

## REVIEW

# Interoceanic differences in adaptation: effects of history and productivity\*

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**ABSTRACT:** Previously published evidence indicated that the degree of habitat specialization and enemy-related adaptation among shallow-water tropical marine species was greatest in the Indo-West-Pacific (IWP), intermediate in the Eastern Pacific (EP), and lowest in the Western Atlantic (WA) and Eastern Atlantic (EA). New data on the incidence of unsuccessful shell breakage (measured as the frequency of shell repair) and on the importance of shell breakage as a cause of death for shallow-water gastropods complicate, but do not invalidate, this picture. Columbelloid and planaxid gastropods conform to the expected interoceanic pattern of shell repair in that the lowest frequencies of repair were found in the Atlantic; but the Cerithiidae and Thaididae showed no interoceanic differences in repair, and the Conidae exhibited a contradictory pattern in which repair was most frequent in the WA and least frequent in the IWP. Great intraregional variation existed in the contribution that breakage made to overall gastropod mortality, as inferred from analyses of dead shells. There was a tendency for breakage to be relatively more important as a cause of death in the IWP and EP than in the WA, but the differences were not statistically significant. A review of other recent literature generally supported the hypothesis that the IWP biotas have undergone more specialization with respect to habitat and enemy-related adaptation than have marine biotas in tropical America. Available historical evidence suggests that these differences are attributable to contrasting geological histories. In the IWP, extensive speciation, especially among well-armored molluscs, took place in the absence of significant extinctions. In the WA, widespread extinctions selectively eliminated armored gastropod taxa, which were not replaced through diversification of Pliocene and Pleistocene survivors. The apparent decline of planktonic productivity in many parts of the WA following uplift of the Central American land bridge during the Pliocene may have contributed to the observed pattern of molluscan extinctions. In the EP, where productivity has remained high, extinction rates were lower, and some highly adapted species have invaded from the IWP. The paper closes with a discussion of future directions in research.

## INTRODUCTION

The tropical shallow-water marine biotas of the world fall into 4 biologically distinct regions that differ not only in their diversity of resident species, but also in such attributes as the size and architecture of individual organisms and patterns of habitat specialization. These regions are: (1) the Indo-West-Pacific (IWP) region, stretching from the Red Sea and East Africa in the west to Polynesia in the east, and from southern Japan

in the north to northern New South Wales (Australia) in the south; (2) the Eastern Pacific (EP), extending from the Gulf of California to northern Peru, and including the Galapagos and other islands off the west coast of tropical America; (3) the Western Atlantic (WA), including the coasts of Florida, the Gulf of Mexico, the West Indies, and the continental east coast of tropical America from Mexico to central Brazil; and (4) the Eastern Atlantic (EA), extending along the west coast of Africa from Senegal to Angola, and including several island groups in the Atlantic (Briggs 1974).

Previous work has suggested that many of the observed differences reflect contrasting geological and biological histories as well as interoceanic patterns of

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planktonic productivity (Vermeij 1978, 1986), which together have resulted in interoceanic differences in the evolutionary impact of competition, predation, and symbiosis. The IWP, where extinction rates have been low and speciation frequent, is thought to have evolved biotas in which the level of expression of predation-related and competition-related traits is high, especially in the highly productive waters adjacent to the continents and large islands of the Indo-Malaysian region. In the WA, which was ravaged by extinctions during the Pliocene and Pleistocene, and where planktonic productivity apparently declined since the closure of the Central American seaway in the Pliocene, traits related to predation and competition have remained or become less well developed. The EP is intermediate between the IWP and WA in the expression of some predation-related traits. Its generally high productivity, low extinction rates, and recent biotic contact with the IWP make this region biotically rigorous, especially in reef environments.

The purpose of this paper is to assess this picture in the light of new data on the successful and unsuccessful predation of shell-breaking gastropods, and in the light of other recently published work. As will be seen, the new data complicate the interoceanic patterns and suggest some modifications in the interpretation of biogeographical differences among the 4 major tropical marine regions.

## GASTROPOD SHELL ARCHITECTURE AND REPAIR

The shells of gastropods often function as effective fortresses of armor against a great variety of predators that break, drill, swallow, or invade their prey. Shell features promoting resistance include large size, a thick shell wall, a high spire (associated with the ability to retract the body far from the apertural edge), tight coiling, a narrow or thick-lipped aperture, a tightly fitting inflexible operculum in the aperture, and strong reinforcing shell sculpture (Vermeij 1978, 1982a, 1987, Palmer 1979, Bertness & Cunningham 1981).

Architectural studies of local assemblages of shallow-water gastropods from rocky bottoms reveal that the incidence and degree of expression of armor (especially of narrow or contracted apertures, compact low spires and tight coiling, and strong external sculpture) are highest in the IWP, intermediate in the EP, and relatively low in the WA and EA (Vermeij 1974b, 1978). A similar pattern is seen among assemblages of high intertidal gastropods (Vermeij 1974a). These interoceanic patterns are evident even within individual gastropod families. They have been documented in the Neritidae, Trochidae, Thaididae, Fasciolaridae, and Conidae (Vermeij 1978, 1979b, Vermeij & Currey

1980). Among gastropods from unconsolidated sediments, armor is again best developed in the IWP, but in contrast to hard-bottom gastropods there is no significant difference in armor between WA and EP assemblages (Vermeij 1978, Vermeij et al. 1980).

Repaired shell breaks provide additional evidence concerning the geography of shell armor. During an unsuccessful attempt by a predator to break a gastropod shell whose outer lip is not internally reinforced, the outer lip and adjacent parts of the shell are often damaged. The gastropod subsequently repairs the injury, but a record of the encounter is preserved as a scar whose course across the outer shell surface departs from the growth-lines marking previous positions of the intact outer lip. The absence of scars indicates one of 3 possibilities: (1) all attacks by shell-breakers were unsuccessful, and the predator was so weak that no damage was caused; (2) all attacks by shell-breakers were successful, that is, they were mortal to the gastropod; and (3) shell-breaking predators were absent (Vermeij 1982b, Schindel et al. 1982, Signor 1985). If explanations (2) or (3) apply, there were no unsuccessful predatory attacks and selection in favour of greater armor as a form of resistance is unlikely. If scars or other signs of sublethal shell damage are present, the potential for selection in favor of increased armor exists. The greater the frequency of repair (number of scars per shell in a sample), the greater this potential is (Vermeij 1982b). It should be emphasized that the incidence of scars, and therefore the potential for selection, depends both on the relative strength of the predator and on its abundance; and that damage does not always result in injury at the lip. I have seen many shells of the thaidid genus *Drupa* whose sharp spines were apparently broken by a fish or other predator while the snail was still alive. Because the mantle edge had grown beyond these spines, the latter were not repaired. The frequency of repair is therefore a conservative measure of unsuccessful shell breakage, especially if the breaking agent is a fish or large crab that attempts to crush the shell outright instead of attacking it at the lip.

Published surveys of the incidence of shell repair show that in *Nerita*, a genus of high intertidal gastropods, the highest frequencies occur in the IWP, followed respectively by the EP, WA, and EA (Vermeij 1978). In the sand-dwelling Terebridae, repair is again most frequent in the IWP, but no differences were detectable among frequencies in the EP and WA (Vermeij et al. 1980). The high frequencies in the IWP were surprising in view of the fact that very slender terebrids, in which frequencies of repair were significantly lower than in squatter species (Vermeij et al. 1980, Signor 1985), are especially well represented in the IWP region. Signor (1985) has suggested that the aper-

Table 1. Frequencies of repair in large rock-dwelling Columbellidae. N: number of shells; Freq.: frequency of repair (number of scars divided by number of shells)

Region and Species	Locality	N	Freq.	
IWP <i>Pyrene versicolor</i>	Pujada Bay, Mindanao	12	0.50	
	Dodinga Bay, Halmahera	13	0.31	
	Moti Island, Molluccas	16	0.31	
	<i>P. spp.</i>	Bagabag Is. Papua New Guinea	12	0.75
	<i>P. ocellata</i>	Honduras Bay, Mindoro	20	0.10
	<i>P. testudinaria</i>	Ulang, Palau	11	0.18
	<i>P. deshayesii</i>	Western Shoals, Guam	12	0.33
EP <i>Anachis rugosa</i>	Chepillo, Panama	10	0	
	<i>A. boivini</i>	Paitilla, Panama	10	0
	<i>A. varia</i>	Playa Venado, Panama	11	0
	<i>A. fluctuata</i>	Isla Perico, Panama	50	0.08
	<i>A. spp.</i>	Paitilla, Panama	42	0.05
WA <i>Columbella mercatoria</i>	Handikurari, Aruba	12	0	
	Piscadera, Curaçao	9	0	
	Santa Cruzbaai, Curaçao	27	0.11	

ture of these slender terebrids is so small that most shell-peeling calappid crabs, which appear to be the chief shell-injuring predators of these gastropods, are unable to gain a purchase on the outer shell lip for peeling. If comparisons were made only among squat species, the interoceanic difference in the incidence of

repair would be even more pronounced than it was with all species included.

In order to explore interoceanic differences in molluscan predation further, I surveyed 5 additional families of shallow-water gastropods with respect to the incidence of scars. Samples of 8 or more shells were

Table 2. Frequencies of repair in large rock-shore Planaxidae. Key as in Table 1

Region and Species	Locality	N	Freq.
IWP <i>Planaxis sulcatus</i>	Majuro, Marshalls	40	0.35
	Dravuni Island, Fiji	15	0.13
	Badisika, Papua New Guinea	16	0.11
	Piti Channel, Guam	17	0
	Jef Bie, Irian Jaya	15	0.13
	Tajandoe, Kei Islands	8	0
	Baclayon, Bohol	9	0.11
	Ravao Is., Papua New Guinea	12	0
	Tipalao Beach, Guam	22	0.14
	Ngerchebal Island, Palau	9	0.22
	Subar Darat, Singapore	11	0
	Nasugbu, Luzon	11	0
	Salu, Singapore	8	0
	Malakal, Palau	10	0.10
	Eilat Lagoon, Israel	8	0
	Ras Muhamad, Sinai	15	0.13
	<i>P. labiosa</i>	Coconut Island, Oahu	8
<i>Supplanaxis niger</i>	Ayem, Irian Jaya	34	0
	Salafai, Pagan	12	0
	Pialama, Pagan	32	0.06
	Anatahan	24	0.04
EP <i>P. planicostatus</i>	Playa Brava, Panama	10	0.40
	Naos Island, Panama	30	0.23
WA <i>S. nucleus</i>	Piscadera, Curaçao	9	0
	Playa Adaro, Venezuela	8	0
	Fort Bay, Saba	9	0
	Cove Bay, Saba	11	0
	Fort Randolph, Panama	12	0
	Cahuita, Costa Rica	11	0
	Rio Bueno, Jamaica	8	0

systematically examined for scars on the body whorl (or, in the case of cerithiids, the last 2 whorls). All samples were taken from my collections except in the case of the Conidae. For the latter family, my material was supplemented with samples in the collections of the U.S. National Museum of Natural History (Washington), Delaware Museum of Natural History, Philadelphia Academy of Natural Sciences, San Diego Natural History Museum, Australian Museum (Sydney), and the collection of A. J. Kohn at the University of Washington (Seattle).

I assumed that scarred shells were collected according to their abundance. This assumption is amply justified for my own collections, but the tendency for collectors to take only perfect specimens might cause the incidence of repair to be underestimated in museum samples. In order to test the assumption that museum samples are not biased with respect to the incidence of scars, I compared the frequencies of repair between my material and museum material in the 2 species of *Conus* for which the number of samples was adequate. As expected, there was no difference in

frequency of repair between my samples and museum lots in either *C. ebraeus* (mean frequency  $0.25 \pm 0.18$  for 7 samples in my collection,  $0.22 \pm 0.15$  for 15 museum samples) or *C. sponsalis* (mean frequencies, respectively,  $0.17 \pm 0.16$  for 7 samples and  $0.11 \pm 0.075$  for 11 samples). Even if repaired shells were underrepresented in museum collections, there is no reason to believe that the bias would be greater for some geographical regions than for others.

Interoceanic patterns more or less consistent with expectation were found in 2 families. Large rock-dwelling Columbellidae (adults 10 to 25 mm long) had significantly lower frequencies of repair in tropical America (WA and EP) than in the IWP ( $p < 0.01$ , Mann-Whitney U-test). No difference was evident between the WA (3 samples of *Columbella mercatoria*) and the EP (Table 1). For large (10 to 40 mm long) rock-dwelling Planaxidae, WA samples (all belonging to *Supplanaxis nucleus*) had significantly lower frequencies of repair than did IWP samples ( $p < 0.03$ , Mann-Whitney U-test; Table 2). The 2 EP samples of *Planaxis planicostatus* both had high frequencies of repair, but

Table 3. Frequencies of repair in small rocky-shore and other epifaunal Cerithiidae. Keys as in Table 1

Region and Species	Locality	N	Freq.	
IWP	<i>Cerithium columna</i>	Pago Bay, Guam	10	0.20
		Majuro, Marshalls	13	0.23
		Majuro, Marshalls	13	0.15
		Majuro, Marshalls	11	0.18
		Pujada Bay, Mindanao	19	0.53
	<i>C. zonatum</i>	Piti Channel, Guam	89	0.04
		Majuro, Marshalls	30	0.23
	<i>C. sejunctum</i>	Pago Bay, Guam	17	0.12
	<i>C. suturale</i>	Pago Bay, Guam	19	0.19
		Agat, Guam	15	0.13
		Bangi Island, Guam	11	0.09
	<i>C. rostratum</i>	Pago Bay, Guam	51	0.10
	<i>C. bavayi</i>	Majuro, Marshalls	17	0.82
	<i>C. trailli</i>	Arakabesan, Palau	12	0.33
	<i>Clypeomorus nympha</i>	Pago Bay, Guam	18	0.17
	<i>C. bifasciatus</i>	Baclayon, Bohol	33	0.76
		Pago Bay, Guam	15	0.20
		Piti Channel, Guam	11	0
		Pujada Bay, Mindanao	11	0.45
Boear, Aru Islands		11	0.18	
<i>C. batillariaeformis</i>		Ravao Is., Papua New Guinea	37	0.43
		Arakabesan, Palau	12	0.25
EP	<i>Cerithium adustum</i>	Playa Brava, Panama	15	1.00
		Playa Brava, Panama	10	0.40
	<i>C. menkei</i>	Anconcito, Ecuador	20	0.45
		Paitilla, Panama	48	0.33
		Chepillo, Panama	22	0.64
WA	<i>C. lutosum</i>	Cahuita, Costa Rica	13	0.46
	<i>C. litteratum</i>	Cahuita, Costa Rica	29	0.10
	<i>C. muscarum</i>	Gasparilla, Florida	13	0.31
	<i>C. atratum</i>	Sanibel Island, Florida	11	0.45
	<i>C. eburneum</i>	Rumaway Bay, Jamaica	26	0.15
	Bahia de Osteones, Puerto Rico	21	0.33	

Table 4. Frequencies of repair in rock-dwelling Thaididae that in the juvenile stage at least have a broadly open aperture. Keys as in Table 1

Region and Species	Locality	N	Freq.	
IWP	<i>Thais aculeata</i>	Palau	14	0
	<i>T. savignyi</i>	Gulf of Eilat	17	0.05
	<i>T. distinguenda</i>	Northern Molluccas	17	0.05
	<i>T. armigera</i>	Manipa, Molluccas	8	0
	<i>Mancinella tuberosa</i>	Pacific islands	10	0
	<i>Purpura persica</i>	Mariana Islands	8	0.13
	<i>Drupa ricinus</i>	Pyramid Rock, Oahu	8	0
		Guam	9	0
		Pagan	14	0.29
		Waimanalo, Oahu	11	0
	<i>D. arachnoides</i>	Guam	9	0
		Palau	19	0.05
	EP	<i>Vasula melones</i>	Playa Brava, Panama	12
		Isla Taboga, Panama	17	0.06
		Playa de Panama, Costa Rica	16	0.06
		Darwin Station, Galapagos	9	0.22
		Ayangué, Ecuador	15	0.07
<i>Stramonita biserialis</i>		Punta Caldera, Costa Rica	14	0
		Punta Carnero, Ecuador	14	0.29
		El Pelado, Ecuador	20	0.05
<i>S. brevidentata</i>		Punta Caldera, Costa Rica	9	0.22
		Punta Carnero, Ecuador	16	0
		Naos Island, Panama	13	0.54
		Playa de Panama, Costa Rica	14	0.07
<i>Mancinella triangularis</i>		Costa Rica and Panama	17	0
<i>M. speciosa</i>		Costa Rica to Ecuador	9	0.11
<i>Plicopurpura pansa</i>		Darwin Station, Galapagos	10	0.10
<i>P. columellaris</i>	Darwin Station, Galapagos	9	0.22	
WA	<i>Stramonita rustica</i>	South Curaçao	13	0
		North Curaçao	15	0
		Guadeloupe	21	0.05
		Lucea, Jamaica	12	0
		Gaibu, Pernambuco	24	0.92
		Recife, Pernambuco	66	0.17
	<i>S. haemastoma</i>	Playa Adaro, Venezuela	12	0.08
		Rio de Janeiro, Brasil	14	0.07
	<i>Mancinella deltoidea</i>	Caribbean Sea	16	0.06
	<i>Plicopurpura patula</i>	Curaçao	9	0
		Panama	9	0
		Eastern Caribbean	8	0.13
	EA	<i>S. haemastoma</i>	Dakar, Senegal	11
		Ghana	29	0.03
		Canal de Vridi, Ivory Coast	17	0.29
<i>Thais nodosa</i>		Ghana	10	0
		Aberdeen Beach, Sierre Leone	10	0

their number was insufficient to establish the position of the EP relative to the other 2 geographical regions (Table 2).

In small epifaunal Cerithiidae (adults 10 to 400 mm long), which are architecturally similar in the 4 tropical regions (Vermeij 1979b), no significant interoceanic differences were found (Table 3). Frequencies of repair tended to be higher in the EP (mean frequency  $0.56 \pm 0.27$ , 5 samples) than in either the WA (mean frequency  $0.30 \pm 0.15$ , 6 samples) or the IWP (mean frequency  $0.25 \pm 0.23$ , 21 samples), but great variation at several

scales – within species, among species, and among localities within each region – swamped any interoceanic difference that may exist.

The Thaididae exemplify the interoceanic differences in architecture well (Vermeij 1979b, Vermeij & Currey 1980), but these differences were not reflected in frequencies of repair (Table 4). Data on rocky-shore species that during the juvenile phase have a broad aperture revealed generally low frequencies of repair. Highest mean frequencies of repair were found in the EP ( $0.125 \pm 0.117$ , 16 samples) and WA ( $0.12 \pm 0.26$ ,

Table 5. Median frequencies of repair in small shallow-water species of *Conus*. S: number of samples; F: median frequency of repair

Region	Species	S	F	
IWP rock	<i>C. rattus</i>	5	0.25	
	<i>C. ebraeus</i>	21	0.23	
	<i>C. lividus</i>	13	0.20	
	<i>C. sponsalis</i>	17	0.11	
	<i>C. miliaris</i>	11	0.09	
	<i>C. flavidus</i>	13	0.10	
	<i>C. abbreviatus</i>	3	0.14	
	<i>C. coronatus</i>	6	0.14	
	<i>C. musicus</i>	1	0.07	
	<i>C. chaldaeus</i>	5	0.17	
	<i>C. miles</i>	1	0.79	
	EP rock	<i>C. brunneus</i>	2	0.58
		<i>C. gladiator</i>	5	0.33
		<i>C. nux</i>	5	0.50
<i>C. diadema</i>		2	0.47	
WA rock	<i>C. princeps</i>	1	0.17	
	<i>C. mus</i>	9	0.55	
IWP sand	<i>C. eburneus</i>	8	0.27	
	<i>C. catus</i>	4	0.46	
	<i>C. pulicarius</i>	22	0.24	
	<i>C. vaultieri</i>	1	0	
	<i>C. achatinus</i>	1	0.40	
	<i>C. piperatus</i>	1	1.03	
	<i>C. arenatus</i>	4	0.25	
	<i>C. fulgetrum</i>	1	0.33	
	<i>C. aristophanes</i>	3	0.39	
	<i>C. tessulatus</i>	5	0.23	
	<i>C. pennaceus</i>	6	0.22	
	<i>C. consors</i>	1	0.08	
	<i>C. figulinus</i>	1	0	
	<i>C. terebra</i>	1	0.15	
	EP sand	<i>C. perplexus</i>	2	0.17
		<i>C. virgatus</i>	1	0.20
		<i>C. ximenes</i>	6	0.16
<i>C. lucidus</i>		1	0.30	
<i>C. regularis</i>		2	0.14	
<i>C. recurvus</i>		1	0.07	
WA sand	<i>C. purpurascens</i>	2	0.22	
	<i>C. floridanus</i>	1	0.38	
	<i>C. spurius</i>	5	0.59	
	<i>C. columba</i>	2	0.41	
	<i>C. jaspideus</i>	13	0.19	

12 samples), but frequencies there were not significantly higher than those in the IWP (mean frequency  $0.05 \pm 0.09$ , 11 samples) or EA (mean  $0.065 \pm 0.13$ , 5 samples; Table 4).

Finally, the Conidae exhibited a pattern opposite to the one expected. A summary of the data on shell repair in this family is given in Table 5; median frequencies for each species are reported instead of frequencies of repair for each sample in order to conserve space. Among small rock-dwelling species, frequencies of repair were significantly higher in tropical America than in the IWP ( $p < 0.05$ , Mann-Whitney U-test). Within tropical America, the 9 samples of the WA

*Conus mus* tended to have higher frequencies of repair than did samples of 5 EP species, but the differences were not statistically significant ( $p > 0.10$ ). Frequencies among sand-dwelling species were also higher in the WA (mean frequency for 4 species  $0.39 \pm 0.16$ ), and again the EP showed strikingly low frequencies (mean for 7 species  $0.18 \pm 0.07$ ). In the IWP, sand-dwellers had intermediate and highly variable frequencies (mean for 14 species  $0.29 \pm 0.25$ ). Analysis of variance failed to reveal significant interoceanic differences ( $p < 0.20$ ).

In summary, the data now available suggest a much less consistent picture than did the original surveys on *Nerita* and terebrids. All kinds of hand-waving rationales could be adduced to 'explain' the contrary results for the Conidae and Thaididae, but until more is known about the agencies that cause breakage, it is pointless to engage in such speculation.

#### PREDATORS OF MOLLUSCS

If IWP gastropods are more heavily armored than those elsewhere in the tropics, predators there may be either more common or more powerful than their counterparts in the EP, WA, and EA. The only predators for which this hypothesis has been even partially tested are brachyuran crabs (Vermeij 1976, 1977, Abele et al. 1981). Comparisons among congeners with large crushing claws whose fingers are beset with molar-like teeth reveal that IWP species of *Carpilius*, *Eriphia*, and *Daldorfia* are both larger in size and relatively larger-clawed than are their EP and Atlantic relatives. EP species of *Eriphia* and *Ozius* are larger and have larger claws than do congeners in the WA. Whether these differences reflect differences in absolute crushing performance has not been demonstrated.

Many important molluscivorous genera have circum-tropical distributions, and may therefore be expected to show similar levels of predatory performance in the various regions. This may apply to the shell-peeling crab *Calappa*, the shell-crushing pufferfish *Diodon* and the loggerhead turtle *Caretta*, as well as to various genera of shell-drilling and shell-entering gastropods. In all these categories of predators, however, the IWP has a far higher diversity than do the other regions. Biogeographical comparisons of predatory performance therefore remain to be done for most types of predator.

#### LETHAL BREAKAGE OF GASTROPOD SHELLS

It could be argued that, if shell-breaking predators are important as selective agents influencing prey shell architecture, they should also be important as agents of

gastropod death (Vermeij 1979a). According to this premise, breakage should account for a higher proportion of gastropod deaths in the IWP than in the EP, and the lowest incidence of death due to breakage should occur in the WA and EA.

In order to obtain rough estimates of the relative importance of shell breakage as a cause of gastropod death, I made large collections of 'dead' shells from sandy and rocky habitats at shallow-water sites in the IWP, EP, and WA. IWP samples were collected in Palau (1975), Guam (1974, 1975, 1979, 1984), eastern Indonesia (1979), Papua New Guinea (1979), the southern Philippines (1979), Majuro Atoll in the Marshall Islands (1978), and Dravuni Island in Fiji (1986). WA samples were taken on the north coast of Jamaica (1974) and in Panama (1978). Samples of EP shells were collected in the Bay of Panama (1975, 1976, 1978, 1986) and in the Gulf of Chiriqui (1978). In addition to my own material, 2 large samples of shells occupied by hermit crabs were collected in the Bahamas (WA) at my request by M. L. Reaka. Details of some of the sites in Guam and Panama may be found in earlier papers (Vermeij 1979a, 1982a, Zipser & Vermeij 1980, Vermeij & Zipser 1986). At each site 'dead' shells (including apical fragments) were collected indiscriminately by hand from rocky surfaces and from the top 1 cm of sediment. More than 90% of the shells obtained in this way were occupied by hermit crabs. Shells less than 5 mm long were ignored, as were 'old' or 'worn' shells that were heavily encrusted or bioeroded on inner surfaces. Each shell was examined for drill-holes and breakage, and was then measured for length to the nearest mm. Shell breakage was considered to be lethal if the damage was sufficient to have killed the original snail occupant, as judged from numerous laboratory observations on damage inflicted by a variety of predatory crabs (Vermeij 1976, 1982a, Zipser & Vermeij 1978, Bertness & Cunningham 1981). Some shells appear to have been 'fatally' broken not by the predators of gastropods, but by agents when the shell was empty or occupied by a hermit crab. In order to estimate the importance of this postmortem artifact, I assessed the incidence of 'lethal' damage in drilled shells. Drilling by gastropods is a cause of death for gastropods but apparently not (or very rarely) for hermit crabs. If many drilled shells were also 'lethally' broken, the postmortem artifact would inflate the estimate of breakage as a cause of death for gastropods. Accordingly, I defined the corrected frequency of lethal breakage as

$$f_b = (n_b/n)(1-f_p)$$

where  $n_b$  = observed number of 'lethally' broken shells;  $n$  = total number of 'dead' shells in the sample; and  $f_p$  = frequency of lethal breakage in the drilled shells in the sample (Vermeij 1982a) Available data

indicate that the postmortem artifact is small, inflating estimates of breakage by 10% or less (Vermeij 1982a).

For each species, I calculated the proportion of shells whose lengths exceeded the largest lethally broken shell in order to estimate the importance of a size refuge from shell-breaking predation. For example, 26% of the 47 dead shells of *Opeatostoma pseudodon* collected at Playa Brava (Gulf of Chiriqui, Panama) exceeded a length of 37 mm, the length of the largest lethally broken shell of this species at that locality.

Data on the incidence of lethally broken shells in the field must be treated with caution. Shells so badly fractured that even the competitively most subordinate hermit crabs (the ones most apt to be found in substandard housing) will not occupy them may be preferentially lost from the population of dead shells. This is especially apt to happen in areas where shell-crushing fishes are important predators, because shells are usually broken into small pieces by them. The ecological importance of lethal breakage is therefore likely to be underestimated in some areas.

Skeptics may point out further that agencies in addition to predation can cause shells to break, and that the incidence of breakage among dead shells is therefore not a reasonable estimate of the contribution of shell-breaking predators to overall mortality. At one level, this criticism misses the point. Gastropods exposed to shell-breaking agencies may adapt to them regardless of whether the agencies are biotic or abiotic. The observation that the postmortem artifact of breakage is small suggests that abiotic agencies are unimportant. This conclusion is reinforced by the observation that dead shells from cold-temperate rocky shores, where potential abiotic agencies of breakage (boulders, strong waves) are common but shell-breaking predators are rare, are rarely found broken despite their thin shells.

Results from my survey of more than 9000 dead shells at 38 localities (Table 6) suggest that breakage is less important as a cause of gastropod death in the WA (mean incidence of breakage  $14.0 \pm 6.7\%$ ) than in the IWP (mean incidence  $27.3 \pm 15.1\%$ ), with the EP having intermediate values (mean incidence  $22.6 \pm 8.4\%$ ), but analysis of variance indicates that the interoceanic differences are not statistically significant ( $p < 0.20$ ). The incidence of breakage among dead shells was 25% or higher at 13 of 27 IWP sites (48%), 2 of 8 EP sites (25%), and none of 4 WA sites. Incidences of 10% breakage or less occurred at 2 IWP sites (7.5%), no EP site, and 2 WA sites (50%).

Bertness's (1982) experimental studies of hermit crabs on the 2 coasts of Panama suggest that shell-breaking predation is less intense in the WA than in the EP. Bertness found that the rate of breakage (number of hermit-crab-occupied shells broken per month) was almost twice as high at Pacific sites as on the Caribbean

Table 6. Incidence of lethal breakage in shallow-water assemblages of dead shells. N: number of dead shells

Region and Locality	N	Incidence
IWP Wom Village, Papua New Guinea	273	28 %
Batanta Is., Irian Jaya	232	10 %
Biak Island, Irian Jaya	103	11 %
Misool, Irian Jaya	70	31 %
Boear. Aru, Irian Jaya	243	20 %
Manipa, Molluccas	49	28 %
Pujada Bay, Mindanao	483	15 %
Agat, Guam	37	34 %
Western Shoals, Guam	60	61 %
Alupang Cove, Guam	172	53 %
NCS Beach, Guam	239	21 %
SW Cocos Island, Guam	226	16 %
Cocos Lagoon, Guam	259	27 %
Tumon Bay, Guam	144	42 %
Piti Channel, Guam	186	58 %
Piti Bombholes, Guam	103	17 %
Inner Pago Bay, Guam, 1979	69	42 %
Outer Pago Bay, 1979	746	47 %
Cave Rock, Guam	284	10 %
Pago Bay boulder zone, 1984	380	6 %
Inner Pago Bay, 1984	364	15 %
Bangi Island, Guam	104	28 %
Gun Beach, Guam	107	17 %
Ocean side, Majuro Atoll	209	17 %
Lagoon 1, Majuro	645	20 %
Lagoon 2, Majuro	249	14 %
Dravuni Island, Fiji	48	49 %
EP Playa Venado, Panama 1986	186	36 %
Playa Venado island, 1978	329	13 %
Playa Venado, 1976	242	21 %
Isla Taboga	139	13 %
Playa Brava, Panama	615	20 %
Naos Island, Panama	63	21 %
Punta Paitilla, Panama	171	24 %
Isla Chepillo, Panama	296	33 %
WA Fort San Lorenzo, Panama	591	10 %
Discovery Bay, Jamaica	63	24 %
Fernando Bay, Bahamas	627	12 %
Dump Reef, Bahamas	357	10 %

coast, and that the maximum size of hermit crab killed by shell breakage was also substantially higher on the Pacific side.

The data in Table 6 revealed considerable variation in the incidence of lethal breakage among sites within each of the 3 studied regions. Spatial variation, as well as temporal variation at time-scales ranging from days to years, was also uncovered by Ortega (1986) and Garrity et al. (1986) in their biogeographical studies of shell-crushing in the EP. Like Bertness et al. (1981), these researchers assessed the fates of shells 24 h after the latter had been glued to intertidal surfaces at various levels of the rocky shore. At some sites, all shells had remained intact, whereas at others more than half had been crushed, apparently chiefly by fishes. These findings, together with mine, suggest that very large

numbers of sites will have to be studied in order to establish with confidence whether the interoceanic trends suggested in Table 6 are real.

If heavily armored species predominate in the IWP, species in that region might be expected to be better adapted to predators than are species elsewhere, and therefore to have a larger size refuge from predation. An analysis of dead shells (Tables 7 and 8) did not bear out this prediction, however. In the first place, some species such as *Drupa morum* (Table 7) with all the hall-marks of well-developed armor (thick shell, strong sculpture, tight coiling, globose shape, heavily fortified apertural rim, and narrow aperture) had no size refuge at all. In the second place, species with a large size refuge (that is, 50 % or more of the dead shells larger than the largest broken dead shell) were no better represented in the IWP than in either the EP or WA. Moreover, there were no differences among any of the localities investigated with respect to the mean magnitude of the size refuge for species (Table 8).

#### HABITAT SPECIALIZATION

With some exceptions, WA species can be described as habitat generalists, occupying a variety of environments that to humans look different, whereas many IWP species are habitat specialists. Although little quantitative information exists on this topic, I offer several examples below.

Consider gastropods living on the blades of sea-grasses. In the WA, grazing gastropods found on sea-grasses are typically also found on the underside of stones and on other hard substrate. Examples of such generalists include *Modulus modiolus*, *Cerithium eburneum*, *Tegula fasciata*, and *Columbella mercatoria*. Of 9 gastropod species that I have collected on sea-grasses in the Caribbean region, only 2 (*Smaragdia viridis* and a species of *Tricolia*) appear to be restricted to this habitat. At least 3 of the 9 Caribbean grass-dwelling species have very close relatives in the EP, where sea-grasses are very rare (den Hartog 1970) and where these gastropods occur on rocky substrata. Of 15 grass-dwelling gastropods that I have collected in the IWP (western Indian Ocean, Indonesia, and Micronesia), at least 8 (53 %) appear to be found only on sea-grasses.

Intimate associations between small guests and large hosts are, on the whole, both more diverse and more specialized in the IWP than in the WA. This topic was reviewed by Vermeij (1983); I shall therefore mention only a few examples here. Whereas 10 fish species are facultatively associated with large stichodactylid sea anemones in the WA, a large number of pomacentrid clownfishes is associated obligately with these hosts in the IWP. Zooxanthella-bearing pelecypods (*Tridac-*

Table 7 Incidence of breakage and estimate of size refuges in dead Thaididae. N: number of dead shells; L: length of longest broken shell in mm; F: frequency of broken shells; S: number of shells larger than L, divided by N

Region and Species	Locality	N	L	F	S	
IWP	<i>Thais</i> sp.	Duyfken Point, Queensland	74	48	0.15	0.015
	<i>Morula squamosa</i>	Inner Pago Bay, Guam	19	12	0.11	0.84
		Outer Pago Bay, Guam	32	15	0.22	0.55
	<i>Drupa morum</i>	Outer Pago Bay, Guam	38	34	0.45	0
		Majuro, Marshalls	13	—	0	—
	<i>D. ricinus-arachnoides</i>	Outer Pago Bay, Guam	45	23	0.51	0.13
	<i>D. grossularia</i>	Majuro, Marshalls	11	—	0	—
	<i>Mancinella tuberosa</i>	Majuro, Marshalls	12	—	0	—
EP	<i>Vasula melones</i>	Playa Brava, Panama	20	34	0.20	0.35
		Paitilla, Panama 1975	16	28	0.25	0.35
		Naos Island, Panama	16	35	0.31	0.31
	<i>Stramonita biserialis</i>	Playa Brava, Panama	13	27	0.23	0.46
		Paitilla, Panama 1975	20	24	0.60	0.20
		Paitilla, Panama 1978	31	21	0.17	0.33
		Playa Venado, Panama	10	25	0.20	0.30
	<i>S. brevidentata</i>	Chepillo, Panama	11	27	0.27	0.18
		Playa Brava, Panama	11	19	0.18	0
WA	<i>S. rustica</i>	Fort San Lorenzo, Panama	55	15	0.07	0.69

Table 8. Size refuges from shell-breaking predation at several shallow-water localities. Magnitude M of the size refuge is the percentage of dead shells of a given species larger than the largest lethally broken shell of that species. Proportion P of species with a large size refuge is the percentage of species in which the magnitude of the size refuge is 50 % or higher

Region and Locality	No. of species	M	P	
IWP	Wom Village, Papua New Guinea	8	26 ± 13 %	0
	Pujada Bay, Mindanao	10	25 ± 29 %	20 %
	Pago Bay, Guam (inshore)	7	32 ± 30 %	29 %
	Pago Bay, Guam (outer part)	11	13 ± 16 %	9 %
	Majuro Atoll, ocean side	7	27 ± 28 %	29 %
	Majuro Atoll, lagoon	10	27 ± 22 %	20 %
EP	Playa Brava, Panama	16	28 ± 26 %	6 %
	Playa Venado, Panama (1978)	8	19 ± 24 %	13 %
	Punta Paitilla, Panama (1975)	8	11 ± 13 %	0
WA	Fort San Lorenzo	9	31 ± 28 %	22 %
	Discovery Bay, Jamaica	6	13 ± 16 %	0

nidae and the cardiid genus *Corculum*) are confined today to the IWP, as are coral-associated shell-dwelling sipunculans. Crabs and shrimps that guard corals against predators are found in the IWP and EP but not in the WA; the EP species are identical to those in the IWP and probably came from the latter region along with many other reef species during the Pleistocene (Glynn 1983). Ho's (1987) analysis of harpacticoid copepods associated with hermit crabs shows that *Sunaristes*, the genus with the most species-specific and specialized associations, is confined to the IWP. Sponges that are net oxygen producers by virtue of their algal symbionts are common and diverse in the IWP but relatively rare in the WA (Wilkinson 1987). Moreover, whereas many sponge species in the IWP are obligately associated with photosynthesizing sym-

bionts, and are morphologically specialized by being flat and thin-walled, most of the WA species appear to be facultative photosynthesizers (Wilkinson 1987).

#### GRAZING AND THE ARCHITECTURE OF SESSILE ORGANISMS

Studies of sessile marine plants and animals point to the conclusion that species in the Pacific and Indian Oceans have more highly developed antipredatory and anti-grazing characteristics than do species in the Atlantic. IWP comatulid crinoids, for example, have higher incidences of spinose arm bases than do species in the WA. This difference is presumably related to partial predation by fishes (Meyer & Macurda 1977, Meyer 1985).

IWP and EP reef-building corals are extensively eaten by fishes, gastropods, sea-stars, and sea urchins. Not only is this predation apparently more intense than in the WA, but several of the major groups of predators of corals (notably sea-stars, gastropods, and pufferfishes of the genus *Arothron*) are absent from the WA (Glynn et al. 1972, Glynn 1982, Glynn & Wellington 1983). It is not known if these interoceanic differences in predation are reflected in coral architecture. Crabs and shrimps that defend host corals from attack by sea-star predators (but not from gastropods or fishes) are common in the IWP and EP, but are unknown in the WA (Glynn 1976, 1982, 1983). Preliminary work by Thomason & Brown (1986) suggests that the degree of development of competitive defenses involving the cnidom of scleractinians is more highly developed in the IWP than in most Caribbean corals. It remains to be determined if the cnidom also plays a role in the corals' defense against predators.

It has been known for some time that large fleshy algae are generally rare in the EP and very abundant in the WA. Hay & Gaines (1984) attribute this rarity to higher grazing intensities and to the greater abundance of grazers in the EP (see also Birkeland 1977).

Limpet-like gastropods living epizoically on the shells of gastropods and hermit crabs differ in the degree to which they excavate home scars on their hosts. In the IWP, the hipponicid *Sabia conica* excavates a pit on the exterior of its host's shell, where it is presumably well protected against incidental grazing and other disturbance. The EP *Crepidula incurva* does not make such excavations; neither do species of *Crepidula* in the WA and EA where, unlike the situation in the IWP and EP, the epizoic mode of life appears to be facultative (Vermeij 1978).

### THE HISTORICAL PERSPECTIVE

The general pattern emerging from the available data on interoceanic differences is that, despite great variations within regions and at other spatial and temporal scales, the degree of habitat specialization and enemy-related adaptation is greatest in the IWP, intermediate in the EP, and low in the WA and EA. With respect to enemy-related adaptation, these differences are most clearly seen in the degree of expression of features that are known to confer survival advantages. Independent evidence from studies of successful and unsuccessful predation is inconsistent; sometimes it corroborates the morphological evidence, but in other instances it contradicts or only very weakly supports the evidence from morphology.

One interpretation of these patterns is that enemies – competitors, predators, disease agents, and sometimes

even prey – have had a greater net influence on shallow-water species in the IWP and to a lesser extent the EP than in the tropical Atlantic. The question of how and when the observed interoceanic differences arose may therefore be recast into a question about how oceanographical conditions and the potentially selective processes of speciation and extinction affected enemy-related evolution in the marine tropics.

It may be useful first to give a brief summary of the Cenozoic history of the tropical ocean. Full details may be found in the works of Berggren & Hollister (1977), Hallam (1981), and Briggs (1987). During the Paleocene and Eocene, a more or less continuous belt of ocean surrounded the earth at low latitudes. Although biotas in different parts of the tropics showed species-level differences, and some biotas were richer than others, there was far less taxonomic divergence and heterogeneity than exists in the modern marine tropics. Tectonic events during the Neogene led to the fragmentation of this circumtropical seaway. During the Early Miocene, the connection between the Mediterranean (Tethys Sea) and Indian Ocean was severed by tectonic activity in southwestern Asia and by the northward movement of Africa. The continent comprising Australia and New Guinea also moved northward, nearing Asia as it did so. The resulting tectonic activity created a complex configuration of islands and narrow sea passages in the Indonesian area. By Middle Miocene time, the Indian and Pacific Oceans had effectively been isolated from each other in this region (Kennett 1983, Kennett et al. 1985). In tropical America, the seaways connecting the Pacific and Atlantic oceans gradually shoaled during Late Miocene to Middle Pliocene time. A continuous land bridge was in place no later than 2.4 million yr before present (Gartner et al. 1987). By the beginning of the Pleistocene, the major tropical biogeographical regions were relatively isolated from each other, either by land masses or by great overwater distances. Perhaps as the result of the northward movement of the plate carrying the Line Islands in the Central Pacific, IWP molluscs and other reef-associated organisms have been able to disperse to the EP (Dana 1975, Glynn & Wellington 1983). In the Atlantic, vigorous oceanic circulation has enabled some EA and IWP taxa to invade the WA beginning in the Pleistocene (Petuch 1981).

The cooling that characterized intervals during the Pliocene and Pleistocene affected biotas in the tropical marine regions very differently. Substantial extinctions affected the WA region during the Pliocene. About 32% of gastropod subgenera found in the WA during the Pliocene disappeared in that region. In the EP, extinction affected only about 15% of Pliocene taxa (Vermeij & Petuch 1986). No extinction at the sub-generic level seems to have taken place in the IWP,

despite the fact that individual species did become extinct and several genus-level taxa became geographically more restricted after the Early Pleistocene (Vermeij 1986).

In tropical America, extinction during and after the Pliocene contributed in an important way to the architectural differences observable between Recent EP and WA faunas. Armored hard-bottom gastropods suffered relatively more than did unarmored types in the WA, whereas in the EP the impact of extinction was somewhat greater among unarmored than among armored types. Thus, although the incidence of armor was the same in the EP and WA during the Pliocene, differential extinction was responsible (at least in part) for the observed difference in the incidence of armor in Recent gastropods from opposite sides of tropical America.

That extinctions in the WA also led to the differential elimination of taxa with specialized habits is suggested by some hints from the fossil record. Associations between shell-dwelling sipunculans and scleractinians that attached to the host shells of these worms are known today only in the IWP and EP, but they have been recorded as fossils from the Miocene of Florida in the WA (Gill & Coates 1977). The obligately mangrove-associated gastropod *Nerita planospira*, which is the sole living representative of the subgenus *Ilynerita*, occurs today only in the tropical southwestern Pacific. In the Gatuncillo Formation of Panama, which has been provisionally dated as Late Eocene, a closely similar species of *Ilynerita* is found, which may also have been obligately mangrove-associated (Vermeij & Collins 1988). Members of the pelecypod family Tridacnidae, which bear algal symbionts, are found today in the IWP region, but during the Miocene the family was also represented in the WA.

Although we are still far from understanding how this selectivity of extinction was brought about in the WA, reductions in phytoplankton productivity correlate in time with the extinctions. Phosphate deposits were widespread in Pliocene sediments of the southeastern United States (Riggs 1984), and the diverse fossil assemblages of the Pliocene of Florida and Panama are replete with large-bodied deposit- and suspension-feeding gastropods and pelecypods, suggesting highly productive waters (Petuch 1986). Micropaleontological and carbon-isotope studies (Keigwin 1982, Gartner et al. 1987) suggest that phytoplankton productivity declined in the WA following the Central American uplift, whereas it remained relatively constant and high in the EP. Areas of the WA in which productivity remained high due to upwelling are precisely the regions that harbor the remnant populations of species which during the Pliocene had much broader geographical ranges in the WA. This is notably the case for

the Caribbean coasts of eastern Colombia and Venezuela (Vermeij 1978, Petuch 1982, Vermeij & Petuch 1986). The EP, in which productivity is also high, also serves as an important refuge for Pliocene taxa that inhabited the WA (Woodring 1966, Vermeij & Petuch 1986). In the IWP region, the continental coasts of the Indo-Malaysian area have served as refuges for taxa that during the Pliocene and Early Pleistocene ranged eastward into the insular Pacific. These continental coasts are characterized by widespread upwelling and extensive terrestrial inputs of nutrients (Vermeij 1986). A reduction in phytoplankton productivity in the WA and perhaps elsewhere may have led to higher larval mortality or to failed larval settlement. Whether and how these effects would selectively place at greater risk taxa with specialized habits or with exceptionally well developed enemy-related traits are questions of great biogeographical interest.

Differential speciation has also played a role in accentuating the interoceanic differences in architecture and perhaps specialization. In contrast to tropical America, where very few (if any) subgenus-level taxa originated during the Pliocene and Pleistocene, a large number of supraspecific groups in the IWP have post-Miocene origins. Not only are many of these groups unknown as fossils from the Miocene, but they are wholly absent from the richly fossiliferous pre-Pliocene strata of Europe, an area with close biogeographical affinities to the present-day IWP. Continuing analyses suggest that the incidence of very heavy armor is exceptionally high among post-Miocene IWP gastropods. Examples of recently evolved highly armored genera include *Drupa*, *Lambis*, *Drupella*, *Morula*, *Conomurex*, and various groups of cowries (Cypraeidae) and miters (Mitridae and Costellariidae). The coral-eating sea-star *Acanthaster* likely also had a post-Miocene origin.

## EPILOGUE

It should be abundantly obvious that great gaping holes exist in our understanding of the nature, magnitude, history, and causes of interoceanic differences in the architecture and ecology of tropical shallow-water marine organisms. We badly need systematically collected data on the absolute performance levels of individuals with respect to locomotion, antipredatory resistance, predatory power, growth rate and other competitive methods, grazing intensity, handling time by predators, likelihood of encounters between individuals and their enemies, and so on. Further studies of differential extinction and speciation are also needed. Intraoceanic differences, particularly in relation to planktonic productivity and its effects, deserve more

attention than they have thus far received. Very little has been done on species and communities in environments other than clear-water reefs and coral-sand lagoons. In view of the vast areas of potential commercial importance of the continental shelves and of coastal muddy habitats, these environments should be targeted for intensive comparative study.

Finally, it must be remembered that human activity may already have modified the selective regimes and ecological relationships of marine species on a very large scale, and that the data we are collecting today may not provide a reliable indication of the conditions that gave rise to the interoceanic differences in predation-related architecture and habitat specialization. Fishing has reduced the abundance of herbivorous and predaceous fishes on a huge geographical scale, especially in the WA, with the result that the competitors and prey of these fishes have probably increased in abundance and evolutionary effect. Hay (1984), for example, argued that overfishing is responsible for the great abundance of *Diadema* and other sea urchins throughout the Caribbean. It is imperative that the human impact on ecological relationships and especially on the selective regime of marine species be intensively studied experimentally using control areas where exploitation by humans is still minor.

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