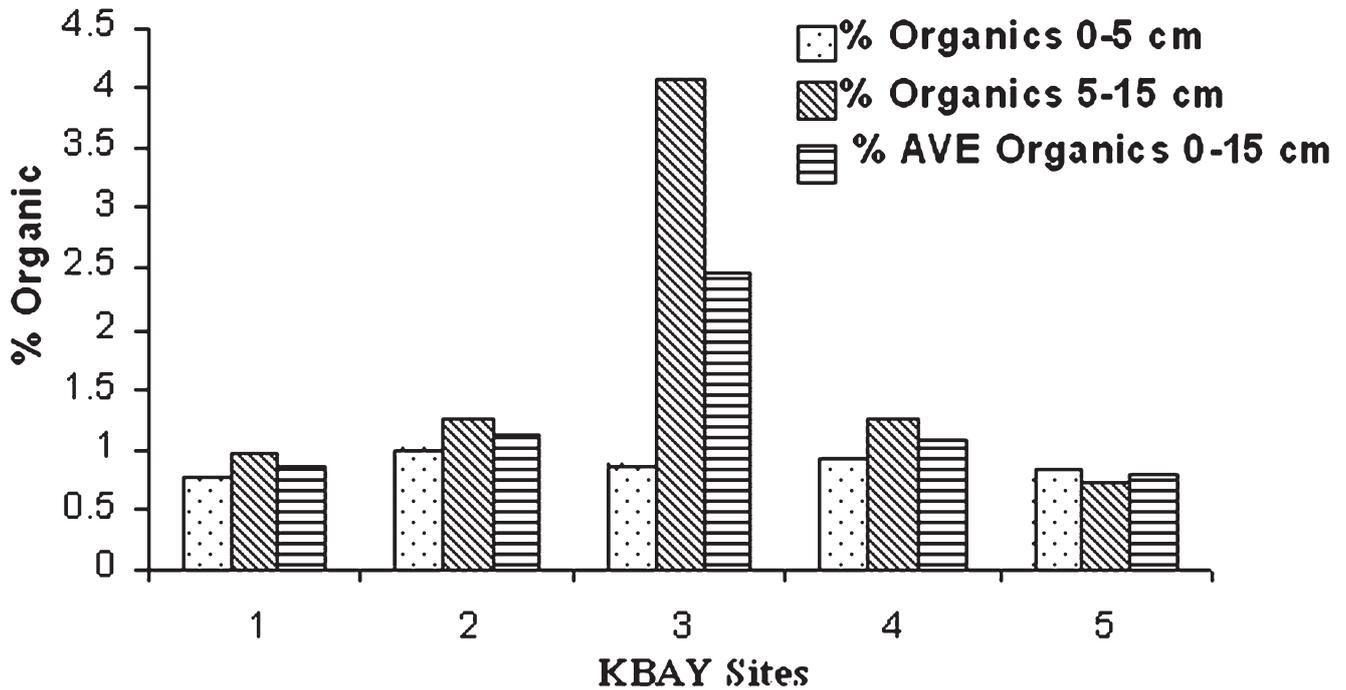


Fig. 7. Comparison of organic sediment component in Kungkrabaen Bay *Laternula truncata* transect quadrats separated into upper (0–5 cm) and lower (5–10 cm) cores. The exceptionally high organic content in the site KBAY3 5–15 cm core depth sample is a presumed artefact.

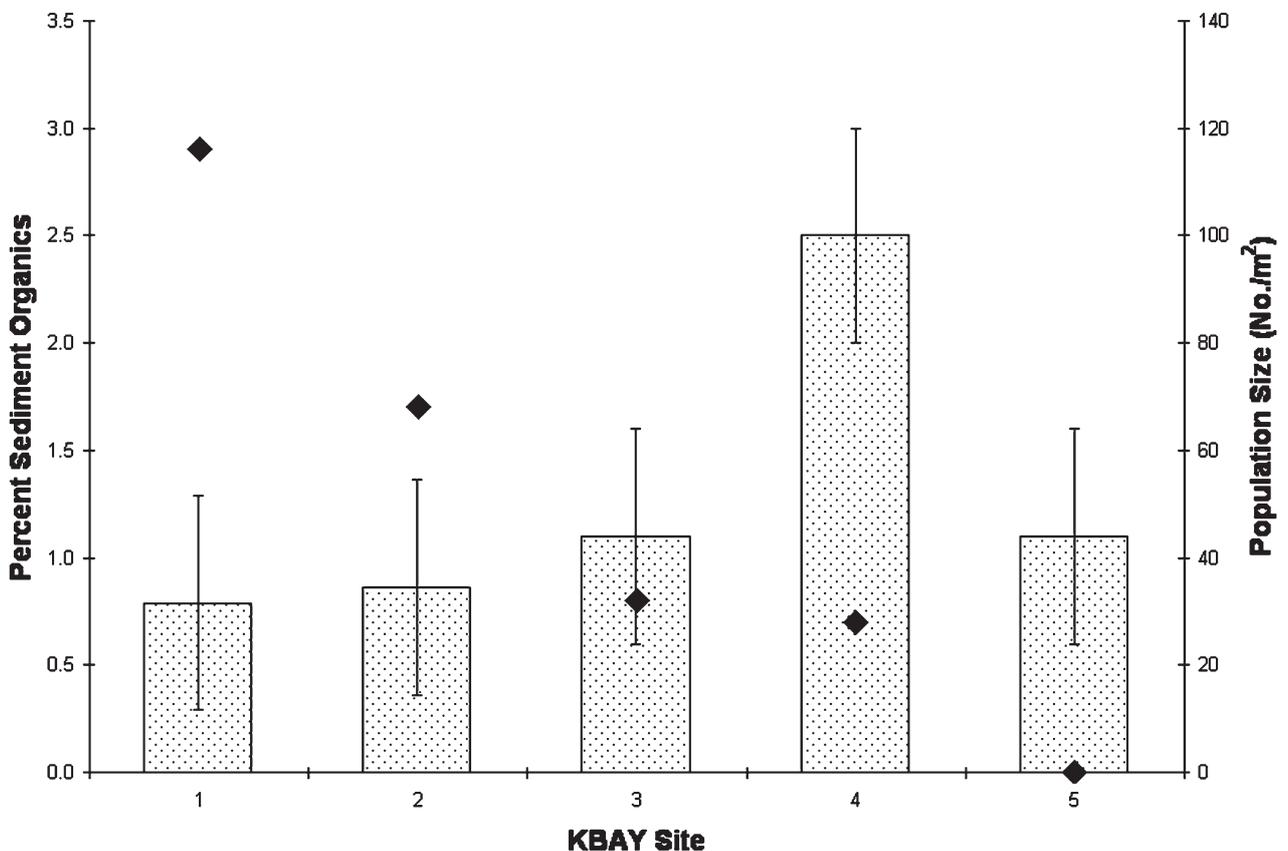


Fig. 8. Kungkrabaen Bay sediment organics along the *Laternula truncata* transect compared to population density in each quadrat site. The arrangement of sites is ordered by decreasing number of *L. truncata*. There is a subtle trend of decreasing number of bivalves as organic content in sediment increases. Solid diamonds = numbers of *L. truncata*/m<sup>2</sup>; stippled bars = percent sediment organic in quadrats.

Table 1. Comparison of sediment organics (top 5 cm, next 10 cm depth), number of *Laternula truncata* specimens per square meter, average size and total numbers, total number of infaunal invertebrate macrofaunal taxa, Shannon-Wiener (S-W) Diversity Index, Simpson Index, and dominant quadrat species for *Laternula truncata* transect sites (KBAY1-KBAY5).

Station	% sediment organics (0-5 cm)	% sediment organics (5-15 cm)	% total organics	n m <sup>-2</sup>	size (L) (n)	No. spp.	S-W Index	Simpson Index	Dominant species
KBAY1	0.76036	0.956	0.8581	68	36.4 (13)	23	2.570	0.893	<i>Gafrarium tumidum</i> , <i>Metapanaeus lysianassa</i>
KBAY2	1.00328	1.251	1.1274	0	0	14	2.208	0.818	<i>G. tumidum</i> , <i>Anomalocardia squamosa</i> , <i>Dasybranchus lumbricoides</i>
KBAY3	0.86776	4.069	2.4687	28	42.6 (4)	12	1.876	0.765	<i>D. lumbricoides</i> , <i>L. truncata</i>
KBAY4	0.92538	1.244	1.0846	32	51.6 (3)	19	1.480	0.594	<i>Glauconome chinensis</i> , <i>Cerithidea cingulata</i> (Gmelin, 1791), <i>Pillucina vietnamica</i> Zorina, 1978
KBAY5	0.84521	0.740	0.7928	116	27.1 (14)	23	1.215	0.461	<i>G. chinensis</i> , <i>L. truncata</i> , <i>D. lumbricoides</i>

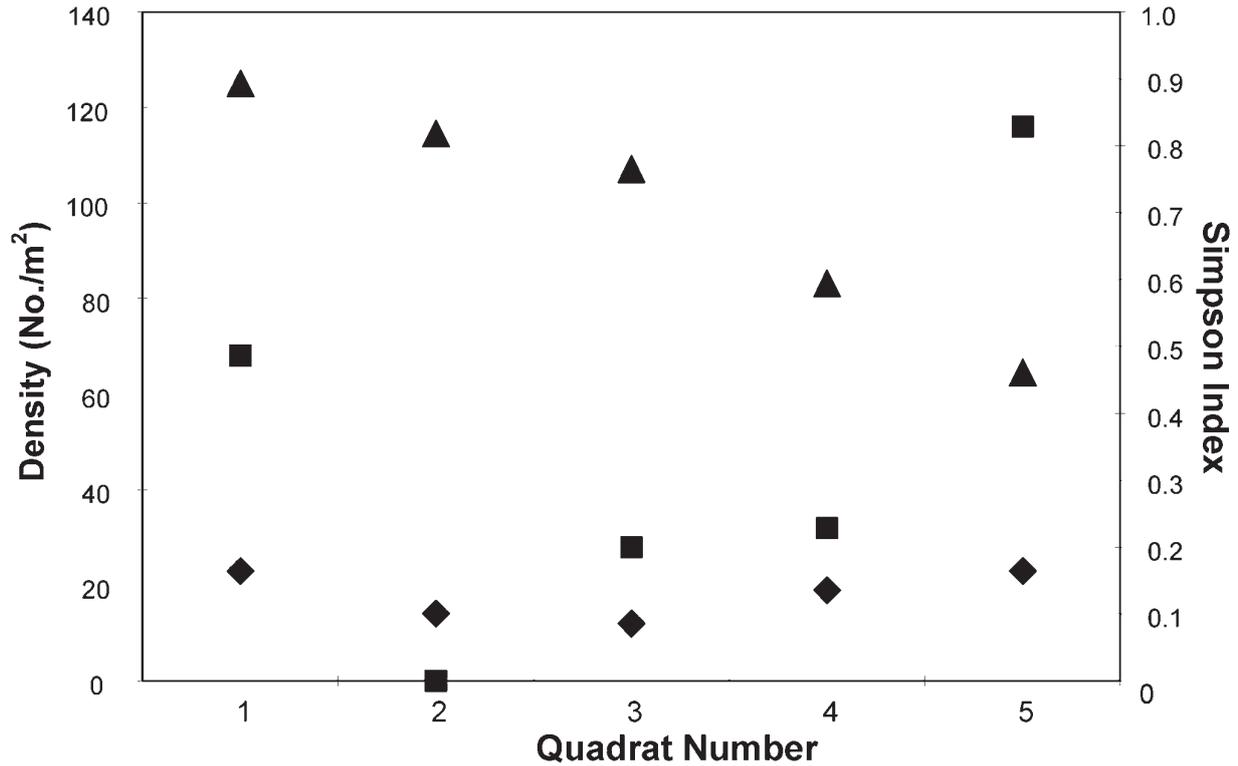


Fig. 9. Overall number of species per transect quadrat in Kungkrabaen Bay plotted against evenness (Simpson Index) and total number of specimens of *Laternula truncata* m<sup>-2</sup>. There is a weak correlation between increasing diversity and a larger population of *L. truncata*. There is an obvious decline in evenness, and hence a rise in dominance, moving from quadrat 1 to quadrat 5. Solid squares = number of specimens of *L. truncata* m<sup>-2</sup>; solid diamonds = total number of infaunal macroinvertebrate species per quadrat sampled (delineated on primary (left) Y-axis as number per quadrat); solid triangles represent Simpson Index.

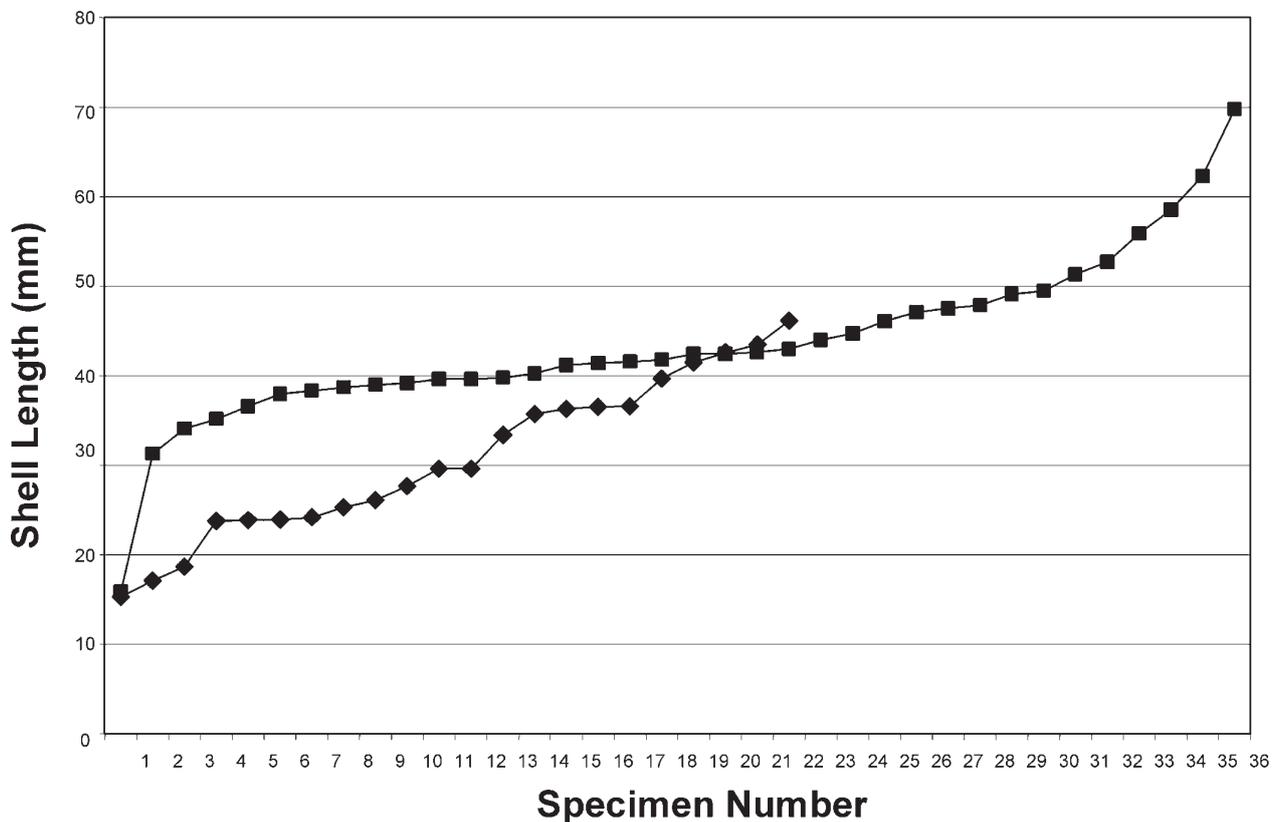


Fig. 10. Comparative size (shell length) related to burrowing success in specimens of *Laternula truncata*. Specimens larger than approximately 45 mm did not reburrow. Solid diamonds represent clams that reburrowed; solid squares represent clams that did not reburrow.

Table 2. Shell, habitat, and behavioural differences between *Laternula truncata* and *L. cf. corrugata* found in Kungkrabaen Bay.

<i>Laternula truncata</i>	<i>Laternula cf. corrugata</i>
Rounded to truncate posterior shell margin; uniform shell form	Oblique to roundly pointed posterior shell margin, sometimes upturned; shell often irregular in form
Shell not eroded (in live specimens)	Shell in living specimens often eroded, white blotches
Maximum size to about 75 mm	Maximum size to about 35 mm
Saddle-shaped lithodesma	No lithodesma
Umbonal slit approximately 36% shell height	Umbonal slit approximately 30% shell height
Pallial sinus approximately 38% shell length	Pallial sinus approximately 29% shell length
Buried deep, 5 or usually more cm; deep pallial sinus	Near surface, siphons often close to substratum surface; relatively shallow pallial sinus
Muddy sand to fine sand areas of relatively open mangrove flat' seaward of mangrove, usually closer to hummocks	Sandy areas within mangrove forest proper
Among mangrove rootlets, pneumatophores; primarily <i>Avicennia marina</i> and <i>A. alba</i>	Among pneumatophores, occasionally among rootlets; primarily <i>Sonneratia alba</i>
None found with bore holes	Some with bore holes
Slow burrower; largest specimens do not reburrow	Rapid burrower, all sizes
Foot rarely seen probing	Active foot, quickly probes
Relatively common	Less common

**Comparisons between laternulid species.** – *Laternula truncata* and *L. cf. corrugata* were found in distinct, nonoverlapping habitats in Kungkrabaen Bay. *Laternula truncata* was found deeply burrowed in finer sediments of the open mangrove flat or commonly near mangrove hummocks composed primarily of *Avicennia marina* and *A. alba*; *L. cf. corrugata* was found near the surface in sandy, more compacted sediments in more protected areas of the mangrove forest dominated by *Sonneratia alba* (i.e., deeper into the forested area of the mangal as opposed to open areas with “islands” of mangrove trees). Table 2 highlights some of the most obvious differences between these two taxa. Aside from obvious size and meristic differences in shell characters, the shells of *L. truncata* were rarely eroded as they were in *L. cf. corrugata*. Of structural and probably taxonomic significance, *L. truncata* possesses a well-developed saddle-shaped lithodesma; no lithodesma was found in *L. cf. corrugata*. Specimens of *L. cf. corrugata* were also more active and, upon extraction from the sediment, relatively quickly reburied. No boreholes were found in any shells of *L. truncata*; some shells of *L. cf. corrugata* were found with boreholes penetrating the valves. These boreholes, sometimes circular, oval, or irregular in outline, were often found along the middle and posterior portions of the valves. We have demonstrated in unpublished experiments that the muricid snail *Chicoreus capucinus* will readily bore into and consume *L. cf. corrugata*. Although both *L. truncata* and *L. cf. corrugata* possess an umbonal slit (Fig. 6) in their shells, the slit is proportionally longer in *L. truncata*, reflecting 36% of the shell height versus 30% in *L. cf. corrugata*.

## DISCUSSION

Other than the polar bivalve *Laternula elliptica*, little is known of the ecology and behaviour of most laternulids.

In Hong Kong, Morton (1976) found *L. truncata* located on the seaward side of mangrove forests. In Kungkrabaen Bay, southeastern Thailand, we found *L. truncata* and *L. cf. corrugata* in distinct, nonoverlapping habitats. In the open mangrove flat, *L. truncata* resides close to and among the rootlets of *Avicennia alba* and *A. marina*. *Laternula cf. corrugata*, on the other hand, is found deeper in the mangrove forest, often associated with *Sonneratia alba*. In addition, whereas the open flat area often showed large numbers of empty shells of *L. truncata* in life positions, no such remnant populations of *L. cf. corrugata* were found in their more protected habitat. The smaller, less deeply buried *L. cf. corrugata* were found in smaller numbers and, when empty valves were found, they sometimes were clearly drilled. The shallow position of *L. cf. corrugata*, boreholes in empty valves in the field, and confirmation of predation by a drilling muricid gastropod (unpubl. data), could offer evidence of shorter lived and more fragile populations than those comprising the deeper burrowing, larger sized, and more densely populated *L. truncata*. The large numbers of vacant shells of *L. truncata*, so evident in this shallow bay, suggests fully grown specimens in a population with little recent recruitment (no small valves were found). In turn, the stability of these life-positioned specimens, with about 20% shell exposed, suggests a quiescent environment with low energy tides and thus little erosion and minimal, if any, short-term entrainment. Or in turn, this could suggest selective displacement during tidal or storm activity, entraining only the smaller, more easily eroded valves. Periodic monsoon activity has been documented to entrain a large number of bivalves of various species in Kungkrabaen Bay (N. Kakhai, pers. obs.). K. Chalermwat (unpubl. data) noted an extensive mat of dense, filamentous green algae covering our transect sites KBAY4 and KBAY5 in May 2006. All bivalves under this mat were recently dead, including the previously dominant *Glauconome chinensis* as well as all

specimens of *Laternula truncata*. During July 2006, the mat had dissipated and there were apparent signs of recovery but with noticeably smaller macroinvertebrate populations (K. Chalermwat, pers. obs.). Although we found a continuum of sizes in our samples from late summer 2005, it is also true that we found no specimens smaller than approximately 15 mm L. Cumulatively, this suggests either a loss of the smallest size classes from the flat (mortality or entrainment), failed recent recruitment(s), or recruitment from outside of the transect area. Microscopic examination of gametes showed that even the smallest specimens in our collections were reproductively mature at time of sampling. A longer temporal sampling program is needed to answer questions concerning recruitment, the lack of evident cohort sizes, and absence of specimens less than 15 mm L in our samples in the Bay.

Habitat transition in the open mangrove flat, especially in light of heavy rains and monsoons, can happen quickly. The mangrove hummocks, site of the densest concentrations of *Laternula truncata*, offer some degree of stability among the rootlets and pneumatophores in the otherwise open sand flat. The habitat deeper in the mangal offers ready protection from storms and erosion for the shallowly buried *L. cf. corrugata*. The shallow burial depth for this bivalve accords it ready access to overlying water during high tides. In an apparent evolutionary trade-off, it also makes this bivalve more readily available to surface predators such as *Chicoreus capucinus*.

Although specimens of *Chicoreus capucinus* were found both in the forested mangal and the associated sand flat, we only found field evidence of borings in *Laternula cf. corrugata*. No specimens of *L. truncata* were found with boreholes. We confirmed (unpubl. data) in a very small series of experiments, that *C. capucinus* would drill and consume *L. cf. corrugata* in less than 12 h; no similar drilling was seen with *L. truncata* within 24 h. Harper & Peck (2003) found that the muricid *Trophon longstaffi* E. A. Smith, 1907, was able to drill and consume specimens of *L. elliptica* but took 29 d to attack and consume the bivalve. In Antarctica, *L. elliptica* is consumed by seastars, buccinid gastropods and fish (Arnaud, 1973; Dayton et al., 1974; Zamorano et al., 1986). Aside from siphon nipping by fish, the presumption is that these polar bivalves were exposed to predation after being exhumed by iceberg scouring, thus leaving them fully exposed to predators. The higher degree of erosion of the shell of specimens of *L. cf. corrugata* could offer *C. capucinus* thinner “target” areas for drilling. Ultimately, predation by this muricid on Thailand mangrove flat specimens of *L. truncata* cannot be discounted despite the lack of borehole evidence. Wells et al. (2001) found that *C. capucinus* consumed *Glaucanome chinensis* by inserting its proboscis into the siphonal apertures. More importantly, Tan & Oh (2002) reported significant predation of both *L. truncata* and *L. cf. boschasina* (Valenciennes in Reeve, 1863) from a Singapore mangal. In these cases only half of all attacks on *L. truncata* were by drilling (80% for *L. boschasina*).

*Laternula cf. corrugata* has been reported in concentrations to 150 m<sup>-2</sup> from soft muds in Pattani Bay near the mouth of the Yaring River in Thailand (Swennen et al., 2001). No other references to this species’ ecology have been found. In the case of the Kungkrabaen Bay population, the sediment was sandy and associated with *Sonneratia alba* but additional information on the ecology of this species awaits further study. The only other such association has been reported by Athalye & Gokhale (1998) who found specimens of *L. navicula* (a possible synonym of *L. cf. corrugata*) associated with *Avicennia marina* among mangals of India.

The study sites on the open flat with less silt/clay in the surface substratum had the densest populations of *Laternula truncata*. The surface silt/clay could be a recent depositional event and thus reflect a prohibitive surface to newly-settling, filter-feeding bivalve larvae and juveniles. The dominance of finer sand in turn could be optimal for burrow construction and/or could be of sufficient porosity to allow the sediment to remain aerobic around the infaunal bivalve. In total, the relatively aerobic sediment, lower organics, and ability to burrow/penetrate the fine sand substratum, could be a requisite sedimentary habitat for *L. truncata*. Periodic deposition of silt/clay into the upper substratum, on the other hand, could inhibit initial larval settlement. This combination could explain the lack of evident size cohorts as well as the dearth of the smallest sized specimens. Except for what we believe to be an organic artifact in KBAY3, quadrat KBAY2 had the highest organic content along the transect and was totally void of specimens of *L. truncata*.

*Avicennia alba* is often considered a pioneer mangal species found along the shore’s edge (Piyakarnchana, 1980) and as such is often part of mangrove hummocks dotting Kungkrabaen Bay. The hummocks, as noted, offer some protection during turbulent tides or storms and as such we might hypothesise that they would also be home to the highest species diversity and/or abundance. Similarly we might speculate that diversity and abundance is highest in areas with complex topography, such mangrove forests. It would thus be reasonable to assume that macroinvertebrate diversity and/or abundance would decrease with distance from mangals into the sand flat proper. Indeed, Angsupanich & Aksornkoae (1996) found only 33 species of macroinvertebrates, from both wet and dry seasons combined, in Ban Don Bay in Suratthani Province, Thailand, but with highest diversity and abundance closer to mangroves. Compare this to our single transect in August retrieving over 40 species. In our study we also found a decrease in the Shannon-Wiener Diversity Index as we moved from our original mangrove hummock quadrat (KBAY1) out slightly from shore towards our terminal hummock (KBAY5). These two hummocks showed very similar sediment types and indeed showed the highest number of species (both with 23 species). However, there was a linear trend from our origin mangrove hummock to the terminal hummock, with Shannon-Wiener Diversity Indices dropping at each station as we moved from hummock to open sand flat and back to hummock with the two hummocks showing indices that dropped from 2.57 to 1.215. Along

the transect, we saw a linear drop in the Simpson Index, indicating a drop in evenness. Specifically, high numbers of *Glauconome chinensis* and *Laternula truncata* drove down evenness and diluted the diversity index. The lowest number of species (12) was found at the transect midpoint (KBAY3). This station also was dominated by *Dasybranchus lumbricoides* and was the farthest distance from either hummock. There was no clear relationship between the presence of *L. truncata* and overall evenness or diversity. Specimens of *L. truncata* were present at KBAY3 (which held the smallest number of total infaunal taxa) and in fact were absent only at KBAY2 where *Gafrarium tumidum* dominated; *G. tumidum* also dominated at KBAY1 where *L. truncata* was common. Biodiversity in mangroves remains understudied and poorly understood. Macintosh et al. (2001) suggested that mangal trees and other plants increase habitat complexity and in turn biodiversity. Similarly, Kathiresan & Bingham (2001) reviewed studies on molluscan diversity, reporting that diversity, at least in some mangals, increased nearer to the high tide zone. On the other hand, Dittmann (2001, 2002) found that diversity in mangals proper was lower than in associated mudflats.

The overall and relative abundances of *Laternula truncata* are at least in part related to rates of predation, which in turn are related to prey accessibility. How accessible an infaunal bivalve is to a surface or near-surface dwelling predator is related to depth of burial, rate of burial, and/or the mechanical ability of a predator to “reach” the prey. There remains contradictory information in the literature about the ability of laternulid bivalves to rebury if excavated from their burrows. Morton (1976: 270) noted that “as adults they possess a vestigial foot and evidently remain immobile in a previously established burrow in a stable substratum.” As recently as 2004, Peck et al. (2004: 357) remarked that although *Laternula elliptica* does reburrow, it was “unexpected” because “other members of the Laternulidae do not burrow.” This misinformation reflects observations by Runnegar (1972), Morton (1973), Savazzi (1990), and Berkman et al. (1991), and suggests earlier observations of only large, more lethargic specimens. Savazzi (1990) reported that *L. spengleri* (Gmelin, 1791) from the Philippines that were 32–63 mm L, would not reburrow. Sufficient evidence exists to discount reports that laternulids are unable to reburrow. Prior to Peck et al. (2004), who reported the “unexpected”, albeit slow, reburrowing behaviour of *L. elliptica*, Zamorano et al. (1986) found that in a population of *L. elliptica* with a density of 40 individuals per m<sup>2</sup> that were removed from the sediment, 30% successfully reburied within 24 hours. After 23 days, 60% of the clams had reburied. Urban & Silva (1995) reported a 48% successful reburial rate of this laternulid in 48 hours. The latter was from a population of only 15 individuals per m<sup>2</sup>, giving some indication that density could play a role in rate of reburial. Peck et al. (2004) found that smaller specimens of *L. elliptica* burrowed much faster than larger specimens, with those 30 mm long or less reburrowing in less than 30 min and those in the 80–90 mm range requiring more than 18 hours. Most recently, Morley et al. (2007) found that *L. truncata* and *L. boschasina* from Singapore were able to rebury themselves

with 80% (20 of 25, approx. 17–46 mm L) and 63% (15 of 24, approx. 11–29 mm L) reburrowed within 24 hours. In our reburial experiments, 37% of all (15–70 mm long) specimens of *L. truncata* had reburied within 24 hours. In the same time frame, 50% of the specimens less than 45 mm L had reburied. Morley et al. (2007) showed a direct correlation in *L. truncata* between shell length and duration to full burial. Based on qualitative field observations and depth of the pallial sinus, we assume smaller laternulids are found closer to the sediment surface, making them more accessible to predators and more vulnerable to hydrodynamic exhumation from within the substratum. Hence, faster reburial offers a possible survival edge in younger specimens.

*Laternula elliptica* is capable of burrowing as deeply as 0.5 m (Zamorano et al., 1986). The latter authors divided the burrowing cycle into three phases: (1) foot extension and penetration into the sediment, (2) foot tip dilation and anchorage, and (3) contraction of the pedal retractors to pull the shell into the sediment. This simple process was seen in *L. truncata* and *L. cf. corrugata* as well (also see Morley et al., 2007). Zamorano et al. (1986) also reported unusual siphonal activity associated with locomotion and burial. This process consisted of levering the tips of the siphons against the substratum to lift the shell and then “looping” the siphons in a process that allows shell rotation while forcing water from the exhalent siphon to create jetting. Zamorano et al. (1986) suggested that this method was used by *L. elliptica* to move the bivalve to another favorable position for reburying after they were excavated by iceberg exhumation. Peck et al. (2004: 365) wrote “Other *Laternula* species are not known to rebury if removed from the sediment, and the behaviours described here are rare or absent in related species, and generally amongst the Bivalvia.” Morley et al. (2007) described this behaviour in *L. truncata*, confirmed in the current work, as a possible assist in initial foot anchorage prior to burrowing. Thus, the behaviour is probably engrained in the genus and functions across the taxon allowing accidentally exhumed individuals to either move away from the source of disruption and possibly to a more secure position where at least smaller specimens are able to rebury and/or in abetting early stages of reburial.

Taxonomy of the laternulids is in need of revision with a serious approach to a unifying character set still wanting. The shell of laternulid bivalves offers an interesting blend of recent and ancient characters. The aragonitic prismatic shell is characteristic of anomalodesmatan, in particular pholadomyoidan, bivalves and is recognised as a primitive shell microstructure dating back to the Ordovician (Cox et al., 1969; Carter, 1980; Prezant, 1981). Morton (1976) examined the shell and hinge structures of the Laternulidae, citing important differences in shell thickness, lithodesma form, shell proportions, and depth of the pallial sinus. He speculated that the variations found are related to functionality and geographic variation. For instance, more fully tropical laternulids [e. g. *Laternula anserifera* (Spengler, 1793), *L. boschasina*] seem to have thinner shells than those whose distributions range into more temperate zones (e. g., *L. elliptica*, *L. navicula*, *L. truncata*). In addition, he described

the shells of the tropical laternulids as being less cylindrical in cross section and this in turn could be related to burrowing habits. According to Morton's measurements, *L. truncata* from a seaward side of a mangrove forest in Hong Kong is relatively long and "transversely rounded" as opposed to *L. elliptica*, which he considered comparatively "short" and "transversely elliptical." The tapered cross-section presented by *L. truncata* offers less resistance to burrowing. Depth of burial is also related to pallial sinus depth (specifically, relative to shell length). Morton (1976) found *L. truncata* to have a pallial sinus to shell length ratio of 0.39. Specimens from Kungkrabaen Bay had a ratio of 0.385, in line with those measured by Morton indicating little intraspecific variation in this character and most likely similar burrowing depths. *Laternula* cf. *corrugata* from Kungkrabaen Bay had a ratio of 0.287 (i. e. 28.7% shell length) confirming a comparatively shallower burrowing depth than *L. truncata*.

The lithodesma is a structure common to the hinge of many anomalodesmatans but is not ubiquitous within the genus *Laternula*. The lithodesma is present in only some species of *Laternula*; for example, it is absent in *L. cf. corrugata* but present in *L. truncata*. In Lyonsiid bivalves it is an elongated, rectangular plate (Prezant & Carriker, 1983) whereas in laternulids, when present, it is boomerang-shaped. The function remains speculative but it is assumed to play a role in stabilization of the ligament, essentially dividing it into two effective compressive units in widening ligaments (Young & Morton, 1980). Morton (1976) also assumed that the lithodesma in laternulids helps align the valves in the absence of hinge teeth. The lack of a lithodesma in *L. cf. corrugata* could reflect its relatively smaller size, however the proposed function of the lithodesma would not necessarily account for the lack of lithodesmas in the relatively large *L. anatina* and *L. elliptica*. The mid-sized *L. erythraea* Morris & Morris, 1993, has a broadly V-shaped lithodesma. *Laternula anatina*, according to Morton (1976), also has a relatively shallow pallial sinus (27% of shell length). It is likely that only a complete analysis of the total suite of characters, including behavioural, will reveal any possible rationale for the distribution of the lithodesma in this family.

Laternulids also possess an umbonal slit that essentially allows the shell to function as four valves (Morton, 1976) thus allowing some flexibility in the shell. Savazzi (1990) found that possession of the slit limits mechanical stresses to the posterior portion of the shell, stresses that occur in part because of the relative immobility of the primary ligament. This has little relevance in laternulids that lack a lithodesma, such as *Laternula* cf. *corrugata* and *L. anatina*. Although the umbonal slit in *L. cf. corrugata* is proportionally shorter than that in *L. truncata*, it still represents almost one third of the shell height and must be considered either functional, even in this shallow burrower, or an evolutionary remnant.

*Laternula* is currently the sole accepted genus within the family Laternulidae. Although Morton (1976) noted eight species within the family, there is no clear delineation as to the total number of species (Prezant & Smith, 1998). To date, there also remains no clear determination of the specific

epithet of *L. corrugata*. Reeve's (1863) original description was based on material collected by Cuming from the island of Ticao, the Philippines. Lamy (1934) suggested that this species is similar to *L. liautaudi* (Mittre, 1844) but did not synonymise the two. [According to P. G. Oliver (pers. comm.), *L. liautaudi* should be in the genus *Exolaternula* as listed in OBIS IndoPacific Molluscan database (<http://data.acnatsci.org/obis/search.php/78253>).] The shell in our specimens, sometimes misshapen and often eroded, has strong similarities to other presumed species within the genus *Laternula*. An examination of Reeve's original plates of his described species of *Anatina* (*Laternula*) shows *L. corrugata* with a fairly smooth outline, unlike the irregular and sometimes misshapen specimens we collected (Fig. 2D). Reeve (1863) also described *Anatina amphora* Reeve, 1863, later synonymised with prioritised *L. anatina*. His figure of "*A. amphora*" shows similarities to our specimens of *L. cf. corrugata* (rounded anterior and upwardly turned, acute posterior margins), however, his figure is likely of a juvenile specimen of *L. anatina*, which shows this general form as opposed to the more truncated posterior margin in larger specimens. The ontogenetic flexibility of the shell of laternulids has yet to be examined but based on limited information in the literature; care must be taken in identifications based solely on shell outline.

In 1980, Piyakarnchana, in an overview of mangals of the country, noted only *Laternula truncata* among laternulids found in Thailand. Some of the general identification guides that contain laternulids have image labels reversed (e.g., Abbott & Dance, 1982, and Swennen et al., 2001) increasing the possibility of errors in the wider literature. In addition, because there is so little literature on laternulids other than *L. elliptica*, some broad generalizations have taken root and help obfuscate their taxonomy. For example, Savazzi (1990: 100), although only examining *L. spengleri* (Gmelin, 1791), indicated that ossicula (i.e. lithodesmas) "are always present in the Laternulidae". Interestingly, *L. spengleri* has a shell shape very much like *L. truncata* and with careful examination could indeed turn out to be a prior name (the type species for the family is *Anatina truncata* Lamarck, 1818, which, to some authors, is considered synonymous with *Solen spengleri* Gmelin, 1791; see Morris & Morris, 1993).

What is clear is that laternulid bivalves are an important part of the biota in the mangals of the southern and eastern seaboard of Thailand, little is known about these organisms in the tropics, and the mangrove forests are increasingly threatened. The complexity of the many tropical mangrove flats is enhanced by the large number of local individuals who harvest a variety of clams and other infaunal macrofauna from the flats. In Kungkrabaen Bay, laternulids did not seem to be a large proportion of the molluscan fauna being harvested but the level of surface sediment turnover through the use of hand tools appeared significant and could possibly impact local substratum stability and hence infaunal composition. Although a few studies have examined the potential impact of local intertidal harvests on shallow water communities (see Logan, 2005), little is known of potential long-term impacts that such collections could have on the populations

of laternulids in the mangrove sand flats or the possible impact on overall infaunal biotic communities. It would be difficult to tease out this variable from organic run-off from shrimp or rice farms or other human-induced impacts within Kungkrabaen Bay, but it is clear that there is a need for additional study of these viable populations of laternulids within this relatively diverse intertidal community.

### ACKNOWLEDGMENTS

The International Marine Bivalve Workshop (with contributions on other molluscan groups) in Chantaburi, Thailand, was organised 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. André Sartori shared important taxonomic information and insight about laternulids. Harlan K. Dean and Nittaya Chaiyanate helped with identifications and confirmations of some of the polychaetes. Thanks to Paul Callomon for help in specimen access at the Academy of Natural Sciences, Philadelphia, and to Joe Youn and Tom Hoskinson for their electronic media expertise. The efforts of Judith Lynn Hunt in tracking down some difficult-to-find references are deeply appreciated. Two anonymous reviewers fine tuned this manuscript, offering important suggestions for improvement, and Paula Mikkelsen helped considerably in refining the text in preparation for publication.

### THAI ABSTRACT

คณะผู้วิจัยศึกษาประชากรหอยสองฝาในกลุ่ม อโนมาโลเดสมาตา ชนิด *Laternula truncata* (Lamarck, 1818) ในพื้นที่ๆ เป็นสันดอนทรายบริเวณอ่าวคุ้งกระเบนในประเทศไทย เพื่อหาข้อมูลเกี่ยวกับขนาดประชากร การแพร่กระจายของหอยที่มีอายุต่างกัน และความสัมพันธ์ต่างๆ ไประหว่างลักษณะของตะกอน และความหลากหลายของสัตว์หน้าดิน คณะผู้วิจัยพบว่าความหนาแน่นของ *L. truncata* ค่อนข้างสูงบริเวณที่เป็นสันดอนทรายปนโคลนโดยหอยจะฝังตัวอยู่ในระดับค่อนข้างลึกอยู่ภายในกระจุกรากของต้นโกงกาง *Avicennia alba* Blume, 1827 และ *A. marina* (Forsskål) Vierhapper, 1907 พื้นที่ดังกล่าวมีกระจุกของต้นโกงกางชนิดดังกล่าวอยู่บนสันดอนทราย ส่วนพื้นที่รอบๆ ที่อยู่ในระดับต่ำกว่าจะมีหอย *L. truncata* ค่อนข้างน้อย การแพร่กระจายของหอยสองฝาชนิดนี้ค่อนข้างเป็นไปอย่างสม่ำเสมอในทุกๆ ขนาดของหอย ยกเว้นหอยขนาดเล็กที่สุด ซึ่งน่าจะบ่งบอกถึงการเพิ่มประชากรจากการลงเกาะใหม่อย่างต่อเนื่อง โดยมีการสูญเสียหอยที่ลงเกาะใหม่บ้าง โดยทั่วไปแล้ว ความหลากหลายของสัตว์หน้าดินขนาดใหญ่รวมทั้งหอย *L. truncata* จะอยู่ในระดับสูงใกล้แนวป่าชายเลน อย่างไรก็ตามความโดดเด่นของสัตว์หน้าดินบางชนิดจะ

เพิ่มขึ้นในแนวสำรวจจากสันดอนแรกผ่านไปยังพื้นที่โล่งไปยังสันดอนป่าชายเลนสันดอนที่สอง นอกจากหอยชนิดดังกล่าวยังมีหอยในวงศ์เดียวกันอีกชนิดหนึ่งคือ *L. cf. corrugata* (Reeve, 1863) ซึ่งอาศัยอยู่ในสิ่งแวดล้อมที่ต่างกัน โดยหอยชนิดที่สองนี้จะฝังตัวตื้นๆ ภายในป่าชายเลนที่มีความหลากหลายของพรรณไม้มากกว่า และอยู่ในพื้นที่ๆ ตะกอนมีองค์ประกอบเป็นทรายมากกว่า จากการศึกษาพฤติกรรมฝังตัวของหอยทั้งสองชนิดพบว่าหอยดังกล่าวทั้งสองชนิดสามารถฝังตัวใหม่ได้อย่างซ้ำๆ หากถูกนำมาวางไว้บนพื้นตะกอน โดยหอยขนาดเล็กสามารถฝังตัวได้เร็วกว่าจนมีคัลล์ตัว หอย *L. truncata* ที่มีขนาดใหญ่ไม่สามารถฝังตัวใหม่หากถูกรบกวนจนหลุดออกมานอนบนพื้น รายงานฉบับนี้มีการเปรียบเทียบความแตกต่างระหว่าง รูปร่าง นิเวศวิทยา และพฤติกรรมบางประการของ *L. truncata* และ *L. cf. corrugata* และอภิปรายถึงการขาดข้อมูลพื้นฐานในการจำแนกชนิดของหอยสองฝากลุ่มนี้ โดยเฉพาะการกำหนดชื่อที่ถูกต้องของ *L. cf. corrugata*

### LITERATURE CITED

- Abbott, R. T. & S. P. Dance, 1982. *Compendium of Seashells*. E. P. Dutton, New York. 411 pp.
- Adal, M. N. & B. S. Morton, 1973. The fine structure of the pallial eyes of *Laternula truncata* (Bivalvia: Anomalodesmata: Pandoracea). *Journal of Zoology, London*, **171**: 533–556.
- Ahn, I.-Y. & J. H. Shim, 1998. Summer metabolism of the Antarctic clam, *Laternula elliptica* (King & Broderip) in Maxwell Bay, King George Island and its implications. *Journal of Experimental Marine Biology and Ecology*, **224**: 253–264.
- Ahn, I.-Y., K. Jaekyoon & K.-W. Kim, 2001. The effect of body size on metal accumulations in the bivalve *Laternula elliptica*. *Antarctic Science*, **13**: 355–362.
- Ahn, I.-Y., J. Surh, Y.-G. Park, H. Kwon, H.-S. Choi, S.-H. Kang, H. J. Choi, K.-W. Kim & H. Chung, 2003. Growth and seasonal energetics of the Antarctic bivalve *Laternula elliptica* from King George Island, Antarctica. *Marine Ecology Progress Series*, **257**: 99–110.
- Aksornkoae, S., 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.
- Aller, R. C., 1974. Prefabrication of shell ornamentation in the bivalve *Laternula. Lethaia*, **7**: 43–56.
- Angsupanich, S. & S. Aksornkoae, 1996. Macro-benthic fauna in shrimp-farms adjacent to mangroves, Kradae Chae Canal, Ban Don Bay, southern Thailand. *Lamer*, **34**: 75–81.
- Ansell, A. D. & R. Harvey, 1997. Protected larval development in the Antarctic bivalve *Laternula elliptica* (King and Broderip) (Anomalodesmata: Laternulidae). *Journal of Molluscan Studies*, **63**: 285–286.

- Arnaud, P. M., 1973. Invertébrés marins des XIIème et XMème Expéditions Antarctiques Française en Terre Adélie. 13. Polyplacophores, Scaphopodes et Pélécy-podes. *Tethys*, **5**: 549–560.
- Athalye, R. P. & K. S. Gokhale, 1998. Macro-benthos from the mudflats of Thane Creek, Maharashtra, India. *Journal of the Bombay Natural History Society*, **95**: 258–266.
- Berkman, P. A., T. R. Waller & S. P. Alexander, 1991. Unprotected larval development in the Antarctic scallop *Adamussium colbecki* (Mollusca: Bivalvia: Pectinidae). *Antarctic Science*, **3**: 151–157.
- Bigatti, C., P. E. Penchaszadeh & G. Mercuri, 2001. Aspects of the gonadal cycle in the Antarctic bivalve *Laternula elliptica*. *Journal of Shellfish Research*, **20**: 283–287.
- Brockington, S., 2001. The seasonal energetics of the Antarctic bivalve *Laternula elliptica* (King and Broderip) at Rothera Point, Adelaide Island. *Polar Biology*, **24**: 523–530.
- Carter, J. G., 1980. Environmental and biological controls of bivalve shell mineralogy and microstructure. In: Rhoads, D. C. & R. A. Lutz (eds.), *Skeletal Growth of Aquatic Organisms Biological Records of Environmental Change*. Plenum Press, New York. Pp. 69–113.
- Cox, L. R., C. P. Nuttall & E. R. Truman, 1969. General features of Bivalvia. In: Cox, L. R. et al., *Part N [Bivalvia], Mollusca 6, Volume 1*. In: Moore, R. C. (ed.), *Treatise on Invertebrate Paleontology*. The Geological Society of America and University of Kansas, Lawrence. Pp. N2–N224.
- Dayton, P. K., G. A. Robilliard & L. B. Dayton, 1974. Biological accommodation in the benthic community at McMurdo Sound, Antarctica. *Ecological Monographs*, **44**: 105–128.
- De Man, J.G., 1888. Report on the podophthalmous Crustacea of the Mergui Archipelago, collected for the Trustees of the Indian Museum, Calcutta, by Dr. John Anderson, F. R. S., Superintendent of the Museum. *Journal of the Linnean Society, London*, **22**: 1–312.
- Dittmann, S., 2001. Abundance and distribution of small infauna in mangroves of Missionary Bay, North Queensland, Australia. *Revista de Biología Tropical*, **49**: 535–544.
- Dittmann, S., 2002. Benthic fauna in tropical tidal flats – a comparative perspective. *Wetlands Ecology and Management*, **10**: 189–195.
- 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.
- Gray, J. E., 1828. Original figures and short systematic descriptions of new and unfigured animals. *Spicilegia Zoologica*, **1**: 6.
- Grube, A. E., 1878. Annulata Semperiana. Beiträge zur kenntniss der annelidenfauna der Anneliden-fauna der Philippinen nach den von Herm Prof. Semper mitgebrachten sammlungen. *Mémoires de l'Académie Impériale des Sciences de St. Pétersbourg*. St.-Petersbourg, série 7, **25**(8): ix, 1–300.
- Harper, E. M. & L. Peck, 2003. Predatory behavior and metabolic costs in the Antarctic muricid gastropod *Trophon longstaffi*. *Polar Biology*, **26**: 208–217.
- Jonkers, H. A., 1999. Aligned growth positions in Pliocene *Laternula elliptica* (King and Broderip) (Bivalvia: Anomalodesmata: Laternulidae). *Antarctic Science*, **11**: 463–464.
- Kang, D.-H., I.-Y. Ahn & K.-S. Choi, 2003. Quantitative assessment of reproductive condition of the Antarctic clam, *Laternula elliptica* (King & Broderip), using image analysis. *Invertebrate Reproduction and Development*, **44**: 71–78.
- Kathiresan, K. & B. Laternula Bingham, 2001. Biology of mangroves and mangrove ecosystems. *Advances in Marine Biology*, **40**: 81–251.
- 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*. Amarin Co., Ltd., Bangkok, Thailand. 339 pp.
- King, P. P. & W. J. Broderip, 1831. Description of the Cirrhipeda, Conchifera and Mollusca, in a collection formed by the officers of H. M. S. *Adventure* and *Beagle* employed between the years 1826 and 1830 in surveying the southern coasts of South America, including the Straits of Magalhaens and the coast of Tierra del Fuego. *Zoological Journal*, **5**: 332–349.
- 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.
- Lamy, É., 1934. Révision des *Anatina* vivants du Muséum National d'Histoire Naturelle de Paris. *Journal de Conchyliologie*, **78**: 145–168.
- Linnaeus, C., 1758. *Systema Naturae per Regna Tria Naturae. Tomus I. Editio Decima, Reformata*. Laurentii Salvii, Stockholm. [ii] + 824 pp.
- Logan, J. M., 2005. Effects of clam digging on macroinvertebrate community structure in a Maine mudflat. *Northeastern Naturalist*, **12**: 315–324.
- Lohan, M. C., P. J. Statham & L. Peck, 2001. Trace metals in the Antarctic soft-shelled clam *Laternula elliptica*: implications for metal pollution from Antarctic research stations. *Polar Biology*, **24**: 808–817.
- 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.
- Menasveta, P., 1997. Mangrove destruction and shrimp culture systems. *World Aquaculture*, **28**: 36–42.
- Mittre, M. H., 1844. Mémoire sur le genre *Anatine*. *Magasin de Zoologie*, 2eme série, **6**: 1–18, 3 pls.
- Momo, F., J. Kowalke, I. Schloss, G. Mercuri & G. Ferreyra, 2002. The role of *Laternula elliptica* in the energy budget of Potter Cover (King George Island, Antarctica). *Ecological Modeling*, **155**: 43–51.
- Montagu, G., 1813. Descriptions of several new or rare animals principally marine, found on the south coast of Devonshire. *Transactions of the Linnean Society of London*, **11**: 18–21.
- Morley, S. A., L. S. Peck, K. S. Tan, S. M. Martin & H. O. Pörtner, 2007. Slowest of the slow: latitudinal insensitivity of burrowing capacity in the bivalve *Laternula*. *Marine Biology*, **151**: 1823–1830.
- Morris, S & N. Morris, 1993. New shells from the UAE's east coast. *Tribulus*, **3.1**: 5–8, figs pp. 18–19.
- Morton, B., 1973. The biology and functional morphology of *Laternula truncata* (Lamarck, 1818) (Bivalvia: Anomalodesmata: Pandoracea). *Biological Bulletin*, **145**: 509–531.

- Morton, B., 1976. The structure, mode of operation and variation in form of the shell of the Laternulidae (Bivalvia: Anomalodesmata: Pandoracea). *Journal of Molluscan Studies*, **42**: 261–278.
- Peck, L. S., H. O. Pörtner & I. Hardewig, 2002. Metabolic demand, oxygen supply, and critical temperatures in the Antarctic bivalve, *Laternula elliptica*. *Physiological and Biochemical Zoology*, **75**: 123–133.
- Peck, L. S., A. D. Ansell, K. E. Webb, L. Hepburn & M. Burrows, 2004. Movements and burrowing activity in the Antarctic bivalve molluscs *Laternula elliptica* and *Yoldia eightsi*. *Polar Biology*, **27**: 357–367.
- Piyakarnchana, T., 1980. *The Present State of Mangrove Ecosystems in Southeast Asia and the Impact of Pollution, Thailand*. Project report SCS/80/WP/94E. Food and Agriculture Organization of the United Nations and United Nations Environment Programme, South China Sea Fisheries Development and Coordinating Programme, Manila. 138 pp. Online version <http://www.fao.org/docrep/field/003/AB751E/AB751E00.htm>.
- Prezant, R. S., 1981. Comparative shell ultrastructure of Lyonsiid bivalves. *The Veliger*, **23**: 289–299.
- Prezant, R. S. & M. R. Carriker, 1983. Functional microstructure of the lithodesma of *Mytilimeria nuttalli* (Bivalvia: Anomalodesmata). *The Veliger*, **25**: 326–329.
- Prezant, R. S. & B. J. Smith, 1998. Subclass Anomalodesmata. In: Beesley, P. Laternula, G. J. B. Ross & A. Wells (eds), *Mollusca: The Southern Synthesis. Fauna of Australia, Volume 5, Part A*. CSIRO Publishing, Melbourne. Pp. 397–429.
- Rees, A. 1802-1830. *The Cyclopaedia, or, Universal Dictionary of Arts, Sciences, and Literature*. Longham, Hurst, Rees, London. 39 Volumes, 5 Volumes of plates, Atlas.
- Reeve, L. A., 1860-1863. Monograph of the genus *Anatina*. *Conchologica Iconica; or Illustrations of the Shells of Molluscos Animals*, **14**: 26 pls.
- Röding, P. F., 1798. *Museum Boltinianum, Pars Secunda Continens Conchlia, sive Testacea Univalvia, Bivalvia et Multivalvia*. Johan Christi Trappii, Hamburg. viii + 199 pp.
- Runnegar, B., 1972. Anatomy of *Pholadomya candida* (Bivalvia) and the origin of the Pholadomyidae. *Proceedings of the Malacological Society of London*, **40**: 45–58.
- Sartori, A. F., F. D. Passos & O. Domaneschi, 2006. Arenophilic mantle glands in the Laternulidae (Bivalvia: Anomalodesmata) and their evolutionary significance. *Acta Zoologica*, **87**: 265–272.
- Savazzi, E., 1990. Shell biomechanics in the bivalve *Laternula Lethaia*, **23**: 93–101.
- Smith, E. A., 1907. Mollusca. II. Gastropoda. *National Antarctic Expedition 1901-1904, Natural History*, **2**: 12 pp., 2 pls.
- 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. & T. M. Oh, 2002. Feeding habits of *Chicoreus capucinus* (Neogastropoda: Muricidae) in a Singapore mangrove. *Bolettino Malacologico*, **28** (supplement 4): 43–50.
- Treadwell, A. L., 1929. New species of polychaetous annelids in the collections of the American Museum of Natural History from Porto Rico, Florida, Lower California, and British Somaliland. *American Museum Novitates*, **392**: 1–13.
- Urban, H. -J. & G. Mercuri, 1998. Populations dynamics of the bivalve *Laternula elliptica* from Potter Cover, King George Island, South Shetland Islands. *Antarctic Science*, **10**: 153–160.
- Urban, H.-J. & P. Silva, 1995. Tolerancia a temperatura maxima de dos molusco antárticos (*Laternula elliptica* y *Nacella concinna*) en Caleta Potter, Isla 25 de mayo (King George), Antártida. *VI Congreso Latinoamericano de Ciencia del Mar*, Mar del Plata, Libro de Resúmenes, p. 112.
- Vierhapper, F. 1907. Denkschriften der Kaiserlichen Akademie der Wissenschaften in Wien. *Mathematisch-Naturwissenschaftliche Klasse*, **71**(1): 321–490.
- 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. *Phuket Marine Biological Center Special Publication*, **25**(1): 31–39.
- Yonge, C. M. & B. Morton, 1980. Ligament and lithodesma in the Pandoracea and the Poromyacea with a discussion on evolutionary history in the Anomalodesmata (Mollusca: Bivalvia). *Journal of Zoology, London*, **191**: 26–292.
- Zamorano, J. H., W. E. Duarte & C. A. Moreno, 1986. Predation upon *Laternula elliptica* (Bivalvia, Anatinidae): a field manipulation in South Bay, Antarctica. *Polar Biology*, **6**: 139–143.
- Zorina, I. P., 1978. New species of bivalve molluscs (Bivalvia) of the Gulf of Tonkin (South China Sea) (in Russian). *Trudy Zoological Institut, Leningrad*, **61**: 193–203.