

Modular growth of a gorgonian coral can generate predictable patterns of colony growth

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Abstract

The modular construction of colonial organisms can generate complex growth patterns that incorporate both growth and partial mortality. These patterns often confound simple age based descriptions of growth but, in some cases, modularity can generate predictable patterns of colony growth that are amenable to modeling approaches more commonly used in unitary organisms. Colonies of the Caribbean gorgonian *Pseudopterogorgia elisabethae* from a 20 m deep population in the Bahamas exhibit such characteristics. Mass was highly predictable from colony height, following a power function with an exponent of 2.1. Age, as determined from counts of annual growth rings was a good predictor of height and mass. The relationship between age and height was modeled using a Von Bertalanffy growth curve. Growth models from both the age:height relationship and from extrapolations of colony growth rates from another Bahamian population yielded similar but more variable results. Based on those data and previously published observations of spawning and survivorship, colonies reach sexual maturity at 5–7 y and can live to over 40 y. Using the Von Bertalanffy function to estimate ages from height facilitates interpretation of size frequency distributions and suggested enhanced recruitment on San Salvador Island following the passage of Hurricane Andrew in 1992. Although simple growth models do not characterize the variance inherent in modular growth, these models can provide useful tools for the interpretation of population data.

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1. Introduction

One of the fundamental properties of plants and many invertebrates is their modular pattern of growth. “Individuals” are constructed from the iterative replication of

modules. Those modules may be leaves, tillers, polyps, zooids or branches among many possibilities, and the individuals can be a single physiologically discrete entity such as an oak tree or coral head, or the more ambiguous entity of strawberry plants that are linked by runners or hydroid colonies linked by stolons, in which the degree of integration can vary dramatically over time (Lasker and Sánchez, 2002; Rinkevich, 2002; Sánchez, 2004). The growth of these individuals can be modeled through the replication, growth and death of the modules (Harper,

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1977). In addition to describing the growth of individuals and colonies, the recognition of modular growth has shaped our understanding of life histories (Harper and White, 1974; Jackson, 1985; Jackson and Coates, 1986) and community structure (Jackson, 1977).

While studies of modular growth have often focused on the plasticity of form and the complexity of both the individual growth and population dynamics of modular organisms (Hughes and Jackson, 1985; Hughes and Connel, 1987; Hughes, 1989; Babcock, 1991; Hughes et al., 1992), other research on the same or similar taxa have successfully analyzed modular taxa using models developed for unitary organisms (Grigg, 1974, 1975, 1977; Caddy, 1993; Mistri and Ceccherelli, 1993, 1994). Form is an emergent property of modular organisms, a feature that makes it possible to examine the growth and dynamics of some modular organisms using either approach. In this paper we characterize the growth of a colonial marine invertebrate, the gorgonian coral *Pseudopterogorgia elisabethae* Bayer, 1961, using a Von Bertalanffy growth model and show how the model can be used to characterize the age and size of individual colonies and with some additional data the age structure of populations as well. The use of a model developed for unitary organisms does not provide a mechanistic description of growth that incorporates the inherently modular organization of the colony, i.e., the formation and growth of the individual modules. Instead, the model summarizes growth in a simple form that facilitates comparisons among species and environments.

Modular organisms are similar to unitary organisms in that they often have highly characteristic forms and upper limits to growth. Among gorgonians species descriptions almost invariably include maximum heights (Bayer, 1961), implying either a functional limit to size set by size-dependent mortality (Birkeland, 1977) or a size- or age-dependent limit to growth. Decreasing rates of growth with colony height have been described by Grigg (1977), Velimirov (1975) and Lasker et al. (2003). Such limits imply an upper limit to size and are an integral component of the Von Bertalanffy growth model, which has been used extensively for fishes and unitary invertebrates, including solitary corals (Chadwick-Furman et al., 2000; Goffredo et al., 2004). While the large literature focusing on complexity of modular growth might suggest otherwise, colonial species with discrete colonies that are not subject to variable levels of partial mortality can also be modeled with the Von Bertalanffy growth function. Thus, a number of authors using either growth rate data or size and age data have fit growth in gorgonians to Von Bertalanffy growth functions (Grigg, 1975; Mistri and Ceccherelli, 1993; Mitchell et al., 1993). When it can be used this approach

allows analyses that can further address the population dynamics, ecology and management of populations (Grigg, 1976, 1984; Abbiati et al., 1992; Santangelo et al., 1993; Mistri and Ceccherelli, 1994).

2. Materials and methods

In May 2005, 81 *Pseudopterogorgia elisabethae* colonies were collected at a depth of 21–23 m at Cross Harbour Ridge on the Little Bahama Bank near Great Abaco (25° 56.91' N, 77° 20.38' W). As *P. elisabethae* at this site is harvested by cropping branches from colonies, care was taken to only collect colonies with no sign of previous collection. Collections were made with the assistance of T. Higgs, one of the commercial collectors. Colonies were dried and then the height (H), mass (M), and base diameter (D) were measured. Height was measured as the greatest distance along the axis from the base to the tip of the colony. Growth rates among the 81 colonies were determined from the relationship between colony height and age using differences in the average heights of colonies of successively greater ages to estimate growth rates.

Colony age was estimated by growth ring analysis (Knuston et al., 1972; Grigg, 1974; García-Rodríguez and Massò, 1986; Abbiati et al., 1992; Mitchell et al., 1993; Mistri and Ceccherelli, 1994; Santangelo et al., 2004). Cross sections cut 1 cm from the colony base were glued onto a support, embedded in epoxy resin, and then polished using a grinder/polisher to enhance the definition of the individual growth rings. The sections were examined and the rings were counted using a dissecting microscope under both incident and ultraviolet lighting to illuminate the growth rings. All concentric bands that were darker than the surrounding tissue were counted as growth rings. Each basal cross section was counted at least three times to estimate interpretation error, and the arithmetic mean value of the count (rounded to a whole number) was used to determine the number of bands, which we have interpreted as annual bands. Although the exact nature of the banding pattern has not been demonstrated for a tropical gorgonian, bands are known to be annual in species from deeper water and from temperate species (Grigg, 1974; Abbiati et al., 1992; Santangelo et al., 1993; Mistri and Ceccherelli, 1993, 1994). Mitchell et al. (1993) presents data indicating that the growth rings are produced annually in *Leptogorgia virgulata*, a semi-temperate species in the Gorgoniidae, the same family as *P. elisabethae*. In order to relate the growth rings to environmental variation at the study site, temperature at Cross Harbour was recorded with a Hobo temperature logger recording a measurement every 2.5 h between May 2004 and November 2005.

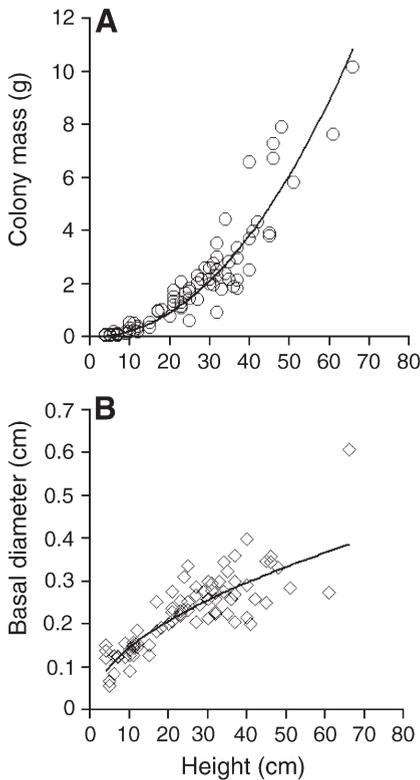


Fig. 1. Dependence of biometric parameters on colony height in the gorgonian coral *Pseudopterogorgia elisabethae*. (A) Colony dry mass, $y=0.002x^{2.075}$ ($r=0.968$, $p<0.001$; $N=81$). (B) Colony base diameter, $y=0.044x^{0.519}$ ($r=0.872$, $p<0.001$; $N=81$).

To monitor the growth of individual colonies, all colonies of *P. elisabethae* along three transects totaling 70 m² of substratum located at depths of 12–15 m in San Salvador, Bahamas (24° 4.00' N, 74° 32.50' W) were tagged (total number of colonies = 181). The colonies were photographed in place at approximately 6 months intervals between December 1997 and December 1999; the growth rate of each colony was calculated by measuring changes in colony height both through sequences of images and direct measurements in the field (for more details on growth rate determination see Lasker et al., 2003). Mortality of these colonies was also determined and has been reported previously (Lasker et al., 2003).

Growth rates based on both the size–age data and the directly observed growth rates were fit to the Von Bertalanffy function (Von Bertalanffy, 1938):

$$H_t = H_\infty(1 - e^{-Kt})$$

where H_t is colony height at age t , H_∞ is asymptotic height (maximum expected height), K is a growth constant, and t is colony age. The exact procedures are

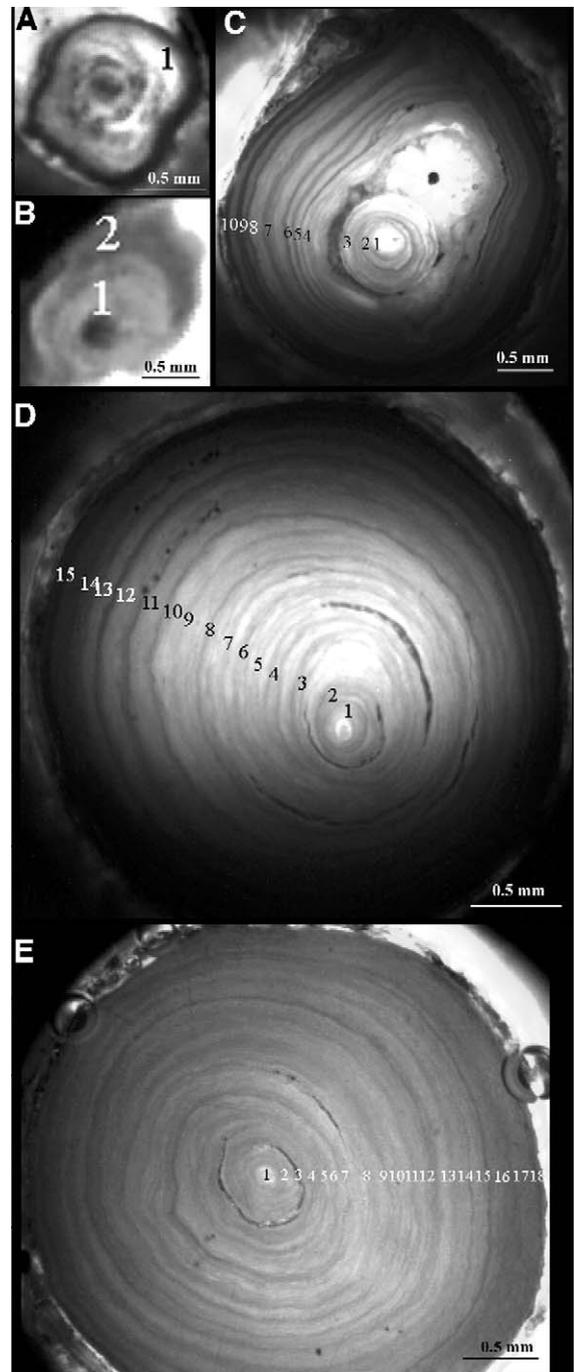


Fig. 2. Cross sections exhibiting annual growth rings of the base of the colony central axis in colonies of *Pseudopterogorgia elisabethae*. Each ring is made up of 2 bands, one is light in color and thick while the other is darker and thinner. The numbers showing the years of growth are next to the darker bands. The peripheral band of all sections is a darker band corresponding to winter growth prior to the May 2005 collection. (A, B) Young colonies 1 to 2 years of age. (C–E) Adult colonies 10, 15, and 18 years old.

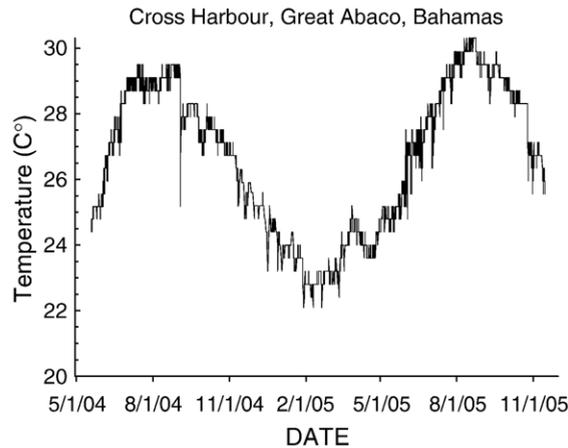


Fig. 3. Temperature at 16 m depth at Cross Harbour, Great Abaco, Bahamas. Note the sharp declines in temperature on September 3, 2004 and October 25, 2005, which correspond to the passage of Hurricanes Frances and Wilma.

described in the manuals of Pauly (1984) and Sparre et al. (1989).

The parameters H_{∞} and K were determined from the age–height data using a Ford–Walford plot. The Ford–Walford plot factors out differences in growth that are age-dependent by plotting size (colony height, H) at age $t+1$ as a function of size at age t (Ford, 1933; Walford, 1946; Gulland and Holt, 1959). Since there were multiple colonies of equal ages mean heights were used for colony size at each age classes. H_{∞} was then calculated as the $H_{\infty} = \text{intercept}/(1 - \text{slope})$, and K as $K = -\ln(\text{slope})$.

Growth rate data from San Salvador were fitted to a Von Bertalanffy growth function using a Gulland and Holt plot, in which growth rate is plotted as a function of colony size. The slope of that function is equal to the

growth constant K ($K = -\text{slope}$), and the maximum expected colony height (H_{∞}) corresponds to the colony height at which there is no growth, i.e., where the growth regression intercepts the x -axis. Only a single growth rate summarizing growth over the entire observation period was used for each colony. All growth rates were normalized to a year. In some cases data were unavailable for the entire 2 y period, usually due to mortality or because the colony first appeared as a recruit.

Population size structure at San Salvador was determined for the colonies present in the 70 m² that were monitored for colony growth. Colonies that were present in July 1999 were used for the analysis. Colony heights were used to estimate age using the Von Bertalanffy growth model derived from the San Salvador data.

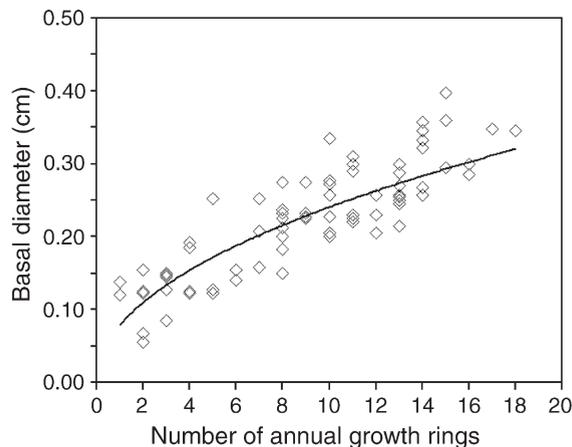


Fig. 4. The relationship between the number of annual growth rings and axis diameter in the gorgonian coral *Pseudopterogorgia elisabethae*, $y = 0.079x^{0.486}$ ($r = 0.839$; $p < 0.001$; $N = 77$).

3. Results

3.1. Colony biometry and growth rings

The height of *Pseudopterogorgia elisabethae* colonies from Cross Harbour was an excellent predictor of dry colony mass (Fig. 1A). For many species, mass is roughly proportional to the cube of the major body axis (Von Bertalanffy, 1938). However, mass was closely related to the square of height among *P. elisabethae* colonies. This relationship, which has been observed in other anthozoan colonies (Grigg, 1976, 1984), is probably a consequence of the relatively simple sub-apical branching pattern and planar growth form of the colony. There also was an inverse exponential relationship between colony height and colony base diameter. This changing height:base diameter relationship indicates allometric growth, with colony height increasing more rapidly than colony base diameter (Fig. 1B).

Growth rings in *P. elisabethae* exhibited a clear alternation between light and dark bands (Fig. 2), and several features of both the environment and the samples indicate that the growth rings in *Pseudopterogorgia elisabethae* axes were generated annually. Firstly, the environment at Cross Harbour is seasonal. Temperatures at 15 m depth ranged from summer highs of over 30 °C to lows approaching 22 °C with a broad period of cool temperatures during the winter and Spring (Fig. 3). Secondly, the samples were collected in May which is the last month of cool water temperatures. The last ring on the samples appears to be a high density band which would be expected from slow growth. Finally the 3 youngest colonies, which had 3 sets of rings, were 6–12 cm in height. Assuming settlement in December when spawning occurs (Gutiérrez-Rodríguez and Lasker, 2004), those colonies would have been 2.5 y old, which would indicate growth rates of 2 to 5 cm y⁻¹. Those growth rates are consistent with observed rates from San Salvador (see below) and are also consistent with the sizes of new 6 month old recruits that have been observed in cleared areas at Cross Harbour (unpublished data).

The youngest colony aged was 1 year old (Fig. 2A) and the oldest 18 y (Fig. 2E). Older colonies were present in the collection, but they could not be aged due to the difficulty of discerning and consistently scoring the extremely thin bands at the outer edge of the axis. The largest colony collected had a basal diameter of 0.608 cm which, relative to colonies of similar height, was unusually large (Fig. 1). The relationship between the number of annual growth rings and the colony base diameter indicated that the annual growth rate of the diameter decreased as the colony aged (Fig. 4).

3.2. Von Bertalanffy growth function

An age–colony height relationship was established, using the growth ring analysis to age colonies (Fig. 5A, B). The relationship was used to calculate the Von Bertalanffy growth function parameters using a Ford–Walford plot (see Sebens, 1983; Mitchell et al., 1993; Goffredo et al., 2004). A Ford–Walford plot factors out differences in growth that are age-dependent by plotting size (colony height, H) at age $t+1$ on the ordinate versus size at age t on the abscissa. The linear regression of this plot produced the equation H_{t+1} (cm) = 0.959 H_t (cm) + 3.308 ($r=0.970$; $p<0.001$), from which H_∞ = intercept/(1 – slope) = 81.7 cm, and $K = -\ln(\text{slope}) = 0.041$. The Von Bertalanffy growth model based on growth ring analysis was depicted in Fig. 5. When the predicted heights for each age class was compared to the

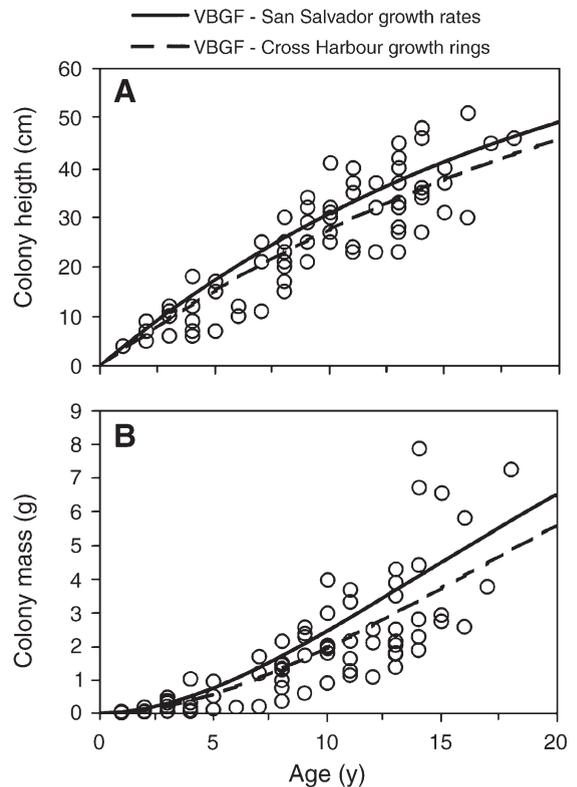


Fig. 5. Age specific growth curves of colonies of the Caribbean gorgonian coral *Pseudopterogorgia elisabethae* in the Bahamas (western Atlantic). The age–size relationship, obtained from the application of the Von Bertalanffy growth model to linear extension rates measured in the field, is compared to age–size data from microscopic analysis of growth rings. (A) Relationship between colony age and colony height. (B) Relationship between colony age and colony dry mass. Marked points (circles) are heights and masses of colonies for colonies collected at Cross Harbour whose age was determined from growth ring analyses.

observed heights (i.e. all colonies not the mean for each age) $r^2=0.78$.

3.3. San Salvador growth rates

The growth rates observed among the colonies from San Salvador provided estimates of growth over the full size range of *P. elisabethae* colonies (Fig. 6). Growth rate decreased as a function of height. The distribution of the growth rates depicted in Fig. 6 suggests a maximum growth rate at any given size with a broad distribution of observed growth rates under that maximum. On average, colonies ranging from 0 to 10 cm in height grew 3.5 cm per year (SE=0.30; $N=84$), colonies ranging from 20 to 30 cm in height exhibited an annual growth rate of 2.6 cm (SE=0.44; $N=31$), while colonies ranging from 40 to 50 cm in height grew 0.5 cm per year (SE=0.06; $N=5$). The growth rates of *P. elisabethae* colonies on San Salvador were markedly variable both among and within size groups (average coefficient of variation within the size classes=72%). The regression of growth rate against height, although highly significant ($p=0.0007$) only explained 6.2% of the total variance in growth rates. That variability is indicative of the effects of modular growth on the trajectory of any single colony. The mean growth rates characterized by the linear regression yielded a growth curve ($H_\infty=76.899$ cm, $K=0.05$), remarkably similar to the data from Cross Harbour (Fig. 5).

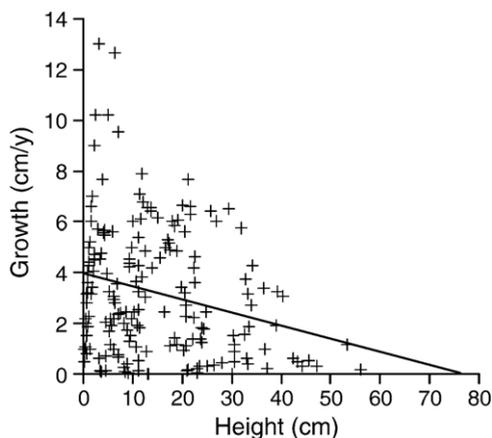


Fig. 6. Growth rates of colonies of *Pseudopterogorgia elisabethae* from San Salvador, Bahamas, plotted as a Gulland and Holt plot for the estimation of Von Bertalanffy growth function parameters K and L_∞ . The observations are independent of one another; i. e., a single colony contributes one point. The ordinate is size increment per unit time $[(H_1 - H_2)/(t_2 - t_1)]$, and the abscissa are mean size for the increments in question $[(H_2 + H_1)/2]$. The linear regression of this plot produced the equation $y = -0.051x + 3.953$ ($r = -0.250$; $p < 0.001$; $N = 181$).

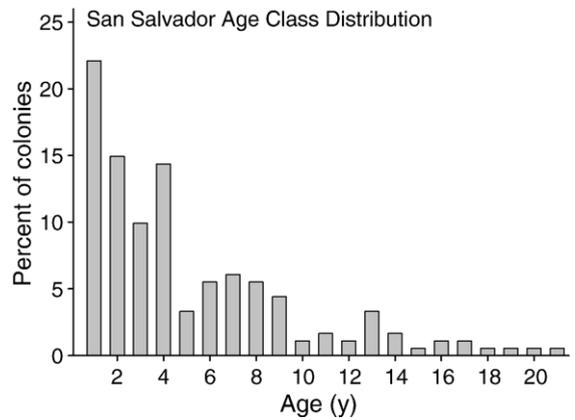


Fig. 7. Age class distribution of *Pseudopterogorgia elisabethae* colonies from San Salvador 1999. Ages of the colonies were estimated from colony heights using a Von Bertalanffy growth function derived from growth rates of colonies at San Salvador.

3.4. Population age structure

The size–frequency distribution of colonies from San Salvador was converted to an age–frequency distribution using the growth curves developed from the observed San Salvador growth rates (Fig. 7). The population was dominated by young individuals, with 64% of the population at or under the age of sexual maturity. The largest colony observed on the transects was estimated to be 21 y.

4. Discussion

4.1. Colony biometry

Colony mass was related to the square of colony height, a pattern that has been observed in other anthozoan colonies (Grigg, 1976, 1984). Volume and thus mass is commonly a cubic function of linear size. Among these branching colonial organisms the cumulative length of the branches (and thus colony mass) is a function of the linear extension of the branches. New branches in gorgonians are generated sub-apically, i.e., immediately below the growing tip (Lasker and Sánchez, 2002), and in the case of *P. elisabethae* the branching is generally in a single plane. Thus expansion of the colony occurs vertically as the original branch axis extends and to the sides as newly generated branches grow. The process of growth is more complex than that simple characterization as not all branches grow and generate new branches equally (Lasker et al., 2003; Sánchez et al., 2004), but the net effect is that the colony expands into an ever growing area and hence the 2nd power relationship between height and mass.

The increment in size of the rings added each year decreased with age and size of the colony (Fig. 4). This was not simply the same amount of gorgonin being laid down more ‘thinly’ due to increasing circumference as extrapolation of the power function that describes the curve in Fig. 4 shows that the cross-sectional area of each year’s ring steadily declines. The decline in the growth rate may simply reflect the overall decline in growth that occurs. Alternatively, it may relate to the functional role of the axis as the colony’s support structure. While the weight of the colony in water is negligible, current flow will generate drag which should be directly proportional to the cross sectional area of the colony. Colony mass, a good index of the total number and length of branches, should also be good predictor of size. Therefore, drag should increase as a 2.08 power of height (i.e., the mass–height relationship in Fig. 1A). Cross sectional area of the axis which will be an index of its strength will increase as a 1.04 power of height (extrapolating area from diameter in Fig. 1B). Those relationships suggest that axis cross-sectional area increases at an approximately 1/2 power of mass (1.04/2.08). If axis strength is a simple function of cross-sectional area and drag a linear function of mass, then colonies become increasingly susceptible to failure from drag stresses as they grow. This suggests that drag may limit colony survivorship in high current environments, and it is interesting to note that in the Bahamas *P. elisabethae* is not commonly found on reefs with open ocean exposures. A complete analysis of forces on the colony, the elastic deformation of the colony and the predicted relationship between the bending moment and strength of the axis should be used to determine whether the allometry of axis growth does lead to increasing risk of axis failure. If that is the case it raises the question of what developmental and evolutionary factors have shaped the colony allometry.

4.2. Colony growth

Modular organisms often follow highly complex growth trajectories that can mask the age–size relationships that are characteristic of unitary organisms. (Hughes and Jackson, 1980; Hughes, 1983, 1984). Disturbances that lead to partial mortality can lead to individuals with identical ages and dramatically different sizes and vice versa. Even when partial mortality is not a frequent event, many modular organisms have overall growth dynamics that are determined by the behavior of multiple growth loci such as the branches of a tree or branching colonial invertebrate. Patterns of growth among those modules can be highly complex. For instance, Lasker et al. (2003) describe how some branches of *P. elisabethae* grow

following a size/age based pattern of decreasing growth while other branches have determinate growth, ceasing extension after several years. These processes can be modeled using module based matrix models that characterize the net growth of individuals/colonies (i.e., Lasker and Sánchez, 2002). An alternative approach that functionally summarizes the transition probabilities of a matrix model is that of Sánchez et al. (2004) in which growth in the number branches is modeled using difference equations that incorporate both limits to growth and the relative numbers of different classes of branches.

The Von Bertalanffy growth function provides a simpler model that requires less information than the detailed characterization of colony form needed in models that differentiate between classes of branches. Implicit in its usage is the ability to use height as an overall index of size (Fig. 1). The similarity of the growth curve generated from two independent data sets from two locations also supports the robustness of the technique for *P. elisabethae*. However, populations of colonies subject to regular disturbance may not fit the Von Bertalanffy growth function, and the variance evident in the growth rate data from San Salvador indicates that the growth model must be used with caution. While the idealized colony may follow a Von Bertalanffy growth function, the utility of analyses based on means will be limited by the variance around those means. Nonetheless, the applicability of the Von Bertalanffy growth function to *P. elisabethae*, as well as a variety of other anthozoans (Grigg, 1976, 1984; Ross, 1984; Babcock, 1991; Chadwick-Furman et al., 2000; Andrews et al., 2002; Goffredo and Chadwick-Furman, 2003; Goffredo et al., 2004), suggests it has potential for characterizing growth in a range of modular organisms.

4.3. Population structure

Bak and Meesters (1998) argue that size–frequency data in taxa such as corals can provide important insights regarding the stability and dynamics of coral populations. Since the data can often fit multiple models, without additional information its interpretation may be complex. The age structure depicted in Fig. 7 generally parallels the pattern of colony survivorship observed at San Salvador during most years, which can be interpreted as an indication of a stationary population. However, the population at San Salvador is not at equilibrium. Annual mortality rates of colonies at San Salvador between December 1997 and July 1999 were 25, 19, 12 and 9% for 1–10, 11–20, 21–30 and 30–40 cm colonies respectively (extrapolated from Lasker et al., 2003). In September 1999, two months after the census reported here Hurricane Floyd, a category 3 storm at that time, crossed over San Salvador. While no

colonies greater than 40 cm height had died in the preceding 18 months, mortality of colonies that were >40 cm height between July and December 1999 was 40%. Four hurricanes in the preceding 20 y passed within 50 km of San Salvador — Hurricanes Bertha (1996 — category 1), Erin (1995 — category 1), Andrew (1992 — a category 5 at the time of closest approach) and Gert (1981 — category 1). While the damage from those hurricanes is unknown, the combination of such variability in mortality rates and annual variation in recruitment make it unlikely that the population is ever at a stable age distribution. Interestingly, there appears to be a small peak in the number of 7 y old colonies that were present in 1999. Those are the colonies that would have recruited in December 1999, 2 months after Hurricane Floyd passed the island. That may reflect more successful recruitment at that time, perhaps due to clearing of the substratum by the hurricane. Conspicuous settlement of new recruits, and population rejuvenation following intense disturbance events, have been reported for a temperate gorgonian (Mistri and Ceccherelli, 1996). The breadth of the peak in the *P. elisabethae* age distribution may be indicative of error in the age assignments and the variability evident in Figs. 3 and 5 both indicate that modularity generates marked variability in colony size. While the use of the Von Bertalanffy model does not capture that variability it does allow interpretation of data that would not have been possible from the size based data alone. Simple models such as the Von Bertalanffy model should be used cautiously in modular taxa, but the presumption that they are not appropriate for modular organisms is overly simplistic.

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