Sea whip coral *Leptogorgia virgulata* in the Mid-Atlantic Bight: Colony complexity, age, and growth

Rebecca P. Wenker[1] and Bradley G. Stevens[1]

[1] Department of Natural Sciences, University of Maryland Eastern Shore, Princess Anne, Maryland, USA

Corresponding Author:
Rebecca Wenker[1]
University of Maryland Eastern Shore, 1 Backbone Road, Princess Anne, Maryland, 21853, USA
Email address: rwenker@umes.edu

Abstract

Sea whip coral *Leptogorgia virgulata* are a common structural component of both natural and artificial hard-bottom reef habitats in the mid-Atlantic region and may serve as essential habitat for commercially valuable species. However, they are slow-growing, easily damaged, and especially vulnerable to damage by passive fishing gear. Despite their potential importance, until recently, sea whips are generally understudied in this region. We examined the colony complexity, length, age, and growth of sea whips from four artificial reef sites in the mid-Atlantic region to gain a better understanding of their biology in the area. There were no significant differences in the bifurcation (R_b) and tributary to source (T/S) ratios between sites, with the $R_b \approx 3$ for all sites, indicating similar complexity between sites. The total length distribution was 8.3 cm to 85.3 cm, and 50% of corals in the range of 34.2-56.4 cm. Age, estimated from annual growth ring counts, ranged from 2 to 15 y, with 50% of corals in the range of 6 to 8 y. The large proportion of middle-sized and middle-aged corals suggests episodic recruitment. Age-length keys showed the trend of age increasing with total coral length, and a von Bertalanffy growth model demonstrated size-dependent growth following the equation: $E[L|t]$ (cm) $=86.1(1-e^{-0.14(t-1.44)})$. This is the first study providing such data for sea whips in the coastal mid-Atlantic region, and the baseline created will be a useful reference to study changes over time.

Introduction

Cold-water corals are an important contributor to benthic habitat complexity on continental shelves and slopes, canyons, seamounts, oceanic banks, and ocean ridges (Freiwald et al. 2004). They have also been observed to colonize man-made structures, such as artificial reefs or shipwrecks (Steimle and Zetlin 2000; Freiwald et al. 2004). These coral habitats often serve as biodiversity hotspots and are used by other species for numerous purposes, including nurseries, feeding and spawning grounds, and refuge sites (Freiwald et al. 2004; Foley et al. 2010; Watling et al. 2011; Baillon et al. 2012). However, these communities have been negatively impacted by fishing activities such as bottom trawling, bottom-set gillnets and longlines, pots, and traps (Van Dolah et al. 1987; Freiwald et al. 2004; Watling et al. 2011; Schweitzer et al. 2018), which can inflict structural damage to the coral or completely remove them from the seafloor.

In the Mid-Atlantic Bight (MAB), ranging from Massachusetts to North Carolina on the U.S. east coast, benthic habitats are primarily flat and homogenous topography composed of sand and mud bedforms. Within this region, hard-bottom reef habitats are scarce, patchy, and widely scattered (Steimle and Zetlin 2000). Reef habitats vary in composition and include both natural rocky bottom and mud outcrops as well as anthropogenic structures such as shipwrecks, pipes, lost cargos, and cable cars that form artificial reefs (Steimle and Zetlin 2000). Due to the relative infrequency of natural hard-bottom substrate, introduced or artificial reef habitat is most likely a significant source of habitat complexity. Artificial reef structures provide multi-dimensionality and can support biological communities that the surrounding soft-bottom habitat

Commented [D1]: The 'm' in "mid-Atlantic" should only be capitalized when talking about the MAB.

Deleted: benthic

Deleted: found

Deleted: Mid

Commented [D2]: You mean like pots and traps? Give examples.

Deleted: Mid

Deleted: Mid

Deleted: there is evidence that

Commented [D3]: Use et al. for more than 2 authors in a citation; check the rest of the manuscript.

Deleted: , Wendt, and Nicholson

Deleted: , Lipcius, and Stevens

Deleted: the coastal waters

Commented [D4]: I assume you're talking about artificial reefs here – but make it clear going forward of which type of reef you're talking about (or if you're talking about both). This is important because your study only involved artificial reefs.

Deleted: R

cannot, including mussels, crabs, lobsters, corals, sponges, and numerous fish species (Sedberry and Van Dolah 1984; Steimle and Figley 1996; Steimle and Zetlin 2000; Fabrizio et al. 2013; Ross et al. 2016). Due to the high utilization of reef habitat by fish species, mid-Atlantic reefs are often well-known and targeted by recreational and commercial fisheries (Steimle and Zetlin 2000).

In the Delaware, Maryland, and Virginia (Delmarva) region of the MAB the sea whip *Leptogorgia virgulata* is a common component of hard-bottom reefs (Steimle and Zetlin 2000; Cullen and Stevens 2017; Schweitzer et al. 2018; Schweitzer and Stevens 2019). These corals can be found along the North American Atlantic coast, and have been observed at depths of 2-59 meters (Bayer 1961; Gotelli 1988; Packer et al. 2017). Sea whips are soft corals, but do have a stiffened axial skeleton and a 3-dimensional structure with branches arranged around a central axis, adding additional height to reef substrate (Bayer 1961; Mitchell et al. 1993; DeVictor and Morton 2010). Annual growth rings are deposited into this axial rod, enabling age estimation (Grigg 1974; Mitchell et al. 1993). Notably, the structural complexity provided by sea whips and the biotic community associated with them may make these corals a significant habitat for many commercially and recreationally valuable species (Van Dolah et al. 1987; Ruppert and Fox 1988; Steimle and Figley 1996; Able and Fahay 1998; Wicksten and Cox 2011; Cullen and Stevens 2017). These include species like snapper *Lutjanus* spp., grouper *Epinephelus* spp., and porgy *Calamus* spp. in the Southeast Atlantic, and black sea bass *Centropristis striata*, tautog *Tautoga onitis*, and lobster *Homarus americanus* in the Delmarva region (Van Dolah et al. 1987; Steimle and Figley 1996; Able and Fahay 1998; Cullen and Stevens 2017). Additionally, Schweitzer and Stevens (2019) found fish abundance to positively correlate with sea whip coverage on Delmarva reef habitats, and that sea whips were the only biogenic structure in the study significantly related to fish abundance.

Several studies have also indicated that healthy sea whips produce a strong chemical defense system, preventing the attachment, settlement, and fouling by epibionts (Targett et al., 1983; Standing et al. 1984; Gerhart et al. 1988; Clare et al., 1999). Sea whips in the Delmarva region show evidence of damage and overgrowth by fouling organisms (personal observation; Schweitzer et al. 2018; Schweitzer and Stevens 2019). This includes overgrowth by organisms such as mussels, bryozoans, ascidians, and sponges, as well as damaged and stripped tissue. The presence of overgrowth and fouling could suggest that the underlying coral tissue has been damaged or killed, and the coral's chemical defense system impaired.

Despite their potential importance to commercially valuable fish and shellfish species, sea whips are generally understudied in the western Atlantic, and little is known about the local reefs nor the sea whip colonies that occupy them. No standard or baseline information exists for comparison in case of major changes to this habitat, whether caused by human or natural disturbance. For example, there is currently no information regarding growth rates, effects of damage or fouling on growth and mortality, or rates of recovery from damage.

In response to this lack of information, this study was undertaken to provide new insights into the biology of sea whip corals. The goals of this project were to determine colony

Deleted: , Pessutti, and Manderson
Commented [D5]: Again, artificial, or natural or both?
Deleted: Mid
Commented [D6]: Artificial or natural or both?
Deleted: , Lipcius, and Stevens
Commented [D7]: Also DeVictor and Morton 2010
Deleted: therefore they are non-reef building
Deleted: . However, they
Deleted: , Dardeau, and Schroeder
Deleted: , Dardeau, and Schroeder
Deleted: , Wendt, and Nicholson
Commented [D9]: Better to say South Atlantic Bight?
Deleted: , Wendt, and Nicholson
Commented [D10]: Since the topic sentence of this paragraph is Delmarva, switch this sentence around so that the Delmarva species are mentioned first.
Commented [D11]: Artificial or natural or both?
Deleted: , Hooper, and Costlow
Deleted: , Rittschof, and Mayo
Deleted: , Lipcius, and Stevens
Commented [D12]: By what?
Deleted: and thus the fisheries that depend on them,
Commented [D13]: Assume this is also true for the southeast Atlantic/South Atlantic Bight, where they are more common? (DeVictor and Morton 2010)
Commented [D14]: Artificial or natural or both?
Deleted: individual
Deleted: s
Deleted: This is especially concerning, because of their value to fish populations, commercial fisheries, and those employed by them...
Deleted: s
Deleted: the

complexity, age, and growth rates of sea whips from four artificial reef sites in the mid-Atlantic region, in order to gain a better understanding of reef ecology in this understudied region.

Materials & Methods

Study sites

Sea whips were collected from four artificial hard-bottom reef sites located approximately 16 km of offshore Ocean City, MD (Table 1; Fig. 1). Samples were taken from the Memorial Barge on October 3, 2016 and August 7, 2017, South Ledges on August 11, 2017, Sussex Wreck on August 10, 2018, and Boom Wreck on October 1, 2018.

Measurement and collecting

All sample collections were made via regular scuba diving. Though sea whips are not a managed species, approval for their collection was obtained from the National Oceanic and Atmospheric Administration. A total of 102 sea whips were collected; 24 from Memorial Barge, 26 from South Ledges, 29 from Sussex Wreck, and 23 from Boom Wreck (Table 1). At each site, two dives were conducted per each sampling day. On the first dive, scuba divers measured size frequency of the corals present by stretching out a 50 meter tape measure along the central axis of the habitat, and selecting the specimen nearest to every 0.5 m mark along the tape in order to obtain a random selection of specimens. Coral colonies were stretched out, and their height (total length, TL) was marked with a pencil on a section of ½ inch diameter PVC pipe marked at 1 cm intervals. This helped ensure that we sampled all size classes in proportion to their abundance at each site. A total of 119 corals were measured in-situ; 29 from Memorial Barge, 28 from South Ledges, 31 from Sussex Wreck, and 31 from Boom Wreck (Table 1). The length of the transect differed per site due to the varying size of each reef structure and abundance of sea whips, though we tried to stretch the tape across areas with higher densities of sea whips.

On the second dive, colonies were selected for estimation of age and colony complexity in a stratified manner. We attempted to remove a similar number of small, medium, and large colonies, based on the initial size frequency analysis. Specimens were collected by either removing the entire colony with its holdfast intact if possible, or by cutting the basal stalk at the point closest to the holdfast with bone cutters. Sampled colonies were placed in a large mesh bag for transport to the surface.

Colony complexity

The total length of all collected coral specimens was measured to the nearest mm, and all branches were counted and labeled for branching analysis. Two measures of colony complexity were obtained for each collected colony: a bifurcation ratio (R_b), and a tributary to source ratio (T/S).

The R_b is the ratio of the number of branches of a given order to the number of branches of the next higher order, a technique originally used to describe stream networks (Strahler 1952, Brazeau and Lasker 1988). Different branch levels were assigned, with the most distal branches

Deleted: Mid

Deleted: the

Deleted: area

Deleted: This project will serve as a source of knowledge in this understudied region, and the baseline information created will be a useful reference to understand their changes over time.

Commented [D16]: Table 1 caption suggested revision:

"Descriptive information of the four artificial reef study sites in the Mid-Atlantic Bight. Includes study site name, location, depth (m), date visited/sampled, number of corals measured in-situ (NI_S), number of corals collected (N_C)."

Commented [D17]: Fig. 1 caption suggested revision:

"Map of the four artificial reef study sites offshore of Ocean City, MD, where corals were collected: Memorial Barge, South Ledges, Sussex Wreck, and Boom Wreck."

Deleted: Sample

Deleted: collection

Deleted: using regular pressurized air

Commented [D18]: What do you mean by "central axis?"

Commented [D19]: ? I can't figure this sentence out. How does measuring coral height of a so-called random sample of in-situ corals "help ensure that we sampled **ALL** size classes **in proportion to their abundance** at each site?" What am I missing here?

Commented [D20]: Doesn't that take some of the randomness out of it?

being primary, the union of two primary branches forming a secondary, two secondary branches connecting to form a tertiary, etc. (Fig. 2). The R_b is then obtained by regressing the log of number of branches versus branch order, and calculating the antilog of the slope of the regression line. Branching networks that display perfectly dichotomous branching have a R_b of 2, and this value increases as branches that do not increase the order of the system are added. A benefit to this ordering technique is that branches with similar functions are grouped in the same order (Mitchell et al. 1993; Brazeau and Lasker 1988). For example, primary branches tend to have younger, non-reproductive polyps, whereas older, reproductive polyps are more frequently found on secondary and tertiary branches (Brazeau and Lasker 1988). We calculated the R_b for each colony, and an average for each site.

While the R_b focuses primarily on overall colony complexity, the T/S ratio is more sensitive to differences at each level of branching. The T/S ratio distinguishes between branches which do or do not increase the order of the system (Mock 1971). A branch that joins another branch of equal order is called a "source" branch, while branches that join a branch of higher order are "tributary" branches (Fig. 2) (Mock 1971; Brazeau and Lasker 1988). Following the methods of Brazeau and Lasker (1988) and Mitchell et al. (1993), we calculated the T/S ratios of primary and secondary branches in each colony by dividing the number of tributary branches by the number of source branches. We then calculated an average primary and secondary T/S ratio per site.

The mean length of in-situ and collected corals were each compared between sites with a One-way ANOVA. The R_b and T/S ratios of collected corals were each compared between sites with a One-way ANOVA. Total length distributions of in-situ corals and collected corals were each compared between sites with two-sample Kolmogorov-Smirnov (KS) tests (R Core Team 2017). Only two sites can be compared simultaneously with a KS test, so 6 tests were conducted to compare all the sites for both in-situ and lab measured corals. We adjusted the critical *P*-value (α) accordingly using the Bonferroni correction method, dividing 0.05 by 6 to get a new critical α of 0.008.

Age analysis

After air-drying colonies in the lab until completely dry, short (≈10 mm) pieces of the axial skeleton were cut from the base of each coral and placed in a single 2x3x1 cm well within a silicon tray. Prior to embedding, the molds were sprayed with a silicon spray and left to dry. Coral pieces were embedded using West System™ #105 Epoxy Resin and #206 Slow Hardener, with a 5:1 ratio of resin to hardener delivered via a 1:1 pump system. The solution was mixed for at least a minute and then poured over the coral sections in the wells until it covered them completely. The epoxy resin blocks were left to dry for at least 8 hours, and then sliced with a diamond bladed saw into sections of approximately 18 µm thickness (range 15-22 µm). Five sections of each basal piece were mounted on glass slides with crystal bond and photographed under a stereo-zoom microscope. Photos were then viewed in Adobe Photoshop to estimate age by counting annuli rings from the center outwards (Fig. 3). Criteria for rings included either of

Deleted: , Dardeau, and Schroeder

Deleted: , Dardeau, and Schroeder

Deleted: with a Dremel tool

Deleted: ,

Commented [d21]: Is this much detail about the resin and hardener really necessary?

Which is basically my point with the rest of my deletions in this paragraph. Do you really need to name product names?

Deleted: , or until thoroughly mixed. Epoxy was

Deleted: A small labeling strip of paper was also placed in each well for future identification. The epoxy resin blocks

Deleted: (Buehler IsoMet Low Speed Precision Cutter)

Deleted: (Leica Application Suite (LAS X), Leica Microsystems).

two criteria (Mitchell et al. 1993): 1) A concentric band darker than the surrounding tissue, or; 2) A change in density or color of the axial rod in the inner region of the cross section. Growth rings were counted out to the growing edge of the coral, this edge not being counted as a ring unless it met the previous criteria.

The in-situ total length measurements were used to assign putative ages to in-situ corals via the Isermann-Knight Method using the age-length key generated from the collected corals (Ogle 2016), described in the following growth methods section. The functions required to assign these ages are included in the FSA, dplyr, and nnet packages in R (Venables and Ripley 2002; R Core Team 2017; Ogle 2016, 2018; Wickham et al. 2018).

Mean ages of in-situ and collected corals were compared between sites using a One-way ANOVA, and a Tukey HSD test was used to determine if any significant differences occurred between sites. Age distributions were compared between sites using two-sample KS tests with a Bonferroni adjusted critical α of 0.008 (R Core Team 2017). Age rings in coral sections were independently counted by two observers to estimate bias (Grigg 1974). In some cases, multiple sections of the same colony were counted; if values differed the average was used. The presence of bias and the proportional agreement between readers was evaluated in R using age-bias plots and three symmetry tests, including McNemar, Evans and Hoenig, and Bowker (Ogle 2016, 2018). The tests differ in how they gather the data for comparison; however, each test produces estimates of the degrees of freedom, a chi-squared value, and a *P* value. The null hypothesis for these tests is that no asymmetry (or bias) occurs within the age estimates. The McNemar test follows the equation

$$\chi^2 = \frac{\left(\sum_{i=1}^{m-1}\sum_{j=i+1}^{m}\left(n_{ij} - n_{ji}\right)\right)^2}{\sum_{i=1}^{m-1}\sum_{j=i+1}^{m}\left(n_{ij} + n_{ji}\right)}$$

where n_{ij} is the observed frequency of the *i*th row and the *j*th column within the table, and n_{ji} describes the frequency observed in the *j*th row and the *i*th column. McNemar uses a maximally pooled approach by adding squared values on both sides of the agreement line and determining if the sums are equal. Evans and Hoenig revised this method by altering the equation to

$$\chi^2 = \sum_{p=1}^{m-1}\frac{\left(\sum_{j=1}^{m-p}\left(n_{p+j,j} - n_{j,p+j}\right)\right)^2}{\sum_{j=1}^{m-p}\left(n_{p+j,j} + n_{j,p+j}\right)}$$

including a new variable p= j-i. This is a diagonally pooled approach which tests for differences in values pooled from off-diagonals that are the same "distance" from the main diagonal. Bowker's test calculates chi-squared without any pooling, and tests for differences between cells that are in the same relative positions above and below the main diagonal using the equation

$$\chi^2 = \sum_{i=1}^{m-1}\sum_{j=i+1}^{m}\frac{\left(n_{ij} - n_{ji}\right)^2}{n_{ij} + n_{ji}}.$$

Precision of the data was evaluated using three indices: percent agreement (PA), average percent error (APE) and the average coefficient of variation (ACV). PA is defined as:

$$\mathrm{PA} = 100 \times \frac{F}{N}$$

Deleted: , Dardeau, and Schroeder

Deleted: Ogle 2018;

Deleted: ; Ogle 2018

Deleted: ,

Deleted: (the probability of rejecting the null hypothesis) where F is the number of corals that readers agreed on age, and N is the number of corals used in the study. APE is defined as:

$$\mathrm{APE} = 100 \times \frac{\sum_{i=1}^{R} \frac{|Xij - Xj|}{Xj}}{R}$$

where R is the number of duplicate ring counts, X_{ij} is the *i*th ring count of the *j*th coral, and X_j is the average age for the *j*th coral. Lower values indicate higher agreement. ACV is defined as:

$$\mathrm{ACV} = 100 \times \frac{\sqrt{\sum_{i=1}^{R} \frac{(Xij - Xj)^2}{R-1}}}{Xj}$$

where symbols are similar to APE. Lower values indicate higher agreement, with ACV < 5% indicating high precision.

Growth

Age-length keys, observed and smoothed, were constructed using the total length and age data from collected corals. These keys show the proportion of ages (ring counts) within bins of 5 cm total length. Observed age-length keys were constructed using raw data, whereas smoothed age-length keys use a multinomial linear regression to model proportions at each age for each length category. The predicted proportion of coral at age for any one length interval is influenced by both the data for that interval and age as well as by data for other intervals and ages – resulting in predicted values that follow a smooth curve. Coral growth rate was determined by examining the relationship between length and age, and fitting that age-length data to a von Bertalanffy growth model using the following equation:

$$E[L|t]=L_\infty(1-e^{-K(t-t0)})$$

where E[L|t] is the expected or average length at age t, L_∞ is the asymptotic average length, K is the Brody growth rate coefficient or exponential rate of approach to L_∞ (yr^{-1}), and t_0 is the age when mean length is zero (model artifact) (Beverton and Holt 1957). Confidence intervals for parameters in non-linear models, like the von Bertalanffy model, are best found through bootstrapping methods and not the model summary. To do this, we followed the methods of Ogle (2016) using the nlstools package (Baty et al. 2015). Von Bertalanffy models have been used to study the growth patterns of other gorgonian coral species (Grigg 1974; Mistri and Ceccherelli 1993, 1994; Goffredo and Lasker 2006; Munari et al. 2013), as well as corals with size-dependent growth (Chadwick-Furman et al. 2000; Goffredo et al. 2004).

The functions required to construct age-length keys are included in the FSA, dplyr, and nnet packages in R (Venables and Ripley 2002; R Core Team 2017; Ogle 2016; Ogle 2018; Wickham et al. 2018). The functions required to perform growth analyses and bootstrapping methods in R are contained in the FSA and nlstools packages (Baty et al. 2015; R Core Team 2017; Ogle 2016, 2018).

Deleted: , Serafin, and Mistri

Deleted: , Goffredo, and Loya

Deleted: , Mattioli, and Zaccanti

Deleted: ; Ogle 2018

Results

Colony complexity

There was no significant difference in mean length and total length distributions between sites for both in-situ (One-way ANOVA, $F(3,115)=1.84$, $p=0.14$; KS test x 6, all $p>0.008$) and collected corals (One-way ANOVA $F(3,98)$, $p=0.71$; KS test x 6, all $p>0.008$). Therefore, we pooled them together into a length-frequency figure containing all 119 corals measured in-situ and the 102 corals collected (Fig. 4). The mean height of in-situ sea whips was 48.6 ± 1.8 cm (mean ± SE), with total length ranging from 7.5 cm to 100.2 cm (Fig. 4), and 50% of in-situ sea whips were in the range of 33.7-61.8 cm. The mean height of collected sea whips was 46.9 ± 1.7 cm. Total length ranged from 8.3 cm to 85.3 cm, with 50% of corals in the range of 34.2-56.4 cm (Fig. 4). Total length frequency of both collected and in-situ sea whips per site are illustrated in Figure 5. No significant differences in the bifurcation (R_b) ratios of *L. virgulata* were found between sites (One-Way ANOVA, $F(1,97)=0.0597$, $p=0.81$) (Table 2). The average R_b ratios of approximately 3 for all sites indicated that for each branch of a given order, there are approximately three branches in the next lower order. For example, for every tertiary branch there are three secondary branches, and for every secondary branch there are three primary branches. There was also no significant difference found between tributary to source (T/S) ratios in primary (One-way ANOVA, $F(1,100)=3.317$, $p=0.072$) and secondary (One-way ANOVA, $F(1,97)=0.348$, $p=0.556$) branches between sites (Table 2).

Age analysis

Neither mean age nor age distribution of collected corals differed significantly between sites (One-way ANOVA, $F(1,100)$, $p=0.55$; KS test x 6, all $p>0.08$). Therefore, data for collected corals from all four sites were grouped together for further analysis (Fig. 6). Estimated age of collected sea whips ranged from 2 to 15 y, with 50% in the range of 6 to 8 y. The distribution of assigned ages for in-situ corals was not significantly different between sites (KS test x 6, all $p>0.08$), however the One-way ANOVA showed a significant difference in mean assigned age between sites (One-way ANOVA, $F(3,115)$, $p=0.013$). Further analysis with a post hoc Tukey HSD test showed that mean age differed significantly ($p= 0.008$) between the Memorial Barge (6.3 y) and South Ledges (8.3 y) sites, with mean ages for other sites not significantly different. Age frequency of both collected and in-situ sea whips per site are illustrated in Figure 7. Three tests of symmetry showed no systematic bias between readers (McNemar $p=0.64$, Evans and Hoenig $p=0.64$, Bowker $p=0.38$) (Table 3). P-values > 0.05 for each test indicate that the null hypothesis has not been rejected, therefore no significant asymmetry was observed. Indices of precision show that percent agreement (PA) between readers was 82.35%, with the remaining 18% differing by only 1 year. The average percent error (APE) was 1.2%, and the average coefficient of variation (ACV) was 1.7%, therefore our age counts can be considered precise (ACV<5%).

Growth

The age-length keys generated from the pooled coral data show the trend of age increasing with total coral length (Fig. 8). In the observed age-length key there are portions that

Commented [d22]: Revisions to Fig. 5:

The results of the ANOVA should be described in the text, not the figure caption. Delete in caption.

Commented [d23]: Revisions to Table 2 caption: Delete this, as it is already explained in the text:

~~"Bifurcation ratios (Rb) are the number of branches of a given order to the number of branches of the next higher order, and tributary to source ratios (T/S) are the number of tributary branches vs. the number of source branches. T/S ratios were calculated for both 1° and 2°, primary and secondary, branches."~~

Deleted: (Fig. 7)

Commented [d24]: Revisions to Fig. 7:

Again, remove statistical results from caption, keep in text.

Deleted:

Deleted: are presented in Table 4.

Deleted: Percent

seem to contradict the overall trend, such as the age 7 and 8 corals in the 65 cm interval following the age 9-13 corals in the three previous intervals. This is a common issue with observed age-length keys, and can be due to highly variable ages within a length interval and small sample sizes in some length intervals. The smoothed age-length key, which applies a multinomial logistic regression model fit to all length intervals and ages, addresses those issues and more clearly shows the trend of increased age with total coral length (Fig. 8).

Coral growth was determined by relating age estimates to total coral length in a von Bertalanffy growth model (Fig. 9; Table 5), using all 102 corals collected. Our model demonstrates size-dependent growth, and the parameters were calculated to be: $L_\infty = 86.1$ cm, $K = 0.14$ yr^{-1}, and $t_0 = 1.44$ y (Table 5). This results in the equation

$$E[L|t]\ (cm) = 86.1(1 - e^{-0.14(t-1.44)})$$

where $E[L|t]$ represents length at age t. Therefore, the curve reaches an asymptotic mean length of 86.1 cm at the exponential rate of approach of 0.14 yr^{-1}. The age at which mean length is 0, or t_0, is 1.44 years. However, t_0 is a modeling artifact and has little biological significance. The maximum observed length of in-situ corals (100.2 cm) was greater than the largest length category in the age-length keys (85 cm). Furthermore, the value of $L_\infty = 86.1$ is intended to estimate the mean size of the largest corals, not the maximum size. Therefore, when assigning ages to the in-situ corals the last length category was treated as all-inclusive. Subsequently, the ages of in- situ corals >85 cm are most likely underestimated.

> **Commented [d26]:** Equation parameters are duplicated in both Fig. 9 and Table 5. Remove from Fig. 9.

Discussion

The mean height of collected sea whips in our study was 46.9 ± 1.7 cm, with a total length distribution of 8.3 cm to 85.3 cm, and 50% of corals in the range of 34.2 to 56.4 cm. In contrast, sea whips studied by Mitchell et al. (1993) in the Gulf of Mexico had a mean size of 18.9 cm and none exceeded 32.5 cm in height. Mitchell et al. (1993) study site was only 1-1.5 m in depth and exposed to more frequent wave action and subsequent sand scouring than our sites, which could have prevented coral growth to larger heights. However, strong and tall communities of gorgonian corals have been documented on habitats exposed to strong surf (Kinzie 1973; Birkeland 1974; Sanchez et al. 1997; Gomez et al. 2014).

> **Deleted:** (Fig. 4)
>
> **Deleted:** , Dardeau, and Schroeder's
>
> **Deleted:** , Díaz, and Zea

Colony complexity

The average bifurcation ratio (R_b) equaled approximately 3 for all study sites, indicating that for each branch of a given order there are approximately three branches in the next lower order. This coincides with the R_b of 3.1 that Mitchell et al. (1993) found for the sea whips in their study, suggesting this may be a characteristic of the species. In many arboreal gorgonians, the distal portion of first order branches include many young, nonreproductive polyps while older, reproductive polyps are more numerous on secondary and tertiary branches (Brazeau and Lasker 1988).

> **Deleted:** , Dardeau, and Schroeder

There was no significant difference found between tributary to source (T/S) ratios in primary and secondary branches between sites. Larger primary T/S ratios at Memorial Barge and

South Ledges indicate that there are more primary than secondary tributary branches in the colonies at each site, which may explain their "bushier" appearance, however it doesn't contribute to changing the overall colony complexity as indicated by the bifurcation ratio. The lower primary T/S ratios at the deeper Sussex and Boom Wreck sites indicate fewer accessory (tributary) branches, but the difference was not significant. This pattern was also seen in Brazeau and Lasker's (1988) study, which looked at the colony complexity of two arborescent gorgonian species, *Plexaura homomalla* and *Plexaura flexuosa,* at shallow and deep sites. They found primary and secondary T/S ratios to decrease significantly with depth, leading to the "bushier" appearance of corals at the shallow site (Brazeau and Lasker 1988). Though the differences were not significant in our study, the reoccurrence of the pattern suggests that the colony complexity of arborescent gorgonian corals, like *L. virgulata*, can change with depth. In corals containing zooxanthellae, this change in colony morphology could serve to reduce self-shading at lower light levels (Brazeau and Lasker 1988). However, *L. virgulata*, like other cold-water corals (citation) lacks zooxanthellae. Therefore, morphological plasticity in this species could be due to other factors related to changes in depth, such as wave stress, current strength, food density, and predation (Lasker et al. 1983; Dai and Lin 1993; West et al. 1993; Sanchez et al. 1997).

Commented [D27]: This is one of the definitions of cold-water or deep-sea corals.

Deleted: , Gottfried, and Coffroth

Deleted: , Harvell, and Walls

Deleted: , Díaz, and Zea

Age Analysis

Our sea whip samples had an age range of 2 to 15 y, with 50% in the range of 6 to 8 y. Agreement on ring counts between readers was high, and there was no systematic bias displayed in ageing by either reader. There was more disagreement at greater ages, most likely because rings towards the outer edge of the coral tend to be smaller in width and closer together (Grigg 1974), making it harder to distinguish between them. However, estimates never differed by more than one year.

Despite our systematic approach to sampling and *L. virgulata*'s annual reproductive season (Adams 1980), we observed very few juveniles and a large proportion of middle-age colonies. This is similarly expressed in the size frequency of corals collected and those measured in-situ, which show fewer colonies in the smaller size classes and a larger proportion in the mid-size classes. The dominance of medium-aged *L. virgulata* colonies is consistent with episodic recruitment, with the high frequency of middle-age colonies representing a past "pulse" in recruitment (Munari et al. 2013). This episodic recruitment may be due to environmental factors influencing the mortality and settlement of coral larvae, newly settled recruits, and/or juvenile colonies. Smaller gorgonian corals have been observed to have higher mortality rates than those in larger size classes (Grigg 1977; Gotelli 1991; Gomez et al. 2014). Yoshioka (1994) observed this trend in gorgonian *Pseudopterogorgia* spp. populations, where larger colonies had a high (96% y^{-1}) and constant survivorship compared to the low (62% y^{-1}) and variable survivorship in smaller colonies. This resulted in episodic variations in *Pseudopterogorgia* population size frequencies. Gotelli (1991) noticed high variation in the number of *L. virgulata* recruits on a monthly scale, as well as low juvenile survivorship. Predation does not appear to be a major factor behind *L. virgulata* juvenile mortality (Patton 1972). Episodic recruitment could

Commented [D28]:

Deleted: , Serafin, and Mistri

potentially explain the significantly different mean ages of the in-situ corals at Memorial Barge and South Ledges. Differential recruitment between the sites could lead to this difference in mean age.

Episodic recruitment can also indicate the instability of the species' environment, as the more variable the environment the more irregular the age structure of a respective population will be (Grigg 1975). One such environmental factor affecting the observed age-frequency in our study could be storm events. Though their effect on gorgonian communities can be unpredictable and highly variable, large storms can produce strong currents and wave action resulting in the burial, sand scouring, breakage, and detachment of corals (Yoshioka and Yoshioka 1987). Detachment and abrasion were a major cause of mortality in Grigg's (1977) study examining populations of the branching gorgonians *Muricea californica* and *Muricea fruticosa,* with colonies able to withstand detachment by strong currents until they reached a threshold height and size. Gotelli (1988) concluded that high sediment concentrations limit recruitment of *L. virgulata* larvae by restricting settlement sites, and that sand was an important source of juvenile mortality due to the burial or damage of young or newly settled individuals. Larger, adult colonies appear to be tolerant of heavy sediment loads, perhaps due to their established holdfast and additional height (Williamson et al. 2011). Storm events could also be the reason why our age frequency and distribution differed from that of Mitchell et al. (1993), whose study population of *L. virgulata* experienced two hurricanes within 8 years of the project.

Additionally, another factor preventing regular recruitment in the population studied by Grigg (1977) was the lack of available hard substrata for settlement, a determining factor of recruitment for many gorgonians (Kenzie 1973). Therefore, recruitment may be regulated by space limitation in habitats where hard substrata is completely occupied, or covered in a soft sediment layer. Coral larvae that do manage to settle may then have to compete with other sessile organisms, and risk mortality by overgrowth (Gomez et al. 2014). On our study sites, the hard substrata of the artificial reef were often covered in beds of mussels, sponges, and the encrusting star coral *Astrangia poculata*, as well as an occasional layer of fine sediment. Sea whip colonies usually grew in the limited spaces between these other organisms, thus new coral recruits may find stiff competition for available substrata on these sites. Years of high *L. virgulata* recruitment may result after a removal or mortality event affects established sessile organisms or sediment layers, clearing space for coral settlement. This was the case in Grigg's (1977) study, where occasional periods of exposed hard bottom due to shifting sediments resulted in fluctuating recruitment of *Muricea.* Large year classes resulted from years of heavy recruitment after substrata exposure. Similarly, large mussels covered one of our study sites (Memorial Barge) in 2016, but when that site was revisited in 2017, the mussels were scarce and much smaller; by 2019, the site was again covered with a deep layer of small mussels. This suggests that mussels may have been removed by winter storms between visits, and replaced by new recruits, which could have direct impacts on coral recruitment.

Growth

Deleted: , Dardeau, and Schroeder's

Commented [D29]: Of course, they're impacted by storm events cause *L. virgulata* occurs fairly shallow as compared to most other cold water/deep-sea corals. Care to speculate other ways that depth or, perhaps temperature, may also be a factor here? Anything from the literature?

Commented [D30]: See comment at end of Conclusion.

Commented [D31]: But what if the *Leptogorgia* was there first, and it was the other organisms that grew in the space between them? Wouldn't it be better to simplify the sentence and say the substrate is crowded with other organisms and the coral may face stiff competition for space?

Commented [D32]: Perhaps too speculative. Mussels attached by byssal threads are pretty tough to dislodge – think about the fact that blue mussels can live in the intertidal zone on rocky coasts. So not sure what could cause their disappearance.

The generated age-length keys show the overall pattern of coral size increasing with age. Anomalies to the trend found in the observed age-length key could be due to variable ages and/or small sample sizes in some length intervals, which are common issues within these keys. The multinomial logistic regression applied in the smoothed age-length key addresses those issues and better shows the trend of increased age with total coral length. Gotelli (1991) also found a correlation between *L. virgulata* colony size and age, with considerable variation in the size of older individuals. Variation of growth rate between colonies, and the subsequent variation in length for colonies of similar ages, may be due to persistent intrinsic differences, minor differences in food supply related to position on the reef, or other differences in the microhabitat (Grigg 1974).

Deleted: generated

For organisms with indeterminate growth and variation of size within an age class, it has been recommended to use population dynamic models based not only on age, but on simultaneous analyses of size and age (Kirkpatrick 1984; Hughes 1984; Hughes and Connell 1987). We accomplished this using a von Bertalanffy growth model illustrating *L. virgulata* size at age. According to this growth function, *L. virgulata* reaches maximum individual length at approximately 20 years of age. Gorgonian corals tend to grow toward a theoretically high size asymptote, with their size and lifespan then being limited ecologically (Grigg 1974; Mistri and Ceccherelli 1993, 1994; Goffredo and Lasker 2006; Munari et al. 2013) – a trend that appears to apply to *L. virgulata*. Other constraints on size may be physical, like the biomechanics of a coral skeleton with a highly branched structure (Chadwick-Furman et al. 2000). Mitchell et al. (1993) produced a growth function for *L. virgulata* based on annuli ring width, and calculated a K parameter equal to 0.094 y^{-1}. This is a lower rate of approach compared to our K value of 0.14 y^{-1}, suggesting the sea whips in our study approach L_∞ at a slightly faster rate.

Deleted: , Serafin, and Mistri

Deleted: , Dardeau, and Schroeder

With no corals over the age of 15, and 50% in the range of 6 to 8 y, our study sites are dominated by middle-age colonies. Our curve seems to be slightly below the rapid, two-year initial growth rate of *L. virgulata* which Adams (1980) observed, where age-2 corals averaged 14 cm in height. However, that study mimicked water conditions of the Gulf of Mexico, so the warmer temperatures could have potentially increased *L. virgulata* growth rate in comparison to our study. This difference could also be due to sample size limitation, as we found only one coral aged 2 y, and no corals younger than that. In general, younger corals were scarce in our samples, with only fourteen corals under 6 y out of the 102 collected. This could have affected the t_0 model parameter, age at length 0 cm. Additionally, only 22.5% of the corals collected were over 8 y, which could potentially alter the rate of approach (K) to L_∞.

The presence of mostly middle-age colonies at our study sites implies that adult survivorship is high for these populations. In Gotelli's (1991) study of *L. virgulata,* the population growth rate (growth rate measured as the proportion of colonies in size class *i* that grew to size class *i* + 1 in the next month) was close to 0.0. Thus, it was clear that adult survivorship was more important to population growth than either recruitment or fecundity. One reason for this could be fluctuating juvenile mortality (Gotelli 1988; Gotelli 1991; Yoshioka 1994). Therefore, the presence of many middle-age adults at our sites could be considered beneficial in terms of maintaining overall population structure and growth. However, Gotelli (1991) did mention that recruitment was important in terms of stabilizing the population growth of *L. virgulata*.

In the Delmarva region of the MAB there is evidence of threats to adult survivorship, and subsequently the population stability of *L. virgulata* populations. Schweitzer et al. (2018) observed commercial fishing activities at 3 sites in this region, and found that 50% of the commercial fishing traps observed came into contact with benthic epifauna, including sea whips, upon retrieval. As a result, sea whips could be damaged or experience breakage, reducing their overall structural complexity and density. Our study sites are not commercially fished, however they are fished recreationally. Observed damage to sea whips at these sites includes fishing lines entangled in biotic overgrowth attached to the corals, lines restricting coral branches, lines cutting into coral tissue, and damaged and stripped tissue in general. Future work will need to be done to examine whether these negatively affect coral survival.

Conclusions

This study currently represents the only measure of colony complexity, age, and growth for *L. virgulata* on artificial reefs in the mid-Atlantic region, and will be a useful reference to study changes over time and/or long-term population trends. However, the number of sites observed and corals analyzed may represent a relatively small fraction of the total number in this region. Therefore, more research into the location and biology of *L. virgulata* in this region is necessary to better verify the coral characteristics presented in our study. While ageing corals via growth ring counts may be a more accurate technique, the growth function generated in our study could be used in the field to estimate age-frequency without removal of specimens. Additionally, measuring in-situ changes in total coral length via tagging studies would give more insight into growth rates of *L. virgulata*. They could also be used to improve our understanding of the capacity for, and rates of recovery of, sea whip populations after damage or removal by either human or natural disturbances. The evidence for episodic recruitment of *L. virgulata* shown in this study suggests that they do not recruit on a regular annual basis, and good recruitment years may only occur at intervals of a decade or longer. Thus, any corals that are damaged or removed due to disturbance by human or natural events may require decades to recover. Changes in fishing patterns, storm events, or climate change may exacerbate or change this pattern. Presently, the most conspicuous human disturbances to *L. virgulata* in the mid-Atlantic result from fishing. However, development of offshore wind-power energy areas may also impact coral populations in the future. In addition, our study only looked at recreationally fished sites. Therefore, it would be beneficial for future studies to examine sea whips at commercially fished sites in order to compare them. Regarding natural disturbance, storm events are most likely the biggest source of damage, and the frequency and intensity of storm events should be considered for long-term modeling, management, and habitat protection. Once the information regarding population distribution, biology, and trends in these waters have been more thoroughly documented, the development of population models for coral communities would be beneficial.

Deleted: , Lipcius, and Stevens

Commented [D33]: I think it is safe to speculate that it already does. You mention fishing effects on corals in the 1st paragraph of the Introduction, and there's plenty of evidence in the literature (beyond what you've already cited) to show what kind of damage can be done. (I don't think it makes a difference whether it's done by commercial or recreational fishing, except perhaps in matter of degree.) Feel free to remind the reader that this is a real problem here (with more citations).

Deleted: Mid

Commented [D34]: What makes you say that? There ain't a lot of hard bottom in the MAB, artificial or otherwise, we know that. Perhaps your sites make up -- well, perhaps not an insignificant portion of hard bottom here! Any possible citations for this?

Commented [D35]: As is true for deeper cold-water corals. (Citations.)

Deleted: Mid

Commented [D36]: Good paper! But there's one thing that needs to be addressed or discussed: might there be a difference, or is there any evidence of a difference (citations?), in growth, colony complexity, age, etc. between colonies inhabiting artificial reefs and those found on natural hard bottoms? I think this is a big gap here. But also, addressing this could lead to all kinds of habitat conservation questions, if one of these habitats is shown to be "better" than the other for the corals. (As you know, these corals are starting to get a lot of attention from both fishers and resource managers.)

Do some digging around and see if this is the case. It's worth discussing and even speculating about, even if there isn't a lot of evidence one way or the other out there.

Don't' confine your answer to only this species, and don't necessarily confine it to the exact parameters you studied.

That's why I was a stickler about adding the word "artificial" when talking about your study sites.

Acknowledgements

The authors would like to thank J. Kogon and the OC Dive Boat crew, as well as J. Dykman, L. Burke, and M. Hutchins.

References

Able, K.W., and M.P. Fahay. 1998. The first year in the life of estuarine fishes in the Middle Atlantic Bight. Rutgers University Press, New Brunswick, New Jersey. https://doi.org/10.2307/1447411.

Adams, R.O. 1980. Investigations of color, morphology and development of the sea whip *Leptogorgia virgulata* (Lamarck) (Cnidaria: Octocorallia: Gorgonacea). Dissertation. Florida State University, Tallahassee, Florida, USA.

Baillon, S., J-F Hamel, V.E. Wareham, and A. Mercier. 2012. Deep cold-water corals as nurseries for fish larvae. Frontiers in Ecology and the Environment 10(7):351-356. https://doi.org/10.1890/120022.

Baty, F., C. Ritz, S. Charles, M. Brutsche, J-P Flandrois, and M-L Delignette-Muller. 2015. A toolbox for nonlinear regression in R: The package nlstools. Journal of Statistical Software 66(5):1-21. Available at http://www.jstatsoft.org/v66/i05/.

Bayer, F.M. 1961. The shallow-water octocorallia of the West Indian Region: A manual for marine biologists. Studies of the Fauna Curacao and Other Caribbean Islands 12: 1-373.

Beverton, R.J.H., and S.J. Holt. 1957. On the dynamics of exploited fish populations. Fishery Investigations. H.M.S.O., London, England.

Birkeland, C. 1974. The effect of wave action on the population dynamics of *Gorgonia ventalina* Linnaeus. Studies in Tropical Oceanography 12:115-126.

Brazeau, D.A., and H.R. Lasker. 1988. Inter- and intraspecific variation in gorgonian colony morphology: quantifying branching patterns in arborescent animals. Coral Reefs 7:139-143. https://doi.org/10.1016/B978-0-12-811963-1.00001-9.

Capezutto, F., L. Sion, F. Ancona, R. Carlucci, A. Carluccio, L. Cornacchia, P. Maiorano, P. Ricci, A. Tursi, and G. D'Onghia. 2018. Cold-water coral habitats and canyons as essential fish habitats in the southern Adriatic and northern Ionian Sea (central Mediterranean). Ecological Questions 29:9-23. https://doi.org/10.12775/EQ.2018.019

Chadwick-Furman, N.E., S. Goffredo, and Y. Loya. 2000. Growth and population dynamic model of the reef coral *Fungia granulosa* Kluzinger, 1879 at Eilat, northern Red Sea. Journal of Experimental Marine Biology and Ecology 249:199-218. https://doi.org/10.1016/S0022-0981(00)00204-5.

Clare, A.S., D. Rittschof, D.J. Gerhart, I.R. Hooper, and J. Bonaventura. 1999. Antisettlement and narcotic action of analogues of diterpene marine natural product antifoulants from octocorals. Marine Biotechnology 1:427-436.

Coull B.C., and J.B.J. Wells. 1983. Refuges from fish predation: experiments with phytal meiofauna from the New Zealand rocky intertidal. Ecology 64:1599-1609.

Cullen, D., and B. G. Stevens. 2017. Use of an underwater video system to record observations of black sea bass (*Centropristis striata*) in waters off the coast of Maryland. Fishery Bulletin 115:408-418. https://doi.org/10.1007/s12562-017-1116-y.

Dai, C-F, and M-C Lin. 1993. The effects of flow on feeding of three gorgonians from southern Taiwan. Journal of Experimental Marine Biology and Ecology 173:57-69. https://doi.org/10.1016/0022-0981(93)90207-5.

Devictor, S.T. and S.L. Morton. 2010. Identification guide to the shallow water (0–200 m) octocorals of the South Atlantic Bight. Zootaxa 2599:1-62.

Diaz, R. J., G. R. Cutter, and K. W. Able. 2003. The importance of physical and biogenic structure to juvenile fishes on the shallow inner continental shelf. Estuaries 36:12-20. https://doi.org/10.1007/BF02691689.

Fabrizio, M.C., J.P. Pessutti, and J.P Manderson. 2013. Habitat associations and dispersal of black sea bass from a Mid-Atlantic Bight reef. Marine Ecological Progress Series 482:241-253. https://doi.org/10.3354/meps10302.

Foley, N.S., V. Kahui, C.W. Armstrong, and T.M. Van Rensburg. 2010. Estimating linkages between redfish and cold water coral on the Norwegian coast. Marine Resource Economics 25:105-20. https://doi.org/10.5950/0738-1360-25.1.105.

Freiwald, A., J.H. Fosså, A. Grehan, T. Koslow, and J.M. Roberts. 2004. Cold-water coral reefs: out of sight – no longer out of mind. UNEP-WCMC Biodiversity Series, 22. https://doi.org/10.5962/bhl.title.45025

Gerhart, D.J., D. Rittschof, and S.W. Mayo. 1988. Chemical ecology and the search for marine antifoulants. Studies of a predator–prey symbiosis. Journal of Chemical Ecology 14:1905-1918.

Goffredo, S., G. Mattioli, and F. Zaccanti. 2004. Growth and population dynamics model of the Mediterranean solitary coral *Balanophyllia europeae* (Scleractinia, Dendrophylliidae). Coral Reefs 23:433-443. https://doi.org/10.1007/s00338-004-0395-9.

Goffredo, S. and H.R. Lasker. 2006. Modular growth of a gorgonian coral can generate predictable patterns of colony growth. Journal of Experimental Marine Biology and Ecology 336:221-229. https://doi.org/10.1016/j.jembe.2006.05.012.

Gomez, G.C., Guzman, M.H., Gonzalez, A. and Odalisca, B. 2014. Survival, growth, and recruitment of octocoral species (Coelenterata: Octocorallia) in Coiba National Park, Pacific Panama. Bulletin of Marine Science 90:623-650.

Gotelli, N.J. 1988. Determinants of recruitment, juvenile growth, and spatial distribution of a shallow-water gorgonian. Ecology 69:157-66. https://doi.org/10.2307/1943170

Gotelli, N. J. 1991. Demographic models for *Leptogorgia virgulata*, a shallow-water gorgonian. Ecology 72(2):457-467. https://doi.org/10.2307/2937187.

Grigg, R. W. 1974. Growth rings: annual periodicity in two gorgonian corals. Ecology 55(4):876-881.

Grigg, R.W. 1975. Age structure of a longevous coral: A relative index of habitat suitability and stability. The American Naturalist 109:647-657. https://doi.org/10.1086/283035.

Grigg, R.W. 1977. Population dynamics of two gorgonian corals. Ecology. 58:278-290.

Hereu, B., M. Zabala, C. Linares, and E. Sala. 2005. The effects of predator abundance and habitat structural complexity on survival of juvenile sea urchins. Marine Biology 146:293-299. https://doi.org/10.1007/s00227-004-1439-y.

Hughes, T.P. 1984. Population dynamics based on individual size rather than age: A general model with a reef coral example. The American Naturalist 123:778-795.

Hughes, T.P., and J.H. Connell. 1987. Population dynamics based on size or age? A reef-coral analysis. The American Naturalist 129:818-829.

Jenkins, G.P., H.M.A. May, M.J. Wheatley, and M.G. Holloway. 1997. Comparison of fish assemblages associated with seagrass and adjacent unvegetated habitats of Port Phillip Bay and Corner Inlet, Victoria, Australia, with emphasis on commercial species. Estuarine, Coastal and Shelf Science 44:569-588. https://doi.org/10.1006/ecss.1996.0131.

Kelaher, B. P., and J. C. Castilla. 2005. Habitat characteristics influence macrofaunal communities in coralline turf more than mesoscale upwelling on the coast of northern Chile. Estuarine, Coastal and Shelf Science 63:155-165. https://doi.org/10.1016/j.ecss.2004.10.017.

Kinzie, R. A. 1973. The zonation of West Indian gorgonians. Bulletin of Marine Science 23:93-155.

Kirkpatrick, M. 1984. Demographic models based on size, not age, for organisms with indeterminate growth. Ecology 65:1874-1884. https://doi.org/10.2307/1937785.

Lasker, H.R., M.D. Gottfried, and M.A. Coffroth. 1983. Effects of depth on the feeding capabilities of two octocorals. Marine Biology 73:73-78.

Luckhurst, B. E., and K. Luckhurst. 1978. Analysis of the influence of substrate variables on coral reef fish communities. Marine Biology 49:317-323. https://doi.org/10.1007/BF00455026.

MacArthur, R.H., and J.W. MacArthur. 1961. On bird species diversity. Ecology 42:594-598.

Mistri, M. and V.U. Ceccherelli. 1993. Growth of the Mediterranean gorgonian *Lophogorgia ceratophyta* (L.,1758). P.S.Z.N.I. Marine Ecology 14:329-340.

Mistri, M. and V.U. Ceccherelli. 1994. Growth and secondary production of the Mediterranean gorgonian *Paramuricea clavata*. Marine Ecology Progress Series 103:291-296. https://doi.org/10.3354/meps103291.

Mitchell, N.D., M. R. Dardeau, and W.W. Schroeder. 1993. Colony morphology, age structure, and relative growth of two gorgonian corals, *Leptogorgia hebes* (Verrill) and *Leptogorgia virgulata* (Lamarck), from the northern Gulf of Mexico. Coral reefs 12(2):65-70. https://doi.org/10.1007/BF00302103.

Mock, S.J. 1971. A classification of channel links in stream networks. Water Resources Research 7:1558-1566. https://doi.org/10.1029/WR007i006p01558.

Munari, C., G. Serafin, and M. Mistri. 2013. Structure, growth and secondary production of two Tyrrhenian populations of the white gorgonian *Eunicella singularis* (Esper 1791).

Estuarine Coastal and Shelf Science 119:162-166. https://doi.org/10.1016/j.ecss.2013.01.007.
Ogle, D. H. 2016. Introductory fisheries analyses with R. CRC Press.
Ogle, D.H. 2018. FSA: Fisheries stock analysis. R package version 0.8.20. Available at https://cran.r-project.org/web/packages/FSA/FSA.pdf
Packer, D.B., M.S. Nizinski, S.D. Cairns, and T.F. Hourigan. 2017. Deep-sea coral taxa in the U.S. northeast region: Depth and geographical distribution. Available at https://repository.si.edu/handle/10088/34997
Patton, W.K. 1972. Studies on the animal symbionts of the gorgonian coral, *Leptogorgia virgulata* (Lamarck). Bulletin of Marine Science 22:419-431.
Pianka E.R. 1978. Evolutionary ecology (5th ed.). HarperCollins, New York, USA.
R Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. Available at https://www.R-project.org/
Ross, S.W., M. Rhode, S.T. Viada, and R. Mather. 2016. Fish species associated with shipwreck and natural hard-bottom habitats from the middle to outer continental shelf of the Middle Atlantic Bight near Norfolk Canyon. Fishery Bulletin 114:45-57. https://doi.org/10.7755/FB.114.1.4.
Ruppert, E.E. and R.S. Fox. 1988. Seashore animals of the southeast. A guide to common shallow-water invertebrates of the Southeastern Atlantic Coast. University of South Carolina Press, Columbia, South Carolina.
Sánchez, J.A., J.M. Díaz, and S. Zea. 1997. Gorgonian communities in two contrasting environments on oeanic atolls of the southwestern Caribbean. Bulletin of Marine Science 61(2):453-465.
Scharf, F.S., J.P. Manderson, and M.C. Fabrizio. 2006. The effects of seafloor habitat complexity on survival of juvenile fishes: species-specific interactions with structural refuge. Journal of Experimental Marine Biology and Ecology 335:167-176. https://doi.org/10.1016/j.jembe.2006.03.018.
Schweitzer, C.C., R.N. Lipcius, and B.G. Stevens. 2018. Impacts of a multi-trap line on benthic habitat containing emergent epifauna within the Mid-Atlantic Bight. *ICES Journal of Marine Science* 75(6):2202-2212. https://doi.org/10.1093/icesjms/fsy109.
Schweitzer C.C., and B.G Stevens. 2019. The relationship between fish abundance and benthic community structure on artificial reefs in the Mid-Atlantic Bight, and the importance of sea whip corals *Leptogorgia virgulata.* PeerJ 7:e7277. https://doi.org/10.7717/peerj.7277
Sedberry, G. R., and R. F. Van Dolah. 1984. Demersal fish assemblages associated with hard-bottom habitat in the South Atlantic Bight of the U.S.A. Environmental Biology of Fishes 11:241-258. https://doi.org/10.1007/BF00001372.
Standing, J.D., I.R. Hooper, and J.D. Costlow. 1984. Inhibition and induction of barnacle settlement by natural products present in octocorals. Journal of Chemical Ecology 10: 823-834. https://doi.org/10.1007/BF00987966.

Steimle, F.W., and W. Figley. 1996. The importance of artificial reef epifauna to black sea bass diets in the Middle Atlantic Bight. North American Journal of Fisheries Management 16(2):433-439. https://doi.org/10.1577/1548-8675(1996)016<0433:tioare>2.3.co;2.

Steimle, F.W., and C. Zetlin. 2000. Reef habitats in the Middle Atlantic Bight: Abundance, distribution, associated biological communities, and fishery resource use. Marine Fisheries Review 62(2):24-42.

Strahler, A.N. 1952. Hypsometric (area-altitude) analysis of erosional topography. Bulletin of the Geological Society of America 63:1117-1142. https://doi.org/10.1130/0016-7606(1952)63.

Targett, N.M., S.S. Bishop, O.J. McConnell, and J.A. Yoder. 1983. Antifouling agents against the benthic marine diatom, Navicula salinicola. Homarine from the gorgonians Leptogorgia virgulata and L. setacea and analogs. Journal of Chemical Ecology 9:817-829. https://doi.org/10.1007/BF00987807.

Van Dolah, R.F., P.H. Wendt, and N. Nicholson. 1987. Effects of a research trawl on a hardbottom assemblage of sponges and corals. Fisheries Research 5:39-54.

Venables, W. N. and B.D. Ripley. 2002. Modern applied statistics with S. Fourth Edition. Springer, New York.

Watling, L., S.C. France, E. Pante, and A. Simpson. 2011. Advances in marine biology (Vol. 60, pp. 44–122). Academic Press, Cambridge, MA, USA. https://doi.org/10.1192/bjp.112.483.211-a.

West, J.M., C.D. Harvell, and A.M. Walls. 1993. Morphological plasticity in a gorgonian coral (*Briareum asbestinum*) over a depth cline. Marine Ecology Progress Series 94:61-69. https://doi.org/10.3354/meps094061.

Wickham, H., R. François, L. Henry, and K. Müller. 2018. dplyr: A grammar of data manipulation. R package version 0.7.6. Available at https://CRAN.R-project.org/package=dplyr.

Wicksten, M. K., and C. Cox. 2011. Invertebrates associated with gorgonians in the northern Gulf of Mexico. Marine Biodiversity Records 4:e79. https://doi.org/10.1017/S1755267211000741.

Williamson, E. A., K.B. Strychar, K. Withers, and B. Sterba-Boatwright. 2011. Effects of salinity and sedimentation on the gorgonian coral, Leptogorgia virgulata (Lamarck 1815). Jounral of Experimental Marine Biology and Ecology 409: 331-338. https://doi.org/10.1016/j.jembe.2011.09.014

Yoshioka, P. M. and B. B. Yoshioka. 1987. Variable effects of hurricane David on the shallow water gorgonians of Puerto Rico. Bulletin of Marine Science 40:132-144.

Yoshioka, P.M. 1994. Size-specific life history pattern of shallow-water gorgonian. Journal of Experimental Marine Biology and Ecology 184:111-122.