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Redwood of the reef: growth and age of the giant barrel sponge *Xestospongia muta* in the Florida Keys

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Abstract The growth of animals in most taxa has long been well described, but the phylum Porifera has remained a notable exception. The giant barrel sponge *Xestospongia muta* dominates Caribbean coral reef communities, where it is an important spatial competitor, increases habitat complexity, and filters seawater. It has been called the 'redwood of the reef' because of its size (often >1 m height and diameter) and presumed long life, but very little is known about its demography. Since 1997, we have established and monitored 12 permanent 16 m diameter circular transects on the reef slope off Key Largo, Florida, to study this important species. Over a 4.5-year interval, we measured the volume of 104 tagged sponges using digital images to determine growth rates of *X. muta*. Five models were fit to the cubed root of initial and final volume estimates to determine which best described growth. Additional measurements of 33 sponges were taken over 6-month intervals to examine the relationship between the spongocoel, or inner-osculum space, and sponge size, and to examine short-term growth dynamics. Sponge volumes ranged from 24.05 to 80,281.67 cm^3. Growth was variable, and specific growth rates decreased with increasing sponge size. The mean specific growth rate was 0.52 ± 0.65 $year^{-1}$, but sponges grew as fast or slow as 404 or 2% $year^{-1}$. Negative growth rates occurred over short temporal scales and growth varied seasonally, significantly faster during the summer. No differences in specific growth rate were found between transects at three different depths (15, 20, 30 m) or at two different reef sites. Spongocoel volume was positively allometric with increasing sponge size and scaling between the vertical and horizontal dimensions of the sponge indicated that morphology changes from a frustum of a cone to cylindrical as volume increases. Growth of *X. muta* was best described by the general von Bertalanffy and Tanaka growth curves. The largest sponge within our transects (1.23 × 0.98 m height × diameter) was estimated to be 127 years old. Although age extrapolations for very large sponges are subject to more error, the largest sponges on Caribbean reefs may be in excess of 2,300 years, placing *X. muta* among the longest-lived animals on earth.

Introduction

Sponges are important components of coral reef ecosystems (Diaz and Rützler 2001). In the Caribbean, sponges rival reef-building corals in diversity and abundance (Targett and Schmahl 1984; Suchanek et al. 1985). They filter large amounts of water (Reiswig 1971; Pile et al. 1997) and compete for space in the benthic community (Suchanek et al. 1985; Engel and Pawlik 2005). Additionally, coral reef sponges serve as habitat for a large number of other invertebrate taxa (e.g., Duffy 1992; Henkel and Pawlik 2005) and host a diverse array of microbes that may take part in primary production or nitrification (Rützler 1985; Diaz and Ward 1997).

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Growth, form, and size influence the ecology and functional significance of an organism in its community (Peters 1983; Werner and Gilliam 1984). In addition, the size of an organism may explain patterns in life histories (Blueweiss et al. 1978). Despite the importance of understanding growth, size, and other demographic data, limited information exists for sponges. Some studies have been conducted on species that are encrusting (Elvin 1976; Ayling 1983; Turon et al. 1998; Garrabou and Zabala 2001; Tanaka 2002), rope-form (Wulff 1985) and tubular (Lesser 2006; Trussell et al. 2006), but less is known about massive species (Reiswig 1973; Hoppe 1988). Studies of sponge growth rates have been hindered by many difficulties: most species grow slowly (Reiswig 1973) requiring long-term monitoring, they have high inter- and intra-specific variation in morphology, and they exhibit indeterminate growth (Sebens 1987). In addition, growth rates of sponges may be highly variable (e.g., Duckworth and Battershill 2001; Garrabou and Zabala 2001), many species do not tolerate or are too large for manipulation, and there are no morphological or internal structures that accrete regularly so as to indicate age.

The giant barrel sponge *Xestospongia muta* is a conspicuous and abundant member of reef communities throughout the Caribbean, where it is an important component of habitat heterogeneity (Humann 1992; Buettner 1996). Populations of this species occupy greater than 9% of the available reef substrate in some regions (Zea 1993); on the reefs off Key Largo, Florida, mean densities of *X. muta* are ~0.2 sponges m^{-2} (McMurray and Pawlik, unpublished data), and the biomass of this species exceeds that of any other benthic invertebrate. Individuals are often very large, with heights and diameters in excess of 1 m, and *X. muta* is believed to be long lived, with anecdotal estimates ranging from 100 to >1,000 years old (Humann 1992; Gammill 1997), although little is known about the growth of this species.

The purpose of this study was to measure growth rates of *X. muta* by applying image-analysis measurement techniques to repeated digital images of sponges in situ. Measurements were conducted across different temporal and spatial scales to identify patterns of sponge growth. Scaling of sponge dimensions was assessed to examine changes in sponge morphology with increased size. Growth functions were fitted to measurement data to describe sponge growth and obtain age estimates for this species.

Materials and methods

Study sites and monitoring

Growth of *X. muta* was studied at permanent 16 m-diameter circular transects on Conch Reef [24′56.996N; 80′27.223W] and Pickles Reef [24′59.272N; 80′24.660W], Key Largo, Florida, as part of a long-term monitoring program begun in 1997. On Conch Reef, 3 transects were established at 15, 20 and 30 m depth, and at Pickles Reef (~6 km from Conch Reef), 3 transects were established at 15 m depth. Because of bottom-time limitations of SCUBA-diving at depth, transects at 20 and 30 m at Conch Reef were set-up using NOAA's underwater habitat "Aquarius" as a base of operations. Subsequent twice-yearly monitoring was undertaken by SCUBA diving from surface vessels using compressed air or nitrox. Within each transect, each sponge was mapped and given a unique stainless steel tag attached with a plastic cable-tie to a masonry nail driven into the limestone substratum next to the base of the sponge. Sponges were surveyed and each was photographed from above and in profile with a digital camera in the spring and fall of each year from 2000 to 2007. Due to inclement weather and limitations presented in the field, every sponge was not always photographed during each field season. A slate was photographed in each digital image, held parallel to the central axis of each sponge in side images and parallel to the plane of the top of the osculum in top images, displaying the unique tag number of each sponge and a 16 cm scale marker. For the purposes of this study, the spongocoel is defined as the central cavity of *X. muta*.

Field measurements

Field measurements were performed on sponges in permanent transects on Conch and Pickles reefs to test the accuracy of the digital image measurement technique (see below), examine the relationship between sponge volume and spongocoel volume, and determine if a seasonal pattern of growth exists for *X. muta*. Initial measurements of 33 sponges were taken in May 2006 and these sponges were revisited in November 2006 and May 2007. The 6 month interval between May and November 2006 was considered the summer season and the final 6 month interval was considered the winter season. Sponge height, base circumference, and osculum diameter were measured with a flexible plastic measuring tape (to ±1.0 mm). Volume was calculated using the equation for the geometric model of a frustum of a cone:

$$V_{\text{sponge}} = \frac{1}{12}\pi h\left(\text{od}^2 + (\text{od})(\text{bd}) + \text{bd}^2\right), \qquad (1)$$

where V_{sponge} = sponge volume (cm^3); h = height (cm); od = osculum diameter (cm); and bd = base diameter (cm) (Fig. 1).

Equation 1 applies to the three most common morphologies of *X. muta*: cylinder, frustum of a cone, and inverse frustum of a cone. Additional measurements of spongocoel depth and inner diameter were performed and spongocoel volume was calculated by applying the equation for the frustum of a cone:

$$V_{\mathrm{spongocoel}} = \frac{1}{12}\pi \mathrm{sd}\left(\mathrm{sb}^2 + (\mathrm{sb})(\mathrm{od}) + \mathrm{od}^2\right), \qquad (2)$$

where $V_{\mathrm{spongocoel}}$ = spongocoel volume (cm^3); sd = depth of spongocoel (cm); sb = spongocoel base diameter (cm); and od = osculum diameter (cm) (Fig. 1).

The relationship between spongocoel volume and sponge volume was described by the allometric equation:

$$V_{\mathrm{spongocoel}} = \alpha V_{\mathrm{sponge}}^{\beta}. \qquad (3)$$

Field data was log$_e$-transformed so that the equation becomes:

$$\log_e V_{\mathrm{spongocoel}} = \log_e \alpha + \beta \log_e V_{\mathrm{sponge}}. \qquad (4)$$

Linear regression was performed to determine the scaling coefficient, α, and the scaling exponent, β of Eq. 4. Because a predictive relationship was sought, ordinary least squares regression (OLS) was used (Sokal and Rohlf 1995; Warton et al. 2006). A logarithmic correction factor was applied to eliminate bias in the scaling coefficient estimate resulting from the conversion from log to arithmetic units (Baskerville 1971; Sprugel 1983). The actual slope was tested against an isometric slope of $\beta = 1$ with a *t*-test. Analysis of covariance (ANCOVA) was used to test for differences between sampling periods with sponge volume as the covariate and measurement period (May 2006, November 2006, May 2007) as a fixed factor.

Specific growth rates were calculated as:

$$G = \frac{V_2 - V_1}{V_1} \times \frac{1}{\mathrm{d}t}, \qquad (5)$$

where G = specific growth rate (year^{-1}); V_1 = initial volume (cm^3); V_2 = final volume (cm^3); and t = time (years). Spearman rank correlation was used to examine the relationship between initial volume and specific growth rate for each season. Differences in specific growth rates between summer and winter seasons were tested with a paired sample *t*-test.

Digital image measurements

A cross-sectional approach was employed to study growth of *X. muta*. Size-increment data were obtained from digital images taken in May 2001 and December 2005, a period spanning 4.5 years. These timepoints were chosen because they included the largest number of measurable sponges with initial and final photographs compared to other field seasons. A total of 104 sponges, representing a broad range of sizes present in the population, were selected for study. Sponges from both Conch and Pickles reefs and from all three depths at Conch Reef were measured, but only sponges with characteristic "barrel" morphologies that had not experienced any obvious damage or tissue loss were included.

Measurements of sponges from digital images were made with UTHSCA Image Tool software. Measurements of sponge height and base diameter were taken from side images and two perpendicular measurements of osculum diameter were taken from top images (to ±1.0 mm). For the two osculum diameter measurements, the first diameter was chosen as the longest possible diameter, with the second perpendicular to the first. Volume was calculated by applying Eq. 1 for a frustum of a cone (Fig. 1).

A paired-sample *t*-test was used to test for differences between volume estimates from digital image measurements and from field measurements, uncorrected for spongocoel volume, for data from November 2006. As digital image estimates assume a solid geometry and do not account for the volume of the spongocoel, Eq. 3 was used to obtain spongocoel volume estimates for sponges measured with digital image analysis. Spongocoel estimates were then subtracted from original sponge volume

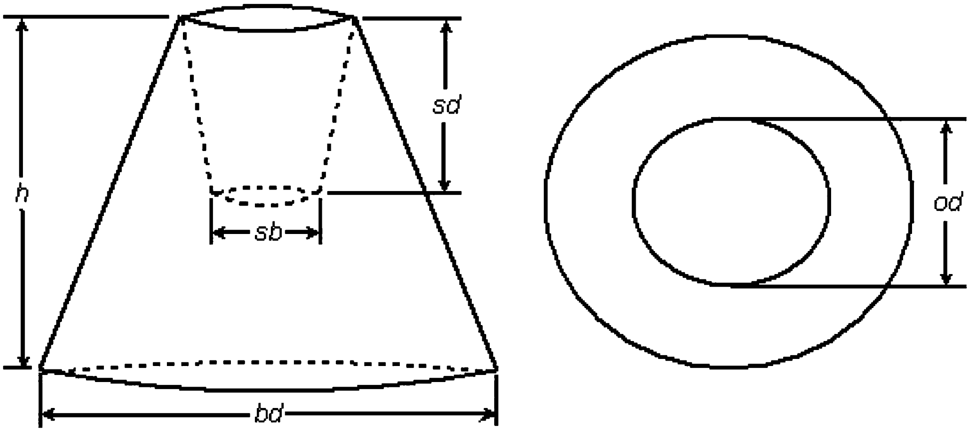

Fig. 1 Frustum of a cone geometric approximation of *X. muta*, side and top view. Measurements used for digital image analysis were: *h* sponge height, *bd* base diameter, *od* osculum diameter. Additional measurements taken in the field were: *sd* spongocoel depth; *sb* spongocoel base diameter

estimates to correct for spongocoel volume. Specific growth rates were calculated by applying Eq. 5. Spearman rank correlation was used to examine the relationship between initial volume and specific growth rate estimates for digital image data, corrected for spongocoel volume.

A Walford (1946) plot was constructed with $\log_e$ final volume on the ordinate and $\log_e$ initial volume on the abscissa. Differences in growth between depths were tested with a one-way ANCOVA with initial volume as the covariate and depth (10, 20 and 30 m) as a fixed factor. Differences in growth between Pickles and Conch reefs at 15 m depth were similarly tested with a one-way ANCOVA. Following Trussell (1997), OLS regressions were used because techniques for model II ANCOVA are unavailable (Sokal and Rohlf 1995).

To examine the relationship between size and morphology, scaling relationships between height, base diameter, and osculum diameter were determined. Relationships between final and initial sizes of each dimension were similarly determined. The geometric mean of initial and final measurements was used in regressions between differing dimensions. Measurements were $\log_{10}$-transformed and reduced-major-axis (RMA) regression was used because of measurement error in the independent variable (Ricker 1973). To test actual slope against an isometric slope of $\beta = 1$, the T statistic and degrees of freedom were calculated with equations from McArdle (1988).

Growth models

Five commonly used growth functions were fit to size-increment data to determine which model best described growth of *X. muta*: the general von Bertalanffy growth formula (gVBGF) (von Bertalanffy 1938; Beverton and Holt 1957; Pauly 1981), specialized von Bertalanffy growth formula (sVBGF) (Richards 1959; Pauly 1981), Gompertz (Gompertz 1825; Winsor 1932), Richards (Richards 1959; Ebert 1980), and Tanaka (Tanaka 1982) growth functions. Growth equations were obtained from Brey (2001) and Tanaka (1982).

For brevity, only the Tanaka growth function will be detailed below, as it best describes indeterminate growth. For the following equations, S_1 is the initial size (cm) and S_2 is the final size (cm) after time interval dt (4.5 years); S_t is a continuous function of t (years) and S_0 is size at time zero.

The Tanaka function (Tanaka 1982):

$$S_2 = \left(1/f^{0.5}\right)\ln\left(2G + 2\left(G^2 + fa\right)^{0.5}\right) + d \tag{6}$$

where $G = (E/4) - (fa/E) + f, \quad E = e^{(f^{0.5})(S_1 - d)}$

Or

$$S_t = \left(1/f^{0.5}\right)\ln\left(2f(T-c) + 2\left(f^2(T-c)^2 + fa\right)^{0.5}\right) + d$$

$$\text{where } T = t/\mathrm{d}t,\ c = (a/E) - (E/4f),\ E = e^{(f^{0.5})(S_0 - d)} \tag{7}$$

is sigmoid with an initial period of slow growth, and a period of exponential growth followed by growth that slows but never reaches an asymptote. The biological meanings associated with the parameters are: a = related to maximum growth rate ($\approx 1/a^{0.5}$); c = age at which growth is maximum; d = shifts size at which growth is maximum; f = measure of the rate of change of the growth rate (Tanaka 1982, 1988). The influence of each parameter on the shape of the curve is demonstrated in Ebert et al. (1999) and Ebert (1999).

The cube root of volume estimates, corrected for spongocoel volume, was used as an average linear size to model growth of *X. muta*. The difference equations of the models were fitted to final and initial linear sizes on a Walford plot by nonlinear regression (NLIN procedure SAS).

The sum of squared error (SSE), coefficient of determination and Akaike (1973) information criterion (AIC) were used to evaluate model fit. The AIC selects the most parsimonious candidate model by evaluating the trade-off between model bias that results from too few parameters versus variance that results from too many (Burnham and Anderson 2002). Therefore, AIC values can be used to evaluate any differences between the 2- and 3-parameter models that may otherwise be neglected through use of the SSE as the sole fitting criteria. In model selection, the model with the lowest SEE and AIC is sought. Because sample size, n, was small with respect to the number of model parameters, K, ($n/K < 40$), the second-order correction, AIC$_c$ was used (Burnham and Anderson 2002). The model selection criteria AIC differences, Δ_i, give a measure of each model relative to the best model; and Akaike weights, w_i, are normalized relative likelihood values which give the probability that a given model is the best of the candidate models (Burnham and Anderson 2002).

Parameter estimates were used to produce size-at-age curves using the integrated forms of the growth functions. Growth functions were then cubed to obtain volume-at-age plots. In contrast to the four determinate models, Tanaka parameters described growth for 4.5 year intervals because the time interval between initial and final sizes is not included in the difference equation for this model. To determine parameters for yearly growth, nonlinear regression was performed to refit the curve. The parameter t_0 was determined by solving each function at $t = 0$. The size of the smallest sponge measured in the dataset was used as size at $t = 0$ for all curves. Analyses were conducted with SPSS (vers. 14.0.0 for Windows, SPSS, Inc., Chicago, IL, USA) and SAS (vers. 9.1.3 for Windows, SAS Institute Inc., Cary, NC, USA) statistical software.

Results

Growth rates

Estimates of volume of individual *X. muta* from field measurements did not significantly differ from estimates using digital images (paired *t*-test; $P = 0.26$, $t_{31} = -1.16$). Initial volume estimates from digital image analysis, corrected for spongocoel volume, ranged from 24.05 to 80,281.67 cm^3. There was a significant negative correlation between specific growth rate and initial volume ($r_s = -0.798$, $P \leq 0.01$). All sponges had positive growth over the study interval and there was large variation in growth rates. The mean (±1 SD) specific growth rate was 0.52 ± 0.65 year^{-1}. Growth rates as fast as 4.04 year^{-1} and as slow as 0.02 year^{-1} were observed. In terms of volume, sponges gained an average of $1{,}955.37 \pm 2{,}221.09$ cm^3 year^{-1}. ANCOVA analysis of log$_e$-transformed initial and final volume data indicated that there was no significant effect of depth ($F_{2,68} = 2.75$, $P = 0.07$) or reef location ($F_{1,60} = 1.55$, $P = 0.22$) on growth rate. Although not significant, mean growth was greater for sponges at 20 and 15 m depths compared to sponges at 30 m.

The initial volumes of sponges measured in the field ranged from 26.69 to 150,492.90 cm^3. Specific growth rate during the summer was negatively correlated with initial volume ($r_s = -0.69$, $P \leq 0.01$), but no significant correlation was found between initial volume and specific growth rate during winter ($r_s = -0.105$, $P = 0.56$). Growth over the entire year was significantly correlated with initial volume, with rates decreasing with increasing volume ($r_s = -0.67$, $P \leq 0.01$). Sponges grew significantly faster in summer compared to winter (paired *t*-test; $P = 0.001$, $t_{32} = 3.65$). Mean (±1 SD) specific growth rates during the summer and winter were 0.94 ± 1.20 and 0.14 ± 0.42 year^{-1}, respectively. The mean specific growth rate over the entire year was 1.15 ± 1.42 year^{-1}. In terms of volume, sponges gained an average of $4{,}195.53 \pm 4{,}080.01$ cm^3 during summer compared to $1{,}472.40 \pm 6{,}173.16$ cm^3 during winter. Growth was variable and three sponges experienced negative growth in summer while ten decreased in size over winter. When these sponges were omitted from analyses, positive growth rates remained significantly greater in the summer compared to winter (paired *t*-test; $P = 0.003$, $t_{19} = 3.37$).

Spongocoel volume

Spongocoel volumes measured in the field ranged from 0.61 to 57,543.51 cm^3 for sponges with non-corrected volumes (i.e., uncorrected for spongocoel volume) of 27.31 and 223,529.96 cm^3, respectively. There was no significant effect of measurement period on the relationship between spongocoel volume and non-corrected sponge volume (ANCOVA; $F_{2,98} = 0.793$, $P = 0.46$). Data from all three measurement periods were therefore pooled and used to determine the parameters of the allometric equation (Eq. 3). Spongocoel volume was found to allometrically increase with increasing sponge volume and is reliably predicted from sponge volume ($t_{97} = 9.73$, $r^2 = 0.97$, $P < 0.001$) (Fig. 2). The allometric equation relating spongocoel volume to sponge volume was determined to be:

$$V_{\text{spongocoel}} = 0.01946 \times V_{\text{sponge}}^{1.214}. \tag{8}$$

Scaling

The ranges of heights, base diameters, and osculum diameters of measured sponges were 2.28–65.79, 3.84–51.95, and 0.48–46.05 cm, respectively. Mean growth rates (±1 SD) were 1.85 ± 1.10 cm year^{-1} in height, 1.45 ± 0.88 cm year^{-1} in base diameter, and 0.98 ± 0.67 cm year^{-1} in osculum diameter. Scaling equations that describe the relationship between sponge dimensions and change in each dimension are given in Table 1. The slopes of regressions of final versus initial size, in terms of height, base diameter, and osculum diameter, were significantly less than 1, indicating that growth in all dimensions decreases with increasing size. For regressions of base diameter versus sponge height, and osculum diameter versus sponge height, slopes did not significantly differ from those predicted for isometry. In contrast, an allometric relationship was found between base diameter and osculum diameter, with increases in osculum diameter occurring faster than increases in base diameter.

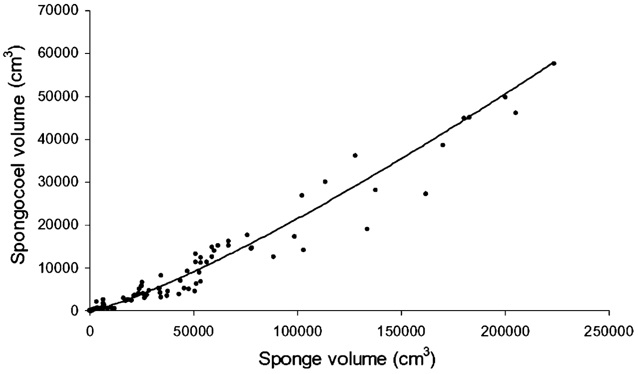

Fig. 2 Relationship between spongocoel volume and sponge volume for sponges measured in the field. *Fitted line* is the allometric equation (Eq. 7)

Table 1 Reduced-major axis regression equations for scaling analysis of linear measurements of *Xestospongia muta*

Regression	r^2	*df*	*T*
log base diameter (Y) versus log height (X)			
$\log Y = 0.82 \log X + 0.27$	0.79^{***}	75	1.95^{NS}
log osculum diameter (Y) versus log height (X)			
$\log Y = 1.21 \log X - 0.52$	0.74^{***}	76	1.62^{NS}
log base diameter (Y) versus log osculum diameter (X)			
$\log Y = 0.68 \log X + 0.61$	0.85^{***}	73	4.40^{***}
log height$_{t+\Delta t}$ (Y) versus log height$_t$ (X)			
$\log Y = 0.80 \log X + 0.42$	0.88^{***}	72	2.94^{**}
log base diameter$_{t+\Delta t}$ (Y) versus log base diameter$_t$ (X)			
$\log Y = 0.74 \log X + 0.47$	0.88^{***}	72	3.73^{***}
log osculum diameter$_{t+\Delta t}$ (Y) versus log osculum diameter$_t$ (X)			
$\log Y = 0.72 \log X + 0.47$	0.89^{***}	72	4.35^{***}

The T statistic was used to test actual slope against an isomeric slope of $\beta = 1$ for each regression

*** $P < 0.001$, **$P < 0.01$, *NS* not significant

Growth models

Because *X. muta* has a variety of morphologies (i.e., low growth form with base diameter greater than height, high growth form with base diameter less than height), no one linear measurement best characterized sponge size. Moreover, the Tanaka growth model failed to converge when modeling volumetric growth. Therefore, the cube root of digital image volume estimates, corrected for spongocoel volume, was used to model growth of *X. muta*. This measurement of size is useful because it inherently accounts for the spongocoel correction and morphology of the sponge.

Parameter estimates for each of the five growth models are presented in Table 2. A number of fitting criteria were used to assess the fit of the models (Table 3). The models, in order of best fit are: gVBGF = Richards > Tanaka > sVBGF > Gompertz (Table 3). The Richards model converged on the gVBGF as one of its special cases. Therefore further mention of the gVBGF will refer to both models. AIC$_c$ values were in agreement with the SSE and did not indicate substantial differences between the models. Akaike weights revealed that there is a 22 and 21% chance, respectively, of the gVBGF and Tanaka being the best of the candidate models. Low Akaike weights are indicative of the large variation in observed growth and inclusion of poor models (e.g., sVBGF and Gompertz) in the set of candidate models.

The gVBGF and Tanaka models were selected for further analysis, as the best of the candidate models, based on model fit. An evidence ratio, the ratio of Akaike weights, indicates that the gVBGF is only 1.07 times more likely to be the best model, given the set of candidate models. A Walford plot of final and initial sizes with the fitted models is presented in Fig. 3. Both models describe initial growth that gradually increases to a maximum and slowly attenuates with increasing size. Initial growth is slightly overestimated and the models start to diverge at larger size classes. The primary difference between the two models is the description of growth for the largest size classes. A plot of the two growth curves for both linear size and volume (Fig. 4a, b) shows the same patterns observed in Fig. 3. The gVBGF describes faster growth for larger individuals and approaches an asymptotic size of 6,612.11 cm. The Tanaka curve describes relatively constant growth rates for larger size classes. Extrapolation of the Tanaka curve to 3,000 years shows slowly attenuating growth that never reaches an asymptote (Fig. 4c). The age estimates obtained from the gVBGF and Tanaka curves for the largest sponge measured over the 4.5 year interval are 53 and 55 years, respectively.

Discussion

Redwood of the reef?

Although *X. muta* is a dominant member of Caribbean coral reef ecosystems, with average densities of ~0.2 individuals m^{-2} (McMurray and Pawlik, unpublished data), and covering >9% of available hard substratum on some reefs (Zea 1993), remarkably little is known of its demography. This species has been anecdotally reported to be long-lived (Humann 1992; Gammill 1997), but no measurement data related to age could be found in the scientific literature. Using our data and the Tanaka growth model, we can confirm the extreme longevity of *X. muta*, and can calculate ages of very large specimens based on their dimensions. The largest sponge

Table 2 Parameter estimates for growth functions fitted to cubed root of final and initial volumes; $n = 104$

gVBGF	Richards	Tanaka	sVBGF	Gompertz
$S_\infty = 66.1211$	$S_\infty = 66.1213$	$a = 0.5548$	$S_\infty = 138.3$	$S_\infty = 52.4541$
$k = 0.0388$	$k = 0.0388$	$f = 0.00254$	$k = 0.0102$	$k = 0.0711$
$d = 1.8972$	$d = -1.8972$	$d = 68.9563$		

Function parameters were estimated by nonlinear regression (NLIN procedure SAS)

Table 3 Growth function fitting criteria

Model	K	r^2	SSE	AIC$_c$	Δ_i	w_i
gVBGF	3	0.935	689.3	202.7	0	0.2213
Richards	3	0.935	689.3	202.7	0	0.2213
Tanaka	3	0.935	690.2	202.8	0.1357	0.2068
sVBGF	2	0.933	705.2	203.1	0.2505	0.1952
Gompertz	2	0.933	708.3	203.5	0.7067	0.1554

K Number of parameters, r^2 coefficient of determination, *SSE* sum of squared error, AIC_C second order correction for the Akaike Information Criterion, Δ_i Akaike differences, w_i Akaike weights

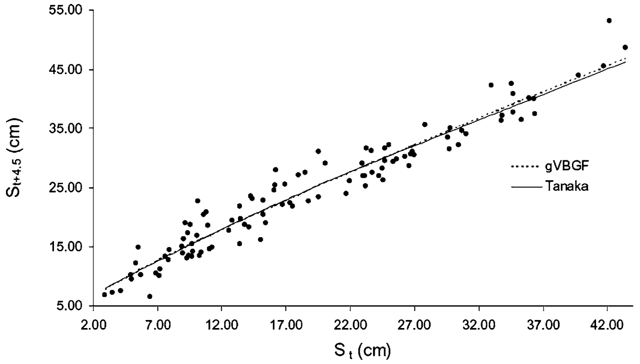

Fig. 3 Walford plot of initial size (S_t) and size 4.5 years later ($S_{t+4.5}$). Plotted sizes are the cube root of volume estimates. *Fitted lines* are the gVBGF and Tanaka function with parameters from Table 2

within our transects (1.23 m high, 0.98 m diameter) is estimated to be 127 years old. In June 2007, we measured two specimens of *X. muta* at 30 m depth off Plana Cay, Bahamas [22′36.441N, 73′37.555W]: one was 170 cm in height, 305 cm in base circumference, and 81.5 cm average osculum diameter, while the second was 140, 300 and 96.5 cm, respectively (Fig. 5). The volume estimates for these sponges, corrected for spongocoel volume, were 662,147.30 and 632,912.80 cm^3; and age estimates, obtained from the Tanaka growth model, were 258 and 242 years, respectively. Size estimates of an even larger specimen of *X. muta* from Curaçao (photograph in Nagelkerken et al. 2000) provide an age estimate of ~2,300 years, although age estimates of sponges of this size are rather significant extrapolations and may be subject to more error than for smaller sponges. Nevertheless, this estimate greatly surpasses the age of the oldest reported individual (non-clonal) animal, the Ocean Quahog *Arctica islandica*, at 374 years (Schone et al. 2005), and places it on par with the oldest known redwood tree, *Sequoia sempervirens* (~2,000 years old) in Humboldt Redwoods State Park, California (HRIA 2006). Considering their large size and great age, "redwood of the reef" is an apt designation for *X. muta*.

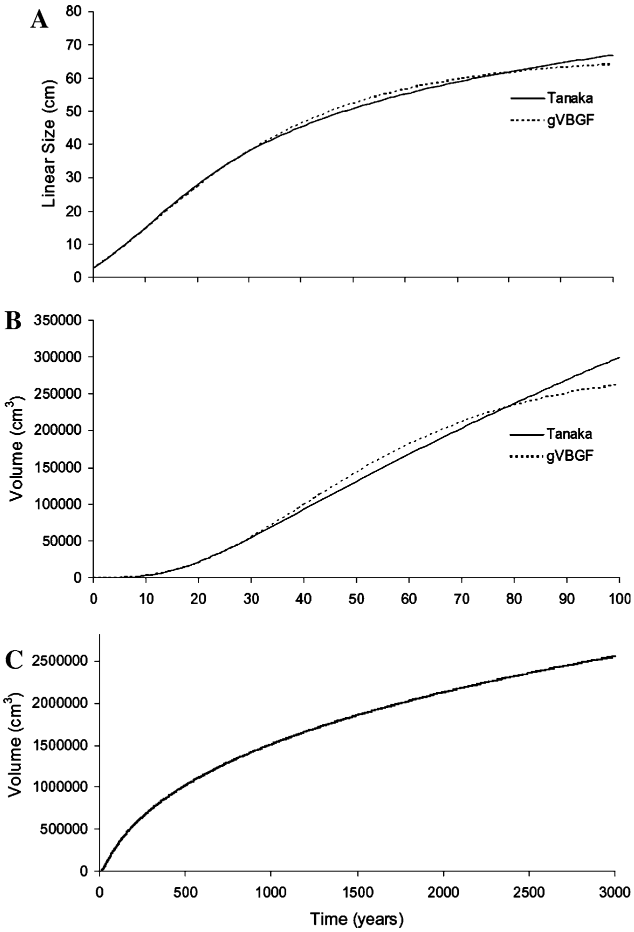

Fig. 4 gVBGF and Tanaka growth curves from parameter estimates in Table 2. **a** Linear size as a function of time; **b** linear sizes from (**a**) cubed for volume as a function of time; **c** same curve as (**b**) with time expanded out to 3,000 years

Growth rates

Specific growth rates of *X. muta* were found to decrease with increasing sponge volume. The same trend has been observed for many sponge species (Reiswig 1973; Hoppe 1988; Leys and Lauzon 1998; Garrabou and Zabala 2001). In contrast, Duckworth and Battershill (2001) found no differences in growth rates among the range of size classes studied. Wulff (1985) observed decreased growth rates with increasing size in only one of three rope-form species. It was hypothesized that relatively constant surface area to volume ratios of rope-form species allow for less influence of size on growth rates (Wulff 1985). For *X. muta*, physiological or mechanical limits may constrain growth in larger size classes while there may be a selective advantage for relatively faster growth of small sponges. The observed variability in growth rates is characteristic of sponges (Reiswig 1973; Dayton et al. 1974; Fell and Lewandrowski 1981; Ayling 1983; Wulff 1985; Hoppe 1988; Leys and Lauzon 1998; Duckworth and Battershill 2001; Garrabou

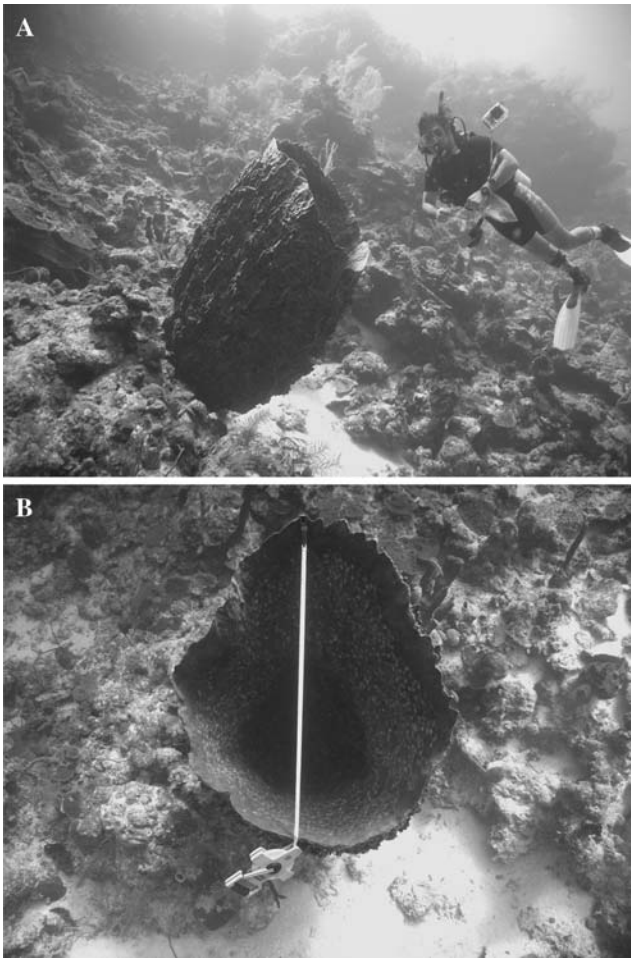

Fig. 5 Specimen of *Xestospongia muta* measured at 30 m depth off Plana Cay, Bahamas **a** side view **b** top view. Distance under tape is 1 m

and Zabala 2001) and other indeterminately growing species (Sebens 1987).

Growth rates did not differ for *X. muta* from three depths (15, 20, 30 m) on Conch Reef. In contrast, a common tube sponge, *Callyspongia vaginalis*, was found to grow significantly faster on the deeper slope of Conch Reef (25 m), where picoplankton concentrations were demonstrated to be higher, compared to shallower parts of the reef (14 m; Lesser 2006; Trussell et al. 2006), prompting these authors to conclude that food availability was the cause of the observed bathymetric growth pattern. Our study bracketed the same depth range on the same reef, but no significant effect of depth on growth of *X. muta* was observed, suggesting that differences in picoplankton abundance (Lesser 2006; Trussell et al. 2006) may not be important determinants of growth for all sponge species.

Cross-species comparisons of sponge growth rates are difficult to make, because specific growth rates decrease with increasing sponge size for *X. muta* (this study) and for other species (e.g., Reiswig 1973; Hoppe 1988), and average growth rates are influenced by the range of sizes measured. Comparisons are further complicated by the different methods used to measure growth rates. Nevertheless, Hoppe (1988) found average volume increases of 7.7–19.4% year^{-1} for *Neofibularia nolitangere*, *Ircinia strobilina*, and *Agelas clathrodes*, all large sponges on the reefs around Curaçao. Reiswig (1973) found increases ranging from <5 to 60% year^{-1} for *Mycale* sp., *Verongia gigantea*, and *Tethya crypta* on Jamaican reefs. The average specific growth rate of 52% year^{-1} for *X. muta* reported in this study is comparable to these species, given the wide interspecific variation in reported growth rates.

In a study documenting regeneration of *X. muta*, Schmahl (1999) monitored the recovery of injured sponges following the grounding of a vessel on the Florida reef tract. Sponges were tracked for 13 months and linear growth in height was measured. Growth was variable, and 27% of the sponges did not grow. Sponges that grew increased an average of 1.94 cm in height, and growth rates were greatest during the peak of warm water temperatures. However, regeneration rates are known to differ from normal growth rates (Hoppe 1988) and involve separate processes (Simpson 1984). In another study that examined regeneration, Walters and Pawlik (2005) found *X. muta* capable of healing the area of a wound at a rate of 6.5% day^{-1}. In the present study, specimens of *X. muta* were specifically chosen to be free of physical injury so that normal rates of growth could be determined, and the average yearly rate of growth in height, 1.85 cm, suggests that normal growth rates may be less than regeneration rates reported by Schmahl (1999) and Walters and Pawlik (2005). Moreover, we observed substantial damage to other specimens of *X. muta* in our permanent transects caused by the movement of rope debris, and these exhibited very rapid subsequent regeneration; in one case, approximately twice the rate observed by Schmahl (1999).

Sponges grew significantly faster in summer compared to winter. This pattern is consistent with findings for smaller species (Elvin 1976; Fell and Lewandrowski 1981; Barthel 1986; Turon et al. 1998; Duckworth and Battershill 2001; Garrabou and Zabala 2001; Tanaka 2002). Johnson (1979) found the opposite pattern of growth for calcareous sponges, while others have found no seasonal growth (Ayling 1983; Hoppe 1988; Tanaka 2002). Based on historical average water temperatures on Conch Reef (Leichter and Miller 1999), faster growth rates of *X. muta* occurred in the summer months when the metabolic rate would be expected to increase.

Trade-offs of energy allocation to processes of reproduction and chemical defense may also influence temporal changes in growth rate. A trade-off between growth and chemical defense has been found for the sponge *Crambe*

crambe in the Mediterranean (Turon et al. 1998), but a relationship between growth and reproduction has yet to be established. The chemical defense of *X. muta* is variable and is not correlated to sponge size (Chanas and Pawlik 1997); however, no study has examined temporal patterns of metabolite production in this species. Likewise, little is known about reproduction of *X. muta*. The age of first reproduction is unknown and little information exists on the timing of reproduction. Spawning has been observed in both spring and late summer (May 2004: Ritson-Williams et al. 2005; May 2005: McMurray, personal observation; and September 2007, O. Rutten, personal communication). Recruitment has also been observed in the spring and fall (Pawlik, unpublished data), suggesting that *X. muta* reproduces at least twice yearly. Growth rates are expected to decrease with increased reproduction if a trade-off in energy allocation between these two processes exists. Energy diverted from growth to gamete production may occur over several months, which could explain lower growth rates in the winter, prior to spawning in May. However, not all sponges in the population spawn during any one season (Pawlik, unpublished data), and some spawn in the fall, so there is not a clear trade-off between reproduction and growth.

Coral reef sponges may obtain food as picoplankton from the water column (Lesser 2006), or derive it from symbiotic algae (Frost and Williamson 1980; Hill 1996). Picoplankton availability as a function of depth may influence spatial differences in growth rates of some tube sponges (Lesser 2006; Trussell et al. 2006) but a similar relationship was not observed for *X muta*, and seasonal picoplankton abundance on Conch Reef would not be expected to vary sufficiently to explain seasonal differences in sponge growth. In a study of the growth of the sponge *Halichondria panacea*, Barthel (1986) found that temporal patterns were explained by water temperature and not correlated with food. Seasonal variation in light levels would be important if photoautotrophic cyanobacterial symbionts provided nutrition to *X. muta*, as has been demonstrated for other coral reef sponges (Wilkinson and Cheshire 1988). While *X. muta* does harbor cyanobacteria, available evidence suggests that they are commensals that do not benefit the host sponge (Thacker 2005; López-Legentil et al. 2008).

Field measurements revealed variable growth of *X. muta*, with shrinkage occurring for some sponges. It has been well documented that sponge growth is highly plastic (Reiswig 1973; Barthel 1986; Turon et al. 1998; Garrabou and Zabala 2001), and shrinkage rates are also known to be lower than rates of growth (Garrabou and Zabala 2001). Plasticity is a common characteristic of indeterminate growth (Sebens 1987). The patterns of seasonal growth and short-term shrinkage events highlight the influence that the temporal scale of measurements has on observed growth rates. Field measurements over half-year intervals revealed dynamic growth processes, while the image-analysis technique, used over a much longer time interval, integrated short-term processes and provided smoothed growth rates.

Spongocoel volume

The spongocoel has been excluded in geometric volume approximations of sponge size in previous studies of large reef species (e.g., Reiswig 1973), and the present study is the first to address scaling of the spongocoel with sponge size. Spongocoel volume was positively allometric with increasing sponge size, necessitating the correction of geometric approximations for spongocoel volume across a broad range of sponge size-classes. In the present study, sponge volumes and growth rates would be overestimated without correcting for this relationship. It is unclear why larger sponges have a proportionally larger spongocoel, but two important functions are likely responsible: water pumping (Reiswig 1971) and reproduction (Ritson-Williams et al. 2005). The spongocoel functions as the excurrent site for water pumped through the sponge. The relationship between pumping rates and spongocoel volume is unknown; however pumping rates are known to increase proportionally with tissue volume (Reiswig 1975). Increased spongocoel volume may aid pumping rates as sponges grow larger, thus potentially reducing physiological problems associated with large size (Schmidt-Nielson 1974). The positive allometry between spongocoel volume and sponge volume also increases the ratio of surface area to sponge volume. The outer surface of a sponge is covered with ostia for water intake, and subsequently, food capture, waste removal, and gas exchange (Reiswig 1971). During reproduction, the spongocoel is the excurrent site for gametes during spawning events (Ritson-Williams et al. 2005). Reproductive output is expected to increase with sponge size and this may require an increasingly larger spongocoel, with a proportionally greater surface area, as sponges grow larger.

Scaling

Scaling relationships between sponge dimensions characterize the form of sponge growth (Schmidt-Nielson 1974). The way in which an organism grows has many ecological implications (Werner and Gilliam 1984). For example, Hoppe (1988) found significantly faster vertical rates of growth compared to horizontal for the sponge *Ircinia strobilina* and attributed this difference as a strategy to avoid competition. In the present study, growth in height, base diameter, and osculum diameter were compared. Both horizontal measures of base and osculum diameter increased at the same rate as vertical growth (height). While a significant allometric relationship was not found between these dimensions, examination of the slopes of the regressions reveals a tendency for base diameter to increase slower than height and for osculum diameter to increase faster than height (Table 1). Osculum diameter was found to widen significantly faster than base diameter. As *X. muta* grows, its morphology changes from a frustum of a cone to a cylinder, or barrel-shape, with osculum diameter equal or larger than base diameter. There are, of course, exceptions to this generality and growth form may be influenced by an array of physical (e.g., water flow) and biological factors (e.g., damage by fish or turtle grazing).

gVBGF and Tanaka growth models

Among all the growth models considered, the gVBGF and Tanaka growth models were found to provide the best fit to the data. The Walford plot of size-increment data (Fig. 3) shows that, indicative of indeterminate growth, all sponges were actively growing. Both curves fit the wide range of size classes measured for the current study. The primary difference in the fit of the two curves lies within the large size-classes: the gVBGF extrapolates growth beyond the largest measured sponge to approach an asymptote, while the Tanaka describes slowly attenuating growth. Much larger individuals of *X. muta* exist on Conch Reef, and throughout the Caribbean, than those included in this study (e.g., Nagelkerken et al. 2000). In fact, estimated volumes for the largest individuals exceed the asymptote of all asymptotic growth curves studied. The Tanaka curve does not have an asymptote and is therefore the most relevant model to describe growth of *X. muta*. The Tanaka function has previously been used to describe growth of other marine invertebrates, including sea urchins (Ebert et al. 1999; Rogers-Bennett et al. 2003) and molluscs (Tanaka 1988).

The growth curve determined for *X. muta* is conservative in several aspects. First, the volume used at time zero, 24.05 cm^3, is an overestimation of true volume at settlement. Measuring growth of recruits is imposed by the limits of detection in the field. Recruits that are approximately 5 cm^3 were frequently observed and larvae of *X. muta* have been reported to be 0.1–0.2 mm in length (Lindquist and Hay 1996). The growth of these earliest stages is presently unknown and may occur over a significant length of time. Because of their plastic nature, a decoupling of sponge size and age may exist in some cases. Sponges have the ability to lose large amounts of volume and regenerate (Henry and Hart 2005). When *X. muta* suffers partial mortality, a ring of multi-oscule remnants may regenerate at the base of the sponge. Through time, remnants have been observed to grow and fuse with reduction in the number of osculae as the sponge grows, although the resulting form is not typical. Should a regenerated sponge grow sufficiently to restore single-osculum morphology, the application of the Tanaka growth curve to establish its age would result in an underestimation.

Can the growth model derived herein be used to estimate the age of specimens of *X. muta* at other locations in the tropical and subtropical Western Atlantic? A definitive answer awaits additional research, but our data indicate little reason to believe otherwise. Physical and biological parameters are remarkably similar on coral reefs throughout the greater Caribbean (e.g., Goreau et al. 1993), which may partially explain the consistency of the flora and fauna over such a large biogeographic region. We detected no differences in growth of *X. muta* as a function of depth, despite differences in temperature and picoplankton availability along this cline (Lesser 2006; Trussell et al. 2006). Seasonal cycles of temperature are common to Caribbean reefs at all latitudes, with an offset of temperature between northern and southern reefs of only a few degrees (Goreau et al. 1993). Further, there is no reason to believe that growth rates of *X. muta* have changed over decadal to millennial scales; our recent transect data show population increases in *X. muta* over the past decade (McMurray and Pawlik, unpublished data), suggesting that sponges are generally healthy. Interestingly, it remains to be seen whether growth and age may reliably be predicted from our data for the closely related Indo-Pacific giant barrel sponge, *Xestospongia testudinaria,* which occur at similar sizes and densities on Australia's Great Barrier Reef (Fromont and Bergquist 1994).

Implications for conservation and management

The worldwide decline of coral reef ecosystems has prompted many local restoration efforts (Jaap 2000; Precht 2006). Funding devoted to restoration can be substantial; for example, one 1994 ship grounding on a coral reef resulted in a $3.9 million remediation settlement (NOAA 1997). Efforts typically focus on reattachment of reef-building corals (e.g., Hudson et al. 2007), but based on our data, greater emphasis should be placed on large coral reef sponges. Future remediation settlements should take into consideration the importance of barrel sponges to habitat complexity, as well as their great age. In addition to damage from vessel groundings, *X. muta* may be affected by the cutting movements of chain, rope, or monofilament fishing line, particularly as these items are dragged during storm events (Schmahl 1999; Chiappone et al. 2002, 2005). After these events, detached large sponges are commonly found, still alive and intact, between reef spurs on sand or rubble where they slowly erode under the action of oscillating currents. We have recently developed new techniques for the reattachment of dislodged *X. muta* to the reef substratum (McMurray and Pawlik 2008).

Perhaps greater than the threat of physical damage affecting *X. muta* populations is the increasing evidence of disease affecting large coral reef sponges (Webster 2007). We recently described a syndrome "sponge orange band" (SOB), that usually results in the death of *X. muta* on which it is observed (Cowart et al. 2006). In fact, the largest and oldest sponge (~130 years) in our permanent transects succumbed to this syndrome within 6 weeks in July 2005 (Cowart et al. 2006). The same syndrome was likely responsible for the death of the very large sponge described from Curaçao by Nagelkerken et al. (2000), estimated at ~2,300 years old. We have observed that the number of sponges affected by this syndrome is highly patchy within sponge populations, and its intensity changes greatly from year to year. It is not clear if this syndrome is a new phenomenon, but if sponges in the population have an equal probability of contracting it in any given year, the likelihood that any individual sponge will survive to a great age would diminish. If diseases of sponges similar to SOB are becoming more prevalent (Webster 2007), we would predict profound changes in the age structure of long-lived coral reef sponges such as *X. muta.*

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References

Akaike H (1973) Information theory and an extension of the maximum likelihood principle. In: Petrov BN, Csaki F (eds) Proceedings of the 2nd international symposium on information theory. Akademiai Kiado, Budapest, pp 267–281

Ayling AL (1983) Growth and regeneration rates in thinly encrusting Demospongiae from temperate waters. Biol Bull 165:343–352. doi:10.2307/1541200

Barthel D (1986) On the ecophysiology of the sponge *Halichondria panacea* in Kiel Bight. I. Substrate specificity, growth and reproduction. Mar Ecol Prog Ser 32:291–298. doi:10.3354/meps032291

Baskerville GL (1971) Use of logarithmic regression in the estimation of plant biomass. Can J Res 2:49–5. doi:10.1139/x72-009

von Bertalanffy L (1938) A quantitative theory of organic growth (inquires on growth laws II). Hum Biol 10:181–213

Beverton RJH, Holt SJ (1957) On the dynamics of exploited fish populations. Fisheries Investigations of the Ministry of Agriculture and Fisheries, Food in Great Britain (2. Sea Fish), 19. Fascimile reprint 1993, Fish and Fisheries Series, Number 11. Chapman and Hall, London

Blueweiss L, Fox H, Kudzma V, Nakashima D, Peters R, Sams S (1978) Relationships between body size and some life history parameters. Oecologia 37:257–272. doi:10.1007/BF00344996

Brey T (2001) Population dynamics in benthic invertebrates. A virtual handbook. Version 01.2. Alfred Wegener Institute for Polar and Marine Research, Germany. http://www.awi-bremerhaven.de/Benthic/Ecosystem/FoodWeb/Handbook/main.html. Accessed 26 March 2007

Buettner H (1996) Rubble mounds of sand tilefish *Malacanthus plumieri* (Bloch, 1787) and associated fishes in Colombia. Bull Mar Sci 58:248–260

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretical approach. Springer, New York

Chanas B, Pawlik JR (1997) Variability in the chemical defense of the Caribbean reef sponge *Xestospongia muta*. In: Lessios HA, Macintyre IG (eds) Proceedings of the 8th international coral reef symposium, vol 2. Smithsonian Tropical Research Institute, Balboa, pp 1363–1368

Chiappone M, White A, Swanson DW, Miller SL (2002) Occurrence and biological impacts of fishing gear and other marine debris in the Florida Keys. Mar Pollut Bull 44:597–604. doi:10.1016/S0025-326X(01)00290-9

Chiappone M, Dienes H, Swanson DW, Miller SL (2005) Impacts of lost fishing gear on coral reef sessile invertebrates in the Florida Keys National Marine Sanctuary. Biol Conserv 121:221–230. doi:10.1016/j.biocon.2004.04.023

Cowart JD, Henkel TP, McMurray SE, Pawlik JR (2006) Sponge orange band (SOB): a pathogenic-like condition of the giant barrel sponge *Xestospongia muta*. Coral Reefs 25:513. doi:10.1007/s00338-006-0149-y

Dayton PK, Robilliard GA, Paine RT, Dayton LB (1974) Biological accommodation in the benthic community at McMurdo Sound, Antarctica. Ecol Monogr 44:105–128. doi:10.2307/1942321

Diaz MC, Rützler K (2001) Sponges: an essential component of Caribbean coral reefs. Bull Mar Sci 69:535–546

Diaz MC, Ward BB (1997) Sponge-mediated nitrification in tropical benthic communities. Mar Ecol Prog Ser 156:97–107. doi:10.3354/meps156097

Duckworth AR, Battershill CN (2001) Population dynamics and chemical ecology of New Zealand Demospongiae *Latrunculia* sp. nov. and *Polymastia croceus* (Poecilosclerida: Latrunculiidae: Polymastiidae). N Z J Mar Freshw Res 35:935–949

Duffy JE (1992) Host use patterns and demography in a guild of tropical sponge-dwelling shrimps. Mar Ecol Prog Ser 90:127–138. doi:10.3354/meps090127

Ebert TA (1980) Estimating parameters in a flexible growth equation, the Richards function. Can J Fish Aquat Sci 37:687–692. doi:10.1139/f80-086

Ebert TA (1999) Plant and animal populations: methods in demography. Academic Press, San Diego

Ebert TA, Dixon JD, Schroeter SC, Kalvass PE, Richmond NT, Bradbury WA et al (1999) Growth and mortality of red sea urchins *Strongylocentrotus franciscanus* across a latitudinal gradient. Mar Ecol Prog Ser 190:189–209. doi:10.3354/meps190189

Elvin DW (1976) Seasonal growth and reproduction of an intertidal sponge *Haliclona permollis* (Bowerbank). Biol Bull 151:108–125. doi:10.2307/1540709

Engel S, Pawlik JR (2005) Interactions among Florida sponges: I. Reef habitats. Mar Ecol Prog Ser 303:133–144. doi:10.3354/meps303133

Fell PE, Lewandrowski KB (1981) Population dynamics of the estuarine sponge, *Halichondria* sp., within a New England eelgrass community. J Exp Mar Biol Ecol 55:49–63. doi:10.1016/0022-0981(81)90092-7

Fromont J, Bergquist PR (1994) Reproductive biology of three sponge species of the genus *Xestospongia* (Porifera: Demospongiae: Petrosida) from the Great Barrier Reef. Coral Reefs 13:119–126. doi:10.1007/BF00300772

Frost TM, Williamson CE (1980) In situ determination of the effect of symbiotic algae on the growth of the fresh water sponge *Spongilla lacustris*. Ecology 61:1361–1370. doi:10.2307/1939045

Gammill ER (1997) Identification of coral reef sponges. Providence Marine Publishing, Inc, Tampa

Garrabou J, Zabala M (2001) Growth dynamics in four Mediterranean demosponges. Estuar Coast Shelf Sci 52:293–303. doi:10.1006/ecss.2000.0699

Gompertz B (1825) On the nature of the function expressive of human mortality, and on a new mode of determining the value of life contingencies. Philos Trans R Soc Lond Ser B 115:513–585

Goreau TJ, Hayes RL, Clark JW, Basla DJ, Robertson CN (1993) Elevated sea surface temperatures correlate with Caribbean coral reef bleaching. In: Geyer RA (ed) A global warming forum: scientific, economic and legal overview. CRC Press, Boca Raton, pp 225–255

Henkel TP, Pawlik JR (2005) Habitat use by sponge-dwelling brittlestars. Mar Biol (Berl) 146:301–313. doi:10.1007/s00227-004-1448-x

Henry L-A, Hart M (2005) Regeneration from injury and resource allocation in sponges and corals—a review. Int Rev Hydrobiol 90:125–158. doi:10.1002/iroh.200410759

Hill MS (1996) Symbiotic zooxanthellae enhance boring and growth rates of the tropical sponge *Anthosigmella varians* forma *varians*. Mar Biol (Berl) 125:649–654. doi:10.1007/BF00349246

Hoppe WF (1988) Growth, regeneration and predation in three species of large coral reef sponges. Mar Ecol Prog Ser 50:117–125. doi:10.3354/meps050117

HRIA (2006) Coast Redwood. Humboldt Redwoods Interpretive Association. http://www.humboldtredwoods.org/. Accessed 20 December 2007

Hudson JH, Anderson J, Franklin EC, Schittone J, Stratton A (2007) M/V Wellwood coral reef restoration monitoring report, monitoring events 2004–2006. Florida Keys National Marine Sanctuary Monroe County, Florida. Marine Sanctuaries Conservation Series NMSP-07-02. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Sanctuary Program, Silver Spring, 50pp

Humann P (1992) Reef creature identification. New World Pub, Jacksonville

Jaap WC (2000) Coral reef restoration. Ecol Eng 15:345–364. doi:10.1016/S0925-8574(00)00085-9

Johnson MF (1979) Recruitment, growth, mortality and seasonal variations in the calcareous sponge *Clathrina coriacea* (Montagu) and *C. blanca* (Miklucho-Maclay) from Santa Catalina Island, California. In: Lévi C, Boury-Esnault N (eds) Biologie des Spongiaires. Colloques Internationaux du CNRS 291, Paris, pp 325–334

Leichter JJ, Miller SL (1999) Predicting high frequency upwelling: spatial and temporal patterns of temperature anomalies on a Florida coral reef. Cont Shelf Res 19:911–928. doi:10.1016/S0278-4343(99)00004-7

Lesser MP (2006) Benthic-pelagic coupling on coral reefs: feeding and growth of Caribbean sponges. J Exp Mar Biol Ecol 328:277–288. doi:10.1016/j.jembe.2005.07.010

Leys SP, Lauzon NRJ (1998) Hexactinellid sponge ecology: growth rates and seasonality in deep water sponges. J Exp Mar Biol Ecol 230:111–129. doi:10.1016/S0022-0981(98)00088-4

Lindquist N, Hay ME (1996) Palatability and chemical defense of marine invertebrate larvae. Ecol Monogr 66:431–450. doi:10.2307/2963489

López-Legentil S, Song B, McMurray SE, Pawlik JR (2008) Bleaching and stress in coral reef ecosystems: hsp70 expression by the giant barrel sponge *Xestospongia muta*. Mol Ecol 17:1840–1849

McArdle BH (1988) The structural relationship: regression in biology. Can J Zool 66:2329–2339

McMurray SE, Pawlik JR (2008) A novel technique for the reattachment of large coral reef sponges. Restoration Ecol (in press)

Nagelkerken I, Aerts L, Pors L (2000) Barrel sponge bows out. Reef Encounter 28:14–15

NOAA (1997) NOAA gears up for reef restoration at Looe Key: university agrees to $3.9 million settlement for damage in Florida Keys Sanctuary. http://www.publicaffairs.noaa.gov/pr97/nov97/noaa97-r423.html

Pauly D (1981) The relationships between gill surface area and growth performance in fish: a generalization of von Bertalanffy's theory of growth. Meeresforsch 28:251–282

Peters RH (1983) The ecological implications of body size. Cambridge University Press, Cambridge

Pile AJ, Patterson MR, Savarese M, Chernykh VI, Fialkov VA (1997) Trophic effects of sponge feeding within Lake Baikal's littoral zone. 2. Sponge abundance, diet, feeding efficiency, and carbon flux. Limnol Oceanogr 42:178–184

Precht WF (2006) Coral reef restoration handbook. CRC Press, Boca Raton

Reiswig HM (1971) In situ pumping activities of tropical Demospongiae. Mar Biol (Berl) 9:38–50. doi:10.1007/BF00348816

Reiswig HM (1973) Population dynamics of three Jamaican Demospongiae. Bull Mar Sci 23:191–226

Reiswig HM (1975) The aquiferous systems of three marine Demospongiae. J Morphol 145:493–502. doi:10.1002/jmor.1051450407

Richards FJ (1959) A flexible growth function for empirical use. J Exp Bot 10:290–300. doi:10.1093/jxb/10.2.290

Ricker WE (1973) Linear regressions in fishery research. J Fish Res Board Can 30:409–434

Ritson-Williams R, Becerro MA, Paul VJ (2005) Spawning of the giant barrel sponge *Xestospongia muta* in Belize. Coral Reefs 24:160. doi:10.1007/s00338-004-0460-4

Rogers-Bennett L, Rogers DW, Bennett WA, Ebert TA (2003) Modeling red sea urchin (*Strongylocentrotus franciscanus*) growth using six growth functions. Fish Bull (Wash DC) 101:614–626

Rützler K (1985) Associations between Caribbean sponges and photosynthetic organisms. In: Rützler K (ed) New perspectives in sponge biology. Smithsonian Institution Press, Washington DC, pp 455–466

Schmahl GP (1999) Recovery and growth of the giant barrel sponge (*Xestospongia muta*) following physical injury from a vessel grounding in the Florida Keys. Mem Queensl Mus 44:532

Schmidt-Nielson K (1974) Scaling in biology: the consequences of size. J Exp Zool 194:287–307. doi:10.1002/jez.1401940120

Schone BR, Fiebig J, Pfeiffer M, Gleb R, Hickson J, Johnson A et al (2005) Climate records from a bivalved Methuselah (*Arctica islandica*, Mollusca; Iceland). Palaeogeogr Palaeoclimatol Palaeoecol 228:130–14. doi:10.1016/j.palaeo.2005.03.049

Sebens KP (1987) The ecology of indeterminate growth in animals. Annu Rev Ecol Syst 18:371–407. doi:10.1146/annurev.es.18.110187.002103

Simpson TL (1984) The cell biology of sponges. Springer, New York

Sokal RR, Rohlf FJ (1995) Biometry: the principles and practice of statistics in biological research, 3rd edn. W. H. Freeman and Co, New York

Sprugel D (1983) Correcting for bias in log-transformed allometric equations. Ecology 64:209–210. doi:10.2307/1937343

Suchanek TH, Carpenter RC, Witman JD, Harvell CD (1985) Sponges as important space competitors in deep Caribbean coral reef communities. In: Reaka ML (ed) The ecology of deep and shallow coral reefs, symposia series for undersea research 3(1), NOAA/NURP, Rockville, pp 55–59

Tanaka K (2002) Growth dynamics and mortality of the intertidal encrusting sponge *Halichondria okadai* (Demospongiae, Halichondrida). Mar Biol (Berl) 140:383–389. doi:10.1007/s002270100703

Tanaka M (1982) A new growth curve which expresses infinitive increase. Pub Amakusa Mar Biol Lab Kyushu Univ 6:167–177

Tanaka M (1988) Eco-physiological meaning of parameters of ALOG growth curve. Pub Amakusa Mar Biol Lab Kyushu Univ 9:103–106

Targett NM, Schmahl GP (1984) Chemical ecology and distribution of sponges in the Salt River Canyon, St. Croix, U.S.V.I. NOAA Tech Mem OAR NURP-1

Thacker R (2005) Impacts of shading on sponge-cyanobacteria symbioses: a comparison between host-specific and generalist associations. Integr Comp Biol 45:369–376. doi:10.1093/icb/45.2.369

Trussell GC (1997) Phenotypic plasticity in the foot size of an intertidal snail. Ecology 8:1033–1048

Trussell GC, Lesser MP, Patterson MR, Genovese SJ (2006) Depth-specific differences in growth of the reef sponge *Callyspongia vaginalis*: role of bottom-up effects. Mar Ecol Prog Ser 323:149–158. doi:10.3354/meps323149

Turon X, Tarjuelo I, Uriz MJ (1998) Growth dynamics and mortality of the encrusting sponge *Crambe crambe* (Poecilosclerida) in contrasting habitats: correlation with population structure and investment in defence. Funct Ecol 12:631–639. doi:10.1046/j.1365-2435.1998.00225.x

Walford LA (1946) A new graphic method of describing the growth of animals. Biol Bull 90:141–147. doi:10.2307/1538217

Walters KD, Pawlik JR (2005) Is there a trade off between wound-healing and chemical defenses among Caribbean reef sponges? Integr Comp Biol 45:352–358. doi:10.1093/icb/45.2.352

Warton DI, Wright IJ, Falster DS, Westoby M (2006) Bivariate line-fitting methods for allometry. Biol Rev Camb Philos Soc 81:259–291. doi:10.1017/S1464793106007007

Webster NS (2007) Sponge disease: a global threat? Environ Microbiol 9:1363–1375. doi:10.1111/j.1462-2920.2007.01303.x

Werner EE, Gilliam JF (1984) The ontogenetic niche and species interactions in size-structured populations. Annu Rev Ecol Syst 15:393–425. doi:10.1146/annurev.es.15.110184.002141

Wilkinson CR, Cheshire AC (1988) Growth rate of Jamaican coral reef sponges after Hurricane Allen. Biol Bull 175:175–179. doi:10.2307/1541905

Winsor CP (1932) The Gompertz curve as a new growth curve. Proc Natl Acad Sci USA 18:1–8. doi:10.1073/pnas.18.1.1

Wulff JL (1985) Patterns and processes of size change in Caribbean Demosponges of branching morphology. In: Rützler K (ed) New perspectives in sponge biology. Smithsonian Institution Press, Washington, pp 425–435

Zea S (1993) Cover of sponges and other sessile organisms in rocky and coral reef habitats of Santa Marta, Colombian Caribbean Sea. Caribb J Sci 29:75–78