

SELECTIVE HERBIVORE INCREASES BIOMASS OF ITS PREY: A CHITON–CORALLINE REEF-BUILDING ASSOCIATION¹

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Abstract. The intimate association between a selective herbivore (the chiton *Choneplax lata*) and its primary prey (the crustose coralline alga *Porolithon pachydermum*) results in increased biomass and accretion of the alga. This process, over ecological and geological time scales, comprises a major component of Caribbean reef-building systems. Manipulative experiments showed that as the chiton grazes the alga it stimulates new meristematic activity and removes sporlings of the competitively superior frondose and filamentous algae, thereby increasing the survival rate of *P. pachydermum* on the intertidal reef crest. Furthermore, in the absence of *C. lata*, overgrowths of frondose and filamentous epiphytes provide an attractive food source for parrotfishes (Scaridae), which accelerates bioerosion of the coralline reef-crest structure due to the deep rasping action of feeding activity. Algal removal experiments suggest that the role of *P. pachydermum* is to provide a predictable food source and refuge substratum, which increases survivorship of the burrowing chiton by minimizing expenditure of energy during foraging and risk to predation.

The chiton/coralline alga association is abundant throughout tropical western Atlantic islands and augments reef-building processes on the shallow algal crest portion of Caribbean reefs. Cover of the *Choneplax/Porolithon* association in the Belize Barrier Reef crest averages 13% (maximum to 70%) with a mean chiton density of 664 individuals/m² within the association. On average, the extensive networks of interconnected chiton burrows extend between 6 and 10 cm deep and contain one *C. lata* for every six openings, with the majority of animals (66%) ranging from 16 to 30 mm in length. Gut contents of the chiton consist predominantly of *P. pachydermum* (51%), followed by bacterial detritus (30%), Cyanophyta (13%), Bacillariophyta (3%), and fleshy microalgae (3%). The close SEM (scanning electron microscope) match between radular morphology of *C. lata* and grazing scars on the thallus surface of *P. pachydermum* shows how the chiton regularly feeds on the coralline alga without causing mortality. Virtually all *P. pachydermum* in the vicinity of *C. lata* burrows contain radular track scars of $\approx 10 \mu\text{m}$ in depth, whereas the photosynthetic, meristematic, and reproductive tissues of the coralline lie below 20 μm . *P. pachydermum* under intense chiton grazing is photosynthetically competent with 0.1 mg C fixed $\cdot \text{g}^{-1}$ organic dry mass $\cdot \text{h}^{-1}$, which is not significantly different from ungrazed material and within the range of rates for other crustose coralline algae. The result is continuous net accretion at a mean rate of 2.3 mm/yr.

Key words: accretion; biomass; Caribbean; chiton–coralline association; *Choneplax lata*; herbivory; *Porolithon pachydermum*; reef-building.

INTRODUCTION

Studies in marine intertidal and subtidal systems have had a substantial impact on the general field of ecology and evolutionary biology, especially in understanding predation, competition, physical disturbance, and physiological stress. As pointed out by Dethier and Duggins (1984), the demonstrable importance of these “negative interactions” may have caused us to overlook more complex indirect factors, particularly among herbivores and their prey, many of which could be positive. In contrast, it is well documented that ter-

restrial plants respond to herbivory in complex ways, often altering their morphology, chemistry, and productivity. For example, terrestrial grassland biomass can be stimulated and maintained by continual herbivory (e.g., McNaughton 1979). Owen and Wiegert (1976, 1981) and Owen (1980) also postulate that herbivores can maximize fitness of their food plants, possibly resulting in mutualisms between grasses and grazers. However, there are few marine examples documenting that a characteristically negative factor such as herbivory may in fact be a positive attribute leading directly to increased growth and biomass of prey species.

In further contrast to terrestrial systems (e.g., Simberloff et al. 1978, Inouye 1982), tightly coupled mu-

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tualisms and commensalisms within or between trophic levels have not been frequently explored in marine environments (Vermeij 1983). Those that have are mainly passive or disproportionately one sided. Some examples are the cropping effects of a limpet, which reduces mortality of the kelp *Egrecia* by decreasing losses due to wave-shearing (Black 1976), a limpet–coralline association that prevents lethal fouling by epiphytes (Steneck 1982), tube-building infauna that facilitate the colonization of other infaunal species (Woodin 1978, Gallagher et al. 1983), turf algae that physically enhance the successful settlement and development of seeds of the surfgrass *Phyllospadix* (Turner 1985) and barnacle-induced substratum irregularities that reduce gastropod grazing on *Fucus* germlings (Lubchenco 1983). Other examples are lowered fish herbivory on young kelp sporophytes when intermixed with aggregations of small early successional algae (Harris et al. 1984), as well as lessened predation on tunicates (Sutherland 1974), bivalves (Bloom 1975, Suchanek 1978, Vance 1978), bryozoans (Osman and Haugsness 1981), algae (Littler et al. 1987), corals (Glynn 1985), amphipods (Hay et al. 1989), and crabs (Cohen 1988, Hay et al. 1990) when associated with other organisms such as hydroids, sponges, bryozoans, epibiotic algae, gorgonians, corals, and macroalgae. Analogous studies on tropical reef seaweeds (Littler et al. 1986) and on temperate algae from a rock jetty (Hay 1986) have convincingly demonstrated that palatable species are protected from herbivores when growing naturally in close association with relatively unpalatable plants. A similar effect has been shown (e.g., Hixon and Brostoff 1982) where algal biomass is increased by damselfish that decrease the intensity of herbivory within territories. Positive biological interactions could be much more widespread than previously suspected, particularly on biotic reefs.

The present study was conducted as part of an investigation of the association between a chiton and a coralline alga and explores the mechanisms by which a herbivore may affect the productivity, growth, and accretion of its principal prey. In this paper, we describe the nature of the association and investigate the role of the chiton *Choneplax lata* (Guilding 1829) in increasing biomass and accretion of the reef-building alga *Porolithon pachydermum* (Foslie) Foslie. The following specific questions are addressed: (1) Is the chiton *Choneplax lata* frequently and predictably associated with the coralline alga *Porolithon pachydermum*? (2) What is the role of the chiton/coralline association in biomass accumulation, carbonate accretion, productivity, and bioerosion on Caribbean reefs? (3) Is survivorship of *Porolithon pachydermum* improved in the presence of *Choneplax lata*? (4) Is survivorship of *Choneplax lata* improved in the presence of *Porolithon pachydermum*? (5) What characterizes this association and the population structure of its associates? (6) Does the chiton regularly feed on

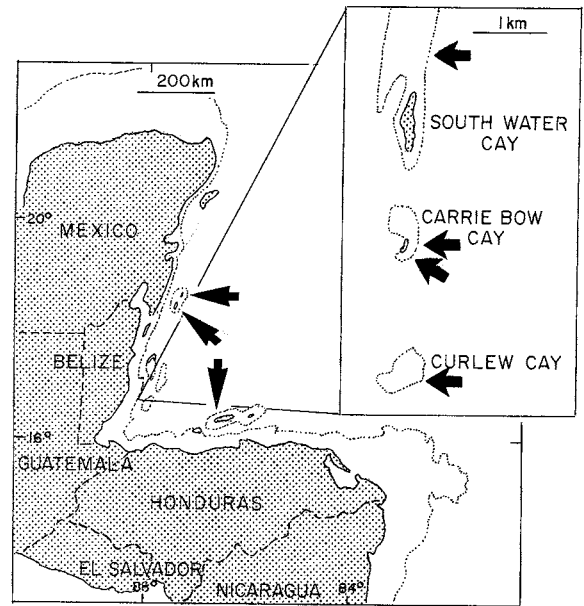


FIG. 1. Map of Caribbean showing location of the seven study sites (dotted lines indicate the outer reef shelf).

Porolithon pachydermum as well as fleshy microalgae? (7) How widespread and important is the association?

STUDY AREAS

The long-term experimental phase of the research was performed at the Smithsonian Institution's field station located on Carrie Bow Cay (CBC), Belize, Central America (16°48' N, 88°05' W; Fig. 1) between February 1986 and June 1991. Carrie Bow Cay is one of several small islands composed of carbonate debris that has accumulated on the outer margin of the Belize Barrier Reef. The island and its surroundings comprise a well-developed biotic reef system removed from major anthropogenic influences and is typical of the Central Province of the Belize Barrier Reef. The topography, geology, and general biology are well known from nearly two decades of study (see Rützler and Macintyre 1982).

The Belizean barrier-reef complex is the largest continuous reef system in the Atlantic Ocean (over 250 km in length and from 10 to 32 km in width). It consists of an almost unbroken barrier reef bordered by an intertidal reef crest extending downward to a submerged ridge and steeply angled fore-reef slope on its seaward margin (Fig. 1, dotted line). The community composition and zonation of the CBC region of the Belize Barrier Reef, despite some variation (Burke 1982), is representative of much of the entire platform. Distinct similarities exist between the Belize Barrier Reef's biological/geological zonation and the barrier reefs of the north coast of Jamaica (Goreau 1959, Goreau and Land 1974), the north coast of Haiti (Burke 1982), the southeast coast of Alarcran (Burke 1982), and the offshore

reefs of the Bahamas, Puerto Rico, the Lesser Antilles, Panama's San Blas Islands, Mexico's Yucatan, and the Bay Islands of Honduras (M. M. Littler and D. S. Littler, *personal observations*).

On the basis of dominant biological and geological characteristics, the barrier reef seaward of CBC can be divided into four major zonal units: back reef, reef crest, inner fore reef, and outer fore reef. Water movement and depth had been suggested initially (Rützler and Macintyre 1982) to be the main factors controlling such biological/geological patterns; however, we now know (Lewis 1986, Cohen 1988, Littler et al. 1989b) that complex biological/physical interactions interplay to determine the zonal patterns. The water over the intertidal reef crest is in an almost constant state of turbulent agitation and the system is strongly affected by waves related to normal trade wind conditions, as well as storms and infrequent hurricanes (see Macintyre et al. 1987 for an analysis of wave hydrodynamics near the Belizean sites studied). The central Belizean study sites (Fig. 1) are located on the intertidal to shallow subtidal reef crest on the east side of Carrie Bow Cay, Tobacco Reef, and Curlew Cay and are representative of the reef crest habitat throughout the Belize Barrier Reef (James et al. 1976, Burke 1982). Reef crests in Mexico and Honduras also were quantitatively sampled during the present study (Fig. 1).

METHODS AND MATERIALS

Experimental manipulations

The role of *Choneplax lata* in the hypothetical chiton/algal mutualism was examined with removal studies. For experimental purposes, we haphazardly collected 15 large ($\approx 0.25 \text{ m}^2$) slabs of reef rock dominated by the *Choneplax/Porolithon* community on 1 March 1987 from within the primary study area located on the CBC algal crest (Fig. 1). These were broken free to allow manipulation and randomize location effects, and transported underwater to the shallow downstream rubble-pavement zone south of CBC where strong westward currents prevail. To test whether the presence of *C. lata* affected neighboring macroalgae on the experimental rock slabs, we haphazardly selected 75 visually similar $9 \times 12 \text{ cm}$ (108 cm^2) plots each containing ≈ 12 burrow apertures. The interspersed and spatially separated plots were marked on 4 March 1987 by nailing numbered aluminum tags to their lower 12 cm long margins. These plots were assigned randomly to three treatments of 25 plots each [chiton removal treatment (experimental test of the role of *Choneplax*), removal controls (to control for removal-methods effects), and natural controls (to control for stochastic events unrelated to removal)]. The labels on one of the removal quadrats and two of the controls were lost and those plots could not be accurately relocated.

Because the chitons occur in an intricate network of burrows (up to 10 cm deep, Fig. 2A, B; see photo on

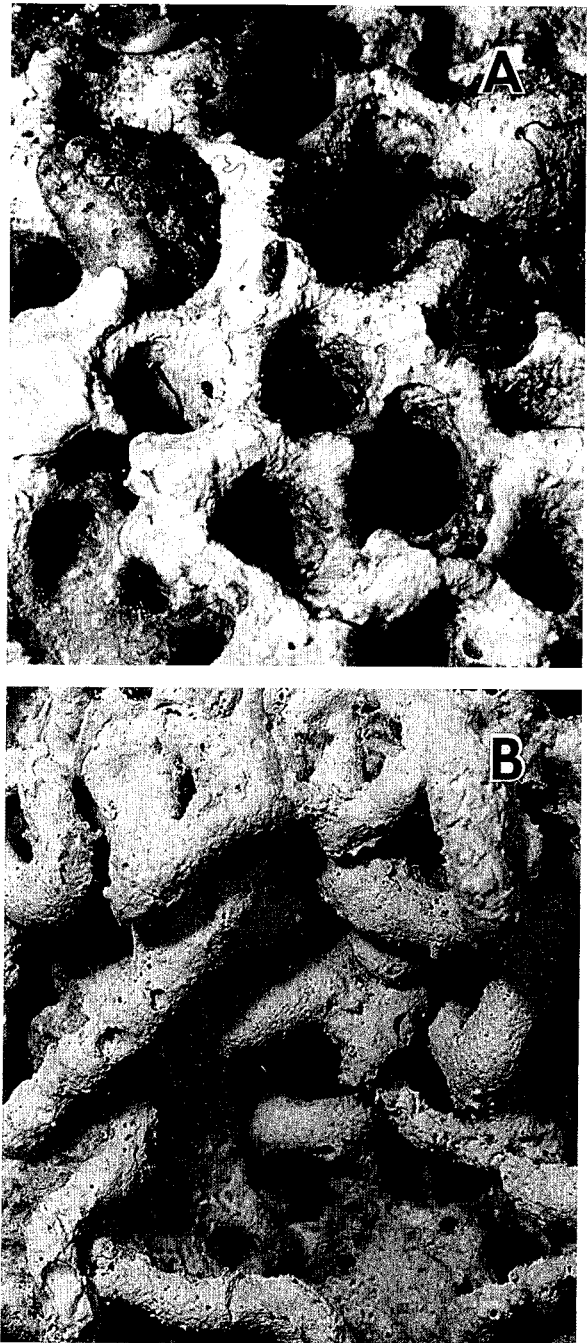


FIG. 2. (A) Reef-crest surface view of *Porolithon pachydermum* showing several *Choneplax lata* and their burrows ($1.5\times$). Note the massive upward accretions between burrows as a result of increased meristematic activity. (B) Underside view of acid-cleared resin casting of *Choneplax lata* burrow complex ($1\times$).

p. 221 of Littler et al. 1989a) and do not emerge predictably, it was not possible to remove them by strictly physical means. We tested the use of quicklime (CaO) as a molluscicide (see North 1976); however, both field and laboratory experiments showed that CaO was more

TABLE 1. Quicklime (CaO) and paradichlorobenzene (PDB) effects on *Choneplax lata* and associated fauna of three large intact reef-crest slabs of the *Choneplax/Porolithon* association following 20 h in running seawater aquaria. The samples treated with CaO and PDB contained 74 and 122 *C. lata* holes, respectively, while the untreated controls had 61 openings. Data for *Porolithon* are percent cover. These chiton mortality data (pseudoreplicated) were not statistically analyzed because all subsequent field experiments contained independent control replicates for PDB effects.

Taxa	Controls		CaO		PDB	
	No. alive	No. dead	No. alive	No. dead	No. alive	No. dead
<i>Choneplax lata</i>	9	0	6	3	0	13
Limpets	2	0	2	0	0	2
Octopus	0	2
Shrimp	4	2	7	0	3	7
Crabs	2	0	1	0	1	0
Amphipods	2	0	3	0	1	0
Worms	2	2	5	1	2	1
Brittle stars	1	1	0	2	3	7
<i>Porolithon pachydermum</i>	100%	0%	10%	90%	100%	0%

effective in killing *Porolithon pachydermum* than it was in eliminating *Choneplax lata* (Table 1). Subsequently, we employed crystals of paradichlorobenzene (PDB), which proved to be an effective molluscicide (Table 1). Crystals were crushed with a mortar and pestle and screened through a 1-mm nylon mesh sieve to produce a granular powder, which was then applied to individual burrows by squeezing from a small hole in the corner of a polyethylene bag. To analyze the toxicity of CaO and PDB to algae and invertebrates, running seawater aquaria containing three natural rock slabs of *C. lata* ($N = 31$) and associated faunas and floras were set up on 2 March 1987 and treated as in the subsequent field removal and control experiments. The aquarium populations were monitored daily over a 5-d period by direct examination. On 6 March 1987, the carbonate slabs were carefully chiseled apart, and living and dead invertebrates were censused.

In the plots selected for chiton removal and removal control, all chiton burrows were filled in the field to the extent possible with the PDB crystals. After 24 h, the 15 large slabs of reef rock containing the chiton populations were taken downcurrent, inverted, and shaken vigorously underwater to allow the remaining crystals to fall free and be swept away to the sandy lagoon by current action. Numerous dead *Choneplax lata* also fell free and were consumed by fishes at this time. The natural controls received the same handling and shaking but were unmanipulated in terms of PDB. Natural densities and size frequencies of *C. lata* (based on the census data) were replaced in the removal-control plots in the field on 6 March 1987. The slabs containing labeled plots were then moved upstream while submerged and permanently secured near their original positions on the reef crest with fast-setting underwater epoxy.

To examine the effectiveness of the molluscicide and whether it had killed other invertebrates, subsamples of the experimental rock slabs were returned to the laboratory on 10 March 1987 and immediately broken

open with rock hammers to assess the control vs. treated populations.

Close-up photographs of the marked plots were taken on 7 March 1987 using an extension tube with a 9×12 cm fixed framer on a 35-mm Nikonos camera equipped with an electronic flash and Kodachrome-25 transparency film. The undisturbed macro-photographic monitoring method as applied here allows for the quantification of understory crusts and microalgae (small epiphytic and epilithic forms) even when they occur in low abundances. The initial quadrat photographs were used to document the species and amount of cover present immediately following the experimental manipulations. After 14 mo, all removal, removal-control, and control quadrats were rephotographed and scored for biotic cover. To allow for maximum artifactual differences due to recruitment, emigration and mortality to develop, the slabs containing all 9×12 cm plots were returned to the laboratory and the chiton populations re-examined 2.5 yr following the initiation of the experiment.

The macro-photosamples were assessed in the laboratory to determine the percent cover of each organism in the 108-cm² quadrats. Scoring was accomplished by projecting the transparencies onto a pattern of randomly spaced dots (average two dots per square centimetre) and was repeated for each photograph following blind movement of the dot grid (≈ 400 dots per quadrat). Reproducibility was high at this micro-scale, seldom varying more than $\pm 5\%$ of the previous value for each of the dominant organisms. The relative changes in percent cover (total and by taxa) were calculated from the differences between 0 and 14 mo.

To test the null hypothesis that the percent cover differences of macroalgal populations in the removal, removal-control, and control quadrats, immediately after manipulation were not statistically different ($P > 0.05$), we used ANOVA followed by Bonferroni, a posteriori, multiple classification analysis (SAS 1985). Tests of treatment effects on the predicted losses or

gains of algal cover (percent cover change) following the removal of *Choneplax lata* (before vs. after 14 mo) also were conducted using ANOVA and Bonferroni analysis on species and total algal cover. All percent cover data were arcsine transformed so that they conformed to the assumptions of parametric statistics (Sokal and Rohlf 1981). Unless otherwise indicated, variability about the mean is expressed throughout as the mean plus or minus the standard error.

The role of living *Porolithon pachydermum* in the hypothetical chiton/algal mutualism was examined by removing *P. pachydermum* on 10 additional haphazardly collected slabs ($\approx 0.25 \text{ m}^2$) of reef-crest rock dominated by the *Choneplax/Porolithon* association. Slabs were taken as above on 15 June 1989 from the CBC algal crest (Fig. 1). The slabs were immediately placed in a 200-L tank of freshwater for 3 d to kill all invertebrates and algae. The slabs were flushed repeatedly and the freshwater changed daily. To determine whether the presence of living *P. pachydermum* affected the survivorship of *C. lata*, we haphazardly selected 50 visually similar $9 \times 12 \text{ cm}$ (108 cm^2) plots containing *C. lata* burrows from the above slabs. A subgroup of 25 of these plots was randomly selected and healthy *C. lata* individuals were added at natural densities and sizes (experimental test of the role of *Porolithon*). The other 25 plots were left as removal controls (for events not related to either *C. lata* or *P. pachydermum*), while an additional 25 independent unmanipulated (physical removal and replacement of slabs only) nearby healthy plots served as natural controls (for stochastic events) containing both the chiton and coralline. The slabs were replaced in the crest, permanently marked, and photographed as described earlier. The labels of nine of the *Porolithon*-removal plots and three of the *Porolithon* + *Choneplax*-removal plots were lost and those quadrats could not be reassessed. After 14 mo, all treatment and control quadrats were rephotographed, assessed for biotic cover, and analyzed as in the chiton-removal study described above. The slabs were then broken free and returned to the laboratory where the population numbers of chitons were determined as indicated earlier.

Bioerosion/accretion

Both sets of manipulative experiments were duplicated simultaneously using unmanipulated controls, *Choneplax*-removal plots, and *Choneplax*-removal controls, as well as *Porolithon*-removal plots and *Choneplax* + *Porolithon*-removal plots ($N = 25$ per treatment). However, in this experiment the carbonate rock substrata and calcareous organisms were stained for 15 min in aquaria with alizarin red (following Stearn et al. 1977), a nontoxic indicator that binds permanently to calcium carbonate. After 24 mo, the experimental substrata were harvested and shipped to the Smithsonian Marine Station at Link Port, Florida where thin cross-sections of each were made at haphazard loca-

tions by a water-lubricated diamond saw. Net accretion and bioerosion were assessed by randomly measuring the growth (thickness) of *P. pachydermum* above or erosional bite scars penetrating below the alizarin red layer. Statistical comparisons were made among all treatments using ANOVA followed by Bonferroni (SAS 1985).

Population census

The natural densities and size classes of *Choneplax lata* were determined on 6 March 1987 by sampling 24, $\approx 0.25\text{-m}^2$ sections (slabs collected haphazardly) of the reef crest at CBC. Burrow openings sometimes coalesce at the surface and were each counted as separate entities when the individual apertures could be recognized. The carbonate slabs were broken apart carefully using rock hammers and chisels and all chitons were censused, lengths measured, and placed in running seawater aquaria. Some of these animals were used in the removal-control experiments. To reveal the nature of the labyrinth of burrows, several burrow castings were made by filling representative burrowed slabs with catalyzed liquid resin and later slowly dissolving the surrounding carbonate with 10% H_2SO_4 .

Gut contents

The majority of chitons (>100) collected during the above population census were preserved in 5% formalin/seawater. Fifteen of these were selected by random draw and the gut contents microdissected onto individual microscope slides and mounted in a 70% Karo corn syrup solution. These were then quantified using methods similar to those of Steneck (1982) at 30 haphazard locations under $100\times$ magnification by scoring the upper end points of 10 lines on an ocular micrometer as random point intercepts.

Scanning electron microscopy

To test the hypothesis that *Choneplax lata* was the source of the grazing, we compared the mosaic pattern of scars on *Porolithon pachydermum* with the radular morphology of *C. lata* on a fine scale. Radulas of chitons collected during February 1986 were prepared for examination under a Hitachi scanning electron microscope (SEM) following microdissection and sputter coating. Concurrently, algal samples were prepared in the same manner from fragmented portions of *P. pachydermum* collected in the vicinity of the burrows to ascertain how the chiton regularly feeds on the coralline without causing mortality. The SEM photomicrographs of grazed *P. pachydermum* also were used to quantify the mean depth and width of rasping by *C. lata* and to reveal alterations in anatomical function in the presence of chitons.

Primary productivity

Fragments of *Porolithon pachydermum* ($\approx 25 \text{ cm}^2$), containing openings of chiton-occupied burrows with

uniform mosaics of radular tracks, were taken from the reef crest of the primary study area (Fig. 1) on CBC. These were compared with previously published data on ungrazed material from the same site to test the hypothesis that chiton grazing does not inhibit photosynthesis of the coralline and to support the longer term growth studies. Care was taken to select individual fragments that were representative of material occurring within the areas assessed for cover. Eight replicate samples plus four blank controls were incubated on the day of collection in the shallow current channel behind the reef crest (27°C, photon flux density of 900–2100 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) between 0900 and 1500 EST. Fragments of *P. pachydermum* were incubated in individual 1.0 L, wide-mouth, glass canning jars that were continuously mixed. Methods concerning the handling of algae, incubation, and O_2 analysis followed the recommendations of Littler and Arnold (1985). Net productivity was measured to within 1 $\mu\text{g O}_2/\text{L}$ with an Orbisphere 2610 O_2 analyzer and calculated as milligrams organic C fixed per gram of thallus organic dry mass per hour, assuming a photosynthetic quotient of 1.0 (to facilitate comparisons with other data).

Long-term growth rates

To determine long-term patterns of carbonate accretion and the potential age of representative *Porolithon pachydermum* crusts at our sites, we radiocarbon dated nine samples from recognizable dead *Acropora palmata* branches at the four different coralline–chiton sites in Belize (Fig. 1) at $\approx 10\text{-m}$ intervals within each site. Individual layers of the coralline alga could be analyzed due to the small sample sizes measurable by accelerator mass spectrometry (AMS). We were particularly interested in using AMS to analyze the lowermost individual layers of *P. pachydermum* adjacent to the intact coral core. The crusts were sectioned by water-lubricated diamond saw, and appropriate strata to be dated were identified under a dissection microscope. Samples were taken from the lower well-preserved subsurface crusts. About 0.01 g of material was removed from each stratum by a fine Dremel grinder point and placed in a labeled vial. The samples were given no pretreatment and reacted with phosphoric acid to produce CO_2 , which was applied to Cu targets. The AMS measurements were made in triplicate on aliquots of each milled sample at the Eidgenössische Technische Hochschule, University of Zürich. Growth rates were calculated by dividing the distance (in millimetres) to the surface by the age (yr BP) of the innermost layer.

Standing stocks

The reef crest was transected on compass headings of 90° magnetic at two sites seaward of the laboratory on CBC (the primary study sites), at one site on Curlew Cay, and at a fourth site on Tobacco Reef 1 km north of Southwater Cay (Fig. 1), beginning on the west margin of the crest in 0.1 m of water and extending 25 m

to the eastward (seaward) border at a depth of 0.9 m. Tidal amplitude is minimal relative to wave height, and average depths between wave peaks and troughs were measured at the time of sampling with a metre stick. Quantitative samples were obtained by photographing 0.15-m² quadrats at every 1.0-m interval across the crest ($N = 24$ per site). Photographs were taken perpendicular to the substratum using a 35-mm Nikonos camera equipped with an electronic flash and Kodachrome-64 transparency film. Simultaneously, field notes and voucher specimens of all macrophytes and turf algae were taken for taxonomic purposes from near each quadrat and placed in individually labeled bags. Vouchers were subsequently studied and deposited in the Algal Collection of the U.S. National Herbarium, National Museum of Natural History, Smithsonian Institution.

Reproducible estimates of cover were obtained in the laboratory by projecting the developed transparencies onto a 40 × 40 cm sheet of white bristol paper containing a stratified grid pattern of dots, each randomly placed within 2-cm² squares, on the side of the reflected light (Littler and Littler 1985). The number of dots superimposed on each species was then scored twice (i.e., replicated after blind movement of the grid) with the percentage cover values expressed as the number of “hits” for each species divided by the total number of dots (≈ 400) scored in the quadrats. Species present in quadrats but not abundant enough to be scored by the replicated grid of point intercepts were assigned a cover value of 0.1%. Our photographic transect measurements were restricted to macrophytes that could be discerned in the field with the unaided eye. However, we did quantify small algae when they occurred in high abundances as components of algal turfs.

We also conducted video-transect surveys (at right angles to the substrata) across reef crests at two sites on Chinchorro Bank, Mexico and one site off Roatan, Honduras. A transparent screen containing a grid of dots was taped to a high-resolution video monitor and the video tapes were scored in stop action after random movements ($N = 24$ quadrats per site). Study areas were located at ship anchorage sites chosen from oceanographic charts without specific habitat knowledge.

RESULTS

Toxicity tests

In the preliminary experiment to examine the efficacy of potential molluscicides, the PDB crystals were totally effective in killing *Choneplax lata* in running seawater aquaria within a 24-h period (Table 1). In the 122 chiton holes, all 13 *C. lata* were dead, as were one juvenile octopus and two limpets. Low numbers of juvenile limpets were the only other invertebrate herbivore found in the assemblage. Of the other invertebrates, 3 out of 10 shrimp were alive, as were one of

TABLE 2. Initial percent cover immediately after experimental manipulation of *Choneplax lata*.

Taxa	A Control†		B Removal control‡		C Removal§		Means (A, B, C)		Multiple classifi- cation analysis
	\bar{X}	SE	\bar{X}	SE	\bar{X}	SE	\bar{X}	SE	
<i>Porolithon pachydermum</i> *	85.6	1.4	77.9	1.4	82.2	2.2	81.8	1.1	A, C > B
Blue-green algae	9.4	1.3	8.7	1.3	10.2	1.5	9.4	0.8	...
<i>Cladophora</i> sp.*	1.6	0.4	4.9	1.4	1.6	0.4	2.8	0.5	A, C < B
<i>Centroceras clavulatum</i> *	1.1	0.2	3.5	0.8	3.1	0.4	2.7	0.3	A < B, C
<i>Amphiroa</i> sp.*	0.5	0.1	1.0	0.2	0.4	0.1	0.6	0.1	A, C < B
<i>Gelidium crinale</i> *	0.1	0.06	1.7	0.7	0.1	0.05	0.6	0.3	A, C < B
<i>Ulva</i> sp.	0.6	0.2	0.5	0.2	0.4	0.1	0.5	0.1	...
Filamentous reds	0.3	0.1	0.7	0.3	0.3	0.1	0.4	0.1	...
<i>Peyssonnelia</i> sp.	0.4	0.3	0.1	0.08	0.07	0.05	0.2	0.1	...
Colonial diatoms	0.1	0.07	0.1	0.1	0.01	0.01	0.1	0.0	...
All others	0.05	0.03	0.8	0.8	0.8	0.8	0.6	0.4	...
Totals	99.8		99.9		99.2		99.7		

* Indicate species with significant differences from the control values ($P < 0.05$, Bonferroni).

† No removal; $N = 23$.

‡ *Choneplax* removed and replaced; $N = 25$.

§ *Choneplax* removed; $N = 24$.

five crabs, one amphipod, two of three worms, and 3 of 10 brittle stars. All *Porolithon pachydermum* retained its natural color and remained healthy as did the various microalgae. A similar pattern was found for the control slab (Table 1), except that no dead *C. lata* or limpets were found. Subsamples of the PDB-treated field samples taken on 6 March 1987 showed 100% mortality of chitons with no dead crustacea, polychaetes, or algae observed. CaO was found unsuitable for chiton removal (Table 1), since its primary effect was to kill *P. pachydermum*.

Chiton-removal plots

In the 72 108-cm² plots selected for experimental manipulations (Table 2), algal cover averaged 99.7%. Of this, 81.8% was the crustose coralline *Porolithon pachydermum*, 9.4% was Cyanophyta, and the remainder was mostly sparse, epiphytic, microscopic algae.

The algal populations of the 24 removal plots did not differ significantly from those of the 23 control plots, with the exception of *Centroceras clavulatum* (*C. Agardh*) Montagne, which contained 2.0% more cover in the experimental plots (significant at $P < 0.05$, Bonferroni). At the start of the experiment (Table 2), the coverages of four algal populations in the 25 removal-control quadrats [*Cladophora* sp., *Centroceras clavulatum*, *Amphiroa* sp. and *Gelidium crinale* (Turn.) Lamour.] were significantly greater ($P < 0.05$, Bonferroni) than those of the 23 controls, whereas cover of *P. pachydermum* was significantly lower ($P < 0.05$, Bonferroni). Fourteen months after the initial experimental manipulations (Table 3), no significant cover differences ($P > 0.05$, Bonferroni) were found among any of the populations of the 23 control and 25 removal-control plots.

When cover differences before and 14 mo following

TABLE 3. Percent cover increases or losses (denoted with a minus sign) relative to initial cover 14 mo after the experimental manipulation of *Choneplax lata*.

Taxa	A Control†		B Removal control‡		C Removal		Multiple classification analysis
	\bar{X}	SE	\bar{X}	SE	\bar{X}	SE	
<i>Porolithon pachydermum</i> *	-1.6	1.1	-0.1	1.8	-16.2	3.0	A, B > C
Blue-green algae	0.3	1.2	4.2	1.4	-1.5	2.0	...
<i>Cladophora</i> sp.*	0.3	0.3	0.1	1.1	10.0	1.6	A, B < C
<i>Centroceras clavulatum</i> *	0.8	0.4	-2.6	0.9	1.1	0.8	A, C > B
<i>Amphiroa</i> sp.	-0.1	0.1	-0.3	0.3	0.6	0.3	...
<i>Gelidium crinale</i> *	0.04	0.06	-0.9	0.4	-0.04	0.46	A, C > B
<i>Ulva</i> sp.*	0.3	0.2	-0.1	0.1	1.8	0.4	A, B < C
Filamentous reds*	0.1	0.09	0.4	0.5	1.3	0.6	A, B < C
<i>Peyssonnelia</i> sp.	-0.1	0.1	0.04	0.04	0.4	0.2	...
Colonial diatoms	0.01	0.03	-0.1	0.1	0.8	0.5	...
All others	0.8	0.8	-0.1	0.3	1.7	1.0	...

* Indicate species with significant differences from the initial values ($P < 0.05$, Bonferroni).

† No removal; $N = 23$.

‡ *Choneplax* removed and replaced; $N = 25$.

§ *Choneplax* removed; $N = 24$.

TABLE 4. Percent cover increases or losses (denoted with a minus sign) relative to initial cover 14 mo after the experimental manipulation of *Porolithon pachydermum*. Both the experimental (*Porolithon* removal and *Choneplax* + *Porolithon* removal) plots initially contained zero living cover.

Taxa	Control†		A <i>Porolithon</i> removal‡		B <i>Choneplax</i> + <i>Porolithon</i> removal§		Multiple classifi- cation analysis
	\bar{X}	SE	\bar{X}	SE	\bar{X}	SE	
<i>Porolithon pachydermum</i> *	-6.9	2.4	22.0	5.8	7.2	1.4	A > B
Blue-green algae*	0.9	0.5	14.3	2.3	3.4	1.0	A > B
<i>Cladophora</i> sp.	3.2	1.1	8.8	1.4	10.2	1.8	...
<i>Centroceras clavulatum</i>
<i>Amphiroa</i> sp.	-0.04	0.04
<i>Gelidium crinale</i>
<i>Ulva</i> sp.*	0.4	0.4	0.0	0.0	0.5	0.2	A < B
Filamentous reds*	2.0	1.4	16.2	4.1	71.1	3.2	A < B
<i>Peyssonnelia</i> sp.
Colonial diatoms
All others	0.8	0.9	0.7	0.5	1.9	0.8	...

* Indicate significant changes between species of the two removal groups ($P < 0.05$, Bonferroni). No significant changes occurred for the unaltered controls based on comparisons with the initial values.

† No removal; $N = 25$.

‡ $N = 16$.

§ $N = 22$.

the manipulations were compared within each experimental group (Table 3), no significant changes ($P > 0.05$, Bonferroni) had occurred in the 23 control quadrats. Only two significant changes ($P < 0.05$, Bonferroni) occurred in the 25 removal controls, with declines in cover of the fleshy algae *Centroceras clavulatum* and *Gelidium crinale*. However, in the 24 chiton-removal quadrats (Table 3), a substantial decrease occurred in the cover of *Porolithon pachydermum* (16.2%, mostly bleached and dead), while the epiphytes *Cladophora* sp. (10.0% increase), *Ulva* sp. (1.8%), and filamentous red algae (1.3%) showed marked gains (all significant at $P < 0.05$, Bonferroni). Small but insignificant increases in the predicted direction were shown by four other herbivore-susceptible species, *Centroceras clavulatum* (1.1%), colonial diatoms (0.8%), *Amphiroa* sp. (0.6%), and the fleshy crustose alga *Peyssonnelia* sp. (0.4%).

The chiton population census after 2.5 yr from the initiation of the chiton-removal experiment revealed the normal mean (± 1 SD) chiton density of 2.0 ± 0.3 chitons per plot (one chiton per six openings) in the control treatments, with 1.4 chitons ± 0.7 per plot (one per four openings) in the removal-control plots and 0.5 chitons ± 0.5 per plot (one per 24 openings) in the removal plots. These deviations from the controls indicate that a differentially low (NS, $P > 0.05$, Bonferroni) level of mortality occurred in the removal-control replacements, whereas limited recruitment (NS, $P > 0.05$) took place in the chiton-removal plots over the 30-mo time span.

Porolithon-removal plots

In the 50 108-cm² initial plots in which *Porolithon pachydermum* was killed, no algal cover was present

at the beginning of the experiment. The 25 unmanipulated control plots showed 98.2% cover of algae dominated by 85.1% *P. pachydermum*, 6.5% Cyanophyta, and the remainder sparse filamentous epiphytes. Fourteen months after the initiation of the experiment, significant cover differences ($P < 0.05$, Bonferroni) were found between all three groups of plots. The major species of the unmanipulated control plots had not changed significantly ($P > 0.05$) in the 14-mo period and were still dominated by *P. pachydermum* (78.2%), along with Cyanophyta and sparse filamentous forms; however, as expected, they contained significantly greater cover of all algal species present ($P < 0.05$, Bonferroni) than did either group of the removal plots, which started with no living cover. The plots with both *Porolithon* and *Choneplax* removed (Table 4) had been colonized sparsely after 14 mo by thin *P. pachydermum* [7.2%, significantly less than the *Porolithon*-removal plots (22.0%), $P < 0.05$, Bonferroni], but mostly by filamentous turf algae (such as *Herposiphonia*, 71.1% cover increase, significantly greater than the experimental *Porolithon*-removal plots at $P < 0.05$, Bonferroni). Importantly, no epiphyte-free patches of *P. pachydermum* occurred where *C. lata* was absent.

In the experimental *Porolithon*-removal plots (with *C. lata* reintroduced), two results prevailed after 14 mo. We noted that 5 of the 16 *Porolithon*-removal quadrats had disproportionately high coverages of *P. pachydermum* relative to the remaining 11. This prompted us to sample the chiton populations in the two groups, which proved to be significantly different ($P < 0.05$) at (mean ± 1 SD) 2.0 ± 0.7 per plot for the 5 quadrats vs. 0.1 ± 0.1 for the other 11 quadrats. This finding warranted a separate analysis of *P. pachydermum* cover for the

two groups. For 11 of the 16 plots (considered separately due to low chitons) no significant cover difference ($7.0 \pm 0.2\%$, $P > 0.05$, Bonferroni) occurred for *P. pachydermum* compared with the *Porolithon* + *Choneplax* removal plots ($7.2 \pm 1.4\%$). However, in the other five *Porolithon*-removal plots (analyzed separately), the association had been restored with *P. pachydermum* successfully colonizing [mean overall cover of $55.2 \pm 2.8\%$ cover (significantly different from the *Porolithon* + *Choneplax* removal, $P < 0.05$)] and being maintained epiphyte-free but grazed (as evidenced by recent radular tracks).

The final population census (at 14 mo) showed normal numbers of *Choneplax lata* in the unmanipulated natural controls (mean $[\pm 1SD]$ of 2.1 ± 0.7 chitons/plot); however, significantly lower numbers ($P < 0.05$, Bonferroni) were present in the experimental *Porolithon*-removals (0.7 chitons ± 0.1 /plot) and *Porolithon*+*Choneplax* removals (0.1 chitons ± 0.1 /plot). In the five *Porolithon*-removal plots where the association had been restored, *C. lata* densities were only slightly below natural levels at 2.0 chitons ± 0.7 /plot (NS compared to controls, $P > 0.05$); whereas in the remaining 11 *Porolithon*-removal plots, *C. lata* densities (0.1 chitons ± 0.1 /plot) were significantly lower than the controls ($P < 0.05$).

Bioerosion/accretion

The unmanipulated controls and *Choneplax*-removal controls [containing living *Porolithon* + *Choneplax* (replaced)] were the only treatments to show net carbonate accretion above the alizarin red layer at $+1.5 \pm 0.1$ and $+1.1 \pm 0.1$ mm $\cdot 24$ mo $^{-1}$ of mean upward growth, respectively (Fig. 3). These both were significantly greater ($P < 0.05$, Bonferroni, $N = 25$ per treatment) than the other three treatments, (but not significantly different from each other, $P > 0.05$). The other treatments all showed significant ($P < 0.05$, Bonferroni) net bioerosion as evidenced by fish or chiton grazing scars. Although the remaining three treatments did not differ significantly from each other ($P > 0.05$, Bonferroni), there was an interesting trend as follows (Fig. 3). The *Choneplax* removal manipulation containing living *Porolithon* showed increased overgrowth of microalgae (as previously shown, Table 3) and lost the least carbonate, due mainly to mortality following overgrowth or to fish rasping scars, at -0.2 ± 0.1 mm/24 mo. The 25 plots in which both *Choneplax* and *Porolithon* had been removed eroded at -0.3 ± 0.1 mm/24 mo, again attributable mainly to fish rasping. The manipulation wherein *Porolithon* was removed and *Choneplax* replaced at natural densities showed the greatest bioerosion at -0.4 ± 0.1 mm/24 mo, with both fish and chiton grazing scars abundant.

Population census

The mean number of apertures per square metre of the chiton/coralline association in the field transects

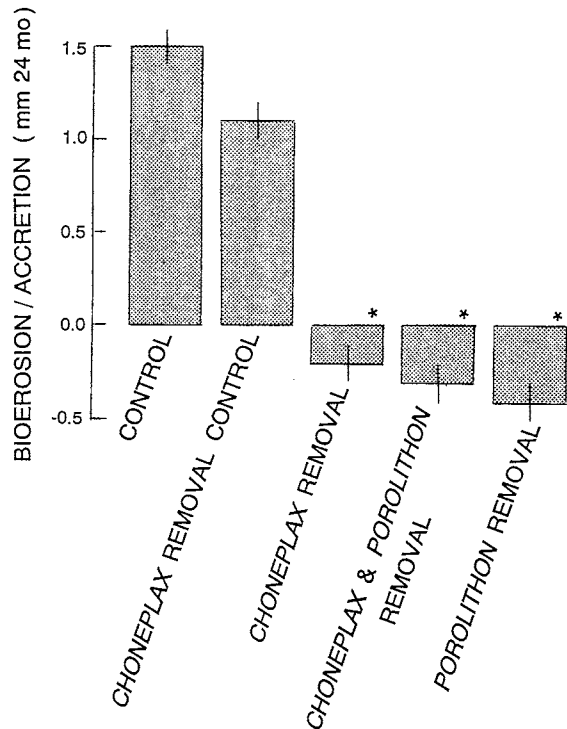


FIG. 3. Net carbonate accretion or bioerosion (negative values) relative to the alizarin red layer per 24 mo (controls = no removals to control for natural stochastic events, *Choneplax* removal control = natural populations of *Choneplax* replaced to control for removal effects, *Choneplax* removal = experimental test, *Choneplax* + *Porolithon* removal = experimental test). Asterisks indicate means significantly different from the unmanipulated controls ($P < 0.05$, Bonferroni).

was 3982 ± 137 ($N = 136$ quadrats), yielding a calculated mean population density of 664 chitons/m 2 of association. The 24 carbonate slabs censused for the *Choneplax*/*Porolithon* association had a total of 2345 burrow apertures containing 387 *C. lata*, giving an average of one animal per six holes. The size frequency distribution (Fig. 4) revealed a length range for *C. lata* from 4 to 43 mm, with 17% of the population from 4 to 14 mm (probably juveniles), 66% from 16 to 30 mm, and 17% from 31 to 43 mm. The chitons appeared to be equally distributed both in size and abundance between the 24 fragments and throughout the 2345 burrows. Castings of representative aggregations of burrows revealed a labyrinth of interconnected tunnels of similar diameter penetrating to a depth of 6–10 cm (Fig. 2B) and with few dead ends.

Gut contents

Porolithon pachydermum was by far the most abundant component of *Choneplax lata* gut contents ($51.0 \pm 4.1\%$, $n = 15$) followed by bacterial detritus (i.e., organic material + bacteria, $28.9 \pm 3.8\%$), Cyanophyta ($12.8 \pm 5.0\%$), Bacillariophyta ($3.2 \pm 1.0\%$),

and fleshy microalgae ($3.1 \pm 0.9\%$). We did not quantify animal matter, although sponge spicules were common and portions of foraminifera and bryozoans were sometimes present.

Scanning electron microscopy

Scanning electron micrograph analyses (Fig. 5) showed that the radular morphology of *Choneplax lata* and the surficial pattern of grazing scars on *Porolithon pachydermum* matched precisely. Fractured sections of the latter, as measured under SEM, revealed an average excavation depth of $10 \pm 2 \mu\text{m}$ and a mean thickness of living *P. pachydermum* of $100 \pm 19 \mu\text{m}$. The intercalary meristem, photosynthetic cells, and reproductive conceptacles of *P. pachydermum* occurred at an average depth of $20 \pm 6 \mu\text{m}$ below the thallus surface and were covered by nonpigmented epithallial cells. Fractured sections also showed (M. M. Littler and D. S. Littler, *personal observations*) that meristematic activity at the margins of grazed burrows increased to resemble those of the more rapidly growing crust margins. This resulted in a vertical columnar growth that deepened the burrows (Fig. 2A).

Primary productivity

The primary productivity of recently grazed *Porolithon pachydermum*, although low ([mean \pm 1 SD] $0.1 \pm 0.01 \text{ mg C fixed} \cdot \text{g}^{-1} \text{ organic dry mass} \cdot \text{h}^{-1}$, $N = 8$) was not significantly different from nongrazed ($P > 0.05$) and within the range of values typical for crustose coralline algae (see *Discussion*), indicating little inhibition of the alga by chiton grazing.

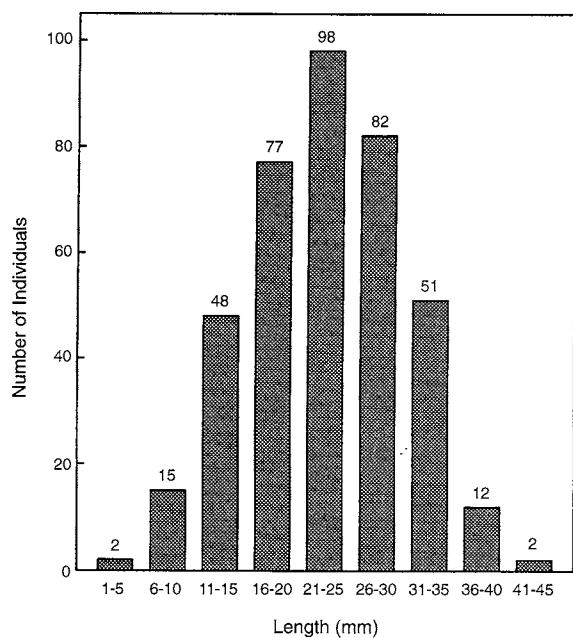


FIG. 4. Population size class distribution of *Choneplax lata* ($N = 387$).

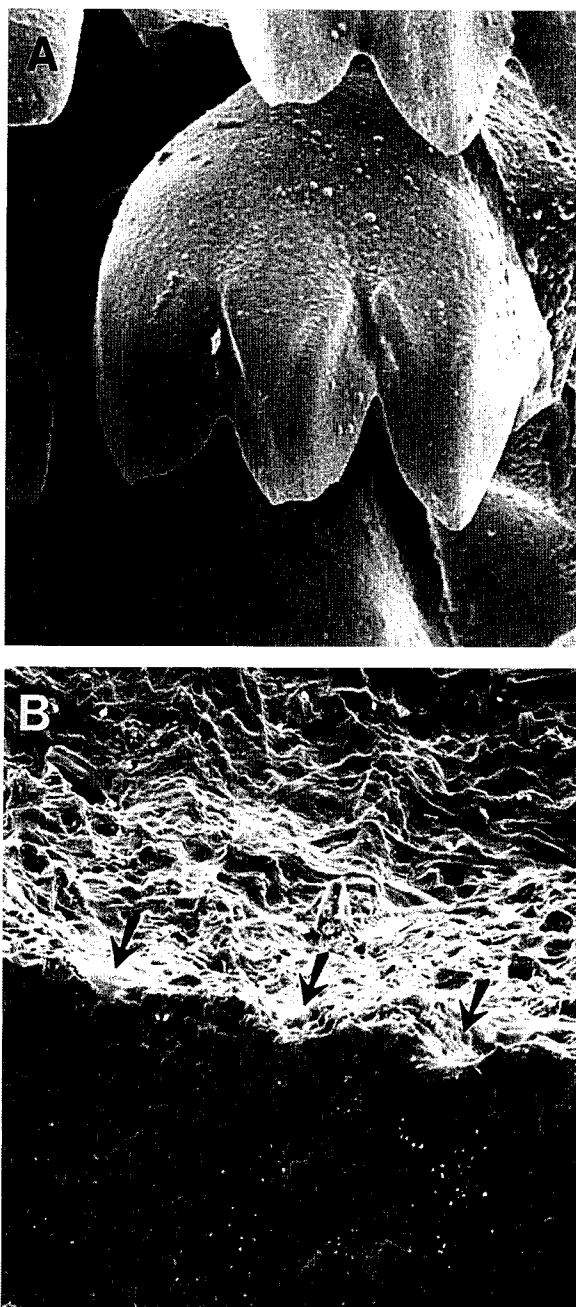


FIG. 5. SEMs ($700\times$) showing (A) the radular morphology of *Choneplax lata* and (B) the surface pattern of grazing scars (arrows) on *Porolithon pachydermum* (oblique view).

Long-term growth rates

Radiocarbon dates were obtained at the four Belize sites for nine samples of *Porolithon pachydermum* (containing normal abundances of *Choneplax lata*) that had overgrown the dead elk-horn coral, *Acropora palmata* Lamarck (Table 5). The lowermost layers were remarkably consistent in ages (mean = $109 \pm 1 \text{ yr BP}$, range = 100–113 yr BP). The calculated net growth (= accretion) rates for the *P. pachydermum* crusts from

TABLE 5. Radiocarbon dates (RCyrBP) \pm 1 SE and corresponding accretion rates of *Porolithon pachydermum* at the four Belize sites. The consistency of the data indicates that just before 100 yr BP numerous *Acropora palmata* branches reached the surface along the Belizean reef crest and were colonized by *Porolithon pachydermum* and *Choneplax lata*.

Sites	RCyrBP (n = 3)	Accretion (mm/yr)
1	107 \pm 1.0	4.0
	107 \pm 1.1	4.0
	109 \pm 0.8	4.0
2	100 \pm 1.4	1.0
	113 \pm 0.8	1.0
3	110 \pm 0.8	1.5
	110 \pm 0.8	1.5
4	110 \pm 0.8	2.0
	112 \pm 0.8	2.0
Means	109 \pm 1.3 (n = 9)	2.3 \pm 0.4 (n = 9)

the nine reef-crest samples ranged from 1.0 to 4.0 mm/yr and averaged 2.3 ± 0.4 mm/yr during the past 109 yr (Table 5).

Standing stocks

The reef crest at the primary study site (CBC, Fig. 1) comprised a narrow habitat (\approx 20 m wide, depth range 0.1–0.9 m) and had a mean-total, projected, macrophyte cover approaching 100% (Table 2). The vertical, plate-like hermatypic corals *Millepora complanata* Lamarck and *Agaricia agaricites* L. also were abundant (5 ± 2 and $7 \pm 2\%$ cover, respectively, Fig. 6) and probably contributed substantially to vertical growth. Toward the seaward margin, *Acropora palmata*

builds to the extreme low tidal level, above which it and other corals are overgrown by the dominant *Choneplax/Porolithon* association (Fig. 6). The uppermost algal portion of the reef is dominated by a pink pavement of *Porolithon pachydermum* ($40 \pm 5\%$ mean cover, maxima to 100%, Fig. 6) containing excavations made by *Choneplax lata* ($15 \pm 3\%$ mean cover, maximum to 60%, Fig. 6). The areas with *P. pachydermum* alone (\approx 25% cover) were mainly on the subtidal portions of the crest front. Other prevalent macrophyte species throughout the 20 m wide reef crest are the turf-forming *Wrangelia argus* (5.5%), the encrusting red alga *Peyssonnelia* sp. (5.0%), and the geniculate coralline *Jania capillacea* (1.4%). Microalgal forms, predominantly *Cladophora* sp. and *Centroceras clavulatum* (with 2.6% cover each), comprise \approx 8.0% cover and occurred as sparse patchy turfs. Blue-green algae (Cyanophyta) were visible on damaged portions of the carbonate substrata and averaged 3.3% cover. *Hali-medea opuntia* (Linnaeus) Lamouroux (1.1%) and *Lobophora variegata* (Lamouroux) Womersley (0.6%) border the leeward (westward) margin of the crest. The encrusting green alga *Codium intertextum* Collins and Hervey is common on the outer (eastward) margin of the reef crest beneath ledges and deep in crevices beyond the range of our photo-samples.

Porolithon pachydermum (alone) and the chiton-coraline association were equally abundant at the five other crest sites as follows (Fig. 6, $N = 24$ quadrats/site): Curlew Cay—total *P. pachydermum* alone = $33 \pm 7\%$ mean cover and the association = $16 \pm 4\%$ mean cover; Tobacco Reef— $15 \pm 5\%$ and $7 \pm 2\%$; Chinchorro Bank, Mexico (North)— $27 \pm 7\%$ and 10

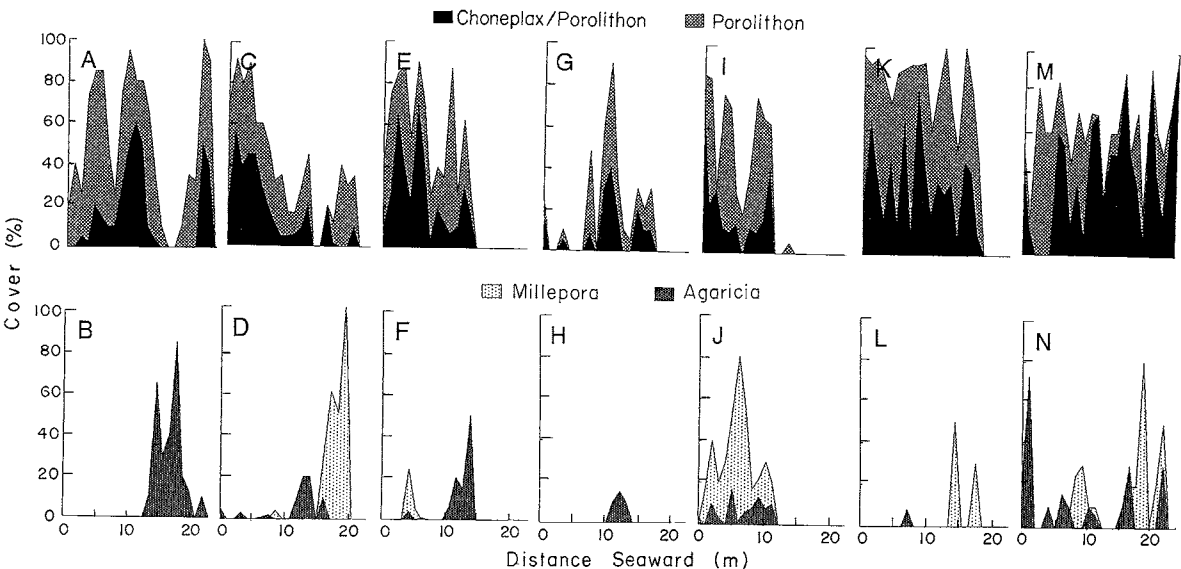


FIG. 6. Standing stocks of dominant cover organisms on seven Caribbean reef crests (upper row = *Porolithon* and *Choneplax*, lower row = *Millepora* and *Agaricia*). (A, B) = CBC North, (C, D) = CBC South, (E, F) = Curlew Cay, (G, H) = Tobacco Reef, Belize; (I, J) = Chinchorro Bank North, (K, L) = Chinchorro Bank South, Mexico; (M, N) = Roatan, Honduras.

$\pm 3\%$, (South) $62 \pm 8\%$ and $27 \pm 5\%$; and Roatan, Honduras— $62 \pm 4\%$ and $42 \pm 6\%$. The corals *Milnepora* spp. averaged $6 \pm 1\%$ cover at the above five sites, while *Agaricia agaricites* cover averaged $4 \pm 1\%$.

DISCUSSION

Most theoretical models currently consider factors such as predation to act directly as negative structuring vectors. Chitons in particular have gained worldwide attention for their negative impacts as abundant grazers along tropical carbonate shorelines, where they contribute substantially to long-term coastal degradation (reviewed in Rasmussen and Frankenberg 1990). However, herbivory as mediated by the chiton *Choneplax lata* on its principal prey, the reef-building alga *Porolithon pachydermum*, is in fact a positive attribute leading to elevated meristematic activity and net growth as well as increased biomass and structural carbonate accretion. For example, the long-term accretion rates (range = 1.0–4.0 mm/yr, mean = 2.3 mm/yr) of the various *Porolithon/Choneplax* samples were within the range of rates (0.1–5.2 mm/yr) previously reported (Adey and Vassar 1975, Littler et al. 1991) for *Porolithon* and other crustose corallines, and reflect substantial upward growth throughout the past 109 yr at CBC. In agreement, Nunn (1993) noted that a vertical growth rate of 1.6 mm/yr is probably representative of most *Porolithon* ridges over geological time periods.

This direct positive phenomenon is conceptually different from the limited marine examples of positive effects (indirect), such as disturbance favoring *r*-selected species (e.g., Sousa 1984), the instances of territorial animals defending a resource (e.g., Hixon 1986) and the selective reduction of competitively dominant organisms by predators (e.g., Dethier and Duggins 1984, Wootton 1993), and will need to be integrated into modern theoretical models as more examples of comparable mutualisms become revealed.

Research in marine intertidal and subtidal systems has been extremely rewarding, but focused primarily on negative interactions (i.e., competition, predation, physical disturbance, physiological stress). As mentioned (Rasmussen and Frankenberg 1990), herbivory by chitons is notorious for its bioerosive potential, leading to substantial coastal retreat. This study establishes the first intimate association between a chiton and a crustose coralline alga and shows the association to be an important component augmenting accretion in shallow Caribbean algal ridges. *Choneplax lata* was found almost exclusively on *Porolithon pachydermum* and the association averaged 15% cover of the crest substratum at the seven study sites. *Porolithon pachydermum* without chitons contributed 25% cover but mainly in deeper seaward areas of the crest accessible to herbivorous fishes (see Lewis 1986 for fish grazing assays on the same CBC system). Numerous studies (e.g., Littler and Doty 1975, Wanders 1976) have documented

that *Porolithon* requires some form of physical disturbance (grazing, wave shear) to remove superior fleshy algal competitors.

We found significantly greater persistence of intertidal populations of the coralline alga *Porolithon pachydermum* in the presence of the rasping chiton *Choneplax lata* (Table 3) compared to populations with the chiton removed. The mutualistic role of the herbivorous chiton is to "service" the coralline by removing superior competitors such as upright frondose and filamentous algae that can overgrow and smother or shade underlying crustose algae in the absence of herbivory (Wanders 1976, Steneck 1982). Overall, shallow *P. pachydermum* with *C. lata* present was less fouled by epiphytes (Table 3) and was more robust (M. M. Littler, D. S. Littler, and P. R. Taylor, *personal observations*) than populations without the chiton. We observed the ungrazed *Porolithon* (chiton-removal) plots to become fouled and bleached during the first 4 mo of our experiments, followed by increased bioerosion due to fish rasping and sloughing during the remaining 10 mo.

The effects of *Porolithon pachydermum* removal on *Choneplax lata* were twofold, depending on stochastic settlement and recruitment events during the experiments (Table 4). Generally, we observed that early-successional thin sheets of *P. pachydermum* and filamentous fleshy algal forms were the first organisms to settle. These did not always lead to the long-term establishment of *C. lata* populations; however, in 5 out of 16 of the removal-control plots (only where *P. pachydermum* became part of the successional sequence), the association was re-established (mean cover of *Porolithon* = 55.2%, mean of 2.0 chitons/plot) during the 14-mo experimental period. Chiton populations remained significantly reduced (mean of 0.1 chitons/plot) in all other cases in the absence of *Porolithon*. Unknown sources of decline by *C. lata* (emigration, predation?) may have caused the differences shown in the *Porolithon*-removal plots (i.e., both *Porolithon* and *Porolithon+Choneplax* removed), but the high mortality and the fact that *C. lata* were not recorded naturally without the coralline, suggests that *P. pachydermum* is required by successful populations of the chiton.

As pointed out by Steneck (1992), the significance of mutualisms can be exaggerated if they are interpreted as coevolved (the "arms race" model) when they may only represent an end point along a genetically constrained adaptive continuum. Several recent studies (reviewed in Steneck 1992) support the alternative hypothesis that trophic specialization and stable coexistence will be most likely between small herbivores (with reduced energy requirements, limited mobility, and high susceptibility to predation) and macroalgae that are large, well defended, nutritionally poor, long lived, and with great regenerative capacity. These criteria are consistent with the intimate chiton-coraline association studied here. Unfortunately, the fossil record is of little use at the species level because the

key chiton diagnostic character, girdle morphology, has not been preserved even though the plates are recorded as early as the Cambrian (Steneck 1983). However, the much later appearance of the genus *Porolithon* (rare in the Miocene and not abundant until the Pleistocene, Johnson 1961) and its present widespread abundance in the absence of chitons (Fig. 6) also do not support the coevolution model, similar to the lack of coevolutionary evidence for a comparable coralline-limpet association (Steneck 1982) and for obligate limpet associations with kelp (Estes and Steinberg 1988).

Sections of the naturally occurring association showed massive chiton-grazed accretions (up to 100 mm thick) of *Porolithon pachydermum*, with recent accretion thicknesses of 30 mm. As mentioned, the mean accretion rate for nine samples of the *Porolithon/Choneplax* mutualism on dead *Acropora palmata* branches was 2.3 mm/yr over a 109-yr period. This demonstrates that chiton grazing does not result in net bioerosion, but instead may be important in augmenting accretion processes leading to Caribbean reef crests. The chiton-removal-control reef surfaces stained with alizarin red were similar in terms of recent accretion layers to the unaltered control sections. Conversely, the surfaces of the chiton-removal substrata showed significantly more ($P < 0.05$, Bonferroni, Fig. 3) surficial parrotfish excavations resulting in substantial new bioerosion of the living and fossil *P. pachydermum*. Such fish-related bioerosion occurred at high-water periods and probably was induced by the increased fleshy algal stocks that represent attractive prey items for parrotfishes (Littler and Doty 1975, Wanders 1976), since the control populations showed fewer parrotfish rasping scars.

Not only is the persistence of *Porolithon pachydermum* improved in association with *Choneplax lata*, but the fitness of *P. pachydermum* is probably also increased, since grazing from the chiton is sufficient to remove epiphytes but not so deep as to cause undue mortality or damage reproductive, photosynthetic, and regenerative tissues. Grazing by the chiton alters the minor meristematic surfaces, which normally function to thicken and repair the thallus, into upward growing major meristems surrounding each burrow aperture. These resemble and function like the main meristem responsible for horizontal spread of the crust margin. The redirected upward growth results in a columnar "swiss cheese" labyrinth of refuge habitats (Fig. 2A) and greatly increases biomass per unit of two-dimensional substratum over the typical flat *P. pachydermum* morphology. Conversely, herbivores such as urchins and parrotfishes, whether feeding on the coralline alga or surficial epiphytes, graze deeply into coralline algal crusts, thereby removing actively growing meristematic, photosynthetic, and reproductive tissues. However, even when severely damaged, the intercalary meristem of *P. pachydermum* shows remarkable regenerative capacity (M. M. Littler and D. S. Littler, *personal*

observations of thick sections). Adey and Vassar (1975) found that herbivory by large mobile fishes with powerful rasping apparatuses increased the mortality of thin juvenile *P. pachydermum* on settlement plates, restricting it to high energy environments such as algal ridges and reef crests.

The close SEM match between radular morphology of *Choneplax lata* (Fig. 5A) and grazing scars on the thallus surface of *Porolithon pachydermum* (Fig. 5B), and the internal anatomical dimensions of *P. pachydermum*, show how the chiton grazes the coralline alga without causing mortality. As indicated earlier, the raised areas surrounding burrows are in fact rings of meristematic tissue, analogous to the main meristem at the margin of the crust, resulting in increased upward growth. Virtually all *P. pachydermum* in the vicinity of *C. lata* burrows contain radular track scars in the thick epithallus layer of $\approx 10 \mu\text{m}$ depth, whereas the intercalary growing area, photosynthetic cells, and reproductive structures of the coralline lie below 20 μm . This aspect of the relationship mirrors that reported for a limpet-coralline mutualism in the Gulf of Maine (Steneck 1982). *P. pachydermum* under intense chiton grazing was photosynthetically competent ($0.1 \pm 0.01 \text{ mg C fixed} \cdot \text{g}^{-1} \text{ organic dry mass} \cdot \text{h}^{-1}$) within the range of rates for other crustose coralline algae. For example, Littler et al. (1987) recorded about the same photosynthetic rate ($0.09 \pm 0.02 \text{ mg C} \cdot \text{g}^{-1} \text{ organic dry mass} \cdot \text{h}^{-1}$) for ungrazed *P. pachydermum* in Belize (NS, $P > 0.05$). The range of previous values reported (Littler et al. 1986) for crustose algae ranges from 0.1 to $0.4 \text{ mg C} \cdot \text{g}^{-1} \text{ organic dry mass} \cdot \text{h}^{-1}$.

The preponderance of *Porolithon pachydermum* in the gut contents of *Choneplax lata* (51%) shows that the chiton continually rasps the coralline, although other microscopic algae (19%) and bacteria (29%) are consumed as well. The coralline is not only an abundant and dependable food source for the chiton but also grows well intertidally in heavy turbulence, providing a further degree of physical escape for the chiton potentially removed from intense predation by subtidal predators. As discussed above, the aggregation of chitons and their meristematically altered burrows within the coralline algae provide essential refuge habitat. Limited recruitment of mature *C. lata* did occur in the chiton-removal plots during 30 mo, but was not substantial. In casual aquarium feeding trials, the night-foraging spiny lobster *Panulirus argus* (Latreille 1804) readily consumed living *C. lata* in all size classes. During the daytime, carnivorous fishes, particularly grey snapper (*Lutjanus griseus*, L. 1758) and bluehead wrasse (*Thalassoma bifasciatum*, Bloch 1791) quickly devoured the chiton.

The *Choneplax lata/Porolithon pachydermum* association covers substantial areas of algal ridges throughout the Caribbean (Fig. 6). Crustose coralline algae are among the most abundant and widespread space occupiers of photic-zone marine hard substrata

worldwide (Littler 1972, Steneck 1986) and this pattern has persisted for many millions of years (Steneck 1983). Barrier and fringing reefs are complex ecosystems that depend on coralline algae for the maintenance of wave-resistant fronts (see, for examples, Tracey et al. 1948, Lee 1967, Maxwell 1968, 1969, Ginsburg and Schroeder 1973, Doty 1974, Littler and Doty 1975, Adey and Burke 1976, Adey 1978*a, b*). The intertidal wave-resistant algal ridge, by reducing erosional forces (Dawson 1961, Ladd 1961, Nunn 1993), is perhaps the most important part of a biotic reef because the protection it affords permits the development of most other shallow-water reef communities, as well as absorbing wave energy that could erode emergent land masses. Crustose coralline algae are the principal cementing agents (Wray 1971) that produce the structural integrity and resilience of the reef front, and their importance in this role cannot be overemphasized.

The crustose coralline alga *Porolithon pachydermum* reaches cover maxima of up to 70% in the crest portion of the Belize Barrier Reef (cf. Littler et al. 1987) but its association with the burrowing chiton *Choneplax lata* had been overlooked (see Littler et al. 1987, 1989*a*). We have collected co-occurring populations of the *C. lata*/*P. pachydermum* association present at comparable abundances (M. M. Littler and D. S. Littler, *personal observations*) from the Florida reef tract and the northern Bahamas southward to Puerto Rico and the Lesser Antilles (Grenadines) and westward to the Mexican Yucatan, the Bay Islands of Honduras, and the San Blas Islands of Panama. In Belize, all portions of the barrier reef crest south and north of Carrie Bow Cay contain abundances similar to those studied here, as do the outer (seaward) reef crests of the three Caribbean atolls, Glovers Reef, Lighthouse Reef and Chinchorro Bank (M. M. Littler and D. S. Littler, *personal observations*). We have found *P. pachydermum* frequently in subtidal areas of high herbivory without the chiton (presumably maintained by other grazers, Wanders 1976); however, in nearly all cases where burrow-forming populations of *C. lata* were observed, *P. pachydermum* was the predominant substratum.

In the Pacific, wave shock in the intertidal and fish grazing subtidally are sufficient to remove large frondose algal competitors from the closely related reef-builder *Porolithon onkodes* (Heydrich) Foslie on Hawaiian algal ridges (Littler and Doty 1975), but abundant rasping limpets are also present in the intertidal, as well as on the algal ridges of Guam and Enewetak Atoll (Littler and Littler 1984: Fig. 9) and probably play a role similar to that of *C. lata*. As in the case of the *Acmæa/Clathromorphum* mutualism (Steneck 1982), we have documented a predator/prey interaction whereby the prey not only survives frequent grazing, but benefits from it. Interestingly, we recently noted similar intimate associations between other species, i.e., *P. onkodes* and the much larger burrowing chiton, *Cryptoplax larvaeformis* (Tyron 1887) that occurs

abundantly (M. M. Littler and D. S. Littler, *personal observations*) throughout the rim of the Great Astrolabe Reef of Fiji, and a small black chiton (unidentified) in association with intertidal *P. onkodes* throughout the northern Papua New Guinea coastline, suggesting that such associations may be important worldwide in tropical waters.

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