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Regional variations in tropical high intertidal
gastropod assemblages

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ABSTRACT

High intertidal gastropod assemblages in the Indo-Malaysian area and western Indian
Ocean have a higher incidence of presumed antipredatory devices (obstructed apertures, in
flexible opercula, low spires, and strong external shell sculpture) than high intertidal gastro-
pods found elsewhere in the tropics. Species numbers of high intertidal gastropods are
greatest in the Indo-Malaysian region, western Indian Ocean, and Caribbean; and lowest in
the South Atlantic and Polynesia. The pattern of regional variation in species number and
shell architecture of high intertidal gastropods contrasts with that of gastropods in other
shallow tropical marine habitats.

Compared to high intertidal gastropods, the generally smaller and more highly disperisible
high intertidal barnacles, bivalves, and algae have a uniformly low species number and
similar form throughout the tropics, and tend to possess broader geographic ranges. Of all
the high intertidal groups studied, gastropod assemblages show the greatest regional variation
in species number and architecture because the high intertidal habitat is more island-like
relative to gastropods than to autotrophs and filter-feeders. High species number, strong sub-
stratum specialization, and high incidence of inferred antipredatory devices among gastro-
pods occur in areas with long stretches of suitable contiguous coastline where climatic condi-
tions have remained stable for long periods of time.

1. Introduction

Among the first investigators to conduct comparative studies of marine
communities on a worldwide scale were Stephenson and Stephenson (1949),
Dahl (1952), and Thorson (1957). They, like their colleagues working in the
terrestrial realm, attempted to show that far-reaching similarities exist in the
morphological and reproductive adaptations of organisms belonging to un-
related taxonomic groups to similar physical conditions, and that, as a con-
sequence, assemblages geographically isolated from one another are similar in
the types of organisms encountered and in the manner by which space and food

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are divided among them. Thus, vertical zonation patterns on tropical rocky shores are generally comparable, and high and low intertidal representatives of a given group generally differ from each other in a predictable way (Vermeij, 1973a).

In earlier work (Vermeij, 1971, 1973b), I found that high intertidal limpets (Acmaeidae, Patellidae, Siphonariidae) and neritid gastropods are restricted either to limestone or to volcanic rock in the Indo-Malaysian region and western Indian Ocean, but that they occur on a wide variety of substratum types elsewhere in the tropics. With the exception of the possibly limestone-restricted West Indian littorinid Echininus nodulosus, other high intertidal gastropods do not appear to exhibit substratum specialization in any part of the tropics. Substratum specialization is confined to species whose soft parts are in contact with the rock surface during exposure to air, and occurs only in areas with large stretches of both kinds of substratum.

Elsewhere (Vermeij, 1974), I have argued that obstructed apertures, elongate apertures, inflexible opercula, low spires, and strong external shell sculpture among low intertidal open-surface rocky-shore gastropods are adaptations reducing successful attacks by crabs, fishes, and other predators which crush the shell or extract the soft parts directly from the aperture. When the incidence of these features was calculated for various assemblages of open-surface gastropods, unexpected and striking differences were observed among tropical provinces which were interpreted to reflect differences in vulnerability of molluscan prey species to predators of a given size, shape, and strength.

In this paper, I analyze high intertidal rocky-shore assemblages of organisms in various parts of the tropics with the following questions in mind:

(1) What patterns exist in species number and in the predation-related morphology of high intertidal gastropods?

(2) How are these regional patterns related to the pattern of substratum specialization?

(3) What regional pattern in species richness exists among high intertidal bivalves, barnacles, and algae, and why are these different from those exhibited by gastropods? and,

(4) How and why do the patterns of regional variation among high intertidal assemblages differ from those in other tropical marine shallow-water settings?

The evolution and biogeographic significance of the answers to these questions are discussed in the present paper.

The high intertidal is here defined as that part of the marine shore which lies at and above high water neap tide level, reaching up to the seaward-most occurrence of flowering plant vegetation.
2. Materials and Methods

Molluscs were collected by hand from high intertidal open rocky surfaces in each of the major tropical biogeographic provinces. A complete sample of the gastropod species was probably obtained at most localities visited. Observations on collected balanomorph barnacles and bivalves, as well as on algae, were supplemented with published information in the literature.

Among morphological measurements taken on gastropod shells are (1) the length: breadth ratio $S$ of the aperture or generating curve; and (2) the greatest linear dimension $l$ of the largest individual for each species at a given locality. In addition, a count was made within each assemblage of gastropod species whose shell possesses either an inflexible calcareous operculum or strong folds or teeth on the apertural margin impeding entrance into the aperture. A third apertural character restricting access to the soft parts, a narrow aperture ($S$ greater than 2.5) was not observed in high intertidal snails despite its common occurrence among low intertidal forms. Among high intertidal species, a calcareous operculum is restricted to the family Neritidae, but obstructed apertures occur in four families (Thaididae, Neritidae, Trochidae, and Ellobiidae). In calculating the relative number of species with apertural modifications, those possessing both an inflexible operculum and an obstructed aperture were counted only once. All species were weighted equally in spite of differences in abundance. The fraction of species with apertural modifications in each assemblage was multiplied by 100 to yield the index $I_{ap}$ of apertural modifications for that assemblage (see also Vermeij, 1974).

3. Results

a. Gastropods. Eight families of gastropods occur in tropical high intertidal assemblages. Of these, the Neritidae and Littorinidae are the most diversified widespread (see Vermeij, 1973a). The Neritidae are most numerous, both in absolute and relative number of species, in the Indo-Malaysian region and the western Indian Ocean; while the greatest absolute and relative diversity of Littorinidae is found in the Caribbean (Vermeij, 1973b). High intertidal representatives of the Planaxidae and Siphonariidae are restricted to the eastern Pacific and parts of the Indo-West-Pacific, while Trochidae and Ellobiidae are represented by a few species in the Caribbean and Indo-West-Pacific. Acmeidae and Thaididae occur at high shore levels in all tropical regions examined except Brazil and West Africa.

Table I. and Fig. 1 present data on $I_{ap}$ values, species number, and some habitat parameters in 26 localities throughout the tropics. Limestone upper-shore communities in the Indo-West-Pacific possess significantly higher $I_{ap}$ values than volcanic shores in the same region ($p < 0.01$, Mann-Whitney U-Test). This effect is most profound where the number of species is high (Palau, northwest Philippines, western Indian Ocean), and is much less pro-
Table I. Shell architecture, species number, and habitat of high-shore assemblages of shelled gastropods.

<table>
<thead>
<tr>
<th>Locality</th>
<th>Rock type</th>
<th>Wave exposure</th>
<th>I&lt;sub&gt;ap&lt;/sub&gt;</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Inner Indo-West-Pacific</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Koror, Palau</td>
<td>volcanic</td>
<td>sheltered</td>
<td>36</td>
<td>11</td>
</tr>
<tr>
<td>Ngemelis, Palau</td>
<td>limestone</td>
<td>rather sheltered</td>
<td>67</td>
<td>12</td>
</tr>
<tr>
<td>Calatagan, Luzon</td>
<td>limestone</td>
<td>rather sheltered</td>
<td>67</td>
<td>9</td>
</tr>
<tr>
<td>Nasugbu, Luzon</td>
<td>volcanic</td>
<td>rather exposed</td>
<td>29</td>
<td>7</td>
</tr>
<tr>
<td>Nyali, Kenya</td>
<td>limestone</td>
<td>rather exposed</td>
<td>62</td>
<td>13</td>
</tr>
<tr>
<td>Nosy-Be, Madagascar</td>
<td>volcanic</td>
<td>rather exposed</td>
<td>58</td>
<td>12</td>
</tr>
<tr>
<td>Pulau Subar Darat, Singapore</td>
<td>volcanic</td>
<td>rather sheltered</td>
<td>38</td>
<td>8</td>
</tr>
<tr>
<td>Peripheral Indo-West-Pacific</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chalan Anite Point, Guam</td>
<td>volcanic</td>
<td>rather exposed</td>
<td>20</td>
<td>5</td>
</tr>
<tr>
<td>Tipalao Beach, Guam</td>
<td>limestone</td>
<td>rather exposed</td>
<td>29</td>
<td>7</td>
</tr>
<tr>
<td>Kahuku Point, Hawaii</td>
<td>limestone</td>
<td>exposed</td>
<td>17</td>
<td>6</td>
</tr>
<tr>
<td>The Fjord, Sinai Peninsula</td>
<td>volcanic</td>
<td>rather sheltered</td>
<td>29</td>
<td>7</td>
</tr>
<tr>
<td>Marset el Et, Sinai Peninsula</td>
<td>limestone</td>
<td>rather sheltered</td>
<td>33</td>
<td>6</td>
</tr>
<tr>
<td>Ras Muhamad, Sinai Peninsula</td>
<td>limestone</td>
<td>rather sheltered</td>
<td>50</td>
<td>4</td>
</tr>
<tr>
<td>Eastern Pacific</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Academy Bay, Galapagos</td>
<td>volcanic</td>
<td>rather exposed</td>
<td>33</td>
<td>6</td>
</tr>
<tr>
<td>Naos Island, Panama Canal Zone</td>
<td>volcanic</td>
<td>rather sheltered</td>
<td>20</td>
<td>5</td>
</tr>
<tr>
<td>Playa de Panama, Costa Rica</td>
<td>volcanic</td>
<td>rather sheltered</td>
<td>13</td>
<td>8</td>
</tr>
<tr>
<td>Western Atlantic</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ilha Fernando de Noronha, Brazil</td>
<td>volcanic</td>
<td>exposed</td>
<td>25</td>
<td>4</td>
</tr>
<tr>
<td>Fort Point, Jamaica</td>
<td>limestone</td>
<td>exposed</td>
<td>23</td>
<td>13</td>
</tr>
<tr>
<td>Boca Playa Canoa, Curacao</td>
<td>limestone</td>
<td>exposed</td>
<td>27</td>
<td>11</td>
</tr>
<tr>
<td>Fort Bay, Saba</td>
<td>volcanic</td>
<td>exposed</td>
<td>38</td>
<td>8</td>
</tr>
<tr>
<td>Pointe des Chateaux, Guadeloupe</td>
<td>limestone</td>
<td>exposed</td>
<td>30</td>
<td>10</td>
</tr>
<tr>
<td>Vieux Habitants, Guadeloupe</td>
<td>volcanic</td>
<td>rather exposed</td>
<td>33</td>
<td>9</td>
</tr>
<tr>
<td>Cahuita, Costa Rica</td>
<td>limestone</td>
<td>rather exposed</td>
<td>36</td>
<td>11</td>
</tr>
<tr>
<td>West Africa</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dakar, Senegal</td>
<td>volcanic</td>
<td>exposed</td>
<td>25</td>
<td>4</td>
</tr>
<tr>
<td>Takoradi, Ghana</td>
<td>sedimentary</td>
<td>rather exposed</td>
<td>20</td>
<td>5</td>
</tr>
</tbody>
</table>

KEY:  I<sub>ap</sub>: Index of species with inflexible operculum or obstructed aperture. 
n: number of species.

nounced in the more peripheral regions with fewer species (Guam, Hawaii, Red Sea). The difference in I<sub>ap</sub> between assemblages on limestone and volcanic rock in the Indo-West-Pacific is almost entirely due to the relatively larger number of Neritidae on limestone as compared to volcanic shores. In the West Indies, I<sub>ap</sub> values and neritid species composition are similar on limestone and volcanic shores. Caribbean and peripheral Indo-West-Pacific values of I<sub>ap</sub> are similar to each other and to those in the tropical eastern Pacific and eastern Atlantic, and are all significantly lower than those in the inner Indo-West-
Figure 1. Relationship between $I_{ap}$ (gastropod apertural modifications) and substratum type in different regions of the tropics. Each point represents one locality.

**KEY:**

$I_{ap}$: Index of gastropod species with calcarious opercula or obstructed apertures. $I_{ap} =$ the fraction of species with apertural modifications times 100.

A: Inner Indo-West-Pacific.

B: Peripheral Indo-West-Pacific (Hawaii, Guam, Red Sea).

C: Eastern Pacific.

D: Western Atlantic, including Brazil.

E: West Africa.

Squares represent limestone substratum; round dots represent volcanic substratum.

Pacific ($p < 0.05$ in all cases). This difference is due not only to the greater importance of neritids in the last-named area, but also to the difference in architecture of Thaididae and Trochidae from different provinces. Of the four thaidids collected in high intertidal assemblages in Madagascar and Kenya (Morula anaxeres, M. fenestrata, M. fusconigra, and M. marginatra), all but M. fusconigra possess strong teeth on the outer lip of the aperture. In the Hawaiian Nucella harpa, the West Indian Purpura patula, and the West American P. pansa and Acanthina brevidentata, such apertural teeth are little if at all developed. The only high intertidal thaidid outside the Indo-West-Pacific with strong teeth on the outer lip is the West American Purpura columellaris, represented in my collections only from Academy Bay, Galapagos.
Among high intertidal trochids, the only species with marked apertural im-
pediments is *Monodonta labio*, represented in my samples from limestone
and volcanic shores in Palau, northwest Philippines, and Singapore, but also
known from southern Japan and Melanesia to Queensland west to the Sey-
chelles.

With the exception of various species of *Tectarius* (Littorinidae) in the Indo-
Malaysian area, *Nerita textilis* in the western Indian Ocean, and *Echininus
nodulosus* in the West Indies, sculpture among high intertidal gastropods is much
less strongly developed than in such low intertidal open-surface genera as
*Drupa*, *Chicoreus*, *Muricanthus*, *Vasum*, *Cymatium*, and some *Trochus*, *Turbo*,
*Cerithium*, *Morula*, and *Thais*. Furthermore, strong sculpture among low inter-
tidal forms often consists of spines, nodes, or thick axial ridges, while in the
high intertidal the sculpture is usually less coarse and massive. For example,
there are from 12–15 spirally arranged tubercles per whorl on the shell of *E.
nodulosus*, in contrast to 7–11 in low intertidal *Thaididae*, *Vasidae*, and
*Trochidae*. The sculpture in most nodulose littorinids and in the trochid
*Monodonta labio* is much finer than that in *Echininus*. Such differences in num-
ber of axial elements per whorl are largely independent of the rate of whorl
expansion of the shell. In most species of *Nerita*, *Littorina*, and *Planaxis*,
sculpture consists of spirally continuous ridges rather than discrete nodes or
tubercles. Despite the general reduction of shell sculpture among high-shore as
compared to low-shore gastropods, it must be pointed out that there tends to
be an interspecific increase in intensity of shell sculpture from low to high shore
levels among Littorinidae and Neritidae, which is probably related to an in-
crease in relative area of heat reflectivity (Vermeij, 1973a).

Low spires and indistinct shell apices (apical half-angle greater than 45°)
occur commonly among low intertidal gastropods, but among high intertidal
species are restricted to some Neritidae, primarily species such as *Nerita
textilis*, *N. spengleriana*, *N. maxima*, *N. insculpta*, and *N. undata* in the western
Indian Ocean and Indo-Malaysian region. Most other high intertidal gastro-
pods possess a prominent apex and high spire.

High intertidal gastropod species number within the Indo-West-Pacific is
highest in the Indo-Malaysian region (Palau and northwest Philippines) and
the western Indian Ocean, decreasing towards more peripheral parts of the
Indian and Pacific Oceans (Tables I.–II.). At least some of this centrifugal
decrease in diversity is associated with the lack of extensive shorelines in the
Central Pacific and parts of the Indian Ocean (Taylor, 1971). The low species
numbers from Singapore (Table I.) and Ceylon (Table II. Atapattu, 1972)
appear to represent a belt of reduced diversity between richer areas to the east
and southwest. In the West Indies, species number is relatively high, the smallest
number (8) being recorded from the small volcanic island of Saba in the eastern
Caribbean (Table I). West African and Brazilian shores (see also Vermeij
and Porter, 1971) possess fewer than 5 species, while those in the eastern
Table II. Numbers of gastropod species from some Indo-West-Pacific localities.

<table>
<thead>
<tr>
<th>Locality</th>
<th>Number of species</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tulear, southwest Madagascar</td>
<td>11</td>
<td>Plante, 1964</td>
</tr>
<tr>
<td>Inhaca Island, Mozambique</td>
<td>about 13</td>
<td>Kalk, 1958</td>
</tr>
<tr>
<td>Aldabra Atoll, Indian Ocean</td>
<td>12 to 13</td>
<td>Taylor, 1970; Hughes, 1971</td>
</tr>
<tr>
<td>Ceylon</td>
<td>8 to 9</td>
<td>Atapattu, 1972</td>
</tr>
<tr>
<td>Queensland (northern mainland coast)</td>
<td>about 10</td>
<td>Endean et al., 1956</td>
</tr>
<tr>
<td>Kwajalein and Majuro, Marshall Islands</td>
<td>6</td>
<td>Kay, 1971</td>
</tr>
<tr>
<td>Raroia Atoll, Tuamotus</td>
<td>3 to 4</td>
<td>Morrison, 1954</td>
</tr>
<tr>
<td>Fangataufa Atoll, Tuamotus</td>
<td>3</td>
<td>Salvat, 1970</td>
</tr>
<tr>
<td>Mururoa Atoll, Tuamotus (before atomic testing)</td>
<td>2</td>
<td>Chevalier et al., 1968</td>
</tr>
<tr>
<td>Fanning Island, Line Islands</td>
<td>4</td>
<td>Kay, 1971</td>
</tr>
</tbody>
</table>

Pacific are intermediate in diversity between South Atlantic and Caribbean assemblages.

In all regions, the number of gastropod species increases with exposure to wave action (see also Plante, 1964). For example, 7 species occur on sheltered volcanic shores near the ORSTOM laboratory at Nosy-Be, Madagascar, while 12 can be found on more exposed volcanic rocks at the nearby village of Ambatoloaka. The relation between the index $I_{ap}$ of apertural modifications and the number of species per high intertidal assemblage varies from weakly positive to weakly negative, in the various regions, and is nowhere significant. No relation exists between $I_{ap}$ and degree of exposure to wave action (Table I).

Comparisons of maximum size distributions of species show that no significant differences exist among any but a few pairs of high intertidal gastropod assemblages. Body size is markedly lower among species in West Africa, mainland Brazil, and Hawaii than elsewhere in the tropics, rarely exceeding 20 mm. The various species of *Tectarius* (1 up to 60 mm) are the largest known Littorinidae, and occur in the southern Philippines, Indonesia, and parts of Melanesia (Rosewater, 1972). The largest high intertidal neritid (*Nerita scabricosta*, $1 = 50$ mm) and siphonariid (*Siphonaria gigas*, $1 = 52$ mm) occur in the eastern Pacific.

b. **Bivalves and barnacles.** Compared to gastropods, the diversity of bivalves and barnacles in the high intertidal is low and constant throughout the tropics. Some oysters (*Ostrea iridescens* in the eastern Pacific, *O. tulipa* in West Africa, *O. cucullata* in the Indo-West-Pacific) and mussels (*Brachidontes dominguensis* in the West Indies, *B. solisianus* in mainland Brazil, *B. puntarenensis* in West America, *B. niger* in West Africa, *B. variabilis* in the Indian Ocean and Red Sea, *B. crebristriatus* in Hawaii) occur abundantly on the shore up to about high water neap level, but do not generally extend above this level. Among
bivalves, only the isognomonid *Parviperna dentifera*, with a wide range throughout the Indo-West-Pacific and Red Sea, occurs in exposed cracks above high water neap. Minute species of the erycinid genus *Lasaea* may occur on the upper shore in the byssus of *Parviperna* or in deep cracks (Taylor, 1971).

Most high intertidal tropical shores save those of small isolated islands or archipelagos such as St. Helena (Colman, 1946), Fernando de Noronha (Vermeij, 1972a), and the Galapagos (Hedgpeth, 1969) are populated by one to three species of chthamalid barnacles. The majority of these belong to the warm temperate to tropical genus *Chthamalus*: *C. dentatus* in West Africa and southwest Madagascar (Lawson, 1966; Plante, 1964); *C. stellatus bisinuatus* in mainland Brazil (da Costa, 1962; Vermeij and Porter, 1971); *C. s. angustitergum* in the Florida Keys (Stephenson and Stephenson, 1950); *C. caudatus*, *C. malayensis*, and *C. withersi* on the mainland coast of Queensland (Endean et al., 1956). In the western Indian Ocean and Red Sea, the only high intertidal barnacle is the monotypic *Tetrachthamalus oblitteratus* (Taylor, 1968, 1971; Fishelson, 1971; Achituv, 1972).

Analysis of latitudinal ranges given by Guiler (1960) for Australian barnacles demonstrates that all high intertidal species on the mainland coast of northern Queensland are restricted to tropical waters, and that all but one of the five low intertidal barnacles there are similarly restricted. This similarity in latitudinal restriction between high and low intertidal species appears also to hold for barnacles on other tropical shores, but there is some evidence that the high-shore species on subtropical coasts extend to higher latitudes than their lower-shore counterparts. At Dakar, Senegal, the high intertidal *C. stellatus* extends north to the British Isles, while the low intertidal *Balanus tintinnabulum* is restricted to warmer waters (see also Sourié, 1954). Lipkin and Safriel (1971) found that high intertidal barnacles on the Mediterranean coast of Israel belong to two warm temperate species of *Chthamalus*, and that the low intertidal to subtidal *Balanus amphitrite* is mostly tropical in distribution and has colonized the Mediterranean through the Suez Canal from the Red Sea. Kalk (1959) and Marsh and Hodgkin (1962) in Mozambique and southwest Australia respectively have also noticed that high-shore communities in these areas are more temperate in appearance than the corresponding low-shore assemblages.

c. *Algae.* High intertidal algae are mostly microscopic Cyanophyta with a cosmopolitan distribution, or moss-like eukaryotic forms distributed throughout the tropics. In Cameroon, West Africa, 4 out of 5 high intertidal eukaryotic algae listed by Lawson (1955) are cosmotropical, the only exception (*Cladophora camerunica*) being a somewhat larger form found only in the lowest part of the zone. Similarly high incidences of pantropical distributions among high intertidal algae are found among the 4 species listed by Stephenson and Stephenson (1950) for the Florida Keys and by Vroman (1968) for the Dutch Windward
Islands, and among the 5 species listed by Lawson (1956) for Ghana. The 4 or 5 high intertidal algae on limestone shores in Tanzania and Kenya (Lawson, 1969) are also known from other tropical coasts. Analysis of latitudinal distributions of algae in the Western Atlantic (compiled from data in Taylor, 1957, 1960) indicates that only one of the four high intertidal eukaryotic algae listed by Vroman (1968) from Guana and Little Bays, St. Maarten, extends to north temperate waters; and only 4 out of 32 low intertidal or shallow subtidal non-epiphytic algae from the same localities extend into the north temperate latitudes. There appears thus not to be a significant difference in extent of latitudinal range between high and low intertidal algae in the tropics, in contrast to the distinctly more tropical aspect of high intertidal snails as compared to lower-shore species (Vermeij, 1972, 1973a, b).

4. Discussion

The incidence of apertural teeth, inflexible opercula, low spires, and strong sculpture among high intertidal gastropods is, in all but one locality (Vieux Habitants, Guadeloupe), lower than among corresponding low intertidal open-surface assemblages. This, together with the lack of elongate apertures among high intertidal species, may reflect a general decrease in the importance and intensity of predation at high shore levels relative to that lower on the shore. Regional variations in these features within high intertidal communities also suggests that intensity of predation is probably higher in the Indo-Malaysian region and western Indian Ocean than elsewhere in the tropics. This suggestion is supported by the abundance of crab-inflicted shell damage on Indo-West-Pacific gastropods as compared to those in the tropical Atlantic. Experimental work is now in progress to test the above hypotheses.

The trend in $I_{ap}$ and the incidence of other presumed antipredatory devices among high intertidal gastropods strikingly parallels that of substratum specialization. In Indo-West-Pacific assemblages with high species number and well-marked substratum specialization (Indo-Malaysian region and western Indian Ocean), $I_{ap}$ is high, while in the more impoverished peripheral Indo-West-Pacific, the Singapore-Ceylon region, and other variably diversified tropical assemblages where substratum specialization is rare or absent (Vermeij, 1971, 1973b; Atapattu, 1972), $I_{ap}$ is uniformly low. No high intertidal algae, barnacles, or bivalves appear to be specialized to particular rock types, despite the fact that high intertidal algae are more luxuriant on shaded limestone than on shaded volcanic substrata (see e.g. Vroman, 1968), and that more intense grazing by fishes on limestone causes barnacles to be more frequent on harder rock types (Newman, 1960; Stephenson, 1961).

The pattern of regional variation in species number and shell architecture seen in high intertidal gastropods contrasts with that in other shallow-water marine habitats. On low intertidal open rocky surfaces, $I_{ap}$ values and the in-
cidence of strong sculpture and low spires are high in the Indo-West-Pacific and eastern Pacific, and significantly lower in the tropical Atlantic (Vermeij, 1974). Species number in this habitat is relatively constant throughout the tropics except in the south Atlantic, where it is markedly lower. In low intertidal undersurface habitats, \( I_{ap} \) and species number appear to vary little and without regional trend (Vermeij, 1974). Mangrove swamps are characterized by gastropod assemblages with uniformly low \( I_{ap} \) values never exceeding 25; species number and mean adult body size of species is highest in the Indo-Malaysian region, lower in the eastern Pacific, and lowest in the Caribbean, West Africa, and the peripheral Indo-West-Pacific (Madagascar, Red Sea, Guam) (Vermeij, 1973c).

Spatial differences in the diversity, taxonomic composition, and architecture of a given group of organisms among mutually isolated but physically comparable communities may result from differences in the nature and intensity of biotic interactions, subtle differences in climate, historical and geographic factors, or some combination of these. From the data presented in this paper, it is evident that these factors do not affect all taxonomic groups equally or in the same way. On the upper shore, the most marked regional variations and the smallest geographic ranges are found among the gastropods which, in contrast to barnacles, bivalves, and algae, are mobile and relatively large and as adults depend for food on other organisms living in situ. High intertidal filter-feeders and algae are sedentary as adults, tend to possess much greater powers of dispersal, and are notably small in adult body size, both in comparison to high intertidal snails and to lower intertidal representatives of their respective groups (Jackson and Vermeij, 1974). In short, high intertidal localities are more like islands for high intertidal gastropods than for bivalves, barnacles, and algae, both from the point of view of dispersability and specialization to particular environmental conditions. Furthermore, tracts of high intertidal shore and of mangrove swamp are less continuously distributed and thus more like islands than are low intertidal open rocky-surface habitats and especially the undersurfaces of low-shore stones.

Briggs (1966) and Vermeij (1974) have argued that the Pacific and Indian Oceans have undergone less fluctuation in climate during the late Tertiary and Pleistocene than did the smaller, more land-locked Atlantic. As noted by Sanders (1968) and Futuyma (1973), stability of physical conditions over long periods of time may result in the proliferation of biotic interactions and in habitat or food specialization as compared to that in temporally more unpredictable areas. It should also be pointed out that, since the probability of extinction of a population is negatively correlated with population size and with area of suitable continuous habitat (given density-independent factors), any given fluctuation in physical regime will have a relatively greater effect on a species in a small habitat patch than on a population in a larger one. The richness of the Indo-Malaysian area in species of high intertidal gastropods, scleractinian
corals (Stehli and Wells, 1971; Rosen, 1971), and mangrove trees and crabs (Macnae, 1968), may be thus in part due to the climatic stability of the area over long periods of time, and to the presence of extensive stretches of suitable habitat on continental shores and on large and small islands. The probable greater importance of predation in high intertidal communities in this region relative to other coasts is consistent with the hypothesis of long-term climatic stability, and might be expected in large habitat patches where relatively small populations of metabolically active predators can be supported (MacArthur and Wilson, 1967). The low diversity of high intertidal gastropods in West Africa, Brazil, and the eastern Pacific may be partly due to the intermittent occurrence of rocky shore there (Lawson, 1966; Vermeij and Porter, 1971; Glynn, 1972). By contrast, long stretches of high intertidal rocks occur in the West Indies, but large climatic fluctuations in the recent geological past may have left insufficient time for the elaboration of biotic interactions such as predation at both high and low shore levels. Despite claims to the contrary (Ladd, 1960), it appears that the present-day trends in diversity or other community properties of shallow-water marine organisms cannot be accounted for solely by the water movements due to currents and winds (see also Briggs, 1967).

In summary, the pattern of variation in community composition is determined by the insularity of the habitat patches, which differs from group to group. The greatest degree of regional variation among the tropical high intertidal groups investigated here is found in the gastropods which, partly because of their large size relative to high intertidal autotrophs and filter-feeders, “see” high intertidal habitats more as islands, and are therefore more affected by present-day geographic relationships. In the comparatively “continental” Indo-Malaysian area and the western Indian Ocean, where long stretches of contiguous suitable shoreline occur and where climatic conditions have apparently remained stable over long periods of time, gastropod species number is high, substratum specialization is well developed, and relatively intense predation by shell-breaking or aperture-intruding predators is inferred from gastropod prey shell form. In other parts of the tropics, where either shorelines are less contiguous or the physical regime has been less constant than in the two Indo-West-Pacific areas, substratum specialization and inferred antipredatory devices among gastropods are little developed, and species number is variable. High intertidal barnacles, bivalves, and algae, which have wider geographic ranges than most gastropods, show great uniformity in species composition and form as compared to gastropods.

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