

SCLEROCHRONOLOGY

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Synonyms

Coral chronometers; Related to Dendrochronology

Definition

Sclerochronology: The term sclerochronology is derived from the Greek words *sklero*, meaning “hard,” and *chronos*, meaning “time.” The field of sclerochronology is the study of periodicities stored in accreted hard parts and skeletons of various extant and extinct organisms. The periodicity can range from daily to annual scales and compose chronologies that span years to centuries, thus providing potentially long records of historical variations. Annual periodicity provides a chronology for determining age, growth rates, and reconstructions of environmental influences. Along with the recorded growth chronologies, the chemical composition of the skeleton also contains temporal records based on isotopic ratios and trace elemental concentrations, which can be used to reconstruct proxy paleoenvironmental and paleoclimatic records. Studies of skeletal growth and geochemical records have been used within the broader fields of ecology, physiology, and paleoclimatology. Sclerochronology is akin to the study of annual growth rings in trees, termed dendrochronology.

Introduction

Sclerochronology encompasses a wide array of organisms within coral reef environments that secrete structures which reflect growth periodicities. These may include, but are not limited to: corals, mollusks, fish, and sclerosponges. The following description is constrained to coral sclerochronology to provide a more focused perspective within the broader field of sclerochronology. It should be noted that early developments in mollusk sclerochronology (Isely, 1913, 1931; Orton, 1923; Davenport, 1938; Bonham, 1965) and fish sclerochronology (Leeuwenhoek, 1685; Pell, 1859; Adams, 1940; Jackson, 2007) paralleled the advances in coral sclerochronology, but because the nature and skeletal correlates of annual records differ substantially between taxa and phyla, descriptions and methods are generally specific to each subfield of sclerochronology.

Scleractinian corals are colonial organisms that secrete calcareous skeletons composed primarily of calcium carbonate, i.e., aragonite. In many species, the coral skeletons possess internal growth banding, density banding, and/or external growth ridges, which record the growth rate of the colony. Coral colonies can live hundreds of years and therefore provide annual chronologies of growth rates over time in response to changing environmental

conditions. Coral sclerochronology encompasses the study of annual density band formation, historical growth records, and reconstruction of environmental records based on density band chronologies and skeletal chemistry of stable isotopes and trace elements.

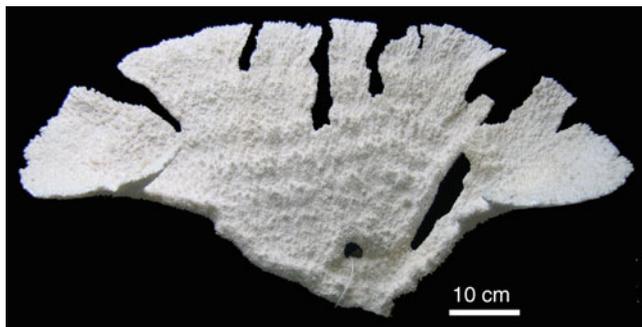
History

The term sclerochronology first appeared in the published literature in 1974 when Buddemeier et al. proposed: “Similar potentials have already been realized in the case of dendrochronology (Fritts et al., 1971); an analogous approach to the study of growth patterns in calcareous exoskeletons or shells could be designated sclerochronology” (Buddemeier et al., 1974). This was followed by a paper in 1976 entitled “Sclerochronology: a tool for interpreting past environments” (Hudson et al., 1976). Though the term sclerochronology may have arisen in the 1970s, the field of study has origins dating back to the nineteenth century when initial observations consisted of the apparently cyclical ridges on the external coral surface that were associated with periodic growth of the colony.

In 1898, referring to *Madrepora palmata* (*Acropora palmata*, Lamarck 1816), R. B. Whitfield remarked “Another feature worthy of mention is seen over all the larger spreading fronds in the form of broad undulations. These mark periods of growth, being thicker and thinner in substance, and are undoubtedly annual growths of the coral, . . .” (Whitfield, 1898); see Figure 1. In an effort to relate these “annual” growth patterns on the colony surface to environmental controls, Whitfield further speculated that they were a result of seasonal variations in water temperature. Vaughan (1915) later confirmed that these surface undulations were in agreement with annual growth rates for this species in the same locale.

Many of the early studies measured coral growth rates, though not directly from skeletal records, in order to address fundamental relationships between coral growth, environmental influences, and reef accretion (Finckh, 1904; Wood Jones, 1908; Mayor, 1918; Edmondson, 1929; Stephenson and Stephenson, 1933; Tamura and Hada, 1934). Much of this work, coupled with observations of cyclical skeletal ridges, led to the concept that corals may present useful chronometers of historical environmental, climatic, and even astronomical change (Wells, 1963; Runcorn, 1966; Shinn, 1966). The utility of corals as chronometers, suggested by these authors, was based on external growth ridges and directly measured growth rates; however, it was not based on internal variations of the skeletal architecture that produce annual density bands, which has come to be the most widely utilized characteristic in coral sclerochronology.

In 1933, the Chinese paleontologist, Ting-Ying H. Ma was the first to note that the internal skeletal architecture of Paleozoic corals (Silurian, Middle and Upper Devonian, and Lower Carboniferous) exhibited periodic variations in the size and densities of skeletal elements (dissepiments and tabulae), which appeared to reflect an annual cyclicity,



Sclerochronology, Figure 1 Example of external growth ridges on *Acropora palmata* reported by R. B. Whitfield in 1898.

and further asserted that these variations were in response to seasonal climatic changes, in particular water temperature (Ma, 1933). Using modern corals, *Favia speciosa* from Japan, Ma found similar patterns characterized by variations in dissepiment thickness and spacing, which appeared as repeating bands within the skeleton (Ma, 1934a, b). Using these internal growth bands, Ma measured growth rates and deduced temporal relationships between growth rates and temperature, where higher growth rates were associated with warmer years and lower growth rates with cooler years. Ma (1937) also assessed corals from different regions (Pacific, Atlantic, and Indian Oceans) and found a spatial relationship between growth and temperature, where corals growing in regions of warmer temperature grew faster than that in regions of cooler temperature. Ma's research represents the first assessment of internal growth banding, a precursor to studies of annual density banding, as well as the spatial and temporal relationship between coral growth rates and water temperature.

A significant advancement in coral sclerochronology occurred in 1972 when Knutson et al. confirmed the annual nature of density banding using corals from Eniwetok Atoll, which were exposed to nuclear weapons testing fallout (Knutson et al., 1972). A combination of X-radiography and radioautography (Bonham, 1965), termed autoradiography by Knutson et al., was used to identify density banding and radioactivity banding, respectively, within medially sectioned skeletal slabs from the coral colonies. The number of density bands in between, and following, the radioactivity bands corresponded with the number of years between nuclear weapons detonations and the date of coral collections, thus providing a straightforward proof of the annual nature of coral density banding. Shortly thereafter, the annual nature of density banding was reconfirmed for different species and by radiometric analysis (Dodge and Thomson, 1974; Moore and Krishnaswami, 1974) and radiometric, staining, and direct measurement (Macintyre and Smith, 1974). Once the basic premise that coral skeletons possessed annual density bands had been established, the field of sclerochronology expanded quickly with novel approaches aimed at developing and understanding the measurement of linear extension rates, bulk

density, and calcification rates, the skeletal structural basis of density banding, environmental correlates of growth rates, coral growth ecology, and the impacts of climate change on coral growth rates.

Prior to the discovery of annual density banding, the chemical composition of coral skeletons had been analyzed for Ca and Sr (Thompson and Chow, 1955), Sr, Ca, and Ba (Bowen, 1956), Co, Ag, and U (Veeh and Turekian, 1968), C and O isotopes (Keith and Weber, 1965; Weber and Woodhead, 1970), Sr, U, Ba, Cu, B, Li, and Zn (Livingston and Thompson, 1971); however, geochemical analyses of coral skeletons as a chronological record had yet to be developed. Similarly, Ra, Th, and Pb were used as a radiometric confirmation of annual density banding, but it was not until the late 1970s when annual chronologies from density banding and geochemistry were used together to derive proxy environmental records (Goreau, 1977; Emiliani et al., 1978). Fairbanks and Dodge (1979) demonstrated annual periodicities in C and O isotopes, which illustrated the sclerochronological reliability and potential for proxy records of temperature stored within the chemical composition of the skeleton. Since this time, research into isotope fractionation, incorporation of trace elements, and the application to proxy reconstructions have rapidly expanded providing extensive contributions to the fields of paleoclimatology, ocean circulation, and climate change (Swart, 1983; Druffel, 1997; Gagan et al., 2000; Swart and Grotoli, 2003; Grotoli and Eakin, 2007).

Fluorescence of the coral skeleton was initially suggested as a recorder of coastal rainfall by P. J. Isdale (1984) (Boto and Isdale, 1985). Though the nature of these fluorescent bands has been brought into question as a possible artifact of skeletal density variations (Barnes et al., 2003; Barnes and Taylor, 2005), skeletal fluorescence (luminescence) has been reported to provide records of runoff (Isdale et al., 1998; Lough et al., 2002), precipitation (Fang and Chou, 1992), and wind speed (Nyberg, 2002), monsoon climate and upwelling (Tudhope et al., 1996), mortality (Hendy et al., 2003), El Niño Southern Oscillation teleconnections (Hendy et al., 2003), rainfall and river flow (Lough, 2007), and hurricane activity (Nyberg et al., 2007).

Growth measurements from density banding

Coral samples for sclerochronology were originally collected as whole colonies; however, the currently preferred method is to collect cores (5–10 cm in diameter) using pneumatic or hydraulic drills (Figure 2) due to the minimal impact on coral colonies when cores are replaced with appropriate plugs. The cores are sectioned into 0.4–0.8-cm thick parallel-sided slabs oriented along the primary growth axis. The slabs are then planed to precise thickness for accurate density determination. Slabs are rinsed profusely after cutting and planing to remove all loose debris that can affect densitometry and geochemical sampling. Methods and quality of X-radiography will vary greatly based on the type of X-ray machine used; however, as a general rule, longer exposure times using slow speed

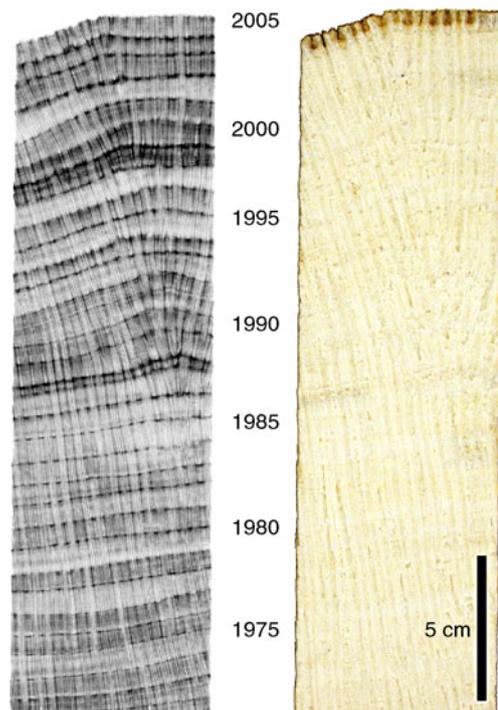


Sclerochronology, Figure 2 Coring of a coral colony using a hydraulic drill to obtain a skeletal record of coral growth rates.

film with a small grain size will produce the highest quality X-radiographs. As an example, using an industrial X-ray film at a source to object distance of >1 m and X-ray machine settings of 70 kVp, 15 mA, and exposure times of 5–10 s will provide good X-radiographs (Figure 3).

Density banding is revealed on X-radiographs of skeletal slabs and is apparent as alternating light (high-density) and dark (low-density) bands on the X-radiograph. A couplet of light and dark bands represents a single year's growth and is most often referred to in the singular form as an annual band. The annual nature of density banding allows three parameters of coral growth to be determined: (1) linear extension rate, (2) bulk skeletal density, and (3) calcification rate. Assessing all three growth parameters provides the most complete understanding of coral growth, and no one parameter is universally representative of the others (Dodge and Brass, 1984).

The annual extension rate is measured from the top of one high-density band to the top of the next high-density band and presented in units of cm/yr. The first extension rate measurements were collected on X-radiographic positive prints using dial calipers and following a linear transect normal to the density bands and along the axis of maximal growth; see review of early growth studies in Buddemeier and Kinzie (1976). X-radiograph densitometry (Buddemeier, 1974; Dodge and Thomson, 1974; Chalker et al., 1985) and gamma densitometry (Chalker and Barnes, 1990) provide xy -data of density and distance along the coral slab, which can also be used to determine



Sclerochronology, Figure 3 X-radiographic positive print with annual density banding (dark bands = high-density, and light bands = low density) and a photograph of the coral slab.

extension rates based on distance from one density maxima (or minima) to the next density maxima (or minima). Annual values can also be derived from the combination of adjacent high-density and low-density bands. Density data can be delimited into high-density and low-density bands by the midpoint, or average value, between maxima and minima and by the zero crossing of the second derivative of the density data, which is the inflection point between bands. High-density and low-density data provide information about growth rates, which may vary independently on a seasonal basis.

Density measurements of coral skeletons are best described as the bulk density over the thickness of a coral slab, as opposed to the density of calcium carbonate skeleton. Density data is presented in units of g/cm^3 . The density of coral skeletons has been measured by a variety of techniques, including X-radiograph densitometry (Buddemeier, 1974; Dodge and Thomson, 1974; Chalker et al., 1985), gamma densitometry (Barnes and Devereux, 1988; Chalker and Barnes, 1990), computerized tomography (Bosscher, 1993; Bessat and Buigues, 2001), buoyant weight technique (Dodge et al., 1984; Barnes and Devereux, 1988), weight and volume (Highsmith, 1979), and mercury displacement (Dustan, 1975).

X-radiograph densitometry, a common method of density determination, is based on the principle that when two materials (e.g., a coral sample and an aluminum standard) are X-rayed and the exposed film exhibits equal optical density for both materials, the density of the sample material can be calculated. Buddemeier (1974) obtained the mass absorption coefficients for both the sample and standard from tabulated values; however, this technique required the exact determination of the applied X-ray voltage and was further complicated by the assumption of an effective X-ray beam energy and the inhomogeneity of the sample and standard. Chalker et al. (1985) avoided such problems by using relative mass absorption coefficients. They determined the relative mass absorption coefficient of the standard and sample by slopes of curves fitted to data of sample thickness vs. densitometer output voltage. Dodge and Kohler (1985) adapted these methods to image processing, which replaces the densitometer output voltages with gray-scale pixel values (0–255), which are converted to relative optical density (ROD) values. The values are not measurements of true optical density (OD), which ranges from 0.0 to 4.0, because OD requires measurement of the incident light intensity before passing through the X-radiograph (Carlton and Adler, 1996).

Once extension rates and density have been measured, the calcification rate is calculated as the product of extension and density and is presented in units of $\text{g}/\text{cm}^2/\text{yr}$. The calcification rate is a measure of the addition of mass, for a give area, over time, with the three growth parameters related by the formula:

$$\text{Extension (cm/yr)} \times \text{density (g/cm}^3\text{)} = \text{calcification (g/cm}^2\text{/yr)}.$$

Skeletal basis of density banding

The construction and growth of coral skeleton is based on the formation of aragonite crystals, at sites of calcification, which are organized into fan-shaped structures called sclerodermites, and represent the building blocks of skeletal architecture (Wells, 1956). The formation of aragonite crystals exhibits a diel pattern, where well-organized and closely arranged needles are formed at night and loosely arranged needles are formed during the day (Barnes, 1970; Gladfelter, 1983). These diel patterns in skeletal accretion produce daily external growth ridges (Barnes, 1972), which have been used as evidence for variation in the number of days per year from the Middle Devonian to present (Wells, 1963). Though daily growth ridges represent a valuable trait for sclerochronology, they are substantively different than the skeletal variations responsible for X-ray revealed annual density banding.

Buddemeier (1974), in his X-radiographic studies of coral skeletons, determined that variations in organic content nor trace element levels were substantial enough to cause the density variations associated with banding and proposed two alternatives for density-band formation: (1) the orderliness in which aragonite needles are deposited, and (2) the variation in size and spacing of the skeletal elements. Barnes and Devereux (1988) presented terminology for categorizing the scale of skeletal variations referring to the organization of aragonite crystals or needles as “microarchitecture” and the organization of skeletal elements (e.g., dissepiments, septa, and thecae) as “meso-architecture.” Barnes and Devereux analyzed the density of coral skeleton (*Porites* sp.) by gamma-densitometry, buoyant weight, and powdered skeleton techniques and found that variations in microarchitecture were insufficient to account for density banding and further suggested that variations in the skeletal mesoarchitecture were responsible for density banding.

Skeletal structures reported to vary in conjunction with density bands include thickness and orientation of trabeculae (Buddemeier and Kinzie, 1975), dissepiment thickness (Macintyre and Smith, 1974; Emiliani et al., 1978), dissepiment and costae thickness (Dodge et al., 1992), and septa and columellae thickness (Helmle et al., 2002), and a general thickening of all skeletal elements (Barnes and Devereux, 1988). It is generally accepted that periodic thickening and/or coalescing of skeletal structures are responsible for density banding and also that the specific structures responsible for producing density bands vary between genera and species. The impact skeletal structures have on the attenuation an X-ray beam passing through a coral slab and the resulting density bands (or false bands) on the X-radiograph has been described by experimental, theoretical, and modeled approaches (Barnes et al., 1989; Barnes and Lough, 1990; Barnes and Taylor, 1993; Taylor et al., 1993; Le Tissier et al., 1994).

Causes of density banding and correlates of coral growth

The environmental or endogenous causes of annual density banding have not been clearly identified. Common hypotheses include temperature, light, productivity, and reproduction. Annual reproductive cycles may cause a metabolic shift from growth to gamete productions, larval development, or tissue repair from spawning. Mendes and Woodley (2002) found *Montastraea annularis* corals from Jamaica, which underwent a bleaching event in 1995–1996, failed to produce a high-density band in 1996 and suggested this was due to the lack of gonad development and spawning in 1996. Alternative explanations for this event could include the bleaching stress, lack of photosynthetic energy contributions, or exceptionally high temperatures. Mendes (2004) conducted a controlled experiment considering temperature, light, and reproduction relative to density banding and concluded that reallocation of energy from growth (extension rate) to reproduction (gonad size) was the likely cause of high-density band formation in *M. annularis* from Jamaica, which occurs in late August to early October. It is important to consider that gonad size, temperature, and light were all at their highest levels during the period of high-density band onset. Characteristics of temperature, light, and spawning cycles generally correlate (Mendes, 2004; van Woesik et al., 2006), which makes it difficult to disentangle the true cause of density band formation.

Temperature and light are the two most commonly cited limiting controls on coral growth rates and therefore are likely to play a dominant role in controlling subannual growth rates responsible for density banding. Weber et al. (1975) and Highsmith (1979) attributed density banding primarily to temperature with high-density bands forming when temperatures were at their peak. Buddemeier (1974) demonstrated strong correlation between density banding and precipitation though he attributed this primarily to the influences of light availability. Klein and Loya (1991) cited temperature and light as combined factors controlling density band formation. Wellington and Glynn (1983) found that light was a better correlate with high-density band formation and further suggested that density banding may be controlled by combined effects of light, productivity, and reproduction. Varying with temperature and light, autotrophic (photosynthesis) and heterotrophic (feeding) energy contributions may control metabolic resources in a cyclical pattern, thus giving rise to annual density banding. Klein et al. (1993) reported that timing of density band formation varied by depth (3 m, 30 m, and 51 m) and attributed this observation to autotrophy/heterotrophy ratios. Temperature and light might also control density banding through the energetic contributions of photosynthesis, where P/R ratios may exceed a threshold for photosynthetic contributions during the summer temperature maximums and/or when light levels exceed a similar threshold.

Correlations between environmental parameters and coral growth records derived from density banding have

included extension rates alone, as well as complete growth assessment, including density and calcification. Correlations of coral growth with environmental variables include depth and light vs. extension (Hubbard and Scaturro, 1985; Huston, 1985; Logan and Tomascik, 1991; Bosscher and Meesters, 1993; Logan et al., 1994); light vs. extension, density, and calcification (Wellington and Glynn, 1983), temperature vs. extension (Jokiel and Coles, 1977; Dodge and Lang, 1983; Guzman and Tudhope, 1998), temperature vs. extension, density, and calcification (Highsmith, 1979; Lough and Barnes, 1997, 2000; Carricart-Ganivet, 2004; Worum et al., 2007; Cooper et al., 2008; Lough, 2008; De'ath et al., 2009); hydraulic energy vs. extension, density, and calcification (Scoffin et al., 1992); precipitation vs. extension (Buddemeier et al., 1974; Fang and Chou, 1992); nutrients vs. extension (Tomascik and Sander, 1985; Klein et al., 1993), and nutrients vs. extension, density, and calcification (Wellington and Glynn, 1983). Coral skeletal records have also been used to assess growth responses to anthropogenic perturbations such as crude oil and oil dispersants (Lewis, 1971; Knap et al., 1983) and runoff and coastal development impacts from turbidity, sedimentation, and sediment resuspension (Dodge et al., 1974; Loya, 1976; Dodge and Vaisnys, 1977; Barnes and Lough, 1999; Carricart-Ganivet and Merino, 2001; Torres, 2001).

Coral sclerochronology is not rooted in a mechanistic understanding of the growth-limiting controls over varying temporal and spatial scales and is therefore prone to errors associated with causation inferred from correlation. No single environmental parameter has been demonstrated to consistently and fully explain the annual variability in extension, density, or calcification, and it is likely that the limiting controls on coral growth are a combination of environmental influences that interact on daily to decadal periods over varying spatial scales. Effective sclerochronology aims to better identify these interactions for constrained time periods and a defined ranges of influence.

Coral growth and climate change

Skeletal deposition of corals and ultimately coral growth rates are generally controlled by environmental and climatic conditions and the chemical composition of the surrounding water. With regard to recently rapid climate change, influences from rising sea surface temperatures and increasing atmospheric carbon dioxide levels have potentially affected coral growth over recent years. Increased carbon dioxide levels have lowered the pH of oceanic surface waters with resultant decreases in the aragonite saturation state (Gledhill et al., 2008), which has been hypothesized to cause decreases in calcification rates of corals and other calcifying organisms (Smith and Buddemeier, 1992; Kleypas et al., 1999). Increased sea surface temperatures are known to exert a positive influence upon coral growth rates (Weber et al., 1975), which

occurs both on spatial (Lough and Barnes, 2000) and temporal (Lough and Barnes, 1997) scales. However, coral growth is also negatively influenced by the metabolic effects of coral bleaching, which occurs above their thermal tolerance (Jokiel and Coles, 1977; Goreau and Macfarlane, 1990).

Records of coral growth consisting of extension, density, and calcification are predominantly short-term, decadal-scale, analyses used to assess site-specific growth ecology (Wellington and Glynn, 1983; Dodge and Brass, 1984; Lough and Barnes, 1992; Scoffin et al., 1992; Carricart-Ganivet et al., 2000; Carricart-Ganivet and Merino, 2001; Worum et al., 2007). Long-term coral growth records have generally been limited to extension rate measurements alone (Hudson et al., 1976, 1994; Dodge, 1981; Hudson, 1981; Dodge and Lang, 1983). Relatively few studies have measured all three parameters of growth for long-term, multidecadal to century-scale records. Lough and Barnes (1997) and Bessat and Buigues (2001) measured extension, density, and calcification over century-scale records and reported a positive relationship between sea surface temperature and calcification over the twentieth century. However, Lough (2008) reported recent declines in 5-year averaged calcification and extension between 1965 and 2005 despite increasing sea surface temperature over the same period. De'ath et al. (2009) analyzed ten multicentury growth records in combination with many shorter and more recent coral growth records (up to 328 colonies) and identified a 14% decline in calcification and 13% decline in extension since 1990. Recent declines in calcification have also been reported in two short-term studies (Cooper et al., 2008; Tanzil et al., 2009). The recent declines reported from coral records of extension and calcification suggest that the positive relationship between sea surface temperature and calcification over the twentieth century may not be holding up under current environmental conditions and that further analyses are necessary to assess the range of these reported declines in coral growth and the role aragonite saturation states may play in these declines.

Summary

The field of coral sclerochronology arose from initial observations of external growth ridges, variations of internal skeletal structures, and apparent relationships between environmental conditions and coral growth. The confirmation of the annual nature of density banding led to modern methods of X-radiography, densitometry, and measurement of growth parameters: extension, density, and calcification. Coral sclerochronology has demonstrated its utility by advancing our understanding of coral growth ecology along with anthropogenic impacts and environmental influences on growth rates. The skeletal basis of density banding revealed on X-radiographs is well described; however, the fundamental cause of density banding has yet to be clearly defined. Based on decades of published research on coral growth rates and

environmental influences, it is clear that coral growth is not a fully controlled by a single environmental limiting factor, in contrast to the analogous field of dendrochronology. The value of coral sclerochronology lies in the ability of corals to store records of growth in their skeleton, over long periods of time, which reflect the sum total of environmental and climatic controls. The field of coral sclerochronology is continually advancing and provides unique records, throughout the tropical and sub-tropical oceans, of potential climatic/environmental change and anthropogenic influence.

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SEA LEVEL CHANGE AND ITS EFFECT ON REEF GROWTH

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Introduction

Over short timescales (minutes to months), sea level changes with tides, waves, atmospheric pressure, wind, and currents. Mean sea level (hereafter “sea level”) is the average level of the sea surface over a specific period (e.g., 1 year) after filtering out these short-term fluctuations. Sea level is determined from a reference level on land (e.g., a benchmark), and defined as an equipotential surface of the gravity field (i.e., the geoid).

At longer timescales (longer than a decade), sea level varies with changes in the volume of seawater and shape of the ocean basins. At timescales of 10³ to 10⁵ years