

187

THE HIGH-LATITUDE CORAL REEFS OF BERMUDA: CHARACTERISTICS AND COMPARISONS

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With 1 figure

ABSTRACT. Bermuda lies at a latitude of 32° N in the sub-tropical north-west Atlantic and supports thriving coral reefs which are truly constructional. Platform margin and lagoonal reefs are dominated by a *Diploria-Montastrea-Porites* coral assemblage seen throughout the Caribbean, with an *Oculina-Madracis* coral assemblage on inshore reefs of Castle Harbour, where waters are more turbid. Although coral coverage may exceed 50% on some platform margin reefs, coverage elsewhere is generally below 25%. The coral fauna, the main reef-building species of which are reproductively active, is reduced in diversity to about one-third that of the Caribbean region, as are the gorgonians. Sclerosponges and thecideid brachiopods are conspicuously absent from reef coelobite communities in Bermuda. Linear skeletal extension (growth) rates for *Porites astreoides*, *Diploria strigosa* and *Scolymia cubensis* in Bermuda are lower than those to the south. Differences in coral competitive hierarchies between Bermuda and Jamaica may reflect differing diversities more than behavioural patterns, while those coral species prone to bleaching in Bermuda are more sensitive to elevated water temperatures than they are at the same temperatures in lower latitudes. Depth ranges of corals in Bermuda are less than those from lower latitudes, but this may be due to a combination of mobile rhodolith substrates and competition for space from fleshy macroalgae below 50 - 60 m depth. Despite their high latitude, Bermuda's reefs show no mixing of tropical and temperate elements, with fleshy macroalgae of tropical or sub-tropical affinities important mainly on fore-reef slope reefs, and dissolved inorganic nutrient concentrations lower than those from other high-latitude reefs. Bermuda's reefs thus share some, but not all, of the characteristics said to typify high-latitude reefs.

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INTRODUCTION

In the last 20 years there have been many studies of high-latitude coral reefs, mainly from Australia, Japan and Hawaii (see CROSSLAND, 1988 for references). JOHANNES *et al.* (1983) and CROSSLAND (1988) have listed some of the physical, chemical and biological factors influencing community structure and reefal processes to be expected in coral reefs across a latitudinal gradient. Factors said to characterize high-latitude reefs are: increased seasonality in light and water temperatures, elevated nutrients, reduced biotic diversity and coverage, reduced grazing and resultant increased diversity, coverage and biomass of calcareous and fleshy macroalgae, with seasonal alternation of temperate and tropical communities at the extremes of latitudinal distribution of reefs. This paper reviews the characteristics of the high-latitude coral reefs of Bermuda in the western Atlantic in the context of these and other factors, to facilitate comparisons between Bermudian and other high-latitude reefs previously described from the Pacific and Indian oceans.

Regional setting of Bermuda

Bermuda lies at a latitude of 32° N, which is beyond the normally-accepted limit for coral reef growth but owes its sub-tropical climate mainly to eddies of the warm Gulf Stream flowing into the Sargasso Sea. This results in a high-latitude outpost of the Caribbean biota. Virtually all scleractinian corals and gorgonians from Bermuda are present in the Caribbean, but only about 40% of Caribbean forms have been found in Bermuda, testifying to the depauperate nature of the Bermudian marine fauna (LOGAN, 1988). Low winter water temperatures, averaging about 18° C, are usually invoked to account for this reduced diversity (LIDDELL and OHLHORST, 1988), but factors such as larval ecology may also be involved (GLYNN, 1973).

Physiographically, Bermuda is an atoll, in that a peripheral annular reef tract and islands form a mostly-submerged 22- by 52-km ellipse surrounding a shallow central lagoon. The main physiographic zones of fore-reef slope, main terrace, rim, and lagoon, described by LOGAN (1988, 1992), all support thriving Recent coral reefs of 5 to 20 m relief which are truly constructional from the base up (GARRETT & HINE, 1979; KUHN *et al.*, 1981; KUHN, 1984), rather than veneers over eolianite, as seen in high-latitude South African reefs described by RIEGL *et al.* (1995).

Coral reef communities

The main reef-building corals in Bermuda are *Diploria strigosa*, *Diploria labyrinthiformis*, *Montastrea annularis*, *Montastrea cavernosa* and *Porites astreoides*, which account for over 90% of the coral cover on each of fore-reef slope, main terrace and rim

reefs, 78% on lagoonal patch reefs and almost 85% on near-shore platform reefs (DODGE *et al.*, 1982; LOGAN, 1988, 1992). This assemblage, named the *Diploria-Montastrea-Porites* coral assemblage, also predominates on Caribbean reefs, with the addition of species of *Acropora*, a genus not found in Bermuda. In inshore Bermudian reefs, such as Castle Harbour, a coral assemblage dominated by branching *Oculina* and *Madracis* species are best adapted to its turbid waters, accounting for almost three-quarters of the total coral cover of about 10%, especially on the steep flanks of pinnacle reefs (DRYER and LOGAN, 1977). Although coral coverage may exceed 50% on the main terrace reefs, coverage elsewhere is generally below 25%, with diversity highest on lagoonal and inshore reefs and lowest on offshore platform margin reefs (LOGAN, 1988, 1992).

Coral reproductive activity

Diploria strigosa, *D. labyrinthiformis*, *Montastrea annularis* and *M. cavernosa* are all reproductively active, showing overlapping summer spawning activity (WYERS *et al.*, 1991) comparable to that recorded for corals from the high-latitude reefs of the Houtman Abrolhos Islands of Western Australia (BABCOCK *et al.*, 1994) and Shikoku Island, Japan (van WOESIK, 1995). Although SMITH (1992) did not observe spawning in *Porites astreoides* from Bermuda, he noted that it is the dominant recruiting species at his study sites and that it broods its planulae before release, suggesting that it is also reproductively active. *D. strigosa* and *M. annularis* have similar spawning seasons in Bermuda and Puerto Rico (18°N), despite the latitudinal difference (WYERS 1985, 1986; SZMANT, 1986).

Reef cryptofaunas

Bermudian reefs offer a variety of cryptic habitats for colonisation by coelobites (cryptobionts). Coelobite communities from rim reefs of the North Rock area of Bermuda were described by LOGAN *et al.* (1984), who compared them with communities previously described by LOGAN (1981) from Grand Cayman reef caves at 19° N. Unlike the more exposed reefal elements, there is little difference in the diversity of cryptic communities between the two areas; the main difference is in the presence of a sclerosponge-thecideid brachiopod community in the darkest recesses of caves in Grand Cayman which is not seen in Bermuda. This distinctive cryptofauna occurs in low-latitude reef caves in both shallow and deep reefs in Jamaica and the Caymans (JACKSON *et al.*, 1971; LANG *et al.*, 1975; LOGAN, 1981).

Coral growth rates

Annual linear skeletal extension (growth) rates in the corals *Porites astreoides*,

Diploria strigosa and *D. labyrinthiformis* have been studied by retrospective techniques from a variety of biotopes in Bermuda by LOGAN and TOMASCIK (1991) and LOGAN *et al.* (1994). Depth-for-depth latitudinal comparison of growth rates of the first two species indicates an inverse relationship between growth rate and latitude, with a similar inverse curvilinear relationship with depth for *P. astreoides* in both Bermuda and Jamaica (LOGAN and TOMASCIK, 1991). TOMASCIK and LOGAN (1990) also found peripheral growth rates in *Scolymia cubensis* to be significantly greater in Barbados (13° N) than in Bermuda. These studies support the findings of others who have also shown growth rate-latitudinal differences (see LOGAN and TOMASCIK, 1991 for references). Reduction in winter water temperatures and light levels with increasing latitude have been invoked to account for these differences.

Coral competitive interactions

Inter-colony boundary disputes between coral species are common, especially on platform margin and fore-reef slope reefs where coral coverage is high. Aggressive behavior between coral species was first described by LANG (1973), who erected a hierarchy of digestive dominance for Jamaican reef corals. Short-term aquarium experiments were combined with observations of long-term and/or induced interactions in the natural environment for Bermudian reef-building corals by LOGAN (1984). While there are some inconsistencies in rank between the two Bermudian hierarchies, the basic groupings of aggressive and weakly-aggressive species are the same. Comparison with Jamaica shows a close similarity at the family level, notwithstanding some differences in the ranking of individual species and the reduced diversity of the Bermudian coral fauna (LOGAN, 1986). The highest-ranked species in both regions are relatively minor components of the reefs, suggesting other factors such as growth rates, larval ecology and induced sweeper tentacle development are also important, while moderately-aggressive species of *Diploria* and *Montastrea* predominate on the reefs. Minor differences in coral competitive hierarchies between Bermuda and Jamaica thus seem to reflect differing coral diversities rather than behavioural patterns.

Coral bleaching

Certain reef corals, such as *Montastrea annularis*, *Diploria labyrinthiformis* and the hydrozoan *Millepora alcicornis* suffered extensive bleaching in Bermuda in 1988, particularly on platform margin rim reefs (COOK *et al.*, 1990). This episode of bleaching coincided with abnormally high summer water temperatures in August and September of that year, but gradually subsided when water temperatures returned to normal levels in December of 1988. COLES *et al.* (1976) showed that the upper thermal tolerances of subtropical Hawaiian corals are lower than those at lower latitudes in the Pacific. It would appear that the temperature

range experienced by Bermudian corals in the summer of 1988 was less than the upper limits recorded during bleaching events for the same species at lower latitudes (LANG *et al.*, 1988; COOK *et al.* (1990), suggesting that high-latitude reef corals in the north-western Atlantic may also be sensitive to elevated temperatures that are within the normal thermal tolerance range for corals at lower latitudes.

Coral depth ranges

On the northern margin of the platform, north of North Rock, FOCKE and GEBELEIN (1978) described the substrate of a locality at 50m depth, noting the general scarcity of reef-building corals (mainly *Montastrea cavernosa* present), the presence of gorgonians and the brown alga *Padina*, and the abundance of coralline algae as the dominant primary framebuilders. Rhodoliths were recorded as common in sand patches, supporting records of previous dredgings of algal balls from 60-80m depth off Bermuda's south shore by CHAVE *et al.* (1962). It is now known that a rhodolith cobble zone occurs seawards of the reefs around the whole Bermuda platform (FRICKE and MEISCHNER, 1985; MEISCHNER and FRICKE, 1988).

FRICKE and MEISCHNER (1985) noted that the two species of *Montastrea* occur below 30m, *M. cavernosa* ranging down to 78m. A deep-water association of *M. cavernosa*, *Agaricia fragilis* and *Scolymia cubensis* occurs below 60m, with occasional *Madracis decactis* and *Stephanocoenia michelinii* ranging down to almost 60m. While 13 species of constructional stony corals, plus *Millepora alcicornis*, occur below 20m depth, there is a significant decrease in coral diversity below 40m, in contrast to areas in lower latitudes, such as Jamaica, where diversity may remain as high as, or higher than, shallow sites at depths greater than 30 m (LIDDELL and OHLHORST, 1988). Since light penetration is relatively high (1% S.I. at 100m depth) and water temperatures are constant enough to be non-limiting, FRICKE and MEISCHNER (1985) concluded that the absence of a suitably firm substrate for coral growth (where mobile rhodolith fields occur), plus competition for space from algae, prevent the establishment of viable deep water reefs below 50-60m around the platform.

Fleshy algae, grazing rates and dissolved inorganic nutrients

Both JOHANNES *et al.* (1983) and CROSSLAND (1988) maintain that high-latitude reefs are typically characterized by a high biomass and diversity of fleshy algae (showing a mix of both tropical and temperate elements), as in the Houtman Abrolhos Islands (28-29° S) off Western Australia. At such latitudes there is increased seasonality in temperature and light, reducing growth rates in corals. Additionally, dissolved inorganic nutrient concentrations are generally higher than at low latitudes. This, plus the scarcity of scarid and acanthurid grazing fishes, contributes to a high biomass of fleshy algae which also inhibits coral growth.

There is significant growth of fleshy algae mainly on fore-reef slope reefs in Bermuda (FRICKE & MEISCHNER, 1985; Logan, 1988, 1992), although whether or not this is seasonal is not known. Five 20-m transects taken in August of 1986 at a depth of 30 m by the author (unpublished data) north-north west of the North Rock beacon show that the phaeophytes *Spatoglossum schroederi* (mean coverage of 17.4%, ± 7.7) and *Lobophora variegata* (5.5%, ± 2.4) are the most abundant forms, contributing to a total fleshy algal coverage of 22.9% ± 5.3) that approximates that of the scleractinian corals at that locality and may inhibit their recruitment and growth, as in Jamaica (HUGHES, 1994). Even some of the shallower rim reefs near the Kitchen Shoals beacon occasionally show dense growth of the rhodophyte *Asparagopsis taxiformis*, while the tops of inshore pinnacle reefs in Castle Harbour are covered with a dense mat of algae, such as *Caulerpa*, *Padina*, *Galaxaura*, *Amphiroa*, *Neomeris*, *Dictyota*, *Styopodium* and *Halimeda* (LOGAN, 1992). However, in all these examples, there is no mixing of tropical and temperate elements, since every element is tropical or sub-tropical in latitudinal distribution (LITTLER *et al.*, 1989). While there are no data on grazing rates from fore-reef slope reefs in Bermuda, dissolved inorganic nutrient levels of nitrogen and phosphorus in reefal areas, whilst very variable, are generally lower (MORRIS *et al.*, 1977, Connelly, unpublished data (Fig. 1)) than those from the Houtman Abrolhos Islands, although they are higher than the range given for low-latitude reef waters by JOHANNES *et al.* (1983).

CONCLUSIONS

Bermudian reefs fit the model of typical high latitude reefs previously described in that corals show reduced diversity, growth rates and depth range, presumably due to marked seasonality in water temperatures and light, and increased susceptibility to bleaching. Sclerosponges and thecideid brachiopods, typical of some shallow and deep low-latitude cryptic reef habitats, are conspicuously absent from such habitats in Bermuda. On the other hand, Bermudian reefs have reproductively-active corals, are truly constructional, lack high concentrations of dissolved inorganic nutrients and show no mixing of temperate and tropical elements in fleshy algae. Moreover, these algae show significant coverage only locally and mainly on fore-reef slope reefs. Bermuda's reefs thus share some, but by no means all, of the characteristics said to typify high-latitude reefs.

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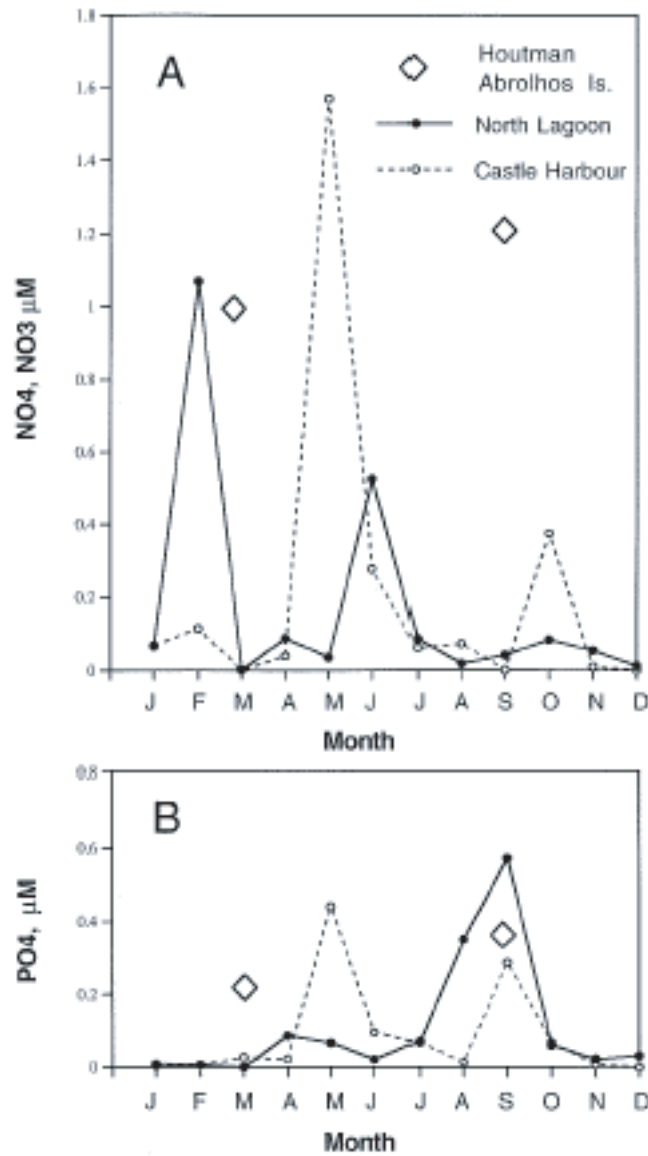


Fig. 1 - Average monthly dissolved inorganic nitrate-nitrite (A) and phosphate (B) from two reef sites in Bermuda (data from Connelly, unpublished), compared to Houtman Abrolhos Islands for September 1979 and March 1980 (JOHANNES *et al.*, 1983).

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