FISH PREDATION AND THE EVOLUTION OF GASTROPOD SHELL SCULPTURE: EXPERIMENTAL AND GEOGRAPHIC EVIDENCE

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Marine gastropod molluscs exhibit a wide range of shell forms, many of which are believed to provide some defense against predation. Vermeij (1974) has suggested that narrow or occluded apertures, low spires, thickened shells and strong sculpture act in various ways to deter the attacks of shell-breaking or shell-entering predators. In addition, Vermeij (1976, 1977a) has presented evidence suggesting that inter-oceanic differences in crab predation intensity may have been responsible for the evolution of less vulnerable shells among Indo-West Pacific gastropods when compared with Eastern Pacific and Tropical Atlantic ones. Similarly, one might expect regional differences in the intensity of a particular mode of predation to lead to geographic variation in the frequencies and degree of development of a mode-specific morphological defense.

Crabs and fishes are almost certainly the most important shell-breaking predators on lower intertidal and subtidal gastropods. Their modes of feeding, however, are rather different. Crabs are able to manipulate shells more precisely and can apply their chelae to a shell in a variety of ways. They should be less deterred by strong external sculpture than by thickened shells, reduced spires, or reinforced or occluded apertures, except when shells are small relative to chelae. On the other hand, fishes that crush gastropods must use their jaws and hence can only apply stress to very restricted portions of a shell in a restricted manner. They should be more effectively deterred by certain types of strong external sculpture than by thickened lips or restrictive apertures. More specifically, stout spines or nodes appear

to reduce susceptibility to being crushed by fish. Such sculpture may act in at least four ways (Fig. 1): 1) it increases the effective diameter of the shell, thus decreasing the mechanical advantage of the predator's crushing apparatus; 2) it distributes the stress over a larger area of the shell; 3) it localizes the stress at the thickest parts of the shell; and 4) it focuses the applied force to a very restricted area of the crushing surface, increasing the chance of damage to the predator. The structural similarity of strong axial ribbing suggests it should perform in a similar manner. Shell thickness and to some degree overall shell shape may also affect susceptibility to crushing. In this paper I directly test the importance of stout spines as a potential defense against crushing by fish. Observations on the type of damage inflicted by crushing fishes serve as the basis for some speculation about how other morphologies might also reduce vulnerability. Finally I consider the geographic distribution of stout spinose sculpture and how it relates to the distribution of shell-destroying fishes.

Experimental studies that examine the importance of gastropod shells as a defense against predation have almost exclusively employed crabs as predators (Ebling et al., 1964; Kitching et al., 1966; Kitching and Lockwood, 1974; Vermeij, 1976; Zipser and Vermeij, 1978; but see Ivlev's 1961 study of freshwater carp, roach and perch on *Limnaea ovata* of different shell thicknesses, p. 102). The present study represents the first experimental examination of the types of shell morphologies that offer an effective defense against shell-crushing fishes and rays. Although I have only

tested two species of fish, I believe the results may be extended to other predators of this type as well.

METHODS

Three experimental approaches may be used to provide independent tests of the function of sculpture in response to a particular stress. The simplest is to compare the relative susceptibilities of two closely related, preferably congeneric species that differ only in degree of sculpture. This approach suffers from the assumption that the sculptural differences represent a single-factor difference between the two species and ignores the possibility that subtle differences might exist in other aspects of the shell, including shape, internal construction and shell composition as a result of their separate evolutionary histories. A second approach compares the relative susceptibilities of normal individuals and individuals whose sculpture has been experimentally altered or removed. However, removal of sculpture may make a shell weaker than a normally unsculptured one of the same shape. Though not entirely free of the complications associated with the first, a third more biologically meaningful approach compares the relative vulnerability of intraspecific variants that have sculpture developed to different extents. While giving a more realistic measure of the effectiveness of a particular sculpture, this last approach is the most logistically difficult because it requires large numbers of individuals exhibiting substantial variation. Also, gastropod species that show marked variation tend to do so in more than one trait simultaneously (Palmer, unpubl.) making tests relevant to a single trait difficult (similar simultaneous variation in several traits has been noted in birds and mammals as long ago as 1877 by A. J. Allen). However, this last approach can circumvent some of the problems of unknown differences in evolutionary history and unwanted weakening of the shells associated with the first two. Since in some cases intraspecific morphological variation has been directly linked to varying levels of
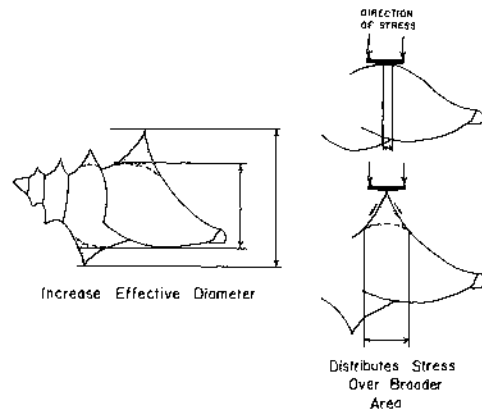

FIG. 1. Two mechanisms by which stout spines might act to reduce susceptibility to crushing by fish. The stippled areas represent shell material not present in unsculptured species. See text for other possible mechanisms.

predation intensity (Gilbert, 1966, 1973; Zaret, 1972; Kerfoot, 1977; Gross, 1978) this final approach can provide a rather sensitive test for the functional significance of a particular sculpture. All three of the above approaches have been used in the present study to compensate for the biases inherent in any particular one.

Two circumtropical spiny puffer species, *Diodon holacanthus* and *Diodon hystrix*, were used to examine defenses against shell crushing by fish. Both species are important predators on gastropods and capable of handling a broad range of shell types (Hiatt and Strasburg, 1960; Randall, 1967; Hobson, 1974). Collected by hand or with nets in the vicinity of Galeta Point on the Caribbean and Taboga Island on the Pacific side of Panama, the fish were held either in running or frequently changed sea water for the duration of the experiments (May 10–June 10, July 20–August 31, 1976). All experiments were conducted at the Smithsonian Tropical Research Institute, Naos Island lab, in the Bay of Panama. *Diodon* are ideal experimental animals for they readily accept individual food items offered by hand once they have been conditioned. Crabs were initially used to condition the fish to this kind of feeding, followed by snails. For each experiment, living gastropods of

FIG. 2. *Thais kioskiformis* positioned on the crushing plates of the skull from a 210 mm *Diodon hystrix*. Note the long lever arm on the upper jaw, a presumed specialization for crushing hard-shelled invertebrates. Articulation points of the upper and lower jaws are indicated by arrows.
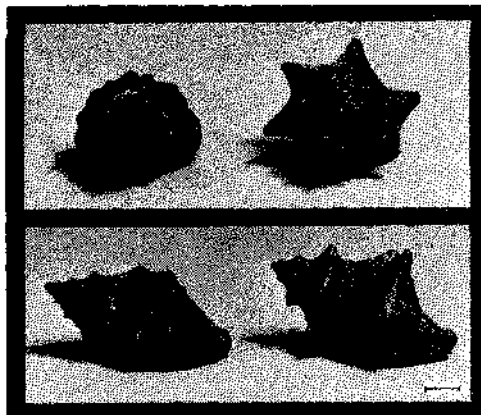

FIG. 3. Two species of *Thais* with different degrees of sculptural development used in experiment one. Left, *T. biserialis*; right, *T. kioskiformis*. Scale bar equals 5 mm.

various sizes were individually tagged on their shells using india ink coated with Dekophane (Rona Pearl Corp., Bayonne, New Jersey, see Spight, 1974) and measured, prior to being offered to the puffers. In all but the fourth experiment, shells were offered individually and their fate recorded. Snails were collected almost exclusively from Venado Beach, approximately 3 km west of the Pacific entrance to the Panama Canal.

The shell parameters measured in these experiments include: 1) length—apex to tip of siphonal canal; 2) aperture length—posteriormost outer edge of the lip to tip of siphonal canal; 3) diameter—distance from the dorsalmost spine tip or edge of the body whorl to the surface upon which the aperture is resting; 4) immersed weight—weight of the whole animal when immersed in sea water, which provides a relative measure of shell weight and hence thickness for animals of the same overall

shape, since tissue weight in seawater is negligible. The correlation between the immersed weight of entire animals and destructively sampled shell dry weight is 0.9997 ($N = 23$; Palmer, unpubl.); and 5) spine length—tip of spine to outer edge of body whorl. Fish sizes are measured as the standard length (tip of snout to caudal peduncle).

When feeding, the *Diodon* take a shell in their mouth and position it on the crushing plates (Fig. 2) by short inhaling and exhaling motions, biting down intermittently until the shell breaks. The shell is repeatedly crushed and its fragments ejected until all that remains is the operculum and a portion of the columella that are still attached to the viscera. Shells that do not break are eventually dropped. If necessary, rejected shells were offered two or more times to a fish on different days to ensure against changes in effort associated with reduced hunger or interest. Rejection was considered final only if a fish

TABLE 1. *Comparison of critical sizes for a congeneric species pair with strongly and weakly developed spines. Critical size range is indicated in parentheses.*

Fish	*Thais kioskiformis* (strong spines)	*T. biserialis* (weak spines)	% Difference
Diodon hystrix (292 mm)	34.8 (33.4–36.3) mm	40.2 (39.8–40.6)	15.5
D. holacanthus (240 mm)	29.7 (28.2–31.2)	32.7 (31.7–33.7)	10.1

made two attempts each greater than 30 seconds or a single attempt longer than 60 seconds duration.

Relative vulnerabilities were assessed using a measure of critical size which was obtained for each experimental group of snails. Critical size is that snail size above which a given fish is incapable of crushing a particular snail species (Vermeij, 1976). Unless specified otherwise, critical size in this paper refers to shell length and provides a measure of the relative size of the animal occupying a shell. The tabled critical sizes correspond to the mean of the largest uneaten and smallest eaten snails, these latter values being indicated in parentheses. In all experiments, except for *T. kioskiformis* in experiment two, the size range of offered snails exceeded the critical size range for a given fish.
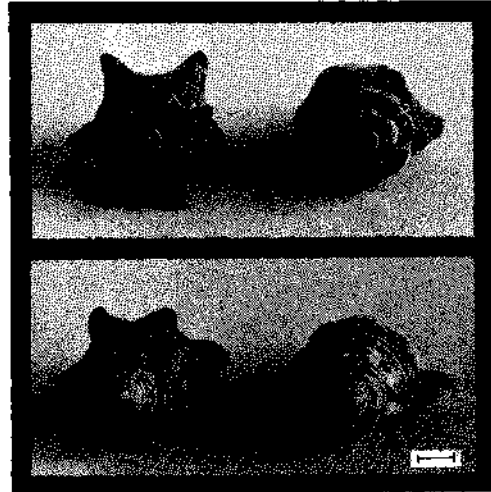

FIG. 4. Normal (left) and experimentally modified shells (right) of *Thais kioskiformis* (top) and *Cymia tecta* (bottom) used in experiment two. Scale bar equals 5 mm.

EXPERIMENTAL RESULTS

I conducted four experiments analyzing the vulnerability of shells to crushing by *Diodon*. In the first, various sizes of two morphologically different muricid species, *Thais kioskiformis* and *T. biserialis*, were offered to two puffer fish. *T. kioskiformis* in Panama has a single row of stout conical spines regularly spaced about the periphery of the shell, while *T. biserialis* exhibits very weakly developed pairs of nodes about the same portion of the shell (Fig. 3). The results (Table 1) show that the critical size of *T. biserialis* is more than 10% larger than that of *T. kioskiformis*. Assuming similar overall shell shape (see Fig. 3) and comparable growth rates

in the two species, *T. kioskiformis* should achieve an earlier escape from predation at this smaller size. Also, simply due to scaling, a 10% difference in length will be equivalent to a 33% difference in volume and hence represents a substantial defensive accomplishment in terms of the amount of animal tissue being defended. Allometric changes in shape could act to increase or decrease this difference.

In a second experiment, comparable size ranges of two morphologically similar species, *T. kioskiformis* and *Cymia tecta*, were divided into two groups prior to being offered to a 240 mm *D. holacanthus*

TABLE 2. *Critical sizes for normal and modified shells. Critical size range is indicated in parentheses. C. tecta was offered to a 330 mm D. hystrix and T. kioskiformis to a 240 mm D. holacanthus.*

| | Critical length | | |
Gastropod	With spines	Spines removed	% Difference
Cymia tecta	25.4 (24.1–26.8) mm	30.5 (28.6–32.4)	19.8
Thais kioskiformis	29.7 (28.2–31.2)	>32.0	≈7.7
	Critical diameter		
Gastropod	With spines	Spines removed	% Difference
C. tecta	17.6 (17.5–17.7) mm	17.5 (16.9–18.1)	−0.01
T. kioskiformis	18.4 (18.1–18.7)	>18.5	≈0.5

TABLE 3. *Factorial analysis of variance on shell characters for groups of eaten and uneaten* Thais kioskiformis *after having been offered to three different puffer fish.* M—Diodon hystrix *(292 mm),* P2—D. holacanthus *(235 mm),* P3—D. holacanthus *(200 mm). The snails in group M are from the third experiment before their spines were filed off (see text). Only snails within the critical size range for each fish were used in these computations. Sample sizes are indicated in parentheses. The sums of squares have been computed according to the "classical experimental design" of SPSS and the main effects have been tested over the residual mean square (RMS). Significant F-ratios are asterisked. The aperture length/shell length ratio acts as a crude measure of whorl overlap as long as aperture shape is constant; lower values correspond to less overlap.*

	Mean shell values			Two-factor analysis of variance		
Shell character	Fish	Eaten	Uneaten	Source of variation	F ratio	P
Shell length	M	34.73 mm (8)	34.97 (7)	***Fish	708.27	<.001
	P2	29.46 (26)	30.12 (14)	Fate	2.41	.125
	P3	22.72 (9)	22.78 (7)	Interaction	1.42	.250
				RMS	0.811	
Aperture length/ Shell length	M	0.629	0.603	Fish	0.14	.867
	P2	0.626	0.607	Fate	3.04	.086
	P3	0.629	0.626	Interaction	0.35	.703
				RMS	0.003	
Spine length	M	3.73 mm	4.15	***Fish	22.34	<.001
	P2	2.87	3.14	*Fate	6.87	.011
	P3	2.36	2.89	Interaction	0.28	.753
				RMS	0.325	
Diameter	M	16.35 mm	16.71	***Fish	119.16	<.001
	P2	15.40	16.37	***Fate	14.86	<.001
	P3	12.38	12.93	Interaction	0.94	.396
				RMS	0.614	
Immersed weight	M	2.60 g	3.53	***Fish	149.64	<.001
	P2	1.82	2.24	***Fate	33.33	<.001
	P3	0.76	1.00	*Interaction	4.27	.018
				RMS	0.121	

and a 330 mm *D. hystrix* respectively. The spines were ground flush with the outer shell surface in one group and left unaltered in the other (Fig. 4). Again, the results show that the critical size is on the order of 10–20% larger when the shell is unprotected by spines (Table 2). However, if shell diameters (the dimension of the shell important to the predator) are compared instead of lengths (the dimension of the shell relating to the size of the animal inside the shell), the critical diameters are very similar (Table 2), at least for *C. tecta.* This suggests that one function of stout spines is to increase the effective diameter experienced by the predator.

In a third experiment, 30 *T. kioskiformis* (length 30.6–36.8 mm) were offered individually to a 292 mm *D. hystrix* for whom the critical size of *T. kioskiformis*

was measured at approximately 35 mm (range 33.4–36.9 mm). Over a period of nine days, snails were repeatedly offered until the *Diodon* had successfully crushed all but seven. The spines of these remaining individuals were then ground flush with their shell as before, and they were offered again. All were successfully crushed except one very thick 36.0 mm individual whose shell was more than 35% heavier than the next heaviest individual. Spine removal clearly increases the vulnerability to being crushed.

The final experiment consisted of offering tagged, premeasured *T. kioskiformis* to two different-sized *Diodon holacanthus.* In this manner, the morphologies of eaten and uneaten shells could be compared. The *T. kioskiformis* were selected to represent a range of morphologies for

individuals close to the critical size of each fish. All the animals were placed in the tank with their respective predator at the same time. Many of the vulnerable shells were eaten within the first 24 hours. At the end of 96 hours, all the surviving *T. kioskiformis* were removed and noted. Table 3 summarizes the results of the third and fourth experiments for individuals falling within the critical size range of each fish. Fate groupings for each character have been considered separately by analysis of variance. Significant differences exist between the eaten and uneaten groups in spine length, body whorl diameter and shell thickness (=immersed weight), indicating that all three factors influence vulnerability to crushing. Whorl overlap, as inferred from the aperture length/length ratio, does not appear to be important. The lack of a significant difference in shell length ($P = 0.125$) shows that within the critical size ranges, these differences in shell characters are not just associated with variations in animal body size. The greatest difference both between fate groups and between fish occurs in immersed weight, suggesting that shell thickness is the most consistent of the three factors at reducing susceptibility to crushing.

The results of all four experiments are thus in agreement. Stout spines reduce vulnerability to crushing by *Diodon*. Other factors such as shell diameter and in particular shell thickness are also important and in some cases may confer an even greater resistance to being crushed (e.g., experiment 3).

DISCUSSION

In addition to the experiments detailed above, complementary insight into the types of morphological defense effective against a particular type of predation can be gained by inspecting individuals that have been only partially damaged. Damaged shells indicate not only the attack site of the predator but also the areas of potential weakness of the prey. I have examined gastropod shells partially damaged by *Diodon* in the lab and by an
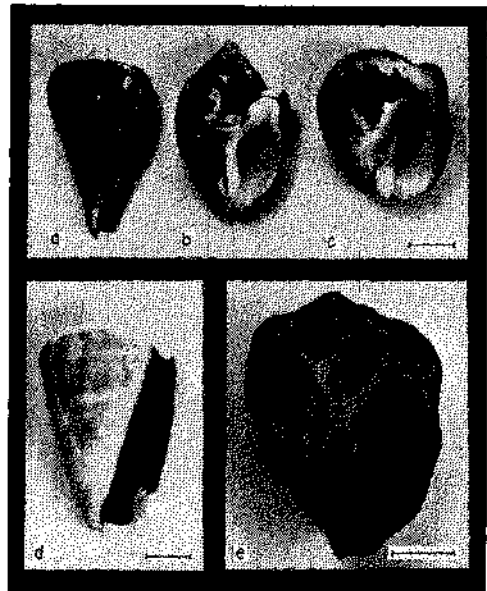

FIG. 5. Species exhibiting reduced and/or reinforced spires: a) *Conus patricius* (Pacific, Panama); b) *Triumphis distorta* (Pacific, Panama); c) *Thais melones* (eastern Pacific, Panama); d) *Strombus luhuanus* (Eniwetok Atoll); e) dorsal half of a *T. melones* shell illustrating the heavily reinforced spire (section made along the axis of coiling). Scale bars equal 10 mm.

unidentified sand-dwelling ray in the field. These indicate that the most vulnerable portions of a shell are the dorsalmost and ventralmost surfaces of the body whorl (i.e., those surfaces furthest perpendicularly from a plane described by the axis of coiling and the outer lip of the aperture), corresponding to its narrowest cross-sectional diameter. Of externally sculptured species exhibiting stout spines or nodes, the strongest are almost always found extending from the shoulder of the whorl and hence present at these locations (see Fig. 7). Pronounced axial ribbing would also reinforce these regions.

At least two other types of morphological defense would appear to be partially effective against shell-crushing fishes. In species widest at or very near the apex, reduced spires with internally thickened apices would distribute the stress over the successive whorls formed by the most pos-

terior portion of the apertural lip. The Conidae (Fig. 5a) best illustrate this type of conformation. Figures 5b–5e illustrate three other species whose adults exhibit reduced reinforced spires. This type of defense should also be effective against crabs that crush entire shells with their master claws (Vermeij, 1974, 1976, 1977a) rather than breaking away successive portions of the aperture (Rossi and Parisi, 1973; Zipser and Vermeij, 1978).

The most generally effective morphological defense against all types of shell-breaking predators is a thickened shell. Since resistance to breaking increases as the third power of thickness for solids (Wainwright et al., 1976, p. 256), slight increases in thickness will confer substantial increased strength to a structure. Molluscan shell material with its multilayer internal organization (Currey, 1976; Currey and Kohn, 1976), may be strengthened even more by equivalent increases in thickness if increased thickness is achieved by selective addition to the layer contributing most to overall resistance. In the present study, the heavier shelled *T. kioskiformis* were the most consistently resistant to crushing by *Diodon* (Table 3). Thick-shelled morphs of *Lepsiella albomarginata* (Kitching and Lockwood, 1974), *Nucella lapillus* (Ebling et al., 1964) and *Thais* (=*Nucella*) *lamellosa* (Palmer, unpubl.) have also been found to be an effective defense against grapsid, portunid and cancrid crabs respectively.

It is important to recognize, however, that material is not added to a shell without some energetic cost either in terms of production or maintenance (reduced mobility and/or increased energy expended carrying a heavier shell). Hence, within the constraints on form imposed by anatomical requirements and limitations of the physical habitat (e.g., drag upon burrowers or dwellers of wave swept rocks), there must be an evolutionary "choice" between investment in a more generally effective defense (uniformly thickened shells) or investment in a more energetically efficient defense (strong external sculpture). The relevant question, then, is:

which morphological strategy offers a greater defense per unit shell material, a thick shell or strong sculpture? The data I have collected indicate only that both shell thickness and stout spines reduce vulnerability to crushing by fish. However, if the material present in the spines were distributed evenly about a shell it seems unlikely that the shell would be equally invulnerable. Strong sculpture, then, would appear to provide a better defense for the same material and maintenance costs. It is within these reduced costs that the advantage of sculpture over thickness lies. A species' morphological strategy should thus reflect a compromise between the competing demands upon energy for both growth and reproduction, and for defense. In addition, since there is a limit to the rate at which shell material can be produced, a snail with a uniformly thick shell necessarily requires more time to achieve a given length than a thin-shelled animal of similar shape. For a thicker shell to be selected for, the risks associated with being smaller for a longer period of time must be offset by the reduced vulnerability conferred by being thicker.

Although all four experiments support the hypothesis that stout spinose sculpture reduces the vulnerability of shells to being crushed by fish, the mechanism by which these spines act remains unclear. Since the critical *diameters* of normal and modified shells are very similar (Table 2), one function would appear to be to increase the shell diameter experienced by the predator (mechanism 1, see introduction). Though they are by no means ruled out, mechanisms two and three are less consistent with the results of experiment two (Table 2). If either of these were important, then the critical diameters of the shells with the spines removed should have been larger, indicating that the spines contributed more to overall shell resistance than just an increased diameter. This interpretation should be accepted only tentatively until more extensive experiments can be conducted. Further experiments on crushing by fish will also be required to distinguish

between the relative contributions of other characters to shell resistance including overall shape, degree of whorl overlap, primary thickness, secondary internal thickening and other types of external sculpture.

Predator-Specificity of Spinose Sculpture

Concerning the predator-specificity of morphological defense, I regard stout spines as primarily if not exclusively effective against shell-crushing fish rather than crabs. Support for this interpretation derives from several observations. First, the proposed mechanisms of spine action would not apply to crushing crabs unless the spiral distance between spine tips was distinctly less than the breadth of the molars of a crab's crusher claw. A claw applied with its plane of movement parallel to the axis of coiling would fit between these spines to a greater or lesser extent depending on the relative sizes of the claw and the shell. Similarly, a claw applied to the body whorl perpendicular to the axis of coiling (Hamilton, 1976) would fall between or outside of spine rows. In both situations, stress would be tangential to the spines. In fact, stout spines could give crabs a better purchase while they attempt to break a shell. Of course when shells are small relative to molar breadth, this argument does not apply. However, it seems likely that sculpture on shells so small would be ineffective against what, relatively, would be a large, powerful crusher claw.

Second, since spine rows are restricted to axially discrete areas about a whorl, they would offer little defense against crabs that 'peel' shells open starting at the aperture (Feare, 1970; Rossi and Parisi, 1973; Zipser and Vermeij, 1978) although they might interfere with claw positioning in the highly specialized calappid crabs (Shoup, 1968; but note the ineffectiveness of *Murex brandaris* spines in interfering with predation by *Calappa granulata* in Rossi and Parisi, 1973, Fig. 4). Unspecialized peeling crabs (Cancridae, Xanthidae) usually insert the fixed finger of the manus of one claw into the aperture and

break outwards (Zipser and Vermeij, 1978; pers. observ.). Spinose shells would still be weak between rows of spines relative to this outwardly directed stress. Finally, spines are not always found in rows. Some Caribbean Strombidae produce very stout dorsal knobs just prior to expansion of the aperture and cessation of growth (see Fig. 7c). The dorsal knobs on two of these species may be related to specific predators: the eagle ray *Aetobatis narinari* on *Strombus raninus* and the loggerhead turtle *Caretta caretta* on *S. gigas* (Randall, 1964).

Geographic Evidence

If certain morphological defenses can be linked to specific types of predation, then the evolutionary importance of a given defense should depend upon the intensity of predation attributable to the relevant type of predator. Absolute measurements of predation intensity are difficult and at best approximate. One crude indication of the evolutionary importance of a defensive morphology is the number of predatory species using the mode of attack against which the morphology is directed. To this end, I have compiled lists* of tropical and temperate fish species that prey on gastropods in appendices I and II respectively. The species are grouped taxonomically along with their size, intensity of feeding on gastropods, geographic region and mode of ingestion (crushing, whole, etc.). Tables 4 and 5 summarize the relevant portions of the appendices.

FIG. 6.   Geographic distribution of the proportions of shell-crushing fish species. The dark area of a circle corresponds to the proportion of species that crush molluscs. The numbers of species eating molluscs are indicated in parentheses. These data consider only those species for which dietary information was given in each study. References to the surveys used for this figure are asterisked in the bibliography. Proportions of shell-crushing species are used instead of numbers of species to guard against possible differences in sampling effort.

In both temperate and tropical waters, numerous teleosts prey on gastropods (Table 4). The mode of ingestion ranges from swallowing whole, to tearing off feet, to outright crushing of the entire shell. Shell crushing is accomplished using either specialized jaws or pharyngeal teeth (Table 5). The actual impact of fish predation on natural populations, however, remains to be measured.

At least five families of rays contain species known to be molluscivorous (Table 5). Species from some of these have been observed to exert an important influence not only on infaunal mollusc populations of soft bottoms (Coles, 1910; Bigelow and Schroeder, 1953; Randall, 1967; Orth, 1975) but also on epifaunal molluscs of coral rubble or reef benches (Randall, 1964; pers. observ.). Interestingly, most of the temperate nearshore Rajidae appear to feed on molluscs only incidentally, their principal food being crustaceans, annelids and fishes (Smith, 1891; Scott, 1901; Holden and Tucker, 1974; McEachran et al., 1976), whereas gastropods may form more than 50% of the diet in some tropical rays (Randall, 1967). Some species of sharks

and chimaerids also prey on molluscs (Table 5).

Vermeij (1977b) has recently discussed the geologic history of shell-crushing predators. He found the marked early Cretaceous increases in morphologically resistant shells to be correlated with a concomitant increase in the number and variety of shell-breaking predators including crabs, stomatopods, and fishes. Schaeffer and Rosen (1961) have indicated that the great diversification in teleost feeding mechanisms occurred in the late Jurassic or early Cretaceous, although there were earlier crushing fishes among the holostean semionotids and pycnodonts. Evidence of shell crushing has also been noted in Cretaceous sharks (*Ptychodus*). They appear to have been responsible for substantial mortality of epifaunal bivalves (Inoceramidae, Speden, 1971; Kauffman, 1972) and presumably would have been capable of crushing gastropods as well. This all suggests that shell crushing by fish has been a relevant source of molluscan mortality for well over 100 million years, quite a sufficient time to have

TABLE 5. *Fish families and the number of species that crush molluscs for tropical and temperate waters.*[2]

Tropical			Temperate		
Family	Crushing mechanism	Number of crushing species	Family	Crushing mechanism	Number of crushing species
Teleosts					
Lethrinidae (grunts)	Jaw teeth	3	Zoarcidae (eelpouts)	Jaw teeth	2
Sparidae (porgies)	Jaw teeth	13	Sparidae (porgies)	Jaw teeth	2
Balistidae (triggerfish)	Jaw teeth	7	Anarhichadidae (wolffish)	Jaw teeth	5
Monacanthidae (filefish)	Jaw teeth	1	Tetraodontidae (smooth puffer)	Jaw teeth	3
Tetraodontidae (smooth puffer)	Jaw teeth	7	Anguillidae (eels)	Pharyngeal teeth	1
Diodontidae (spiny puffer)	Jaw teeth	4	Cyprinodontidae (killfish)	Pharyngeal teeth	1
Albulidae (bonefish)	Pharyngeal teeth	1	Sciaenidae (croakers)	Pharyngeal teeth	1
Ogcocephalidae (batfish)	Pharyngeal teeth	1	Embiotocidae (surf-perch)	Pharyngeal teeth	2
Branchiostegidae	Pharyngeal teeth	1	Labridae (wrasses)	Pharyngeal teeth	4
Carangidae (jacks)	Pharyngeal teeth	2	Callionymidae (dragonets)	Pharyngeal teeth	1
Leiognathidae	Pharyngeal teeth	1	Stromateidae (butterfish)	Pharyngeal teeth	1
Nemipteridae (breams)	Pharyngeal teeth	1	Pleuronectidae (flounder)	Pharyngeal teeth	5
Gerridae (mojarra)	Pharyngeal teeth	1			
Pomadasyidae (grunts)	Pharyngeal teeth	13			
Sciaenidae (croakers)	Pharyngeal teeth	2			
Aplodactylidae	Pharyngeal teeth	1			
Labridae (wrasses)	Pharyngeal teeth	34			
Blenniidae (blennies)	Pharyngeal teeth	1			
Gobiidae (gobies)	Pharyngeal teeth	3			

TABLE 5. *Continued.*

	Tropical			Temperate		
Family	Crushing mechanism	Number of crushing species		Family	Crushing mechanism	Number of crushing species
Rays						
Dasyatidae (stingrays)	Jaw teeth	4		Myliobatidae (eagle rays)	Jaw teeth	1
Gymnuridae (butterfly rays)	Jaw teeth	2		Rajidae (skates)	Jaw teeth	1
Myliobatidae (eagle rays)	Jaw teeth	2				
Rhinopteridae (cow-nosed rays)	Jaw teeth	1				
Sharks						
Heterodontidae (horned sharks)	Jaw teeth	1		Triakidae (smooth dogfish)	Jaw teeth	2
Ratfish						
(No tropical species)				Chimaeridae	Jaw teeth	3

Summary

	Tropical			Temperate			
	Total crushing	Total surveyed	Proportion	Total crushing	Total surveyed	Proportion	Probability[1]
Families	24	43	0.56	16	38	0.42	$P = 0.109$
Species	107	157	0.68	35	119	0.29	$P < 0.001$

[1] Probabilities computed from a one-tailed test comparing arcsine transformed proportions.

[2] Fish families containing molluscivorous species none of which crush their prey (number of species in parentheses): TROPICAL—Charcharhinidae (3), Sphyrnidae (3), Engraulidae (1), Batrachoididae (1), Gadidae (1), Holocentridae (9), Syngnathidae (3), Serranidae (1), Pseudochromidae (1), Apogonidae (2), Sillaginidae (1), Lutjanidae (1), Mullidae (6), Chaetodontidae (1), Pomacentridae (4), Uranoscopidae (1), Clinidae (3), Acanthuridae (2), Ostraciidae (1); TEMPERATE—Squalidae (2), Muraenidae (1), Batrachoididae (1), Gobiesocidae (1), Gadidae (9), Ophidiidae (1), Gasterosteidae (1), Syngnathidae (4), Scorpaenidae (5), Triglidae (3), Hexagrammidae (3), Congiopodidae (1), Cottidae (5), Serranidae (1), Notothenidae (1), Citelidae (1), Nototheniidae (3), Clinidae (2), Stichaeidae (3), Pholididae (1), Bothidae (7) and Soleidae (5). Note that the sum of the species numbers in parentheses and those in the crushing species column will not add up to the "total surveyed" because some of the families containing crushing species also include species that do not crush their prey.

TABLE 4. *The proportions of fish species and families that include gastropods in their diet from tropical and temperate feeding surveys.*

	Tropical teleosts					
Locality	Species including gastropods	Total surveyed	Proportion	Families including gastropods	Total surveyed	Proportion
India[1]	6	28	0.21	4	16	0.25
Marshall Islands[2]	52	228	0.23	18	53	0.34
Hawaii[3]	27	166	0.16	9	33	0.27
Baja California[4]	12	46	0.26	11	24	0.46
West Indies[5]	70	205	0.34	17	53	0.32
		Mean	0.24		Mean	0.33

	Temperate teleosts					
Locality	Species including gastropods	Total surveyed	Proportion	Families including gastropods	Total surveyed	Proportion
Alaska[6]	8	39	0.21	6	18	0.33
California[7]	18	45	0.40	9	21	0.43
Scotland[8]	14	49	0.29	8	28	0.29
Denmark[9]	16	28	0.57	10	13	0.77
		Mean	0.37		Mean	0.46
	Mann-Whitney U $P > 0.10$ (two-tailed)			Mann-Whitney U $P > 0.10$ (two-tailed)		

[1] Nath (1966), [2] Hiatt and Strasburg (1960), [3] Hobson (1974), [4] Hobson (1968), [5] Randall (1967), [6] Simenstad et al. (1977), [7] Quast (1968), [8] Scott (1901), [9] Blegvad (1916). References 3, 5 and 9 are detailed studies giving volume or weight measures of each prey category.

exerted an important influence on gastropod shell form.

Reconsidering the summaries of tropical and temperate molluscivorous fishes, one can see that the proportion of all species preying on gastropods is roughly comparable (Table 4). If, however, the proportions of molluscivorous species that crush shells are compared, there is a highly significant difference (Table 5). The proportion of shell-crushing fishes is substantially greater in the tropics. Figure 6 further illustrates this point, where the proportion of shell-crushing species of those that eat molluscs has been plotted for those studies surveying the diets of many fish in one area. In tropical waters (arbitrarily defined as lying between 30°N and 30°S latitude) the proportion of shell-crushing species ranges from 42% to 100% (mean 63.8%) and is significantly greater than that observed in temperate surveys (range 0% to 59%, mean 25.2%, $P < 0.001$, Mann-Whitney U test). Interestingly, the two highest temperate values (45% for southern Japan and 59% for North Car-

olina) not only lie close to this arbitrary boundary but were obtained along coasts swept by strong tropically derived western boundary currents (Kuroshio Current and Gulf Stream respectively). That these regions are distinctly more tropical in nature than other north-temperate coasts of equivalent latitude is evidenced by the pronounced northward extension of reef building coral genera within them (Fig. 9 of Newell, 1971). Excluding these two surveys from the analysis, the lower proportion of temperate shell-crushing fish becomes even more dramatic (range 0%–37%, mean 19.8%).

The above interpretation assumes that all shell-crushing fish species are equally abundant and prey equally heavily on gastropods. While there are no directly comparable quantitative data on relative abundances, there are some for diets. The deviations from the assumption of equal feeding intensity, however, further emphasize the pattern already noted. The appendices show that gastropods compose greater than 30% of the diet of nearly one-
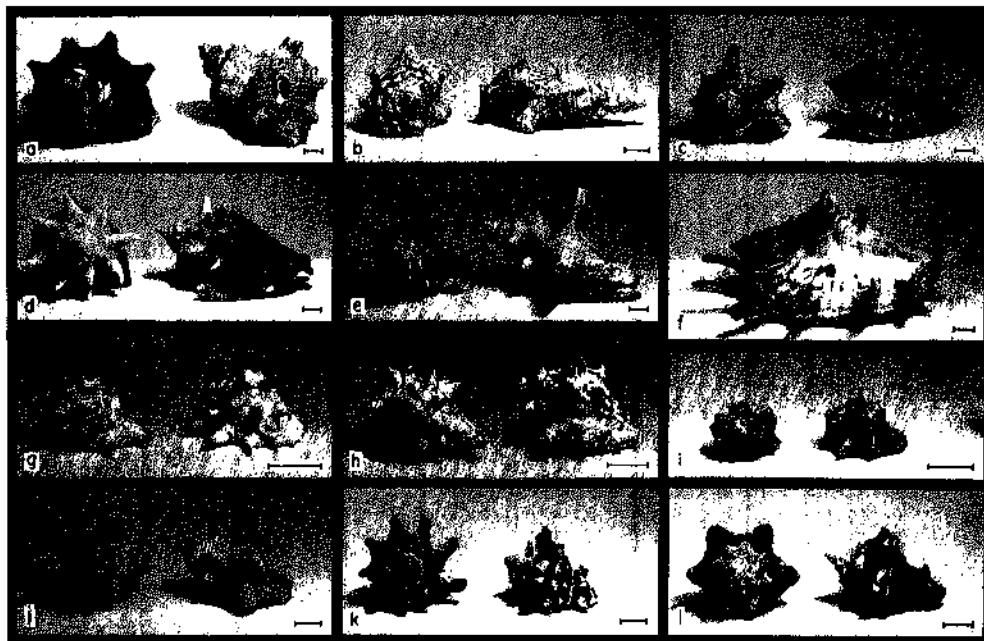
FIG. 7. Species exhibiting stout spinose sculpture from all three orders of marine prosobranchs. Archeogastropoda: a) *Turbo cornutus* (Indo-Pacific). Mesogastropoda: b) *Cerithium nodulosum* (Indo-Pacific), c) *Strombus raninus* (Caribbean), d) *Strombus pugilis* (Caribbean), e) *Strombus gigas* juvenile (Caribbean), f) *Lambis lambis* (Indo-Pacific). Neogastropoda: g) *Drupa ricinus* (Indo-Pacific), h) *Thais luhuanus* (Indo-Pacific), i) *Thais triangularis* (Eastern Pacific), k) *Vasum turbinellum* (Indo-Pacific), l) *Vasum ceramicum* juvenile (Indo-Pacific). Scale bars all 10 mm.

third of the tropical shell-crushing species (16 of 51) for which quantitative feeding data (percent weight or volume of food type) are available. In 32 of these 51 species, gastropods formed more than 10% of the diet. This is in sharp contrast with the admittedly meagre data for temperate fish, where only one of the shell-crushing species for which there are quantitative data had significantly more than 10% of the diet composed of gastropods ($N = 6$). None had more than 30% gastropods in its gut. A similar trend towards greater specialization in the tropics has been observed in the Labridae by Bakus (1969), who also noted a greater tendency toward omnivory among temperate fishes in general. Hence, not only are there more species of shell-crushing fish in the tropics but they appear on the average to be more specialized. The dietary differences I have described above are greater than would be

expected by chance alone ($P = 0.023$ and $P = 0.007$ for 10% and 30% gastropods in the diet, respectively; comparison of arcsine transformed proportions).

It is tempting to attribute the almost exclusively tropical occurrence of stout spinose or nodulose sculpture to this increased intensity of predation by tropical crushing fishes and rays. Such sculpture has evolved independently in all three orders of marine prosobranchs, occurring in numerous genera including *Turbo, Cerithium, Strombus, Lambis, Muricanthus, Ocenebra, Thais, Purpura, Drupa* and *Vasum* (Keen, 1971; Hinton, 1972; Abbott, 1974). Figure 7 illustrates a variety of forms exhibiting this sculpture, all of which are tropical or subtropical. In fact, within the muricid subfamily Thaididae (Keen, 1971), a pronounced inverse relationship exists between the proportion of species exhibiting spinose or nodulose
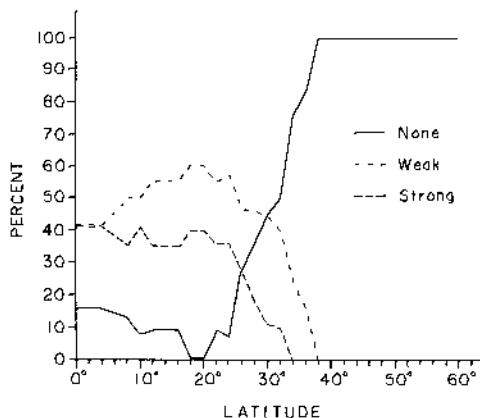
FIG. 8. Proportions of species in the Thaididae (Keen, 1971) exhibiting stout spinose or nodulose sculpture as a function of latitude along the west coast of North America. None—no spinose or nodulose sculpture; weak—sculpture detectable, to approximately 2 mm from body whorl; strong—nodes or spines greater than 2 mm long in adult specimens. Temperate species were taken from the Purpurinae of Abbott (1974) which includes the same genera. The number of species ranges from 12 at the equator to a maximum of 15 at 26°N, to 7 at 38°N, to 4 at 60°N.

sculpture and latitude along the eastern Pacific coast from Columbia to Alaska (Fig. 8). Identical trends exist in the western Atlantic from the Caribbean to Labrador as well as south to Argentina (as compiled from Rios, 1970, and Abbott, 1974), although there are considerably fewer species along these shores. To some extent this reflects a general decrease in the frequency of strong sculpture with increasing latitude (Graus, 1974). However, along the eastern Pacific coast, it also reflects a shift from spines to bladelike varices as in *Thais* (=*Nucella*) *lamellosa* and *Ceratostoma foliatum*. Such varices are the predominant sculptural element in the higher latitude Trophoninae (Abbott, 1974). In *C. foliatum* these varices appear to reduce the probability of being eaten by fish that rip off snail feet, because they increase the chance of landing upright after having been dropped (Palmer, 1977). Their function in other species remains to be satisfactorily explained.

CONCLUSIONS

The experimental and geographic evidence all point in the same direction. Shell-crushing fishes have played an important role in the evolution of gastropod shell sculpture. Though I have suggested other aspects of shell form that may have been influenced by this kind of predation, their effectiveness awaits further experimentation. The evidence for stout spines is clear. Stout spinose or nodulose sculpture reduces vulnerability to being crushed by fish. The high frequencies of this type of sculpture correlated with the increased intensity of shell crushing by fishes in tropical waters suggest that fish predation has also influenced the geographic distribution of sculptural types. While similar correlated geographic differences have been noted between crabs and gastropods among tropical oceans (Vermeij, 1976, 1977a), latitudinal patterns in shell form have remained poorly explained (Graus, 1974; Vermeij, 1973, 1977a; but see Vermeij and Veil, 1977, on latitudinal trends in bivalves and also Vermeij, 1978, for further discussion).

Interpreting large-scale geographic patterns is difficult because so many factors change simultaneously (Pianka, 1966). Since stout spines appear to be most effective against a specific mode of predation, geographic variation in the frequency of species exhibiting them should reflect variation in the intensity of that mode of predation. I believe the increase, with decreasing latitude, in both the numbers and degree of dietary specialization of shell-crushing fishes provides a convincing explanation for the observed geographic distribution of stout spinose sculpture in marine gastropods.

SUMMARY

Two general types of shell-breaking predation on marine gastropods are distinguished. The first is best typified by crabs which exhibit several modes of attack and are capable of breaking shells in a variety of ways. A second is illustrated by teleost fishes and rays that crush shells in their

jaws and are restricted in the manner of attack. Several experiments demonstrate that stout spines or nodes about the periphery of a snail's shell significantly reduce its vulnerability to predators of the latter group. Other morphologies are considered and their potential effectiveness against shell crushing by fish discussed. Species of teleost fishes and rays that crush their gastropod prey are found not only to be more numerous in tropical oceans than temperate ones, but also appear to be more specialized in their diet. The nearly exclusive tropical occurrence of stout spinose or nodulose sculpture supports the hypothesis (Vermeij, 1974, 1978) that geographic variation in predation intensity may lead to regional differences in the frequencies of certain defensive morphologies.

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