

Distribution, Diversity, and Abundance Patterns of Intertidal Benthic Molluscs on Rocky Shores (Phuket Island, Thailand)

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ABSTRACT: A total of 51 mollusc species were encountered along the south-western coast of Phuket Island (Thailand). The taxa were dominated by gastropods, which are well adapted for the zones recognized on the shore. Multivariate cluster analysis shows that faunal composition and species diversity changes between the four zones recognised and a faunal turnover is found in the middle of the intertidal area, which is the boundary between relative wet and relative dry substrate. Mollusc density, species diversity and functional diversity increases below this boundary due to less stressed environmental conditions, supporting the hypothesis that the functional diversity decreases with increasing stress. In contrast faunal composition and species diversity is similar for all microhabitats. This finding does not support the hypothesis of increased species diversity with increased structural complexity. This shows that there is a different relationship between gastropod diversity and microhabitat diversity compared to other intertidal rocky shore biota.

KEY WORDS: Phuket Island, Thailand, tropical rocky shore, molluscs, zonation, intertidal.

INTRODUCTION

The zonation of molluscs on rocky shores at Phuket Island is similar to the zonation pattern recognized globally (Stephenson and Stephenson, 1972). The zonation is controlled by environmental factors such as exposure to air, wave action, temperature, and wetness/dryness of the substrate. These factors interact and overlap in complex ways to form specific environmental conditions for the intertidal biota. The zonation thus results from preferential larval settlement and adult movement as a consequence of their physiological

tolerance to environmental conditions, competition, and predation. In general, the upper limit of species on the shoreline is regulated by physical factors and the lower limit by biological factors (Levinton, 2001). There is thus an increased environmental stress from the lower wetter zones to the higher drier zones along rocky coasts, which can be used to investigate changes in the ecological patterns along a natural stress gradient. These studies are important as marine ecosystem degradation is rapidly increasing due to the impact of pollution and global warming on marine ecosystems

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functioning. Studies on ecosystems with natural environmental stress can be used for comparative analyses with ancient ecosystems in order to increase knowledge of ecosystem evolution as a response to the changing global environment. The topological complexity of rocky shores also provides a great variety of different microhabitats and niches for the colonizing fauna and flora, which leads to co-existence of competitors, thereby contributing to the high biotic diversity normally found on rocky shores (Connor and McCoy, 1979; Huston, 1979; Johnson *et al.*, 2003; Kostylev *et al.*, 2005; Levinton, 2001). This study was carried out as part of a paleoecological comparison with Cretaceous rocky shore fauna since the fauna from Thailand is very similar to 80 million year old fauna from Sweden.

The aim of the study is to investigate the benthic intertidal mollusc species with respect to their tolerance to environmental conditions and their vertical zonation, to determine the preferred microhabitats of the fauna, and to compare the diversity and abundance patterns of the fauna at five study sites, in four zones encompassing six microhabitats. Finally to investigate whether gastropods follow the hypothesis of an increase in species diversity with an increase in topological complexity.

The study sites

The study was conducted along the SW coast of Phuket Island, located in the Andaman Sea adjacent to the

western coast of the Thai Peninsula, southern Thailand (fig. 1). The island has a monsoonal climate with a dry season dominated by a NE-monsoon from November to April and a rainy season dominated by a SW-monsoon from May to October (Yesaki and Jantarapagdee, 1981). During the rainy season the SW coast of Phuket Island experience strong onshore winds which create continuous moderate to high wave action with wave heights up to 3 m. During the dry season the SW coast experiences limited wind and reduced wave intensity, frequency, and heights. The tides around Phuket Island are diurnal, and during the study period the tidal range varied from 0.3 to 3.6 m above the lowest low water level recorded at Phuket Island (2010 tide table from Ko Thaphao Noi). The coastal water temperature ranges from 26–31°C and salinity from 32–33‰ (Limpsaichol, 1981; Scoffin *et al.*, 1992). Three current systems are observed in the coastal areas during the NE-monsoon: an offshore oceanic current, a laminar tidal current, and a near-shore turbulent current (Charoenlaph, 1982). Five sites representing different degrees of exposure to the dominant current systems were studied (fig. 1). All sites are exposed to high wave action during the rainy season but the topography of the rocky shores creates sheltered areas between and behind the rocks. The rocky shores at all four sites are composed of granite with pegmatite veins, and with intervening quartz sand.

Yanui

The N-S oriented Yanui beach is located about 1 km north of Promthep Cape at the southernmost tip of Phuket Island (fig. 1). Granitic headlands form the rocky shore at each end of the beach, and granite boulders ranging from 0.5–2 m in diameter lie along the beach. A small basement peninsula is located in the middle of the beach. A lagoon with many pools and horizontal algal flats develops at low tide between the peninsula and the mainland. The intertidal rocky shore mollusc fauna from the peninsula and from the granitic basement at each end of the beach were studied.

Naiharn

The NW-SE oriented Naiharn beach is located about 2 km north of Promthep Cape (fig. 1). Granite headland and boulders form rocky shores at each end of the beach and are surrounded by quartz sand. The intertidal rocky shore mollusc fauna in the north-western end of the beach were studied.

Ao Sane

The W-E oriented Ao Sane beach is located about 0.5 km west of Naiharn (fig. 1). Granite headlands are located at each end of the beach, and granite boulders, 0.5–4 m in diameter lie along the entire beach. The intertidal rocky shore mollusc fauna from the boulders along the beach and the basement at the eastern end of the beach were studied.

Kata Noi

The N-S oriented Kata Noi beach is located about 5 km north of Promthep Cape (fig. 1). Granite headlands and boulders are located at each end of the beach and are surrounded by quartz sand. The intertidal rocky shore mollusc fauna at the southern end of the beach was studied.

Rawai

The SW-NE oriented Rawai beach is located on the eastern side of Phuket Island about 2 km north of Promthep Cape (fig. 1). Granitic basement is located in each end of the beach and form the rocky shore. The sediment on the tidal flat is siltier compared to the other localities. The intertidal rocky shore mollusc fauna from the south-western end of the beach were studied.

MATERIALS AND METHODS

Fieldwork was conducted continuously from February to December 2010. Living molluscs were collected from the rocky intertidal zone on both exposed and protected surfaces at all study sites. Soft tissue was removed and shells were cleaned for organic material using chlorine bleach. The collection of the intertidal mollusc shells are housed at the Phuket Marine Biological Center.

Six microhabitats were identified on the rocky shores: 1) horizontal surfaces, dipping 0–20°; 2) slopes, dipping 21–69°; 3) vertical surfaces, dipping 70–90°; 4) small boulders, everywhere on and between boulders

smaller than about 1 by 1 m, including the sandy patches between them; 5) Rock pools, depressions that retain water at low tide; 6) Crevices, slits or small holes in the rocks. Three timed visual search periods of 30 minutes was conducted to count the total number of species in each microhabitat at each study site and to determine the preferred microhabitats for all species. Counting was conducted during the afternoon low tide and the three counts of each microhabitat were spread out over the study period. Five levels of abundance of species in the microhabitats were defined: 1 = very rare (1 – 2 individuals), 2 = rare (3 – 10 individuals), 3 = less abundant (11 – 30 individuals), 4 = abundant (31 – 50 individuals), 5 = very abundant (> 51 individuals). An abundance table were constructed using the highest number of specimens of each species counted in a microhabitat at one of the five study sites (Table 1).

Four zones are easily recognized at all five study sites comprising the uppermost *Nodilittorina* Zone, the barnacle zone, the oyster zone, and the lowermost algae crust zone primarily consisting of micro algae (fig. 2). Abundance analyses of species in each zone were conducted using a non-timed visual search during the entire study time (Table 1). Non-timed visual search was chosen to provide a better understanding of the species abundance in the zones. Four levels of abundance were defined: 1 = single (only one or two specimens of a species observed once or twice in a

certain zone during the study period); 2 = few (few specimens of a species observed in a certain zone several times or every time fieldwork was done); 3 = average (relatively many specimens of a species observed in a certain zone every time fieldwork was done); and 4 = abundant (the species can be found in huge amounts in a certain zone every time fieldwork was done) (Table 1). The density of molluscs in each zone was determined to show a trend and is not actual numbers. It is calculated by replacing each level of abundance with a number, single were set to 0,5, few to 1, average to 2, and abundant to 4. These numbers are multiplied by the number of species found in each abundance level (Table 1) so four abundant species will give the number 16 and four few species 4. The calculated numbers for each abundance level in a zone is then added to give the density trend number. The density of the *Nodilittorina* zone is thus; (1 abundant species $\times 4 = 4$) + (4 average species $\times 2 = 8$) + (5 few species $\times 1 = 5$) = 17 (See fig. 2).

Multivariate cluster analyses of the distribution of the mollusc fauna were conducted in order to obtain a better visual understanding of the similarity between the five study sites, between the six microhabitats, and between the four zones. The analyses were made using the statistical software PAST (PAleontological STatistics) based on binary data (present/absent) using Horn's coefficient of similarity (fig. 3).

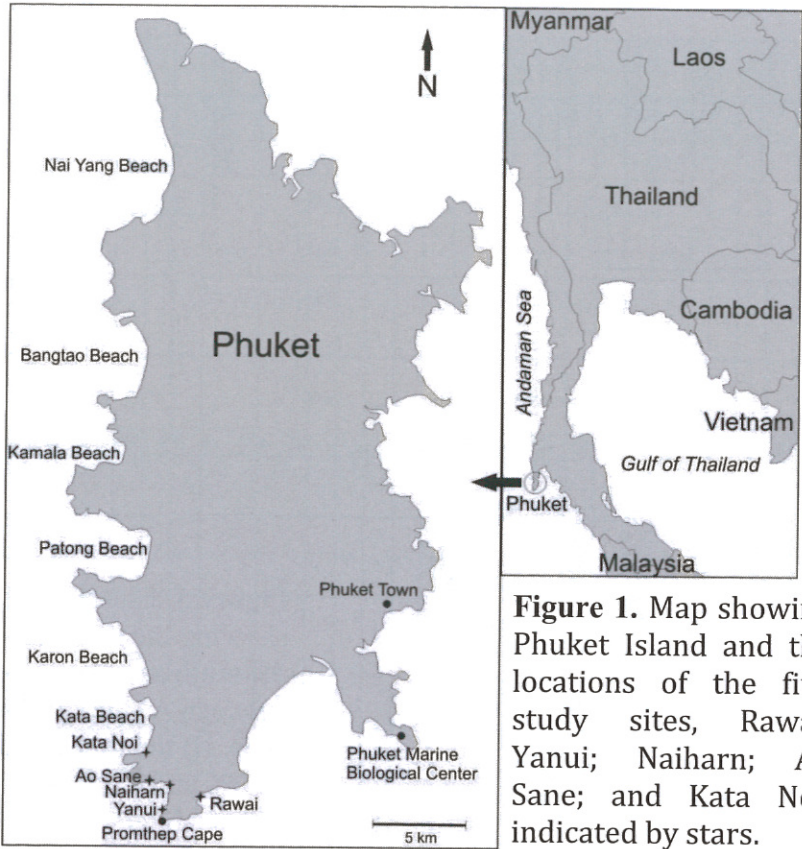


Figure 1. Map showing Phuket Island and the locations of the five study sites, Rawai; Yanui; Naiham; Ao Sane; and Kata Noi, indicated by stars.

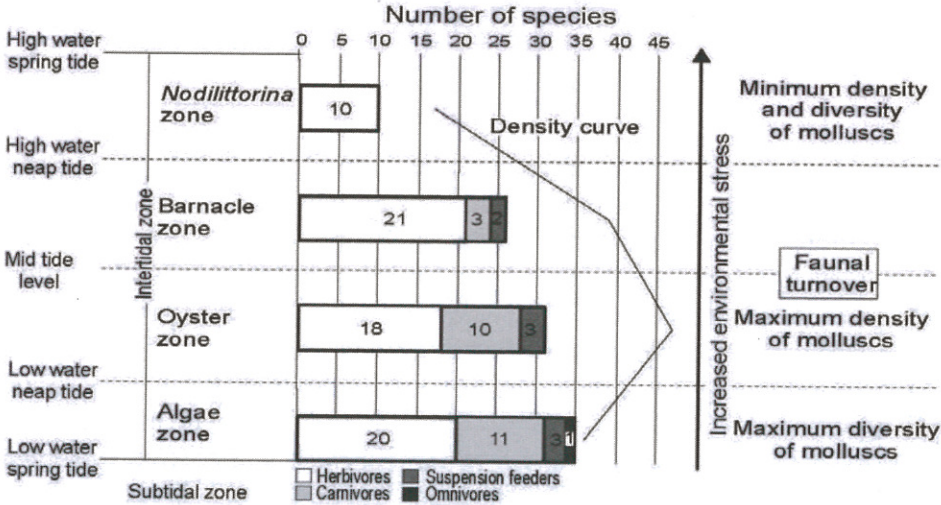


Figure 2. The four ecological zones along the intertidal rocky shores of Phuket Island showing species diversity, density, and functional diversity of the mollusc fauna. The density curve is not based on actual numbers but is a trend calculated from the abundance of species in each zone (see text).

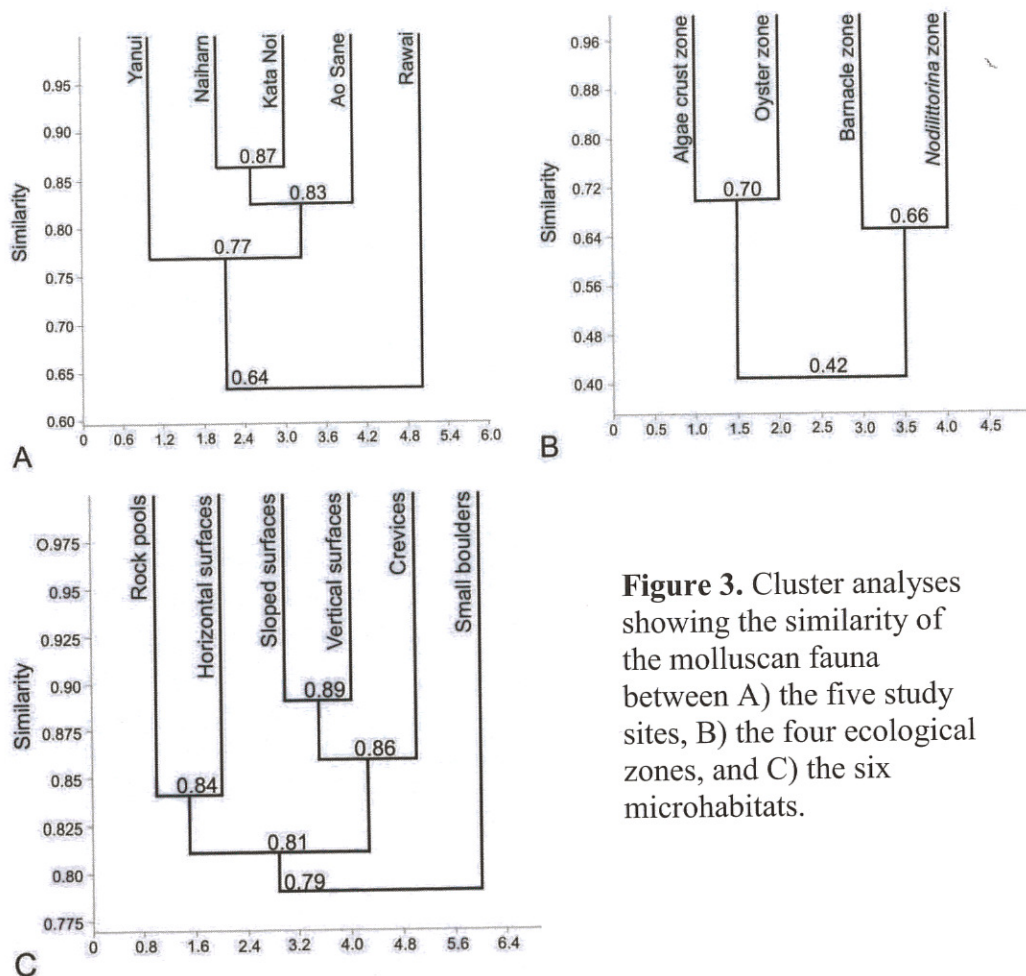


Figure 3. Cluster analyses showing the similarity of the molluscan fauna between A) the five study sites, B) the four ecological zones, and C) the six microhabitats.

Table 1. List of the studied intertidal mollusc fauna, their functional characteristics, their distribution between the studied rocky shores, and their distribution and abundance in microhabitats and zones. **Functional characteristics:** SS – Sessile suspension feeder, MO – Mobile omnivorous, MC – Mobile carnivorous, MH – Mobile herbivorous. **Microhabitats:** 1 = very rare (1 – 2 individuals), 2 = rare (3 – 10 individuals), 3 = less abundant (11 – 30 individuals), 4 = abundant (31 – 50 individuals), 5 = very abundant (> 51 individuals). **Zones:** 1 = single (only one or two specimens of a species have been observed once or twice in the zone), 2 = few (few specimens of a species have been observed in the zone several times or every time), 3 = Average (relatively many specimens of a species have been observed every time in the zone), 4 = abundant (the species can be found in huge amounts every time in the zone).

Table 1

Species	Functional characteristics	Study sites					Microhabitats							Zones			
		Yanui	Ao Sane	Nai-ham	Kata	Rawai	Vertical surfaces	Horizontal surfaces	Slopes	Small boulders	Rock pools	Crevices	Nodi-littorina	Barnacle	Oyster	Algae	
		X	X	X	X	X	5	5	5	5	5	5	-	3	4	4	
<i>Saccostrea cucullata</i>	SS	X	X	X	X	X	5	5	5	5	5	5	-	2	4	2	
<i>Isognomidae</i> sp. A	SS	X	X	X	X	X	5	3	5	5	5	5	-	4	4	3	
<i>Mytilidae</i> sp. a	SS	X	-	X	X	-	5	5	5	-	5	5	-	-	4	3	
<i>Cellana radiata</i>	MH	X	X	X	X	-	5	5	5	5	3	5	-	3	3	3	
<i>Cerithium zonatum</i>	MH	X	-	-	-	-	-	-	-	1	-	-	-	-	-	1	
<i>Clypeomorus petrosa</i>	MH	X	X	X	X	X	-	2	-	5	3	-	-	-	3	3	
<i>Clypeomorus purpurastoma</i>	MH	X	-	-	-	-	-	3	-	1	-	-	-	-	-	2	
<i>Clypeomorus tuberculatus</i>	MH	X	-	-	-	-	-	-	-	1	-	-	-	-	-	1	
<i>Conus ebraeus</i>	MC	X	-	-	-	-	-	3	-	1	-	-	-	-	-	2	
<i>Engina mendicaria</i>	MC	X	-	-	-	-	-	3	-	1	-	-	-	2	2	2	
<i>Ergalutax margaritcola</i>	MC	X	X	X	-	-	1	1	-	2	1	-	-	-	2	2	
<i>Littoraria scabra</i>	MH	X	-	-	-	X	5	-	-	2	2	5	-	-	2	2	
<i>Littoraria undulata</i>	MH	X	X	X	X	X	5	5	5	5	5	5	3	3	-	-	
<i>Mancinella tuberosa</i>	MC	X	X	X	X	-	3	2	2	1	1	1	-	-	2	1	
<i>Mauritia mauritiana</i>	MO	-	-	X	-	-	-	-	-	1	-	-	-	-	-	1	
<i>Miliuriconus aristophanes</i>	MC	X	-	-	-	-	-	3	-	2	-	-	-	-	-	2	
<i>Mitra pica</i>	MC	X	-	X	-	-	-	1	1	-	-	-	-	1	1	1	
<i>Morula anaxeres</i>	MC	X	X	X	X	-	1	2	1	2	1	2	-	-	2	2	
<i>Murcla granulata</i>	MC	X	X	X	X	-	3	3	3	1	2	3	-	-	2	2	
<i>Murcla musiva</i>	MC	X	X	X	X	-	1	1	2	4	1	1	-	-	2	-	
<i>Nerita albicilla</i>	MH	X	X	X	X	X	5	4	4	5	5	5	-	3	3	2	
<i>Nerita chamaelton</i>	MH	X	X	X	X	X	5	5	5	5	5	5	2	3	3	2	
<i>Nerita costata</i>	MH	X	X	X	X	-	5	5	5	3	5	5	2	3	3	2	
<i>Nerita litterata</i>	MH	-	-	-	X	-	-	-	-	1	-	-	-	-	-	1	
<i>Nerita plicata</i>	MH	X	-	-	-	-	1	-	-	-	-	-	-	-	1	-	
<i>Nerita polita</i>	MH	X	X	X	X	X	2	1	5	5	2	1	-	3	3	2	
<i>Nerita squamulata</i>	MH	-	-	-	-	X	-	-	-	2	-	-	-	-	-	1	
<i>Nerita undata</i>	MH	-	X	-	-	-	1	-	-	2	-	1	-	-	1	-	
<i>Nerita undulata</i>	MH	X	-	X	X	X	5	-	-	5	3	5	2	3	3	2	

Table 1 continued

<i>Nodittitorina leucosticta</i>	MH	-	X	X	X	X	5	5	5	2	1	-	3	3	-	-
<i>Nodittitorina millegriana</i>	MH	X	X	X	X	X	5	5	5	5	1	4	3	3	-	-
<i>Nodittitorina trochoides</i>	MH	X	X	X	X	X	5	5	5	5	5	5	4	4	-	-
<i>Notoacmea flammea</i>	MH	X	X	X	X	-	2	1	3	5	-	-	-	2	2	2
<i>Onchidina</i> sp.	MH	X	X	X	X	X	-	5	2	2	1	1	-	-	-	2
<i>Patelloida mufria</i>	MH	X	X	X	X	-	2	-	2	2	1	1	-	2	2	-
<i>Patelloida saccharina</i>	MH	X	X	X	X	-	5	4	3	2	1	-	-	2	2	-
<i>lana</i>																
<i>Peasiella roepstorffiana</i>	MH	X	X	X	X	X	5	5	5	5	-	3	3	2	-	-
<i>Planaxis niger</i>	MH	-	X	X	X	X	5	1	3	3	-	3	2	2	2	-
<i>Planaxis sulcatus</i>	MH	X	X	X	X	X	4	5	5	5	5	5	2	2	3	2
<i>Semiricinula marginata</i>	MC	X	X	X	X	-	5	3	2	3	3	4	-	2	2	2
<i>Siphonaria normalis</i>	MH	X	X	X	X	X	5	5	5	5	5	5	-	3	2	2
<i>Siphonaria</i> sp. c	MH	X	X	X	X	-	5	1	5	5	-	-	-	2	2	2
<i>Smuraginella calyculata</i>	MH	X	X	X	X	-	5	2	2	1	4	1	-	2	-	-
<i>Thais bitubularis</i>	MC	-	-	-	X	-	1	-	1	-	-	-	-	-	1	-
<i>Thais virgatus</i>	MC	X	X	X	X	-	5	5	5	3	5	5	-	2	3	2
<i>Trochus maculatus</i>	MH	-	-	X	X	-	-	-	-	1	-	-	-	-	-	1
<i>Trochus</i> sp.	MH	-	X	-	-	-	-	-	-	1	-	-	-	1	-	-
<i>Virgicomus flavidus</i>	MC	-	-	-	X	-	-	-	-	1	-	-	-	-	-	1
<i>Zierliana woldemarii</i>	MC	-	X	-	-	-	-	-	-	1	-	-	-	1	-	-
<i>Patellidae</i> sp.	MH	-	X	-	-	-	-	-	-	5	-	-	-	2	2	-
<i>Cerithium</i> sp.	MH	-	-	X	-	-	-	-	-	-	2	-	-	-	-	1
Total no. of species	51	37	33	34	31	17	33	34	30	42	33	28	10	26	31	35
Total no. of species in each abundance group	MS=3 MO=1 MC=14 MH=33						1=7 2=3 3=2 4=0 5=21	1=7 2=4 3=7 4=3 5=13	1=3 2=6 3=4 4=1 5=16	1=9 2=10 3=4 4=1 5=18	1=13 2=5 3=4 4=1 5=10	1=8 2=1 3=3 4=2 5=14	1=0 2=5 3=4 4=1	1=2 2=12 3=11 4=1	1=4 2=15 3=9 4=3	1=10 2=21 3=3 4=1

RESULTS

Three species of bivalves and 48 species of gastropods were identified in the intertidal zone (Table 1). Four different functional characteristics of the fauna were found; sessile suspension feeders; mobile omnivores; mobile carnivores; and mobile herbivores. All species are epifaunal since the rocks of the study area are composed of granite, excluding boring and burrowing life habits. A total of 37 species of molluscs were found at Yanui, 33 at Ao Sane, 34 at Naiharn, 31 at Kata Noi, and 17 at Rawai (fig. 4). The density of molluscs is similar at all five study sites.

The cluster analysis based on Horn's coefficient of similarity grouped the western study sites together with a similarity of 0.77, whereas the eastern study site Rawai is an outlier with a similarity to the western sites of 0.64 (fig. 3a)

The zonation

The intertidal rocky shores are composed of four zones (fig. 5). The uppermost *Nodilittorina* zone is partly subaerial and lies between high water spring tide and high water neap tide. Ten mobile herbivorous mollusc species, dominated by *Nodilittorina trochoides*, are found in this zone (fig. 5). The underlying barnacle zone is well within the intertidal zone and extends from high water neap tide level marked by the presence of barnacles, to a sharp lower boundary in the mid tide levels where oysters become dominant. The zone is inhabited by 26 mollusc species, 21

mobile herbivores, three mobile carnivores, and two sessile suspension feeders (fig. 2). The next zone extends from the mid tide levels to low water neap tide and is dominated by the oyster *Saccostrea cucullata* and inhabited by 31 mollusc species, 18 mobile herbivores, 10 mobile carnivores, and three sessile suspension feeders (fig. 2). The oyster zone extends downwards to the algae zone, where a less sharp boundary lies about the low water neap tide level (fig. 5). Oysters are less dominant and the algal crust more evident below this boundary. The algae crust covers the rock surfaces and lowermost oysters and provides a source of food for the herbivorous fauna. A total of 35 mollusc species are found in the algae crust zone, 20 mobile herbivores, 11 mobile carnivores, three sessile suspension feeders, and one mobile omnivore (fig. 2). The faunal composition of the zones did not change during the study period.

The cluster analysis based on Horn's coefficient of similarity grouped the zones into two clusters, the *Nodilittorina* and the barnacle zones together and the oyster and algae crust zones together, with a similarity between the two groups of 0.42. The *Nodilittorina* zone and the barnacle zone have a similarity of 0.66 and the oyster zone and algae zone of 0.70 (fig. 3b)

The microhabitats

Six microhabitats were recognised and found at all study sites except for Kata Noi where rock pools are

absent. A total of 33 mollusc species were found on vertical surfaces, 34 on horizontal surfaces, 30 on slopes, 42 on small boulders, 33 in rock pools, and 28 in crevices (fig. 6). A total of 19 species inhabit six microhabitats and of these 14 are very abundant (fig. 7). Seven species inhabit five microhabitats; five species inhabit four, three species three, and five species two. Twelve species inhabit one microhabitat and nine of these are single individuals. The faunal composition of the

microhabitats did not change during the study period.

The cluster analysis based on Horn's coefficient of similarity placed the small boulder microhabitat as an outlier, with a similarity to the other microhabitats of 0.79. The remaining five microhabitats are grouped in two clusters, one including rock pools and horizontal surfaces with a similarity of 0.84, and another including slopes, vertical surfaces, and crevices with a similarity of 0.86 (fig. 3c).

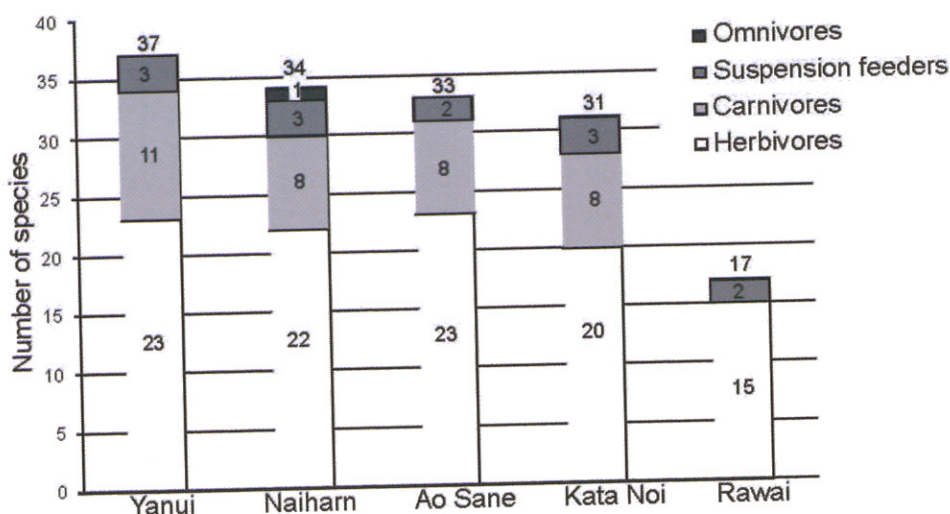


Figure 4. Species diversity and functional diversity at the five study sites.

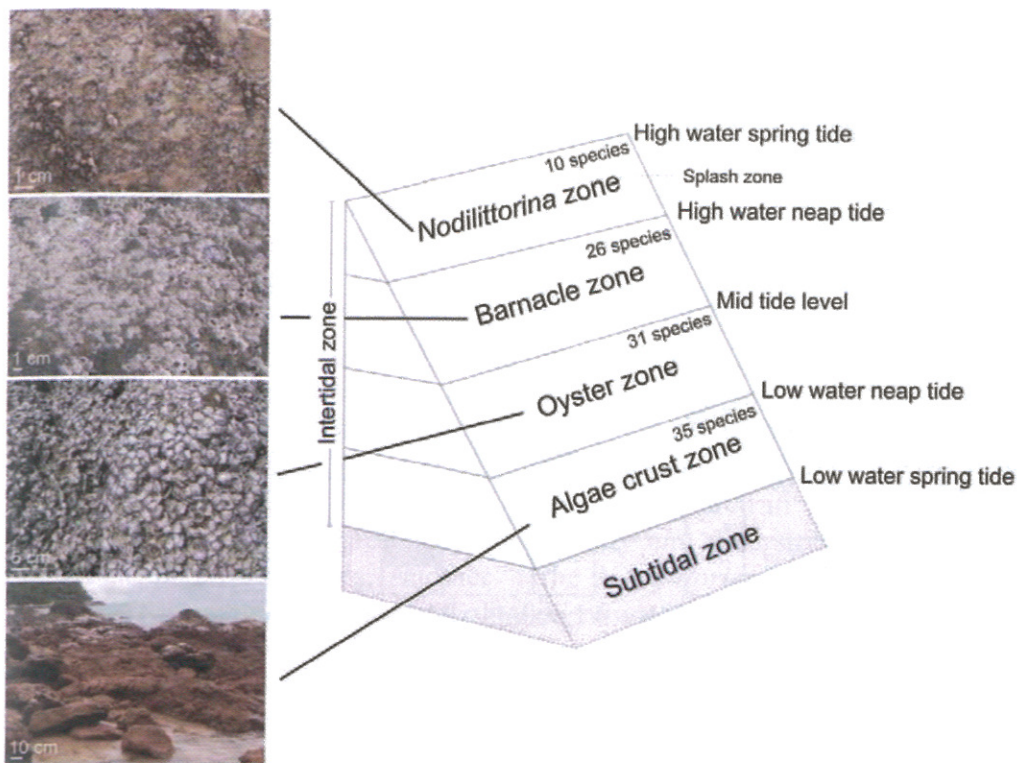


Figure 5. The four zones along rocky shores in the southern part of Phuket. Top photo: *Nodilittorina trochoides* in clusters in the *Nodilittorina* zone at Ao Sane. Middle photo top: barnacle zone at Naiharn. Middle photo bottom: *Saccostrea cucullata* in the oyster zone at Yanui. Bottom photo: The brownish algae zone at Yanui underneath the whitish oyster zone.

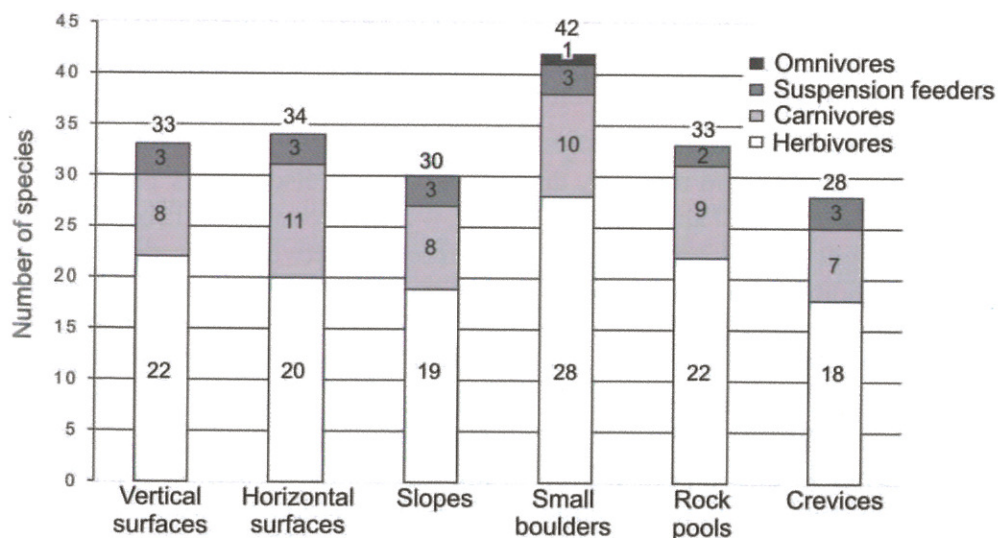


Figure 6. Species diversity and functional diversity at the six microhabitats.

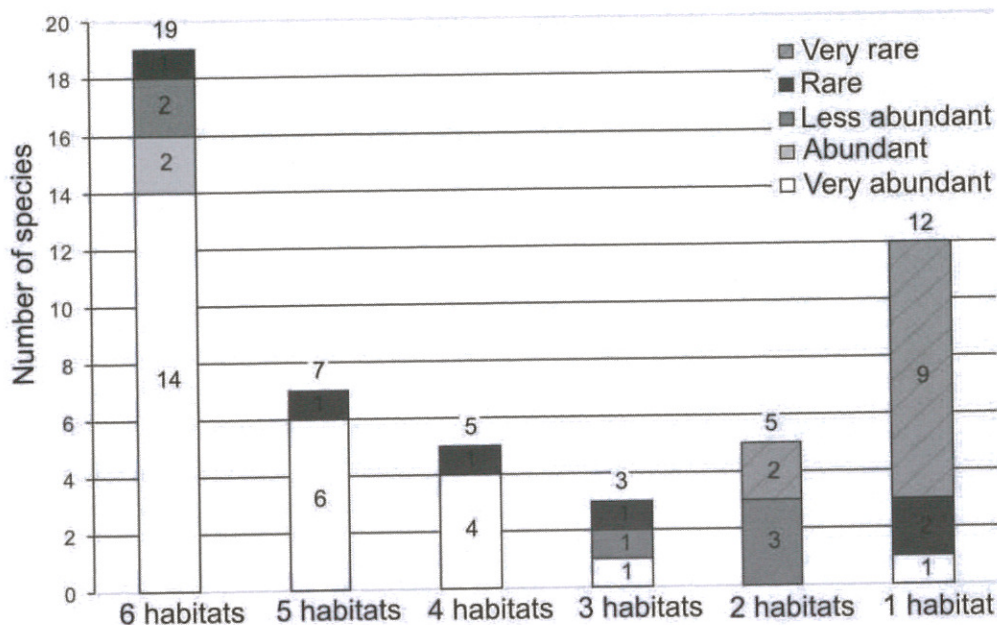


Figure 7. Number of species found in number of microhabitats. Subdivision of columns show number of species in each abundance level from very rare to very abundant, using the highest abundance level of a species found in one of the microhabitats.

DISCUSSION

The study sites

The species diversity and functional diversity of molluscs are similar at Yanui, Naiharn, Ao Sane, and Kata Noi despite the different orientations of the localities. The diversity ranges between 31 and 37 mollusc species and 29 of these are found regularly at all study sites (fig. 4, Table 1). The remaining eight species are rare or single individual specimens. The cluster analysis of the study sites shows a dissimilarity of 0.77 in the faunal composition between Yanui and the three other western localities (fig. 3a). This is due to the higher diversity at Yanui caused by the large occurrence of single individual species. The dissimilarity between

the other three western localities, Ao Sane, Naiharn, and Kata in the cluster analysis is primarily due to a difference in faunal composition, since the species diversity and functional diversity is similar (fig. 4; Table 1). The species diversity at the eastern locality Rawai is much lower with only 17 species represented out of which 15 also occurs regularly at the western localities (Table 1). The difference between the diversity at Rawai and the other sites is thus due to the absence of certain species at Rawai. Some of the absent species are found in the most exposed parts of the western rocky shores with the highest wave action, including *Cellana radiata*, *Nerita costata*, *Notoacmea flammea*, *Patelloida mufria*, and *Patelloida saccharina*

lanx. Not surprisingly no species preferring high wave energy settings are found at Rawai, which is located on the leeward side of the island. Unexpectedly, no mobile carnivores were found at Rawai, which is difficult to explain (fig. 4). All common carnivorous gastropods found at the western study sites belong to the Muricidae, which feed on bivalves, gastropods, and barnacles. A high density of both bivalves and gastropods are found at Rawai, whereas the density of barnacles is lower compared to the density at the western sites. Another difference is a higher density of crustaceans at Rawai.

The similarity in abundance, species diversity, and functional diversity of the western sites shows that orientation of the rocky shores on the windward side of the island is insignificant for these patterns. The lower similarity between the western sites and the eastern site, Rawai, shows that orientation of the rocky shores is important for patterns on a larger scale between the western windward side and the eastern leeward side of the island. In contrast, the density of molluscs is similar at the five study sites. In comparison, subtidal sediment characteristics (and the infauna) differ on the northern, central, and southern parts of the west coast bays (Hylleberg *et al.*, 1985).

The zonation

The *Nodilittorina* zone comprises 10 species, which are all mobile herbivores and of these five are

common and belong to the Littorinidae (fig. 2, Table 1). Many species from this family are adapted to arid conditions and are known to inhabit the uppermost intertidal zone on rocky shores (Stephenson and Stephenson, 1972). The remaining five species belong to the *Nerita* and *Planaxis* and occur rarely, indicating that this is not their preferred habitat. The *Nodilittorina* zone is barren in many places with only about 5% of the rock covered by *Nodilittorina* species gathered in clusters. The low density and diversity of molluscs in the *Nodilittorina* zone is due to the extreme environmental conditions. The granitic substrate becomes very hot during daytime and the zone is only wetted during spring high tide and during high wave activity. The marine species in this zone must thus be able to survive extreme heating of their body tissue and resist desiccation. Competition for suitable space, i.e. cracks and crevices, is high in this zone

The barnacle zone is characterized by a higher density and diversity of molluscs compared to the *Nodilittorina* zone and the presence of sessile suspension feeders and mobile carnivores (fig. 2). Bivalves are represented by only few specimens of *Saccostrea cucullata* and Isognomonidae sp. A. The low density of bivalves suggests that they are less resistant to extreme environmental conditions compared to gastropods. Species of Littorinidae and *Nerita*, together with *Cellana radiata* and *Siphonaria normalis* are the only common species in the

barnacle zone (Table 1). Other species in this zone are rare and occur primarily in crevices or in wet areas.

The oyster zone comprises the highest density of molluscs and oysters almost completely cover the rock (fig. 5). The increase in density and species diversity compared to the two zones above, the *Nodilittorina* zone and the barnacle zone is due to less extreme environmental conditions, as the zone occupies the space from the mid tide level to neap low water level. The five species of Littorinidae, which are abundant in the *Nodilittorina* and barnacle zones are absent in the oyster zone, probably due to competition for space with other molluscs. The mobile carnivorous gastropods occur in abundance in the oyster zone with 10 species represented. All three species of suspension feeding bivalves are represented in this zone.

The algae zone comprises the highest species- and functional diversity of molluscs due to more favourable conditions and the presence of rare subtidal species such as *Trochus maculatus*, *Miliariconus aristophanes*, and *Conus ebraeus*. The zone is primarily covered by algae crust and scattered oysters and gastropods, and the density of molluscs is lower compared to the oyster zone probably due to higher predation pressure by fish and crustaceans (fig. 2).

Dissimilarity in the faunal composition between the four zones can easily be recognized in the

cluster analysis (fig. 3b). The two lower zones, the oyster and the algae crust zone, are grouped together and the two upper zones, the *Nodilittorina* and the barnacle zone, are grouped with a similarity between the groups of 0.42. This indicates that there is a faunal turnover between the barnacle and the oyster zone in the middle of the intertidal zone, which is also the boundary between relatively wet and relatively dry substrate (fig. 2). The change in faunal composition is forced by the ability of the fauna to adapt to different environmental factors. Only four species, *Nerita chamaelion*, *Nerita costata*, *Nerita undulata*, and *Planaxis sulcatus* were found in all four zones and are thus able to survive these very different physical stresses together with biological factors such as competition for space and predation. This limited number of species which are able to survive in all four zones shows that the intertidal mollusc fauna are well adapted to each of the different environments the intertidal zone provides. The intertidal zonation thus increases the species diversity of the mollusc fauna in this ecosystem with different species able to live in different zones.

The microhabitats

A total of 26 species inhabit 5 or 6 microhabitats, of these 20 species are very abundant, indicating that all microhabitats are all well suited for these species (fig. 7). An increase in abundant species is observed going from 1 towards 6 inhabited habitats (fig. 7). This indicates that the molluscan fauna have no preferred

microhabitats and species which inhabit only one microhabitat are primarily single individual species.

The faunal composition is relatively similar for all microhabitats with a minimum similarity of 0.79 between the small boulder habitat and the other five microhabitats in the cluster analysis (fig. 3c). Furthermore, both species diversity and functional diversity are similar for all six microhabitats indicating that a higher number of microhabitats would not increase species diversity or functional diversity of the mollusc fauna, especially not if single individual species are excluded from the study (fig. 3c, fig. 6). This diversity pattern does not follow the hypothesis that the topological complexity of rocky habitats contribute to within-habitat diversity (Connor and McCoy, 1979; Huston, 1979; Levinton, 2001; Johnson *et al.*, 2003; Kostylev *et al.*, 2005). Kelaher (2003) found a negative relationship between the structural complexity of the substrate and gastropod species richness along rocky shores in Sydney, Australia. A negative relationship is not found in this study, where 94% of the studied species are gastropods, but an increase in diversity with an increase of microhabitats is not found either. This suggests that there is a different relationship between gastropod diversity and microhabitat diversity compared to other intertidal rocky shore biota. The high species diversity and the community structure of molluscs along the rocky shores of southern Phuket Island

reflect the intertidal environmental zonation and do not reflect the high diversity of microhabitats.

CONCLUSIONS

It is necessary to understand the ecology of different ecosystem with respect to faunal distribution, abundance and diversity to increase the knowledge of evolution of ecosystem as a response to the changing global environment. This study suggests that the main factor controlling species diversity and community structure of rocky shore mollusc faunas is the tide and not the structural complexity of the substrate and only four species are able to live in all four zones. A faunal turnover is found in the middle of the intertidal zone between the barnacle and the oyster zone, which is also the boundary between relatively wet and relatively dry substrate. Below this boundary an increase in mollusc density, species diversity, and functional diversity occur. Also large scale orientation of the shore control species diversity and community structure as diversity decrease on the Eastern leeward side of Phuket Island compared to the Western windward sites. The faunal composition, species diversity, and functional diversity of the mollusc fauna, which are primarily gastropods, are similar for all the microhabitats suggesting that all microhabitats are well suited for the fauna and increased structural complexity of the rocky shores is not accompanied by an increase in gastropod diversity as expected for rocky biotas.

ACKNOWLEDGEMENTS

The study was funded by the Faculty of Science, University of Copenhagen and the Carlsberg Foundation. I would like to thank the National Research Council of Thailand for help with permission of my research in Phuket, the staff of Phuket Marine Biological Center for provision of facilities and help, and Dr. Somchai Bussarawit for help getting organized in Thailand. Dr. Kresten Anderskov, Dr. Bodil Lauridsen, Professor Finn Surlyk, and Professor Jørgen Hylleberg Kristensen are thanked for constructive comments to the manuscript.

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