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TAPHONOMIC SIGNATURES ON MODERN CARIBBEAN BIVALVE SHELLS AS INDICATORS OF ENVIRONMENTAL CONDITIONS (BELIZE, CENTRAL AMERICA)

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ABSTRACT

Taphonomic signatures on modern bivalve shells, such as traces of drilling organisms, encrusters, fragmentation, and abrasion function as indicators of environmental differences on Belize atoll reefs. Glovers Reef, Lighthouse Reef, and Turneffe Islands are three adjacent Caribbean atolls showing variations in geomorphology, lagoonal depth, sedimentation, mangrove growth, sea-grass cover, and exposure to winds and currents, as well as differences in their lagoonal development and age. A variety of bivalve assemblages characterize lagoonal subenvironments and also mirror the above-mentioned environmental variations. Taphonomic signatures, such as shell-size distribution, disarticulation, sorting, boring traces, encrustations, fragmentation, and abrasion, were identified on bivalve shells from a total of 111 surface sediment samples. Shell-size distribution and sorting of right and left valves indicate *in situ* deposition of populations on each atoll. Increasing residence times of shells on the sediment surface due to decreasing sedimentation rates from Turneffe Islands to Lighthouse Reef to Glovers Reef cause an increase in taphonomic shell signatures.

INTRODUCTION

Taphonomic shell features and bivalve taphocoenoses are very useful indicators for reconstructing ancient environments (e.g., Schäfer, 1962; Fürsich and Flessa, 1987; Feige and Fürsich, 1991; Kidwell and Bosence, 1991). Parsons-Hubbard (2005) and Best and Kidwell (2000b) describe taphonomic signatures of mollusk assemblages from carbonate reef environments in the Caribbean Sea as more useful indicators of original depositional environments than taxonomy or life-habit grouping. The combined effect of various processes controls the single diagnostic signature of an environment. Shell preservation depends on several factors, such as water agitation, bioturbation, and sedimentation rate. Furthermore, environmental variations (mainly sediment composition), bivalve life habits, and shell types affect the taphonomy of bivalves (Best and Kidwell, 2000a, 2000b). Taphonomic features often co-occur predictably, defining so-called taphofacies, which characterize various depositional environments and environmental gradients (Brett and Baird, 1986; Kidwell et al., 1986; Fürsich and Oschmann, 1993). In addition, present-day environments show extensive temporal sediment mixing (time averaging) on the scale of hundreds to thousands of years, having an influence on bivalve taphonomy (Flessa et al., 1993; Flessa and Kowalewski, 1994; Kidwell et al., 2005).

Studies on coral reef taphonomy were discussed by Scoffin (1992). Perry (1999a) investigated coral-reef framework preservation in Discovery Bay, Jamaica. Greenstein and Pandolfi (2003) studied the taphonomy of reef-coral death assemblages in the Florida Keys reef tract. Taphonomic signatures, such as encrustation, bioerosion, and cementation, producing distinct facies and water-depth zonation on the reefs of Campeche Bank (Mexico) were described by Blanchon and Perry (2004). A limited number of studies dealt with the taphonomy of mollusks from several different settings in the Caribbean Sea and nearby areas (Callender et al., 2002; Staff et al., 2002; Walker et al., 2002; Leonard-Pingel, 2005; Parsons-Hubbard, 2005), excluding atoll environments.

The Belize atolls Glovers Reef, Lighthouse Reef, and Turneffe Islands are particularly suitable for a taphonomic investigation of bivalve shells because they include small areas showing distinct environmental zonation. These lagoonal environments are characterized by different bivalve shell assemblages (Hauser et al., 2007). For these reasons, this actuopaleontological study was designed in order to study the nature and origin of taphonomic shell features in these Caribbean atoll reefs. Furthermore, this project explores the question of whether taphonomy reflects the same pattern of environmental zonation as bivalve assemblages and also investigates controlling factors of variation of taphonomic features in various lagoonal environments. Results of this work may be used for paleoenvironmental reconstruction in the younger fossil record.

STUDY AREA

Climate and Oceanography

The Caribbean atolls Glovers Reef, Lighthouse Reef, and Turneffe Islands are situated east of the Belize Barrier Reef (Central America; see Fig. 1). Climate in Belize is subtropical with air temperatures between 24°C in winter and 27°C in summer (Purdy et al., 1975). Winds average 7 knots in October and 13 knots in March and blow from the east and northeast most of the year; however, hurricanes mainly approach from the east and southeast (Gischler and Hudson, 1998). The tidal range is ~30 cm, which is microtidal (Stoddart, 1962).

On the atolls, rainfall averages 175 cm per year (Stoddart, 1962; Purdy et al., 1975) and is highest from May to November and lowest from February to April (Gischler et al., 2003). Lagoonal water temperatures average 27.81°C and follow the seasons (Hauser et al., 2007). Salinity in atoll lagoons is elevated compared to the surrounding ocean. It is largely controlled by rainfall and evaporation and varies significantly among the atolls. During the rainy season, comparatively low salinities (38.32–41.07 practical salinity units) were measured in the restricted lagoons of Glovers Reef and Turneffe Islands, where water exchange with the open sea is limited. Storms and hurricanes cause a noticeable decrease in salinity. During the dry season, salinity increases up to 41.32 practical salinity units in April in the restricted North Lagoon of Turneffe Islands.

Reef Development, Geomorphology, and Environment

Glovers Reef, Lighthouse Reef, and Turneffe Islands differ significantly in geomorphology, sediment composition, and lagoonal development (Gischler and Hudson, 1998; Gischler and Lomando, 1999; Gischler, 2003). Reef growth and topography, as well as Pleistocene karst formation, follow NNE-striking tectonic structures in the underlying bedrock (Purdy, 1974; Lara, 1993; Esker et al., 1998). Because of higher average rainfall in southern Belize, the karst relief is better developed in the south than in the north. This trend is also apparent on the three atolls, and relief is higher (10–12 m) on Glovers Reef and lower (4–5 m) on

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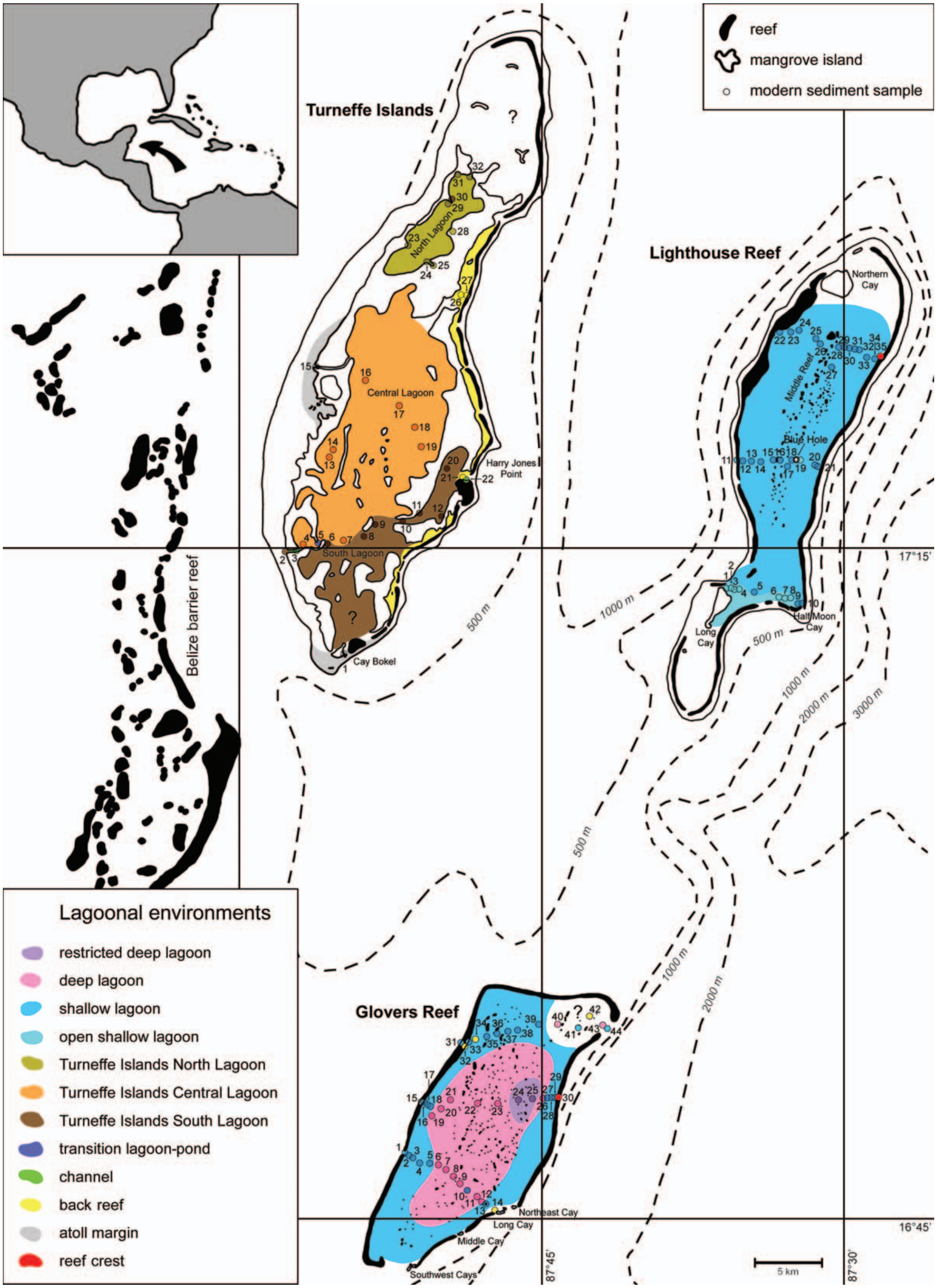

FIGURE 1—Map of the study area with locations of the box-core samples and zonation of lagoonal environments based on Q-mode cluster analyses (Hauser et al., 2007). Glovers Reef: restricted deep lagoon, deep lagoon, shallow lagoon, back reef, and reef crest. Lighthouse Reef: shallow lagoon, open lagoon, and reef crest. Turneffe Islands: North Lagoon, Central Lagoon, South Lagoon, transition lagoon-pond, channel, back reef, and atoll margin.

Turneffe Islands and Lighthouse Reef (Gischler et al., 2000). Reef development began when the rising postglacial sea flooded topographic highs on limestone islands. Investigations of Gischler (2003) dated the flooding of Glovers Reef from ca. 8.5 ka, Lighthouse Reef from ca. 7 ka, and Turneffe Islands from ca. 6 ka. The initial flooding stage is characterized by dense red mangrove swamps.

Glovers Reef is the oldest atoll and 260 km^2 in size. Six islands cover 0.6 km^2 along the southern windward reef margin. The inner lagoon is up to 20 m deep and flattens to the margin. It is covered by $\sim$860 patch reefs and surrounded by a reef crest with three tidal channels in the east (Gischler, 2003). The shallow marginal lagoon is loosely covered with sea-grass meadows of *Thalassia testudinum*, whereas sea-grass growth is sparse in the deeper central part. Surface sediments from Glovers Reef have ^{14}C ages from 1.4 ka to modern (Gischler and Lomando, 2000). Lagoonal sediment samples provide ^{14}C-ages of up to 0.500 ka (average $= 0.375$ ka), proving the effect of time averaging on the sediment as well as on the enclosed shell deposits.

Lighthouse Reef is the smallest atoll and covers 200 km^2 with five islands making up 7.5 km^2. In the south, one opening in the windward reef crest permits a permanent water exchange with the Caribbean Sea. The leeward reef is broken by numerous small channels and one wide opening in the south. The inner lagoon of this atoll is divided into a shallow ($\leq$3 m) western and a deeper (3–9 m) eastern part by the Middle Reef, a north-south trending, $\sim$20-km-long area of patch reefs. Sea-grass cover is more dense in the eastern lagoon than in the western part.

Turneffe Islands include the youngest and biggest atoll. It covers an area of 525 km^2, 125 km^2 of which are islands, mainly grown over with red mangroves (*Rhizophora mangle*). A narrow reef crest with over 20 channels is developed on the eastern side, but in the north, the reef is wider and not interrupted by channels. Except for the northern part, this atoll is situated leeward of Lighthouse Reef. Therefore, inner lagoons are largely protected from winds and currents. A small lagoon in the north and a bigger one, divided into a central and a southern part, are surrounded by mangrove rims with numerous channels (bogues) and ponds. Lagoonal depths reach 6 m (Gischler, 1994). Only in the North Lagoon do rare coral patch reefs develop. The bottom of the lagoons is covered with dense sea-grass meadows and the calcareous alga *Halimeda*. Lagoonal surface sediments on Turneffe Islands are darker and have higher organic carbon content than those on Glovers Reef and Lighthouse Reef (Gischler and Lomando, 1999). They smell intensely of H_2S, indicating a deficiency of oxygen. An overview of the environmental zonation on the atolls based on Q-mode cluster analyses is shown in Figure 1.

MATERIALS AND METHODS

In March and April, 2000, 111 modern sediment samples were taken along E-W transects in the lagoons of Glovers Reef, Lighthouse Reef, and Turneffe Islands (Fig. 1) using a grab sampler (Hydro-Bios, Kiel; volume $=$ 3.4 L). On each sample location, two grab-sampler volumes (6.8 L) were taken from the boat or by snorkeling along the reef crests. Each locality was pinpointed using a global positioning system device (model Magellan 2000; accuracy $=$ 30.8 m). Water depths were measured using a rope with a metric scale, and bottom-water temperatures by holding a contact thermometer in the fresh sediment samples.

During field work, the samples were carefully sieved (mesh width $=$ 1 mm). In the laboratory, they were washed in fresh water and oven dried at 50°C. Bivalve shells, gastropod shells, and fragments of both were picked from the sediment under a binocular microscope, and their volumetric contents were measured. Fragments with $>$50% of the shell, or with characteristic features preserved, were regarded as complete valves or individuals, respectively, because such fragments can clearly be assigned to one valve of a bivalve or to a gastropod. For bivalves, the characteristic features were the umbo, hinge, and pallial line; for the gastropods, the characteristic features were the apex and the aperture.

Compared to gastropods, shells of bivalves provide more information about the life habit of the animal. Shell form and concavity as well as the existence or nonexistence of a pallial sinus indicate whether the species has an epifaunal, infaunal, shallow-burrowing, or deep-burrowing lifestyle; therefore, this study focused on bivalves only. Taxonomic identification was based on Warmke and Abbott (1961), Meinkoth (1981), Rehder (1981), Abbott (1986), and Redfern (2001). According to Patterson and Fishbein (1989), the statistical error depends on the number of individuals in a sample and ranges from 1% to 6% for samples containing 300 shells, which is also regarded here as sufficiently significant for statistical studies. Therefore, large samples were divided into smaller fractions using a sample splitter.

In addition to identifying different bivalve species, we investigated their shell sizes; percentages of right, left, and articulated valves; and taphonomic signatures on the shells. Such signatures include traces of drilling gastropods (*Oichnus* isp.) and the boring sponge *Cliona* (*Entobia* isp.); encrusting organisms, particularly foraminifera; coralline red algae; algae; polychaetes; and biofilms, as well as fragmentation and abrasion of the shells. Fragmented and abraded valves were classified into three degrees by percent fragmentation and abrasion respectively: (1) 0%–33.3%, (2) 33.3%–66.6%, and (3) 66.6%–100%. The level of abrasion is based mainly on loss of shell sculpture.

Q-mode cluster analyses were made using MVSP (Kovach Computing Services, 2001, ver. 3.1) to distinguish different bivalve shell assemblages characterizing diverse lagoonal zones (Hauser et al., 2007) and to find out whether there are differences in the distribution of taphonomic signatures on the shells among these environments.

RESULTS

Shell Size, Disarticulation, and Sorting of Valves

Shell-size distribution on the atolls is right skewed (Figs. 2A–C). On Glovers and Lighthouse Reefs most of the valves are 0.3 cm in size. On Turneffe Islands the maximum size is between 0.2 and 0.3 cm.

Sorting of right and left valves in the lagoonal environments of the atolls is almost 1:1 (Figs. 3A–C). One valve (left or right) predominates along the reef crests of Glovers Reef and Lighthouse Reef, the atoll margin of Turneffe Islands, the back reef of Glovers Reef, and the open southern part of Lighthouse Reef lagoon. Relatively high amounts of articulated valves ($>$5%) were found in the back reef of Glovers Reef, along the reef crest and in the open lagoonal part of Lighthouse Reef, as well as in the transition between lagoon and pond on Turneffe Islands.

Boring Traces

Traces of predating gastropods, including those of muricids (*Oichnus simplex*) and naticids (*Oichnus paraboloides*), were distinguished from dwelling burrows of the boring sponge *Cliona* (*Entobia* isp.; Fig. 4A). *Oichnus simplex* differs from *O. paraboloides* in shape; muricid drillings are cylindrical in outline whereas naticid drillings are conical (Figs. 4B–C). Shells drilled by gastropods normally show only one boring, mostly situated in the middle of the valve or the umbilical region.

In comparison to Glovers Reef and Lighthouse Reef, only a few boring traces were found in the bivalve shells in Turneffe Islands lagoons (Fig. 5A). Drillings of predators as well as dwelling burrows are much more abundant on Lighthouse Reef and reach their highest percentages on Glovers Reef. In all atoll lagoons, *Entobia* isp. shows higher abundances than *Oichnus* isp. Among the gastropod drillings, *O. paraboloides* clearly predominates on the atolls.

In the lagoonal environments of Glovers Reef, traces of *Cliona* increase in abundance from the restricted, deep lagoon toward the shallow marginal zones (Figs. 5B-D). On Lighthouse Reef, *Entobia* isp. is most abundant along the reef crest. The distribution of *Oichnus* isp. shows no such trend.

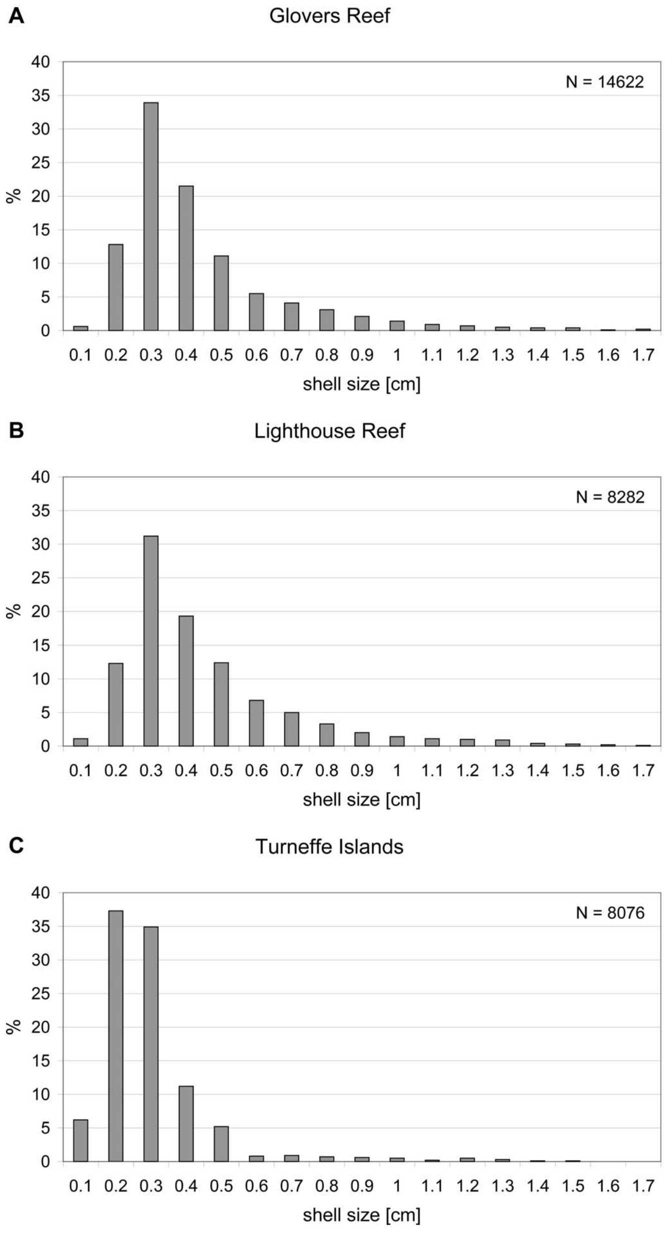

FIGURE 2—Shell-size distribution on the Belize atolls studied. N = number of valves investigated.

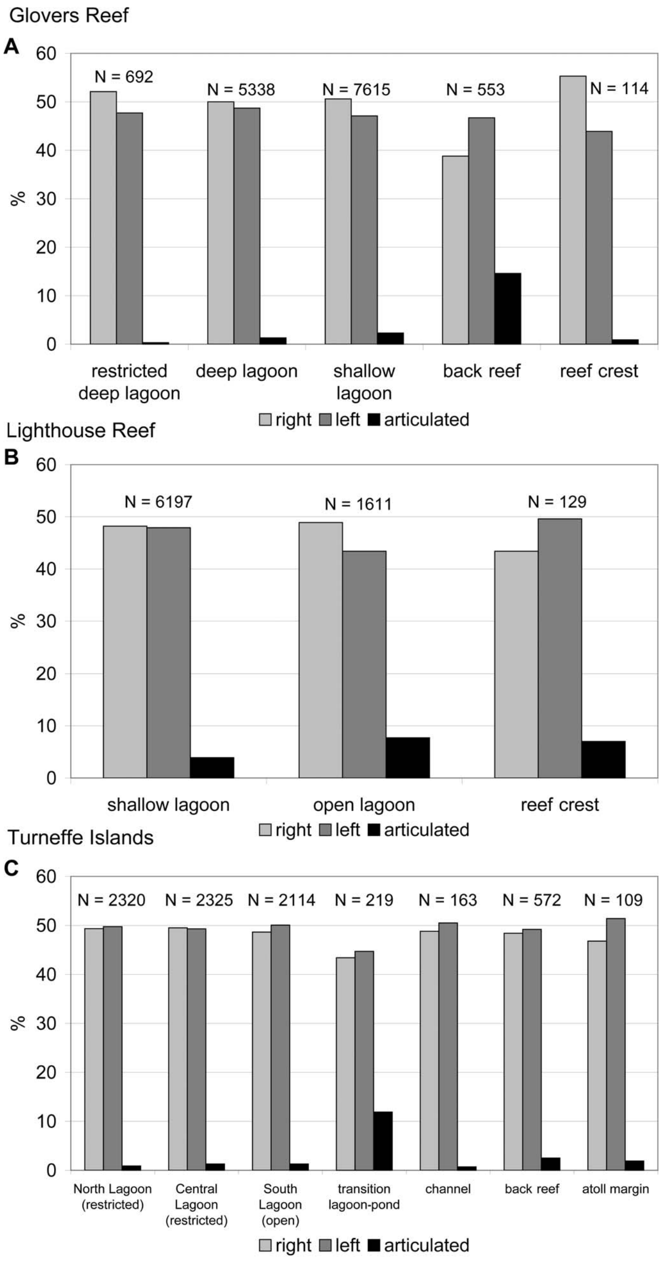

FIGURE 3—Preservation of right, left, and articulated valves in the lagoonal environments of the three atolls. N = number of valves investigated; an articulated valve was counted as one valve.

Encrustations

Abundance of Encrusted Valves.—The abundance of encrusted valves increases from Turneffe Islands to Lighthouse Reef to Glovers Reef (Fig. 6A). On Turneffe Islands, encrustations are very rare, and therefore, this atoll is not considered further in the following.

The distribution of encrusted valves in the lagoonal environments of Glovers Reef and Lighthouse Reef resembles that of *Entobia* isp. (Figs. 6B–D). On Glovers Reef, the number of encrusted valves increases from the restricted, deep lagoon toward the shallow marginal zones. It is highest along both reef crests of Glovers Reef and Lighthouse Reef.

Types of Encrusters.—Bivalve shells found on the atolls are encrusted with foraminifera, coralline red algae, algae, tubes of polychaetes, and a few bryozoans (Figs. 7A–F). The shells are often coated with biofilms consisting mainly of fungal hyphae, diatoms, sponge spicules, and coccoliths (Figs. 8A–D). Biofilms are the most abundant encrustations on bivalve shells in Glovers Reef and Lighthouse Reef lagoons (Figs. 9A–B). With the exception of the Glovers Reef back-reef area, the number of valves coated with biofilms decreases from the restricted central lagoonal parts toward the exposed marginal zones of both atolls.

Encrusting foraminifera are more common on Lighthouse Reef shells. On both atolls, their number, as well as the number of coralline red algae and polychaete tubes, increases toward the shallow marginal lagoons. The most abundant foraminifera encrusting the bivalve shells on the three atolls are *Planorbulina acervalis*, *Rosalina* spp., and *Cornuspiramia antillarum*. Taxa that are less abundant or restricted to only a few localities are *Homotrema rubrum*, *Cymbaloporetta* spp., and *Amphisorus hemprichii* (Figs. 10A–F).

Rosalina is the predominant encrusting foraminifer on Glovers Reef (Fig. 11A). On Lighthouse Reef, this genus is only rarely found. *Planorbulina* is also very common on Glovers Reef but shows its highest numbers on Lighthouse Reef, where *Cornuspiramia* is also comparatively

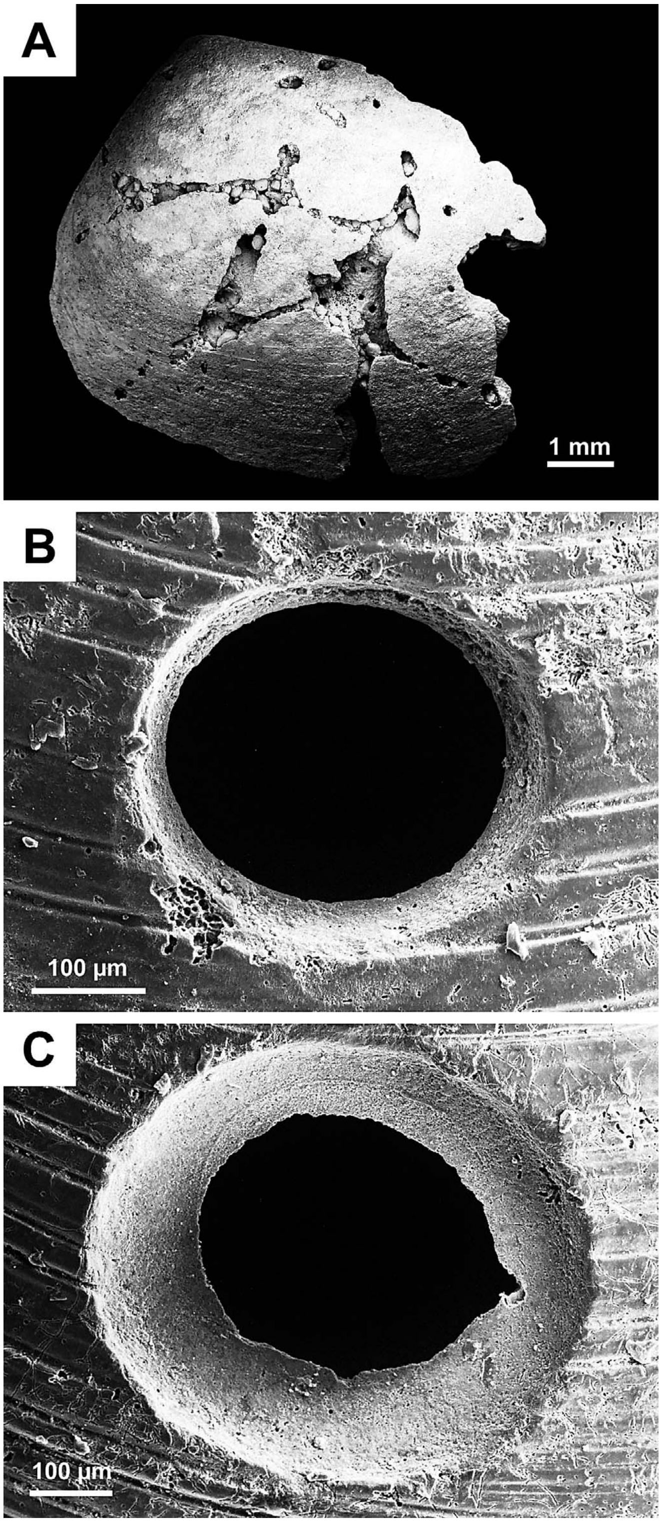

FIGURE 4—Boring traces. A) Traces of the boring sponge *Cliona* (*Entobia* isp.) on a shell of *Tellina gouldii* from sample station L7. B) Boring traces of predating gastropods of the family Muricidae (*Oichnus simplex*, cylindrical). C) Boring traces of predating gastropods of the family Naticidae (*Oichnus paraboloides*, conical).

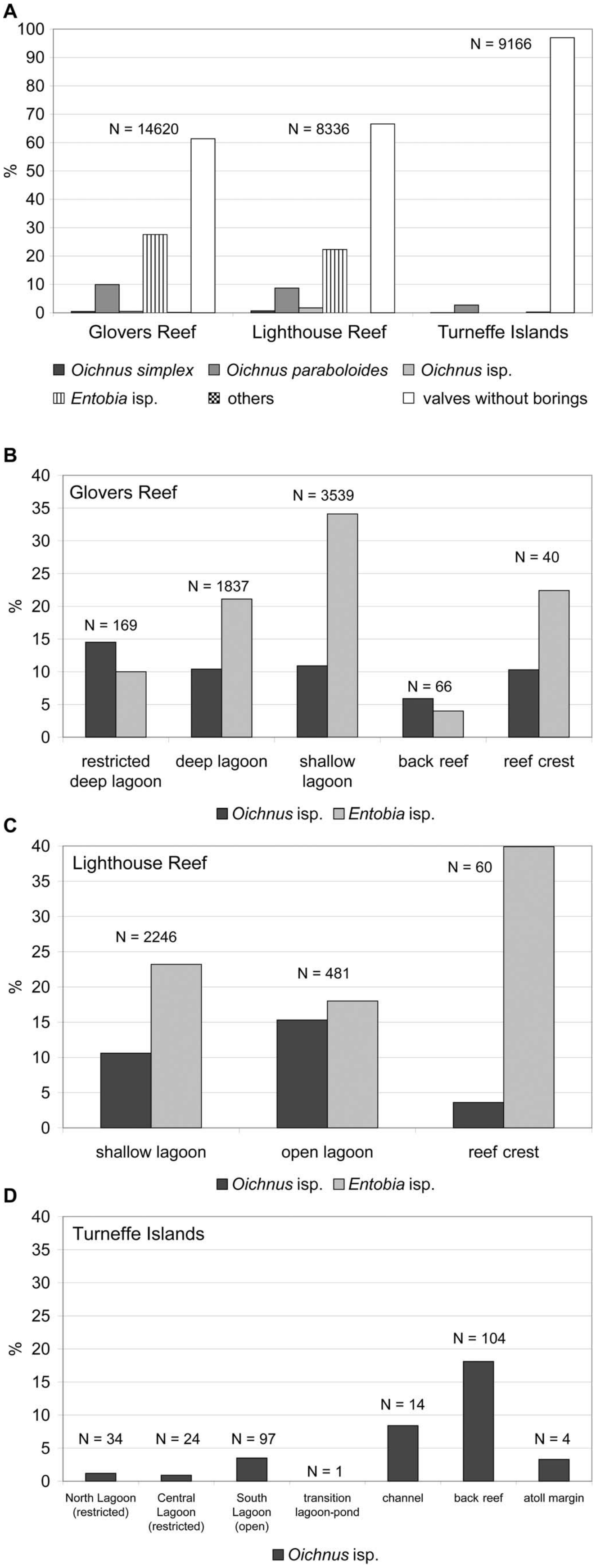

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FIGURE 5—Percentages of boring traces on bivalve shells. A) Comparison of all three atolls; N = number of valves investigated. B–D) Percentages of *Oichnus* isp. (mainly *Oichnus paraboloides*) and *Entobia* isp. in the lagoonal environments of the three atolls; N = number of drilled valves.

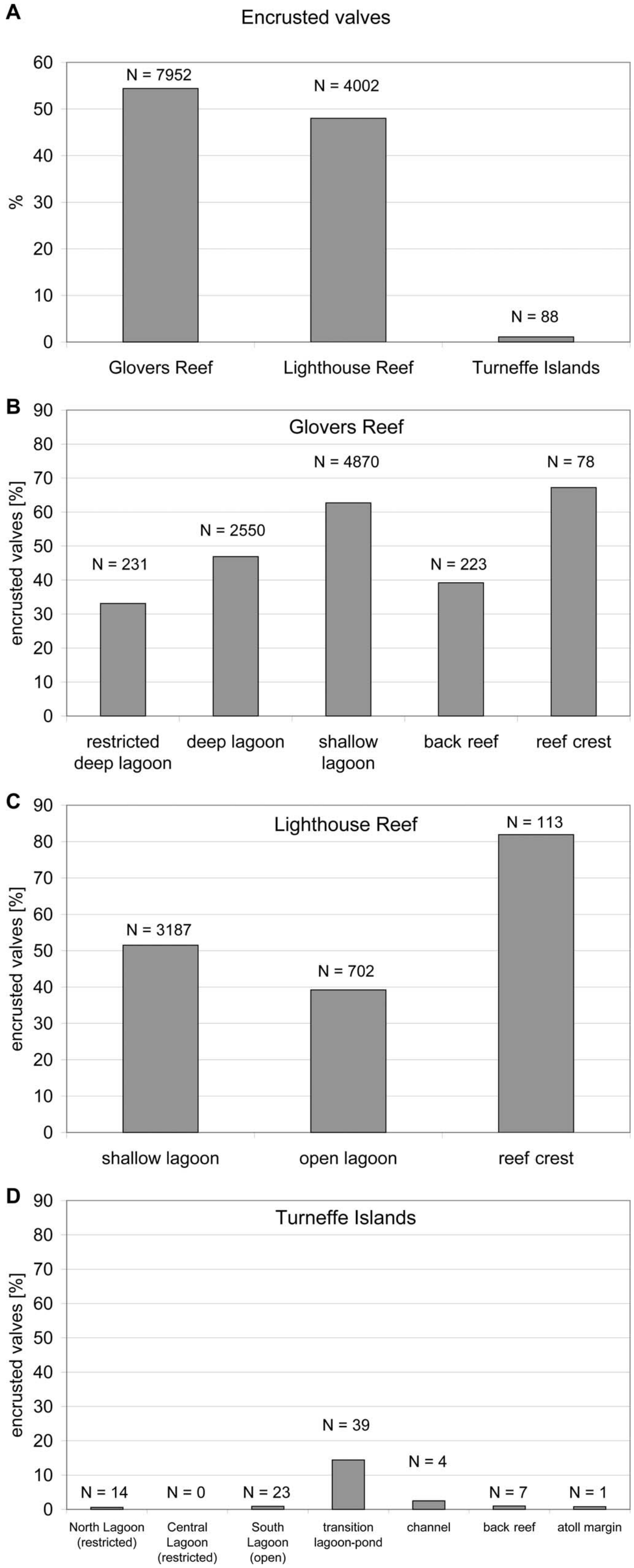

FIGURE 6—Percentages of encrusted valves. A) Comparison of all three atolls. B–D) Distribution of encrusted valves in the lagoonal environments of the three atolls; N = number of encrusted valves.

abundant. With the exception of the reef crests, the percentages of *Planorbulina* and *Cornuspiramia* increase from the restricted, deep lagoonal environments of Glovers Reef and Lighthouse Reef toward the open, shallow marginal zones (Figs. 11B–C). In the opposite direction, the abundances of *Rosalina* increase. In addition to these three foraminifers, *Homotrema rubrum* is a common encrusting species along the windward reef crests of both atolls. On the shells found along the reef crest of Lighthouse Reef, *Cymbaloporetta* spp. and *Amphisorus hemprichii* are also very abundant.

Fragmentation and Abrasion

The abundance of highly fragmented bivalve shells increases from Turneffe Islands to Lighthouse Reef to Glovers Reef (Fig. 12A). In the lagoonal environments on Glovers Reef, shell breakage increases from the restricted, deep lagoon toward the back reef (Figs. 12B–D). On Lighthouse Reef, no such trend is visible, and valves are only slightly fragmented. In Turneffe Islands lagoonal environments, nearly all bivalve shells are ≤33.3% fragmented.

The percentage of abraded valves also increases from Turneffe Islands to Lighthouse Reef to Glovers Reef (Fig. 13A). On Glovers Reef, abrasion increases from the restricted, deep lagoon toward the shallow, marginal zones (Figs. 13B–D). In the back-reef area of this atoll, only a few shells are abraded. Along the reef crest, the abundance of abraded valves is comparable to that in the deep lagoonal part. On Lighthouse Reef, an increase of shell abrasion was observed from the shallow lagoon toward its open shallow zone and reef crest. In the lagoonal environments of Turneffe Islands, nearly all bivalve shells show abrasion level 1.

DISCUSSION

Shell-Size Distribution

The atoll lagoons are predominantly inhabited by small bivalves that are either juveniles or dwarfs. Right-skewed shell-size distribution (Fig. 2) is indicative of *in situ* populations with a constant death rate (Richards and Bambach, 1975). Such distributions also depend on the individual growth rate (Craig and Hallam, 1963; Craig, 1967). High abundance of small shells found on Turneffe Islands may also be an indicator for dwarfism caused by oxygen depletion and salinity fluctuations toward brackish and hypersaline conditions (Oschmann, 1993; Schöne, 1999) within the restricted atoll of Turneffe Islands. The dark lagoonal sediments smelling of H_2S on this atoll also indicate anaerobic sulfate reduction within the substrate. Waves and currents causing sediment transport and winnowing small valves have little influence on Turneffe Islands lagoons. Only a few tellinids with elongate shells and large average shell sizes were found in the lagoons of this atoll.

Disarticulation and Separation of Valves

The 1:1 ratio of right and left valves in the atoll lagoons is indicative of an arbitrary distribution of *in situ* populations, and sorting by transport can be largely excluded. Only in the open marginal lagoonal zones is one valve slightly more abundant than the other, and some influence of transport due to waves and currents is visible.

In spite of higher water-agitation levels in the open marginal zones of Glovers Reef and Lighthouse Reef lagoons, many valves are preserved articulated. These zones are mainly inhabited by deep burrowing bivalves (*Tellina*, *Ervilia*), which protect themselves from waves and currents by living in the sediment, resulting in the preservation of complete shells. High amounts of articulated valves were also found on firm substrate in the transition between lagoon and pond on Turneffe Islands (sample T5). This sample predominantly contains taxodont epifaunal genera (*Arcopsis*, *Barbatia*).

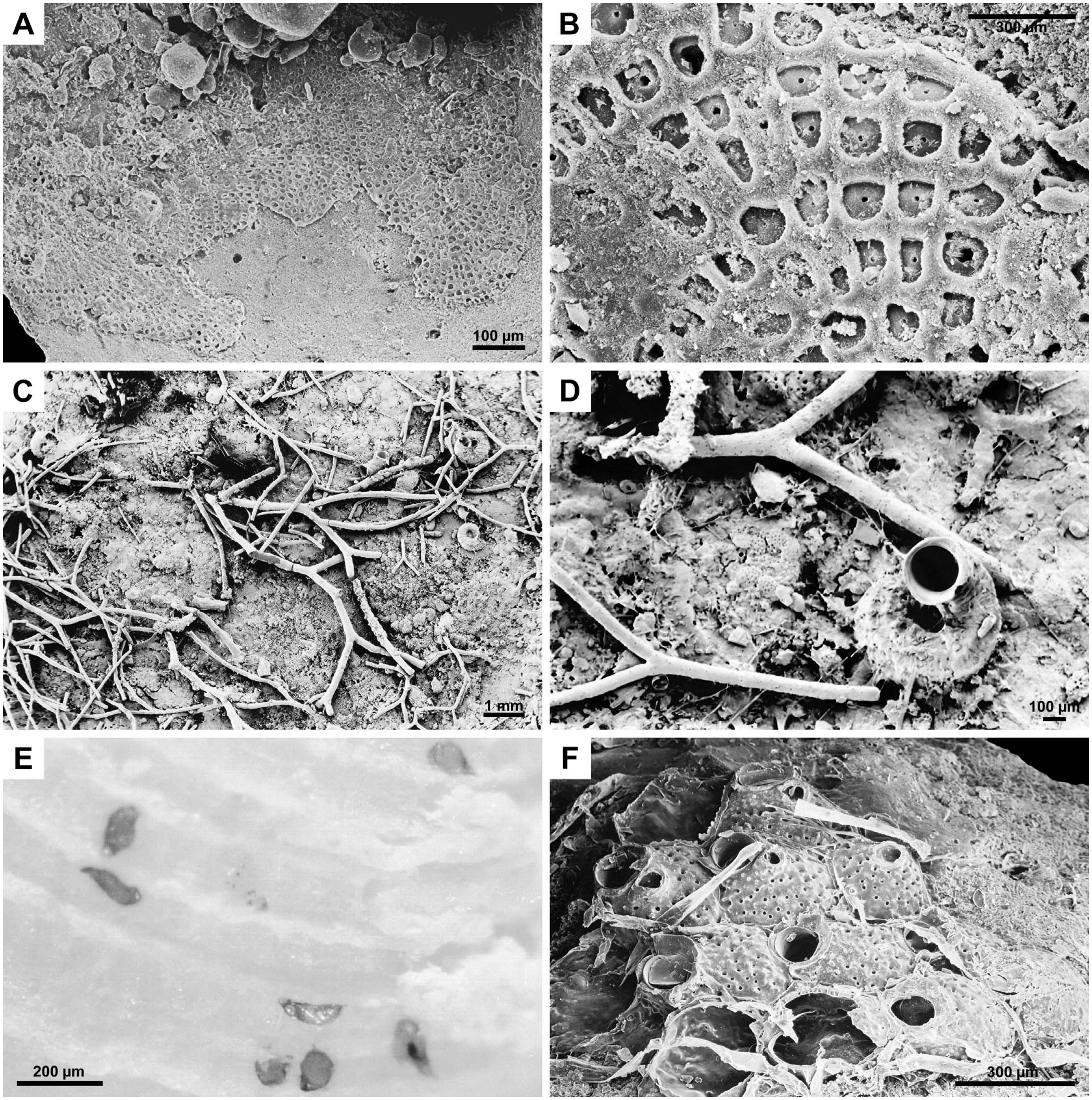

FIGURE 7—Encrusting organisms on bivalves. A) Unidentified species of coralline red algae. B) Higher magnification of alga in A. C) Branched specimen of *Jania*, a coralline red alga (left) and serpulid tubes (right). D) Higher magnification of *Jania* and serpulid tube from C. E) Patches of green attributed to algal growth on the outside of *Chione cancellata* shells. F) Bryozoans assignable to *Hippopodina*.

Drillings

Predatory gastropod drillings found on bivalve shells were produced during the lifetime of the bivalves and caused their death. Therefore, only one hole is usually found in articulated bivalve shells. Exceptions—those articulated bivalves with more than one drilling—are presumably the result of further attempts by the gastropod to kill the animal (Kowalewski et al., 2000). Most of the bivalve species found on the atolls live within the substrate. Therefore, *Oichnus paraboloides* caused by infaunal naticids is overwhelmingly more abundant than *O. simplex* produced by epifaunal muricids. Several factors such as size, biomass, or shell thickness of the bivalve play a significant role in the selection of prey by drilling gastropods (Kitchell et al., 1981). Therefore it is difficult to interpret the distribution of *Oichnus* isp. on the atolls and in their lagoonal environments. The abundance of *O. paraboloides* increases from Turneffe Islands to Lighthouse Reef to Glovers Reef possibly because of increasing numbers of smooth and thin-shelled bivalves, such as tellinids or *Parvilucina* sp. A in the same direction. Their shells are easier to drill than those of polymorphic and thick-shelled species.

Dwelling burrows of *Cliona* were generated after the death of the bivalve. The shell serves as a substratum to the boring sponge. The increase in *Entobia* isp. frequency from Turneffe Islands to Lighthouse Reef to Glovers Reef presumably results from a decrease in sedimentation rate in the same direction. The calculated average Holocene sedimentation rates are 0.82 $m \cdot ka^{-1}$ on Turneffe Islands, 0.53 $m \cdot ka^{-1}$ on Lighthouse

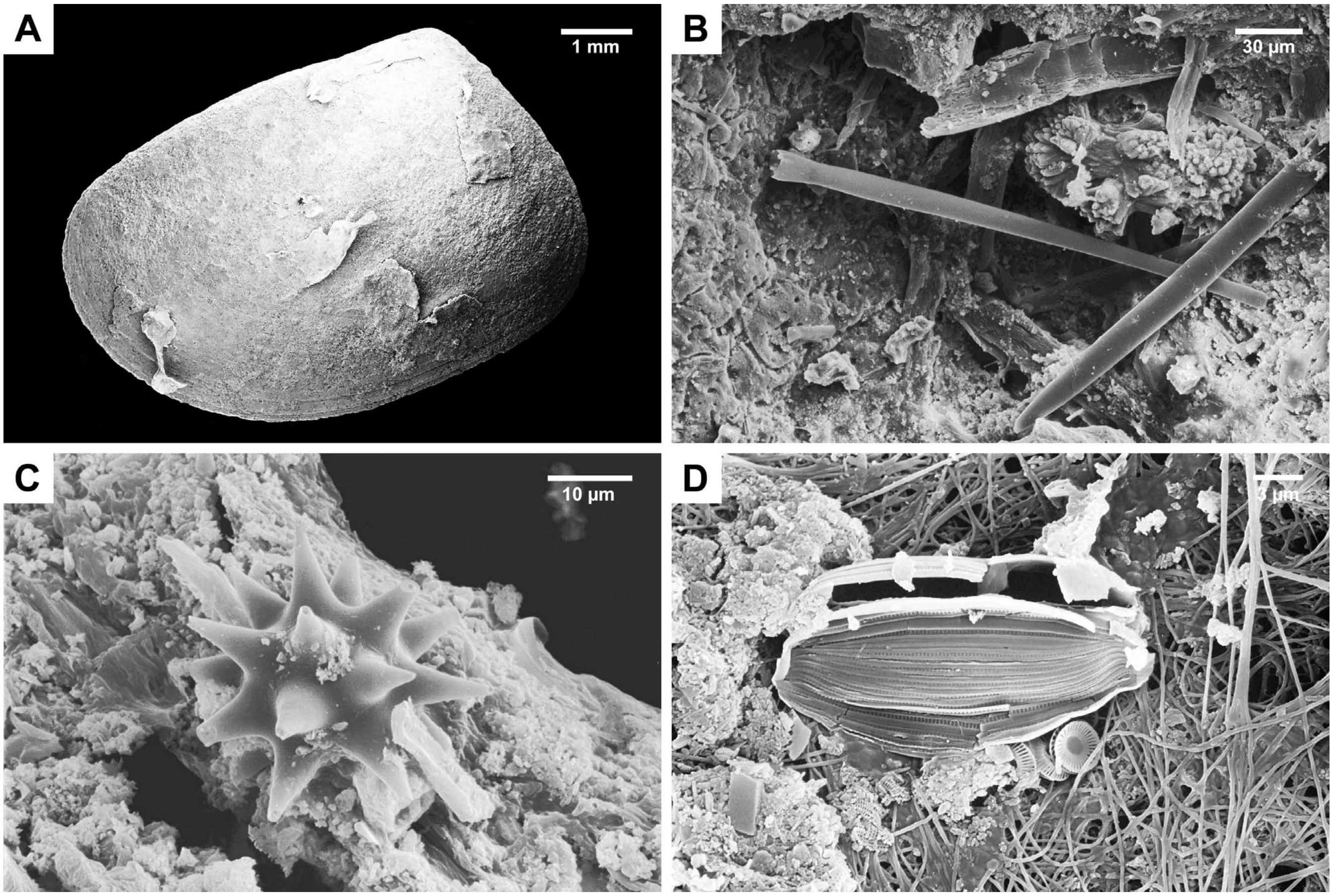

FIGURE 8—Biofilms coating shell surface of *Tellina gouldii* from location L34. A) Overview of shell with encrusting biofilms. B–C) Sponge spicules in biofilms, including monaxones (B) and sphaerasters (C). D) Diatoms, coccoliths, and fungal hyphae in a biofilm.

Reef, and 0.46 m·ka^{-1} on Glovers Reef (Gischler, 2003). Surface samples taken on the Belizean atolls reached 15 cm into the sediment and therefore we calculate average time spans of 326 years on Glovers Reef, 283 years on Lighthouse Reef, and 183 years on Turneffe Islands, based on sedimentation rates. Therefore, shells in Glovers Reef lagoon have a longer residence time on the sediment surface and longer serve as substratum for *Cliona* than those on Lighthouse Reef and Turneffe Islands. On Glovers Reef, a comparable trend is visible from the restricted, deep lagoon toward the marginal zones, which are more exposed to waves and currents. With increasing water agitation, the sedimentation rate presumably decreases. This again results in longer residence times of shells on the sediment substrate. The same situation is also clearly visible along the reef crests of Glovers Reef and Lighthouse Reef, where many valves show boring traces of *Cliona*.

Encrustations

The increasing numbers of encrusted valves from Turneffe Islands to Lighthouse Reef to Glovers Reef are probably related to decreasing sedimentation rates in the same direction, as discussed above. Longer residence times of bivalve shells on the sediment surface of Glovers Reef and Lighthouse Reef lead to more frequent and persistent colonization of the shells by encrusting organisms, such as foraminifera, coralline red algae, other algae, polychaetes, or bryozoans. On reef crests, sedimentation is minimal and encrustations are therefore very common. With increasing wave and current activity from the deep toward the shallow lagoonal parts of Glovers Reef, less sediment is deposited, and shells on the sediment surface are available for encrustation over a longer period of time.

The distribution of encrusting organisms on Glovers Reef and Lighthouse Reef shells presumably depends on the influence of wave and current activity in the lagoonal zones as well as on the exposure to light. Foraminifera, coralline red algae, and polychaetes preferably colonize shells in shallow lagoonal environments exposed to light, waves, and currents. The reason for this pattern could be higher nutrient input into these zones. Permanent exchange of seawater provides an optimal suspension nutrition for filter-feeding polychaetes and suspension-feeding, permanently attached foraminifera. Autotrophic algae and coralline red algae preferably inhabit shallow water areas because of need for exposure to light. Motile foraminifera, which feed on bacteria, fungi, diatoms, and algae (Lipps, 1975, 1983), also prefer living in this environment probably for both nutrient input and light availability. In contrast, biofilms preferably coat the shells in restricted lagoonal environments. This observation corresponds to results of Perry (1999b), who described the accumulation of micrite envelopes subject to low-energy, organic-rich, vegetation-stabilized environments.

Encrusting foraminifera on bivalve shells reflect the fluctuations in wave and current activity on the atolls as well as in lagoonal environments. This is probably linked to different life habits of the species. *Planorbulina acervalis* and *Cornuspiramia antillarum* live permanently attached to the substrate. Consequently, they are well adapted to high-energy environments like the open, shallow lagoonal zones of Glovers Reef and Lighthouse Reef. *Rosalina* spp. is a motile foraminifer that moves on the substrate with the help of its pseudopodia and temporarily attaches to the substrate by an organic glue (Langer, 1993). It is less able to withstand waves and currents than permanently attached forms and therefore characterizes low-energy environments. *Homotrema rubrum*,

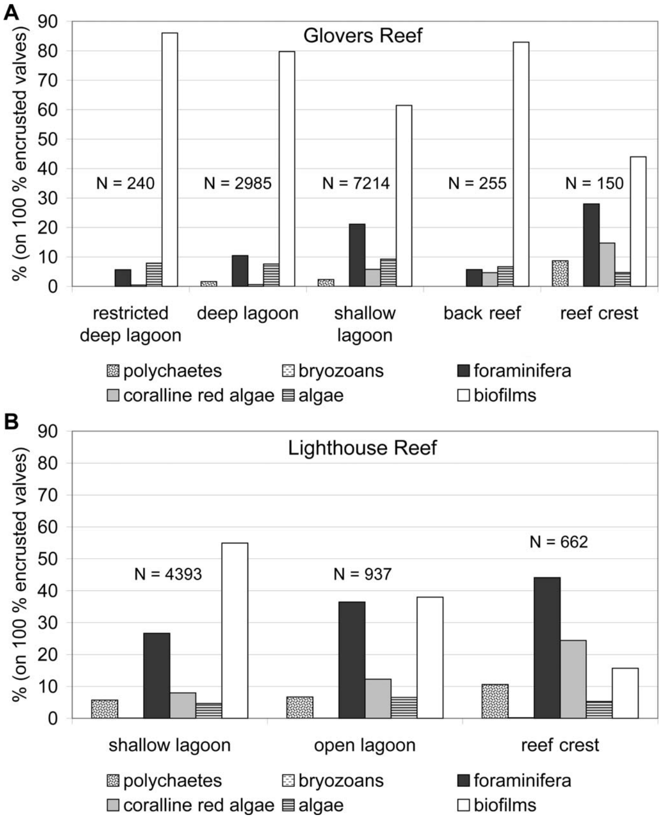

FIGURE 9—Percentages of encrusting organisms on encrusted valves from Glovers Reef (A) and Lighthouse Reef (B). N = number of encrusters. The distribution of encrusters on Turneffe Islands is not shown because their abundance was too low to give any significant information.

found along the reef crests of Glovers Reef and Lighthouse Reef, is a typical species of zones highly exposed to waves and currents (Gischler et al., 2003). The bivalve shells deposited along the reef crest of Lighthouse Reef represent a transported dead assemblage (Hauser et al., 2007), probably encrusted by foraminifera derived from the fore-reef area.

Fragmentation

Fragmented valves may function as indicators of wave and current activity in the atoll lagoons. The present study takes into consideration the fact that thin-shelled bivalve species can break even in low-energy environments, whereas thick-shelled forms can withstand higher wave and current energy. We also considered shell breakage that occurred during rinsing and sieving the samples, even though these procedures were carried out very carefully. Shell-crushing predation—for example, by crabs or fishes—cannot be excluded but is very unlikely because most of the investigated shells are 1–5 mm in size and therefore too small to be suitable for predators. In addition, angular shell fragments, which are indicative of predation (Oji et al., 2003), derive from larger valves, but these were only rarely found.

The increase of shell breakage from Turneffe Islands to Lighthouse Reef to Glovers Reef is probably again connected to the decreasing sedimentation rates in the same direction. Longer residence times on the sediment surface increase the probability of fragmentation due to longer exposure to waves and currents.

On Glovers Reef, increasing fragmentation from the restricted deep lagoon toward the shallow back-reef area can be explained by increasing water agitation toward the atoll margin. The back reef is predominantly inhabited by the thin-shelled bivalves *Tellina similis* and *T. candeana* (Hauser et al., 2007), which may also cause high amounts of broken shells with fragmentation levels 2 and 3. Along the reef crest of Glovers Reef, thick-shelled, epifaunal bivalves (*Barbatia*, *Arcopsis*) are common, and shell breakage is less common as compared to the back reef. In Lighthouse Reef environments, the abundance of broken shells shows only a little variation, possibly related to the uniform influence of waves and currents in the lagoonal zones of this atoll. As a consequence of low water agitation and low abundances of thin-shelled tellinids (<5%), fragmentation level 1 reaches nearly 100% in the lagoonal environments on Turneffe Islands.

Abrasion

The degree of abrasion is yet another useful indicator of wave and current activity, and it is independent from the thickness and stability of the shell. As with fragmentation, we have to consider that artificial abrasion caused by rinsing and sieving may also alter the shell material.

Owing to decreasing sedimentation rates from Turneffe Islands to Lighthouse Reef to Glovers Reef, shell abrasion increases in the same direction. A long residence time on the sediment surface leads to higher levels of shell abrasion caused by sediment relocation or bioturbating organisms. The increase of highly abraded valves from the restricted lagoonal zones of Glovers Reef and Lighthouse Reef toward the open zones exposed to winds and currents is probably combined with an increase of water agitation, thus causing reworking of shells. The back-reef area of Glovers Reef is mainly inhabited by translucent, smooth-shelled tellinids (Hauser et al., 2007), on which abrasion is only barely observable. Toward the reef crest of this atoll, increasing wave and current activity causes slightly higher abrasion levels in comparison to the back reef. Nevertheless, abrasion along the reef crest is not as high as in the shallow marginal lagoon of Glovers Reef. Low abrasion levels on Turneffe Islands are probably a consequence of the restricted mangrove-rimmed lagoons of this atoll.

Summary of Observed Taphonomic Features

Figure 14 summarizes the effect of the main controlling factors—that is, water depth (combined with exposure to light) and water agitation—on the distribution of taphonomic shell signatures. With decreasing water depths and higher energy levels, we observed an increase in shell size, fragmentation, abrasion, and boring traces of *Cliona*, as well as increased encrustations of the foraminifers *Planorbulina* and *Cornuspiramia* and coralline red algae. In contrast, the abundances of *Rosalina* and encrusting biofilms on the shells decrease toward shallow, more highly agitated water areas. High abundances of small valves in restricted lagoonal environments may be caused by oxygen depletion and salinity fluctuations. Combined with increasing water agitation, longer residence times of the shells on the sediment surface lead to an increase in *Entobia* isp., encrustations, fragmentation, and abrasion.

Previous Studies on Mollusk Taphonomy

When we compare our results with those from previous studies, it becomes obvious that there is a lack of standardized sampling methods and sample treatment. In Table 1, results of other studies dealing with taphonomic signatures on mollusk shells in nearby areas are compared with those of our study. Most studies were done on shells in different ecological settings using different sampling methods than the present study. Many included different sets of taphonomic features, investigated only large shells, or gave no information about shell sizes.

The taphonomy of mollusks from several carbonate reef and lagoon systems of St. Croix and Mona Island in the northeastern Caribbean Sea using nonmetric multidimensional scaling was discussed by Parsons-Hubbard (2005) with regard to paleoenvironmental interpretations of fossil shell material and the stability of paleoenvironments. Twenty-eight samples were taken from the taphonomically active zone of six depositional environments using a diver-operated airlift and collecting only particles >4 mm. Modern shells were compared with those from reef cores

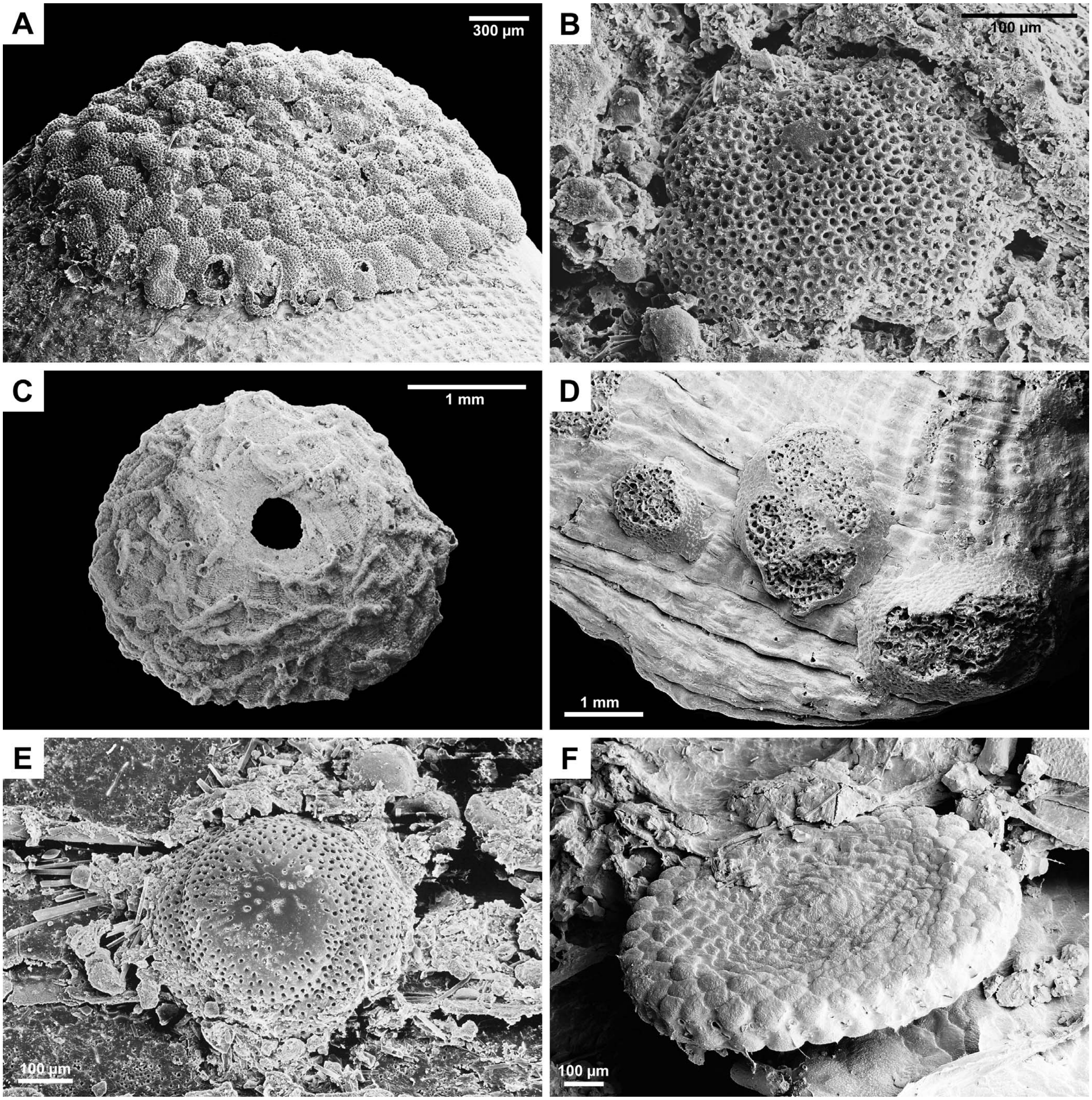

FIGURE 10—Encrusting foraminifera on bivalves. A) *Planorbulina acervalis*. B) *Rosalina* spp. C) *Cornuspiramia antillarum*. D) *Homotrema rubrum*. E) *Cymbaloporetta* spp. F) *Amphisorus hemprichii*.

collected for another study. Parsons-Hubbard (2005) uses a hierarchical approach to place unknown shell samples into their appropriate environment. Highly encrusted shells are assigned to the reef, as were those found on the Belize atolls. Less intensely encrusted shells showing high levels of abrasion were suggested to indicate a beach environment. In our study, highly abraded valves also show intense encrustation caused by long residence times on the sediment surface in areas of agitated water. The remaining samples taken by Parsons-Hubbard (2005) derived from localities based on surface degradation. Microborings, dissolution, and loss of color or luster are indicators of an open shelf. Rhizome etchings can be found only in sea-grass beds, and the presence of periostracum or ligament is indicative of mud environments. Such features have not been observed on Belize shells.

Several studies compared taphonomic signatures on mollusks in different habitats with various water depths on Lee Stocking Island, Bahamas (Callender et al., 2002; Staff et al., 2002; Walker et al., 2002). Samples were taken using two 1-cm-mesh bags attached to a 1.5 m polyvinyl chloride pole. Typically, mesh bags contained five molluscan individuals of five different species. The investigated arrays were relocated and rephotographed after 1 and 2 years, and loose bivalve shells were scattered freely on the sediment surface to measure rates of shell movement and burial. Sampling methods are somewhat different from our study, and the numbers of investigated shells are smaller and shell sizes are bigger. Shells in deep-water sites below the photic zone showed low degrees of discoloration, little edge alteration, and varying degrees of dissolution (Callender et al., 2002). Shells from shallow photic zone sites showed

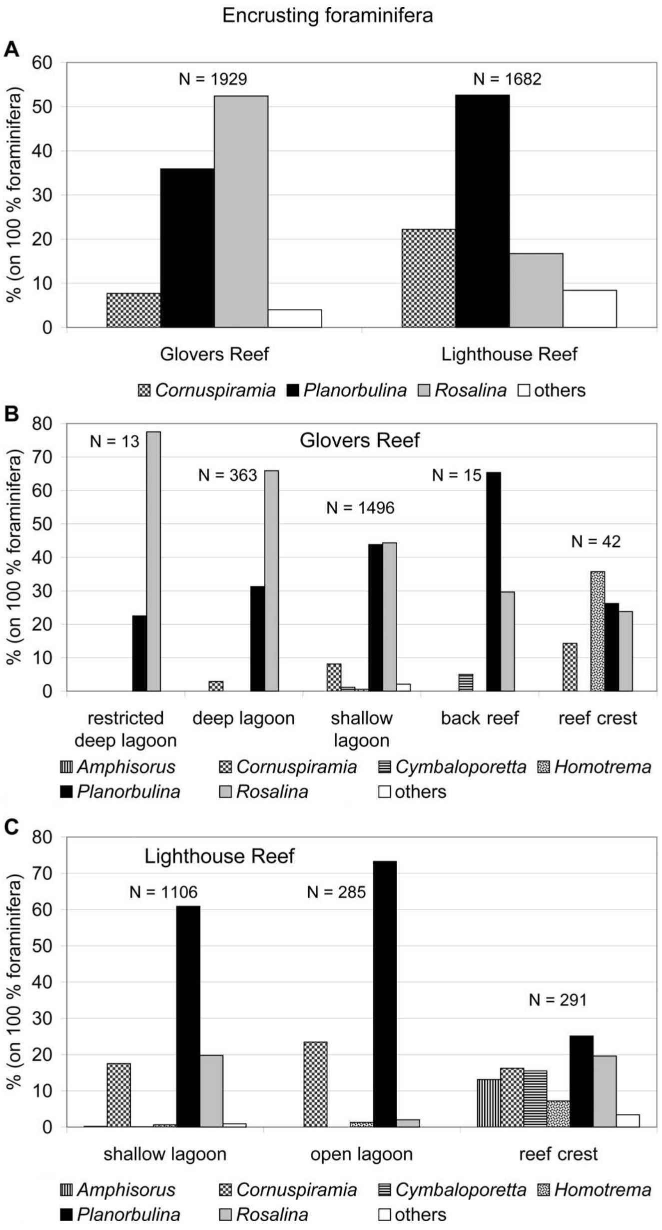

FIGURE 11—Distribution of encrusting foraminifera on shells encrusted by foraminiferans at the two reefs listed. A) Percentages of the most abundant foraminifera. B) Distribution of the most abundant taxa in the lagoonal environments of each atoll. N = number of encrusting foraminifera.

the opposite trend owing to higher energy levels, as was found in our study. Staff et al. (2002) also discussed the influence of time averaging on the levels of taphonomic signatures. The study of Walker et al. (2002) describes higher rates of predation in shallow-water areas than in deep-water areas, which also matches the results of the present study.

Leonard-Pingel (2005) described taphonomic indicators on mollusk shells of fossil sea-grass beds on San Salvador Island (Bahamas), in the Laguna de Términos (Mexico), in the Florida Keys, and along the Florida Gulf Coast. The author investigated bulk samples from *Thalassia* beds and adjacent barren environments taken from the upper 10–20 cm of sediment. In addition to modern environments, two putative fossil sea-grass localities were sampled. Only bioclasts >4 mm of the four most abundant taxa of both bivalves and gastropods were used in the taphonomic analysis. This author suggests that high rates of bioerosion, moderate-to-high rates of dissolution and edge chipping, moderate-to-low rates of edge rounding, and low rates of abrasion are characteristic of

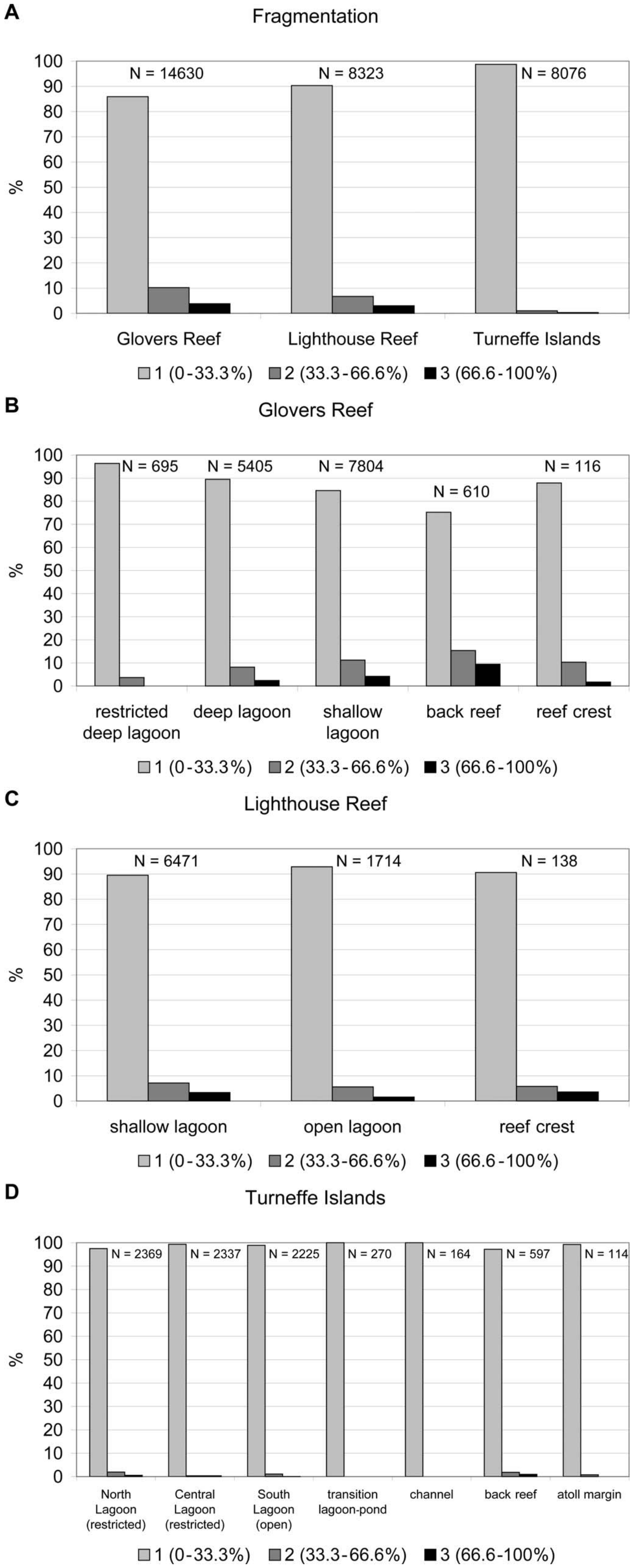

FIGURE 12—Percentages of broken valves with different degrees of fragmentation (A) on all three atolls and (B–D) in the lagoonal environments of each atoll. N = number of investigated valves.

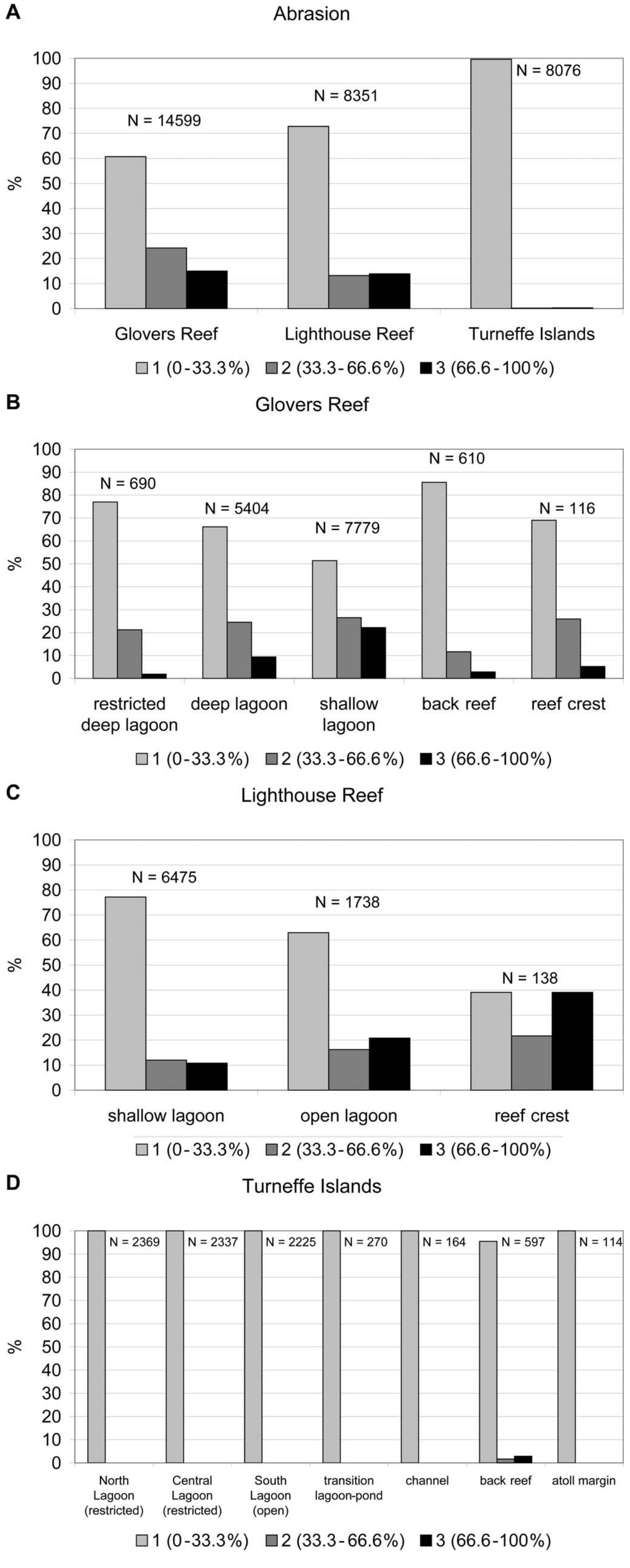

FIGURE 13—Percentages of abraded valves with different degrees of abrasion on (A) all three atolls and (B–D) in the lagoonal environments of each atoll. N = number of investigated valves.

mollusks in fossil sea-grass beds (Leonard-Pingel, 2005). Since the lagoonal Belize samples were not taken in order to compare environments with or without sea-grass growth, the results from Leonard-Pingel (2005) are not directly comparable with ours.

In the Upper Chesapeake Bay (east coast of North America), different types of mollusk shell damage were described as controlled by extrinsic and intrinsic factors in the death assemblage (Lockwood and Work, 2006). The authors collected one to two samples from each of four sampling sites that represented two distinct habitat types differing in salinity, grain size, and water depth. They found infaunal bivalves to be more damaged than epifaunal ones owing to internal, fine-scale surface alteration. Calcitic specimens of epifaunal forms exhibit higher levels of external encrustation than noncalcitic, infaunal shells, as found on bivalves in the atoll lagoons offshore from Belize. Specimens with high levels of shell organics, which were not measured in the shells from Belize atolls, show more fragmentation and edge modification than specimens with low levels of shell organic content.

Aguirre and Farinati (1999) analyzed disarticulation, fragmentation, and abrasion of four bivalve species exhibiting different shell shape, thickness, habitats, and life habits from bulk samples taken along the coast of Buenos Aires Province (Argentina). In contrast to Lockwood and Work (2006), they found infaunal bivalves to be better preserved than epifaunal forms. Infaunal species living in silty sand substrates are less fragmented and abraded than infaunal bivalves living in coarser grained substrates. As in our study, the authors describe breakage and abrasion as direct consequences of reworking more than of transport. They correlate abrasion with the age of the shell and time of exposure on the sediment surface. Disarticulation and abrasion serve as differentiating factors between transported and *in situ* associations. Weak taphonomic signatures are interpreted as indicators of younger shells or a less energetic habitat.

Compared with the above results, the present study shows higher resolution because the Belize atolls exhibit a wide range of habitats situated in relatively small areas, and these were densely sampled. Therefore, our results represent a more clearly developed habitat zonation based on different bivalve assemblages. Furthermore, our data set includes a high number of both individuals and investigated species, in contrast to most of the studies discussed above, which dealt predominantly with a few abundant species from comparatively few sampling localities.

CONCLUSIONS

Taphonomic shell signatures on the Belize atolls were characterized by the following:

1. Slightly higher abundances of small valves in the restricted lagoons of Turneffe Islands may indicate dwarfism due to oxygen depletion and salinity fluctuations.
2. The right-skewed shell-size distribution as well as the nearly 1:1 ratio of right and left valves on Glovers Reef, Lighthouse Reef, and Turneffe Islands are indicators for *in situ* populations on the three atolls.
3. The degree of disarticulation of shells mostly depends on the burrowing depth of the bivalves. Deep burrowing forms are often preserved articulated due to a life position that is protected from waves and currents.
4. Most of the investigated bivalves in this study live infaunally. Therefore, *Oichnus paraboloides*, which is caused by predating infaunal naticids, clearly predominates compared to *O. simplex*, which is produced by epifaunal muricids.
5. Decreasing average sedimentation rates from Turneffe Islands to Lighthouse Reef to Glovers Reef cause longer residence times for bivalve shells on the sediment surface. Increasing water agitation in the lagoonal environments results in the same effect. On the shells, this leads to an increase in *Entobia* isp., encrusting organisms, fragmentation, and abrasion (Fig. 14). The distribution of encrusters also depends on the exposure to light—partly because some are autotrophic and partly because some feed on autotrophic organisms.

TABLE 1—Comparison between this and previous studies on mollusk taphonomy in the Caribbean and other areas. Only those taphonomic features that were investigated in the present study are included (dashes = no information given).

Author	Setting	Sampling method	Shell size	Disarticulation
Parsons-Hubbard, 2005	St. Croix and Mona Island (northeastern Caribbean; carbonate reef and lagoon systems)	diver-operated airlift	>4 mm	—
Callender et al., 2002	Lee Stocking Island (Bahamas; shelf and fore-reef slope)	1 cm mesh bags attached to a 1.5 m PVC pole	>1 cm	—
Staff et al., 2002	Lee Stocking Island (Bahamas; shelf and fore-reef slope)	1 cm mesh bags attached to a 1.5 m PVC pole	>1 cm	—
Walker et al., 2002	Lee Stocking Island (Bahamas; shelf and fore-reef slope)	1 cm mesh bags attached to a 1.5 m PVC pole	>1 cm	—
Leonard-Pingel, 2005	San Salvador Island (Bahamas), Laguna de Términos (Mexico), Florida Keys and Florida Gulf Coast (fossil sea-grass beds)	bulk samples	>4 mm	—
Lockwood and Work, 2006	Upper Chesapeake Bay (North America)	Wildco and hand-operated boxcorers	—	very common
Aguirre and Farinati, 1999	Buenos Aires Province (Argentina; coast)	bulk samples	—	indicator of transport
Hauser et al. (this study)	Glovers Reef, Lighthouse Reef and Turneffe Islands (Belize; atoll lagoons)	grab sampler (6.8 L)	>1 mm; left-skewed shell size distribution indicative of *in situ* populations	indicator of transport, but also dependent on bivalve's burrowing depth; 1:1 ratio of right and left valves indicative of *in situ* populations

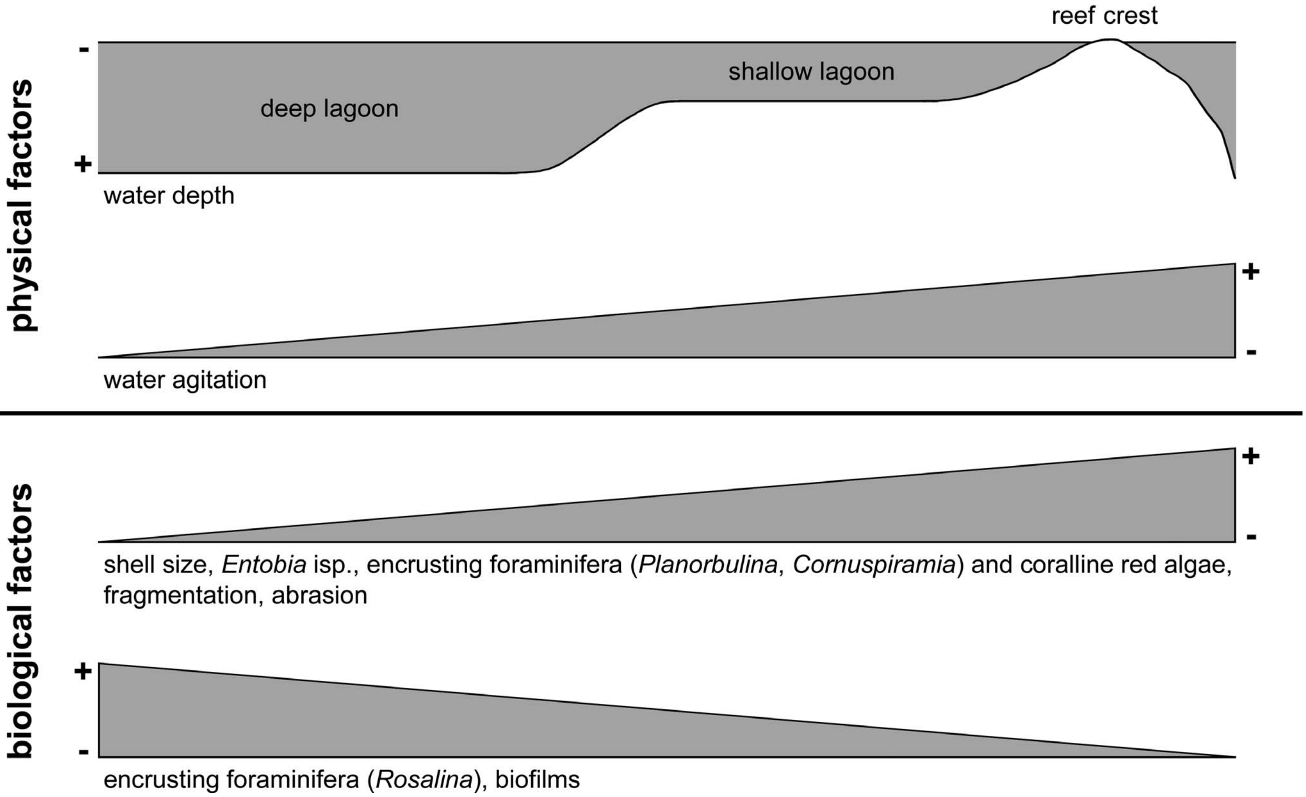

FIGURE 14—Distribution of taphonomic signatures on bivalve shells by environmental factors, such as water depth (combined with the exposure to light) and water agitation.

TABLE 1—Continued.

Author	Borings	Encrustations	Fragmentation	Abrasion
Parsons-Hubbard, 2005	*Cliona* borings in reef environments, rarely bored shells in lagoons	highest encrustation along the reef, indicator of exposure on the sediment surface	highest in beach and reef environments, lowest in sandy lagoons	highest in beach samples, increase from lagoon toward fore reef, indicator of high energy environments
Callender et al., 2002	—	—	chipped edges only	varies significantly and shows no obvious trend
Staff et al., 2002	—	—	chipped edges only	increases in the second year of sampling
Walker et al., 2002	most predation on shells (by crabs, fishes and stomatopods) in shallow shelf depths (≤30 m)	—	—	—
Leonard-Pingel, 2005	—	—	moderate-to-high rates of edge chipping	moderate-to-low rates of abrasion and edge rounding
Lockwood and Work, 2006	—	calcitic specimens with greater external encrustation than non-calcitic ones	high-shell-organic-content specimens show more fragmentation and edge rounding than low-shell-organic-content ones	—
Aguirre and Farinati, 1999	—	—	less on infaunal species living in silty sand than on those living in coarser grained sediments, due to reworking	less on infaunal species living in silty sand than on those living in coarser grained sediments, due to reworking
Hauser et al. (this study)	infaunal bivalves preyed upon by infaunal gastropods causing *Oichnus paraboloides*; abundance of *Entobia* isp. depends on shell's residence time on sediment surface	depends on shell's residence time on sediment surface and on exposure to light; encrusting forams are excellent indicators of wave and current activity	depends on shell's residence time on sediment surface	depends on shell's residence time on sediment surface

6. Encrusting foraminifera serve as excellent indicators of the wave and current activity in lagoonal zones. *Planorbulina acervalis* and *Cornuspiramia antillarum* indicate high energy levels, whereas *Rosalina* spp. characterizes low-energy environments. *Homotrema rubrum* occurs only along the highly exposed reef crests of the atolls.

This study of taphonomic features on bivalve shells supports the results of previous work on modern bivalve shell assemblages (Hauser et al., 2007). Within an atoll, taphonomic patterns reflect environmental zonation defined by distinct assemblages (Fig. 1). A comparison between the atolls, however, provides slightly different results because time averaging has great influence on the distribution of bivalve species and the development of taphonomic shell signatures.

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