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SPATIAL, TEMPORAL AND TAXONOMIC VARIATION IN CORAL GROWTH—IMPLICATIONS FOR THE STRUCTURE AND FUNCTION OF CORAL REEF ECOSYSTEMS

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Growth is a fundamental biological trait, generally considered to have an important role in structuring populations and communities. Accordingly, many studies have quantified growth rates of scleractinian corals, but using a variety of different methods and measures that may or may not be comparable. The purpose of this review is to compile extensive data on the growth of corals, to relate disparate methods of measuring coral growth, and to explore spatial, temporal, and taxonomic variation in growth rates. The most common metric of coral growth is linear extension, measured as unidirectional change in branch length or colony radius. Rates of linear extension vary greatly among corals, being highest among arborescent *Acropora* species. This is not unexpected given the limited carbonate investment in producing long, slender branches compared to solid hemispherical colonies. However, differences in the way that extension rates are actually measured (e.g., linear extension of individual branches vs. changes in the mean solid radius of massive corals) could potentially bias interspecific comparisons of coral growth. The most comparable measure of growth, which gives unbiased estimates of growth across different growth forms, is average annual calcification or change in weight normalized to a measure of size. Surprisingly, even calcification rates appear to be much higher for branching *Acropora* compared to other coral genera, which contributes to the high extension rates recorded for this genus. Despite inconsistencies and incompatibilities among studies of coral growth, there is clear evidence that coral growth rates vary spatially and temporally, largely in response to light and water quality (e.g., turbidity), temperature, and aragonite saturation state. Ongoing changes in environmental conditions (e.g., due to climate change) are expected to have generally negative consequences for the growth of scleractinian corals, which may be further exacerbated by shifts in assemblage structure towards relatively slow-growing species.

Introduction

Scleractinian (hard) corals are fundamental to the geomorphology, biodiversity, and structure of coral reef ecosystems (Goreau 1963, Hoegh-Guldberg 2004, Pratchett et al. 2008). Most notably, scleractinian corals are major contributors to the formation of reef structures (Goreau 1963), as framework builders (Wells 1957) and often contribute disproportionately large amounts to carbonate production (Hart & Kench 2007). Hard corals also contribute to both the productivity (Anthony et al. 2008) and structural complexity of coral reef habitats (Pratchett et al. 2008), providing essential resources (food and shelter) for many reef organisms (Jones et al. 2004, Cole et al. 2008, Rotjan & Lewis 2008, Stella et al. 2011), as well as mediating biological interactions among coral-associated organisms (e.g., competition, Munday 2001, Holbrook & Schmitt 2002; predation, Caley & St. John 1996, Coker et al. 2009), thereby promoting coexistence of many species. Consequently, the biodiversity and abundance of reef-associated fauna (such as fishes) are positively correlated with both the abundance and diversity of scleractinian corals (Jones 1988, Munday 2000, Holbrook et al. 2000, 2002, 2008, Jones et al. 2004, Messmer et al. 2011). Sustained declines in the cover of scleractinian corals (Gardner et al. 2003, Bellwood et al. 2004, Bruno & Selig 2007, De'ath et al. 2012, Jackson et al. 2014) are therefore a critical concern.

Coral reefs are among the world's most threatened ecosystems (Pandolfi et al. 2003), with 19% of reefs having lost more than 90% of their live coral cover (Wilkinson 2008). A further 15% of reefs face a similar prospect within the next 10 to 20 years (Wilkinson 2008). Sustained declines in the abundance (as evaluated through percentage cover) of scleractinian corals are commonly attributed to elevated rates of coral mortality (e.g., Bruno & Selig 2007, De'ath et al. 2012) associated with increasing frequency, severity, and variety of disturbances. Perennial causes of coral mortality, such as natural chronic and acute disturbances, are now compounded by a range of anthropogenic disturbances, which can cause extensive and widespread coral mortality (Hughes et al. 2003). Also important are the physiological stresses imposed by these disturbances, as well as environmental changes, including both climate change and deterioration in water quality (e.g., De'ath et al. 2009, Carilli et al. 2010, Pandolfi et al. 2011) and their interaction (Crain et al. 2008). On Australia's Great Barrier Reef (GBR), for example, De'ath et al. (2009, 2013) reported that growth rates of massive *Porites* corals declined about 11% from 1990 to 2005. The causes of this decline are not yet clear but may be linked to recent increases in seawater temperatures and ocean acidification. Significant declines in coral growth rates, especially if accompanied by declines in other demographic rates (e.g., fecundity and recruitment), will contribute greatly to sustained declines in the abundance of corals (Hughes & Tanner 2000) or, at the very least, constrain the capacity of corals to recover from periodic disturbances (Hoegh-Guldberg et al. 2007, Hughes et al. 2007).

Studies of growth rates of corals (defined herein as any changes in the physical dimensions of discrete colonies) have a long history, extending to the 1800s (reviewed by Buddemeier & Kinzie 1976) and were initially motivated by questions related to the formation and maintenance of reef structures and carbonate frameworks and the fundamental knowledge that reef accretion is inexorably linked to coral growth (Darwin 1874, Dana 1890). Studies of coral growth continued through the early 1900s (Mayor 1924, Edmondson 1929, Stephenson & Stephenson 1933), when long-term studies of individual colonies revealed high spatial and temporal variation in growth rates. In light of this, Stephenson & Stephenson (1933) concluded that coral growth must be measured over extended periods (several years), and averaged across multiple colonies, to reliably detect spatial and taxonomic differences. Thereafter, many studies produced data on time-averaged growth rates for different coral species (e.g., Hubbard & Scaturo 1985), and there emerged a strong dichotomy between 'fast-growing' and 'slow-growing' species, which was partly explained by differences in gross morphology (Buddemeier & Kinzie 1976). Increasingly, however, coral species have been categorized into broadly defined functional groups based on gross colony morphology (such as 'massive', 'bushy', and 'columnar'; e.g., Bellwood et al. 2004), response to disturbances (i.e., winners and losers; Loya et al. 2001), or life-history traits, including growth rate (Darling et al. 2012). 'Characteristic' growth rates have been assigned to such functional groups (e.g., bushy and branching corals are fast growers while massive corals are slow growers). However, even within these functional groups there is substantial inter- and intraspecific variation in growth rates.

The purpose of this review is to synthesize extensive research on the growth rates of scleractinian corals and assess the broader utility of species- and location-specific growth rate measurements to 1) distinguish functional groups of scleractinian corals and 2) understand the changes in the structure and function of coral assemblages attributed to global climate change. Possible effects of global climate change (De'ath et al. 2009, Cooper et al. 2012) have resulted in renewed interest in coral growth, but as yet, there is no theoretical framework within which the effects of climate change on the growth of different coral taxa in different locations (e.g., across latitudinal gradients) can be explained. Despite long-term changes in environmental conditions on coral reefs (e.g., increasing sea-surface temperature [SST]), the reported effects on growth rates of tropical scleractinian corals are equivocal. For example, the growth rates of corals have already declined in some locations and for some taxa (Bak et al. 2009, De'ath et al. 2009, Tanzil et al. 2009, 2013, Cantin et al. 2010, Manzello 2010) as SSTs have increased, but in other cases, warming is associated with increased coral growth rates (Cooper et al. 2012). Reconciling these observations requires simultaneous consideration of multiple environmental drivers of coral growth, which vary in their spatial and temporal effects (van Hooidonk et al. 2013), as well as accounting for alternative measures of coral growth (e.g., linear extension versus calcification).

Contrasting measures of coral growth

A variety of methods have been developed, and are in common use, to quantify 'growth' of reef-building corals (Buddemeier & Kinzie 1976, Holcomb et al. 2013), defined herein as a change in linear dimension, planar area, volume, or mass of the skeleton. For the purposes of this review, we exclude consideration of the effects of environmental conditions on the growth of coral tissue, although we recognize that the growth of tissue and the growth of skeleton are functionally and mechanistically intertwined. The diversity of techniques and approaches for measuring growth rates of corals is partly necessitated by differences in the way that corals grow (e.g., some species deposit carbonate in successive and strikingly different layers that preserve the entire history of annual growth, while in other species these effects are less evident; Table 1), but the specific method(s) selected for measuring coral growth rate also depend on the temporal resolution required (Holcomb et al. 2013) and the specific biological or ecological question(s) motivating the research. Coral biologists and geomorphologists are generally focused on rates of carbonate accretion that lead directly to changes in skeletal weight, as well as, or in place of, measures of changes in overall colony dimensions, such as volume, area, or linear dimensions (e.g., Houlbrèque et al. 2004, Browne 2012). Conversely, ecologically driven research on coral growth, investigating, for example, competition, predation risk, and susceptibility to disturbance, is generally focused more on the change in overall colony dimensions (most often the 'area of occupancy'; Gilmour et al. 2013) rather than change in skeletal mass, or calcification.

While changes in the overall size of scleractinian colonies are fundamentally dependent on the deposition of calcium carbonate (i.e., calcification), the relationship between colony growth and calcification is complex. Calcification (and the associated change in weight of the coral skeleton) does not always relate directly to changes in the overall dimensions of a colony because 1) aragonite (the mineral form of $CaCO_3$ forming the skeletons of scleractinians) is not always laid down in areas of active linear extension (e.g., secondary thickening or infilling in *Acropora*; Gladfelter 1982); 2) differences in gross morphology and the primary axis of growth lead to differing levels of colony expansion for the same quantities of aragonite deposition; 3) the porosity or density of the skeleton varies within and among colonies, and as a function of environmental conditions, thereby

Table 1 Coral taxa reported to have regular growth bands that may or may not be used to retrospectively measure rates of linear extension or calcification throughout the life of the colony

Corals with distinct growth bands, known to record annual growth	*Acropora palmata* (Gladfelter & Gladfelter 1979)
	Agaricia agaricites (Stearn et al. 1977)
	Astrea (= *Montastraea*) *curta* (Harriott 1999)
	Balanophyllia europaea (Goffredo et al. 2009)
	Cladocora caespitosa (Kružić et al. 2012)
	Coelastrea (= *Goniastrea*) *aspera* (Babcock 1988, 1991)
	Colpophyllia natans (Huston 1985)
	Cyphastrea serailia (Harriott 1999, Roberts & Harriott 2003)
	Diploastrea heliopora (Corrège et al. 2004, Cantin et al. 2010)
	Diploria labyrinthiformis (Dodge & Thomson 1974)
	Dipsastraea (= *Favia*) *pallida* (Highsmith 1979, Harriott 1999)
	D. speciosa (Knutson et al. 1972, Buddemeier et al. 1974)
	Gardineroseris planulata (Guzmán & Cortés 1989)
	Goniastrea favulus (Babcock 1988, 1991)
	G. retiformis (Buddemeier et al. 1974)
	G. (= *Favia*) *stelligera* (Buddemeier et al. 1974)
	Hydnophora microconos (Buddemeier et al. 1974)
	Lobactis (= *Fungia*) *scutaria* (Jokiel & Tyler 1992)
	Lophelia pertusa (Mortensen et al. 1998)
	Montastraea cavernosa (Highsmith et al. 1983)
	Orbicella (= *Montastraea*) *annularis* (Dodge et al. 1974)
	O. faveolata (Saenger et al. 2008)
	O. franksi (Saenger et al. 2008)
	Paragoniastrea (= *Goniastrea*) *australensis* (Harriott 1999)
	Pavona clavus (Wellington & Glynn 1983)
	P. duerdeni (Jokiel & Tyler 1992)
	P. gigantea (Guzmán & Cortés 1989, Wellington & Glynn 1983)
	P. varians (Guzmán & Cortés 1989)
	Platygyra daedalea (Simpson 1988)
	P. lamellina (Buddemeier et al. 1974)
	P. daedalea (= *rustica*) (Knutson et al. 1972)
	P. sinensis (Babcock 1988, 1991)
	Plesiastrea versipora (Burgess et al. 2009)
	Pleuractis (= *Fungia*) *granulosa* (Chadwick-Furman et al. 2000)
	Porites astreoides (Stearn et al. 1977, Hubbard & Scaturo 1985)
	P. australiensis (Lough & Barnes 2000)
	P. columnaris (Klein & Loya 1991)
	P. compressa (Grigg 1998, Domart-Coulon et al. 2006)
	P. lobata (Buddemeier et al. 1974)
	P. lutea (Highsmith 1979)
	P. mayeri (Alibert & McCulloch 1997)
	P. nodifera (Al-Rousan et al. 2002)
	P. solida (Barnes & Lough 1989)
	Psammocora profundacella (= superficialis) (Guzmán & Cortés 1989)
	P. haimiana (= *togianensis*) (Knutson et al. 1972)

(Continued)

Table 1 (Continued) Coral taxa reported to have regular growth bands that may or may not be used to retrospectively measure rates of linear extension or calcification throughout the life of the colony

	Pseudodiploria (= *Diploria*) *strigosa* (Guzmán et al. 1991, Logan et al. 1994)
	Siderastrea siderea (Stearn et al. 1977)
	Solenastrea hyades (Moore & Krishnaswami 1972)
	Stephanocoenia sp. (Moore & Krishnaswami 1972)
Corals with apparent growth bands, but of uncertain chronology	*Astreopora myriophthalma* (Buddemeier et al. 1974)
	Fungia fungites (Buddemeier et al. 1974)
	Herpolitha (as '*Herptolitha*') *limax* (Buddemeier et al. 1974)
	Isopora spp. (K. Anderson & N. Cantin, unpublished data)
	Oulophyllia crispa (= *aspera*) (Buddemeier et al. 1974)
	Pocillopora eydouxi (Buddemeier et al. 1974)
	P. meandrina (Jokiel & Tyler 1992)
	Sandalolitha (= *Parahalomitra*) *robusta* (Buddemeier et al. 1974)

obscuring the relationship between skeletal mass and skeletal volume (Buddemeier et al. 1974); and 4) branching corals vary in solidity (i.e., the amount of interbranch space included within the overall 'displacement' volume of the entire colony; Barry 1965), which has direct ramifications for the total amount of carbonate that must be accreted to extend their maximum dimensions (e.g., mean solid radius; Maragos 1978).

For corals that deposit distinct bands of aragonite that preserve the chronology of growth throughout their lives (e.g., *Porites* spp., De'ath et al. 2009, Cooper et al. 2012; *Diploastrea heliopora*, Cantin et al. 2010; Table 1), retrospective measures of growth have proved important in establishing temporal trends in the growth rates of individual colonies (e.g., De'ath et al. 2009, Carilli et al. 2010). For corals that do not deposit aragonite in regular bands, such that the skeletons do not reveal the lifelong chronology of growth, then growth (change in weight, volume, area, or linear dimensions) must be evaluated through direct measurements of individual colonies over time (e.g., Bak et al. 2009). Hence, intrinsic differences in the ways that different coral species calcify have led to taxonomic biases in the methods used to measure growth rates of corals and the amount of data available (Buddemeier & Kinzie 1976).

Retrospective measures of coral growth bands

Banding in the skeletons of scleractinian corals, and its relationship to cyclical growth processes, was first recognized in the eighteenth and nineteenth centuries (e.g., Donati 1751, Whitfield 1898). When examining fossil and modern corals, Ma (1933, 1934) noted regular variations in the size and spacing of skeletal elements, which he speculated were linked to seasonal variation in water temperatures (Ma 1937). By studying massive corals collected in Enewetak Atoll following nuclear weapons testing, Knutson et al. (1972) confirmed that "regular alternating dark and light bands" were deposited annually. This discovery of annual low- and high-density band pairs "rendered almost trivial the previously unsolved problem of measuring long-term growth rates and growth histories" (Buddemeier & Kinzie 1976, p. 199), although it is recognized that such banding is limited to a subset of corals (50 of ~ 750 reef-building scleractinian species or ~ 7%) that mainly have a massive or hemispherical colony morphology (see Table 1). Although Stimson (1996) showed that the distance between concentric crests on the upper colony surface was representative of annual growth increments for some non-massive species (e.g., *Acropora spicifera*, plate-forming *Montipora* spp., and foliaceous *Merulina* spp.), such proxies of annual growth are not universally apparent in these corals and are therefore of limited use in detecting growth variation.

Annual density banding is now widely recognized as an important tool for measuring growth rates of certain scleractinian corals (see Table 1) and has proved useful in relating spatial and temporal variation in growth to environmental variables (e.g., Lough & Barnes 2000, Cooper et al. 2012). The principal advantages of this approach are 1) some coral colonies are several metres in height, and with average growth rates of about 1–2 cm yr^{-1}, they can record skeletal accretion over decades to centuries (timescales that are unfeasible for direct observation); 2) because derived growth measures are retrospective, they represent growth under natural conditions and are not affected by potential changes in growth rate due to coral collection and handling, as occurs in experimental studies; 3) coral skeletons can be preserved after death, allowing retrieval of growth measurements for periods in the distant past (e.g., Brachert et al. 2006 observed "ghost structures" of annual bands in *Porites* from the late Miocene); and 4) the density banding chronology provides the basis for reconstructing environmental conditions based on geochemical (e.g., Sr/Ca) and isotopic (e.g., $\delta^{18}O$) tracers incorporated into the $CaCO_3$ skeleton during growth (Lough 2010). Indeed, geochemical analyses to reconstruct changes in climatic conditions are often the primary motive for collecting cores from massive corals (Lough & Cooper 2011), rather than measuring coral growth *per se*. Despite the widespread use of the growth chronologies provided by annual density bands in massive corals, we still do not have a clear understanding of the environmental or endogenous factors that control band formation (Helmle & Dodge 2011).

Early studies of growth of massive corals with density banding were based on collection of whole colonies (Dodge et al. 1974). Given the size of some colonies and the need to preserve them *in situ*, collection of a coral core from the top of a colony is now the preferred approach. One of the first reports of successful coral core collection (Hudson et al. 1976) used a hydraulic coring system adapted from the reef substratum corer of Macintyre (1975). Subsequently, several lightweight, air-powered drilling systems have been developed and are now routinely used (Stearn & Colassin 1979). For large colonies, the drilling rig is mounted perpendicular to the surface of the colony (Figure 1) and successive cores removed in 50–70 cm length sections (Isdale & Daniel 1989). Useful short (25–50 cm long) cores can also be obtained using handheld drills (Fabricius et al. 2011). Cores are typically 5–10 cm in diameter to increase the chances of obtaining clear banding patterns along a major growth axis (Lough & Barnes 1992, Helmle & Dodge 2011). The resulting hole is filled with a tapered, conical concrete plug (~7 cm in length) that has been presoaked in seawater; the plug is hammered into position so the top is as flush as possible with the colony surface. Plugging the hole prevents bioeroders and sediment invading the core hole, and living coral tissue will, in most cases, recolonize the surface of the plug within 1 to 3 years (Matson 2011). Cores are then mounted (e.g., on aluminium trays with plaster of Paris), and successive slices are removed using a milling machine. Ideally, slices should be one to three times as thick as the average diameter of the coral polyp to capture the mesoscale skeletal architectural features that form the annual density bands (Barnes & Devereux 1988). For *Porites*, for example, slice thickness is typically 6–7 mm.

After preparation and slicing of the core, coral skeletal slices are X-rayed to visualize the annual density banding (Helmle & Dodge 2011). Not all colonies of coral species that exhibit banding have clear annual bands; banding can often be distorted by convoluted skeletal growth, macroarchitectural features, major injuries, or the presence of boring organisms within the skeleton (Lough & Barnes 1992). As such, it is best to collect at least two cores from each coral colony, as well as coring multiple colonies from a given site. Converting the X-ray negative to a positive print visualizes the high-density bands as dark and low-density bands as light areas of skeleton (Figure 1).

Linear extension rate is the simplest, and most often reported, measure of growth that can be measured directly from X-ray negative or positive prints. Using X-radiographs, band width is defined as the linear distance between adjacent bands with equivalent density (e.g., between the tops of adjacent high-density bands; Aller & Dodge 1974). This method has been largely superseded by measures obtained from densitometry (see the next paragraph). Linear extension has also been measured from luminescent lines (D'Olivo et al. 2013, Tanzil et al. 2013) that are visible when coral

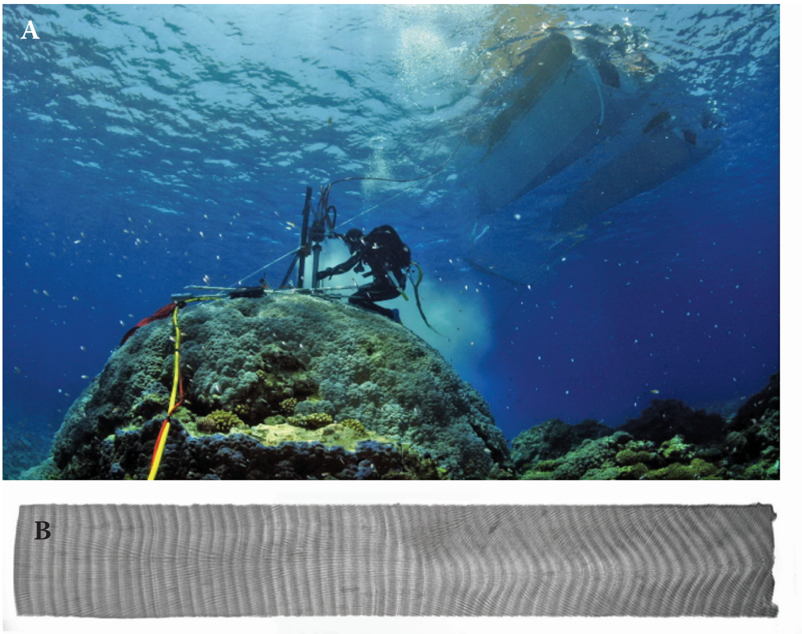

Figure 1 (A) Drilling rig used to extract long (>2 m in ~ 70 cm sections) cores from large colonies of massive *Porites* colonies at Rowley Shoals, Western Australia. (B) Positive X-radiograph of a thin slice (7 mm) of the top approximately 70 cm section of a representative core from Tantabiddi Reef, Western Australia, illustrating the annual high- and low-density band pairs. The estimated age of this coral is 178 years, but it should be noted that for massive *Porites*, any individual coral polyp has an average life expectancy of just 5 years (Drake & Barnes 1993.)

slices are viewed and photographed under ultraviolet light. In some locations, such as the nearshore GBR, the occurrence and intensity of luminescent lines reliably record seasonal river flood events (Lough et al. 2002) due to the incorporation of humic acids from soils into the coral skeleton (Boto & Isdale 1985, Grove et al. 2010). High-intensity luminescent lines associated with major river flood events can also provide additional dating control of annual density banding patterns in nearshore and midshelf reefs (Hendy et al. 2003, Cantin & Lough 2014). Finally, linear extension rates have also been measured from high-resolution geochemical or isotopic sampling of the coral skeleton (e.g., Storz & Gischler 2011), although the use of such tracers is rare.

The first reported continuous measurement of skeletal density along massive coral slices was based on quantitative scanning densitometry of X-radiographs (Buddemeier 1974). This ‘photo’, ‘optical’, or ‘X-ray’ densitometry involves scanning of the X-radiographs (now digital) alongside appropriate $CaCO_3$ standards to obtain absolute skeletal density. Measurements of aluminium bars on the same radiograph as the coral slice, or exposing the film without the coral slice present, allow corrections to be made for non-uniform irradiation of the film, known as the ‘heel effect’ (Chalker et al. 1985). More recently, Duprey et al. (2012) presented an accurate digital detrending approach that circumvents the need for these standards, although this has not, as yet, been generally adopted. X-ray densitometry has been further developed and combined with freely available band identification software (Helmle et al. 2002; Coral*XDS*, http://www.nova.edu/ocean/coralxds). Skeletal density can also be measured continuously by gamma densitometry, which is based on measurement of the attenuation of a beam of gamma photons through the thickness of the slice (Chalker & Barnes 1990, Draschba et al. 2000). For example, the custom-built gamma densitometer at the Australian Institute of Marine Sciences (AIMS) uses ^{241}Am as the source of gamma photons, providing absolute skeletal density measurements at 0.0254 cm intervals along the skeletal slice and has primarily been used for extracting growth characteristics of *Porites* spp. from tropical coral reefs off the eastern and western coasts of Australia (Lough & Barnes 2000, Cooper et al. 2012). Comparable skeletal density measurements have been reported from gamma and X-ray densitometry of the same coral slices (Carricart-Ganivet & Barnes 2007, Tanzil et al. 2013).

Computerized tomography (CT) scanning has also successfully been used to measure variation in skeletal density (Logan & Anderson 1991, Bessat & Buigues 2001). As with X-ray densitometry, this technique requires scanning standards of known density to convert the CT scan density measure (in Hounsfield units) to absolute skeletal density. The main limitation to the use of CT scanning is the cost and availability of CT scanners, which are specialized and expensive compared to readily available medical X-ray units. An advantage of CT scanning is that it generates images along freely chosen sections through the skeleton (Bosscher 1993); thus, an optimum measurement track can be selected that avoids areas of distorted or unclear annual banding. CT densitometry can also be undertaken on the whole coral core rather than on slices of the core and has been successfully applied to several massive coral species with different corallite sizes, such as *Siderastrea siderea* (Saenger et al. 2009), *Diploastrea heliopora* (Cantin et al. 2010), *Porites astreoides* (Crook et al. 2013), and massive *Porites* (Carilli et al. 2012). Annual linear extension rates can then be derived from continuous measurements of density versus distance along a core, or along a slice of a core, as the linear distance between equivalent points in adjacent annual bands (e.g., annual density maxima or minima; Figure 1B). Note that this measure of linear extension assumes that particular features of the annual density banding patterns are formed at the same time each year, which may not necessarily be true if skeletal density is controlled by exogenous factors.

Using X-radiography or gamma or CT densitometry, annual calcification rates (total $CaCO_3$ deposition) can be derived as the product of average annual skeletal density and annual linear extension rate. Overall, these three growth variables (linear extension, skeletal density, and overall calcification) are interrelated, but the relationship between them appears to vary with species. For instance, both *Porites* in the Indo-Pacific and *Montastraea* in the Atlantic show an inverse relationship between linear extension rate and average skeletal density (Scoffin et al. 1992, Lough & Barnes 2000, Carricart-Ganivet & Merino 2001), but variation in overall calcification rate is mainly driven by variation in linear extension rate for *Porites* (Scoffin et al. 1992, Lough & Barnes 2000, Elizalde-Rendón et al. 2010) compared with variation in skeletal density for *Orbicella* (= *Montastraea*) (Carricart-Ganivet 2004, Dávalos-Dehullu et al. 2008, Carilli et al. 2010). Consequently, all three parameters should be measured to fully describe coral growth characteristics for a particular species and location (Dodge & Brass 1984).

Direct measures of linear extension

Growth rates must be measured directly for corals that do not exhibit regular density bands in their skeletal structure (e.g., *Acropora pulchra*; Roche et al. 2010). This requires direct measurements of linear dimensions, area, volume, or weight, repeated over time to calculate a time-averaged rate of growth (Shinn 1966, Gladfelter et al. 1978, Barnes & Crossland 1980, Kinzie & Sarmiento 1986). Moreover, the only way to detect temporal changes in the growth of these corals is to compare direct measurements taken years to decades apart (Edmunds 2007, Bak et al. 2009, Anderson et al. 2014). Measuring linear extension (or branch extension; Simpson 1988) by taking repeated measurements from a fixed reference point to the branch tip or colony margin is one means to quantify changes in physical dimensions of coral skeletons. Using this technique, reference points can be natural features (Hughes & Jackson 1985) but are more often established by placing a permanent tag (e.g., plastic bands or cable ties) near the growing tip or colony margin (Shinn 1966, Yap & Gomez 1981, Simpson 1988, Edmunds 2007, Al-Hammady 2013). This method allows for repeated and continuous measurements of linear extension through time (Bak et al. 2009), although there are concerns that permanent tagging of individual branches (depending on the technique employed) could interfere with the translocation of carbon and energy to the growing branch tips (Oliver et al. 1983), thereby impeding growth. Notably, Oliver (1984) showed that extension rates of tagged branches of *Acropora* depended on the placement of the tag relative to the branch tip, with tags closest to the branch tip causing the greatest reductions in growth.

Given the widespread use of tagging to directly measure linear extension (Table 2), several studies have explicitly focused on resolving potential bias in this method (e.g., Reed 1981, Oliver 1984, Simpson 1988). To test the effect of tagging on growth rates of individual branches, Simpson (1988) directly compared linear extension rates of *Acropora muricata* (= *formosa*) between branches that were tagged versus nearby branches stained with alizarin red (discussed further in this chapter) and showed that tagged branches grew 15% slower than stained branches in the first month, but thereafter there was no significant difference in growth rates. Similarly, Reed (1981) quantified linear extension for *Oculina varicosa* over a 1-year period and found no difference in growth estimates for branches or colonies that were tagged versus stained with alizarin red. To minimize short-term effects of tagging, it is prudent to tag colonies at least 1 month in advance of initiating growth measurements (*sensu* Bak et al. 2009). Another important consideration is the number of branches per colony that should be tagged and measured to obtain reasonable estimates of linear extension; corals exhibit substantial intra- and intercolony variation in growth (Oliver 1984), and increasing the number of tagged branches per colony, as well as the number of colonies considered, can provide estimates of growth rates that are more precise. For *Acropora muricata* (= *formosa*), Simpson (1988) recommended tagging and measuring at least seven branches per colony to account for within-colony variation. However, many studies do not report the number of branches tagged

Table 2 Details of studies employing tagging methodology to measure linear extension rate in corals

Species	No. of branches (colonies)	Distance from tip (cm)	Mortality (% of branches)	Duration	Reference
Acropora cervicornis	13 (1)	10	—	1 year	Shinn 1966
	1 (18)	—	—	88 days	Torres et al. 2007
A. hemprichii	— (15)	—	—	16 months	Ebeid et al. 2009
	— (4)	—	—	—	Al-Hammady 2013
A. muricata	—	—	—	250 days	Oliver 1984
(= *formosa*)	30	3	56.6	344 days	Charuchinda & Hylleberg 1984
	— (24)	—	—	13 months	Jinendradasa & Ekaratne 2000
	60 (1)	—	60	2 years	Suresh & Mathew 1993
	30–40 (8)	5	—	13 months	Simpson 1988
A. palmata	49	15	—	2 years	Bak et al. 2009
A. pharaonis	— (15)	—	—	16 months	Ebeid et al. 2009
A. pulchra	2 (5)	—	—	2 years	Yap & Gomez 1985
A. yongei	3 (29)	1–3	9	4 months	Anderson et al. 2012
Isopora (= *Acropora*) *cuneata*	3 (32)	1–3	3	4 months	Anderson et al. 2012
Pocillopora damicornis	3 (32)	1–3	3	4 months	Anderson et al. 2012
Porites heronensis	3 (30)	1–3	3	4 months	Anderson et al. 2012
Seriatopora hystrix	3 (30)	1–3	10	4 months	Anderson et al. 2012
Stylophora pistillata	— (15)	—	—	16 months	Ebeid et al. 2009
	3 (31)	1–3	7	4 months	Anderson et al. 2012

per colony (Table 2), and for those that do, the number of branches per colony is often fewer than seven (Torres et al. 2007).

An inherent limitation of studies that measure linear extension based on a limited number of individually tagged branches is that any damage to the specific focal branches will lead to underestimates of growth. Given that injuries accumulate through time (affecting an ever-increasing proportion of branches), the effective duration of tagging studies is limited. For example, Charuchinda & Hylleberg (1984) found that only 13 (of 30) tagged branches of *Acropora muricata* were undamaged after 344 days, greatly affecting the power of their statistical analyses. Many studies explicitly exclude branches that exhibit no (or sometimes negative) growth, attributing this to extrinsic disturbances (e.g., injuries) or intrinsic effects on growth (such as physiological stresses or changes in pigmentation; Shinn 1966, Neudecker 1981, Bak et al. 2009) or both. At Lord Howe Island, Anderson et al. (2012) found that a disproportionate number of tagged branches of *Seriatopora hystrix* died during the course of a 6-month growth study, largely due to the spread of algae that had initially colonized plastic cable ties attached to individual branches (Table 2). In some cases, the algae had spread to immediately adjacent branches, while other branches were otherwise healthy.

To circumvent potential issues associated with placing permanent tags on coral branches, vital dyes or stains (e.g., alizarin sulphonate, calcein, and oxytetracycline) can be used to mark the underlying coral skeleton at a given time (reviewed by Holcomb et al. 2013), from which all subsequent growth is clearly visible and measurable (Figure 2). These stains are incorporated into the skeleton through calcification, so corals must be exposed to the stain during a period of active growth (Holcomb et al. 2013). For alizarin sulphonate (commonly referred to as alizarin red), staining is achieved by exposing whole, live colonies to a dilute solution (ca. 10–15 mg L^{-1} alizarin red in seawater; Barnes 1972, Dustan 1975) for at least 3 hours in sunlight (Table 3), depending on the species, light intensity, and seawater temperature. At high-latitude reefs, such as Lord Howe Island (31°S), where low temperatures and light intensity potentially limit rates of calcification, staining may be largely ineffective at normal exposure times of 3–4 hours (Harriott 1999). Anderson et al. (2014) therefore increased exposure times to 8 hours and successfully stained a broad range of different coral species at this location (Figure 2).

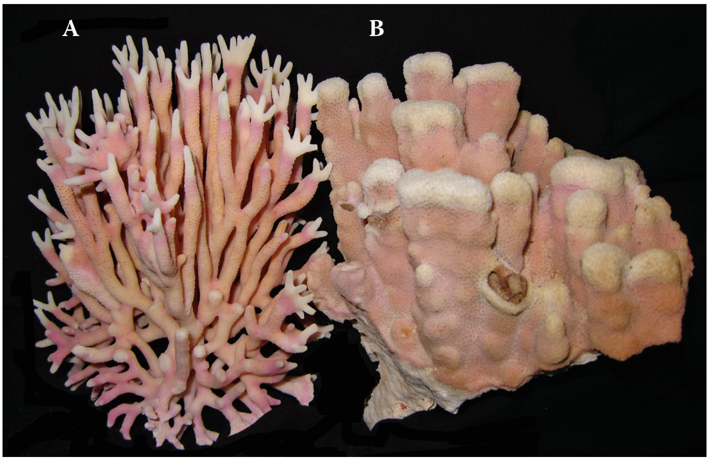

Figure 2 Alizarin staining to reveal subsequent rates of radial extension across the entire surface of a (A) branching coral (*Seriatopora hystrix*) and (B) columnar coral (*Porites heronensis*). Corals were stained in March 2010 (6–8 hours immersion in 10 mg L^{-1} of alizarin stain mixed in seawater), then reattached to reef substratum in lagoon habitats (4 m depth) at Lord Howe Island. Corals were retrieved in May 2011 and immediately bleached to reveal newly accreted carbonate (in white) above the distinct stain line (pink).

Table 3 Spatial and taxonomic variation in exposure time (hours) used for staining *in situ* with alizarin red

Exposure (hours)	Species	Location	Reference
3	*Acropora muricata* (= *formosa*)	Magnetic Island, Davies Reef, GBR	Oliver 1984
4	*A. muricata*, *Montipora aequituberculata*, *Turbinaria mesenterina*	Middle Reef, GBR	Browne 2012
4	*Acropora palmata*, *A. prolifera*, *A. cervicornis*	US Virgin Islands	Gladfelter et al. 1978
4–6	*A. cervicornis*	US Virgin Islands	Gladfelter 1984
5	*Pocillopora damicornis*	Panama	Glynn & Stewart 1973
5–6	*Acropora aspera*	India	Suresh & Mathew 1995
6–8	*A. muricata*, *Pocillopora damicornis*, *Porites cylindrica* (= *andrewsi*)	Guam	Neudecker 1981
6–8	*Acropora yongei*	Houtman Abrolous	Marsh 1992
7–8	*A. yongei*, *Pocillopora damicornis*, *Isopora* (= *Acropora*) *cuneata*, *Porites heronensis*, *Seriatopora hystrix*, *Stylophora pistillata*	Lord Howe Island	Anderson et al. 2014
8	*Acropora muricata*, *Pocillopora damicornis*	Houtman Abrolous (winter)	Crossland 1981
24	*Porites lutea*	Thailand	Charuchinda & Chansang 1985
24	*Orbicella* (= *Montastraea*) *annularis*, *Porites astreoides*	US Virgin Islands	Gladfelter et al. 1978
36–48	*Orbicella annularis* (28 m water depth)	Jamaica	Dustan 1975
48	*Lophelia pertusa* (deep-water coral)	Mexico	Brooke & Young 2009

One limitation of this technique is that alizarin red is toxic to corals (Lamberts 1978), and prolonged exposure or excessive concentrations may ultimately kill corals or suppress growth. In one study, Dodge et al. (1984) stained *Orbicella* (= *Montastraea*) *annularis* in aquaria using 10 mg L^{-1} of alizarin red for 24 hours (longer than most *in situ* studies) and showed that calcification rates were suppressed for 6 days thereafter. In contrast, Holcomb et al. (2013) investigated the effects of different dyes on the temperate coral *Astrangia poculata* and found that alizarin red did not significantly affect coral growth but did cause a reduction in polyp extension during staining. Similarly, Marsh (1992) found no adverse effects of alizarin red on *Acropora yongei*, and several studies of massive corals have found no difference between growth rates estimated using X-radiography of density bands compared with growth measured using staining (e.g., *Orbicella annularis*; Mendes & Woodley 2002, Mendes 2004), suggesting that staining does not have lasting or ecologically important effects on growth rates. However, care should be taken to use the minimum exposure time that will result in effective staining for different corals and in different locations.

Major benefits associated with the use of dyes (e.g., alizarin red) to directly measure rates of linear extension are that 1) this method is not specific to any type or size of coral (cf. retrospective measures described previously), and it can be used on all corals from newly settled polyps to large colonies with any growth form (Holcomb et al. 2013); 2) patterns of coral growth (e.g., major axes of linear extension and effects of localized injuries on subsequent growth) can be readily observed across the entire colony or proportion of the colony that was stained, revealing major areas of growth and also accounting for any portions of the colony where growth was compromised due to injuries or damage; and 3) it is possible to determine the actual amount of calcium carbonate that was added to achieve the observed rates of linear extension, providing direct links between these two commonly used metrics of coral growth (discussed further in the section on calcification rates). To measure calcification rates, all white (unstained) carbonate deposited post-staining may be separated from the stained skeletal material and then weighed (Gladfelter 1984, Browne 2012). Alternatively, skeletal extension rates are multiplied by skeletal density to estimate calcification rates (Morgan & Kench 2012). These methods provide highly conservative measures of calcification rate because any calcium carbonate deposited below the stain line cannot be discerned (Manzello 2010), and it can also be difficult to separate the stained and unstained portions of the skeleton. The major drawback of using vital dyes is that corals must be sacrificed to record change in physical dimensions, meaning that, unless colonies are subsampled through time, the method generates a single time-averaged estimate of coral growth across the period between staining and subsequent collection (Morgan & Kench 2012).

Regardless of measurement technique, a major issue relating to measuring average annual skeletal extension rates of corals is that these data are not directly comparable among corals with different growth forms (Browne 2012). Notably, different measurements are taken depending on the way that the coral colonies grow (Figure 3). For complex branching corals (arborescent and caespitose forms), each branch grows throughout the life of the colony (Wallace 1999); therefore, skeletal extension is measured based on the change in the length of individual and often randomly selected branches ('branch extension'; Oliver et al. 1983, Harriott 1998). In contrast, branch length is finite in other, more-prostrate branching corals (tabular, digitate, and to a lesser extent, corymbose forms), such that growth is only apparent when measuring linear extension of new branches on the periphery of the colony or when measuring change in horizontal dimensions.

When comparing skeletal extension rates between branching and non-branching corals, the problem is more acute. It is possible, for example, that the widely reported differences in extension rates between branching versus massive (or hemispherical) colonies are simply due to the fact that branch extension essentially reflects 1-dimensional growth (especially for very slender branches), whereas skeletal extension in hemispherical colonies represents growth in three dimensions simultaneously. In most cases, skeletal extension is measured in only one direction (e.g., cores from

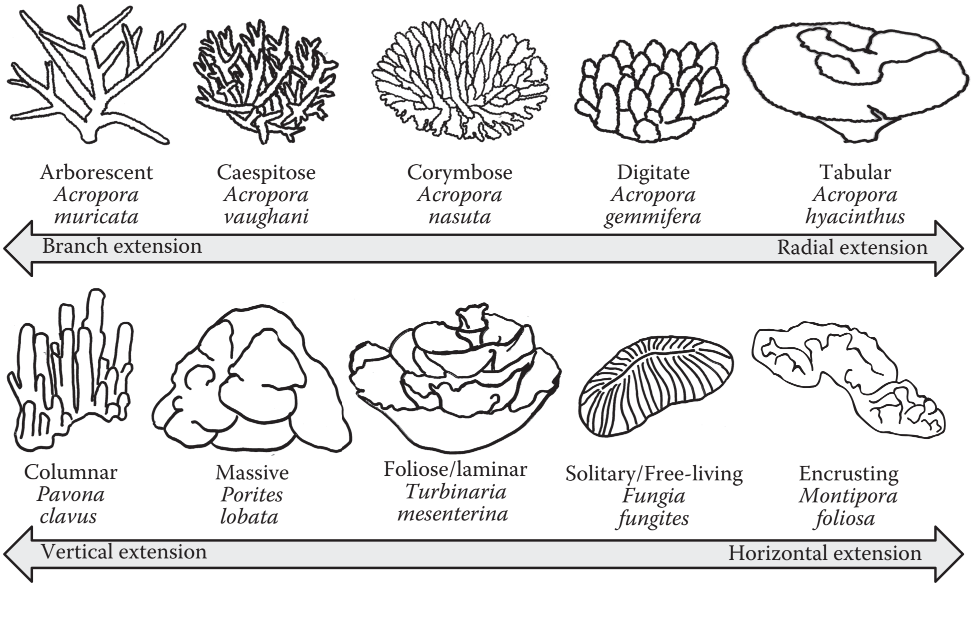

Figure 3 Major growth forms of scleractinian corals arranged according to their major growth axis. Change in area of occupation (standardized for colony size by calculating change in arithmetic mean radius) is the most suitable growth metric for corals to the right.

massive corals are almost invariably taken vertically from the top of the colony; Lough & Cooper 2011), which may over- or underestimate extension rates compared to studies that average skeletal measurements taken in multiple directions and at multiple locations across the colony (e.g., Morgan & Kench 2012). In massive *Porites*, for example, linear extension and calcification rates are about 15% higher along the vertical growth axis compared to the horizontal growth axis, likely related to light availability (Lough & Barnes 2000). Moreover, the terms 'skeletal extension' and 'branch extension' are often used interchangeably (Morgan & Kench 2012), and in some multispecies studies, it is not always clear what exactly has been measured for each different coral type, leading to further confusion about the relationship between linear extension and environmental conditions for different species.

Changes in horizontal planar area or area of occupancy

Growth of colonial organisms, such as corals, is achieved largely through the addition of polyps or modules, the size of which is species specific. In scleractinian corals, there is theoretically no intrinsic limit to the number of polyps within a colony and, hence, few intrinsic limits to colony size (i.e., growth is theoretically indeterminate, although some corals may senesce; Rinkevich & Loya 1986). However, there are many extrinsic factors that limit colony size, particularly the decrease in mechanical stability as colony size increases, a feature that is particularly apparent in colonies with tabular or corymbose morphologies (Madin & Connolly 2006, Madin et al. 2014). Furthermore, competition, predation, disease, and disturbance are all extrinsic factors that limit colony growth and potentially decrease realized growth rates. In addition, the vulnerability of a colony to agents of partial mortality increases with colony size because the probability of encountering such agents increases with the size of colonies (Jackson 1979, Jackson & Hughes 1985). A large proportion of polyps within a colony can die, yet the colony can still survive. This 'partial mortality' means that, unlike most unitary organisms, coral colonies can decrease as well as increase in size. The incidence of partial mortality is often high, particularly in some morphologies, such as massive corals (Hughes & Jackson 1985, Babcock 1991, Bythell et al. 1993, Baird & Marshall 2002). Consequently, methods that can detect decreases as well as increases in colony size, such as arithmetic mean radius (AMR; Figure 4) or changes in weight (as might be determined from a buoyant weight technique, described in the next section), are important in the study of coral demography.

Expressing growth as linear extension accurately captures the way that some corals grow; tabular, digitate, encrusting, and laminar corals tend to grow in a predictable way (in ideal conditions), adding polyps to the periphery of the colony (Stephenson & Stephenson 1933). Consequently, rates of radial extension should be largely independent of colony size (Figure 4B), whereas many other growth measurements (e.g., changes in the horizontal planar area of colonies, which is equivalent to the 'shaded substratum area' or 'projected area'; Jackson 1979) effectively decline with increases in colony size. Importantly, proportional increases in the horizontal planar area of corals decline rapidly with colony size (Figure 4A), potentially explaining why many early studies reported that small colonies "grow" more quickly than larger ones (e.g., Stephenson & Stephenson 1933). As change in planar area represents the amount of new reef 'space' that a coral colony occupies over a certain growth interval, it is particularly relevant, and widely used, for ecological studies of competition (e.g., Connell 1973, Connell et al. 1997) and population structure (e.g., Bak & Meesters 1999). Changes in planar area can be readily converted to change in AMR to provide a size-independent measure of linear growth.

Changes in the projected area of scleractinian corals are most commonly determined from planar photographs of individually tagged or identifiable colonies taken at repeated intervals (e.g., Madin et al. 2014). To do this, it is critical that a 2-dimensional scale bar is included within the photograph, that this scale bar is placed level with the upper surface of the colony, and that the image is recorded with a camera held in a fixed position with the focal plane parallel to the colony surface.

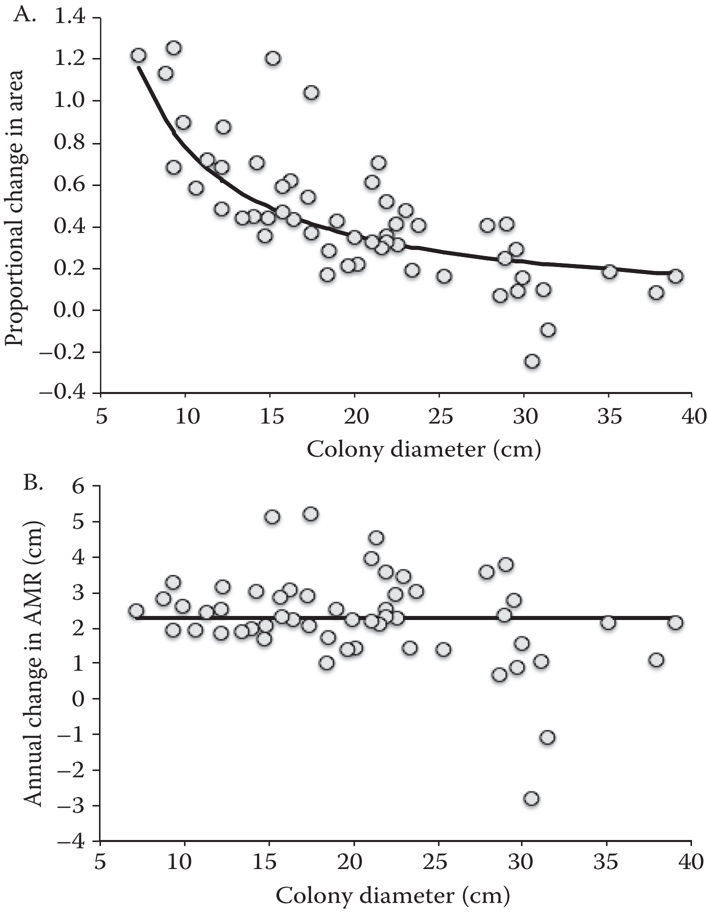

Figure 4 (A) Proportional change in area and (B) annual change in arithmetic mean radius (AMR) versus initial diameter for the digitate coral *Acropora millepora* measured over 524 days (April 2009 to October 2010) at the Keppel Islands, inshore Great Barrier Reef (J. Tan unpublished data). Rather than representing the line of best fit, trend lines indicate the theoretical relationship assuming constant radial growth of 2.28 cm yr^{-1}.

The planar area at each time point is estimated by reference to the scale bar. The AMR is then calculated from each image, and it is the change in the estimated radius (not absolute or proportional changes in planar area) that is used to quantify growth. While this process sounds simple, there are a number of issues to consider to precisely and accurately estimate the planar area and linear extension from photographs, including 1) barrel distortion (a lens effect that causes images to be distorted in shape), which can lead to underestimates of planar area (especially for larger colonies) but can be corrected based on the make and model of the camera used; 2) differences in the placement of the scale relative to the surface of the colony (e.g., if the scale in one image sits above the surface of the colony and is flush with the surface of the colony in the next image, the second area estimate will be larger); 3) differences in the lens-to-subject distance for successive photographs of the same colony, which is often corrected by attaching a measuring rod to the camera housing to maintain a fixed distance; and 4) errors associated with changes in perspective, whereby only photographs taken from directly above and parallel to the surface of the colony will provide accurate estimates of planar area.

The main advantage of estimating rates of linear extension from planar colony area is that colony area is an important determinant of colony fate and fitness, influencing fecundity (Babcock

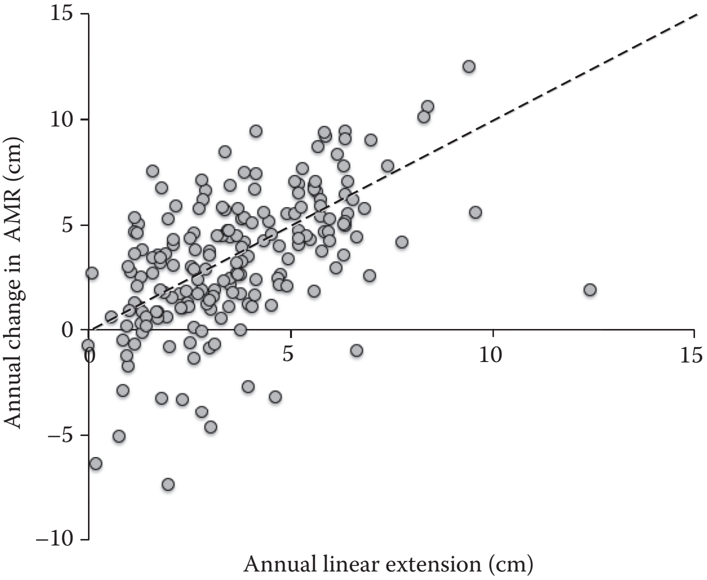

Figure 5 Relationship between linear extension and change in arithmetic mean radius (AMR) for *Acropora hyacinthus* on the Great Barrier Reef. Direct estimates of linear extension were derived by placing tags close (within 5 cm) to the circumference of the colony and recording change in the minimum distance from the tag to the circumference after 1 year (K. Anderson unpublished data). AMR was calculated based on change in projected (planar) area determined from photographs of each colony taken 1 year apart.

1991, Hall & Hughes 1996) and probability of mortality (Madin et al. 2014). There is likely to be a strong positive relationship between skeletal extension rates of corals measured using direct estimates of linear extension and AMR, but direct estimates will not effectively capture negative growth (Figure 5). Conversely, AMR aggregates positive (vegetative growth) and negative growth (injury and partial mortality), providing an ecologically relevant measure of realized growth.

Measuring colony area also allows simultaneous exploration of the size structure of coral populations, which can provide important insights into aspects of coral demography, such as population regulation (Bak & Meesters 1999). It is not clear, however, whether estimates of coral growth derived from planar area are comparable among corals with different growth forms. Changes in the area of substratum occupied by coral colonies is considered robust for comparing among corals that have a generally circular projected area and tend to grow primarily in the horizontal plane (e.g., digitate, corymbose, and tabular *Acropora*; and encrusting corals). However, whether it is possible to derive meaningful estimates of growth from the planar area of colonies with complex shapes (e.g., arboresent *Acropora*) needs to be examined in more detail. Measurement of planar area also disregards vertical growth, which can be the main axis of growth for some corals (e.g., columnar corals) when not constrained by water depth. The relationship between growth rates measured from planar area and other measures of growth (e.g., direct measures of linear extension and calcification) is also unclear and rarely investigated. It is important, therefore, to establish a common metric of coral growth when comparing corals with different growth forms (e.g., comparing strategies of energy allocation, Leuzinger et al. 2003; defining the functional role of coral species with respect to framework building, Wells 1957). However, many of the aforementioned methods and measures of changes in the physical dimensions of coral colonies (linear dimensions, area, and volume) are not directly comparable across all corals. The most universal and broadly comparable measure of coral growth probably relates to change in weight or calcification.

Change in weight or calcification

As the growth of scleractinian corals is fundamentally dependent on the deposition of calcium carbonate, change in weight is one of the most direct and unequivocal measures of coral growth. Moreover, measurements made directly in the currency of calcification rate (i.e., the mass of $CaCO_3$ accreted per unit time) relate directly to the stoichiometry of the mineral and can be more easily compared among coral species and among different studies. Moreover, calcification rate can be equated to linear extension if gross colony morphology and skeletal porosity are known (see section on calcification rates). Early measures of calcification relied on weighing freshly collected corals in air (Gardiner 1901, Finckh 1904), and this technique was still being used in the 1970s (Franzisket 1970). By the 1950s, however, T.F. Goreau had pioneered the use of radioactive ^{45}Ca to measure $CaCO_3$ deposited by corals (Goreau 1959), although the difficulties of working with radioactive materials, the requirement for destructive sampling of the coral to complete the analysis, and environmental hazards associated with using radioactive isotopes *in situ* (Goreau & Goreau 1959) have limited adoption of this technique. Even now, it is rarely used in coral biology (Marshall & Clode 2004, Al-Horani et al. 2007), although contemporary interest in coral calcification rates may renew attention to this valuable tool.

Measuring the weight of corals in air has the obvious and significant limitation of subjecting corals to prolonged aerial exposure. To avoid this problem, Bak (1973) weighed corals submerged in seawater and then estimated the dry weight of corals through *in situ* calibration with lead weights. Later, estimates of dry weight were calculated from 'buoyant weight' by the Archimedes' principle (Jokiel et al. 1978), accounting for the density of both seawater and the coral skeleton. Jokiel et al. (1978) described several configurations of the buoyant weight technique in which resolutions of between 0.1 mg and 2 g could be attained with specimens ranging in weight between 10 g and 5 kg, respectively. Spencer Davies (1989) published further refinements in the buoyant weight technique, making use of electronic top-loading balances and considering the effects of tissue weight on the estimates of skeletal weight. Using this method, Spencer Davies (1989) championed a non-destructive tool with 1% error and a temporal resolution of 24 h with 3–4 cm long branches of *Porites porites*. Buoyant weighing is now regularly used for experimental measurement of growth of small coral fragments ('nubbins'; Birkeland 1976) and larger colonies *in situ* (Bak 1973, Herler & Dirnwöber 2011).

An alternative non-destructive technique to quantify calcification rates is to measure changes in the total alkalinity (A_T in units of µmol kg^{-1}) in the seawater immediately surrounding a coral (Smith 1973, Smith & Kinsey 1978). A_T describes the summed capacity of the ions in seawater to neutralize hydrogen ions (H^+) and is affected by at least 13 ions, including CO_3^{2-} (Chisholm & Gattuso 1991). Because calcification represents the withdrawal of CO_3^{2-} from the dissolved inorganic carbon (DIC) pool of seawater, it affects A_T, with the stoichiometry of the reaction equating 2 molar equivalents of A_T to 1 mole of $CaCO_3$ (Smith & Kinsey 1978, Chisholm & Gattuso 1991).

Important advantages of the 'alkalinity anomaly technique' compared to alternative techniques for measuring coral calcification are that it can be used non-destructively in incubations lasting only a few hours (Smith & Kinsey 1978, Chisholm & Gattuso 1991) and does not require the addition of any reagents to seawater during incubations. The technique also enables comparison of day and night calcification rates and is particularly widely used in experimental studies of the effects of various environmental variables on calcification rates (e.g., Tentori & Allemand 2006). Mostly, however, the alkalinity anomaly technique is used to measure community-level or ecosystem-level rates of calcification (Bates 2002, Hata et al. 2002, Dove et al. 2013). The greatest limitation when using alkalinity anomaly to quantify calcification rates of individual corals is the limited duration of such studies, whereby calcification is typically measured over much less than 24 hours and often only during light or dark cycles, not both (Goreau & Goreau 1959).

Variability in coral growth

Despite difficulties in comparing measures of growth across the diverse group of scleractinians, rates of change in linear colony dimensions (linear or radial extension) vary greatly within and among coral taxa (Edmunds 2007, Morgan & Kench 2012). For example, Morgan & Kench (2012) recorded a more than 20-fold variation in extension rates among 12 different coral species in the Maldives, ranging from 2 mm yr^{-1} for the mushroom coral *Fungia fungites* up to 50 mm yr^{-1} for *Acropora nasuta*. It remains unclear to what extent these differences in linear or radial extension can simply be explained by differences in gross morphology as opposed to inherent differences in energy allocation to growth or contrasting effects of calcification rates and skeletal density. As in many studies, Morgan & Kench (2012) concluded that colony morphology was the major determinant of interspecific differences in skeletal extension rate, showing that branching corals (represented by *Acropora austera* and *A. muricata* [= *formosa*]) had average annual extension rates five times that of massive corals (represented by *Porites lobata*). Similarly, a multispecies comparison of corals in both the Atlantic and Pacific Oceans indicated high among-species variability, with growth rates of about 12 cm yr^{-1} for branching *Acropora* in the Pacific compared with about 0.5 cm yr^{-1} for massive species of *Porites* and *Favia* (Huston 1985). The problem, however, is that extension rates of branching *Acropora* and massive *Porites* are not directly comparable and are biased in favour of rapid growth of *Acropora*. This is because extension rates for branching corals are measured along selected branches, which may or may not sum to changes in the mean solid radius of the colony. For massive corals, however, extension rates are based on radial extension, which generally occurs across the entire surface of the colony, requiring significant production of calcium carbonate. Importantly, calcification rates may actually be higher for massive corals than for branching corals (Buddemeier & Kinzie 1976). At the very least, skeletons produced by massive corals are likely to persist much longer after the coral has died, directly contributing to the reef framework (Wells 1957).

Linear or radial extension

In preparing this review, a database comprising more than 740 records of coral growth was assembled from the literature, focusing on reported rates of extension and calcification. These data have global coverage, ranging from Lord Howe Island off south-eastern Australia to Kaneohe Bay in Hawaii, from the Red Sea across to the eastern Pacific and throughout the Atlantic Ocean. Comparison of linear extension rates (mm yr^{-1}), estimated from density banding patterns, alizarin red staining, direct tagging, photographic analysis, or a combination of these techniques (Table 4), reveals a unimodal distribution of growth rates with a geometric mean of approximately 16 mm yr^{-1} (Figure 6A). Gross colony morphology clearly influenced annual extension rates; massive species accounted for 62% of the lowest quartile of growth records, and branching species accounted for 92% of the upper quartile (Figure 6). Nevertheless, some massive species do attain high rates of radial extension, while extension rates of branching species are not uniformly high; massive species account for 5% of the upper 25% of growth records, and branching species account for 8% of the lower 25% of growth records (Figure 6). These data suggest that additional factors (e.g., environmental conditions and species-specific differences in the way $CaCO_3$ is accreted beneath the coral tissue layers) interact with gross colony morphology to influence annual extension. It is clear, for example, that branching *Acropora* have higher rates of linear extension than other branching corals, but branching corals generally grow faster than massive corals regardless of whether comparison is made within (e.g., branching vs. massive *Porites*) or among taxonomic groups (Figure 6).

Among the branching morphologies, variation in branching pattern also influences growth rates, with annual extension highest for the open branching (arborescent) and tabular *Acropora* (90 ± 6.3 mm and 73 ± 12.2 mm, respectively; mean extension ± standard error; Figure 6). Species

Table 4 Annual extension rates reported for 148 coral taxa, based on direct measurements following tagging or staining, changes in overall colony dimensions, retrospective measurements of density banding couplets using X-radiography, or a combination of methods

Species	Location, region	Sampling date	Methodology	Annual extension rate (mm yr^{-1})	Reference
Acropora abrotanoides	Yap, Micronesia			125–130	Huston 1985
A. aspera	Java, Southeast Asia	1980–1981	Alizarin	34.95–52.65	Brown et al. 1985
	India, Central Indian Ocean	1988–1989	Alizarin	43.5	Suresh & Mathew 1995
A. austera	Maldives, Central Indian Ocean	2010–2011	Tagging	62.9	Morgan & Kench 2012
A. cerealis	Enewetak Atoll, Micronesia	1972–1976	Tagging	42.9	Stimson 1985
A. cervicornis	Jamaica, Western Caribbean	2000–2008	Digital imagery	102	Crabbe 2009
	Jamaica, Western Caribbean	2006–2009	Digital imagery	111.2	Crabbe 2010
	Eastern Caribbean and Atlantic	1979–1980	Alizarin	100	Gladfelter 1984
	Eastern Caribbean and Atlantic	1977	Alizarin	71	Gladfelter et al. 1978
	Bahamas, Northern Caribbean		Alizarin, digital imagery	45–145	Glynn 1973
	Florida Keys, Northern Caribbean			40–45	Huston 1985
	Jamaica, Western Caribbean		Direct, calipers	100–120	Lewis et al. 1968
	Florida Keys, Northern Caribbean	1961–1962	Tagging	109–110	Shinn 1966
	Eastern Caribbean and Atlantic	2001	Tagging	142.35	Torres et al. 2007
	Jamaica, Western Caribbean	1978	Alizarin	35–159	Tunnicliffe 1983
A. cytherea	Maldives, Central Indian Ocean		Direct, radial	58.1	Clark & Edwards 1995
	Solitary Islands, Australia	1994–1995	Alizarin	20.9	Harriott 1999
	Johnston Atoll, Polynesia	1976	X-radiography, growth ridges	66.7–93.2	Jokiel & Tyler 1992
A. digitifera	Maldives, Central Indian Ocean	2010–2011	Alizarin	37.6	Morgan & Kench 2012
A. divaricata	Maldives, Central Indian Ocean		Direct, radial	41.5	Clark & Edwards 1995
A. elseyi	Waikiki aquarium, Polynesia	1992	Digital imagery	127	Atkinson et al. 1995
	GBR, Australia		Alizarin	38	Oliver 1985

(Continued)

Table 4 (Continued) Annual extension rates reported for 148 coral taxa, based on direct measurements following tagging or staining, changes in overall colony dimensions, retrospective measurements of density banding couplets using X-radiography, or a combination of methods

Species	Location, region	Sampling date	Methodology	Annual extension rate (mm yr^{-1})	Reference
A. eurystoma	Red Sea, Middle Eastern Seas	2001–2002	Alizarin	16.46–52.8	Bongiorni et al. 2003
A. florida	GBR, Australia		Alizarin	45	Oliver 1985
A. gemmifera	Maldives, Central Indian Ocean	2010–2011	Alizarin	24	Morgan & Kench 2012
A. granulosa	Egypt, Middle Eastern Seas	1998	Alizarin	5.9–9.24	Kotb 2001
A. hemprichii	Red Sea, Middle Eastern Seas	2011–2012	Tagging	4.75–15.04	Al-Hammady 2013
	Red Sea, Middle Eastern Seas	2001–2002	Tagging	9.6	Ebeid et al. 2009
A. humilis	Maldives, Central Indian Ocean		Direct, radial	19.3	Clark & Edwards 1995
	Enewetak Atoll, Micronesia	1972–1976	Direct, diameter	22.9	Stimson 1985
	Johnston Atoll, Polynesia	1976	X-radiography, growth ridges	9.6–23.7	Jokiel & Tyler 1992
A. hyacinthus	Maldives, Central Indian Ocean		Direct, radial	43.3	Clark & Edwards 1995
	Enewetak Atoll, Micronesia	1975–1978	Direct, diameter	99.3	Stimson 1985
A. intermedia (= *nobilis*)	GBR, Australia		Alizarin	41	Oliver 1985
A. lamarcki	Maldives, Central Indian Ocean	2010–2011	Alizarin	32.4	Morgan & Kench 2012
A. muricata (= *formosa*)	GBR, Australia	2009–2010	Alizarin	63	Browne 2012
	Thailand, Southeast Asia	1984–1986	Alizarin	36–68.4	Chansang et al. 1992
	Thailand, Southeast Asia	1981–1982	Tagging	80	Charuchinda & Hylleberg 1984
	Western Australia, Australia	1979–1980	Alizarin	37–42.9	Crossland 1981
	GBR, Australia	1985	Alizarin	40.15	Dennison & Barnes 1988
	Western Australia, Australia	1979–1980	Alizarin	52–79	Harriott 1998
	Sri Lanka, Central Indian Ocean	1997–1998	Tagging	117.54–120.96	Jinendradasa & Ekaratne 2000
	Maldives, Central Indian Ocean	2010–2011	Tagging	58.5	Morgan & Kench 2012
	Guam, Micronesia	1976–1977	Alizarin	33	Neudecker 1981
	GBR, Australia		Tagging	52.8	Oliver 1984

(Continued)

Table 4 (Continued) Annual extension rates reported for 148 coral taxa, based on direct measurements following tagging or staining, changes in overall colony dimensions, retrospective measurements of density banding couplets using X-radiography, or a combination of methods

Species	Location, region	Sampling date	Methodology	Annual extension rate (mm yr^{-1})	Reference
A. muricata	GBR, Australia		Alizarin	71.3	Oliver 1985
(=*formosa*)	GBR, Australia	1981–1982	Alizarin	80–166	Oliver et al. 1983
	Western Australia, Australia	1982–1983	Alizarin, tagging	137	Simpson 1988
	India, Central Indian Ocean	1988–1989	Tagging	80.5	Suresh & Mathew 1993
A. nasuta	Maldives, Central Indian Ocean	2010–2011	Alizarin	52.8	Morgan & Kench 2012
	Enewetak Atoll, Micronesia	1976–1977	Direct, diameter	39.2	Stimson 1985
A. palmata	Eastern Caribbean and Atlantic	1971–1973	Tagging	88	Bak 1976
	Eastern Caribbean and Atlantic	1977–1978	Tagging	88	Bak 1983
	Eastern Caribbean and Atlantic	2002–2004	Tagging	74–90	Bak et al. 2009
	Jamaica, Western Caribbean	2000–2008	Digital imagery	71	Crabbe 2009
	Jamaica, Western Caribbean	2006–2009	Digital imagery	65	Crabbe 2010
	Jamaica, Western Caribbean	2005–2012	Digital imagery	62.5	Crabbe 2013
	Eastern Caribbean and Atlantic	1977	Alizarin	47.3–99.3	Gladfelter et al. 1978
	Florida Keys, Northern Caribbean			25–40	Huston 1985
	Florida Keys, Northern Caribbean	1992–1996	Digital imagery	69	Lirman 2000
A. pharaonis	Red Sea, Middle Eastern Seas	2001–2002	Tagging	14.7	Ebeid et al. 2009
A. prolifera	Eastern Caribbean and Atlantic	1977	Alizarin	59.2–81.8	Gladfelter et al. 1978
	Florida Keys, Northern Caribbean			37	Huston 1985
A. pulchra	Waikiki aquarium, Polynesia	1992	Digital imagery	206	Atkinson et al. 1995
	Yap, Micronesia			101–172	Huston 1985
	Philippines, Southeast Asia	1980–1981	Tagging	166	Yap & Gomez 1985
A. robusta	Solitary Islands, Australia	1994–1995	Alizarin	22.4	Harriott 1999
	GBR, Australia		Alizarin	55	Oliver 1985

(Continued)

Table 4 (Continued) Annual extension rates reported for 148 coral taxa, based on direct measurements following tagging or staining, changes in overall colony dimensions, retrospective measurements of density banding couplets using X-radiography, or a combination of methods

Species	Location, region	Sampling date	Methodology	Annual extension rate (mm yr^{-1})	Reference
A. solitaryensis	Solitary Islands, Australia	1994–1995	Alizarin	16.7	Harriott 1999
A. spicifera	Western Australia, Australia	1990	Direct, crest to crest	104.2–123.6	Stimson 1996
Acropora spp.	Lord Howe Island, Australia	2010–2011	Alizarin, tagging	42.42–62.04	Anderson et al. 2012
	Samoa, Polynesia	1917–1920	Digital imagery	30–76	Mayor 1924
A. valenciennesi	Sulawesi, Southeast Asia	2001–2002	Tagging	71–333	Crabbe & Smith 2005
A. valida	Solitary Islands, Australia	1994–1995	Alizarin	23.6	Harriott 1999
	Johnston Atoll, Polynesia	1976	X-radiography, growth ridges	45	Jokiel & Tyler 1992
A. yongei	Lord Howe Island, Australia	1994–1995	Alizarin	49.4	Harriott 1999
	Western Australia, Australia	1991–1992	Alizarin	69.3	Marsh 1992
Agaricia agaricites	Eastern Caribbean and Atlantic	1971–1972	Tagging	24	Bak 1976
	Eastern Caribbean and Atlantic	1981	X-radiography	1.6–1.7	Hubbard & Scaturo 1985
	Jamaica, Western Caribbean	1977–1978	Alizarin, digital imagery	4.5–6.5	Hughes & Jackson 1985
	Jamaica, Western Caribbean	1985	X-radiography	0.8–1.6	Huston 1985
	Eastern Caribbean and Atlantic	1974–1975	Alizarin, X-radiography	3.5–4.8	Stearn et al. 1977
A. lamarcki	Jamaica, Western Caribbean	1977–1978	Alizarin, digital imagery	4.5–5.5	Hughes & Jackson 1985
Agaricia spp.	Jamaica, Western Caribbean	2000–2008	Digital imagery	2.47	Crabbe 2009
Astrea (= *Montastraea*) *curta*	Lord Howe Island, Australia	1994–1995	X-radiography, alizarin	2.5–2.7	Harriott 1999
Astreopora myriophthalma	Enewetak Atoll, Micronesia	1972	X-radiography	7.5–13	Buddemeier et al. 1974
Balanophyllia europaea	Palinuro, Mediterranean	2003–2005	Annual bands, CT scan	0.96–1.49	Goffredo et al. 2009
Cladocora caespitosa	Adriatic Sea, Mediterranean	2002	X-radiography	3.46	Kružić et al. 2012
Coelastrea (= *Goniastrea*) *aspera*	GBR, Australia	1982–1984	X-radiography	3.9–4.1	Babcock 1988, 1991

(Continued)

Table 4 (Continued) Annual extension rates reported for 148 coral taxa, based on direct measurements following tagging or staining, changes in overall colony dimensions, retrospective measurements of density banding couplets using X-radiography, or a combination of methods

Species	Location, region	Sampling date	Methodology	Annual extension rate (mm yr^{-1})	Reference
Colpophyllia natans	Jamaica, Western Caribbean	2000–2008	Digital imagery	6.34	Crabbe 2009
	Jamaica, Western Caribbean	1985	X-radiography	9.2–10.5	Huston 1985
Cyphastrea ocellina	Hawaiian Archipelago, Polynesia	1987	Alizarin	4.145	Romano 1990
C. serailia	Lord Howe Island, Australia	1994–1995	X-radiography, alizarin	2.6–3.4	Harriott 1999
	Australia		X-radiography	7.2–10.4	Roberts & Harriott 2003
Dendrogyra cylindrus	Florida Keys, Northern Caribbean	1994–1995	Direct, vertical	20	Hudson & Goodwin 1997
Diploastrea heliopora	Red Sea, Middle Eastern Seas	2008	CT scan	1.8	Cantin et al. 2010
	Vanuatu, Melanesia		X-radiography	2–5	Corrège et al. 2004
Diploria labyrinthiformis	Jamaica, Western Caribbean	2000–2008	Digital imagery	4.33	Crabbe 2009
	Northern Caribbean	1973	X-radiography	3.6	Dodge & Thomson 1974
	Florida Keys, Northern Caribbean	1948–1982	X-radiography	3.5	Ghiold & Enos 1982
	Eastern Caribbean and Atlantic	1981	X-radiography	3.3–4.6	Hubbard & Scaturo 1985
	Bermuda, Northern Caribbean	1990	X-radiography	3.25	Logan & Tomascik 1991
	Bermuda, Northern Caribbean	1991	X-radiography	3.71	Logan et al. 1994
Dipsastraea (= *Favia*) *pallida*	Lord Howe Island, Australia	1994–1995	X-radiography, alizarin	3.3–4.6	Harriott 1999
	Enewetak Atoll, Micronesia	1979	X-radiography	5.7	Highsmith 1979
D. (= *F.*) *speciosa*	Enewetak Atoll, Micronesia	1972	X-radiography	4.5–8.5	Buddemeier et al. 1974
	Enewetak Atoll, Micronesia	1971	X-radiography	4.6	Knutson et al. 1972
	Japan, Southeast Asia	1966–2007	X-radiography	6.6	Seo et al. 2013
Favia sp.	Maldives, Central Indian Ocean		Direct, radial	7.5	Clark & Edwards 1995
	Sulawesi, Southeast Asia	2001–2002	Tagging	2.86–12.73	Crabbe & Smith 2005
	Sulawesi, Southeast Asia		Digital imagery	8.27	Crabbe et al. 2006

(Continued)

Table 4 (Continued) Annual extension rates reported for 148 coral taxa, based on direct measurements following tagging or staining, changes in overall colony dimensions, retrospective measurements of density banding couplets using X-radiography, or a combination of methods

Species	Location, region	Sampling date	Methodology	Annual extension rate (mm yr^{-1})	Reference
Favites sp.	Maldives, Central Indian Ocean		Direct, radial	9.6	Clark & Edwards 1995
Fungia fungites	Enewetak Atoll, Micronesia	1972	X-radiography	10–12	Buddemeier et al. 1974
	Maldives, Central Indian Ocean	2010–2011	Alizarin	2	Morgan & Kench 2012
Gardineroseris planulata	Costa Rica, Western Caribbean	1985–1987	X-radiography, alizarin	10.4	Guzmán & Cortés 1989
	Panama, Western Caribbean	2003–2006	Alizarin	6.1	Manzello 2010
Goniastrea (= *Favia*) *stelligera*	Enewetak Atoll, Micronesia	1972	X-radiography	8–12	Buddemeier et al. 1974
G. edwardsi (= *parvistella*)	Enewetak Atoll, Micronesia	1972	X-radiography	10–12.5	Buddemeier et al. 1974
	Enewetak Atoll, Micronesia	1950–1971	X-radiography	12.5	Knutson et al. 1972
G. favulus	GBR, Australia	1982–1984	X-radiography	3.8–4.3	Babcock 1988, 1991
G. retiformis	Enewetak Atoll, Micronesia	1972	X-radiography	6–9	Buddemeier et al. 1974
	Enewetak Atoll, Micronesia	1979	X-radiography	6.8	Highsmith 1979
	Enewetak Atoll, Micronesia	1971	X-radiography	7.8	Knutson et al. 1972
Heliofungia actiniformis	Indonesia, Southeast Asia	2005–2006	Alizarin	5.7	Knittweis et al. 2009
Herpolitha limax	Enewetak Atoll, Micronesia	1972	X-radiography	10	Buddemeier et al. 1974
Hydnophora microconos	Enewetak Atoll, Micronesia	1972	X-radiography	11.5	Buddemeier et al. 1974
	Maldives, Central Indian Ocean	2010–2011	Alizarin	6.3	Morgan & Kench 2012
Isopora cuneata	Lord Howe Island, Australia	2010–2011	Alizarin, tagging	17.15–21	Anderson et al. 2012
Leptastrea purpurea	Maldives, Central Indian Ocean	2010–2011	Alizarin	1.8	Morgan & Kench 2012
Lithophyllon (= *Fungia*) *concinna*	GBR, Australia		Alizarin	3.6–11.3	Oliver 1985
Lobactis (= *Fungia*) *scutaria*	Hawaiian Archipelago, Polynesia		Direct	4.6–16.4	Edmondson 1929

(Continued)

Table 4 (Continued) Annual extension rates reported for 148 coral taxa, based on direct measurements following tagging or staining, changes in overall colony dimensions, retrospective measurements of density banding couplets using X-radiography, or a combination of methods

Species	Location, region	Sampling date	Methodology	Annual extension rate (mm yr^{-1})	Reference
Lobactis (= *Fungia*) *scutaria*	Johnston Atoll, Polynesia	1976	X-radiography, growth ridges	5.9–10.3	Jokiel & Tyler 1992
Lophelia pertusa	Gulf of Mexico, Northern Caribbean	1979–2013	Digital imagery	19.9	Larcom et al. 2014
Madracis mirabilis	Jamaica, Western Caribbean		Tagging	22	Bruno & Edmunds 1997
Meandrina meandrites	Jamaica, Western Caribbean	2000–2008	Digital imagery	1.22	Crabbe 2009
Merulina sp.	Western Australia, Australia	1990	Direct, crest to crest	17.2–29.3	Stimson 1996
M. ampliata	Singapore, Southeast Asia	1999–2000	Alizarin	10.2–24.6	Dikou 2009
Millepora tenera	Johnston Atoll, Polynesia	1976	X-radiography, growth ridges	18.5	Jokiel & Tyler 1992
Montastraea cavernosa	Jamaica, Western Caribbean	2000–2008	Digital imagery	6.45	Crabbe 2009
	Belize, Western Caribbean		X-radiography	4.36	Highsmith et al. 1983
Montipora sp.	Sulawesi, Southeast Asia	2001–2002	Tagging	1.75–9.74	Crabbe & Smith 2005
	Sulawesi, Southeast Asia		Digital imagery	6.91	Crabbe et al. 2006
	Enewetak Atoll, Micronesia	1972–1978	Direct, diameter	21.7	Stimson 1985
	Western Australia, Australia	1990	Direct, crest to crest	40.3–51.8	Stimson 1996
M. aequituberculata	GBR, Australia	2009–2010	Alizarin	29	Browne 2012
M. capitata	Hawaiian Archipelago, Polynesia	1996–1997	Alizarin	25.2–42.7	Grottoli 1999
	Hawaiian Archipelago, Polynesia		Alizarin	26.51	Rodgers et al. 2003
	Hawaiian Archipelago, Polynesia	1990	Direct, crest to crest	32.5	Stimson 1996
M. digitata	GBR, Australia	1980–1981	Alizarin	30.5	Heyward & Collins 1985
	Philippines, Southeast Asia	2005–2006	Tagging	33.8	Shaish et al. 2010
M. verrilli	Johnston Atoll, Polynesia	1976	X-radiography, growth ridges	17.2	Jokiel & Tyler 1992

(Continued)

Table 4 (Continued) Annual extension rates reported for 148 coral taxa, based on direct measurements following tagging or staining, changes in overall colony dimensions, retrospective measurements of density banding couplets using X-radiography, or a combination of methods

Species	Location, region	Sampling date	Methodology	Annual extension rate (mm yr^{-1})	Reference
M. verrucosa	Hawaiian Archipelago, Polynesia		Direct	14	Edmondson 1929
	Hawaiian Archipelago, Polynesia	1983	Alizarin	16.45–29.2	Cox 1986
Mussismilia braziliensis	Brazil, Eastern Caribbean and Atlantic	1998–2004	Alizarin	8	Kikuchi et al. 2013
Orbicella (= *Montastraea*) *annularis*	Eastern Caribbean and Atlantic	1971–1972	Tagging	8	Bak 1976
	Eastern Caribbean and Atlantic		X-radiography	1.56–10.41	Baker & Weber 1975
	Eastern Caribbean and Atlantic	1990–1991	X-radiography	2–16	Bosscher & Meesters 1992
	Gulf of Mexico, Western Caribbean	1977–1991	X-radiography	8.7	Carricart-Ganivet & Merino 2001
	Caribbean, Western Caribbean	1970–1979	X-radiography	8.6–8.9	Carricart-Ganivet 2004
	Mexico, Western Caribbean	1981–1995	X-radiography	8.2–9.1	Carricart-Ganivet et al. 2000
	Jamaica, Western Caribbean	2000–2008	Digital imagery	7.85	Crabbe 2009
	Western Caribbean	2000–2001	Direct, vertical	4.8–6	Cruz-Piñón et al. 2003
	Eastern Caribbean and Atlantic	1970–1979	X-radiography	9.8	Dodge & Brass 1984
	Jamaica, Western Caribbean		X-radiography	6.2–8.8	Dodge et al. 1974
	Jamaica, Western Caribbean	1971–1972	Alizarin	1.54–6.68	Dustan 1975
	Eastern Caribbean and Atlantic	1987–1989	X-radiography	9.75	Eakin et al. 1994
	Eastern Caribbean and Atlantic	1977	Alizarin	6.6–8.3	Gladfelter et al. 1978
	Panama, Western Caribbean	1985	X-radiography	8	Guzmán et al. 1991
	Belize, Western Caribbean		X-radiography	6.34	Highsmith et al. 1983
	Eastern Caribbean and Atlantic	1981	X-radiography	0.7–11.9	Hubbard & Scaturo 1985
	Gulf of Mexico, Northern Caribbean	1888–1907	X-radiography	6.8–8.9	Hudson & Robbin 1980

(Continued)

Table 4 (Continued) Annual extension rates reported for 148 coral taxa, based on direct measurements following tagging or staining, changes in overall colony dimensions, retrospective measurements of density banding couplets using X-radiography, or a combination of methods

Species	Location, region	Sampling date	Methodology	Annual extension rate (mm yr^{-1})	Reference
Orbicella (= *Montastraea*) *annularis*	Florida Keys, Northern Caribbean	1928–1978	X-radiography	6.3–11.2	Hudson 1981
	Florida Keys, Northern Caribbean	1986	X-radiography	8.3	Hudson et al. 1994
	Jamaica, Western Caribbean	1977–1978	Alizarin, digital imagery	3–4.5	Hughes & Jackson 1985
	Florida Keys, Northern Caribbean			6	Huston 1985
	Jamaica, Western Caribbean	1985	X-radiography	2.8–12.2	Huston 1985
	Florida Keys, Northern Caribbean	1970	X-radiography	17	Knutson et al. 1972
	Jamaica, Western Caribbean	1995–1996	Alizarin, X-radiography	8.55	Mendes & Woodley 2002
	Jamaica, Western Caribbean	1994–1996	Alizarin, X-radiography	8.76	Mendes 2004
	Eastern Caribbean and Atlantic	1981–1982	X-radiography	7.56	Tomascik & Sander 1985
	Eastern Caribbean and Atlantic	1983	X-radiography	8.8–12.4	Tomascik 1990
	Curacao, Eastern Caribbean and Atlantic	1991–1993	X-radiography	5.35–11.58	van Veghel & Bosscher 1995
Orbicella (= *Montastraea*) *faveolata*	Mesoamerican Reef, Western Caribbean	2006	Annual bands, CT scan	9.5	Carilli et al. 2010
	Mexico Caribbean, Western Caribbean	2000–2001	Direct, vertical	6–7.2	Cruz-Piñón et al. 2003
	Florida Keys, Northern Caribbean	1960–2007	X-radiography	8.1	Flannery & Poore 2013
	Florida Keys, Northern Caribbean	1937–1996	X-radiography	7.9	Helmle et al. 2011
	Mexico, Western Caribbean	1835–2002	X-radiography	11.2	Horta-Puga & Carriquiry 2014
	US Virgin Islands, Eastern Caribbean and Atlantic	1995–2006	X-radiography	8–12.6	Saenger et al. 2008
Orbicella (= *Montastraea*) *franksi*	Jamaica, Western Caribbean	2000–2008	Digital imagery	5.63	Crabbe 2009
	Bermuda, Northern Caribbean	1998–2001	X-radiography	2.3	Saenger et al. 2008
Oulophyllia crispa (= *aspera*)	Enewetak Atoll, Micronesia	1972	X-radiography	20–22	Buddemeier et al. 1974

(Continued)

Table 4 (Continued) Annual extension rates reported for 148 coral taxa, based on direct measurements following tagging or staining, changes in overall colony dimensions, retrospective measurements of density banding couplets using X-radiography, or a combination of methods

Species	Location, region	Sampling date	Methodology	Annual extension rate (mm yr^{-1})	Reference
Paragoniastrea (= *Goniastrea*) *australensis*	Lord Howe Island, Australia	1994–1995	X-radiography, alizarin	2.8–2.9	Harriott 1999
	Peel Island, Australia		X-radiography	5.6	Roberts & Harriott 2003
Pavona clavus	Costa Rica, Western Caribbean	1998–2000	Alizarin	6.1	Gateno et al. 2003
	Costa Rica, Western Caribbean	1985–1987	X-radiography, alizarin	9.6	Guzmán & Cortés 1989
	Costa Rica, Western Caribbean	1996–1997	Alizarin, X-radiography	17.8	Jimenéz & Cortés 2003
	Panama, Western Caribbean	2003–2006	Alizarin	9.8	Manzello 2010
	Gulf of Chiriqui/ Panama, Western Caribbean	1975–1979	X-radiography	9.3–13.2	Wellington & Glynn 1983
	Panama, Western Caribbean	1978–1979	Alizarin	14.92–18.42	Wellington 1982
P. duerdeni	Johnston Atoll, Polynesia	1976	X-radiography, growth ridges	8.6–11.8	Jokiel & Tyler 1992
P. gigantea	Costa Rica, Western Caribbean	1985–1987	X-radiography, alizarin	8.3	Guzmán & Cortés 1989
	Panama, Western Caribbean	2003–2006	Alizarin	9.2	Manzello 2010
	Gulf of Panama, Western Caribbean	1975–1979	X-radiography	8.5	Wellington & Glynn 1983
	Panama, Western Caribbean	1978–1979	Alizarin	11.67–12.83	Wellington 1982
P. maldivensis	Johnston Atoll, Polynesia	1976	X-radiography, growth ridges	11–13.1	Jokiel & Tyler 1992
P. varians	Costa Rica, Western Caribbean	1985–1987	X-radiography, alizarin	3.5	Guzmán & Cortés 1989
	Panama, Western Caribbean	2003–2006	Alizarin	3.2	Manzello 2010
Pectinia alcicornis	GBR, Australia	1985	Alizarin	1.2	Oliver 1985
Platygyra daedalea	Western Australia, Australia	1963–1983	X-radiography	15–16	Simpson 1988
P. daedalea (= *rustica*)	Hawaiian Archipelago, Polynesia	1971	X-radiography	22	Knutson et al. 1972
P. lamellina	Enewetak Atoll, Micronesia	1972	X-radiography	6.7–8	Buddemeier et al. 1974
P. sinensis	GBR, Australia	1982–1984	X-radiography	6.4–6.8	Babcock 1988, 1991

(Continued)

Table 4 (Continued) Annual extension rates reported for 148 coral taxa, based on direct measurements following tagging or staining, changes in overall colony dimensions, retrospective measurements of density banding couplets using X-radiography, or a combination of methods

Species	Location, region	Sampling date	Methodology	Annual extension rate (mm yr^{-1})	Reference
Platygyra spp.	IndoPacific, IndoPacific	1974	X-radiography	4.9–12	Weber & White 1974
Plesiastrea versipora	South Australia, Australia		X-radiography	4.14	Burgess et al. 2009
Pleuractis (= *Fungia*) *granulosa*	Red Sea, Middle Eastern Seas	1992–1995	Direct, growth rings	3.4	Chadwick-Furman et al. 2000
Pocillopora acuta (= *bulbosa*)	GBR, Australia	1932	Direct	25	Manton 1932
P. damicornis	Lord Howe Island, Australia	2010–2011	Alizarin, tagging	6.6–14.8	Anderson et al. 2012
	Western Australia, Australia	1979–1980	Alizarin	12.2–14.3	Crossland 1981
	Hawaiian Archipelago, Polynesia	1929	Direct	13.9	Edmondson 1929
	Gulf of Panama, Western Caribbean	1971–1972	Alizarin, digital imagery	32–52	Glynn & Stewart 1973
	Panama, Western Caribbean	1974		33.6–39.6	Glynn 1976
	Western Caribbean	1971–1974	Alizarin	30.8–38.6	Glynn 1977
	Galapagos, Eastern Pacific		Alizarin	22.4	Glynn et al. 1979
	Costa Rica, Western Caribbean	1985–1987	X-radiography, alizarin	29.8–34.6	Guzmán & Cortés 1989
	Solitary Islands/Lord Howe Island, Australia	1994–1995	Alizarin	12.4–16.1	Harriott 1999
	Costa Rica, Western Caribbean	1987–1999	Alizarin	38–66.8	Jimenéz & Cortés 2003
	Egypt, Middle Eastern Seas	1998	Alizarin	6.6–7.39	Kotb 2001
	Panama, Western Caribbean	2003–2006	Alizarin	27.8	Manzello 2010
	Hawaiian Archipelago, Polynesia		Direct, radial	13	Maragos 1972
	Thailand, Southeast Asia	1983	Alizarin	14.29	Martin & Le Tissier 1988
	Guam, Micronesia	1976–1977	Alizarin	29	Neudecker 1981
	GBR, Australia		Alizarin	36.6–43.2	Oliver 1985

(Continued)

Table 4 (Continued) Annual extension rates reported for 148 coral taxa, based on direct measurements following tagging or staining, changes in overall colony dimensions, retrospective measurements of density banding couplets using X-radiography, or a combination of methods

Species	Location, region	Sampling date	Methodology	Annual extension rate (mm yr^{-1})	Reference
P. damicornis	Hawaiian Archipelago, Polynesia	1987	Alizarin	16.4	Romano 1990
	Western Australia, Australia	1982–1983	Alizarin, tagging	45	Simpson 1988
	Enewetak Atoll, Micronesia	1972–1976	Direct, diameter	26.4	Stimson 1985
	Western Australia, Australia	1989	Alizarin	9–15	Ward 1995
	Panama, Western Caribbean	1978–1979	Alizarin	46.07–54.25	Wellington 1982
P. elegans	Costa Rica, Western Caribbean	1985–1987	X-radiography, alizarin	34.8	Guzmán & Cortés 1989
	Costa Rica, Western Caribbean	1996–1997	Alizarin	41.2–52.1	Jimenéz & Cortés 2003
	Panama, Western Caribbean	2003–2006	Alizarin	27.4	Manzello 2010
P. eydouxi	Enewetak Atoll, Micronesia	1972	X-radiography	50	Buddemeier et al. 1974
	Costa Rica, Western Caribbean	1996–1997	Alizarin	30.8	Jimenéz & Cortés 2003
	Johnston Atoll, Polynesia	1976	X-radiography, growth ridges	50.4	Jokiel & Tyler 1992
	Samoa, Polynesia	1917–1920	Digital imagery	20–47	Mayor 1924
P. inflata	Costa Rica, Western Caribbean	1996–1997	Alizarin	31.5	Jimenéz & Cortés 2003
P. ligulata	Hawaiian Archipelago, Polynesia		Direct	14.5	Edmondson 1929
P. meandrina	Hawaiian Archipelago, Polynesia		Direct	14.8	Edmondson 1929
	Costa Rica, Western Caribbean	1996–1997	Alizarin	34.2–44.6	Jimenéz & Cortés 2003
	Johnston Atoll, Polynesia	1976	X-radiography, growth ridges	23	Jokiel & Tyler 1992
	Maldives, Central Indian Ocean	2010–2011	Alizarin	18.7	Morgan & Kench 2012
	Hawaiian Archipelago, Polynesia		Alizarin	6	Rodgers et al. 2003
Pocillopora spp.	Samoa, Polynesia	1917–1920	Digital imagery	23–36	Mayor 1924

(Continued)

Table 4 (Continued) Annual extension rates reported for 148 coral taxa, based on direct measurements following tagging or staining, changes in overall colony dimensions, retrospective measurements of density banding couplets using X-radiography, or a combination of methods

Species	Location, region	Sampling date	Methodology	Annual extension rate (mm yr^{-1})	Reference
P. verrucosa	Maldives, Central Indian Ocean		Direct, radial	25.1	Clark & Edwards 1995
	Red Sea, Middle Eastern Seas	2006–2007	Alizarin	17.88	Mass & Genin 2008
	Red Sea, Middle Eastern Seas	2006–2007	Alizarin	37.6	Mass & Genin 2008
	Enewetak Atoll, Micronesia	1972–1976	Direct, diameter	37.2	Stimson 1985
Porites (branching)	Yap, Micronesia			8–10	Huston 1985
P. astreoides	Jamaica, Western Caribbean	1981–1982	Alizarin	3.1–7.3	Chornesky & Peters 1987
	Jamaica, Western Caribbean	2000–2008	Digital imagery	4.07	Crabbe 2009
	Jamaica, Western Caribbean	2006–2009	Digital imagery	4.25	Crabbe 2010
	Western Caribbean		Annual bands, CT scan	3	Crook et al. 2013
	Mexico/Cuba, Western Caribbean	1997–2004	X-radiography	3.54–3.69	Elizalde-Rendón et al. 2010
	US Virgin Islands, Eastern Caribbean and Atlantic	1977	Alizarin	3–8.9	Gladfelter et al. 1978
	Panama, Western Caribbean	1985	X-radiography	5.25	Guzmán et al. 1991
	Belize, Western Caribbean		X-radiography	4.75	Highsmith et al. 1983
	US Virgin Islands, Eastern Caribbean and Atlantic	1981	X-radiography	1.9–3.1	Hubbard & Scaturo 1985
	Jamaica, Western Caribbean	1977–1978	Alizarin, digital imagery	7.8–8	Hughes & Jackson 1985
	Jamaica, Western Caribbean	1985	X-radiography	2.2–6.3	Huston 1985
	Florida Keys, Northern Caribbean			3.5–14	Huston 1985
	Bermuda, Northern Caribbean	1989	X-radiography	2	Logan & Tomascik 1991
	Barbados, Eastern Caribbean and Atlantic	1974–1975	Alizarin, X-radiography	5.9–6.5	Stearn et al. 1977
P. australiensis	Japan, Southeast Asia	1992–1994	X-radiography	12	Mitsuguchi et al. 2003

(Continued)

Table 4 (Continued) Annual extension rates reported for 148 coral taxa, based on direct measurements following tagging or staining, changes in overall colony dimensions, retrospective measurements of density banding couplets using X-radiography, or a combination of methods

Species	Location, region	Sampling date	Methodology	Annual extension rate (mm yr^{-1})	Reference
P. columnaris	Gulf of Eilat, Middle Eastern Seas	1986–1988	X-radiography	5.68	Klein & Loya 1991
P. compressa	Hawaiian Archipelago, Polynesia	1983	Alizarin	29.2–32.85	Cox 1986
	Hawaiian Archipelago, Polynesia	2003–2004	X-radiography	5.9	Domart-Coulon et al. 2006
	Hawaiian Archipelago, Polynesia		Direct	7.3–10.8	Edmondson 1929
	Hawaiian Archipelago, Polynesia		X-radiography	7.66–8.13	Grigg 1998
	Hawaiian Archipelago, Polynesia	1996–1997	Alizarin	23.3–34	Grottoli 1999
	Hawaiian Archipelago, Polynesia		Alizarin	18.22	Rodgers et al. 2003
P. cylindrica	Philippines, Southeast Asia	1994–1995	Alizarin	30.42	Custodio & Yap 1997
	Philippines, Southeast Asia	2001–2002	Tagging	12.85	Dizon & Yap 2005
	Maldives, Central Indian Ocean	2010–2011	Alizarin	7.4	Morgan & Kench 2012
P. cylindrica (= *andrewsi*)	Guam, Micronesia	1976–1977	Alizarin	25	Neudecker 1981
P. evermanni	Hawaiian Archipelago, Polynesia		Direct	11.6	Edmondson 1929
P. furcata	Florida Keys, Northern Caribbean			9–22.8	Huston 1985
	US Virgin Islands, Eastern Caribbean and Atlantic	1979–1980	Alizarin	53.3	Meyer & Schultz 1985
P. heronensis	Lord Howe Island, Australia	2010–2011	Alizarin, tagging	9.91–21.29	Anderson et al. 2012
	Lord Howe Island, Australia	1994–1995	Alizarin	10.5	Harriott 1999
P. lichen	Maldives, Central Indian Ocean		Direct, radial	16.3	Clark & Edwards 1995

(Continued)

Table 4 (Continued) Annual extension rates reported for 148 coral taxa, based on direct measurements following tagging or staining, changes in overall colony dimensions, retrospective measurements of density banding couplets using X-radiography, or a combination of methods

Species	Location, region	Sampling date	Methodology	Annual extension rate (mm yr^{-1})	Reference
P. lobata	GBR, Australia	1993	X-radiography	8–19	Alibert & McCulloch 1997
	GBR, Australia		X-radiography	7.6–18.8	Barnes & Lough 1989
	Enewetak Atoll, Micronesia	1972	X-radiography	7.8–11.5	Buddemeier et al. 1974
	Maldives, Central Indian Ocean		Direct, radial	12.1	Clark & Edwards 1995
	Java, Southeast Asia	1989–1994	X-radiography	11.7–16.3	Edinger et al. 2000
	Hawaiian Archipelago, Polynesia		Direct	7.1	Edmondson 1929
	Mexico Caribbean, Western Caribbean	1995–2006	X-radiography	4.33	Elizalde-Rendon et al. 2010
	Japan, Southeast Asia	1980–1993	X-radiography	5.3	Fallon et al. 1999
	Hawaiian Archipelago, Polynesia		X-radiography	10.1	Grigg 1998
	Hawaiian Archipelago, Polynesia	1885–2001	X-radiography	3.02–13.49	Grigg 2006
	Hawaiian Archipelago, Polynesia	1996–1997	Alizarin	5.8–7.8	Grottoli 1999
	Costa Rica, Western Caribbean	1985–1987	X-radiography, alizarin	11.7	Guzmán & Cortés 1989
	Johnston Atoll, Polynesia	1976	X-radiography, growth ridges	7.1	Jokiel & Tyler 1992
	Gulf of Eilat, Middle Eastern Seas	1986–1988	X-radiography	7.48	Klein & Loya 1991
	Maldives, Central Indian Ocean	2010–2011	Alizarin	14.8	Morgan & Kench 2012
	Philippines, Southeast Asia	1981	X-radiography	13	Pätzold 1984
	Hawaiian Archipelago, Polynesia		Alizarin	8.07	Rodgers et al. 2003
	American Samoa, Polynesia	2004–2005	Alizarin	1.2–9.8	Smith et al. 2007
	Hawaiian Archipelago, Polynesia		X-radiography	3–13	Grigg 1982

(Continued)

Table 4 (Continued) Annual extension rates reported for 148 coral taxa, based on direct measurements following tagging or staining, changes in overall colony dimensions, retrospective measurements of density banding couplets using X-radiography, or a combination of methods

Species	Location, region	Sampling date	Methodology	Annual extension rate (mm yr^{-1})	Reference
P. lutea	GBR, Australia	1993	X-radiography	12–15	Alibert & McCulloch 1997
	Thailand, Southeast Asia	1990–1991	Alizarin	9.33–24.99	Allison et al. 1996
	Gulf of Aqaba, Middle Eastern Seas	1990–1995	X-radiography	15.2	Al-Rousan et al. 2002
	Moorea, Polynesia	1801–1990	Core analysis, CT scan	10.9	Bessat & Buigues 2001
	Enewetak Atoll, Micronesia	1972	X-radiography	5–13.5	Buddemeier et al. 1974
	Thailand, Southeast Asia	1984–1986	Alizarin	11.1–24.3	Chansang et al. 1992
	Thailand, Southeast Asia	1982–1983	X-radiography	15.4–18.4	Charuchinda & Chansang 1985
	Maldives, Central Indian Ocean		Direct, radial	11.2	Clark & Edwards 1995
	Palmyra Island, Polynesia	1880–2000	X-radiography	20	Cobb et al. 2001
	Sulawesi, Southeast Asia	2001–2002	Tagging	3.98–15.26	Crabbe & Smith 2005
	Sulawesi, Southeast Asia		Digital imagery	9.76	Crabbe et al. 2006
	Hawaiian Archipelago, Polynesia		Direct	11.6	Edmondson 1929
	Gulf of Aqaba, Middle Eastern seas		X-radiography, CT scan	3–8.4	Heiss 1995
	Enewetak Atoll, Micronesia	1979	X-radiography	7.6	Highsmith 1979
	Enewetak Atoll, Micronesia	1985	X-radiography	9–12	Hudson 1985
	Johnston Atoll, Polynesia	1976	X-radiography, growth ridges	7.8	Jokiel & Tyler 1992
	Enewetak Atoll, Micronesia	1971	X-radiography	13.5	Knutson et al. 1972
	Western Australia, Australia	1994	X-radiography	13	Müller et al. 2004
	Republic of Palau, Micronesia	1950–2008	X-radiography	17.73	Osborne et al. 2013
	Red Sea, Middle Eastern Seas	1991–2001	X-radiography	5.66	Rosenfeld et al. 2003
	Thailand, Southeast Asia	1984–1986	Alizarin, X-radiography	13.7–23.2	Scoffin et al. 1992

(Continued)

Table 4 (Continued) Annual extension rates reported for 148 coral taxa, based on direct measurements following tagging or staining, changes in overall colony dimensions, retrospective measurements of density banding couplets using X-radiography, or a combination of methods

Species	Location, region	Sampling date	Methodology	Annual extension rate (mm yr^{-1})	Reference
P. lutea	Japan, Southeast Asia	2002–2008	X-radiography	3.41	Sowa et al. 2013
	Japan, Southeast Asia	1997–1998	X-radiography	7	Suzuki et al. 2000
	Thailand, Southeast Asia	2003–2005	Alizarin, X-radiography	15.31–21.59	Tanzil et al. 2009
	China, Southeast Asia	1980–2006	X-radiography	11.3	Zhao et al. 2014
P. mayeri	GBR, Australia	1993	X-radiography	13	Alibert & McCulloch 1997
P. nigrescens	Maldives, Central Indian Ocean		Direct, radial	17.8	Clark & Edwards 1995
P. nodifera	Red Sea, Middle Eastern Seas	1990–1995	X-radiography	11.2	Al-Rousan et al. 2002
P. porites	Florida Keys, Northern Caribbean			8.3–20	Huston 1985
	Jamaica, Western Caribbean	1987	Alizarin	13.3	Spencer Davies 1989
P. rus	Philippines, Southeast Asia	1994–1995	Alizarin	24.33	Custodio & Yap 1997
P. solida	GBR, Australia	1938–1982	X-radiography	7.2	Lough & Barnes 1990
Porites spp.	Gulf of Aqaba, Middle Eastern Seas	2011–2012	X-radiography	10.09	Al-Rousan & Felis 2013
	GBR, Australia		X-radiography	8.02–14.01	Barnes & Lough 1993
	GBR, Australia	1980–2003	X-radiography	13–15.1	Cantin & Lough 2014
	GBR, Australia	2003	X-radiography	12.8–15.2	Cooper et al. 2008
	GBR, Australia	2005	X-radiography	12.4–14.3	De'ath et al. 2009
	GBR, Australia	1981–2002	X-radiography, luminescent	7.1–16.6	D'Olivo et al. 2013
	Red Sea, Middle Eastern Seas	1971–1991	X-radiography	4.18–14.39	Heiss 1996
	GBR, Australia	1979–1986	X-radiography	12.9	Lough & Barnes 2000
	Indonesia, Southeast Asia	1979–1984	X-radiography	10	Maier et al. 2004
	Samoa, Polynesia	1917–1920	Digital imagery	17–44	Mayor 1924
	Japan, Southeast Asia		X-radiography	6.35	Sowa et al. 2014
	Thai-Malay Peninsula, Southeast Asia	1980–2010	X-radiography, luminescent	18.81	Tanzil et al. 2013
	Thailand, Southeast Asia	1989–1990	Alizarin, fluorescent bands	22.33	Tudhope et al. 1992

(Continued)

Table 4 (Continued) Annual extension rates reported for 148 coral taxa, based on direct measurements following tagging or staining, changes in overall colony dimensions, retrospective measurements of density banding couplets using X-radiography, or a combination of methods

Species	Location, region	Sampling date	Methodology	Annual extension rate (mm yr^{-1})	Reference
Psammocora haimiana (= togianensis)	Enewetak Atoll, Micronesia	1972	X-radiography	29–30	Buddemeier et al. 1974
	Enewetak Atoll, Micronesia	1971	X-radiography	29	Knutson et al. 1972
P. profundacella (=superficialis)	Costa Rica, Western Caribbean	1985–1987	X-radiography, alizarin	6.2	Guzmán & Cortés 1989
	Peel Island/ Wellington Point, Australia		X-radiography	2–2.5	Roberts & Harriott 2003
P. stellata	Hawaiian Archipelago, Polynesia		Direct	5.7	Edmondson 1929
	Costa Rica, Western Caribbean	1996–1997	Alizarin	9.5–18.7	Jimenéz & Cortés 2003
Pseudodiploria (= Diploria) clivosa	Florida Keys, Northern Caribbean			4–8.8	Huston 1985
	Eastern Caribbean and Atlantic	1987–1989	X-radiography	4.45	Eakin et al. 1994
	Panama, Western Caribbean	1985	X-radiography	5.6	Guzmán et al. 1991
	Florida Keys, Northern Caribbean			3.5–10	Huston 1985
	Bermuda, Northern Caribbean	1991	X-radiography	3.33	Logan et al. 1994
Sandalolitha (= Parahalomitra) robusta	Enewetak Atoll, Micronesia	1972	X-radiography	12	Buddemeier et al. 1974
Seriatopora hystrix	Lord Howe Island, Australia	2010–2011	Alizarin, tagging	19.49–19.53	Anderson et al. 2012
	Lord Howe Island, Australia	1994–1995	Alizarin	16.7	Harriott 1999
	Enewetak Atoll, Micronesia	1972–1976	Direct, diameter	22.1	Stimson 1985
Siderastrea radians	Florida Keys, Northern Caribbean			1.5–5	Huston 1985
S. siderea	Belize, Western Caribbean	1995–2008	X-radiography	4.02	Castillo et al. 2011
	Jamaica, Western Caribbean	2000–2008	Digital imagery	7.47	Crabbe 2009
	Panama, Western Caribbean	1991–1992	X-radiography	4.7	Guzmán & Thudhope 1998
	Panama, Western Caribbean	1985	X-radiography	4.8	Guzmán et al. 1991

(Continued)

Table 4 (Continued) Annual extension rates reported for 148 coral taxa, based on direct measurements following tagging or staining, changes in overall colony dimensions, retrospective measurements of density banding couplets using X-radiography, or a combination of methods

Species	Location, region	Sampling date	Methodology	Annual extension rate (mm yr^{-1})	Reference
S. siderea	Eastern Caribbean and Atlantic	1981	X-radiography	1.5–3.1	Hubbard & Scaturo 1985
	Florida Keys, Northern Caribbean			1.5–2.3	Huston 1985
	Florida Keys, Northern Caribbean	2010–2012	Alizarin, buoyant weight	2.6	Kuffner et al. 2013
	Barbados, Eastern Caribbean and Atlantic	1974–1975	Alizarin, X-radiography	4.1–5.4	Stearn et al. 1977
Solenastrea hyades	North Carolina, Northern Caribbean		X-radiography	15	Moore & Krishnaswami 1972
Stephanocoenia sp.	Eastern Caribbean and Atlantic	1981	X-radiography	1.8	Hubbard & Scaturo 1985
	Jamaica, Western Caribbean		X-radiography	5	Moore & Krishnaswami 1972
Stylophora pistillata	Lord Howe Island, Australia	2010–2011	Alizarin, tagging	11.62–20.6	Anderson et al. 2012
	Red Sea, Middle Eastern Seas	2001–2002	Alizarin	15.05–17.72	Bongiorni et al. 2003
	Red Sea, Middle Eastern Seas	2001–2002	Tagging	19.4	Ebeid et al. 2009
	Egypt, Middle Eastern Seas	1998	Alizarin	6.51–9.24	Kotb 2001
	Red Sea, Middle Eastern Seas	1989–1990	Alizarin	24.61	Liberman et al. 1995
Turbinaria frondens	Solitary Islands, Australia	1994–1995	Alizarin	14	Harriott 1999
T. mesenterina	GBR, Australia	2009–2010	Alizarin	11	Browne 2012

with more complex branching patterns, which have higher rates of secondary branching (caespitose; Figure 3), display greater interspecific and intergeneric variation in growth rates. For the caespitose *Acropora*, growth rates varied in the range 38–127 mm yr^{-1} for a single species (*Acropora elseyi*) observed at Lizard Island (northern GBR; Oliver 1985) compared with the Waikiki aquarium in Oahu, Hawaii (Atkinson et al. 1995), suggesting that environmental conditions do influence extension rates. Columnar morphologies (i.e., species that form thick pillars with greater skeleton deposition per unit of tissue) also grow slower, on average, than the arborescent forms. However, as for the caespitose morphologies, there is some evidence of taxonomic variation in growth, with columnar *Montastraea* and *Pavona* growing more slowly than other genera with similar morphology (Figure 6). The distinct difference in growth rates between corymbose and tabular *Acropora* is somewhat unexpected based on branching patterns alone. These branching morphologies are similar (Figure 3), wherein corymbose colonies have small branches that project upwards from densely

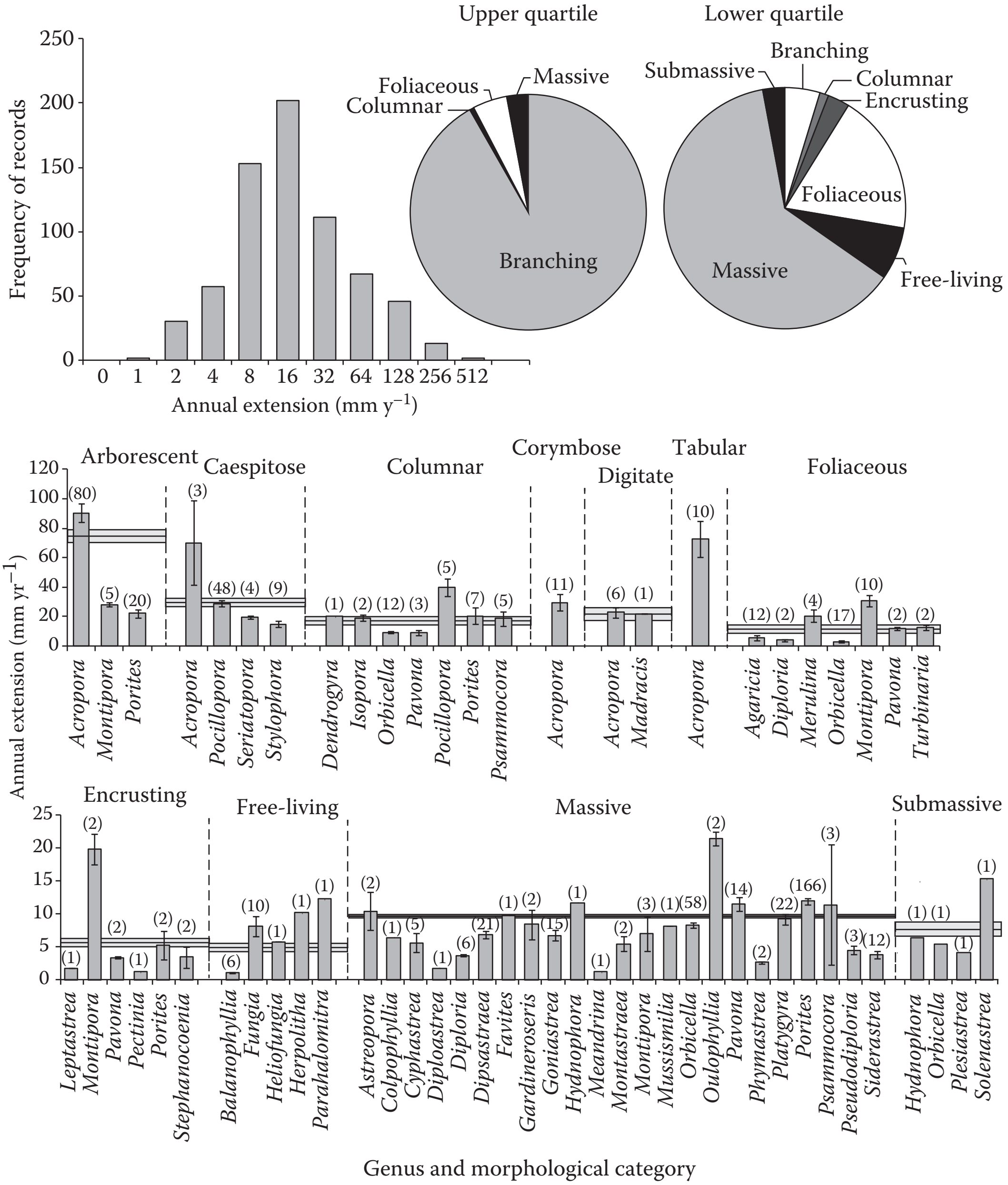

Figure 6 Variation in annual extension rates (millimetres) of corals with different gross morphology. Top panel shows the distribution of reported extension rates across all coral taxa (note the geometric scale showing the lower limit of each extension rate class), with pie charts showing the representation of corals with different growth forms in the upper (faster-growing taxa) and lower quartile (slower-growing taxa). Lower panel shows mean (± standard error [SE]) extension rates recorded for reef-building corals by genus and growth form. Numbers in brackets indicate the number of records for each genus. Grey horizontal bars indicate mean (±SE) extension rates for distinct growth forms (averaged across relevant taxa). No distinction is made between branch extension, radial extension, or AMR. Source data presented in Table 4.

calcified basal branches. However, tabular morphologies have shorter branchlets and, typically, a smaller base of attachment compared with the longer (and sometimes anastomosing) branchlets of the corymbose morphs (Wallace 1999). Evidently, species' investment in a broader base of attachment to the substratum, as evident in corymbose and digitate branching morphologies, as well as in massive and encrusting morphologies, is associated with lower annual extension rates of the colony (Figure 6).

Calcification rates

Pronounced differences in skeletal extension rates of scleractinian corals, as described previously, are generally attributed to differences in 1) growth form and associated patterns of calcification (Jackson 1991); 2) the extent to which skeletons are porous or perforate (Hughes 1987); and 3) physical conditions (e.g., light and water motion). In contrast, calcification rates are considered to be broadly similar (or at least much less variable compared to linear extension) across different coral species and growth forms (Maragos 1972, Buddemeier & Kinzie 1976). However, small differences in mass-specific calcification rates can translate into large differences in extension (Buddemeier & Kinzie 1976), and marked interspecific differences in calcification rate have been recorded in some studies. Goreau & Goreau (1959) recorded a 3-fold difference in the calcification rates of branching versus massive corals on the basis of measurements of calcium uptake by small, standardized fragments of 13 coral species in Jamaica. Considerable interspecific variation in calcification rates has also been recorded with long-term measures (over 13 months; February 2010 to March 2011) of skeletal extension (Morgan & Kench 2012). Morgan & Kench (2012) reported calcification rates ranging from 0.22 g cm^{-2} yr^{-1} for *Leptastrea purpurea* (an encrusting coral) up to 2.96 g cm^{-2} yr^{-1} for *Acropora nasuta* (a corymbose coral). This 13-fold difference in calcification rate among sympatric species is at least equivalent to the interspecific variation in reported rates of linear extension.

Comparisons of calcification rates (g cm^{-2} yr^{-1}; Figure 7) measured over more than 1 year and quantified from either X-radiography for massive corals with preserved density banding or directly estimated from the physical dimensions and density of skeletal material accreted within a known period (e.g., after staining; Table 5) reveal a unimodal distribution of calcification rates with a geometric mean of 1.45 ± 0.99 g cm^{-2} yr^{-1} (mean ± standard deviation [SD]). Data in Morgan & Kench (2012), who reported both annual extension and calcification rates for 32 colonies across 12 species, indicated that there is an asymptotic relationship between species-specific estimates of average annual calcification and average annual extension (Figure 8). This shows that enhanced extension rates of *Acropora* corals are at least partially attributable to higher overall calcification rates and not just to their morphology or unique (perforate) skeletal structure. Nevertheless, the effect of gross morphology on calcification rates is complex and confounded by taxonomic differences. Among species of *Acropora*, arborescent growth forms (e.g., *A. palmata* and *A. muricata*) exhibit the highest rates of calcification (2.93 ± 1.12 g cm^{-2} yr^{-1}, mean ± SD) but are within the range of variation recorded for other more compact (corymbose and digitate) species of *Acropora* (Figure 7). For *Porites*, however, average annual calcification rates appear to be much higher for massive species (e.g., *P. lobata* and *P. astreoides*) than branching species (e.g., *P. cylindrica*).

Spatial variation in coral growth

Spatial variation in coral growth is apparent at many different scales (reviewed by Buddemeier & Kinzie 1976), generally reflective of the broad range of environmental parameters that influence coral growth (see 'Environmental constraints on coral growth' section below), and the spatial scales over which these parameters vary. However, there is also considerable variability in growth rates among conspecific and sympatric corals (Goreau & Goreau 1959, Huston 1985, Babcock 1991, Clark & Edwards 1995), which is attributed to inherent differences in the growth and disturbance

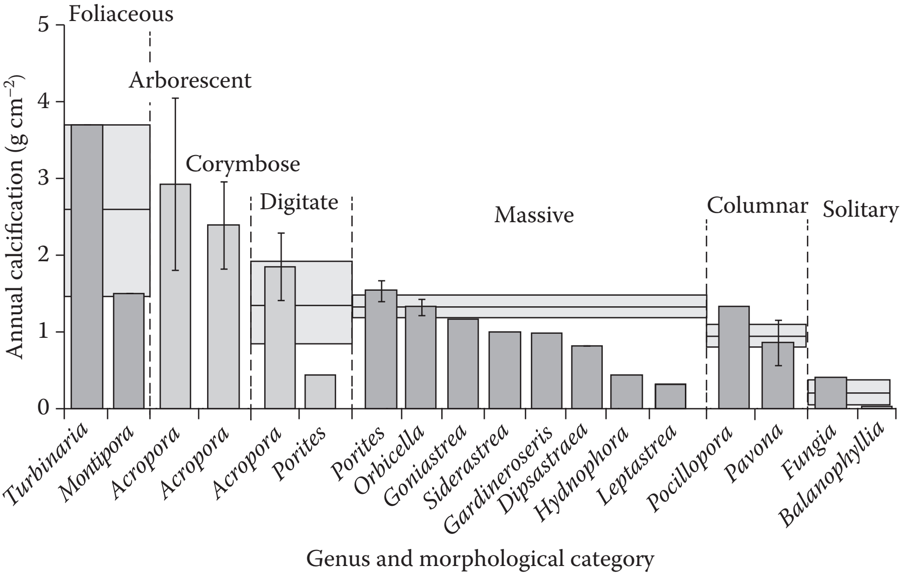

Figure 7 Average annual calcification rates (g cm^{-2}) based on either X-radiography for massive corals with preserved density banding or directly estimated from the physical dimensions and density of skeletal material accreted within a known period for branching and other corals. Grey horizontal bars indicate mean (± SE) calcification rates for distinct growth forms (averaged across relevant taxa). Source data presented in Table 5.

history of individual colonies. Competition, for example, with both other corals (Tanner 1997) and macroalgae (Tanner 1995) can substantially reduce fitness and growth rates of corals. Tanner (1997) showed that increases in the proportional area of *Acropora hyacinthus* subjected to experimentally induced contact with congeners were less than half (28–48% yr^{-1}) that of colonies located more than 15 cm away from potential competitors (95% yr^{-1}). Moreover, coral colonies within the same habitat and location are often subject to different levels of predation and other chronic injuries (Pisapia et al. 2014), which can ultimately have an impact on growth (Cox 1986, Henry & Hart 2005).

Spatial gradients in the growth rates of corals are particularly apparent in relation to water depth due to increased prevalence of faster-growing species in shallow waters (Bak 1976), but also consistent declines in the linear extension and calcification rates of individual coral species with increasing depth (Huston 1985), reflecting the strong effect of light in promoting coral calcification (Allemand et al. 2011). Maximum growth rates for most coral species tend to occur in water ≤10 m deep (e.g., 10 m for *Orbicella annularis*, Barnes & Taylor 1973; <5 m for *Acropora cervicornis*, Gladfelter et al. 1978; 1–5 m for *Porites astreoides*, Huston 1985), although Huston (1985) showed that the average annual growth rate of *Montastraea cavernosa* was significantly higher at 20 m than at 10 m or 30 m, while *Agaricia agaricites* showed no change in growth rate with depth (from 0 to 30 m).

There are at least three mechanisms by which light intensity may enhance calcification. These mechanisms can operate through 1) a direct energetic pathway, as increasing light generally increases photosynthesis, and photosynthetically fixed carbon can be used as a respiratory substrate to support the energy costs of calcification; 2) an organic carbon pathway that provides the precursors of the organic matrix necessary to build the skeleton; or 3) the removal of protons from the site of calcification to maintain pH conditions and stoichiometry favouring deposition of $CaCO_3$ (Allemand et al. 2011). In addition to these effects, the bulk density of coral skeletons can vary with depth, being generally higher in deeper water (Baker & Weber 1975), and in response to turbulence to reduce the risks of breakage (Brown et al. 1985); together these effects modulate a trade-off

Table 5 Calcification rates reported for scleractinain coral species throughout the tropics, based on direct measurements following tagging or staining, changes in overall colony dimensions, retrospective measurements of density banding couplets using X-radiography, or a combination of methods

Species	Location, region	Date sampled	Method	Calcification rate (g cm^{-2} yr^{-1})	Reference
Acropora austera	Maldives, Central Indian Ocean	2010–2011	Direct, water displacement	1.82	Morgan & Kench 2012
A. digitifera	Maldives, Central Indian Ocean	2010–2011	Alizarin, water displacement	2.29	Morgan & Kench 2012
A. gemmifera	Maldives, Central Indian Ocean	2010–2011	Alizarin, water displacement	1.42	Morgan & Kench 2012
A. lamarcki	Maldives, Central Indian Ocean	2010–2011	Alizarin, water displacement	1.83	Morgan & Kench 2012
A. muricata (= *formosa*)	GBR, Australia	2009–2010	Alizarin, water displacement	6.30	Browne 2012
	Maldives, Central Indian Ocean	2010–2011	Direct, water displacement	1.71	Morgan & Kench 2012
A. nasuta	Maldives, Central Indian Ocean	2010–2011	Alizarin, water displacement	2.96	Morgan & Kench 2012
A. palmata	Eastern Caribbean and Atlantic	1977	Staining, weight	0.82–1.89	Gladfelter et al. 1978
Balanophyllia europaea	Mediterranean, Mediterranean	2003–2005	CT, annual bands	0.10	Goffredo et al. 2009
Dipsastraea (= *Favia*) *pallida*	Enewetak Atoll, Micronesia	1979	X-radiography, mercury displacement	0.82	Highsmith 1979
Fungia fungites	Maldives, Central Indian Ocean	2010–2011	Alizarin, water displacement	0.41	Morgan & Kench 2012
Gardineroseris planulata	Panama, Western Caribbean	2003–2006	Alizarin, buoyant weight	0.98	Manzello 2010
Goniastrea retiformis	Enewetak Atoll, Micronesia	1979	X-radiography, mercury displacement	1.16	Highsmith 1979
Hydnophora microconos	Maldives, Central Indian Ocean	2010–2011	Alizarin, water displacement	0.43	Morgan & Kench 2012
Leptastrea purpurea	Maldives, Central Indian Ocean	2010–2011	Alizarin, water displacement	0.31	Morgan & Kench 2012
Montipora aequituberculata	GBR, Australia	2009–2010	Alizarin, water displacement	1.5	Browne 2012
Orbicella (= *Montastraea*) *annularis*	Mexico and Western Caribbean	1977–1991	X-radiography, freezing method	1.39	Carricart-Ganivet & Merino 2001
	Mexico and Western Caribbean	1970–1990	X-radiography, freezing method	1.4–1.43	Carricart-Ganivet 2004
	Mexico and Western Caribbean	1977–1995	X-radiography, freezing method	1.39–1.53	Carricart-Ganivet et al. 2000
	Eastern Caribbean and Atlantic		X-radiography	0.32–1.76	Baker & Weber 1975
	Eastern Caribbean and Atlantic	1970–1979	X-radiography, gamma densitometry	1.23	Dodge & Brass 1984

(Continued)

Table 5 (Continued) Calcification rates reported for scleractinain coral species throughout the tropics, based on direct measurements following tagging or staining, changes in overall colony dimensions, retrospective measurements of density banding couplets using X-radiography, or a combination of methods

Species	Location, region	Date sampled	Method	Calcification rate (g cm^{-2} yr^{-1})	Reference
O. faveolata	Florida Keys, USA, Northern Caribbean	1937–1996	X-radiography, densitometry	0.91	Helmle et al. 2011
	Mexico, Western Caribbean	1985–2009	X-radiography, gamma densitometry	0.97–1.51	Carricart-Ganivet et al. 2012
O. franksi	Mexico, Western Caribbean	1977–2005	X-radiography, gamma densitometry	0.84	Carricart-Ganivet et al. 2012
Pavona clavus	Guiri-Guiri, Pacific Costa Rica, Western Caribbean	1998–2000	Alizarin, x-radiography	2.00	Gateno et al. 2003
	Gulf of Chiriqui, Western Caribbean	1975–1979	X-radiography	0.11	Wellington & Glynn 1983
	Gulf of Panama, Western Caribbean	1975–1979	X-radiography	0.17	Wellington & Glynn 1983
	Panama, Western Caribbean	2003–2006	Alizarin, buoyant weight	1.64	Manzello 2010
P. gigantea	Gulf of Panama, Western Caribbean	1975–1979	X-radiography	0.12	Wellington & Glynn 1983
	Panama, Western Caribbean	2003–2006	Alizarin, buoyant weight	1.35	Manzello 2010
P. varians	Panama, Western Caribbean	2003–2006	Alizarin, buoyant weight	0.63	Manzello 2010
Pocillopora meandrina	Maldives, Central Indian Ocean	2010–2011	Alizarin, water displacement	1.33	Morgan & Kench 2012
Porites astreoides	Mexico and Western Caribbean	1998–2009	X-radiography, gamma densitometry	0.79–0.81	Carricart-Ganivet et al. 2012
	Mexico and Western Caribbean	1998–2006	X-radiography, digitized image	0.52–0.71	Elizalde-Rendon et al. 2010
	Mexico and Western Caribbean		Annual bands, CT Scan	0.48	Crook et al. 2013
P. cylindrica	Maldives, Central Indian Ocean	2010–2011	Alizarin, water displacement	0.44	Morgan & Kench 2012
P. lobata	American Samoa, Polynesia	2004–2005	Buoyant weight	0.19–1.39	Smith et al. 2007
	Java, Southeast Asia	1989–1994	X-radiography, buoyant weight	1.39–2.19	Edinger et al. 2000
	Maldives, Central Indian Ocean	2010–2011	Alizarin, water displacement	1.38	Morgan & Kench 2012
P. lutea	Aqaba, Middle Eastern Seas		X-radiography, CT scan	0.49–0.94	Heiss 1995
	Enewetak Atoll, Micronesia	1979	X-radiography, mercury displacement	1.07	Highsmith 1979
	Thailand, Southeast Asia	1990–1991	Alizarin, volumn displacement	0.6–1.4	Allison et al. 1996

(Continued)

Table 5 (Continued) Calcification rates reported for scleractinain coral species throughout the tropics, based on direct measurements following tagging or staining, changes in overall colony dimensions, retrospective measurements of density banding couplets using X-radiography, or a combination of methods

Species	Location, region	Date sampled	Method	Calcification rate (g cm^{-2} yr^{-1})	Reference
	Thailand, Southeast Asia	2003–2005	Staining, X-radiography, buoyant weight	2.21–2.82	Tanzil et al. 2009
	Thailand, Southeast Asia	1984–1986	Staining and core analysis	2.07–2.78	Scoffin et al. 1992
	Moorea, Polynesia	1801–1990	CT scan	1.25	Bessat & Buigues 2001
	Japan, Southeast Asia	2002–2008	X-radiography	0.54	Sowa et al. 2013
P. mayeri	GBR, Australia	1993	X-radiography	1.6–1.7	Alibert & McCulloch 1997
P. nodifera	Red Sea	1990–1995	X-radiography, gamma densitometry	0.92	Al-Rousan et al. 2002
Porites spp.	GBR, Australia	1980–2003	X-radiography, gamma densitometry	1.58–1.91	Cantin & Lough 2014
	GBR, Australia	1990–2005	X-radiography, gamma densitometry	1.51–1.76	De'ath et al. 2009
	Northern GBR, Australia	2003	X-radiography, gamma densitometry	1.59–1.96	Cooper et al. 2008
	Phuket Thailand, Southeast Asia	1989–1990	Annual fluorescent bands	2.27	Tudhope et al. 1992
	GBR, Australia	1979–1986	X-radiography, gamma densitometry	1.63	Lough & Barnes 2000
	Rib Reef, Australia, Australia	1989–2002	X-radiography, gamma densitometry	1.51	Carricart-Ganivet et al. 2012
	GBR, Australia	1981–2002	X-radiography, water displacment	1.15–1.94	D'Olivo et al. 2013
	Thai-Malay Peninsula, Southeast Asia	1980–2010	X-radiography, gamma densitometry	2.08	Tanzil et al. 2013
Siderastrea siderea	Florida Keys	2010–2012	Alizarin, buoyant weight	0.99	Kuffner et al. 2013
Turbinaria mesenterina	GBR, Australia	2009–2010	Alizarin, water displacement	3.70	Browne 2012

between linear extension rates and skeletal density. In some species, the effects of depth-related declines in photosynthetic rate on calcification may be alleviated by photoadaptation (Dubinsky & Falkowski 2011) and increasing exploitation of a diverse array of heterotrophic modes of feeding to supplement carbon requirements.

One notable consequence of depth-dependent changes in calcification rates of corals is the occurrence of pronounced changes in colony morphology (Barnes 1973, Rosenfeld et al. 2003, Anthony et al. 2005, Pandolfi & Budd 2008, Einbinder et al. 2009). Within a species, colonies typically become thinner, flatter, and morphologically less complex with increasing depth, presumably to make maximal use of limited light availability (Anthony et al. 2005) or because calcification rates decline with depth. However, despite the intuitiveness of this hypothesis, it is possible that

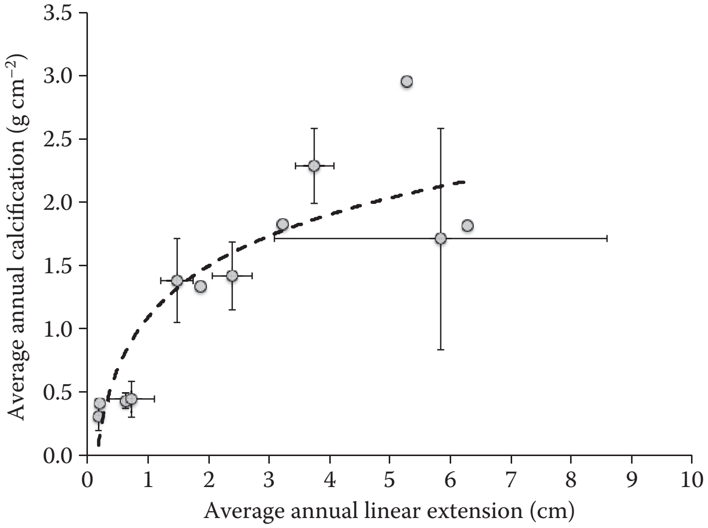

Figure 8 Relationship between average annual extension rate and average annual calcification rate for 12 coral species: *Leptastrea purpurea*, *Fungia fungites*, *Hydnophora microconos*, *Porites cylindrica*, *P. lobata*, *Pocillopora meandrina*, *Acropora gemmifera*, *A. lamarcki*, *A. digitifera*, *A. nasuta*, *A. muricata*, and *A. austera* (in order of mean extension rate). (Redrawn from data in Morgan, K.M. & Kench, P.S. 2012. *Marine Environmental Research* **81**, 78–82.)

deep and shallow morphologies might be genetically distinct (i.e., sibling species; e.g., Barnes 1973 vs. Knowlton et al. 1992), which cautions against assuming that depth-dependent changes in calcification are the sole cause of such changes in phenotype.

Another important gradient over which coral growth is reported to vary is distance off shore, from nearshore reefs dominated by terrestrial influences to outer-edge reefs dominated by oceanic influences (Scoffin et al. 1992, Lough et al. 1999, Lough & Cooper 2011), which relates to variation in wave energy, light, turbidity, nutrient levels, and salinity regimes together with pollution and other anthropogenic disturbances. Two conflicting patterns of changing growth characteristics along inshore-to-offshore gradients have been reported: 1) greater linear extension rates in clearer, less-turbid waters (e.g., *Orbicella* [= *Montastraea*] *annularis* in Jamaica, Aller & Dodge 1974, Dodge et al. 1974; *O. annularis* at Key Largo, Hudson 1981; *Porites* sp. in Indonesia, Tomascik et al. 1993; *Porites* sp. at Mayotte Island, Preiss et al. 1995); versus 2) greater rates of linear extension in more turbid, inshore waters (e.g., *Orbicella annularis* in the southern Gulf of Mexico, Carricart-Ganivet & Merino 2001; *Porites* sp. on the GBR, Lough et al. 1999; *Porites* sp. in Thailand, Scoffin et al. 1992). These contrasting patterns in growth characteristics along inshore-to-offshore gradients are likely due to the complexity associated with simultaneous spatial variation in a range of different environmental drivers (e.g., light, turbidity, wave action, and nutrients), which are likely to vary in importance among location and among coral species (Lough & Cooper 2011).

At larger spatial scales, there are apparent differences in the growth rates of corals with latitude, variously ascribed to large-scale gradients in light, temperature, and seawater chemistry (Grigg 1981, Logan & Tomascik 1991, Kleypas et al. 1999b). Anderson et al. (2014) reported that linear extension rates of *Acropora* and *Pocillopora* corals at Lord Howe Island (31.5°S), which is the world's southernmost coral reef, were one-third to a half of extension rates reported for tropical congeners. Examining massive *Porites lobata* across about 10° of latitude (from 19°N to 29°N) in the Hawaiian Archipelago, Grigg (1981) found a significant inverse relationship between both linear extension and calcification rates and latitude. Grigg (1981) showed that extension rates in *P. lobata* declined 1.08 mm yr^{1} per degree of latitude and attributed these changes to changes in both light and temperature, which together accounted for about 54% of the variance in calcification rates. Similarly, Lough & Barnes (2000) found that both linear extension and calcification rates of massive *Porites* decreased with increasing latitude across 245 similar-size colonies from 29 reefs on the GBR; this decrease was attributed largely to changes in temperature along this gradient (12°S to 21°S). Although irradiance covaries with SST across latitude, Lough & Barnes (2000) found that latitudinal variation in growth rates of massive *Porites* was most strongly correlated with SST.

Temporal variation in coral growth

Temporal variation in coral growth is apparent at scales ranging from diel patterns associated with switches from autotrophy to heterotrophy in light versus dark (e.g., Barnes & Crossland 1980), to strong seasonal patterns represented by the annual density bands apparent in many coral species (Table 1) and increasingly apparent long-term trends linked to global climate change (e.g., Bak et al. 2009). Buddemeier & Kinzie (1976) explicitly reviewed diurnal, weekly, monthly, and annual variability in coral growth. Until the mid-1970s, short- to intermediate-term variability in coral growth was well known, and discussion focused on the merits of extrapolating short-term (hourly) measurements of calcification rates to provide meaningful longer-term estimates of radial extension. Interestingly, similar arguments still apply today, but the more important concern is the extent to which results from laboratory studies conducted under carefully controlled environmental conditions (and often over short time frames) relate to field conditions, where there are fluctuations in a wide range of environmental parameters. This distinction is particularly important when predicting responses of corals to projected climate change, based on short-term experimental exposure to elevated temperatures and reduced pH (Pandolfi et al. 2011).

The most significant change in research on coral growth since the work of Buddemeier & Kinzie (1976) is the emerging focus on global climate change and long-term trends (interdecadal) in growth rates. Today, there is significant interest in documenting long-term trends in the growth of individual corals (Edmunds 2007, Cooper et al. 2008, 2012, De'ath et al. 2009, Cantin et al. 2010, Tanzil et al. 2013) or testing for interdecadal changes in the annual growth rates of coral species (not necessarily the same colonies) from the same location (Bak et al. 2009, Tanzil et al. 2009, Manzello 2010, Anderson et al. 2014) to establish effects of sustained changes in temperature, seawater chemistry, or both on coral growth.

Information on long-term trends (i.e., over decades to centuries) in growth rates of corals mainly comes from cores taken from long-lived massive corals (mostly *Porites*), which enable detailed analysis of long-term trends in growth of individual corals. In some studies, temporal trends in coral growth are determined from a single core or coral colony (Bessat & Buigues 2001, Saenger et al. 2009, Storz & Gischler 2011), but it is unclear to what extent these patterns reflect general responses to changing environmental conditions, as opposed to patterns of growth specific to the individual colony. Hereafter, all data presented on long-term trends in coral growth based on retrospective analysis of density banding in coral cores come from studies that examined multiple colonies and often multiple cores per colony. Within such studies, there are two distinct signals that point to the effects of climate-induced changes in temperature and seawater chemistry on coral growth: 1) sustained changes in annual extension or calcification (Cooper et al. 2008), considered indicative of long-term changes in local environmental conditions (Lough & Cantin 2014), versus 2) interruptions in growth associated with distinct stress events (e.g., bleaching; Cantin et al. 2010, Cantin & Lough 2014).

Cooper et al. (2008) presented the first evidence that calcification rates of massive *Porites* may be declining, based on cores from 10 colonies located in nearshore environments in the northern GBR (14–18°S). They reported a decrease of about 20% in calcification rates from 1988 to 2003, and while they did not directly attribute observed declines in coral growth to either ocean warming or ocean acidification, they did note that these corals were regularly exposed to temperatures well beyond their thermal optima. Further south, sampling of massive *Porites* at three reefs (Pandora, Rib, and Myrmidon) at increasing distances from the mainland revealed a significant decrease in calcification rates between 1961–1965 and 2001–2005 at both Pandora and Myrmidon, but not Rib (Lough 2008). Thereafter, De'ath et al. (2009, 2013) reported widespread and significant declines in calcification rates of corals with massive gross morphologies from 1990 to 2005, based on 328 *Porites* growth records from 69 reefs in the GBR. The magnitude of this decline was initially overestimated (~14%) due to errors in estimating the widths of outermost bands, but even after correcting for this, declines in coral growth during this period (11%) were still substantial, significant, and unprecedented in at least the past 400 years (De'ath et al. 2013). Again, the authors did not specifically attribute the decline to ocean warming or acidification but ruled out several local factors (e.g., declining water quality) that might otherwise account for recent declines in coral growth. Although critical of the findings of De'ath et al. (2009), D'Olivo et al. (2013), when examining recent growth rates in the central GBR, concluded that inshore growth rates have significantly declined (which they attributed to declining water quality) and that midshelf and offshore growth rates "appear to be undergoing a transition from increasing to decreasing rates of calcification, possibly reflecting the effects of CO_2 driven climate change" (D'Olivo et al. 2013, p. 999).

While retrospective measures of coral growth in long cores of massive *Porites* tend to reveal contemporary declines (mostly since 1990) in annual extension and calcification, there are exceptions to this trend. For example, Cooper et al. (2012) reported no significant change in regional average calcification rates between 1900 and 2010, based on 27 *Porites* cores from six reefs in Western Australia at latitudes between 17°S and 28°S. Rates of SST warming varied, however, between reef sites, being only about 0.02°C per decade in the northernmost Rowley Shoals and about 0.10°C per decade in the southernmost Houtman Abrolhos Islands. The rates of change in calcification also varied regionally and appeared to match the rates of SST warming. Only small changes in calcification rate occurred at sites of less SST warming, whereas significant increases in calcification rate occurred at the two most southerly sites where warming was greatest. Massive *Porites* corals at Rowley Shoals and the Houtman Abrolhos Islands have unusually high calcification rates, especially given the relatively low temperatures at these locations. This suggests that the effects of ocean warming on coral growth may vary with latitude, and that corals on high-latitude reefs may initially respond to increasing temperatures with increasing growth rate, as was previously suggested by Buddemeier & Kinzie (1976). Whether such increases in rate of calcification can be sustained over longer timeframes (cf. GBR, where calcification initially increased then declined; Lough & Barnes 2000) is debatable, especially given the 2011 thermal stress event that affected coral reefs in Western Australia and resulted in significant coral bleaching (Feng et al. 2013, Wernberg et al. 2013).

Aside from sustained declines in growth rates, corals may respond to acute temperature stress events with a temporary cessation or reduction in growth (Carilli et al. 2009, D'Olivo et al. 2013), especially after bleaching. Carilli et al. (2009), for example, examined cores taken from 92 colonies of *Orbicella* (= *Montastraea*) *faveolata* across the Mesoamerican Reef in 2006. The majority of colonies exhibited high-density stress bands associated with the 1998 bleaching event (Carilli et al. 2009). Moreover, most of the cores showed a decrease in rate of linear extension that persisted for 2–8 years after the bleaching. This stress event, evident in the coral growth records, appeared to be unprecedented in the previous 75–150 years at least (Carilli et al. 2010). Seemingly healthy colonies of *Diploastrea heliopora* in the Red Sea also exhibited a distinct skeletal signature that could be linked to extreme temperatures in 1998 (Cantin et al. 2010). Annual average extension in the period 1998–2008 was 30% lower than in the period 1925–1997, and Cantin et al. (2010) concluded that further increases in local temperatures may lead to complete cessation of calcification within 30–60 years, assuming that the thermal acclimation capacity of corals is limited (as indicated by Rodolfo-Metalpa et al. 2014).

Growth records from massive *Porites* in the central GBR also showed anomalies associated with the 1998 bleaching event. D'Olivo et al. (2013) reported a 40% reduction in linear extension rates of massive *Porites* after bleaching, which lasted for 3 years. Cantin & Lough (2014) also found distinct signatures of recent disturbances in cores of corals from the central GBR, including partial mortality and abrupt declines in linear extension and calcification rates, detected as abnormally narrow high-density bands, associated with both the 1998 and 2002 bleaching events. The occurrence and magnitude of these depressions in coral growth varied among sites and years, but all corals recovered and were growing at normal rates within 4 years. The extent to which growth of massive *Porites* colonies is disrupted (in duration and severity) following severe thermal stress is ascribed to individual differences in their thermal history (Castillo et al. 2011, 2012, Carilli et al. 2012). Carilli et al. (2012) showed that corals from sites with low temperature variability showed a 45% decline in linear extension and calcification rates and extensive partial mortality, whereas coral from sites with high interannual SST variability showed no partial mortality and only about 20% decrease in calcification and linear extension rates after bleaching.

For corals where the entire growth history is not preserved in the skeleton (e.g., most *Acropora* species), the only way to detect temporal changes in growth rates is to measure growth rates directly at specific intervals (e.g., Edmunds 2007, Bak et al. 2009). Not surprisingly, there are few data on long-term changes in growth rates of branching corals. However, the data available suggest that branching corals are equally, if not more, susceptible to sustained changes in environmental conditions (Manzello 2010). For instance, Bak et al. (2009) reported a 7.2–10.7% reduction in linear growth of *A. palmata* from 1971–1973 to 2002–2004 in the Caribbean, which, aside from acute disturbances (e.g., disease epidemics), might be partly due to ongoing declines in aragonite saturation of seawater, as was documented at nearby locations (Gledhill et al. 2008). At nearby, but offshore locations, the average annual SST had also increased 0.8°C from 1971–1973 to 2002–2004, but this was not considered to have influenced the temporal decline in coral growth (Bak et al. 2009). Similarly, Manzello (2010) attributed declines in skeletal extension of *Pocillopora damicornis* (0.9% yr^{-1}) from 1974 to 2006 in Pacific Panama to ocean acidification rather than increasing temperatures. Between 2004 and 2006, annual extension rates of six coral species (*P. damicornis*, *P. elegans*, *Pavona clavus*, *P. gigantea*, *P. varians*, and *Gardineroseris planulata*) were up to 53% lower than in the 1970s and 1980s in the same locations (Manzello 2010). In the Indo-Pacific, interdecadal declines in average annual extension rates have been documented for *Acropora yongei* and *Pocillopora damicornis* (values in 2010/2011 were 30% of that recorded in 1994/1995) at Lord Howe Island, but growth rates of two other species (*Seriatopora hystrix* and *Porites heronensis*) had increased (albeit slightly) over the same period (Anderson et al. 2014). Environmental drivers of these observed changes in the growth rates of reef-building corals are unclear, but it is notable that average annual SST increased 0.15°C from 1994/1995 to 2010/2011 at Lord Howe Island. Also, declines in aragonite saturation are expected to have an impact on high-latitude locations first (Orr et al. 2005) and may already be limiting calcification of faster-growing corals at Lord Howe Island, as these are known to be adversely affected by changes in aragonite saturation (Fabricius et al. 2011).

Functional importance of coral growth

Investigating coral growth provides insight into how corals respond to changing environmental conditions and how they allocate energy to different metabolic processes (Leuzinger et al. 2012, Madin et al. 2012). The size of colonies is an important determinant of the fate and fitness of individual colonies (e.g., Hughes & Jackson 1980, Hughes 1984, Hall & Hughes 1996), such that fundamental changes or differences in growth rates should influence population and community ecology. Declines in extension rates of newly settled corals (e.g., Albright et al. 2008) will almost certainly lead to increased rates of early post-settlement mortality (Babcock & Mundy 1996, Penin et al. 2010) by extending the time that individuals are exposed to size-specific agents of mortality, such as incidental predation by grazing fishes and physiological stress. However, the extent to which interspecific variation in coral growth influences the relative or absolute abundance of coral species is unclear (Maragos 1972, Hughes 1984) and may warrant specific examination.

The specific role of coral growth in the function and performance of scleractinian corals may be difficult to discern simply by comparing demographic rates among the few well-studied species (Babcock 1991). Similarly, in other systems (e.g., terrestrial plant systems), investigations into how species diversity and composition relate to ecosystem function have failed to produce general principles (Lawton 1999, Simberloff 2004, McGill et al. 2006), often attributed to the complexity and diversity of species-specific functional roles. To address this limitation, community ecologists are increasingly focused on trait-based approaches for comparing functional diversity among locations, habitats, and assemblages (e.g., McGill 2006). It is anticipated that functional diversity (rather than species richness) will provide much greater insights into ecosystem processes (Hooper et al. 2005, Cadotte et al. 2011), such as differences in resilience to environmental disturbances among habitats, locations and assemblages (Folke et al. 2004). Accordingly, there is a concerted push to compile data on a wide range of species traits for scleractinian corals (Baird et al. 2009, Díaz & Madin 2011, Edmunds et al. 2011), largely with a view to understanding the selective effects of different disturbances (e.g., bleaching and disease) on the structure and function of coral assemblages. Functional analyses of scleractinian corals do, however, lag well behind those of many other groups of organisms (e.g., terrestrial plants).

Growth and functional classifications of reef corals

Coral species have been variously assigned to guilds (Fagerstrom 1991), functional groups (Murdoch 2007), and adaptive strategies (Darling et al. 2012) based on a range of different traits. However, growth rate is often the predominant trait used to distinguish, and categorize, scleractinian corals. Most recently, Darling et al. (2012) compared 11 traits across 143 species to distinguish various life-history strategies, which were broadly aligned with the three adaptive strategies (competitors, ruderals, and stress tolerators) proposed by Grime (1977). Aside from growth form (which in itself is linked to variation in growth rate; Figures 6 and 7), the most influential trait distinguishing these groups was average annual growth rate or, more specifically, annual extension rate (mm yr^{-1}). Darling et al. (2012) noted that both coral growth and skeletal density depend on environmental conditions but did not explicitly test for potential biases related to spatial (geographic) variation in temperature, light, or any other environmental factors.

If growth-related traits are to be included in analyses of coral function(s), it is important to gain a better understanding of the functional relationships between coral growth and various environmental drivers. Such understanding has been achieved in plant ecology by measuring growth-related traits under controlled conditions (Grime & Hunt 1975), resulting in the quantification of comparative traits such as maximum potential growth rate R_{max} (Evans 1972). For scleractinian corals, this requires 1) extensive laboratory-based trials to establish comparative growth rates under carefully controlled and standardized environmental conditions and 2) the establishment and analysis of a comprehensive trait database (see, e.g., the LEDA Traitbase for Northwest European flora; Kleyer et al. 2008), which includes specific information about the location, timing, and relevant environmental conditions for each estimate of coral growth. Environmental factors known to influence coral growth rates include temperature (Glynn & Stewart 1973, Weber & White 1974, Lough & Barnes 2000, Tanzil et al. 2009); depth/light (e.g., Wellington 1982, Oliver et al. 1983, Houlbrèque et al. 2003, Hoogenboom et al. 2010); prey availability (Wellington 1982); competition (Neudecker 1977); water flow (Nakamura & Yamasaki 2005, Schutter et al. 2010); and sedimentation (Rogers 1990, Crabbe & Smith 2005). If growth rate is considered to be an important functional and adaptive trait of scleractinian corals, then it is essential to establish the degree of intra- and interspecific variation in coral growth rates across natural ranges for each of these environmental variables.

Growth versus abundance of scleractinian corals

The extent to which interspecific differences in the growth rates of corals actually influence their patterns of abundance is rarely tested, and anecdotal observations are highly conflicting (e.g., Goreau & Goreau 1959 vs. Maragos 1972). There are also no substantive datasets with which to relate spatially and temporally explicit measures of coral growth to variability in the relative abundance of different corals. This may be unnecessary if there are strong and consistent taxonomic differences in coral growth regardless of location (e.g., Figure 6) and interspecific differences in the growth rates of corals can clearly play a role in structuring coral assemblages under certain conditions (e.g., Connell et al. 2004, Bode et al. 2012). It has been shown, for example, that in some tidal pools fast-growing corals outcompete slower-growing corals (Connell et al. 2004) and thereby dominate the coral assemblage. However, there are also many factors that may moderate the outcomes of competitive interactions and prevent fast-growing corals from monopolizing available space (Connell et al. 2004). The question is whether stochastic and extrinsic processes (e.g., disturbance) generally obscure the role of specific traits in structuring populations and communities or whether it is the diversity and complexity of traits that make it difficult to resolve the individual contribution of coral growth. The prevailing view among coral ecologists is that species composition is largely structured by disturbance, at least within contemporary reef environments (Karlson & Hurd 1993, Pandolfi 2002). Perhaps a more valid test of the importance of coral growth is therefore the extent to which growth affects the rate of recovery across different corals in the aftermath of major disturbances.

Rates of recovery for coral assemblages devastated by major disturbances depend on the relative contributions of recruitment versus growth of remnant corals (Connell et al. 1997, Halford et al. 2004, Linares et al. 2011). In the Indo-Pacific, it is invariably fast-growing *Acropora* and *Pocillopora* species that contribute most to rapid increases in coral cover. Following localized bleaching in the central GBR in 2001/2002, coral cover increased by up to 10% yr^{-1} due to rapid increases in the cover of tabular *Acropora hyacinthus*, which was almost entirely attributable to growth of existing colonies (Linares et al. 2011). By 2010, the proportional cover of *Acropora* (relative to combined cover of all other reef-building corals) was much higher than it was immediately prior to the disturbance. The corollary of these results is that if all corals are severely depleted in cover, then recovery will be conditional on recruitment and subsequent growth of new colonies, which will greatly extend the time (4–5 years) until regeneration of coral cover becomes apparent (e.g., Gilmour et al. 2013). However, even in these cases, fast-growing corals (e.g., *Acropora* and *Pocillopora*) will tend to make a disproportionate contribution to initial increases in total coral cover (e.g., Connell et al. 1997). Gilmour et al. (2013) showed that cover of *Acropora* spp. increased from less than 5% to more than 20% within a decade after catastrophic bleaching at Scott Reef, Western Australia, while there was negligible change in the cover of Poritidae during this period, although slow-growing corals would presumably recover given sufficient time. Interestingly, in the Caribbean, examples of reef recovery following catastrophic disturbances are becoming increasingly rare (Idjadi et al. 2006).

Environmental constraints on coral growth

Although scleractinian corals occur throughout the world's oceans (Dodds et al. 2009), tropical coral reefs only form under specific environmental conditions, which occur primarily in shallow, warm tropical waters (Kleypas et al. 1999b, Lough & Barnes 2000). Among the range of factors that vary with latitude, temperature plays a fundamental role in controlling rates of metabolic processes for all organisms (e.g., Angilletta 2009). In general, rates of physiological processes, like respiration and calcification, display a non-linear threshold relationship with temperature (e.g., Pörtner 2002). Insolation is also an important driver of coral calcification because light availability influences photosynthesis by symbiotic algae, which in turn promotes calcification both by providing energy for calcification (Barnes & Chalker 1990) and by removing H^+ ions that are produced during calcium carbonate precipitation (Allemand et al. 2011). Consequently, factors that reduce light penetration into seawater (e.g., turbidity associated with terrestrial run-off and sediment resuspension) can influence calcification rates. As corals are mixotrophic organisms that obtain part of their nutritional requirements through feeding on plankton and suspended particulate matter and absorbing dissolved nutrients (Ferrier-Pagès et al. 2011), the availability of these sources of nutrition can also directly influence coral calcification. Finally, net accretion of calcium carbonate is critically dependent on the availability of carbonate ions in seawater (Tambutté et al. 2011), which is in turn influenced by seawater temperature and pH, which control the relative concentrations of different inorganic carbon molecules (i.e., dissolved CO_2, bicarbonate HCO_3^-, and carbonate CO_3^{2-}). Each of these environmental factors, and their specific effects on coral growth, are discussed next.

Temperature

Temperature is an important factor affecting calcification, and thereby growth rates, in scleractinian corals (e.g., Weber & White 1974, Jokiel & Coles 1977, Edmunds 2005, Tanzil et al. 2013), including deep-water azooxanthellate species (Naumann et al. 2014). The typical relationship with temperature for any measure of performance, including growth, is a parabolic curve: Moderate increases in temperature may have beneficial effects on performance, while exposure to increasing temperatures above the thermal optima will generally result in rapid declines in performance (Deutsch et al. 2008). Optimal temperatures for calcification and growth (generally around 25–28°C) are often close to the long-term maximum summer temperature experienced at a given location (Weber & White 1974, Jokiel & Coles 1977, Tanzil et al. 2013). The majority of studies on the effect of temperature on coral calcification and growth simply compared locations (mainly different latitudes) that have differing temperature regimes. Within the range of naturally occurring temperatures, and when these remain below thermal optima, calcification rates show fairly constant rates of increase with increasing temperature. For instance, for massive *Platygyra* sp. sampled from 21 locations across the Indo-Pacific, rates of linear extension increased from 4.9 mm yr^{-1} at 23.9°C to 12.0 mm yr^{-1} at 29.3°C, with an estimated increase in growth of 0.9 mm yr^{-1} $°C^{-1}$ (Weber & White 1974). Similarly, for *Orbicella* (= *Montastraea*) *annularis* in the Caribbean, extension rates increased 0.94 mm yr^{-1} $°C^{-1}$ across an SST range of 25–29°C (Weber & White 1977). More recent studies of massive corals have revealed similar trends. For Indo-Pacific *Porites* (based on multiple samples at 49 reef sites from Hawaii to the southern GBR), average linear extension and calcification rates significantly increased with increasing average SST, while average skeletal density decreased, giving a temperature sensitivity of 2.98 mm yr^{-1} $°C^{-1}$ for extension rate and 0.33 g cm^{-2} yr^{-1} $°C^{-1}$ for the calcification rate across an SST range of 23.1–29.5°C (Lough 2008). In the Gulf of Mexico, the calcification rate of *Orbicella annularis* showed a temperature sensitivity of 0.57 g cm^{-2} yr^{-1} $°C^{-1}$, although concomitant increases in skeletal density meant that linear extension of this species actually declined with increasing SST (Carricart-Ganivet 2004).

Sustained declines in calcification or linear extension of massive *Porites* have been reported from very warm waters (>28.5°C) around the Thai-Malay peninsula (Tanzil et al. 2013). Based on 70 cores from six locations, Tanzil et al. (2013) reported a region-wide decline of about 19% in calcification and about 15% decline in linear extension rates between 1980 and 2010. Similarly, in the South China Sea (8°N), there have been sustained declines in calcification rates of massive *Porites* from 1920 to 1980, with a slight increase from 1980 to 2000 (Shi et al. 2012). Calcification rates also decreased in the Arabian Gulf between 1987–1990 and 1999–2002 (Poulsen et al. 2006) and at Misima Island, Papua New Guinea between 1984–1988 and 1989–1993 (Barnes & Lough 1999).

The observed linear relationship between average Indo-Pacific *Porites* calcification rates and average SST (for SST below the thermal optimum; Lough & Barnes 2000) has been extrapolated to assess whether corals are calcifying as expected in different reef environments. For example, Lough & Cantin (2014) suggested that calcification rates observed at two southern reefs off the coast of Western Australia, as reported by Cooper et al. (2012), were significantly higher than expected assuming constant temperature-performance relationships across all locations. Although caution must be used when extrapolating relationships observed under specific conditions to other environments, this suggests that other factors, such as improved water clarity or local acclimation to lower temperatures, might offset the effects of spatial temperature gradients. Indeed, such factors were proposed to explain the high calcification rates of southerly coral reefs in previous studies (e.g., Smith 1981), and the observation that optimal temperatures for coral growth are close to local summer maximum temperatures suggests that there is considerable thermal acclimation. Nevertheless, a significant constraint in projecting effects of increasing temperature on scleractinian corals is limited data with which to establish temperature-performance relationships across the full range of current and projected temperatures for different coral species and populations (Hoeke et al. 2011). It is unclear, for example, whether latitudinal differences in growth rates simply reflect direct physiological effects of temperature (i.e., assuming that coral species, regardless of locations, have a similar temperature-performance relationship) or whether corals are locally adapted, such that different populations have different temperature-performance curves and different thermal optima.

Light

Along with temperature, light is among the most important physical factors affecting the growth rates of zooxanthellate corals (Baker & Weber 1975). Pioneering work by Goreau (1959) demonstrated that light, acting through the endosymbiotic algae of hermatypic corals, considerably increases the rate of calcification and suggested that the decrease in light intensity with depth below the ocean surface limits the absolute rate at which these corals calcify (Goreau 1961, 1963). Similarly, Muscatine (1973) considered light to be the primary environmental factor that controls the depth distribution of corals and the rates of overall reef accretion. At large spatial scales, such as along latitudinal gradients, it is difficult to tease apart the relative importance of changes in temperature versus changes in insolation as drivers of changes in coral growth rates. However, when observed along depth gradients, the relationship between light intensity and coral growth is non-linear, with the highest growth rates observed at moderate light levels typically experienced at water depths of greater than 5 m (Baker & Weber 1975). In very shallow water, light intensities are well above the level required to saturate photosynthesis and tend to inhibit calcification (Barnes & Taylor 1973), likely due to photoinhibition (e.g., Hoogenboom et al. 2009).

Within the coral growth database compiled for this review, water depth was recorded with resolution of at least 3 m for more than 450 growth records for 108 different species worldwide. Across species with massive colony morphologies and other non-branching morphologies (including free-living, foliose, encrusting, and columnar forms), there is an overall negative correlation between depth and annual extension rates (Kendall's rank correlation, $\tau = -0.27$, $p < .001$, $n = 210$ and $\tau = -0.36$, $p < .001$, $n = 102$ for massive and other morphologies, respectively). However, there is a wedge-shaped distribution of growth rates for these morphologies, with high variation in annual extension rates observed in shallow, high-light, environments (Figure 9). This variation might reflect among-species variation in the underlying relationships between photosynthesis and light (i.e., depth) and between calcification and depth. Alternatively, these data indicate that several other factors influence coral growth in shallow waters but that light availability likely limits the growth of massive and other non-branching morphologies in deeper waters. In contrast, there is no clear relationship between depth and annual extension for the branching morphologies ($\tau = 0.01$, $p = .85$, $n = 148$). The absence of a clear trend for these species could be related to the smaller depth range (30 m compared with 60 m for massive and other non-branching morphologies; Figure 9). Alternatively, variation in growth for these species is likely to be linked to differences in colony

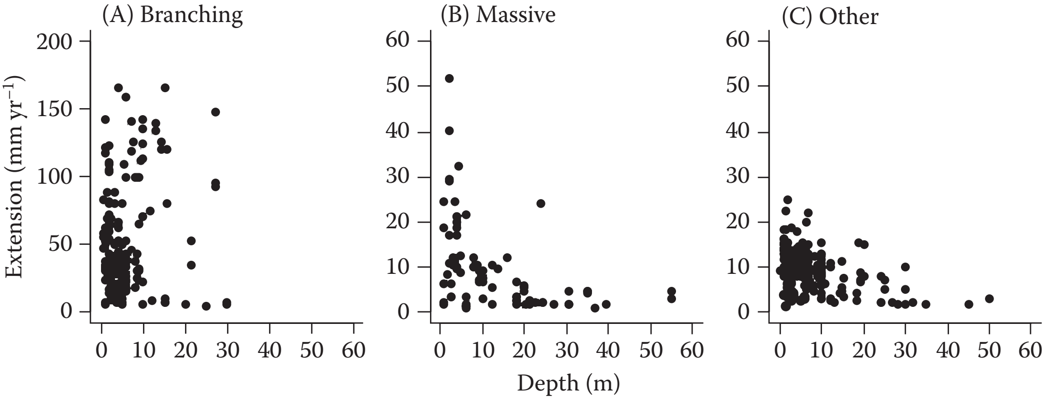

Figure 9 Relationship between depth and average annual extension rates for branching, massive, and other non-branching colony morphologies. Points are individual growth records for different species in different studies. Note differences in scale on the *y*-axis.

morphology (e.g., capacity for self-shading in erect and branching corals), corallite-level morphological features, difference in tissue optical properties, or species-specific concentrations of screening pigments (Kaniewska et al. 2008, 2011).

Water quality

Increasing anthropogenic transformation of coastal environments, such as land clearing, coastal development, and dredging, are directly contributing to increased sedimentation and pollution in nearshore environments (Hughes et al. 2003, Hassan et al. 2005). These activities increase the suspended particulate matter, nutrients, and turbidity present in seawater, which can directly reduce coral growth by smothering coral tissues as well as indirectly reducing growth by decreasing light availability for photosynthesis (reviewed by Fabricius 2005) or increasing susceptibility to disease (Pollock et al. 2014). Not surprisingly, therefore, several studies have documented comparatively low rates of linear extension or calcification in nearshore environments with particularly high levels of suspended sediments (Dodge et al. 1974, Tomascik & Sander 1985, Tomascik 1990, Hudson et al. 1994, Carricart-Ganivet & Merino 2001, Jiménez & Cortés 2003, Crabbe & Smith 2005, Guzmán et al. 2008, Ebeid et al. 2009, Sowa et al. 2014). The majority of these studies have focused on massive corals where retrospective measurements of coral growth rates are related to changes in annual variation in rainfall and flood events (McCulloch et al. 2003, D'Olivo et al. 2013).

On inshore reefs of the GBR, declines in calcification rates (of ~ 0.6% per decade in the period 1930–2008) of massive *Porites* were observed (D'Olivo et al. 2013). Early declines in calcification and growth in these nearshore habitats were directly attributed to high sediment and nutrient loads from river discharges (D'Olivo et al. 2013). However, such effects are compounded by thermal stress. On the central GBR, declines in linear extension rates of *Porites* due to the 1998 mass bleaching were only observed among corals from inshore reefs (not mid- or outer-shelf reefs), which are regularly affected by river discharge during flood events (Cantin & Lough 2014). Although such studies on massive *Porites* have been used as a proxy for overall reef health (Dodge et al. 1974, Tomascik & Sander 1985), some have documented similar growth rates on polluted and unpolluted reefs (although bioerosion had led to net erosion of polluted reefs; Edinger et al. 2000). Also noteworthy is the observation that skeletal density and calcification rates of *Orbicella annularis* may decrease with increasing turbidity, though extension rates are maintained (Carricart-Ganivet & Merino 2001). Also, some corals (notably *Fungia horrida*) have been shown to ingest sediment and may derive additional nutrition from sediments with high organic matter content, possibly offsetting the energetic cost of sediment removal (Rosenfeld et al. 1999).

Increased sedimentation due to declining water quality is generally expected to lead to reductions in coral growth as most corals expend substantial energy in actively clearing sediments. Active sediment rejection behaviour (e.g., ciliary transport of particles, mucus production, tissue expansion, tentacle manipulation of particles, extrusion of mesenteries, and pulsing of tissues) has been observed in a wide range of Indo-Pacific (Stafford-Smith & Ormond 1992) and Caribbean (Hubbard & Pocock 1972, Bak 1976) species. While corals with enhanced capacity for sediment rejection will be more tolerant of high turbidity, this exacts an energetic cost that is likely to reduce growth rates.

Prey acquisition

While light has traditionally been thought to be an important limiting factor for coral growth, corals obtain carbon and nutrients from a variety of sources (reviewed by Goreau et al. 1971, Muscatine 1973, Houlbrèque & Ferrier-Pagès 2009). Among-colony variation in rates of heterotrophic feeding can influence growth: Overall skeletal growth of *Stylophora pistillata* was 30% higher in colonies that were experimentally fed with natural zooplankton (Ferrier-Pagès et al. 2003), and growth of *Goniastrea retiformis* was 10% higher in colonies that were provided with suspended particulate matter as a food source (Anthony & Fabricius 2000). Moreover, the provision of a heterotrophic food source can allow corals to maintain active calcification when kept in almost-complete darkness for several months (Hoogenboom et al. 2010). Aside from providing a direct supply of nutrients to the coral host, heterotrophic feeding by scleractinian corals can also stimulate photosynthesis (Ferrier-Pagès et al. 2003, Houlbrèque et al. 2003, 2004) by relieving nutrient limitation of symbionts, leading to elevated symbiont densities, elevated concentrations of photosynthetic pigments, or both (e.g., Dubinsky et al. 1990).

The extent to which corals rely on autotrophic versus heterotrophic carbon sources is thought to vary among coral species, although there are few data that directly quantify these differences. Among the Scleractinia, which include asymbiotic, facultatively symbiotic, and obligately symbiotic corals, species range between those that are exclusively reliant on heterotrophic feeding (e.g., *Tubastraea* and *Madrepora*) to those that can obtain 100% of their daily energy requirements from photosynthesis (e.g., *Montipora capitata*; Grottoli et al. 2006). Early work divided corals along an autotrophy-heterotrophy continuum based on polyp size and the surface area-to-volume ratio of particular colony morphologies (Porter 1976). However, more recent work indicates that even species with very small polyps (e.g., *Montipora* and *Pocillopora*) can consume significant amounts of particulate matter under certain conditions (Anthony 2000, Grottoli et al. 2006). Although all corals are capable of heterotrophic feeding, there is pronounced interspecific variation in feeding rates (Ferrier-Pagès et al. 2011). This is likely related to differences in the way that coral species capture food. Some species directly capture particles using their tentacles (e.g., *Stylophora*), others extrude filaments for external digestion of prey (e.g., *Galaxea*; Wijgerde et al. 2011), and others appear to use mucous nets (Lewis & Price 1975) or ciliary movement to transfer particles to the mouth of the polyp (e.g., *Mycetophyllia reesi*, a species that lacks tentacles; Goldberg 2002). Further research is required to assess the mechanisms that underlie variation in feeding rates (such as polyp size, colony morphology, tentacle size, and nematocyst density) and how this variation influences among-species variation in calcification and growth.

The use of multiple feeding modes provides corals with additional capacity to adjust their physiology to suit local environmental conditions. For instance, some species increase their heterotrophic feeding rates in deeper water where light is limited (Grottoli 1999, Palardy et al. 2005, 2008) or along turbidity gradients, which are associated with reduced light levels together with increased availability of suspended particulate matter (Anthony 2000). This capacity to switch to a more heterotrophic feeding mode may enhance coral survival during bleaching events. In one study, Grottoli et al. (2006) observed that plankton feeding was slightly upregulated in two species of *Porites* in Hawaii after bleaching but substantially increased in *Montipora capitata* to a level at which heterotrophic feeding was sufficient to meet the coral's basic metabolic costs. As corals can use heterotrophic carbon to fuel calcification, this capacity for upregulation of heterotrophic feeding during periods when photosynthetic carbon supply is reduced (e.g., during bleaching events or periods of high turbidity) potentially mitigates some of the negative impacts of climate change on coral growth. However, sufficiently high heterotrophic feeding rates have only been documented for one coral species, *Montipora capitata*, to date (Grottoli et al. 2006). Moreover, increased reliance on plankton feeding depends critically on an abundant plankton supply at a time when the phenology and distribution of plankton appear to be changing rapidly (Richardson 2008).

Seawater chemistry

Since the Industrial Revolution, atmospheric CO_2 has increased from a preindustrial value of 280 ppm to 391 ppm in 2011, and is continuing to rise at a rate of about 0.5% per year (Forster et al. 2007, Hartmann et al. 2013). Depending on global actions to limit greenhouse gas emissions, the atmospheric concentrations of CO_2 could be between 400 and 900 ppm by 2100 (Moss et al. 2010). As about 30% of anthropogenic carbon dioxide is absorbed into the oceans (Stocker et al. 2013), increasing atmospheric CO_2 has profound impacts on the carbonate chemistry of the oceans (Gattuso et al. 1999). The relative concentration of calcium and carbonate ions in seawater is typically expressed as an aragonite saturation state, or Ω_{arag}, and the chemistry of calcium carbonate crystal deposition dictates that calcification can occur only when $\Omega_{arag} > 1$ (e.g., Gattuso et al. 1999, Tambutté et al. 2011).

Several different forms of inorganic carbon are present in seawater in a dynamic equilibrium that depends on pH (e.g., Gattuso et al. 1998). As atmospheric CO_2 dissolves into seawater, carbonic acid is produced, which then breaks down into hydrogen and bicarbonate ions, decreasing the pH and reducing availability of carbonate ions (Kleypas et al. 1999a, Kleypas & Langdon 2013). Therefore, declines in Ω_{arag} linked to increasing partial pressure of carbon dioxide (CO_2) in seawater, as seawater absorbs CO_2 from the atmosphere, are likely to affect coral calcification (Gattuso et al. 1998). Indeed, a doubling of CO_2 from preindustrial levels will reduce the concentration of carbonate ions in surface waters by 30% (Langdon et al. 2000), reducing Ω_{arag} from historical levels of more than 4.0 typically found in coral reef waters to less than 2.8 (Kleypas et al. 1999a).

There is still a great deal of work to be done to increase our understanding of the effects of ocean acidification on marine calcifiers. Overall, the literature reveals a generally negative effect of near-future ocean acidification on growth, but there are highly variable responses among different taxa (Kroeker et al. 2013, Comeau et al. 2013, 2014). Experimental studies suggest that there is a consistent negative effect of ocean acidification on calcification of reef corals (e.g., Pandolfi et al. 2011, Chan & Connolly 2013, Comeau et al. 2013, 2014). In addition, field studies of the composition of coral communities close to volcanic seeps, where there is a natural elevation of pCO_2 and a decrease in pH, have shown that coral diversity declined close to volcanic seeps although coral cover varied little, and massive *Porites* growth rates were unaffected by proximity to seeps (Fabricius et al. 2011). In the Mediterranean, scleractinian corals were absent from low-pH (7.4–7.5) areas close to natural CO_2 vents, with coincident reductions in abundance of sea urchins and coralline algae (Hall-Spencer et al. 2008). Similarly, Caribbean corals showed reductions in calcification along natural gradients in pH and Ω_{arag} (Crook et al. 2013). However, the suggestion that a fixed Ω_{arag} threshold exists for coral calcification (Hoegh-Guldberg et al. 2007) is contradicted by thriving reefs in locations where aragonite saturation levels are naturally low (Manzello et al. 2008, Comeau et al. 2013). Moreover, predictions of the effects of ocean acidification on reef accretion often do not take into account the ability of corals to regulate the pH of their calcifying medium (McCulloch et al. 2012). Detailed studies of regulation of the medium between the skeleton and the lower tissue layer where calcification takes place revealed that the decrease in pH in this medium was gradual relative to changes in pH in the external seawater, and that corals may therefore be able to partially mitigate the effects of ocean acidification (Venn et al. 2013). McCulloch et al. (2012) further suggested that the energetic cost of pH regulation will be minimal.

Projected changes in coral growth

Coral reefs are reported to be among the most sensitive ecosystems to the ongoing effects of global climate change (Walther et al. 2002) because scleractinian corals (which are the main habitat-forming organisms on tropical reefs) bleach, and often die, following even moderate and temporary increases in ocean temperatures. In 1998, for example, 90% of corals bleached and died across vast tracts of reef in the Indian Ocean, and the temperatures that caused this widespread coral mortality are expected to become a regular (even annual) occurrence in coming decades (Donner 2009, Donner et al. 2009). This does not necessarily mean that there will be annual episodes of significant and widespread coral bleaching (Hughes et al. 2003, van Hooidonk et al. 2013), as there is already evidence of corals acclimatizing, through physiological changes, or adapting, through genetic change, to changing thermal regimes (Pandolfi et al. 2011, Guest et al. 2012). For example, coral assemblages subject to severe bleaching appear less susceptible to bleaching during subsequent thermal anomalies of equivalent magnitude (Pratchett et al. 2013). Nonetheless, corals living in warmer waters, above their thermal optima, may grow more slowly (Anthony et al. 2011). Indeed, one of the expected trade-offs for corals that associate with thermally tolerant genotypes of zooxanthellae (e.g., *Symbiodinium* type D; Berkelmans & van Oppen 2006) is reduced growth (Little et al. 2004, Jones & Berkelmans 2010). Jones & Berkelmans (2010) showed that colonies of *Acropora millepora* experimentally infected with type-D *Symbiodinium* grew 29–38% (depending on environmental conditions) slower than conspecifics infected with type-C2 *Symbiodinium*. Moreover, increasing temperatures above the thermal optima for corals (discussed previously), as well as bleaching itself, will suppress growth (e.g., Cantin & Lough 2014).

The specific effects of increasing ocean temperatures on coral growth are expected to vary both spatially and taxonomically. At high latitudes (on subtropical reefs), increases in ocean temperatures may initially lead to increased rates of coral growth (e.g., Cooper et al. 2012), especially if growth is constrained during the coolest months by a minimum temperature threshold for net calcification (Figure 10). There are limited data on seasonal variation in growth rates of corals at high latitudes, but it is often assumed that reef-building (hermatypic) corals cease growing when exposed to temperatures below 17–18°C (Lough & Barnes 2000), which has been used to account for the constrained latitudinal extent of most reef-building corals (Stehli & Wells 1971). If so, then sustained warming may reduce or eliminate the period that corals are not growing, leading to overall increases in annual growth (Figure 10B). Alternatively, where growth of corals is constrained largely by maximum summertime temperatures (e.g., at low latitudes), then sustained increases in ocean temperatures will be expected to have generally negative effects on coral growth, if not survivorship (Figure 10B). This thesis is partly supported by documented changes in interdecadal growth rates of long-lived corals, such as *Porites* (Figure 10A), whereby ocean warming has already resulted in declines in the calcification rates of corals in low latitudes and naturally warmer locations (e.g., Red Sea, Cantin et al. 2010; Thai-Malay peninsula, Tanzil et al. 2013). Moreover, equatorial species diversity of corals decreased during the previous interglacial (130–115 ka), when SSTs exceeded present values by at least 0.7°C (Kiessling et al. 2012).

Cooper et al. (2012) documented increased growth of massive *Porites* at Coral Bay, Western Australia (23.2°S), as well as at the Houtman Abrolhos Islands (28.3°S), which are the southernmost locations where cores have been taken from massive corals. This initial increase in growth rates may not, however, be sustainable given recent observations of mass bleaching in response to thermal stress at these high-latitude coral reefs (e.g., Moore et al. 2012). While there are no

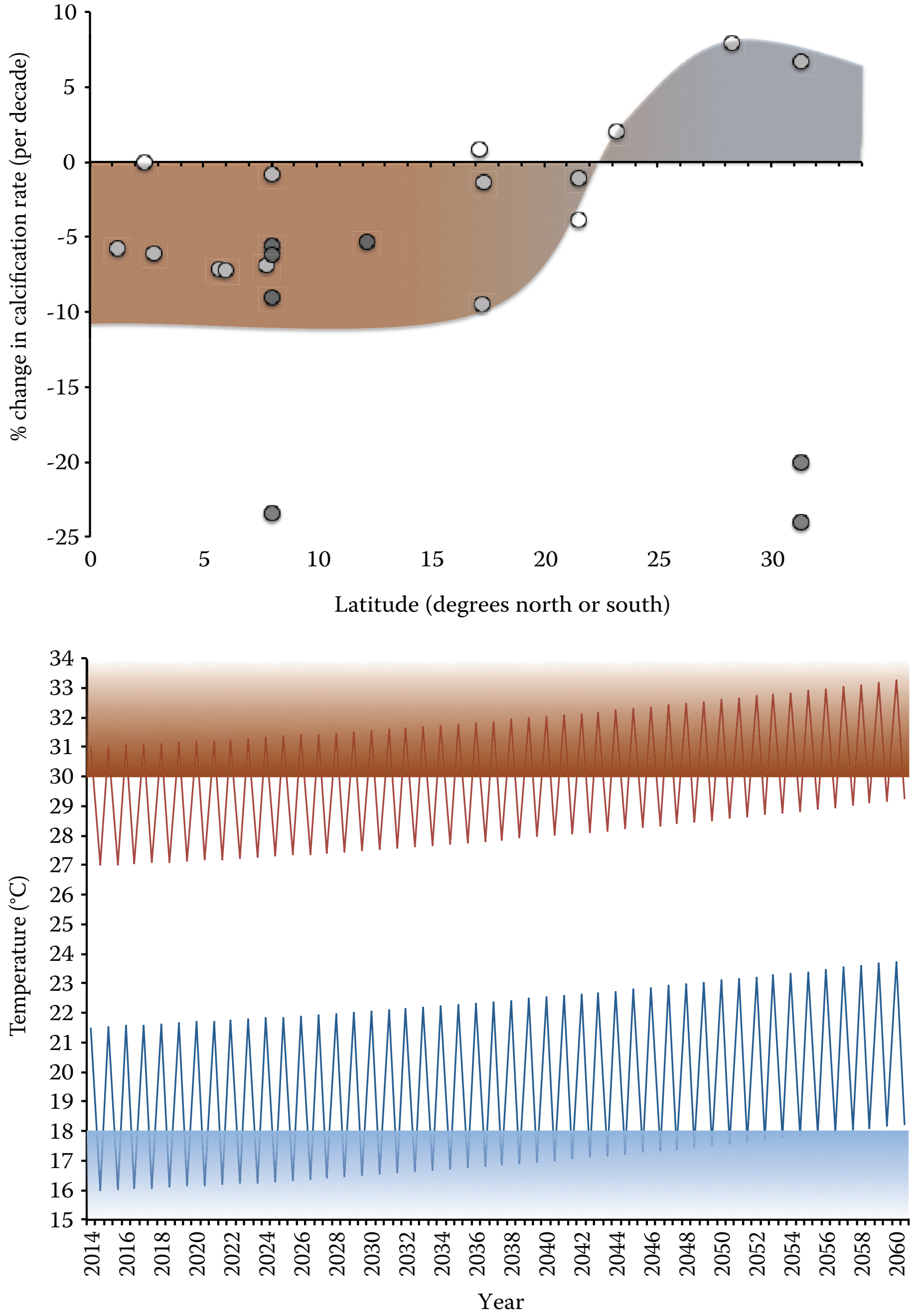

Figure 10 (Top) Latitudinal variation in observed changes in coral growth (percentage change in calcification or extension) based on retrospective measures (open circles) and temporally discrete direct measurements (shaded circles). (Bottom) Potential latitudinal differences in effects of increasing temperature on coral growth assuming fixed maximum and minimum temperature thresholds for coral growth. Ocean warming at high-latitude reefs (indicated in blue) may result in higher rates of coral growth as corals spend less time exposed to temperatures below the minimum temperature threshold for net growth. At low latitudes (orange), meanwhile, corals will be increasingly exposed to temperatures above the maximum thermal threshold and are likely to grow more slowly with ongoing warming.

massive *Porites* growing at Lord Howe Island (31°S), Anderson et al. (2014) directly measured linear extension of columnar *P. heronensis* and found that average annual growth in 2010–2011 was 9.7% higher (11.52 mm) than equivalent measurements taken in 1994–1995 (10.50 mm). While there was significant intercolony variation in annual extension rates for *P. heronensis* in 2010–2011, the temporal change in growth rate (6.5% per decade) is similar to that reported by Cooper et al. (2012) at Houtman Abrolhos Islands. If, however, direct measures of linear extension and calcification are compared across latitudes for corals that do not have records of growth preserved in the skeletons (e.g., *Acropora*), then this trend is no longer apparent (Figure 10). For example, the greatest magnitude of proportional change in coral growth (–20.0% per decade) has been recorded for branching corals (*A. yongei* and *Pocillopora damicornis* at the high-latitude reef, Lord Howe Island; Anderson et al. 2014). One possible explanation for these results is that low and declining levels of aragonite saturation are already limiting calcification at high latitudes, and that these effects are stronger than any beneficial effects of increasing temperature (van Hooidonk et al. 2014).

Experimental tests of the effects of declining aragonite saturation on coral calcification were reviewed by Chan & Connolly (2013), who found that calcification rates decline by 10–25% per unit decrease in aragonite saturation from 4 to 2. Projected differences in rates of decline were largely dependent on the method used to measure calcification, while rates were consistent across fast- and slow-growing coral species (Chan & Connolly 2013). Resulting changes in the calcification and growth of reef-building corals will become manifest at different times in different locations (van Hooidonk et al. 2014) owing to inherent geographic variation in background levels of aragonite saturation (Andersson et al. 2008, Pelejero et al. 2010). Notably, however, the reefs that are likely to be least affected by ocean warming will be the first and worst affected by declining aragonite saturation due to already low saturation states at high latitudes.

Declines in the calcification rates of individual corals due to declining growth rates might be further compounded by shifts in assemblage structure towards comparatively slow-growing species (Riegl & Purkis 2009, Comeau et al. 2014). Most disturbances (e.g., climate-induced coral bleaching, outbreaks of crown-of-thorns starfish, and severe tropical storms) have disproportionate effects on erect branching corals, such as *Acropora* and *Pocillopora* (Loya et al. 2001, McClanahan et al. 2004, Pratchett et al. 2014), suggesting that increasing incidence of acute disturbances may lead to increasing dominance of massive corals, such as *Porites* (e.g., Alvarez-Filip et al. 2011). However, resilience depends not only on species' resistance to disturbance, but also their capacity to recover in the aftermath of major disturbances (Hughes et al. 2003, Baker et al. 2008, Pandolfi et al. 2011). This is especially important after severe disturbances that cause high rates of mortality across a broad range of different coral species; the long-term persistence of different species will depend more on their capacity for recovery (Hughes et al. 2003, Baker et al. 2008) rather than on minor differences in rates of mortality.

Virtually all studies that have forecast changes in the structure of coral assemblages due to climate change, whether based on qualitative frameworks or quantitative projections, have focused on interspecific differences in susceptibility to disturbance (e.g., Marshall & Baird 2000, Loya et al. 2001) and the proportion of colonies that bleach or die in a given population. Persistent shifts in the relative abundance of different corals may, however, be further affected by differential effects of environmental change on key demographic processes, such as growth (De'ath et al. 2009, Carricart-Ganivet et al. 2012). If, for example, the recovery capacity of *Acropora* is compromised, then even moderate increases in the frequency of acute disturbances (e.g., climate-induced coral bleaching) could lead to even more rapid shifts in dominance towards more robust and resistant taxa. Such shifts in assemblage structure would have significant effects on topographic structure and habitat complexity, with potentially important effects on fishes and mobile invertebrates that associate with live coral habitats (Pratchett et al. 2008, Stella et al. 2011). Even moderate changes in the calcification rates of corals, especially if these are combined with directional shifts in the composition of coral assemblages, could also have important effects on reef accretion.

Consequences for habitat structure

Just as not all corals contribute equally to framework building (Wells 1957), corals are not equivalent when it comes to creating habitat for reef-associated organisms (e.g., reef fishes). Branching corals (e.g., branching *Porites* and arborescent *Acropora*) provide the greatest range of different microhabitats and therefore support the greatest diversity of different fishes and mobile invertebrates (Coker et al. 2014). Moreover, *Acropora* and *Pocillopora* corals (which are the predominant genera of branching corals throughout much of the Indo-Pacific) are the preferred prey for corallivorous fishes and invertebrates (Cole et al. 2008, Rotjan & Lewis 2008). Selective depletion of these faster-growing corals may therefore lead to corresponding shifts in the composition of local fish assemblages (if not overall declines in the abundance of fishes), as has been shown in Moorea, French Polynesia (Berumen & Pratchett 2006). Coral assemblages on the northern coast of Moorea have been subject to multiple disturbances (including bleaching, tropical cyclones, and outbreaks of crown-of-thorns starfish) over the last 30 years, which have had a disproportionate effect on *Acropora* corals (Adjeroud et al. 2002, Berumen & Pratchett 2006, Pratchett et al. 2013). As *Acropora* became increasingly scarce, coral-feeding butterflyfishes that specialize on *Acropora* (e.g., *Chaetodon trifascialis* and *C. reticulatus*) have become increasingly rare. In contrast, generalist coral-feeding butterflyfishes, especially those that specialize on *Pocillopora* (e.g., *Chaetodon pelewensis*), have been resilient to shifts in composition of coral assemblages (Berumen & Pratchett 2006). Similarly, Bellwood et al. (2006) showed that some fishes (habitat generalists) increase in abundance following localized coral depletion, which may compensate for the loss of specialist fishes with strong dependence on corals. However, extensive coral loss almost invariably leads to net declines in the abundance and diversity of coral reef fishes (reviewed by Wilson et al. 2006, Pratchett et al. 2008), and these declines are particularly pronounced when coral loss is associated with pronounced declines in topographic structure and habitat complexity (e.g., Sano et al. 1987, Graham et al. 2006).

Branching corals that are important in providing habitat for coral reef fishes and invertebrates (*Acropora* and *Pocillopora*) are disproportionately susceptible to mechanical damage and dislodgement (Madin & Connolly 2006). Projected increases in the severity of tropical cyclones with climate change (Emanuel 2005, Christensen et al. 2013, but see also Klotzbach 2006) are likely to cause fundamental shifts in the relative abundance of corals with different shapes (Madin et al. 2008). Notably, the tabular coral *Acropora hyacinthus*, which is a dominant coral on exposed reef crests in the Indo-West Pacific (Linares et al. 2011), is particularly susceptible to hydrodynamic forces and is expected to decline in abundance with increased frequency of severe tropical storms (Madin et al. 2008). If declines in calcification also lead to weaker skeletons (Hoegh-Guldberg et al. 2007), then corals will have even greater sensitivity to physical damage caused by tropical cyclones (Madin et al. 2008). This will lead to not only fewer but also smaller and flatter corals on reefs in the future, which will directly impact habitat availability for reef-associated organisms.

Consequences for reef accretion

Reef accretion results in the construction of a 3-dimensional biogenic structure on the seafloor. It is constrained at its upper bound by sea level itself, and the distance from the accreting reef surface to sea level is often referred to as ‘accommodation space’, or the remaining potential for vertical reef growth. Reef accretion is a function of the biogenic accumulation of carbonate and sediment on the one hand and the sum of its physico-chemical and biological destruction, dissolution, or transport away from the accreting reef on the other (Perry et al. 2008). Thus, reef accretion depends on a number of processes that facilitate either production of calcium carbonate or its removal from the reef. Although corals, and in some cases coralline algae, are the primary framework builders in modern reef accretion, this has not always been the case, with many reef-building episodes throughout the more than 500-million-year history of metazoans characterized by non-coral reef builders. For example, many Cretaceous reefs were built primarily from the remains of large bivalves (rudists), which formed extensive 3-dimensional structures above the surrounding seafloor (Wood 1998). Today, however, scleractinian corals dominate reefs, so it is important to understand the degree to which carbonate production is dependent on both the cumulative growth of corals on the reef and the relative contribution to that carbonate production among different coral taxa.

Of particular concern for degraded coral reefs around the world are the expected changes in coral assemblage composition and structure due to climate change, as well as the ongoing changes brought about by more local stressors (Pandolfi et al. 2011). Will this change in taxonomic structure affect the ability of coral reefs to accrete? For example, are the rate and magnitude of reef accretion any different between reefs characterized by a fast-growing assemblage dominated by branching corals (e.g., *Acropora* spp.) versus a slower-growing assemblage dominated by massive corals (e.g., Faviidae)? Few studies have documented differences in reef-scale calcification among reefs with different benthic composition. In one such study, reef flats dominated by coralline algae tended to have lower calcification rates than areas dominated by massive *Porites* colonies (Atkinson & Grigg 1984). Similarly, Gattuso et al. (1996) measured higher calcification on a hard-coral-dominated reef compared with a reef with low coral cover. However, such studies did not elucidate the relative importance of changes in coral cover and species composition compared with other environmental factors that also vary among reefs. Given the importance of reef accretion rate to the longevity of coral reefs, the impending changes to taxonomic composition on coral reefs due to climate change and other stressors, and the presumed integral relationship between coral growth and reef accretion, it is important to consider how reef coral assemblage structure is related to reef accretionary rates.

Much of what we know about rates of reef accretion comes from the Holocene fossil record of the past 10,000 years (Montaggioni 2005). Using a paleo-reconstruction of water depth, Hubbard (2009) assessed the relationship between depth and accretion rates on Caribbean Holocene reefs dominated either by fast-growing branching corals (i.e., *Acropora cervicornis*) or by slower-growing massive corals (e.g., *Orbicella annularis*). Even though maximum reef accretion rate decreased with depth in his analyses, Hubbard (2009) found no correlation between water depth and accretion rate for either assemblage due to large variance in accretion across all depth ranges. Importantly, the difference between the regression lines for branching and massive corals was not statistically significant (Figure 11). In another study of the Holocene fossil reefs of Belize, accretion rates increased with *increasing* paleo water depth, and reef accretion in reef settings characterized by massive corals occurred *faster* than those characterized by branching acroporid corals (Gischler 2008). Thus, the common view that reefs characterized by shallow branching corals *always* show the highest accretion rates (e.g., Schlager 1981) is not supported in the Caribbean Sea. However, more recent studies from the Indo-Pacific (Tahiti) did show a higher rate of reef accretion associated with *Acropora*-dominated reefs (Camoin et al. 2012, Blanchon et al. 2014). We clearly need a much greater understanding of the regional variability associated with the relationship between coral growth rate, dominance, and reef accretion rates.

The relationship between biodiversity of reef corals and spatial distribution of reef growth in the fossil record may also inform projections of changes in reef growth following widespread degradation of coral reefs. In a study of Oligocene-to-Neogene sections from the Panama Paleontology Project in the Caribbean (Johnson et al. 2008), there were no clear patterns between coral diversity and reef development through this time interval (~28.5–1.0 million years ago). Even though the taxonomic composition of coral assemblages has varied through time in this dataset, no clear pattern emerged between intervals with a regional distribution of extensive coral reef development and coral community composition. One potential implication of this result is that processes involved in carbonate production may be less important to overall reef growth in space and time when considered against the negative processes of bioerosion, dissolution, mechanical breakdown, and off-reef

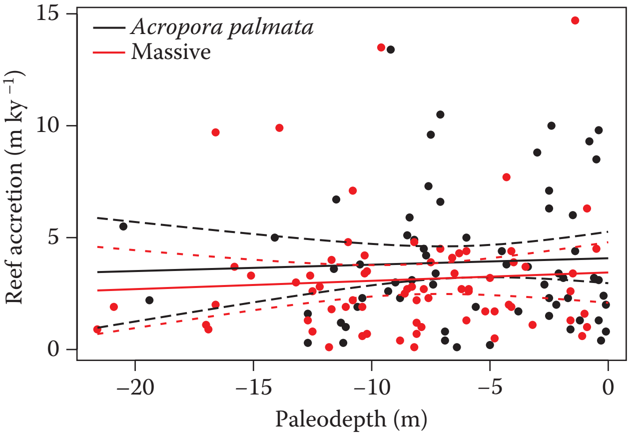

Figure 11 Reef accretion rates in metres per thousand years (m ky^{-1}) for paleo coral assemblages dominated by branching corals, specifically *Acropora palmata*, or massive corals. Notably, there is no apparent relationship between rates of reef accretion and paleodepth for either assemblage type, and there is no significant difference in mean accretion rate between assemblage types. (Redrawn based on data in Hubbard, D.K. 2009. Depth-related and species-related patterns of Holocene reef accretion in the Caribbean and Western Atlantic: a critical assessment of existing models. In *Perspectives in Carbonate Geology: A Tribute to the Career of Robert Nathan Ginsburg*, P.K. Swart et al. (eds). Chichester, UK: Wiley, 1–18.)

transport, as well as environmental limitations associated with light, accommodation space, and wave energy.

Concern over the effects of ongoing and future climate change on coral reefs has led to studies of the net carbonate production rates of living reefs (as a proxy for reef accretion), with particular attention paid to increased rates of coral bioerosion and decreased rates of coral calcification. For example, Perry et al. (2013) found a Caribbean-wide trend of decreasing net carbonate production from which they calculated reef accretion rates that were far lower than during the Holocene in the same areas. Future work needs to take into account the differences in sea-level dynamics between Holocene and modern settings. For example, the rise in sea level since the Last Glacial Maximum (LGM) has resulted in some of the highest reef accretion rates ever recorded (Macintyre & Glynn 1976), and care must be taken when comparing estimates of modern accretion rates, within a period when sea level has only fluctuated by 1 or 2 m over the past several thousand years, with estimates of ancient values during periods of rapid sea-level rise. Available space on the substratum, and other environmental factors including temperature, wave energy, and light intensity, are all determinants of reef growth and destruction.

Conclusions and future directions

The role of coral growth (calcification and associated increases in the physical dimensions of individual colonies) in structuring coral populations and assemblages, or even reef ecosystems, is difficult to isolate from multiple other factors. The abundance of corals (typically measured as areal coverage) depends on processes that contribute to both increases (e.g., reproduction, recruitment, and vegetative growth) and decreases (e.g., injury and mortality) in population size. Moreover, there is likely to be as much variation (spatial, temporal, and taxonomic) in exposure and susceptibility to disturbances, or repair responses (Meesters et al. 1996, Garzón-Ferreira et al. 2005, Madin et al. 2014, Pisapia et al. 2014), as there is variability in growth rates. There may also be direct trade-offs between growth and mortality (e.g., faster-growing, erect, branching corals are disproportionately susceptible to hydrodynamic forces caused by severe storms; Madin & Connolly 2006). Systematic declines in coral growth would, however, be expected to compound the effects of increasing frequency of major disturbances, leading to fewer and smaller corals (e.g., McClanahan et al. 2008), which will have important ramifications for the structure and function of reef ecosystems (Wilson et al. 2006, Pratchett et al. 2008).

A key area for future research is to explicitly investigate the influence of vegetative growth in structuring populations and assemblages of scleractinian corals. One way to do this is to document demographic rates (e.g., growth, injury, and mortality) across a large number of individually tagged colonies in a given population or assemblage (e.g., Babcock 1991, Edmunds & Elahi 2007, Madin et al. 2014). Given the work involved, this has only ever been done for a few specific coral species, but also, previous such studies have recorded long-term changes in colony size (typically maximum diameter or area; e.g., Hughes & Tanner 2000, Edmunds & Elahi 2007), providing estimates of realized growth that are confounded by injury and partial mortality. Alternatively, experimental approaches that quantify maximum potential growth rates of species can be combined with field estimates of realized growth under different environmental conditions to establish the extent to which abundance is limited by intrinsic maximum growth rate or environmental constraints on growth; integral projection models offer great potential for this kind of work (Edmunds et al. 2014).

Calcification rates provide the most direct and readily comparable measure of growth across different reef-building corals (e.g., branching vs. massive corals), especially when measured or averaged over longer periods to dampen marked diel and seasonal differences. Calcification rates can also be measured at the reef scale for coral assemblages under natural field conditions (e.g., Gattuso et al. 1996), providing a means to relate species-specific calcification of individual colonies to larger-scale reef accretion rates. Moreover, calcification rates can often be measured (or at least approximated) alongside routine estimates of linear extension (e.g., based on bandwidth for cores from corals with annual density banding; Aller & Dodge 1974). However, most of the existing data on coral growth is for average annual skeletal extension rates (Table 4), based on measurements of branch, radial (realized and actual), vertical, or horizontal extension. In many studies, skeletal extension is measured in only one direction (e.g., cores from massive corals are almost invariably taken vertically from the top), which may over- or underestimate (depending on the primary growth axis) extension rates relative to studies that average skeletal measurements taken in multiple directions and at multiple locations across the colony (e.g., Morgan & Kench 2012). For example, Lough and Barnes (2000) showed that linear extension in massive *Porites* was 15% higher along the vertical axis of the colony compared to the horizontal axis. To maximize the utility of skeletal extension estimates for comparing across taxa and among studies, it is important to record both horizontal and vertical extension, or at the very least, it should be clear exactly what was measured. Similarly, for complex branching corals, it would be useful to have information on both average annual branch extension and changes in the AMR across a wide range of species and different-size colonies to test if (or how) these two metrics actually relate to each other. Even if there is no apparent relationship, then at least AMR can be used in multispecies comparisons. Consistent and comparable data on growth rates of reef-building corals should then be compiled into a single global database (e.g., https://coraltraits.org).

An important and ongoing area of research is to test for long-term trends in coral growth that may be attributable to environmental changes. Sustained declines in the linear extension and calcification of some corals are already apparent (Edmunds 2005, Bak et al. 2009, De'ath et al. 2009, Tanzil et al. 2009, 2013, Cantin et al. 2010, Manzello 2010), despite relatively moderate environmental changes that have been recorded to date. However, effects of climate change will vary spatially (e.g., with latitude) and taxonomically (Cooper et al. 2012, Anderson et al. 2014). Therefore, much more research is required to discern these differences effectively as well as to account for climate change impacts beyond ocean warming (e.g., ocean acidification), linking long-term measurements of coral growth to measurements of temperature and seawater chemistry within the very habitats and locations where corals are sampled. Much more research is also required to quantify long-term changes in growth rates across a broader range of different coral species, especially those corals that are not amenable to retrospective measures of coral growth (e.g., *Acropora*, *Pocillopora*) but nonetheless are important habitat-forming species. Existing observational and experimental data tend to suggest that climate change and ocean acidification will have mostly negative effects on coral growth. Even at high-latitude reefs where there may be initial beneficial effects of increasing temperatures (Figure 10), low and declining levels of aragonite saturation are expected to constrain coral growth (Chan & Connolly 2013). These relatively short-term studies do not, however, provide insights into the capacity of corals to adapt or acclimatize to changing environmental conditions. Just as there are indications that corals may be becoming less susceptible to bleaching (Guest et al. 2012, Pratchett et al. 2013), growth rates of corals may re-adjust or even increase after a period of acclimatization to altered environmental conditions.

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