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Coral populations and growth patterns: Responses to sedimentation and turbidity associated with dredging

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ABSTRACT

Analysis of coral growth patterns and populations in Bermuda reveals that living coral abundance on the reefs of Castle Harbor, a location where extensive dredging occurred during 1941-1943, is much reduced in comparison to external North-South reefs. Dead corals, sampled in the harbor, have skeletal patterns of growth which are similar and which show a marked decline in growth for several years prior to death. For the brain coral genus *Diploria*, both *D. strigosa* and *D. labyrinthiformis* are fairly evenly represented on contemporary North-South reefs and in the assemblages of dead corals from Castle Harbor, while *D. labyrinthiformis*, a species demonstrably more capable of rejecting accumulated sediment, is the predominant living form inside the harbor. Age distributions of Castle Harbor living corals exhibit no members older than approximately 60 years and show abruptly decreasing numbers of individuals in the older age classes. The North-South living, and Castle Harbor dead corals show a longevity of at least 250 years and a gradual decrease in the numbers of individuals from younger to older age classes. This evidence, coupled with information on the effects of sedimentation on corals, suggests that the process of dredging and its aftereffects created catastrophically detrimental conditions for the Castle Harbor coral population and produced mass coral mortality.

1. Introduction

Among the important factors determining coral abundance, growth, and distribution is sedimentation. The importance of this parameter for coral ecology, particularly in relation to man's activities, is still not completely understood. In this paper we examine the influences of a large scale sediment producing event on coral growth and coral populations. We first review and examine the expected response of corals to sedimentation and turbidity; while it is clear that increased sedimentation has a deleterious effect, quantitative data on individual and population responses are not generally or readily available. We next present a study of Bermuda corals from undisturbed reefs and from reefs in an area where extensive dredging occurred some 35 years ago. Our analysis involves comparison of coral abundance, species distribution, growth patterns, and age distribution of both living and dead coral assemblages between the two areas. Our results indicate the effect of the sedimentation/

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turbidity event associated with dredging has had important ecological consequences to the corals in the affected area and that only partial recovery of the population is evident at present.

2. The effects (observed and expected) of sedimentation and turbidity on corals

a. Individual effects. Most corals can withstand a low sediment supply to the living surface; very high sedimentation rate, however, is lethal (Marshall and Orr, 1931; Mayer, 1918; Edmonson, 1928). Dodge *et al.* (1974) and Aller and Dodge (1974) found the growth rate of the hermatypic coral *Montastrea annularis* to be low in areas of high resuspension of bottom sediments. Apparently, at least for some corals, sedimentation affects growth rate. Many species have an ability to remove sediment which has fallen on their tissues. Yonge (1931) has discussed a coral's ability to clear itself of sand. Hubbard and Pocock (1972) have provided information on the efficiency of various corals at removing different size classes of sediment and have ranked species according to their sediment rejection capacity. Bak and Elgershuizen (1976) have compared the rejection of clean and oil-soaked sediment by various Caribbean corals and present maximum and minimum species dependent rejection rates.

Sedimentation and turbidity (either naturally occurring or man-induced) are detrimental to corals for a variety of reasons. Hermatypic corals are dependent to a certain extent on light for their growth and well-being. Turbidity, as a result of light scattering from sediment particles in the water column, reduces illumination and hence a vital source of energy. In addition, rejection of sediment particles by a coral requires time and energy which could otherwise be used for food capture, growth, skeletal repair, or reproduction. The efficiency of the removal process, at least for hemispherical corals, is expected to depend on coral size. Corals remove coarse sediment particles by distension of the coenosarc with water, thus allowing sediment to slough off. Small grains are removed by direct ciliary action (Hubbard and Pocock, 1972). Both processes require an expenditure of energy. Neither Hubbard and Pocock (1972) nor Bak and Elgershuizen (1976) report coordinated transport of sediments by the shortest route from point of impact to edge. Observation of motion picture films of Hubbard and Pocock's experimental corals and some direct observations in aquaria show no directional routing of the sediment and suggest that the sediment removal process can be approximated as a random walk. On small or young corals a random walk rejection procedure would be efficient, because hemispherical type corals with a small radius would have a high chance of quickly removing particles. In larger and older corals, however, this type of mechanism for sediment rejection would require disproportionately more energy (Vaišnys, Dodge and Shadle, in preparation). These considerations help explain not only why growth would be lowered with increase in sedimentation rate (as the coral puts more energy into sediment rejection) but also why larger and hence older corals

would have a lower chance of survival than smaller and hence younger ones. Yonge (1936) discussed apparently coordinated sediment removal for *Manicina areolata*, which is, however, a species highly adapted for unattached life in a high sedimentation and sediment resuspension environment.

b. Population effects. Some evidence indicates that high turbidity and sedimentation act to decrease coral abundance, alter growth forms to a more branching habit, and decrease species diversity. Roy and Smith (1971) found that while very turbid water did not prohibit the presence of corals in Fanning Lagoon, coral coverage was decreased in comparison with a clear water area. In addition ramose corals were found to be more abundant in the turbid area and diversity was slightly diminished. Loya (1976) found significantly lower coral species diversity on a Puerto Rico reef which he suggested was caused by the "major detrimental effects of sedimentation and water turbidity in the area." Sedimentation and turbidity effects were also suggested as a possibility to explain the reduced living coral coverage in the area. The conclusions of these workers are in agreement with the more qualitative work and reviews of Endean (1976) and Stoddart (1969) and suggestions of Johannes (1972, 1975).

c. The effects of dredging and other human activities. In light of the above discussion, the effects of dredging and other human sediment and turbidity producing activities are expected to be deleterious to both individual corals and populations composed of them. There seems to be a dearth of systematic information and no direct studies are readily available. The following expectations are consistent with our prior discussion and qualitative reviews given by Endean (1976) and Johannes (1972, 1975). Any activity which increases sedimentation and turbidity might reasonably lead to decreased growth rate and increased mortality of individual corals. Coral populations would be expected to show a decrease in overall abundance, a relative decrease in the number of large corals, and preferential species representation corresponding to the rankings of Hubbard and Pocock (1972) or Bak and Elgershuizen (1976). As a consequence of a major event such as dredging, there might be simultaneous mortality of large numbers of corals, as well as preferential survival of the youngest corals present at dredging time.

3. Methods

a. Study area and collection procedures. The island of Bermuda is situated at the northern most Atlantic limit of vigorous hermatypic coral growth. Reef formation is conspicuous; the reefs are composed of and populated by an abundant coral fauna. The most common and abundant species are the brain corals *Diploria strigosa* and *Diploria labyrinthiformis*. Descriptions of various Bermuda reef environments and reefs have been provided by Upchurch (1970), Scoffin and Garrett (1974), Garrett *et al.* (1971), and others.

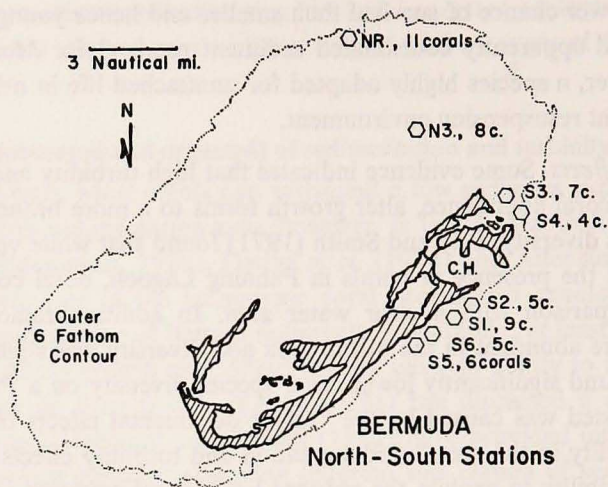


Figure 1. Sketch map of the Bermuda platform showing station locations. To the right of the hexagon station designation are the station numbers and the numbers of living corals collected and used in the age-frequency analysis, respectively.

Castle Harbor is a semi-enclosed basin located in the northeast portion of Bermuda, averages 9 meters in depth, and ranges to as deep as 16 meters. Reefs in the harbor lie 1-3 meters below high water, are shoal-like near shore, and become pinnacle or knoll-like toward the harbor center. A detailed description of several of these reefs is provided by Frazier (1970). There is a sparse cover of various hermatypic corals, one of the most common being *Diploria spp.* We have observed on the Castle Harbor reefs abundant, large, rounded boulders which are the skeletons of dead corals, usually of the genus *Diploria*. These heads range up to 1.5 meters in height and generally are more numerous, and on the average larger and more aggregated, than living *Diploria* coral heads present in the harbor today.

One of the reasons for interest in Castle Harbor is the construction of Kindley Airfield from 1941-1943 by dredging the harbor. The history of the U.S. Navy (now Air Force) base (obtained at base office) reveals that approximately 415 acres of land (portions of St. David's Is. and all of Coopers Is. and Long Bird Is. as well as numerous smaller nearby islands) formed the nucleus of the base and airfield. Dredges were used to break up the bottom of Castle Harbor and the coral (rock) and sand were then pumped ashore through pipes floated on pontoons. An estimated 16-20 million cubic yards of fill were pumped to form the hard packed airfield foundation.

Specimens of *Diploria spp.* were collected at selected stations on the Bermuda platform during the period May-June, 1974. Figure 1 shows station locations outside Castle Harbor and numbers of usable corals collected at each station. South

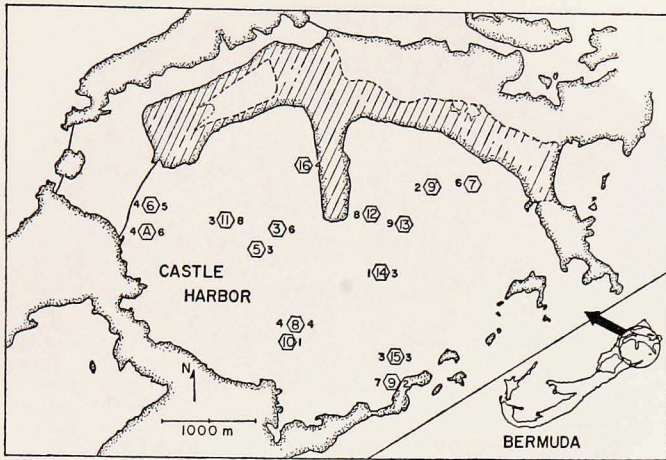


Figure 2. Sketch map of Castle Harbor, Bermuda showing station locations. Station numbers are inside the hexagons. Number of corals collected and used in the age frequency analysis are to the right (living) and to the left (dead) of the hexagons. The shaded land area approximates the amount of land created by dredging during 1941-1943 for airport construction.

and East stations (labeled S) were selected as representative points along a continuum of reef and coral growth. The extreme north station (NR) was located near North Rock along the northern reef tracts while station N3 was located at reef knolls in the central lagoon (3 Hill Shoals). Figure 2 shows the station locations on major patch reefs inside Castle Harbor with appropriate numbers of living and dead *Diploria spp.* collected at each. The shaded land area is an approximation of land created by dredging.

At all stations corals were collected from a 2-5 meter depth range. Whole colonies consisting of well-rounded hemispheres were primarily selected. Collection was made by one or two snorkle or scuba divers using hammers to dislodge specimens; no winches or special lifting equipment were used other than a very occasional rope lift to the boat by one man. In general, the plan was to collect at any one station the largest specimens which were revealed by a brief survey of 200-300 square meters and which could be manipulated by one or two men. In Castle Harbor, the largest living corals were small enough to be collected. Dead harbor corals, on the other hand, were often massive and collection was limited to a much smaller size range than was actually present. Further biasing toward small size in the collection of dead corals was caused by their frequent aggregation, good cementation, and partial burial into the reef framework. Outside the harbor, at North-South stations, living *Diploria* heads were on the average larger and more abundant than living Castle Harbor corals. The largest heads present were too large for collection.

b. Specimen preparation, X-radiography, and measurement procedures. Annual

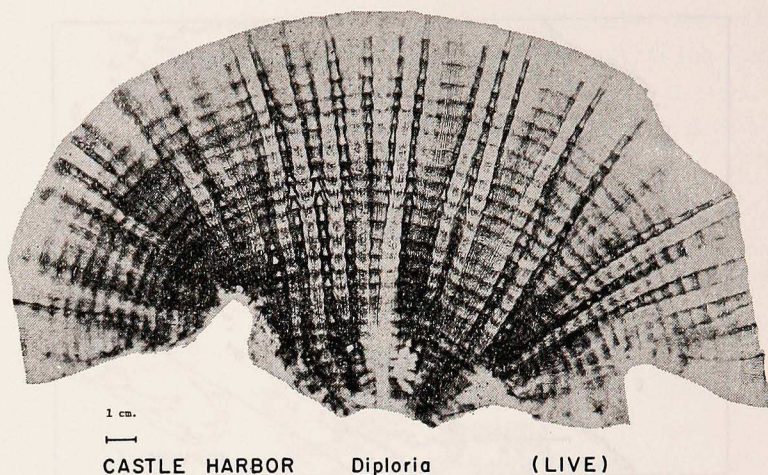


Figure 3. X-radiograph positive of living (when collected) specimen of *Diploria labyrinthiformis* from Castle Harbor, Bermuda showing well developed annual growth bands.

density bands are present in coral skeletons (Knutson *et al.*, 1972; Dodge and Thomson, 1974) and these were used for determination of the age of coral specimens and determination of growth patterns. Coral heads were sectioned with a diamond bit rock saw to obtain a 1-2 cm slab which included a plane intersecting the midpoint of the coral's base (point of colony origin) and the point of highest relief on the growing surface. Thick slabs were resectioned to a uniform thickness of approximately .5 cm and X-radiographed on Kodak AA X-ray film to reveal the density bands.

Band widths were measured with calipers on each living specimen X-radiograph positive (see Fig. 3) along 2-4 straight line transects drawn parallel to corallites. Years were assigned to each annual band (consisting of a high and low density couplet) with the uppermost band of each living coral being assigned the year of collection. Since most heads were nearly hemispherical, there was no one transect which exactly conformed to an axis of maximum growth. All transect lines were drawn and measured from equivalent portions of the coral head in terms of growth rate and in the zone of maximum growth. Often bands near the point of origin of the colony were obscured due to poor sectioning, breakage, or bioerosional features; however, a birth year could be extrapolated from the general hemispherical shape and known growth rate in younger portions. In general this extrapolation involved less than 9 years. Only corals with a birth date prior to 1951 were used in this study. Approximately 30% of specimens were excluded from analysis due to small size, lack of good hemispherical shape, lack of clear banding, or faulty sectioning. The average growth pattern of a coral—referred to as a chronology—was constructed by averaging the measurements on all the transects year by year.

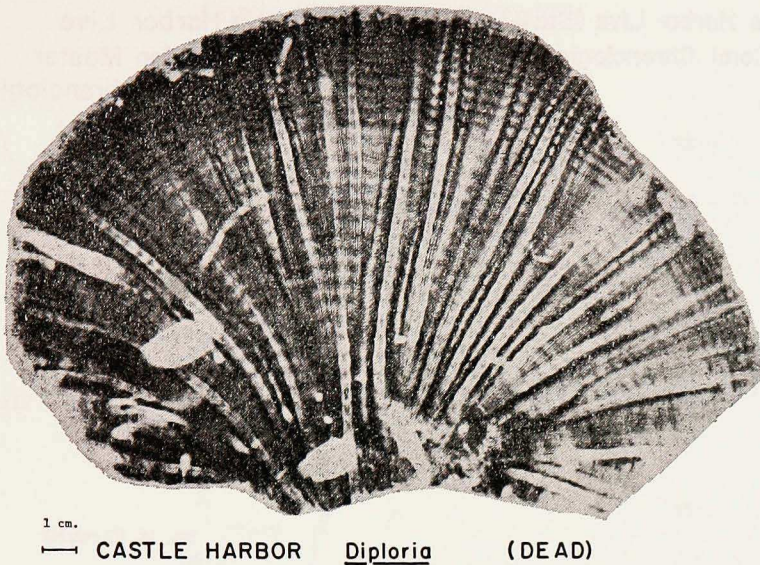


Figure 4. X-radiograph positive of dead (when collected) specimen of *Diploria labyrinthiformis* from Castle Harbor, Bermuda showing an abruptly decreasing growth rate toward the surface of death. Note bioerosion at the surface of the coral.

It is estimated that the assignment of dates to bands is in error by no more than ± 1 year; to facilitate intercomparisons between corals, each coral chronology time series was smoothed by a 3 year moving average. The formula used for the moving average is: $a_j = (b_{j-1} + b_j + b_{j+1})/3$ where b_k is a raw band width index at year k and a_k is the moving averaged value for that year.

Station growth patterns were constructed by averaging the band width chronologies of all corals at that station year by year. To allow comparison of individuals having different long term growth rates, the banding patterns were normalized to their lifetime average before constructing the station chronology.

Dead coral X-radiographs (Fig. 4) were analyzed in similar manner. Growth bands were labeled by band formation (i.e. time since birth) rather than absolute time since neither date of death nor birth are known. As in the case of the living coral chronologies, individual coral chronologies were smoothed by a 3 year moving average and normalized to their respective means. Although annual bands were in general distinct in the dead corals, the uppermost portion of the heads (surface of death) was often obscured. Bioerosion (sponge, worm, and clam borings), epibiont growth, and a pronounced lowering of growth rate at the death surface were all factors in creating uncertainty in the determination of the uppermost (youngest) bands, i.e., those corresponding to the several years immediately prior to death.

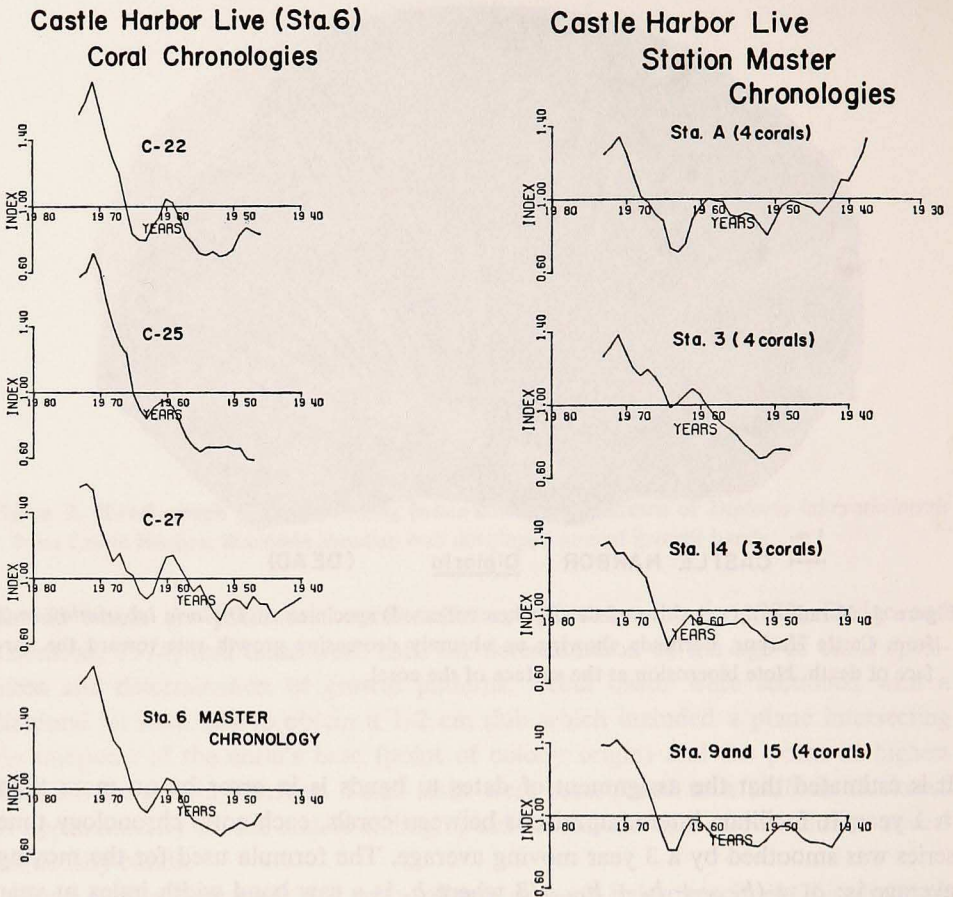


Figure 5. Band width chronologies (time series of band widths, each plotted as index value or the percentage of the average coral growth rate) for typical coral colonies at Station 6 in Castle Harbor. The station summary or chronology is also shown. This is the average by year of coral chronologies at the station.

Figure 6. Examples of typical station chronologies in Castle Harbor.

Since for the dead corals the absolute time of formation of the bands is unknown, no station chronologies were prepared.

4. Results

a. Pattern analysis. Previous work by Dodge and Thomson (1974) and Dodge and Vaišny (1975) indicated, and this study confirms, that contemporary Bermuda *Diploria* corals record similar patterns of growth from year to year. Figure 5 is an example of how typical individual live coral chronologies obtained at Castle Harbor Station 6 compare to each other and to the station master chronology. The patterns

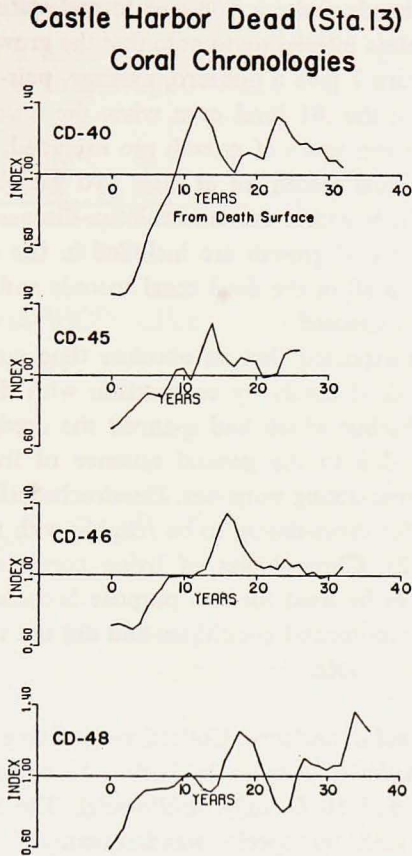


Figure 7. Chronologies of several representative dead corals from Station 13 in Castle Harbor. Yearly growth rates (normalized to the coral mean) are plotted from left to right beginning at the band approximately coincident with death.

of coral growth at a given station are similar. Averaging the corals year by year into a station chronology enhances those aspects of the growth response which are common to corals of a given area. Figure 6 presents examples of representative station chronologies, each composed of 3 or 4 living corals.

Figure 7 gives typical examples of chronologies of several dead corals from Station 13. Annual band widths beginning approximately at the surface of death are plotted for each coral from left to right. Although, as mentioned in the methods section, there is an uncertainty of several years in the location of the death surface and the absolute time of band formation is not independently known, the growth patterns seem to have common features. Particularly obvious is the decline in growth prior to death which was observed in most Castle Harbor dead corals. The uncer-

tainties in dating of the bands make a standard formal statistical analysis not very meaningful. It is nevertheless interesting to note that the growth patterns of the dead corals represented in Figure 7 give a nonzero, average, pair-wise correlation coefficient significant at least at the .01 level even when the unsmoothed data are used and even when the last seven years of growth are excluded, provided a slight shift in the records for best visual match (of at most two years) is allowed. It will be remembered that this shift is within the uncertainties discussed in the methods section. If the last seven years of growth are included in the comparison, there is a distinct common feature in all of the dead coral records and the formal correlation is, of course, significantly increased.

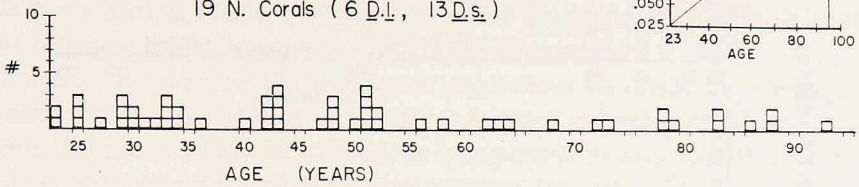
It had originally been expected that an absolute time could be assigned to the banding patterns of the dead corals by comparison with the banding patterns of living specimens in the harbor which had spanned the dredging event. This, however, proved impossible due to the general absence of living harbor corals old enough to be used for cross-dating purposes. Dendrochronologists typically require a minimum of 50 years for cross-dating to be reliable with wood specimens of unknown age (Fritts, 1972). Chronologies of living corals outside of the harbor, although longer, could not be used for this purpose because these corals were responding to different environmental conditions and did not compare especially well to the Castle Harbor living corals.

b. Species composition and abundance. Collections of living corals were only made for the two species of *Diploria*. Outside the harbor 55 corals were used in the age analysis (45 *D. strigosa* and 10 *D. labyrinthiformis*). The collections were biased toward more *D. strigosa* since this species was frequently able to be dislodged more easily from the reef. Qualitative observations suggest that *Diploria spp.* compositions at the South stations are approximately 60-70% *D. strigosa* and 30-40% *D. labyrinthiformis*; the more northern sites had the two species in roughly equal proportions. Inside Castle Harbor 45 specimens of *D. labyrinthiformis* were collected. Observations indicated virtually no *D. strigosa* living in the harbor older than about 15 years and these were rare.

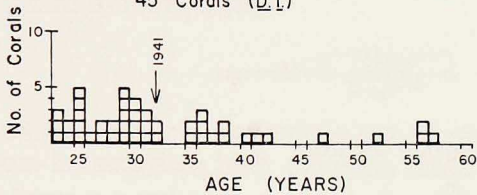
Of the 51 dead specimens collected in Castle Harbor, 43 were *D. labyrinthiformis*, 7 were *D. strigosa* and 1 was *Stephanocoenia michilini*. Species identification of the dead corals was usually impossible until after collection and it is thus expected that species composition of the collected corals is representative of the dead corals in that age (size) range.

Qualitative observations of living corals indicate that both species of *Diploria* corals on reef areas outside Castle Harbor are both more abundant and have greater coverage than those on reefs in the harbor. Other workers (Frazier, 1970; Johannes, 1972, 1975) have made similar observations. We estimate the proportion of easily recognizable dead corals to living ones in Castle Harbor to be at least a

NORTH and SOUTH LIVE

36 S. Corals (4 D.L., 32 D.S.)19 N. Corals (6 D.L., 13 D.S.)

CASTLE HARBOR LIVE

45 Corals (D.L.)

CASTLE HARBOR DEAD

51 DEAD Corals (43 D.L., 7 D.S., 1 S.m.)

Figure 8. Age distribution of collected corals for the various sites. The inset for each diagram describes our best estimates of the efficiency of collecting corals at each site. Collection efficiency at all ages not indicated by the curve is zero. We estimate the shape of the curves is more accurate than the absolute numerical assignment to collection efficiency.

factor of 10, whereas readily observable dead corals at the North-South sites are estimated to make up at most 10% of the living coral population.

c. Age-distributions of collected corals. Figure 8 presents the age distributions of the collected corals for North-South, Castle Harbor live, and Castle Harbor dead corals. Included for each site is an inset which describes our best estimate of the collection efficiency. The estimate of absolute collection efficiency is more uncertain than the estimate of the relative collection efficiency given by the shape of the curves. As previously mentioned in the Methods section, for the North-South stations collection was directed toward obtaining the largest possible specimens at any given station. Due to time available underwater with snorkel and actual site varia-

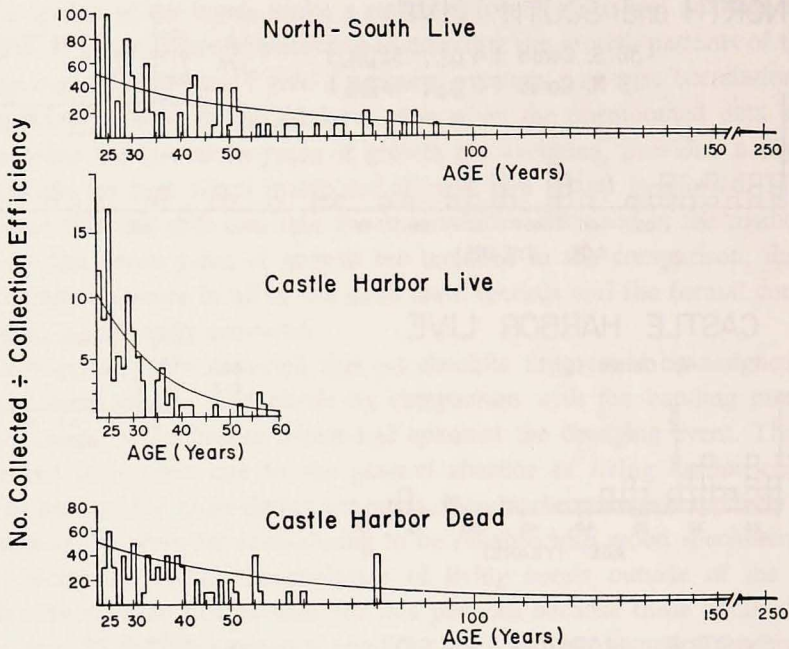


Figure 9. Observed age distributions divided by the collection efficiencies at each site. The smooth curves are those of stable age distributions and are described in the text.

tions, corals of varying ages were included in the collection. Slightly more collection emphasis was placed on older corals in the 23-93 year collection range. For the Castle Harbor live corals, as with other sites, collection was concentrated in the oldest age ranges and our collection efficiency was somewhat lower in the younger age classes of the collection. Ages of the Castle Harbor dead corals are more biased toward younger values by collection limitations. Dead coral skeletons were frequently extensively bioeroded, had rough edges, and were partially cemented into the reef frame or extensively aggregated. All of these factors acted to decrease the ages of physically manipulatable and hence collectable corals.

While for corals older than approximately 90 years the collection efficiency was essentially zero, observations were taken at each site which gave information on that part of the coral population. In the North-South areas large living specimens were observed on the reefs (uncollectable due to their size) in dimensions equivalent to ages of 250-300 years. (Vertical growth rates of Bermuda corals are about .35cm/yr.; Dodge and Vaišnys, ms. in preparation). These observations are supported by those of Scoffin and Garrett (1974) who report *Diploria* heads up to a meter in height on the North reefs. For the Castle Harbor live corals our observations revealed no living corals larger than those collected. For the Castle Harbor dead

corals we observed specimens ranging to heights in excess of 1 meter or approximately 250-350 years old. Johannes (1972) also reports observation of large dead corals in the harbor. Frazier (1970) has reported the presence of *Diploria* heads up to two meters in height incorporated into the reef framework.

To make a comparison of the different populations we divide the observed age-frequency distributions at each site by the associated collection efficiency. Figure 9 presents the results of this calculation. It is important to note that the uncertainty associated with the calculated histograms will vary inversely with the actual number of specimens collected at any given age. In the figure we also show stable age distributions often used in simple population models, specifically those which may be represented by the equation:

$$n_x = N \frac{e^{-rx}(1-e^{-r})}{1-e^{-r\lambda}} \quad (\text{Cole, 1954}).$$

λ is the longevity, r is the intrinsic rate of natural increase (given by the difference between instantaneous birth and death rates), and n_x is the number of individuals aged between x and $x+1$ years. N is the total number in the whole population. The values of r and λ for the curves of Figure 9 were chosen so that the curves approximate the observed age histograms (corrected for collection efficiency) and reflect the presence of old corals which were observed but not collected.

5. Conclusions

There is a striking difference in the appearance of living coral population age structures inside and outside the harbor, or for that matter between the living harbor coral population today as compared to that which was once living there. The low r (estimated to be about .025) and large λ (estimated at 250 years) for the North-South living and Castle Harbor dead corals suggests a stable, long lived, steady state population distribution. The relatively greater r (estimated at .08) in the Castle Harbor live population as compared to the others probably indicates a population in the phase of high recruitment and possible repopulation; the low λ (estimated at about 60 years) indicates an event occurring λ or less years ago that wiped out many of the then existing corals. These conclusions are further strengthened by our observations mentioned in the previous sections that the density of living corals in Castle Harbor is less than for external sites, and also that the proportion of living to dead corals in the harbor is much less than for those same external reefs.

The event which so disturbed the Castle Harbor corals must have been harbor-wide since all stations were affected; on the other hand it must have been confined to the harbor since outside corals were apparently unaffected. The most likely event which could have produced these manifestations is the dredging of the harbor beginning in 1941 for airfield construction. The date when dredging began is shown in Figure 8 and it may be noted that corals which survived the event were never

older than 20 years at dredging time and in general much younger. As discussed earlier the deleterious effects of increased sedimentation should be disproportionately more severe for larger and hence older corals. The observations suggest that the corals greater than approximately 10 cm in height could not survive the increase in sedimentation associated with dredging.

Our data on species distributions offers support that dredging was the event in question. Hubbard and Pocock (1972) report that *D. labyrinthiformis* is more capable at removing particles in the fine sand to granules range than *D. strigosa*. In an event of increased and prolonged sedimentation associated with the dredging itself, and possible resuspension aftereffects, *D. labyrinthiformis* would be expected to be the better competitor. We find both species are well represented in living form on reefs external to Castle Harbor, while *D. labyrinthiformis* is clearly dominant as the living member of the genus inside the harbor. This was not the case in the past in Castle Harbor where we find *D. strigosa* to be present in the dead coral population and relatively abundant. In addition a large (approximately 56 year old) specimen of *Stephanocoenia michilini* was present in the dead coral collection. This is notable because of the extreme scarcity and small size of live colonies of this species in the harbor today, whereas it is reported living in sizes up to a meter in height on external reefs (Scoffin and Garrett, 1974).

The analysis of growth patterns offers further corroboration of the above conclusions and also provides information about the response of individual corals to the disturbance. The marked decline in growth prior to death in the dead corals is presumably indicative of the length of the death process. In many cases the decline is longer than the actual duration of dredging. One possible explanation is that the active dredging is followed by a period of higher than normal turbidity and resuspension lasting for a number of years due to the destabilization of the bottom and disruption of bottom fauna. Thus even if the high turbidity and sedimentation accompanying the active dredging process does not cause sudden death, the higher sedimentation and turbidity following the event may create such stressful (but initially sublethal) conditions that corals do not survive. Jokiel and Coles (1974) suggest that coral deaths resulting from heated water effluent continued for several years where "exposure to increased thermal loading did not appear to kill (all) the corals outright but gradually weakened and eliminated them over a period of time." Another possibility is that observed coral behavior is a response to either nutrient or sediment supply changes brought about because of altered harbor circulation. These considerations show that the effect of man induced sedimentation must be weighed against the viability of nearby corals and coral reefs when making environmental decisions.

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