

SCLEROCRONOLOGY: A DATA SOURCE FOR REEF SYSTEMS MODELS

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INTRODUCTION

Ecosystem modelling necessarily deals with time-dependent data: fluxes, rates, concepts of stability, and so forth. This aspect of ecology separates quantitative and predictive science from its descriptive precursors; this area also presents the greatest experimental difficulties. Few systems have been thoroughly monitored over time periods comparable to the lifetimes of their longest-lived major components; similarly, it is unusual to find adequate data on all phases of seasonal, diurnal, and other cycles. As a result, much modelling is done with an implicit steady-state assumption and with assumed "average" values. Although these assumptions run counter to the common observations that few systems are in long-term equilibrium and extremes are likely to be more important than means in shaping the long-term characteristics of an ecosystem, it is a limitation imposed by the difficulty of developing an adequate data base from real-time observation.

Retrospective analysis of environmental conditions or organism growth is a field pioneered by the dendrochronologists; the purpose of this paper is to review and analyze the extent to which growth patterns may provide useful data for modelling efforts in coral-reef ecosystems.

To be of maximum utility, an organism must show growth patterns with a known and reliable time base, be capable of relation to a specific location or environment, and have a lifetime (and pattern period) long enough to provide a worthwhile extension of feasible real-time observations. Although many organisms show growth patterns of some sort, these criteria reduce the presently available selection to two groups: Molluscs, particularly the tridacnid clams (Bonham, 1965; Panella, 1975); and hermatypic corals. Of these, the corals are by far the more widely distributed and extensively investigated, and will be the sole class of organisms specifically discussed in this paper. It should be kept in mind, however, that many of the observations may also apply to other organisms whose growth patterns remain to be investigated.

AGE AND GROWTH RATE DATA

It is now well established that many reef corals have skeletal density variations with annual periodicity (Knutson *et al.*, 1972; Buddemeier *et al.*, 1974; Moore and Krishnaswami, 1974; Macintyre and Smith, 1974; Dodge and Thomson, 1974); skeletal density bands with

lunar periodicity (Buddemeier and Kinzie, 1975) have also been reported, but are not yet established as a reliable internal chronometer. The daily growth increments reported by Barnes (1972) appear to be too unreliable to serve as more than a secondary confirmation of other chronologies.

One of the most unequivocal uses of growth patterns is the determination of growth rates, ages and age-size relationships. The distribution of ages in a community (among both the living and the dead but persisting members) as a function of species and microenvironment provides another dimension for the study of population dynamics and community structure development. The ability to establish valid age-size relationships by representative growth pattern analysis provides novel opportunities for placing descriptive surveys on a temporally quantitative basis.

Average colony growth rates are another parameter of potential interest for coral reef system models. These rates reflect competitive strategies and their probable success, provide a basis for intra-community niche comparison, and may be compared with the fairly extensive literature on coral growth rates (Buddemeier and Kinzie, 1976) to provide information about the general suitability of the growth environment or specific, potentially growth-controlling, environmental factors. Additionally, growth rates in conjunction with skeletal density and composition analysis provide information on calcification rates, and skeletal studies may also be used to determine rates of bioerosion.

GROWTH PATTERN ANALYSIS

Interest in the potential significance of the observed variability in the approximately annual growth band dimension was stimulated by the example of dendrochronology, wherein systematic pattern variations have been used to construct geographically extensive master chronologies and to reconstruct past climatic variations. The hope has thus been raised that sclerochronology (analysis of exoskeletal growth patterns) might provide similar capabilities in the marine environment.

To date, results have not been completely clear-cut; while individual traumatic events have been shown to be recorded in coral skeletons (Macintyre and Smith, 1974; Moore and Krishnaswami, 1974), only a few attempts at correlation of growth patterns with each other or with environmental records have been made. In a preliminary survey based on growth bands in corals from Enewetak Atoll, Buddemeier *et al.* (1974) found no master pattern correlation. Dodge and Thomson (1974) showed dimensional and density pattern correlations in corals from Bermuda; these two sets of results suggest that external growth control and pattern correlations are more likely to be documented in environments which are marginal in terms of the optimum conditions for coral growth and which show substantial variability. The question of what environmental parameters control growth pattern formation remains a subject for debate and experimentation. Aller and Dodge (1974) have shown that

sedimentation can affect the average growth rates of corals; Weber and White (1974; in press) have demonstrated similar effects for temperature in field studies, as have Clausen and Roth (1975) in the laboratory. Buddemeier (1974) has suggested that seasonal light variations may be a factor in locations where water temperatures remain within the optimum range throughout the year. In general, this is an area of research which shows promise, especially in marginal or stressed environments, but in which much more work will be required to determine whether coral growth patterns can serve as more than a qualitative indicator of non-specific environmental conditions.

SKELETAL COMPOSITION

Interpretation of the isotopic, mineralogical, and chemical composition of coral skeletal carbonate in terms of the conditions of the external environment at the time of deposition is at once one of the most promising and most problem-ridden uses of sclerochronology. If skeletal composition can be calibrated in terms of ambient conditions, then band-dated samples would permit reconstruction of environmental records; and this information might permit further refinement in interpretation of the band pattern variations.

Detrital inclusions within the skeleton have been used to identify times and natures of alterations in the sedimentation pattern (Barnard *et al.*, 1974; Moore and Krishnaswami, 1974). It also seems likely that corals function as reliable samplers for many dissolved materials in the water. This fact has been most thoroughly demonstrated for various natural and artificial radionuclides (Knutson and Buddemeier, 1973; Moore and Krishnaswami, 1974; Dodge and Thomson, 1974; Noshkin *et al.*, 1975), and the implication is strong that many other trace or minor elements should be similarly "sampled." However, the mechanism for this sampling remains unclear; working with some of the same samples analyzed by Noshkin *et al.* (1975), Levy *et al.* (1975) found that the heavy nuclides were concentrated in "hot spots" rather than distributed uniformly through the skeletal band. This could be due to incorporation of detrital particles or (less likely) to patchiness of calcification in the presence of rapidly fluctuating concentrations of the dissolved species. In either event, further investigation is indicated before assuming that small coral samples necessarily represent short-term ambient water characteristics.

Other skeletal composition factors which have been investigated include Sr/Ca ratios (Weber, 1973; Houck, 1975), Mg/Ca ratios (Weber, 1974a; Houck, 1975), ^{13}C content (Land *et al.*, 1975; Weber and Woodhead, 1970; Weber, 1974b; Walsh, 1975) and ^{18}O content (Weber and Woodhead, 1970, 1972; Walsh, 1975). While there may be slight environmental effects on Sr and Mg content, it seems safe to say that these parameters promise to yield little information of utility to modellers, at least in the near future.

The stable isotope studies of corals are somewhat more controversial. It seems clear that the ^{18}O content is related to the water temperature at the time of calcification and that ^{13}C content is related to photosynthetic activity. However, these relationships are not simple, consistent, or even monotonic. Position within the colony, calcification rates on a microstructural level, and other factors appear to affect isotopic compositions; and those trends which have been established have uncertainty levels high enough to require analysis of a very large number of samples in order to establish reasonable confidence levels.

Although not without promise, all skeletal composition parameters appear to suffer from the same complications when viewed as potential environmental indicators. The calcification process of the corals is sufficiently complicated and dynamic that all of the skeletal constituents move through several metabolically controlled steps, often with a significant time lag between uptake and deposition (Cooksey and Cooksey, 1972; Chalker, 1975). Environmental conditions such as light and temperature undoubtedly affect different stages of the calcification process in different ways. The responses are further complicated by species and individual differences in corals and by specific adaptation to microenvironmental conditions. All in all, the stable isotopic composition of coral skeletons shows some promise and potential, but a great deal of further work is required to make such measurements reliably useful as environmental indicators.

SUMMARY AND CONCLUSIONS

From the foregoing it can be seen that retrospective studies of coral skeletons can directly and rather unequivocally provide information on coral ages and growth rates, and on certain aspects of water chemistry and sedimentation at the time of skeletal deposition. It seems likely that growth pattern analysis can yield some index of general environmental variability and suitability for coral growth. It is possible that the combination of skeletal composition and growth pattern analysis will eventually permit quantitative retrieval of some types of environmental data. An optimistic view of this potential is presented by Weber *et al.* (1975); however, this possibility is still far from being realized.

An important point is the need for feedback of information from those interested in time-dependent reef ecosystem modelling to those researchers interested in growth pattern studies of corals and other organisms. Viewed from a narrowly "coral research" point of view, there are many interesting problems; if some of those problems have broader ramifications than others, it is up to the potential users of the data to communicate their needs to the potential data producers.

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