The *Journal of Marine Research* is an online peer-reviewed journal that publishes original research on a broad array of topics in physical, biological, and chemical oceanography. In publication since 1937, it is one of the oldest journals in American marine science and occupies a unique niche within the ocean sciences, with a rich tradition and distinguished history as part of the Sears Foundation for Marine Research at Yale University.

Past and current issues are available at [journalofmarineresearch.org](http://journalofmarineresearch.org).

Yale University provides access to these materials for educational and research purposes only. Copyright or other proprietary rights to content contained in this document may be held by individuals or entities other than, or in addition to, Yale University. You are solely responsible for determining the ownership of the copyright, and for obtaining permission for your intended use. Yale University makes no warranty that your distribution, reproduction, or other use of these materials will not infringe the rights of third parties.

This work is licensed under the Creative Commons Attribution-NonCommercial-ShareAlike 4.0 International License. To view a copy of this license, visit [http://creativecommons.org/licenses/by-nc-sa/4.0/](http://creativecommons.org/licenses/by-nc-sa/4.0/) or send a letter to Creative Commons, PO Box 1866, Mountain View, CA 94042, USA.
Holocene reefs and sediments of Castle Harbour, Bermuda

by Stephen Dryer and Alan Logan

ABSTRACT

Quantitative studies on the corals of Holocene fringing, pinnacle and knoll coral-algal reefs of Castle Harbour, Bermuda, show that only about 10% of the available reef substrate is coral-covered. Of this, about 70% of the total coral-covered area is occupied by corals belonging to the *Madracis-Oculina* assemblage.

Three morphologic-ecologic reef types, distinguished by shape, amount of coral cover and coral species present, are recognized: 1) the fringing reefs occurring close to shore, and characterized by the lowest diversity and total coral cover (5%) in Castle Harbour; 2) the northwestern reefs (mostly pinnacle reefs), characterized by the most prolific coral cover (13%) in Castle Harbour; and 3) the southeastern reefs (mostly knoll reefs), exhibiting the greatest diversity in coral species in Castle Harbour, although total coral cover is only 8%. Coral distribution, both horizontally and vertically, is controlled by several factors, mainly energy conditions, substrate inclination and exposure to sedimentation. Five major habitats for coral colonization are recognized: 1) horizontal surfaces, 2) vertical surfaces; 3) bottom wall; 4) cavity and crevice; 5) off-reef, and each is characterized by corals of distinctive growth form.

The sediments associated with the reefs are mostly sandy muds or muddy sands with a gradual, but ill-defined, decrease in sediment size with increasing distance from the reefs. *Halimeda* and molluscs make up the major part of the biotic constituents of the sediments.

The homogeneous nature of cores in Castle Harbour suggests that, sedimentologically, this area has left little record of the dredging activities for Kindley Air Field in 1941-43. The larger massive coral species may have been killed by this event, however, while the more adaptable branching species were gradually able to assume predominance. It is tentatively suggested that reduced species diversity and coral coverage in Castle Harbour, compared to North Lagoon

1. Department of Geology, University of New Brunswick, Saint John, N.B., Canada.
patch reefs, may reflect stressful conditions brought about by high turbidity and sedimentation rates since the dredging.

1. Introduction

Biological and sedimentological studies of a quantitative nature on Holocene coral reefs and associated environments are relatively rare, mainly because of the complex nature of coral reef growth, the logistical problems associated with underwater studies and lack of a universally-accepted sampling method applicable to reef developments in different geographic areas (Stoddart, 1971).

The coral-algal reefs and sediments of Castle Harbour, a semi-enclosed body of water at the eastern end of Bermuda (Fig. 1) were chosen for detailed study using quantitative methods. The only biological or sedimentological studies previously published on these reefs are two short-term student projects (Frazier, 1970; Robelen, 1970) of limited scope. The present study allows comparisons to be made with Bermudian open-water lagoonal patch reefs and their sediments (Garrett, Smith, Wilson and Patriquin, 1971; Jordan, 1973) and with the sediments of Harrington Sound (Neumann, 1965), a virtually enclosed body of water south-west of Castle Harbour (Fig. 1). In addition, as Castle Harbour was significantly altered by dredging from 1941-1943 for the construction of U.S. Naval Air Station Bermuda (Kindley Air Field), it is of interest to determine, as far as possible, the effects of this activity on the organisms and sediments in the harbor.

The main objectives of this study were:
1. To determine the abundance, diversity, geographic and bathymetric distribution of the main reef-building coral species on both the fringing and patch reefs of Castle Harbour.
2. To determine any textural and compositional trends which might exist for the sediments of the harbor.
3. To determine, as far as possible, the effects of the dredging on the corals and sediments.

2. Study area

The Bermuda Islands lie about 1000 km ESE of Cape Hatteras at approximately 32°20'N and 64°40'W. Their physiography and geology have been well described by several authors, such as Land, Mackenzie and Gould (1967) and Stanley and Swift (1967, 1968), while the general disposition of reefs and sediments across the Bermuda Platform has been outlined by Upchurch (1970). More recently a comprehensive review of all aspects of the Bermuda marine environment studied so far by various authors has been compiled by Morris et al. (1977).

The marine fauna and flora of Bermuda are unquestionably Caribbean in aspect, but greatly reduced in diversity, only 22 of the 72 coral species recorded by Goreau and Wells (1967) from Jamaica, for instance, being found in Bermuda. Many of
the reef organisms, particularly the corals, are probably close to minimum tolerance level water temperatures during the winter, and this may account for the absence of the genus Acropora from this region, as well as other distinctive Caribbean coral species.

The Bermuda Islands enclose or partially enclose three large bodies of water: Great Sound, Harrington Sound, and Castle Harbour. Of these, Harrington Sound is the smallest and most land-locked, having direct communication to North Lagoon only through a narrow inlet. Great Sound is the largest and least enclosed and communicates with North Lagoon through its large northeastern opening, while Castle Harbour is somewhat intermediate in position, both in size and circulation. Communication with North Lagoon is mainly through a narrow unnamed passage in the northwest, while a wider opening in the southeast between a series of small islands offers access to the open ocean east-southeast of Bermuda.

Castle Harbour, the study area, is roughly oval in shape, with its long axis (4.8km) trending approximately west-northwest-east-southeast. It has an overall area of about 10.5km², an average depth of about 8.2m and an average tidal range of 1 meter (Morris et al., 1977).

Gees and Medioli (1970) conclude from their seismic survey that Castle Harbour is of volcanic origin, as previously suggested by Land et al. (1967), while other workers suggest that Castle Harbour originated as a series of solution sinks (Agassiz, 1895; Bigelow, 1905; Bretz, 1960). According to the survey of Gees and Medioli, the depth of the basaltic basement ranges from 30m below mean sea level at the harbor edge to about 90m near its center. The shallow and irregular nature of the sub-bottom suggests that this could be the remnant of an ancient caldera. Sediments resting on this basement are lens-shaped, with the greatest thickness in the center (60m), tapering off to approximately 30m at the edges. The reefs appear to be resting on an ancient peneplain of post-Walsingham age Pleistocene marine limestones and aeolianites and surrounded by unconsolidated sediment aprons.

**a. Pre-dredging conditions.** Castle Harbour was dredged along its northern perimeter from 1941-1943 to provide fill for Kindley Air Field, resulting in almost continuous land area from Longbird Island to Cooper’s Island (Fig. 1). This dredging altered the physical and perhaps the biological character of Castle Harbour, the latter aspect being rather difficult to assess because no detailed qualitative or quantitative studies of either reefs or sediments were made prior to the dredging. However, it is of interest to determine the physical changes brought about by the dredging, as they must have affected the hydrography of the harbor. Comments of early naturalists are also included, as they are the only indications of pre-dredging biological conditions in Castle Harbour.

**Hydrography.** Although almost completely surrounded by land, Castle Harbour, until the dredging, maintained free communication on three sides with the ocean;
thus protection was provided from storm waves without loss of water circulation. The eastern opening was protected by the land forming Castle Point and Castle, Southampton, Nonsuch and Cooper’s Islands (Heilprin, 1889). The scouring action
of the tides and the influx of fresh sea water made conditions in the deep channels between the islands favorable for benthic organisms, according to Bigelow (1905).

In the north the channels known as "The Reaches" gave access to either St. George's Harbour or Ferry Reach, but because of abundant coral growth and heavy silting, were not useful for navigation (Heilprin, 1889). The accumulation of silt may indicate that this passage was of secondary importance in the overall circulation pattern.

The opening to Ferry Reach, south of Longbird Island, provided an opening to North Lagoon. Judging by the shallow depth along the present causeway, major water flow may have been restricted to a single passage immediately south of Longbird Island. This passage now accounts for almost all communication between Ferry Reach and Castle Harbour, having been artificially deepened during and after the dredging (Fig. 4, top).

While it is not proven, it seems logical to assume that the eastern end of Castle Harbour was of primary importance in water exchange. Bigelow (1905) mentions that tidal currents in this area moved in both directions. The northern and western passages were probably of secondary importance during periods of stormy weather. Todd (1939) found that the sediments in Castle Harbour were coarser than those in any of the other Bermudian inner lagoons and attributed this fact to its free circulation but protected position.

**Comments of early naturalists.** Castle Harbour was a favorite collecting ground for naturalists who visited Bermuda and it is informative to summarize some of their comments, as they are the only published records of conditions before the dredging. Verrill (1902), for instance, remarked on the clarity of the waters of the harbor and the presence of numerous living brain corals in shallow water near the Causeway, while both Heilprin (1888, 1889) and Agassiz (1895) referred to the abundance of very large living colonies of *Diploria*.

**b. Post-dredging conditions.** The onset of World War II resulted in an agreement between the United States and Britain giving the United States an armed forces base on Bermuda. To the 1.7 square kilometers of land which included a portion of St. David's Island, all of Cooper's Island, Longbird Island, and scattered small islands, a further 3 square kilometers was added by dredging fill from Castle Harbour. Large suction dredges broke up the bottom and pumped the material (rock and sediments) to shore through pipes floated on pontoons. An estimated 12-15 million cubic meters of substrate were removed in this manner from 1941-1943 (Block, 1969).

The geographic changes resulting from the dredging can be seen by comparing the two maps of Castle Harbour shown in Figure 1.

**Hydrography.** When the dredging was completed, there was continuous land be-
between Longbird Island and Cooper’s Island, with a long runway extending southward nearly a kilometer into Castle Harbour. Castle Harbour was reduced in size by about one fifth (Morris et al., 1977). Water circulation was virtually restricted to the passageway immediately south of Longbird Island and, in the southeast, to the openings between the islands. Detailed data on present hydrographic conditions in Castle Harbour are gradually becoming available (Morris et al., 1977) and the following generalities can be made:

i) The water is turbid, with visibility rarely exceeding about 6 meters (pers. observations), although Verrill’s remarks (1902) suggest that Castle Harbour waters were clearer in earlier times. Morris et al. (1977) have recently discussed the factors which affect water clarity and defined the term “extinction coefficient” (k), which

Figure 2. Annual variation in light levels (% of surface illumination) during 1976-77 at A. Castle Harbour; B. Harrington Sound; C. North Lagoon; D. Great Sound (after Morris et al., 1977).
expresses the transparency of oceanic waters. Low values of $k$ indicate greater water transparency, with less light absorption, than high values (although fine-grained suspended material has the ability to scatter light without greatly affecting the measured vertical extinction, according to Holmes, 1957). Their measurements for Bermuda waters show higher values of $k$ in Castle Harbour (0.28) than in Harrington Sound (0.18-0.21) or North Lagoon (0.22-0.24); moreover, light levels, expressed as a percentage of surface illumination, attenuate more rapidly with depth in Castle Harbour (Fig. 2A) than in Harrington Sound (Fig. 2B) or North Lagoon (Fig. 2C), but are comparable with some parts of Great Sound (Fig. 2D). The suspended detritus comprises both particulate inorganic and organic fractions; the inorganic minerals are derived from bottom sediments stirred up by waves and surge and consist of aragonite and calcite (high and low-Mg) of approximately the same composition as the fine fraction of bottom sediments (Chave and Suess, 1967). Standard staining techniques (Friedman, 1959) performed by us on selected samples in the region of the dredging indicate preponderance of aragonite grains in all size fractions, suggesting that calcified green algae, bivalves, gastropods and corals are major contributors to the sediments (see later data on sediment biotic composition).
Chave (1962) likewise found greater percentages of aragonite than calcite in almost all size fractions he examined from Castle Harbour sediments. The fine fraction (<62µ), which might be expected to be easily re-suspended, is made up primarily of 25-50µ faceted aragonite chips, probably produced by sponge boring (Futterer, 1974), together with <5µ aragonite needles, presumably derived from the breakdown of calcified green algae. Low-Mg calcite, typical of local Pleistocene limestones, is more common than high-Mg calcite in lagoonal samples and less common in near-reef areas (Chave, 1962), suggesting that if dredging is the cause of the siltiness, the break-up of the limestone floor of Castle Harbour may have contributed directly to the fines. Halimeda and coralline algae increase the proportion of high-Mg calcite in near-reef areas.

The particulate organic fraction is mainly of dead material and Morris et al. (1977) have mapped the distribution of suspended solids and their percentage organic composition in Castle Harbour (Figs. 3A, 3B). Highest concentrations of suspended solids occur in the northern dredged area, in the vicinity of the runway extending into the harbor. While theoretical calculations of tidal flushing times for Castle Harbour by Morris et al. (1977), under simple mixing conditions, range from 12-117 days, it is clear that either the reduced circulation caused by the landfill is allowing finer material to accumulate than previously or, more likely, the large amounts of sediments churned up by the dredging result in almost continuous re-suspension of the fines, producing turbidity of Castle Harbour waters.

ii) One other possible source of some of the fine material is the washings from the Government Quarry, on the south side of Castle Harbour, where crushed limestone is produced for building purposes. However, due to the localized nature of this operation (10m³ of flow/day, according to Morris et al., 1977), it is not believed that this silt travels more than a few meters into the harbor or significantly contributes to the turbidity.

iii) There is a vigorous flow of water (estimated maximum velocity of 0.3-1.0 knots, according to Morris et al., 1977) through the passage south of Longbird Island at both the ebb and the flow of the tide. The waters of reefs close to the shore along the Longbird Causeway are amongst the clearest in Castle Harbour, probably due to their proximity to this passage.

iv) Mackenzie, Kulm, Cooley and Barnhart (1965) demonstrated that there is only limited transport of sand-size particles into Castle Harbour from the reefs outside the southeastern entrance. The percentage of tests of Homotrema rubrum, a distinctive pink sessile foraminifer living on the outer reefs, but not in Castle Harbour, decreased rapidly in the sediments of Castle Harbour. Thus there undoubtedly is some transport of sediments into the harbor, probably on the flood tide, but the current energy may not be high enough to move it very far (estimated maximum velocity of 0.4-0.6 knots, almost symmetrical on ebb and flow, according to Morris et al., 1977).
Bathymetry. Most parts of Castle Harbour are less than 10 meters deep. Notable exceptions are the regions where dredging was most active; here depths of more than 10 meters are recorded (Fig. 1). These areas form a narrow zone following the northwestern shoreline from the Longbird passage to just past the tip of the jutting runway. An isolated dredged region is situated in the northeastern part of Castle Harbour. Just east of Walsingham Bay is another area of deeper water, with a maximum depth of 15.5m (Morris et al., 1977), but it is likely that most of this area is not a product of the dredging because, in general, the slope into the depression here is gradual compared to the sharply defined drop-offs in the northern dredged areas. Also, isolated soundings in this area on early maps of Bermuda show depths in excess of 10m.

c. Castle Harbour Reefs. Castle Harbour contains numerous offshore coral-algal patch reefs (Fig. 4, bottom) and a conspicuous inshore fringing reef system extending more or less continuously along the western and southern shorelines of the harbor (Fig. 4, top). The greatest density of off-shore reefs is found toward the center of the harbor, but for the most part distribution appears to be random. The dredging very likely removed many reefs from the northern portion and at the same time essentially made inshore reefs of some that had previously been some distance from land.

The off-shore patch reefs may be divided into two morphologic types: pinnacle and knoll.

Pinnacle reefs are usually about 4-5 meters high and approximately the same distance in diameter, roughly circular in outline, and often with vertical or steep-sided walls. The tops are in shallow water of 1-2m and show irregular relief, the topographic highs often formed from dead heads of large Diploria colonies. Large sand pockets or sand channels are rare. A well-marked notch indented 1-2m is usually present at the base of the pinnacle reef.

Knoll reefs are only about 1-2m high (and their tops are therefore deeper than the pinnacle reefs) but may be up to 10-15m wide. They show considerable variation in morphology; in addition, they are irregular in outline and lack conspicuous vertical walls.

The fringing reefs occur in shallow water approximately 1-1.5m deep and are found close to shore. The outer edge is a somewhat elevated rim, the area shorewards of the rim being almost flat. In aerial photographs they are characterized by a rather distinctive lobation of the seaward edge (Fig. 4, top).

Both fringing and patch reefs are probably constructional throughout, rather than coral veneers over aeolianite topographic highs. Frazier (1970) examined two Castle Harbour pinnacle reefs dissected by dynamite and found that all material observed was of reefal origin, most of it comprising large Diploria. The pinnacle form may be caused by upward growth of corals and calcareous algae to satisfy
Figure 4. (top). Aerial view of fringing reefs from Causeway to Government Quarry. Note sharply-defined dredged areas south of Longbird Island; (bottom). Aerial view of offshore pinnacle reefs east of Tucker’s Town Bay (photographs by P. Garrett).
light requirements as sea level gradually rose during the Holocene transgression, as previously suggested for Bermuda's North Lagoon patch reefs by Wilson (1969). The fringing reefs may have responded to these conditions by upward and shoreward growth as land areas were gradually flooded.

3. Methods

The corals living on Castle Harbour reefs were sampled quantitatively by a continuous quadrat method using a transect line of "rope ladder" type, the "rungs" being one meter apart and 30cm wide. The transect line was run randomly from the top of the reef to its base, along a straight line; one or more transects were taken per reef. The position of a coral colony within the transect line was noted and its length and width recorded from which its surface area could be obtained. From this procedure, the following parameters could later be calculated:

1. Percentage of reef surface covered by all corals (% total coral cover).
2. Percentage of total coral cover occupied by each coral species (% individual coral cover).
3. Percentage of depth interval occupied by each coral species.

The Shannon-Weaver Diversity Index was used in this study (Pielou, 1966; Loya, 1972; Porter, 1972), since it is a measure which takes into account the number of species present and their relative abundance.

Sediment samples were taken at 5m intervals along transects on the flanks of reefs, beginning at the base of the reef and continuing into the off-reef areas of the Castle Harbour inner lagoon.

Core samples of sediments were taken about 25-40 meters from the reefs in lagoonal areas, using a hand-held corer capable of obtaining a core up to one meter in length. Areas of obvious bioturbation were avoided in the coring program. The cores were later divided into 5cm sections for subsequent examination. All sediment samples were treated by standard sedimentological methods, such as those adopted by Neumann (1965) and MacIntyre (1967). The biotic composition of the grains was determined by reflected light, using 300-grain counts of the 2-4mm size fraction, and in most samples unknowns comprised less than 5%, testifying to the suitability of this method for Bermuda sediments. The grains were divided into eight categories: Halimeda spp., molluscs, Homotrema rubrum, corals, coralline algae, foraminifera (other than H. rubrum), others (such as echinoids, serpulids, bryozoans, etc.) and unknowns.

4. Results and discussion

a. Patterns of coral distribution. Data obtained from 36 continuous quadrat coral transects on Castle Harbour reefs, representing a total areal coverage of over 80m², showed a mean percentage total coral cover of approximately 10% for all available
Table 1. Quantitative data on coral coverage and importance rank, morphologic-ecologic divisions of Castle Harbour reefs (averaged for all depths).

<table>
<thead>
<tr>
<th>Coral Species</th>
<th>Fringing reefs, (B1-8)</th>
<th>NW reefs, (B9-13,15,16)</th>
<th>SE reefs, (B14,17-28)</th>
<th>All reefs, (B1-28)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>% Coral Cover</td>
<td>% Coral Indiv.</td>
<td>Rank</td>
<td>% Coral Cover</td>
</tr>
<tr>
<td>Isophyllia spp.</td>
<td>0.49</td>
<td>8.97</td>
<td>5</td>
<td>0.64</td>
</tr>
<tr>
<td>Oculina diffusa</td>
<td>1.18</td>
<td>21.61</td>
<td>1</td>
<td>2.44</td>
</tr>
<tr>
<td>Madracis mirabilis</td>
<td>0.94</td>
<td>17.22</td>
<td>3</td>
<td>6.68</td>
</tr>
<tr>
<td>M. decactis</td>
<td>1.17</td>
<td>21.43</td>
<td>2</td>
<td>0.85</td>
</tr>
<tr>
<td>Porites astreoides</td>
<td>0.20</td>
<td>3.66</td>
<td>8</td>
<td>0.34</td>
</tr>
<tr>
<td>Agaricia frigilis</td>
<td>0.59</td>
<td>10.81</td>
<td>4</td>
<td>0.68</td>
</tr>
<tr>
<td>Siderastrea radians</td>
<td>0.25</td>
<td>4.58</td>
<td>7</td>
<td>0.01</td>
</tr>
<tr>
<td>Faviafragum</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>0.01</td>
</tr>
<tr>
<td>Diploria labyrinthiformis</td>
<td>0.40</td>
<td>7.33</td>
<td>6</td>
<td>0.28</td>
</tr>
<tr>
<td>D. strigosa</td>
<td>0.07</td>
<td>1.28</td>
<td>10</td>
<td>—</td>
</tr>
<tr>
<td>Montastrea cavernosa</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>M. annularis</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Dicchoenia stokesi</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Stephanocoenia michelini</td>
<td>0.17</td>
<td>3.11</td>
<td>9</td>
<td>0.03</td>
</tr>
<tr>
<td>Porites porites</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>0.44</td>
</tr>
<tr>
<td>Siderastrea siderea</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>0.002</td>
</tr>
<tr>
<td>Millepora alcicornis</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>0.64</td>
</tr>
<tr>
<td>Meandrina meandrites</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Totals</td>
<td>5.46</td>
<td>100</td>
<td>13.04</td>
<td>100</td>
</tr>
</tbody>
</table>
Table 2. Percentage coral cover/m² of most abundant coral species on fringing reefs (#1-8) over discrete depth intervals, with representative area surveyed per depth interval. Shannon-Weaver Diversity Index $H'$ (base $e$) = 0.6932 $H'$ (base 2).

<table>
<thead>
<tr>
<th>Depth (m)</th>
<th>0.5-</th>
<th>1.0-</th>
<th>1.5-</th>
<th>2.0-</th>
<th>2.5-</th>
<th>3.0-</th>
<th>3.5-</th>
<th>4.0-</th>
<th>4.5-</th>
<th>5.0-</th>
<th>5.5-</th>
<th>6.0-</th>
<th>6.5-</th>
<th>7.0-</th>
<th>7.5-</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>M. mirabilis</td>
<td>0.21</td>
<td>0.21</td>
<td>0.01</td>
<td>3.54</td>
<td>6.06</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>M. decactis</td>
<td>0.01</td>
<td>0.25</td>
<td>1.00</td>
<td>1.46</td>
<td>22.58</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Isophyllia spp.</td>
<td>0.18</td>
<td>1.27</td>
<td>0.72</td>
<td>0.83</td>
<td>0.03</td>
<td>0.50</td>
<td>0.28</td>
<td>2.93</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A. fragilis</td>
<td>0.22</td>
<td>1.75</td>
<td>1.48</td>
<td>5.01</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>P. astreoides</td>
<td>2.78</td>
<td>0.66</td>
<td>0.10</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>D. labyrinthiformis</td>
<td>1.25</td>
<td>3.34</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Others (11 species)</td>
<td>0.00</td>
<td>0.03</td>
<td>0.51</td>
<td>0.05</td>
<td>0.32</td>
<td>0.64</td>
<td>0.26</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>11.33</td>
</tr>
<tr>
<td>Total/m²</td>
<td>4.21</td>
<td>5.52</td>
<td>1.66</td>
<td>2.54</td>
<td>7.97</td>
<td>5.06</td>
<td>1.76</td>
<td>9.00</td>
<td>27.87</td>
<td>2.93</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Representative area surveyed (m²)</td>
<td>2.00</td>
<td>5.00</td>
<td>7.00</td>
<td>7.00</td>
<td>7.06</td>
<td>6.28</td>
<td>4.38</td>
<td>2.72</td>
<td>2.00</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
<td></td>
</tr>
<tr>
<td>$H'$ (base $e$)</td>
<td>0.77</td>
<td>1.06</td>
<td>1.47</td>
<td>0.70</td>
<td>1.02</td>
<td>0.84</td>
<td>0.96</td>
<td>0.86</td>
<td>0.53</td>
<td>0.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Shannon-Weaver Diversity Index $H'$ (base $e$) = 0.6932 $H'$ (base 2).
Table 3. Percentage coral cover/m² of most abundant coral species on northwestern patch reefs (#9-13,15,16) over discrete depth intervals, with representative area surveyed per depth interval. Shannon-Weaver Diversity Index $H'$ (base $e$) = 0.6932 $H'$ (base 2).

<table>
<thead>
<tr>
<th>Depth (m)</th>
<th>0.5-</th>
<th>1.0-</th>
<th>1.5-</th>
<th>2.0-</th>
<th>2.5-</th>
<th>3.0-</th>
<th>3.5-</th>
<th>4.0-</th>
<th>4.5-</th>
<th>5.0-</th>
<th>5.5-</th>
<th>6.0-</th>
<th>6.5-</th>
<th>7.0-</th>
<th>7.5-</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>O. diffusa</td>
<td>0.10</td>
<td>0.38</td>
<td>0.82</td>
<td>0.61</td>
<td>0.24</td>
<td>8.33</td>
<td>2.79</td>
<td>0.59</td>
<td>1.62</td>
<td>3.51</td>
<td>7.89</td>
<td>5.03</td>
<td>4.35</td>
<td>4.00</td>
<td></td>
</tr>
<tr>
<td>M. mirabilis</td>
<td>0.37</td>
<td>4.86</td>
<td>5.21</td>
<td>14.13</td>
<td>23.32</td>
<td>6.36</td>
<td>2.68</td>
<td>4.31</td>
<td>2.92</td>
<td>9.78</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>M. decactis</td>
<td>0.20</td>
<td>0.02</td>
<td>0.91</td>
<td></td>
<td></td>
<td>0.61</td>
<td>4.80</td>
<td>1.88</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Isophyllia spp.</td>
<td>2.97</td>
<td>2.76</td>
<td>0.55</td>
<td>0.26</td>
<td>0.25</td>
<td>0.03</td>
<td>0.41</td>
<td>0.47</td>
<td>0.34</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A. fragilis</td>
<td>0.06</td>
<td>1.32</td>
<td>0.84</td>
<td>3.02</td>
<td>0.97</td>
<td>0.12</td>
<td>0.13</td>
<td>0.75</td>
<td>0.09</td>
<td>0.06</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>P. astreoides</td>
<td>0.46</td>
<td>1.07</td>
<td>0.84</td>
<td>0.46</td>
<td>1.08</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>D. labyrinthiformis</td>
<td>0.29</td>
<td>0.19</td>
<td></td>
<td>0.33</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>2.82</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Others (11 species)</td>
<td>0.60</td>
<td>5.17</td>
<td>0.13</td>
<td>0.03</td>
<td>6.95</td>
<td>0.00</td>
<td>0.00</td>
<td>0.02</td>
<td>0.07</td>
<td>0.00</td>
<td>0.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total/m²</td>
<td>4.70</td>
<td>14.61</td>
<td>9.97</td>
<td>16.33</td>
<td>34.86</td>
<td>16.63</td>
<td>10.80</td>
<td>7.40</td>
<td>5.73</td>
<td>16.20</td>
<td>8.11</td>
<td>5.03</td>
<td>4.35</td>
<td>4.00</td>
<td></td>
</tr>
<tr>
<td>Representative area surveyed (m²)</td>
<td>6.00</td>
<td>8.04</td>
<td>9.00</td>
<td>9.00</td>
<td>9.00</td>
<td>9.20</td>
<td>10.00</td>
<td>10.00</td>
<td>9.06</td>
<td>7.10</td>
<td>5.60</td>
<td>2.30</td>
<td>2.00</td>
<td>1.00</td>
<td></td>
</tr>
<tr>
<td>$H'$ (base $e$)</td>
<td>1.24</td>
<td>1.46</td>
<td>1.53</td>
<td>0.58</td>
<td>0.98</td>
<td>1.09</td>
<td>1.23</td>
<td>1.12</td>
<td>1.21</td>
<td>0.97</td>
<td>0.15</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td></td>
</tr>
</tbody>
</table>
Table 4. Percentage coral cover/m² of most abundant coral species on southeastern patch reefs (#14,17-28) over discrete depth intervals, with representative area surveyed per depth interval. Shannon-Weaver Diversity Index $H'$ (base e) = 0.6932 $H'$ (base 2).

<table>
<thead>
<tr>
<th>Depth (m)</th>
<th>0.5-</th>
<th>1.0-</th>
<th>1.5-</th>
<th>2.0-</th>
<th>2.5-</th>
<th>3.0-</th>
<th>3.5-</th>
<th>4.0-</th>
<th>4.5-</th>
<th>5.0-</th>
<th>5.5-</th>
<th>6.0-</th>
<th>6.5-</th>
<th>7.0-</th>
<th>7.5-</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>O. diffusa</td>
<td>0.63</td>
<td>1.67</td>
<td>0.79</td>
<td>0.23</td>
<td>0.95</td>
<td>1.74</td>
<td>1.34</td>
<td>3.31</td>
<td>3.37</td>
<td>6.90</td>
<td>2.48</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>M. mirabilis</td>
<td>0.60</td>
<td>0.64</td>
<td>0.95</td>
<td>0.37</td>
<td>1.02</td>
<td>3.89</td>
<td>0.07</td>
<td>0.27</td>
<td>0.12</td>
<td>0.24</td>
<td>0.23</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>M. decactis</td>
<td>0.17</td>
<td>3.25</td>
<td>0.20</td>
<td>0.40</td>
<td>2.20</td>
<td>1.60</td>
<td>0.22</td>
<td>3.03</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Isophyllia spp.</td>
<td>4.56</td>
<td>1.25</td>
<td>2.51</td>
<td>1.80</td>
<td>0.82</td>
<td>1.16</td>
<td>0.34</td>
<td>0.51</td>
<td>1.42</td>
<td>0.21</td>
<td>1.06</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A. fragilis</td>
<td>0.59</td>
<td>0.10</td>
<td>0.95</td>
<td>0.20</td>
<td>0.31</td>
<td>0.02</td>
<td>0.91</td>
<td>0.44</td>
<td>0.06</td>
<td>0.17</td>
<td>0.34</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>P. astreoides</td>
<td>1.45</td>
<td>0.86</td>
<td>0.32</td>
<td>0.33</td>
<td>0.72</td>
<td>0.49</td>
<td>0.05</td>
<td>0.09</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>D. labyrinthiformis</td>
<td></td>
<td>0.06</td>
<td>1.04</td>
<td></td>
<td></td>
<td>0.46</td>
<td>0.12</td>
<td>0.10</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Others</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(11 species)</td>
<td>0.00</td>
<td>0.42</td>
<td>0.36</td>
<td>0.22</td>
<td>0.21</td>
<td>0.30</td>
<td>2.55</td>
<td>1.01</td>
<td>0.06</td>
<td>0.52</td>
<td>1.16</td>
<td>6.43</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total/m²</td>
<td>7.24</td>
<td>5.43</td>
<td>5.20</td>
<td>7.33</td>
<td>5.27</td>
<td>8.00</td>
<td>7.92</td>
<td>7.35</td>
<td>5.47</td>
<td>11.07</td>
<td>5.27</td>
<td>12.60</td>
<td>94.29</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Represented area surveyed (m²)</td>
<td>2.00</td>
<td>3.00</td>
<td>5.00</td>
<td>11.00</td>
<td>12.02</td>
<td>15.00</td>
<td>15.18</td>
<td>14.34</td>
<td>14.00</td>
<td>10.20</td>
<td>5.92</td>
<td>2.00</td>
<td>1.00</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$H'$ (base e)</td>
<td>1.03</td>
<td>1.68</td>
<td>1.53</td>
<td>1.56</td>
<td>1.98</td>
<td>1.46</td>
<td>1.91</td>
<td>1.74</td>
<td>1.12</td>
<td>1.02</td>
<td>1.48</td>
<td>0.98</td>
<td>0.00</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
substrates, although values range from less than 2% to over 30%. Thirty-three of the 36 transects indicated total coral cover of less than 17%. Of the corals present, three species contribute about 70% of the total coral cover. These are *Madracis mirabilis* (33%), *Oculina diffusa* (26%) and *Madracis decactis* (12%). This is the *Madracis-Oculina* assemblage of Garrett et al. (1971).

In terms of numbers of species present, diversity in Castle Harbour is high, but using a diversity index taking into account both species present and their abundance (such as the Shannon-Weaver Diversity Index), Castle Harbour yields low values when compared to other regions on the Bermuda Platform, particularly North Lagoon patch reefs (Settgas, *unpubl. report*, 1974).

As previously mentioned, both inshore fringing reefs and offshore patch reefs (comprising pinnacles and knolls) are present in Castle Harbour and were so recognized by Frazier (1970). It is possible, however, to subdivide the patch reefs on morphological grounds into two geographic groups:

a) Northwestern patch reefs, mostly of the pinnacle type.

b) Southeastern patch reefs, variable in morphology but mostly knoll reefs.

These essentially morphologic distinctions between fringing reefs, northwestern patch reefs and southeastern patch reefs are supported by data from the coral transects (Tables 1-4). The fringing reefs are lowest in both diversity and total coral cover, the dominant corals being *Isophyllia* spp., *Porites astreoides* and *Diplopora labyrinthiformis* on the shallow upper surfaces and *Oculina diffusa*, *Madracis decactis*, *Madracis mirabilis* and *Agaricia fragilis* on the deeper protected areas beneath the rim. Corals occupy only about 5% of the overall available reef surface, however. Coral growth seems to have been more prolific at the outer edge of the reefs and consequently a discontinuous rim of massive corals has been built up. This rim is defined by large, but mostly dead coral heads of the genus *Diplopora* (Fig. 5).

The northwestern reefs are characterized by *Madracis mirabilis*, which accounts for over 50% of the total coral cover. In terms of coral growth, these reefs are the most prolific in Castle Harbour, with overall mean values of total coral coverage approximating 13% of the available substrate.

The southeastern reefs exhibit the greatest diversity in coral species, although total coral cover is only 8%, with *Oculina diffusa* the most abundant species present. The Shannon-Weaver Diversity Index was highest in these reefs, maximum values occurring between 2.5 and 4m depth (Table 4). The northwestern reefs have a much lower overall Diversity Index, with a maximum at depths between 1.5 and 2.5m, corresponding approximately to the edge of the reef and the upper part of the steep walls (Table 3). Similarly the fringing reefs have the highest Diversity Index values at depths between 1.5-2.0m, corresponding to the growing edge of the reef (Table 2). Porter (1972) demonstrated a general increase in coral diversity toward the edge of Panamanian reefs, which he termed the “edge effect.” A similar phenomenon has been described in qualitative terms from Jamaican reef terrace edges by Goreau and
Figure 5. Fringing reef west of Tucker's Town Bay at a depth of 2m, dead Diploria heads just below the outer rim (knife handle 15cm long).

Wells (1967) and from the seaward edges of terraces on Grand Cayman Island by Rigby and Roberts (1976). While on a much smaller scale, it seems that the “edge effect” can also be detected in Castle Harbour.

Frazier (1970) maintained that corals on two Castle Harbour pinnacle reefs he examined in detail were not evenly distributed and suggested that certain species characterized vertically-disposed zones, which he called the Isophyllia zone, the Madracis zone and the Oculina zone. His Isophyllia zone represents the upper surface of the reef and is dominated by massive corals, primarily species of Isophyllia and Isophyllastrea (the latter not found by us) and secondarily, by the species Diploria labyrinthiformis and Porites astreoides. The Madracis zone is found on the upper sides of the reefs and is dominated by Madracis decactis, although Oculina diffusa is usually present but subordinate. His Oculina zone forms the lower sides of the reefs and is divided into two sub-zones, the O. diffusa sub-zone and the O. varicosa sub-zone. Species of Madracis are often found in the O. diffusa sub-zone, but are subordinate to the characteristic species. Our coral transect data2 (Tables 2-4) indicate that this simple depth-zone classification of Frazier’s cannot be applied

universally within Castle Harbour, although it is most applicable to some of the northwestern patch reefs (Table 3).

Furthermore, we believe the term “zone” is inappropriate here because it implies controlling factors constituting a vertical environmental gradient. Dana (1976) concluded that the coral distribution in the Holandes Cay lagoon reefs of Panama was in response to habitat differences resulting from variations in conditions of light, water energy and sedimentation, as well as selective larval settlement and differential mortality rates. We agree with Dana and have used the term “habitat” here rather than “zone.”

We have recognized five major habitats of coral growth associated with Castle Harbour reefs (Fig. 6).

**Horizontal Surfaces** (Frazier’s *Isophyllia* zone). The tops of the reefs make up most of the horizontal surfaces, although such surfaces may be present at several levels. They are populated mainly by massive, encrusting or thick-branching forms, since delicate branching forms would be easily broken by surge action. The major coral species are *Isophyllia* spp., *Porites astreoides* and *Diploria labyrinthiformis*, with subsidiary *Porites porites* and *Siderastrea radians*. The deeper horizontal surfaces of the southeastern reefs may support colonies of *Montastrea cavernosa* and *M. annularis*, although these forms are not common. Hubbard and Pocock (1972), on the basis of experiments on sediment-rejection capabilities of corals, have suggested that species of such genera as *Isophyllia*, *Diploria*, *Montastrea*, *Porites* and *Siderastrea* dominate the upper surfaces of patch reefs because of their low growth form and ability to remove coarse sediment particles quickly and efficiently.

**Vertical Surfaces** (Frazier’s *Madracis* zone). These areas are probably the most prolific in Castle Harbour, in terms of coral growth. Between depths of 1.5 and 3.5m, representing most of the steep walls, *Madracis mirabilis* is by far the most dominant species, contributing (for all of the harbor) between 27% and 62% of the total coral coverage, with large areas populated almost entirely by this species. *M. mirabilis* has a branching growth form which presents the least amount of horizontal surface to sedimentation (see later discussion).

*Oculina diffusa* and *Madracis decactis* are of secondary importance between 1.5 and 3.5m but are more important at slightly greater depths. *M. decactis* seems to prefer shaded regions, and Scatterday (1974) noted that this species was most prominent in reef cavities off Bonaire, Netherlands Antilles.

**Bottom wall** (Frazier’s *Oculina* zone). While *M. mirabilis* is still present, it is *O. diffusa* and *M. decactis*, both delicate branching forms, which represent most of the coral cover on the lower parts of the reef walls, down to the interface with the reef sediment slope. *M. decactis* is found mainly under the shaded overhangs at the base.
Figure 6. Habitats and main coral distribution on a typical Castle Harbour pinnacle reef and adjacent sediments.
of the reef. We found *O. varicosa* so rarely that it seems inappropriate to consider its presence to be definitive of any particular habitat.

*Cavity and crevice.* Minor openings on otherwise horizontal surfaces (such as the tops of reefs) may house small, nonprotruding, branching corals, while overhangs on vertical surfaces provide a niche for the cup-shaped coral *Agaricia fragilis*, which is the dominant coral in these cryptic environments. Occasional encrusting colonies of *M. decactis* may also occur.

*Off-reef.* Large colonies of branching *Oculina diffusa* occur on, and partially within, the sediment off the reefs. Scattered colonies of *M. mirabilis*, *Isophyllia* spp. and *Siderastrea radians* may also be found in off-reef areas, usually attached to coral rubble, otherwise coral growth is rare in this habitat.

*b. Sediment facies and composition.* Eighteen sediment transects were performed in Castle Harbour from selected patch or fringing reefs, beginning at the reef-sediment interface and sampling toward the inner lagoon in various directions (see Fig. 1, top) at 5m intervals. A total of 104 sediment samples were collected and processed.

The size classification of sediments used by Folk (1968) was adopted. Approximately 65% of the sediments were classified as gravelly muddy sands, with the rest of gravelly sands, gravelly muds and gravelly sandy muds. The coarsest samples are usually found close to the reefs, with a gradual increase lagoonwards in mud content and a decrease in gravel and sand (Fig. 7). Several transects (T2, T4-7, T9-10, T13-T14) reveal a band of coarser material about 5m wide surrounding the reefs, and at a distance of 5-10m from the reef base. The reason for the presence of this band is not yet understood but it probably results from off-reef currents.

Robelen (1970) maintained that the distribution of sediments in Castle Harbour is a function of the distribution of living species and the winnowing effect of currents. We also infer the presence of off-reef currents to account for limited lagoonward transportation of sediments from the base of the reef, but have been unable to detect them during our summer field seasons.

The 2-4mm sieved fractions of the samples were examined to establish the biotic composition of the sediments. On the average approximately one-half of the grains consists of fragments of species of *Halimeda*, probably derived from the reef rather than the inner lagoon floor, where *Halimeda* and other calcified green algae are not common. A further one-third of the sediments is composed of mollusc fragments of two types: thick heavy shells of reef-dwelling molluses and thinner, more delicate shells of infaunal inner lagoon dwellers. These proportions are similar to those obtained by Barnhart (1963) from three isolated stations in Castle Harbour.

From Figure 8 it can be seen that the content of *Halimeda* fragments in the sediments increases with increasing distance from the base of the reef to a distance of
about 10m, where it levels off at approximately 50%. Fragments which have recently become detached from living plants are easily moved, perhaps because of decompositional gases trapped in the pores of the segments. After a period of time such fragments become less buoyant and therefore more difficult to resuspend.

Evidence of bioerosion is extensive on all hard substrates, and boring activities of sponges and bivalves, for instance, must be responsible for much of the breakdown of coral heads.

Sixteen cores were taken in areas of Castle Harbour floored by inner lagoon sediments and all showed strong textural and compositional homogeneity from top to bottom, suggesting stable conditions during the time period represented by the depth of the cores. The cores are compositionally similar to the sediment samples obtained from the transects, with Halimeda and molluscs accounting for 70-80% of the fragments in the 2-4mm sieve fraction (present in nine of the sixteen core samples).
c. Postulated dredging effects. Several authors (Laborel, 1966; Frazier, 1970; Mattraw, 1970; Johannes, 1972) have suggested that the dredging of Castle Harbour altered its biological character. Frazier noted that some Diploria colonies obtained from the interior of two pinnacle reefs dissected by blasting were much larger (up to 2 meters in diameter) than any now found living in the harbor. Likewise, Mattraw remarked that these dissected reefs contained abundant Millepora alcicornis which is presently much less common in Castle Harbour. On the basis of laboratory experiments involving the tolerances of living M. alcicornis to fine suspended sediments, Mattraw suggested that its present relative scarcity is due to increased siltiness in Castle Harbour since the dredging. The presence of huge dead Diploria colonies exposed on the reefs (Johannes, 1972; pers. observations) indicates that either conditions in Castle Harbour have changed and are no longer favorable for such growth, or some event killed the corals and recovery is still incomplete.

Evidence from studies in other regions suggests that high turbidity and sedimentation rates may be responsible for decreased coral abundance and species diversity, as well as changes in growth form. Roy and Smith (1971) noted that coral coverage and diversity were reduced in areas of turbid water in Fanning Lagoon, Pacific, compared to that in clearer water, while branching (ramose) growth forms predominated in corals from turbid water areas. Loya (1976) also invoked turbidity
and sedimentation effects to explain reduced diversity and coral coverage on a Puerto Rico reef. We suggest that in Castle Harbour the predominance of branching corals belonging to the genera Madracis and Oculina is a response of two opportunistic forms (presenting a minimum surface area on which sediments can settle) to increased rates of turbidity and sedimentation following the dredging. Furthermore, it is possible, though difficult to prove, that our relatively low values of the Shannon-Weaver Diversity Index for Castle Harbour reefs (especially on the reef tops) compared to North Lagoon Reefs (Settgas, unpubl. report, 1974) may reflect the stressful conditions of high turbidity and sedimentation rates present in Castle Harbour since the dredging.

Dodge and Vaišnys (1975, 1977) concluded that there was a catastrophic mortality of Diploria colonies in Castle Harbour between 1941-43, based on a study of annual banding characteristics. They demonstrated that most living colonies post-date the dredging and living colonies older than 45 years are rare, while outside Castle Harbour colonies with ages of up to 300 years are not uncommon. Theoretical calculations by these authors on energy requirements for self-cleaning in Diploria indicate that survival decreases with increasing colony size. This agrees with their field observations that corals younger than 12 years at the time of dredging seem to have survived the event.

The available evidence thus appears to suggest that the dredging has been responsible for changes in the growth, abundance and distribution of some coral species in Castle Harbour. It is generally postulated that the increase in fine suspended sediment was responsible, yet experiments by Hubbard and Pocock (1972) have shown that many corals can effectively remove large amounts of sediment from their surfaces by mucus secretion followed by a reversal of ciliary currents. It is possible therefore, that high concentrations of suspended sediments per se did not directly cause mortality, but that decreased light penetration resulting from the suspended material promoted stressful conditions for corals already near their minimum temperature requirements and under increased sedimentation (Dodge and Vaišnys, 1977). Survival of individual corals was probably a reflection of colony size, growth form, sediment-cleaning efficiency, light requirements and sensitivity to low winter water temperatures, but it is impossible to be more definitive until information is available on long-term survival rates of various corals under stressful conditions.

An indirect consequence of the dredging has been the previously-mentioned changes in circulation patterns in Castle Harbour, which may have a greater long-term effect on the coral communities than the factors already mentioned. If such changes have led to a significant reduction in circulation, then it is unlikely that the reefs will ever be restored to pre-dredging conditions. At present, it seems that either the flushing action of the currents is constantly re-suspending silt that was produced by the dredging or the present production of fine sediment (from a source
as yet uncertain) is taking place at a rate equal to or greater than that at which the currents can remove it. In either case negligible improvements for coral growth can be expected.

However, it would be desirable to conduct quantitative investigations on the corals in Castle Harbour several years from now and compare the results with this study, to show whether or not conditions are improving for the recovery of the reefs.

The dredging does not seem to have affected the sediment regime in Castle Harbour to any significant degree. Both the textural and compositional data of the cores suggest that there have been few changes while the last 40-45cm of sediment have accumulated, which almost certainly represents a time period which began before the dredging. Robelen (1970, p. 85) believed he could distinguish an organically-bound silt layer in the upper four inches (10cm) in his northern Castle Harbour cores, which was not present in the southern cores. He attributed this difference between northern and southern cores to “fundamental changes in bottom conditions as a result of dredging.” We did not find the organically-bound silt layer in any of our cores and remain unconvinced that any major change in sediment regime attributable to the dredging is present.

d. Comparisons with other regions on the Bermuda Platform. The patch reefs of North Lagoon and their associated sediments have been described by Garrett et al. (1971), Jordan (1973) and Scoffin and Garrett (1974). The patch reefs are up to 200 meters in diameter and are larger, more exposed and in water of greater depth than those of Castle Harbour. Large areas of sediment on the upper surfaces of lagoonal patch reefs are common, while cavities play a more important role in these reefs than in Castle Harbour patch reefs.

In terms of number of taxa, diversity of corals in Castle Harbour reefs is higher than in North Lagoon reefs, but coral cover is lower, values ranging from 10-45% on lagoonal reefs (Garrett et al., 1971). The dominant reef-building corals on lagoonal reefs are Diploria, Montastrea, and Porites astreoides, these forms (accounting for about 60% of total coral cover (Scoffin and Garrett, 1974), being grouped as an assemblage by Garrett et al. This assemblage is very impoverished at present in Castle Harbour. The Oculina-Madracis assemblage of Garrett et al. characterizes the deeper lagoonal patch reefs and the lower faces of the shallow patch reefs, accounting for about 26% of total coral cover (Scoffin and Garrett, 1974). In Castle Harbour, this assemblage predominates below depths of 2m, especially on steeply-inclined or vertical faces.

Both Garrett et al. and Jordan (1973) found a general decrease in grain size down the reef flanks off North Lagoon patch reefs. Garrett et al. noted that these reef-flank sediments were finer than the surrounding lagoonal sediments and referred to this as a “halo of fines.” Jordan, too, noted this phenomenon and attributed it to the winnowing of fines from the reef top. No such halo of fines exists
around Castle Harbour patch reefs where inner lagoonal sediments are much finer than the reef flank sediments.

Lateral changes in sediment composition lagoonwards on patch reefs of North Lagoon are similar to the changes seen in Castle Harbour. Coral and coralline algae fragments decrease lagoonwards in both areas, foraminifera (other than *H. rubrum*) increase lagoonwards, and *Halimeda*, the major constituent of the sediment from both regions, increases away from the reefs, while the molluscan fraction is less important in North Lagoon reefal sediments (15%) than in Castle Harbour (30%). *Homotrema*, of course, is much more important in North Lagoon reef sediments.

Studies in Harrington Sound by Neumann (1965) have shown the existence of four well-defined ecological zones from the shoreline: the Rocky Zone, the Shallow Sandy Zone, the *Oculina* Zone and the Subthermocline Zone. As Castle Harbour is generally less than 10m deep, its sediments most resemble those from the Shallow Sandy Zone of Harrington Sound. Compositionaly, Castle Harbour sediments are predominantly of *Halimeda* and molluscs, while in Harrington Sound the *Halimeda* fraction is low, molluscs making the greatest contribution to the sediments. Because of significant differences in depth and hydrography, close biological and sedimentological similarities between the two bodies of water would not be expected.

5. Summary

The fringing reefs and patch reefs studied in Castle Harbour show very low percentages of coral cover, among the lowest on the Bermuda Platform. Most of the corals present belong to the *Madracis-Oculina* assemblage, dominated by branching corals. Three morphologic-ecologic reef types can be distinguished by differences in shape, amount of coral cover and coral species present, the coral distribution being controlled by several factors, mainly energy conditions, substrate inclination (which allows five major habitats to be recognized) and exposure to sedimentation.

Sediments associated with the reefs are mostly sands with a significant fraction of fines, the proportion of fines increasing with increasing distance from the reefs. *Halimeda* and molluscs are the predominant biotic constituents in all size fractions.

The effects of dredging for the construction of Kindley Air Field in 1941-43 do not appear to be reflected in the sediments obtained by coring. However, the predominance of branching forms and the recent death of many of the larger massive coral species, such as *Diploria*, together with the presently reduced coral species diversity and coral coverage in Castle Harbour (compared to North Lagoon patch reefs) may be attributed, at least in part, to the high turbidity and sedimentation rates following the dredging.

Acknowledgments. We acknowledge the cooperation of the staff of the Bermuda Biological Station and the field assistance of R. E. Dodge and J. Dryer. The work was supported by National Research Council of Canada Grant A-4331 to Logan. This contribution is No. 744 of the Bermuda Biological Station.
REFERENCES


Received: 14 November, 1977; revised: 3 March, 1978.