Temperature-mediated transitions between isometry and allometry in a colonial, modular invertebrate

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The evolutionary success of animal design is strongly affected by scaling and virtually all metazoans are constrained by allometry. One body plan that appears to relax these constraints is a colonial modular (CM) design, in which modular iteration is hypothesized to support isometry and indeterminate colony size. In this study, growth rates of juvenile scleractinians (less than 40 mm diameter) with a CM design were used to test this assertion using colony diameters recorded annually for a decade and scaling exponents (b) for growth calculated from double logarithmic plots of final versus initial diameters. For all juvenile corals, b differed significantly among years, with isometry ($b=1$) in 4 years, but positive allometry ($b>1$) in 5 years. The study years were characterized by differences in seawater temperature that were associated significantly with b for growth, with isometry in warm years but positive allometry in cool years. These results illustrate variable growth scaling in a CM taxon and suggest that the switch between scaling modes is mediated by temperature. For the corals studied, growth was not constrained by size, but this outcome was achieved through both isometry and positive allometry. Under cooler conditions, positive allometry may be beneficial as it represents a growth advantage that increases with size.

Keywords: isometry; allometry; scaling; scleractinia; temperature

1. INTRODUCTION

The variation in phenotypic traits with organism size has fascinated biologists for more than a century (Dubois 1897; Gould 1966; Schmidt-Nielsen 1989; Gayon 2000). This interest quickly led to the realization that, most traits scale disproportionately with size and in 1936, the term ‘allometry’ was coined to describe the general case of scaling as a power function of size (Huxley & Teissier 1936). Such relationships have pervasive and far-reaching effects on biological systems (Schmidt-Nielsen 1989; Gayon 2000), but some of the most important consequences of allometry originate in the constraints it imposes over ontogenetic and evolutionary time on organism size (Gould 1966); it is rare for these constraints to be relaxed.

One example of a group of organisms with the potential to avoid allometric constraints is provided by metazoans with a colonial modular (CM) design, such as bryozoans, colonial ascidians and colonial scleractinians (Jackson 1979; Hughes 2005). The critical feature of these taxa that is necessary to avoid allometry is the iterative propagation of modules that are conserved in size, so that colonies grow indeterminately while modules retain their area to volume relationship (Jackson 1979; Sebens 1987; Hughes 2005). All things being equal, colony scaling then is a summation of module properties, with the result that scaling is hypothesized to be isometric (Jackson 1979; Hughes & Hughes 1986; Sebens 1987). Surprisingly, there have been few experimental tests of this assertion and while some studies support isometry in bryozoans (Hughes & Hughes 1986; Barnes & Peck 2005) and corals (Elahi & Edmunds submitted), in a larger number of cases

scaling has been found to be allometric (Jokiel & Morrissey 1986; Sebens 1987; Kim & Lasker 1998; Vollmer & Edmunds 2000), and in some cases both isometry and allometry have been reported (Muñoz & Cancino 1989; Nakaya *et al.* 2003) or predicted (Patterson 1992). Such contradictions may reflect, in part, the likelihood that scaling characteristics are context specific for CM taxa, for example, varying as a function of flow regime and colony morphology (Patterson 1992; Kim & Lasker 1998; Barnes & Peck 2005) and the degree of integration among modules (Nakaya *et al.* 2003).

Arguably, the best example of a CM design is provided by colonial scleractinians, which in shallow tropical seas construct reefs with substantial ecological significance (Knowlton & Jackson 2001). Of central importance to reef construction is the exploitation by corals of their CM design to achieve indeterminate growth (Hughes 1984), with a subset of species forming massive colonies that function as primary framework builders (Goreau 1959). While individual modules (i.e. polyps) theoretically can maintain constant growth regardless of colony size, in practice their growth can be limited by colony morphology, which leads to self-shading with regards to resource acquisition (Patterson 1992; Kim & Lasker 1998) and a shortage of space necessary to accommodate dividing polyps (Barnes 1973). However when corals are small, notably when they are in a juvenile life stage, their growth is unlikely to be affected by self-shading or surface area limitations and indeed rapid growth in this life stage is important to gain an escape in size from the mortality risks of being small (Jackson 1977).

In this study, juvenile scleractinians were used to study scaling in organisms with a CM design, specifically to test the null hypothesis that the scaling of growth does not

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depart from isometry. Because scaling relationships typically are described by equations of the form $Y = aX^b$, where Y is the trait of interest, X is size, a is a constant and b is the scaling exponent, isometry can be defined by changes in Y that are proportional to X and allometry by changes in Y that are disproportional to X . Importantly, isometry can be distinguished from allometry using inferential statistics to test the scaling exponent for departures from an expected value, which for isometry is unity ($b=1$) when X and Y have the same dimensions (Gould 1966). Thus, to test for departures from isometric growth in juvenile corals, I assessed growth as the change in diameter of colonies at the start and end of nine, year-long intervals spanning a decade (1996–2005) and quantified the scaling of growth using the slopes (b) of the lines fitted to the double logarithmic plots of the colony diameters in successive years. According to the hypothesis of isometry in CM taxa, such plots should display a straight line with a slope of 1 and, assuming that growth occurs, a non-zero intercept that reflects a growth increment independent of initial size. Because my earlier research indicated that the dynamics of juvenile corals was related to seawater temperature (Edmunds 2004), I tested the nine scaling exponents for an association with seawater temperature. The results of these analyses demonstrate that scaling of growth in a CM taxon is isometric, at least some of the time. Most interestingly however, the data reveal a transition between scaling modes that is associated with seawater temperature, and therefore may be relevant to understanding the effects of rising seawater temperature on coral reefs.

2. MATERIAL AND METHODS

(a) *Growth of juvenile corals*

The growth of juvenile corals was determined using a tagging procedure on the shallow reefs (less than 9 m depth) along the south coast of St John, US Virgin Islands (Edmunds 2000, 2004). Juvenile corals were defined as colonies ranging in size from the smallest that could be detected (approx. 2 mm diameter) to 40 mm diameter and only colonies with approximately circular outlines were selected in order to avoid asexual fragments (which typically have fractured surfaces). Within this size range, the smallest colonies were difficult to identify to species, and therefore corals were identified to genus.

The first corals were tagged in May 1996 and thereafter tagging and measuring was completed in July (1999–2001) or August (all other years). Juvenile corals were selected randomly for tagging, marked by cementing a numbered aluminium disk to the adjacent rock and their sizes recorded with callipers (± 0.1 mm) as the mean of the two major diameters at the margins of the tissue, which sometimes stopped short of the edge of the corallum. One year later, the tags were relocated, and the marked corals assessed for condition and, if alive, again were measured. Because 22–46% of the tagged corals died each year (Edmunds 2004), more corals were tagged than eventually were available for the measurement of growth. Both the sample size and the relative taxonomic composition of the population of tagged coral varied from year to year, but *Porites* and *Agaricia* were the most frequently tagged genera in all years.

(b) *Seawater temperature*

Seawater temperature was recorded using loggers, and a continuous record from 1989 to 2005 was obtained by pooling data from different instruments placed at locations between 9 and 14 m depth within Great Lameshur Bay. A Ryan Industries thermistor (± 0.3 °C accuracy) was deployed at 11 m depth from January 1989 to April 1997 and from November 1997 to August 1999. An Optic Stowaway (± 0.2 °C accuracy, Onset Corporation) was deployed at 9 m depth from June 1997 to October 1997, August 1999 to August 2003 and August 2004 to August 2005 and a Tidbit (± 0.2 °C accuracy, Onset Corporation) was deployed at 14 m depth from August 2003 to August 2004. Due to a logger failure in May 1997, temperature records for this month were obtained from a dive computer. To characterize the thermal regime, temperature records for each ca 12 month period between the summer field surveys, including those periods over which juvenile corals were censused (1996–2005), were summarized by month and day and used to generate six parameters: the mean monthly temperature, the standard error of the monthly temperatures, the warmest monthly temperature, the coolest monthly temperature and the number of thermally extreme days (both hot and cold) each year. Days were categorized as ‘hot’ when they exceeded the local coral bleaching threshold of 29.3 °C, as determined by the United States National Oceanic and Atmospheric Administration, National Environmental Satellite Data and Information Service (NOAA/NESDIS; http://orbit-net.nesdis.noaa.gov/orad/sub/sst_series_virginpath.html), and ‘cold’ when they were at or below an arbitrary value of 26.0 °C (the 12th percentile of all the daily temperatures).

(c) *Statistical analyses*

The scaling of growth was evaluated using the linear relationships between the logarithms of the initial and final diameters. This approach relies on the initial diameter serving as a tractable measure of size for the purpose of allometric analyses (Gould 1966), and its choice was driven by the inability of measuring biomass—a measure of size used more frequently in allometric studies (Schmidt-Nielsen 1989)—in a non-destructive manner. The scaling analyses were completed first for all the juvenile corals together, then for *Porites* and finally for a subset of corals obtained by excluding *Porites*. The second and third analyses were completed simply to gain insight into the possibility that the results for all the juveniles were biased by the most abundant genus (*Porites*, which accounted for 21–76% of the tagged corals each year). Model I regression techniques were used to test for a linear relationship between diameters and ANCOVA was used to test for differences in slopes among years. The statistical assumptions of these procedures were tested through graphical analyses of the residual variation. Because the diameters were measured with error, the slopes (b) of the relationships were calculated by Model II Reduced Major Axis (RMA) techniques with the standard error provided by Model I techniques (Sokal & Rohlf 1995). A two-tailed t -test then was used to determine whether the scaling relationships were isometric (i.e. $b=1$) or allometric (i.e. $b \neq 1$).

To gain insight into the potential role of seawater temperature in mediating changes in the scaling of growth, the relationship between temperature and b was explored with Pearson correlation. To reduce the risks of Type I errors in repeated testing with different aspects of the temperature

Figure 1. Growth of all juvenile corals between 1996 and 2005. Values are displayed on logarithmic axes as the final size (mm; ordinate) against the initial size (mm, abscissa). The axes are identical in all graphs and for clarity they are labelled only on the 2002–2003 panel. Regression lines were fitted by RMA techniques and the b -values display the slopes of these lines.

record, principal component analysis (PCA) was used to collapse the six parameters of seawater temperature into a smaller number of principal components (PCs). PCA was carried out on the correlation matrix of the log-transformed data, using a $\log(x)$ transformation for the parameters derived from the monthly records and a $\log(x+1)$ transformation for the number of extreme thermal days. Two correlation analyses were completed, first between the values of b and PC1 and second between the values of b and PC2. The component loadings were used to determine the relative influence of each temperature parameter on each PC and hence provide a biological interpretation of any significant correlations.

3. RESULTS

The initial and final diameters of 58–249 juvenile corals were recorded every year. All had an initial diameter less than 40 mm, but some grew out of this size range during their study year, some declined in size, and a few did not change in size. For each period, less than 26% grew to more than 40 mm diameter, less than 36% shrank and less than 8% remained the same size.

For all juvenile corals, the final size was strongly and positively related to the initial size (figure 1), and all of the regressions were significant ($F \geq 47.84$, d.f. = 1 and ≥ 55 , $p < 0.001$). However, the slopes of the regressions differed significantly among years ($F = 6.26$, d.f. = 8, 1175, $p < 0.001$), with RMA slopes ranging from 1.006 in 2002–2003 to 1.268 in 1999–2000. The RMA slopes for 1996–1997, 1997–1998, 2000–2001 and 2002–2003 do not differ significantly from 1 ($t < 1.140$, d.f. ≥ 60 , $p \geq 0.26$; s.e. for slopes shown in figure 4), and therefore describe isometric relationships. In contrast, the RMA slopes for 5 of the 9 years—1998–1999, 1999–2000, 2001–2002, 2003–2004 and 2004–2005—differ significantly from

1 ($t > 2.03$, d.f. ≥ 55 , $p \leq 0.048$; s.e. for slopes shown in figure 4), and therefore describe allometric relationships. The biological significance of these differences is illustrated by a contrast of the relationship between the actual growth increment (mm yr^{-1}) and initial size in 2 years for which large numbers of corals were measured and growth scaling varied (figure 2). In brief, isometric growth scaling in 2002–2003 ($b = 1.006$ in figure 1) corresponds to a mean growth increment of 5.4 mm yr^{-1} that is independent of initial size ($r = 0.032$, d.f. = 213, $p > 0.050$), while allometric growth scaling in 2004–2005 ($b = 1.112$ in figure 1) corresponds to an annual growth increment that is related positively to size ($r = 0.221$, d.f. = 186, $p < 0.010$) and increases from near-zero at less than 10 mm diameter to ca 10 mm at greater than 35 mm diameter (figure 2).

The results for *Porites* (data not shown) were similar to those for the juveniles of all taxa, although the strength of the relationships between initial and final diameter were weakened by smaller sample sizes. The final sizes of colonies again were positively related to the initial size ($F \geq 5.77$, d.f. = 1 and ≥ 13 , $p < 0.032$), and their slopes differed significantly among years ($F = 3.64$, d.f. = 8, 490, $p < 0.001$) and ranged from 0.979 in 1997–1998 to 1.328 in 2001–2002. However, in contrast to the results for all of the juveniles, the RMA slopes for *Porites* differed significantly from 1 in only 3 of the 9 years ($t > 2.11$, d.f. ≥ 34 , $p \leq 0.042$)—1999–2000, 2001–2002 and 2003–2004—and therefore the scaling of growth in this genus was allometric in 1/3 of the years, but isometric in 2/3 of the years. When *Porites* was excluded from the analysis of juvenile corals, the final sizes of the colonies remaining still were related positively to the initial size ($p < 0.001$), the slopes of these relationships differed significantly among years ($p = 0.015$), and the RMA slopes differed significantly from 1 ($p < 0.05$) in one of the 9 years (data not shown).

Figure 2. Growth of all juvenile corals in 2 years (2002–2003 and 2004–2005) selected to illustrate isometric and allometric growth scaling (respectively) for years characterized by large sample sizes (more than 188 corals) for growth measurements. 2004–2005 differed from 2002–2003 with respect to seawater temperature, notably with more variable monthly temperatures, a colder winter, and a greater number of days that were either cold (less than or equal to 26.0 °C) or hot (greater than 29.3 °C; figure 3). Growth rates are displayed as the difference between final and initial diameters and are plotted against the initial diameter; growth rates were both positive (i.e. size increased) and negative (size decreased). Growth rates were independent of size in 2002–2003 (dashed line at a mean growth rate of 5.4 mm yr⁻¹), but were related positively to size in 2004–2005 (solid line fitted by Bartlett's three-group method, which is a technique suitable for Model II regressions with low correlation coefficients (Sokal & Rohlf 1995)).

(a) Seawater temperature

Seawater temperature displayed a complex pattern of variation between 1989 and 2005 (figure 3). The mean temperatures for the *ca* 12 month periods between censusing trips were significantly and positively correlated with time ($r=0.780$, d.f. = 14, $p=0.004$), and increased from 27.2 ± 0.3 °C in 1989/90 to 28.0 ± 0.4 °C in 2004/05 ($\pm$ s.e., $n=12$). Additional parameters that characterized seawater temperature also varied among sampling years, but the patterns of variation differed among parameters. The highest monthly seawater temperature also was correlated positively with time ($r=0.527$, d.f. = 14, $p=0.036$), and increased from 28.5 °C in 1989/90 to 29.3 °C in 2004/05, but neither the lowest monthly seawater temperature, nor the standard error of the monthly seawater temperatures, varied consistently over time ($r \leq 0.196$, d.f. = 14, $p > 0.466$). The number of days that were categorized either as hot or cold was affected by time (2×16 contingency table, $\chi^2=379$, d.f. = 15, $p < 0.001$), so that towards the end of the study there were more hot days per year (and fewer cold days) than when the study began (figure 3).

A PCA was used to collapse the six temperature parameters with the goal of facilitating an unambiguous test of the hypothesis that the scaling of growth in juvenile corals is independent of seawater temperature. The PCA was completed using the temperature records for the 10 years that juvenile corals were surveyed and it created two PCs that together explained 87% of the variation in

Figure 3. Seawater temperature in Great Lameshur Bay between 1989 and 2005. All values were recorded daily using *in situ* loggers placed at 9–14 m depth and are grouped by *ca* 1 year between sampling periods. (a) Number of extreme thermal days in the year between sampling periods; hot days are greater than 29.3 °C and cold days are less than 26.0 °C. (b) Mean monthly seawater temperatures (filled circles; $\pm$ s.e., $n=12$) together with the hottest (high) and coolest (low) months in each 12 month period.

seawater temperature (table 1). Based on the component loadings (table 1), PC1 was strongly and positively related to the standard error of the monthly temperature variation and the number of cold days and also was strongly negatively related to lowest monthly temperature. High values of PC1 corresponded to years characterized by variable monthly temperatures, cold winters and large numbers of 'cold' days. PC2 was strongly and positively associated with the mean monthly temperature, and therefore, high values of PC2 corresponded to years with high-mean seawater temperatures (table 1).

The scaling of growth in all juvenile corals was strongly and positively associated with PC1 for temperature ($r=0.835$, d.f. = 7, $p=0.005$; figure 4), but was unrelated to PC2 ($r=-0.113$, d.f. = 7, $p=0.772$). For *Porites*, *b* also increased with PC1 for temperature, although the relationship was not statistically significant ($r=0.611$, d.f. = 7, $p=0.081$), and again was unrelated to PC2 ($r=-0.117$, d.f. = 7, $p=0.764$); the *b* values for the subset of corals obtained by excluding *Porites* were unrelated to either PC ($p > 0.050$). Based on the results from all of the juvenile corals, larger scaling exponents were associated with large values for PC1, which in turn corresponded to years with colder winters, more cold days per year, and greater variance of mean monthly temperatures. Because the five steepest scaling relationships differed significantly from 1 and are

Table 1. Principal component analysis of six characteristics of the seawater temperature in Great Lameshur Bay between 1996 and 2005. (Daily records of seawater temperature were used to create the six characteristics for each year: mean monthly temperature, standard error of monthly temperature, minimum monthly temperature, maximum monthly temperature, the number of hot days (i.e. greater than 29.3 °C), and the number of cold days (less than 26.0 °C). The PCA was performed on log-transformed data.)

parameter	PC1	PC2
eigen value	3.08	2.16
explained variance (%)	51.27	35.96
component loadings		
mean monthly temp.	−0.23	0.82
s.e. of monthly temp	0.95	0.21
minimum monthly temp	−0.85	0.44
maximum monthly temp	0.63	0.64
no. hot days	0.66	0.67
no. cold days	0.77	−0.63

Figure 4. Relationship between the RMA slopes ($b \pm \text{s.e.}$) for the scaling relationship of growth in juvenile corals (pooled taxa) and multivariate seawater temperature (PC1). Slopes were taken from the scaling relationships for the 9 study years (figure 1), with those differing significantly from 1 marked with asterisks (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$); s.e. values were derived from Model I regressions (Sokal & Rohlf 1995). The multivariate temperature was derived from a principal component analysis of six parameters characterizing seawater temperature between 1996 and 2005 (figure 3 and table 1). The slopes of the scaling relationships are correlated significantly with multivariate seawater temperature ($p = 0.005$), with warmer conditions associated with isometry and cooler conditions with positive allometry. The regression line was fitted by an RMA technique; the vertical dashed line indicates a possible 'break-point' between isometry and positive allometry.

characteristic of allometry, while the four remaining were not statistically discernable from 1 and are characteristic of isometry, the relationship between b and temperature for all juvenile corals (figure 4) illustrates a transition between scaling modes that is associated with temperature.

4. DISCUSSION

The differential variation with size of area- and volume-dependent traits is a primary cause of allometric constraints on organism size (Schmidt-Nielsen 1989), and biologists have long been interested in body plans that achieve an 'escape' from such constraints. CM designs provide the best-known example of a body plan for which these constraints are relaxed (Hughes 2005), and for this reason (as well as many others) they have attracted considerable research attention (Jackson 1977, 1979; Hughes 2005). The present analysis provides examples of both scaling modes in a CM taxon and, together with previous reports of allometry for this body plan (referenced in the introduction), demonstrates that the biological implementation of modularity does not provide an unequivocal escape from allometry. There are well-known explanations for this discrepancy (described below), but this is the first study to demonstrate repeated transitions between scaling modes for a CM taxon under ecologically relevant conditions defined by habitat and temporal scale. Interestingly, because the allometry is positive ($b > 1$) for the size class of scleractinians studied—describing a growth advantage that is amplified by size (figure 2)—it potentially is beneficial rather than constraining under the cooler regime in which it occurs. Perhaps this is why the overall growth of juvenile corals in St John is related positively to the number of cold days in the year preceding the year during which growth occurs (Edmunds 2004). Although larger corals were not the subject of the present study, an analysis of growth in a full size range of coral colonies shows that positive growth allometry in cooler years does not extend to colonies more than 40 mm diameter (P. J. Edmunds, unpublished data), thereby avoiding the biologically implausible outcome of exponentially increasing organism size.

While CM designs create the possibility for isometry, in practice this potential may be realized infrequently due to the emergent properties of colony design (Kim & Lasker 1998; Lasker & Sanchez 2002). Using the reef coral *Pocillopora damicornis*, Jokiel & Morissey (1986) were among the first to demonstrate allometry for a CM taxon (data re-analysed in Patterson 1992 and Vollmer & Edmunds 2000), yet even in the 1980s the assumption of independence among modules that is necessary for isometry was known to be violated by translocation of metabolites among modules in corals (Pearse & Muscatine 1971), hydroids (Rees *et al.* 1970) and bryozoans (Best & Thorpe 1985). The translocation of metabolites among modules now is accepted as a common feature of CM taxa (reviewed in Oren *et al.* 2001), and because such translocation can be facultative, as occurs when resources are mobilized to support healing (Oren *et al.* 2001), the extent of translocation potentially could mediate scaling modes. This possibility recently was demonstrated for the colonial ascidian *Botrylodes simodensis*, which switches metabolic scaling from allometric to isometric when the translocation pathway through the common vascular system degenerates (Nakaya *et al.* 2003). The assumption of conserved module dimensions, which also is necessary for isometry, probably is violated in some cases as well. For example, in colonial scleractinians biomass can vary *ca* twofold between seasons (Fitt *et al.* 2000), which probably alters polyp volume by changing the depth of skeleton occupied by living tissue (Barnes & Lough 1992). This effect (i.e. changes in tissue thickness) has been

hypothesized to drive allometric metabolic scaling in juvenile colonies of the coral *Siderastrea siderea* (Vollmer & Edmunds 2000). Finally, it is important to note that scaling in CM taxa also can be modified simply through the interactions between colony morphology (Lasker & Sanchez 2002) and the environment. For instance, metabolic scaling for a cylindrical colony in an aquatic environment switches from isometric to allometric when mass transfer characteristics are changed by the transition from turbulent to laminar flow (Patterson 1992), and for bryozoans, the mode of metabolic scaling depends on whether the colony is encrusting or arborescent (Barnes & Peck 2005), or whether or not it is feeding (Muñoz & Cancino 1989). Interference among modules for resource acquisition provides yet another mechanism through which scaling in CM taxa might depart from isometry (Kim & Lasker 1998).

The important conclusions from the aforementioned studies are that not only is modularity itself insufficient to assure isometry (Vollmer & Edmunds 2000), but also that the scaling can be ontogenetically labile in CM taxa, and therefore not a fixed characteristic of body design as often is assumed (Glazier 2005). There are multiple hypotheses that can account for scaling in specific body plans or individual traits (Gould 1966; Schmidt-Nielsen 1989; Glazier 2005), but in the present case however, the putative mechanism(s) underlying the scaling trends must have the capacity to explain allometry and isometry for a single trait in one taxon, and over a decade, multiple transitions between scaling modes that plausibly could be mediated by temperature. Two possibilities—that the results reflect the consequences of measuring different coral genera each year, or changes in colony shape—are inconsistent with the data. First, although the relative abundance of the genera analysed varied each year, *Porites* and *Agaricia* were most frequently measured over all 9 intervals ($58 \pm 6\%$ of all corals per year (mean $\pm$ s.e., $n=9$)), and the inclusion of *Porites* in the analyses was not critical to the conclusion that growth scaling varied among years, although this genus contributed to the detection of a greater number of scaling exponents that differed significantly from 1. Second, while changes in the scaling of growth as measured by change in diameter could be mediated by a trade-off with colony height, analysis of the aspect ratio (height/diameter) of 48 juvenile colonies of *Porites* and *Diploria* indicated that the shape was independent of size (P. J. Edmunds, unpublished data).

One mechanism that could explain the present results is the possibility that the growth of juvenile corals is affected by directed translocation of metabolites among coral polyps (Oren *et al.* 2001), which probably is a result of flagella-powered fluid transport within the gastrovascular cavity (GVC; Gladfelter 1983). The translocation of metabolites among polyps would promote polyp integration and conceivably could support positive growth allometry as a result of the increase in resources that are available for transport in larger colonies (Oren *et al.* 2001). With this hypothesis, warmer years might impede polyp integration through a reduced supply of metabolites available for transport, or a reduction in fluid transport among modules (see Nakaya *et al.* 2003), both of which would favour polyp autonomy. For reef corals, temperature is well known for its ability to modulate the availability of metabolites by mediating carbon supply (i.e. through

photosynthesis) and demand (i.e. through respiration; Coles & Jokiel 1977; Iglesias-Prieto *et al.* 1992), but the implications of elevated temperature for translocation are unknown. Interestingly in hydroids, high temperature has the potential to disrupt polyp–polyp transport by creating ‘dynamical chaos’ in the contractions of stolons that connect the polyps and provide continuity through a common GVC (Buss & Vaisnys 1993).

An alternative mechanism that also is consistent with the present results is the possibility that cooler years promote wintertime increases in biomass (Fitt *et al.* 2000) that plays an important role in fuelling skeletal growth in the following months. As wintertime ‘fattening’ of coral tissue would represent an absolutely larger reserve of metabolites in bigger compared to smaller colonies, conceivably this could support positive growth allometry when reserves are translocated in support of increasing colony diameter. Although the proximal causes of seasonal differences in coral biomass are unknown, the strong likelihood that temperature is a key factor raises that possibility that wintertime fattening would be reduced in mild winters, thereby undermining the potential for juvenile corals to display positive growth allometry (i.e. growth then would scale isometrically). As there are high mortality risks associated with small size for reef corals (Jackson 1977), a mechanism reducing the progression of colonies through the risky small size classes—such as a loss of positive growth allometry—could have negative implications for population growth.

In summary, by using a decade of *in situ* growth data for juvenile corals, this study identifies a hitherto unknown plasticity of scaling for a CM taxon and suggests that the transitions between scaling modes is related to temperature. Clearly, it is important to examine other CM taxa for the presence of similar trends before claims of generality can be made, but for colonial scleractinians the present analyses already justify the completion of manipulative experiments designed to address three core issues. First, a test of the role of tissue thickness in growth scaling is required, for example, through an experimental manipulation of biomass achieved through differential feeding (Houlbreque *et al.* 2004). Second, the role of polyp–polyp translocation in growth scaling should be explored, perhaps by incubating corals under conditions that modify transport through the GVC as can be achieved by varying the viscosity of seawater (Krueger & Dudgeon 2005). Finally, and most importantly is the need for an experimental analysis of the effect of temperature on the scaling of growth, specifically to test for a cause-and-effect relationship between these variables. If a cause-and-effect relationship is supported, then the present analysis may be relevant in evaluating the effects of global climate change on coral reefs.

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