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Bioerosion of gastropod shells: with emphasis on effects of coralline algal cover and shell microstructure

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Abstract. Organisms boring into fifty nine species of gastropod shells on reefs around Guam were the bryozoan *Penetrantia clionoides*; the acrothoracian barnacles *Cryptophialus coronorphorus, Cryptophialus zulloi* and *Lithoglyptis mitis*; the foraminifer *Cymbaloporella tabellaeformis*, the polydorid *Polydora* sp. and seven species of clionid sponge. Evidence that crustose coralline algae interfere with settlement of larvae of acrothoracican barnacles, clionid sponges, and boring polychaetes came from two sources: (1) low intensity of boring in limpet shells, a potentially penetrable substrate that remains largely free of borings by virtue of becoming fully covered with coralline algae at a young age and (2) the extremely low levels of boring in the algal ridge, a massive area of carbonate almost entirely covered by a layer of living crustose corallines. There was a strong negative correlation between microstructural hardness and infestation by acrothoracian barnacles and no correlation in the case of the other borers. It is suggested that this points to a mechanical rather than a chemical method of boring by the barnacles. The periostracum, a layer of organic material reputedly a natural inhibitor of boring organisms, was bored by acrothoracican barnacles and by the bryozoan. The intensity of acrothoracican borings is shown to have no correlation with the length of the gastropod shell.

Introduction

This paper presents a portion of a study investigating the interactions among boring organisms (those that penetrate a hard substrate and live within it), gastropod shells, and crustose coralline algae. An earlier part of this study has shown that the borers involved, and the percentage of shells bored by them, are three species of acrothoracican barnacles (*Cryptophialus coronophorus*, c.f. *Cryptophialus zulloi*, and *Lithoglyptis mitis*) (55%); the bryozoan *Penetrantia clionoides* (58%); the foraminifer *Cymbaloporella tabellaeformis* (15%); seven species of clionid sponge (9%); and the polychaete *Polydora* sp. (10%) (Smyth 1988 a, b; Smith 1990). The gastropod shells involved are fifty nine species that occur intertidally and subtidally in the waters around Guam. Crustose coralline algae are hard, calcified red algae that deposit calcium carbonate within and between cell walls and are important structural components of reefs in that they play a critical cementing function in the consolidation of reef components. They are usually the most common carbonate components on reefs in terms of reef surface area occupied (Milliman 1974). Tropical reef snails at sites with high surf are heavily encrusted with coralline algae yet we know almost nothing about the ecology of these encrusters when occupying gastropod shells. Most studies of growth, competition, and mortality of encrusting fauna and flora have been done on artificial panels, solid rock, attached shells, and algal fronds.

My interest in the factors inhibiting boring into gastropod shells stems from initial field observations that coralline-encrusted shells appeared to be less bored than were non-encrusted shells from the same sites. This suggested that living crustose coralline algal cover might cause a reduction in shell boring. Corallines might protect shells in one of three ways; (1) by interfering with settlement, (2) by interfering with penetration, (3) by smothering the borers.

It has been reported that organisms encrusting coral inhibit the development of or smother the endolithon (Bromley 1978; Bertram 1936; MacGeachy and Stearn 1976; MacGeachy 1977). Unfortunately, there is ambiguity in these studies because of lack of information regarding the encrusters. MacGeachy (1977), for example, reports "sponges will be present only if the sponge larvae settle before the substratum has been entirely encrusted" but the encrusters were not identified. On the other hand, a number of reports claim that encrusters do not have an inhibitory effect on borers (Highsmith 1981; MacGeachy and Stearn 1976; Risk and Sammarco 1982).

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Evidence of a relationship between larval settlement and presence of coralline algae has been presented in a number of papers (see Morse and Morse 1984). These studies have dealt with the induction of settlement of larvae of molluscs (that feed on these algae) by substances emanating from the corallines. To my knowledge, there has not been a study dealing with inhibition of settlement by corallines.

There has been no previous study presenting a comparison between coralline encrusted and non-encrusted shells at the same site, though a previous portion of this study (Smyth 1988 a) compared coralline-encrusted and non-encrusted areas on the same shell, and found that the boring bryozoan, *Penetrantia clionoides*, only bores into those parts of the shell surface devoid of coralline algae. This borer is particularly common on the left side of the aperture in hermited shells (78% of which are bored by this organism) where corallines cannot proliferate because of constant abrasion against the substrate as the hermit crab carries the shell.

Given that boring organisms must contend with properties of the substrate such as degree of hardness, proportion of organic matrix, and surface area available, a hypothesis was formulated at the initiation of this study that microstructural differences would be reflected in different rates of excavation success by the borers. Specifically, shell hardness was expected to be directly related to resistance to boring. There are a number of studies documenting the microstructure of gastropod shells (Bøggild 1930; Srinivasan 1941) yet I know of only one study that attempts to establish a relationship between shell microstructure and the extent of boring (White 1969). The latter study claimed that hardness was not a significant factor in determining penetration success by the acrothoracican *Trypetesa lampas* into gastropod shells.

The high proportion of organic matrix in the periostracum has been reported to deter predation (Bottjer 1981; Cobb 1969). Shell surface area would also be expected to influence the level of boring in terms of surface area available for settlement of the larvae of the boring organisms. The literature suggests that shell size is significant in terms of boring intensity (White 1969) with older shells being more heavily bored. The latter study was conducted in the temperate zone and it appeared that it would be interesting to pursue if there were complexities involved in this tropical situation that would override mere surface area effects.

Smith (1990) reports on the incidence of boring in 1874 gastropod shells in the waters around Guam. This paper examines factors that influence the degree to which shells are bored. Specifically, the aims of this study were: (1) to determine the extent to which encrustation by coralline algae and shell microstructure influence boring into gastropod shells and (2) to determine the intensity of boring in shells of different size.

Methods

Living gastropods, shells occupied by hermit crabs (herein termed "hermited shells"), and empty shells, were collected at fifteen sites, at eight locations, around Guam. Ten of the study sites were in the intertidal (four were algal ridges) and five were shallow subtidal sites. Areas were chosen randomly at each site and all shells within the area were collected. Limpets were collected, on the algal ridge in Pago Bay, by placing a drop of formalin at the inhalent canal and lifting the limpet from the substrate as it raised itself away from the irritant. All other gastropods collected, as well as characteristics of the study sites, are presented in Smyth (1990). Shells were preserved by oven-drying or by immersion in 4% buffered formalin or in 70% ethanol. As each shell was examined under the light microscope, its identification, dimensions, the borers present, their intensity, position, and extent of coralline cover were recorded. Having noted surface characteristics, color, conceptacle dimensions and shape, chips from the corallines were prepared for scanning electron microscopy in order to measure diameters and lengths of epithallial, perithallial, and hypothallial cells thus allowing species identification according to the criteria of R. Steneck (personal communication). These chips were glued onto glass cover slips with a dilute water-soluble glue (trade name, "Elmer's Glue-All", Borden Inc.). The cover slip was then attached to a standard aluminium stub by carbon paint. The specimens were later sputter-coated under vacuum, first with a thin layer of carbon and then with gold palladium. They were viewed with Cambridge Stereoscan Electron Microscopes, Models 100 and 250.

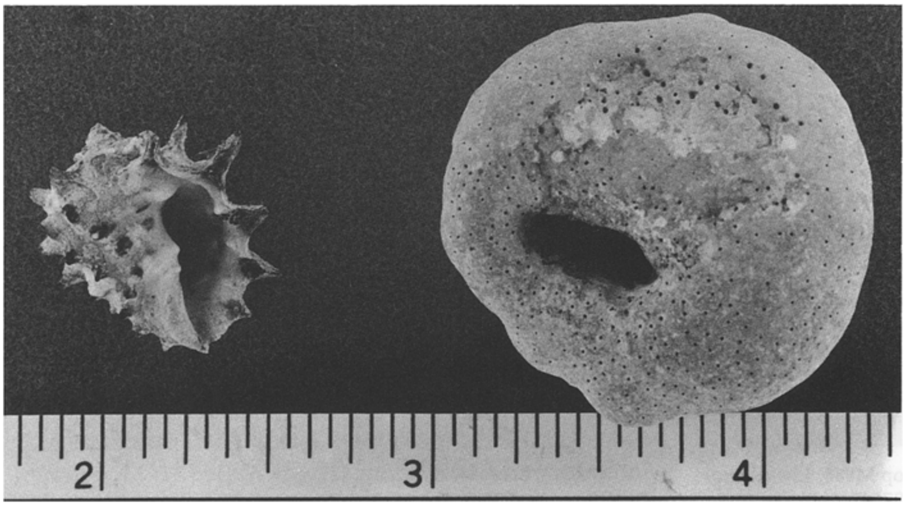

Fig. 1. Ventral view of coralline-covered and non-encrusted *Drupa* sp. of similar dimensions. Scale measures in sixteenths of an inch

The gastropods have been divided into six distinct shell-structure groups, based on superfamilies, for the purpose of analyses of microstructure. Taxonomy follows Cernohorsky (1978). The superfamilies and included genera are; Conacea (*Conus*); Volutacea (*Mitra, Vasum*); Tonnacea (*Bursa, Cymatium, Distorsio*); Buccinacea (*Cantharus, Latirus, Peristernia*); Muricacea (*Chicoreus, Drupa, Drupella, Morula, Cronia, Coralliophila*); Trochacea (*Trochus, Tectus, Turbo, Astrea*).

Quadrat sampling, to establish the density of both limpets and *Drupa* sp., was carried out using a 50 cm × 50 cm quadrat frame placed randomly on the surface of the algal ridge.

In order to facilitate detailed examination of the algal ridge substrate for borers (impossible to achieve in situ because of high surf), a total of 99 samples of crustose coralline algae, was collected at randomly chosen sites along the algal ridge in Pago Bay. Samples, taken from the surface to a depth not greater than 30 mm into the substrate, were collected using a geologist's hammer and chisel. The substrate and its associated gastropods were bagged immediately, rinsed in distilled water, and oven-dried prior to examination for presence of the boring organisms. The surface area of each piece was determined by measuring the projected area on a sheet of graph paper with a millimeter grid.

Results

A layer of living coralline algae covers the coralline ridge itself and encrusts the gastropods on the ridge (Fig. 1). Representatives of five genera of corallines are involved: *Hydrolithon reinboldi, Hydrolithon* sp., *Neogoniolithon* sp., *Paragoniolithon* sp., *Porolithon onkodes*, and *Lithoporella* sp.

Data for limpets are presented in Table 1. The species involved and their densities were; *Patella flexuosa*, 42/m^2; *Cellana radiata orientalis*, 24/m^2. This compares with values of 9/m^2 for *Drupa ricinus* and 0.5/m^2 for *Drupa morum*. The latter two were chosen for comparison because they are the two most common non-docoglossan gastropods at this site. The size range for these limpets was: *P. flexuosa*, 4 mm–27 mm and *C. radiata orientalis*, 8 mm–23 mm.

Field observations indicated that recently settled limpets become covered with coralline algae very rapidly. Comparisons with *Drupa* sp. show that young limpets are significantly more encrusted than are young drupes. This comparison is made because 78% of the bored non-docoglossan shells on the ridge were representatives of the genus *Drupa*. These limpets are inconspicuous on the algal ridge as a consequence of the near total encrustation by coralline algae which results in them merging in with the surrounding living crusts. It is only when moving that they can be distinguished from the algal ridge itself.

Table 1. Data for limpets presenting total number of shells examined in each category, the density of each on the algal ridge in Pago Bay, the proportion bored, and the total number of acrothoracican barnacles involved

Species	Number of shells examined	Density of limpets	Number (%) of shells bored	Total number of barnacles (*C. zulloi*)
Patella flexuosa	214	42.4/m^2	0	0
Cellana radiata orientalis	61	24.0/m^2	2 (3%)	9

Of 214 specimens of *Patella flexuosa* collected, all of which were totally encrusted by corallines, not one was bored. Sixty-one specimens of *Cellana radiata orientalis* were collected, two of which were bored by acrothoracican barnacles. Both bored shells were exceptional in not having a complete cover of coralline algae. The coralline cover on both was patchy, appearing as if the coralline had been damaged by grazers. One specimen, 11.2 mm in length, contained 5 acrothoracicans. Three of these were c.f. *Cryptophialus zulloi* while the identity of the other two is uncertain because they were recently settled specimens. The other bored shell, 9.1 mm long, contained four acrothoracicans, all *C. zulloi*.

This low level of boring indicates that the early and rapid encrustation of the limpets by coralline algae seals off the substrate, affording little opportunity for settlement of larvae of boring organisms. At the site where these limpets were collected, 69% of non-docoglossan living gastropods were bored (Smyth 1990). This high level of boring in a substrate showing much less encrustation by corallines is in sharp contrast to a level of 0.7% for limpets.

The massive area of carbonate known as the algal ridge is covered with a layer of living crustose coralline algae except in zones where that layer has been damaged by grazing organisms or by physical factors.

The surface area of each of the 99 pieces of crustose coralline algae, removed from the living upper layer of the algal ridge, ranged from 1.53 cm^2 to 304.28 cm^2. The total surface area of this algal ridge material, collected for microscopic examination, amounted to 7341 cm^2. All but two of the pieces had an intact cover of crustose coralline algae. These two pieces were encrusted by different species of corallines but both samples had discontinuities in the crust. These discontinuities appeared to have resulted from the activities of grazing organisms. At points where the coralline was damaged, acrothoracicans had bored into the two pieces, 128 cm^2 and 117 cm^2 respectively, in area. The first portion of the ridge contained one specimen of *Cryptophialus coronophorus* and three of *C. zulloi*. The second piece was bored by three specimens of *C. zulloi*. The borehole apertures of these barnacles were confined to a rectangular area of 0.2 cm^2 and 0.1 cm^2 respectively, on each piece. No other borers of any kind were found in this material nor were any seen during examination of the algal ridge in situ. It is clear that it is only where the living coralline cover is damaged that borers have access to the algal ridge.

The carbonate structure of the ridge itself can be bored by acrothoracicans, sponges and *Polydora* sp., as indicated by examination of dislodged pieces of the algal ridge. In contrast with the above-mentioned pieces, where the surface exposed to the water column is covered in living crustose corallines, these dislodged pieces have exposed surfaces that are not covered with a layer of living coralline algae. Sponge papillae, for instance, were seen in coralline algae on such pieces. As boring progressed the papillary openings were formed through the upper living layer of coralline from beneath it, indicating that the physical nature of the substrate is not a deterrent to borers. The results showed no evidence that acrothoracican barnacles, the boring bryozoan, or boring sponges, can penetrate a surface covered with living coralline algae.

In considering the reactions of the various boring groups to coralline algae, a diversity of behaviors is seen. Recently settled acrothoracicans, identifiable by the discarded cyprid plates on the surface, were never seen on the coralline crusts. Once established in the gastropod shell or in parts of the algal ridge (both substrates now being overgrown by living coralline tissue) acrothoracican barnacles maintain borehole openings through the coralline crust as the latter grows. The boreholes are contained entirely within the shell or the algal ridge material with a "chimney" through the crust.

Borings by *Polydora* sp. occurred randomly on the outer surface of non-docoglossan gastropod shells having a heavy encrustation of corallines. Detailed examination of the burrows indicated that they extend laterally through both the shell material itself and the coralline. They wind their way throughout the coralline material and have no difficulty penetrating it. The thickest coating of corallines seen on individual shells occurred at the Sargassum Belt in Pago Bay and it is here that *Polydora* sp. proved to be most common, occupying 45% of bored shells.

The foraminifer *C. tabellaeformis* and the boring sponges occurred commonly in shells with little encrustation.

Observations in the field indicated a pungent odor emanating from particular crustose corallines (both on shells and on the ridge itself), suggesting the possibility of chemical interactions with organisms on the algal surface. This odor is so distinctive and strong that it is readily perceived while standing on the algal ridge at low tide.

The majority of the shells in this study have crossed-lamellar structure. Specifically, the shell microstructure of the six groups under consideration here is as follows (after Bøggild 1930; Currey 1976; and this study): Trochacea – upper layer prismatic, under layer nacreous; Volutacea, Tonnacea, Buccinacea, Muricacea – crossed lamellar; Conacea – crossed lamellar.

Data on the incidence of borers in the six shell groups are presented in Tables 2–4. The shell groups are ranked in order of decreasing hardness where hardness is measured by the size of the depression left when a diamond is pressed down with a known force (Currey 1976). The data show a strong negative correlation ($P < 0.001$, Test for a Linear Trend in Proportions, Snedecor and Cochran 1967) between microstructure hardness and infestation by acrothoracicans (Table 2). The same association occurs for the individual acrothoracican species. No correlation with shell microhardness is seen for the sponges, polydorids, the bryozoan, and the foraminfier. For living gastropods and hermited shells considered sep-

Table 2. Percent boring in each shell-structure category. Data for living gastropods and for hermited shells are combined here. The six shell groups are ranked from left to right in order of decreasing shell hardness

	Conacea (%)	Volutacea (%)	Tonnacea (%)	Buccinacea (%)	Muricacea (%)	Trochacea (%)
Acrothoracicans	9	24	43	52	64	84
C. coronophorus	0	4	14	18	28	68
C. zulloi	0	5	11	22	38	60
L. mitis	7	19	32	42	31	70
Boring sponges	7	12	32	22	5	10
Polydora sp.	3	8	11	0	10	2
P. clionoides	64	57	82	90	57	62
C. tabellaeformis	22	34	7	0	9	6

Table 3. Percent boring in living gastropods grouped into shell-structure categories. The five shell-structure groups are ranked from left to right in order of decreasing shell hardness. The Buccinacea were excluded here because of the small sample size

	Conacea (%)	Volutacea (%)	Tonnacea (%)	Muricacea (%)	Trochacea (%)
Acrothoracicans	12	15	33	69	100
C. coronophorus	0	0	17	28	93
C. zulloi	0	0	8	47	87
L. mitis	9	12	17	17	83
Boring sponges	0	5	0	1	7
Polydora sp.	9	12	17	9	0
P. clionoides	64	51	83	32	40
C. tabellaeformis	21	34	17	8	3

Table 4. Percent boring in hermited shells grouped into shell-structure categories. The shell groups are ranked from left to right in order of decreasing shell hardness

	Conacea (%)	Volutacea (%)	Tonnacea (%)	Buccinacea (%)	Muricacea (%)	Trochacea (%)
Acrothoracicans	4	33	50	51	58	67
C. coronophorus	0	7	12	18	28	45
C. zulloi	0	10	12	23	28	36
L. mitis	4	26	44	41	46	58
Boring sponges	15	19	56	23	9	12
Polydora sp.	0	5	6	0	11	3
P. clionoides	65	62	81	90	83	82
C. tabellaeformis	23	33	0	0	11	12

arately, the same pattern as for the overall data is seen (Tables 3 and 4).

Acrothoracican and bryozoan borings were seen in the periostracum, an area containing a high proportion of organic material. It should be noted that many of the shells in this study have a thin periostracum. Yet, even species of *Conus*, which have the thickest periostracum in this study, were bored.

Regression analysis showed that there was no correlation between number of female acrothoracica (males are dwarf, much reduced in structure, and are attached to wall of borehole) and length of living and hermited *Drupa* sp. The size range of the drupes was 13 mm–30 mm and the number of female acrothoracica per shell varied from 0 to 109. Acrothoracicans were used for this analysis because a common borer was required and the colonial nature of the bryozoans made them inappropriate.

Discussion

This study has presented preliminary observations on the complex interactions that influence the degree to which shells are penetrated by boring organisms. In summary, the data for limpets, for the algal ridge substrate, and for the location of bryozoan borings, together support the hypothesis that corallines inhibit settlement of the larvae of boring organisms. At least in the case of acrothoracican barnacles, this study has found that shell microstructure and age of shell are also significant. Each of these factors cannot be considered in isolation. For example, the effects of shell age are manifested more in the level of encrustation than in the mere surface area effects, older shells having a greater amount of encrustation than do younger shells.

Limpet shells are a dominant resource for borers in terms of available substrate because of their high density. They are for the most part, however, unavailable to boring organisms because encrustation by corallines rapidly seals off the substrate. Similarily, in the case of the algal ridge itself, this study has shown that though acrothoracicans, sponges, and *Polydora* sp. are capable of boring into the ridge material they do not normally do so. This study has shown that the massive area of carbonate in the algal ridge is potentially penetrable by borers but that the coating of living crustose corallines is protective. Therefore, though there are many different kinds of substrate available both intertidally and in the shallow subtidal for colonization by boring organisms, they go untapped because of the coralline algal cover.

Absence of borehole apertures on the surface of the coralline crusts does not indicate whether or not they are underneath, having been smothered. In considering if coralline algae cause a reduction in shell boring by smothering the borers, an earlier part of this study has shown that bryozoans are the only group smothered (Smyth 1988 a) and that this is a rare event. As bryozoans are colonial, the smothering of some zooids does not terminate the bioerosion.

Having established that the reduction in shell boring in the presence of coralline algae is not a consequence of smothering by the algae, we must consider whether they interfere with settlement or penetration. A previous paper has shown that the boring bryozoan only bores into those parts of the shell surface devoid of coralline algae (Smyth 1988 a). In hermited shells, 78.1% of which were bored by the bryozoan, the boreholes were concentrated almost entirely in the bare patches on the left side of the aperture where corallines cannot proliferate because of the constant abrasion against the substrate as the hermit crab carries the shell. In living gastropods, 35.8% of which were bored by the bryozoan, this borer was found in the bare patches that occasionally appear in the coralline anywhere on the shell surface. In very rare instances, zooids were found buried under coralline algae. When the pattern of growth was examined, it was clear that these proliferated from the intense growth in the bare zone but later became overgrown by corallines. It is apparent that abrasion did not continue to occur in those particular areas, perhaps as a consequence of a change in the way the shell was being carried. This would occur when a new hermit crab moves in.

Evidence from the Bryozoa, therefore, indicates that the reduction in the level of boring is not a smothering effect. In considering if corallines reduce shell boring by interfering with settlement or penetration, these data show that the physical nature of the corallines does not deter boring and that the deterrent may be chemical, emanating from the thin surface layer of living coralline algal material. The odor observed on the algal ridge is suggestive of such a phenomenon. The odor of marine algae is difficult to pursue at a chemical level (W. Fenical personal communication) and is usually the composite of 100+ small molecules. In considering the possible implications of this odor, it is interesting to note that Crisp (1984) points out that, for certain larvae, the shape of the surface is a minor consideration in comparison with its surface chemical properties. Observations made on the attachment of oyster larvae in natural water have shown that chemicals are capable of repelling these larvae (Costlow and Tipper 1984). This interesting observation merits further investigation.

Colonization of new substrate by boring sponges can occur by proliferation of already-established sponge tissue from one substrate to another. Sponge infestation of these shells, however, most likely occurs by larval settlement, given the necessity of undisturbed abutting surfaces for proliferation of the sponge tissue. The larva involved is a solid, ciliated parenchymella (Pomponi 1980).

Previous studies have addressed whether corallines protect coral substrates. Bertram (1936), Highsmith (1981) and MacGeachy and Stearn (1976) reported that corallines do not protect coral skeletons from borers. These statements were based on the presence of clionid sponge openings in corallines. As emphasised earlier this, in itself, provides no support for their statements.

Previous studies reporting borers in corallines would appear to contradict the results of this study but absence of detail regarding the substrate makes evaluation difficult. In their study of coral borers in *Acropora* sp., for example, Risk and Sammarco (1982) report that boring sponges and sipunculans penetrate corallines, though no details are presented in order to facilitate determination of where the boring might have been initiated. Wells and Tomlinson (1966) found the acrothoracican, *Kochlorine floridana*, in *Lithothamnium* sp. and *Goniolithon* sp. in the Gulf of Mexico. No details are presented regarding the substrate, resulting in uncertainty regarding presence or absence of a coating of living coralline tissue. *Cliona viridis* is reported to excavate burrows in coralline algae in deep water in the vicinity of Rovigno (Hartman 1957). *Polydora armata* bores in "coralline hummocks" (Hartman 1941). *Boccardia columbiana* is reported from *Lithophyllum sp.* and *B. proboscidea* was found in a *Lithophyllum* encrusting rock (Woodwick 1963).

The negative correlation between acrothoracican intensity and shell hardness suggests that these barnacles are more dependent upon mechanical means of boring than are the other borers. The acrothoracicans are the only borers in this study with obvious structures for abrasion of the shell; these being the mantle teeth. Of the borers occurring here, the method of boring is known only for the boring sponges. Conclusive evidence for chemical etching has been presented for these sponges (see Smyth 1990).

The majority of the shells collected here have crossed-lamellar structure, the hardest of the structural types. Crossed lamellar structure is dominant amongst gastropod taxa. Fifty four of the sixty superfamilies examined by Currey and Taylor (1974) have shells consisting exclusively or largely of crossed-lamellar structure. These authors show that only two gastropod superfamilies possess nacreous structures. Based on the assumption that predation exerts the main selective pressure on shells, Currey (1976) assumes that there is selective pressure on shells to be strong and is, therefore, puzzled as to why the majority of shells are hard but not very strong. The results of this study suggest that borers may be a greater selective force than previously believed and that, consequently, there may be greater selective pressure to be hard than to be strong. The relative invulnerability of species with crossed lamellar structure is consistent with its extremely widespread distribution among shallow water gastropods. A portion of this study (Smyth 1990) has shown that boring levels are significantly higher at such sites than at deeper sites.

In contrast with the results in this study, White (1969) states that the hardness of the gastropod shell is not relevant to the penetration success of the acrothoracican barnacle, *Trypetesa lampas*. However, she considered the hardest shells to be those most difficult to fracture with a hammer. This measures brittleness, not hardness. Microscopic hardness, specifically, is the feature of importance to the borer.

A shell with a high content of organic matrix is highly susceptible to penetration by borers (Cobb 1969; Rützler and Rieger 1973; Warburton 1966; Yonge 1955). The results in this study agree with these earlier reports as the less hard shells are more heavily bored. The literature suggests that the periostracum, a layer of organic material, functions as protection for the mollusc shell against boring organisms. Most studies of the secondary functions of periostracum have been carried out on shells with a prominent, thick periostracum and in these the protective function has usually been apparent (Clark 1976). Cobb (1969) speculated that the high proportion of organic material in the periostracum of *Mytilus edulis* could deter penetration. Bottjer (1981) shows that the thick, hairy periostracum of *Fusitriton oregonensis* serves as a deterrent to borers. Microborings in the brachiopod *Terebratella sanguinea* first penetrate the shell at points where the periostracum has been stripped away (Curry 1983). The periostracum of shells in this study has been shown to be penetrable by the boring bryozoans, but it must be noted that few of the species collected here have prominent periostraca.

It is reasonable to assume that, all other things being equal, older shells are more heavily bored than are younger shells because of the greater probability of settlement of borers on older shells. A number of studies support this. Boekschoten (1966) concluded that infestation is related to age. *P. ciliata* was not found boring in shells of *Littorina littorea* shorter than 10 mm (Orrhage 1969).

There in an absence of infestation of small *Haliotis* shells by *Cliona celata californiana* (Hansen 1970). Oyster shells younger than three years do not contain *Cliona* (Warburton 1958). Larger shells of *Buccinum undatum* are more likely to be infested by *Trypetesa lampas* than are smaller ones, but no significant regression exists in the case of *Neptunea antiqua* (White 1969). It is obvious from the present study that the situation is considerably more complex for these tropical shells than for the above-mentioned temperature species in that the effects or shell age/size cannot be considered in isolation and must be considered in conjunction with shell microstructure and coralline algal cover.

In conclusion, the significance of this study lies in its determination of a reduction in boring levels in gastropod shells as a consequence of encrustation by coralline algae. Another portion of this research suggests that the reproductive output of corallines on shells is higher than that on surrounding stationary hard substrates (Smyth in preparation). It, therefore, appears that both groups may be enjoying increased fitness by virtue of this association.

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References

Bertram GCL (1936) Some aspects of the breakdown of coral at Ghardaga, Red Sea. Proc Zool Soc London 106:1011–1026

Boekschoten GJ (1966) Shell borings of sessile epibiontic organisms as palaeoecological guides (with examples from the dutch coast). Palaeogeogr Palaeoclimatol Palaeoecol 2:333–379

Bøggild OB (1930) The shell structure of the mollusks. K Dan Vidensk Selsk Skr Natruvidensk 2:233–326

Bottjer DJ (1981) Periostracum of the gastropod *Fusitriton oregonensis*: natural inhibitor of boring and encrusting organisms. Bull Mar Sci 31:916–921

Bromley RG (1978) Bioerosion of Bermuda reefs. Palaeogeogr Palaeoclimatol Palaeoecol 23:169–197

Cernohorsky WO (1978) Tropical Pacific Marine Shells. Pacific Publications, Sydney

Clark GR (1976) Shell growth in the marine environment: approaches to the problem of marginal calcification. Am Zool 16:617–626

Cobb WR (1969) Penetration of calcium carbonate substrates by the boring sponge *Cliona*. Am Zool 9:783–790

Costlow JD, Tipper RC (1984) Marine biodeterioration: an interdisciplinary study. Naval Institute Press, Annapolis

Crisp DJ (1984) Overview of research on marine invertebrate larvae, 1940–1980. In: Costlow JD, Tipper RC (eds) Marine biodeterioration: an interdisciplinary study. Naval Institute Press, Annapois, pp 103–126

Currey JD (1976) Further studies on the mechanical properties of mollusc shell material. J Zool London 180:445–453

Currey JD, Taylor JD (1974) The mechanical behaviour of some molluscan hard tissues. J Zool London 173:395–406

Curry GB (1983) Microborings in recent brachiopods and the functions of caeca. Lethaia 16:119–127

Hansen JC (1970) Commensal activity as a function of age in two species of california abalones (Mollusca: Gastropoda). Veliger 13:90–94

Hartman O (1941) Some contributions to the biology and life history of Spionidae from California. Hancock Pacific Exped 7:289–322

Hartman WD (1957) Ecological niche differentiation in the boring sponges (Clionidae). Evolution 11:294–297

Highsmith RC (1981) Coral bioerosion at Enewetak: agents and dynamics. Int Rev Hydrobiol 66:335–375

MacGeachy JK (1977) Factors controlling sponge boring in Barbados reef corals. Proc 3rd Int Coral Reef Symp 2:477–483

MacGeachy JK, Stearn C (1976) Boring by macro-organisms in the coral *Montastrea annularis* on Barbados reefs. Int Rev Hydrobiol 61:715–745

Milliman JD (1974) Marine carbonates. In: Milliman JD, Muller G, Forstner U (eds) Recent sedimentary carbonates. Springer, Berlin Heidelberg New York, pp 1–375

Morse ANC, Morse DE (1984) Recruitment and metaborphosis of *Haliotis* larvae induced by molecules uniquely available at the surfaces of crustose red algae. J Exp Mar Biol Ecol 75:191–215

Orrhage L (1969) On the shell growth of *Littorina littorea* (Linne) (Prosobranchiata, Gastropoda) and the occurrence of *Polydora ciliata* (Johnston) (Polychaeta Sedentaria). Zool Bidr Uppsala 38:137–153

Pomponi SA (1980) Cytological mechanisms of calcium carbonate excavation by boring sponges. Int Rev Cytol 65:301–319

Risk MJ, Sammarco PW (1982) Bioerosion of corals and the influence of damselfish territoriality: a preliminary study. Oecologia 52:376–380

Rützler K, Rieger G (1973) Sponge burrowing: fine structure of *Cliona lampa* penetrating calcareous substrata. Mar Biol 21:144–162

Smyth MJ (1988a) *Penetrantia clionoides*, sp. nov. (Bryozoa), a boring bryozoan in gastropod shells from Guam. Biol Bull 174:276–286

Smyth MJ (1988b) The foraminifer *Cymbaloporella tabellaeformis* (Brady) bores into gastropod shells. J Foraminiferal Res 18:277–285

Smith MJ (1990) Incidence of boring organisms in gastropod shells on reefs around Guam. Bull Mar Sci 46 (in press)

Snedecor GW, Cochran WG (1967) Statistical methods, 6th edn. Iowa State University Press, Ames, Iowa

Srinivasan PS (1941) The elastic properties of molluscan shells. Q J Indian Inst Sci 4:189–221

Warburton FE (1958) Control of the boring sponge on oyster beds. Progress Reports of the Atlantic Coast Stations. Fish Res Board Can 69:7–11

Warburton FE (1966) The behavior of sponge larvae. Ecology 47:672–674

Wells HW, Tomlinson JT (1966) A new burrowing barnacle from the western Atlantic. Q J Florida Acad Sci 29:27–37

White F (1969) Distribution of *Trypetesa lampas* (Cirripedia, Acrothoracica) in various gastropod shells. Mar Biol 4:333–339

Woodwick KH (1963) Comparison of *Boccardia columbiana* Berkeley and *Boccardia proboscidea* Hartman (Annelida, Polychaeta). Bull S Calif Acad Sci 62:132–139

Yonge GM (1955) Rock-boring organisms. In: Sognnaes RF (ed) Mechanisms of hard tissue destruction, publ 75. Am Assoc Adv Sci, Washington, DC, pp 1–24