Giant ephemeral anemones? Rapid growth and high mortality of corkscrew sea anemones *Bartholomea annulata* (Le Sueur, 1817) under variable conditions

O'Reilly E. a,1, Titus B.M. a,b,1, Nelsen M.W. a, Ratchford S. c, Chadwick N.E. a,⁎

a Department of Biological Sciences, 101 Rouse Life Sciences Building, Auburn University, Auburn, AL 36849, United States
b Division of Invertebrate Zoology, American Museum of Natural History, New York, NY 10024, United States
c College of Science and Math, University of the Virgin Islands, St. Thomas, USVI 00802, United States

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**ABSTRACT**

In shelter symbioses, the recruitment, growth, and lifespan of host organisms influence the life history characteristics of symbiotic guests. Corkscrew sea anemones *Bartholomea annulata* (Le Sueur, 1817) host diverse crustacean ectosymbionts in the Tropical Western Atlantic, some of which are cleaner shrimps that attract and clean Caribbean reef fishes. These sea anemones potentially function as short-lived cleaning stations due to their high mortality and short lifespans relative to that of many reef fishes. A combination of methods (field monitoring, population modeling, manipulative field experiments) was applied to quantify variation in rates of recruitment, growth, shrinkage, and mortality of this anemone. Population projections at reef sites on St. Thomas, U. S. Virgin Islands, indicated that the most important contributors to population growth were the recruitment and fate of the smallest individuals. Field experiments revealed that recruitment and growth varied significantly with reef site, but that lifespan did not. Population modeling demonstrated effects of body size and habitat on life history traits, with smaller anemones growing faster than large ones, and both very large and small individuals dying more frequently than medium-sized ones. The combined data reveal that *B. annulata* is among the shortest-lived sea anemones, with most individuals surviving < 12 months, and maximum lifespan of only ~1.5–2 years at all examined sites. Together, these patterns suggest that this anemone exhibits characteristics of a weedy species; individuals grow and reach adult body size rapidly and populations have rapid turnover. Life history and recruitment data for crustacean symbionts of *B. annulata* indicate that this host may be long-lived enough to mediate multiple generations of crustacean associates, fulfilling the expectations of an evolutionarily stable host. The short lifespan of these anemones relative to those of many reef fishes may cause fishes to search frequently for new cleaning stations on Caribbean coral reefs.

1. Introduction

Symbioses cause ecologically and evolutionarily important adaptations that impact all aspects of a symbiont's life history (Herre et al., 1999; Hoeksema and Bruna, 2006; Thrall et al., 2007). Typically, symbioses involve relatively small guest symbionts living with comparatively large hosts (Hernández et al., 2012). The degree of mobility and host specificity of the guest, in conjunction with the size, lifespan, and population dynamics of the host, greatly affect the degree to which symbiotic partners co-evolve (Thompson, 1994; Thrall et al., 2007). Host size and lifespan may regulate the intraspecific group size, reproductive opportunities, parental care, and lifespan of the guest (Hernández et al., 2012). Therefore, in most sessile marine symbioses, hosts should be longer-lived than guests so that each individual can host at least one full generation of guest symbionts. However, this prediction remains largely untested because the lifespans and survival rates of most sessile marine organisms remain unknown.

On tropical coral reefs, giant sea anemones are conspicuous and often engage in charismatic and ecologically-important symbioses with fishes and crustaceans (Chadwick et al., 2008; Colombara et al., 2017). While some guest symbionts may be highly mobile (e.g., anemone-fishes) and transition easily from one host species to another (Huebner et al., 2012), smaller invertebrate guests may be functionally sessile post-recruitment. Thus, it is expected that the population dynamics of
the anemones (i.e., recruitment, growth, maximum size and longevity) will be critically important for mediating intraspecific group size, reproductive opportunity, fecundity, and generation time for macro-invertebrate host species such as crustaceans (Baeza and Thiel, 2007; McKeon and O'Donnell, 2015).

Population dynamics of some temperate sea anemones are known, especially for *Anthopleura* spp. in the northeastern Pacific (Sebens, 1983), indicating that they may live for > 100 yrs. and have high recruitment rates of 3–25 individuals m−2 yr−1 (Sebens, 1982). However, recruitment rates are poorly characterized for many tropical genera, and may be highly variable and species-specific (Dixon et al., 2017; O'Reilly and Chadwick, 2017), with members of some taxa able to produce both sexual and asexual recruits (Fautin, 2002; Jennison, 1981; Scott et al., 2014). On coral reefs, the limited available substrate space and potentially intense competition for space with reef-building corals (Scott et al., 2014). On coral reefs, the limited available substrate space and potentially intense competition for space with reef-building corals (Chadwick and Arvedlund, 2005; Chadwick and Morrow, 2011) may severely limit anemone recruitment. Sea anemones in general have been described as potentially long-lived (> 50 yrs., Ottaway, 1980; Sebens, 1983; Shick, 1991), and those that produce asexual clones could further prolong the lifespan of the genet, even if the ramet is short-lived (Jackson and Coates, 1986; Bythell et al., 2018). Thus, sea anemones as symbiotic hosts may provide long-term stability, and fit the general expectations of large symbiotic host species.

Large sea anemones in the tropical Indo-Pacific, all of which host clownfishes in the genus *Amphiprion*, have received the most attention in terms of characterizing their patterns of recruitment, growth, survival, and effects of hosting symbionts on their life history characteristics (Dixon et al., 2017; Scott et al., 2011; Szczubak et al., 2013). They are expected to have stable population sizes and extended lifespans, given that associated fishes may live for multiple decades (Buston and García, 2007). However, recent evidence indicates that some Indo-Pacific anemones may live only 3–9 years, and exhibit high turnover of individuals even if they are stable in terms of population size (Dixon et al., 2017; McVay, 2015). In contrast, Caribbean anemones host diverse, shorter-lived crustaceans (> 15 species, Briones-Fourzná et al., 2012; Colombaro et al., 2017; Hermkind et al., 1976), and extended host lifespan may not be required for symbiotic stability because the crustaceans can be either highly mobile (Chadwick et al., 2008; Huebner et al., 2012) or short-lived (only 1–2 yrs., Bauer, 2004; Gilpin and Chadwick, 2017).

Corkscrew sea anemones *Bartholomea annulata* (Le Sueur, 1817) fill an important ecological niche in that they harbor obligate cleaner shrimps that remove parasites from reef fishes (Huebner and Chadwick, 2012a, 2012b; Limbaugh et al., 1961; McCammon et al., 2010). The cleaner shrimps receive protection from living among the anemone tentacles, and may benefit the anemone by attracting fishes for cleaning, which in turn excrete dissolved nutrients absorbed by the host (Cantrell et al., 2015). *Alpheus* snapping shrimps also form mutualisms with these anemones, in which both partners benefit by receiving mutual shelter from predation (McCammon and Brooks, 2014). Individuals of *B. annulata* are the most common large sea anemones in the Tropical Western Atlantic, and are habitat generalists that occur in small pockets at the rock-sand interface along the margins of coral reefs, as well as in sea grass beds and mangrove habitats (Briones-Fourzná et al., 2012; Jennison, 1981; Sebens, 1976). Food is acquired with these anemones adapt to specific habitats, as a conceptual framework for understanding the ecology and evolution of this symbiotic system.

2. Methods

2.1. Field population monitoring

To explore patterns of recruitment, growth, and mortality in situ for *B. annulata*, two sites were established at St. Thomas, US Virgin Islands (USVI), and monitored every 3 mo for 1 yr (March 2007–March 2008): Brewers Bay (BB: 18° 20′ 27.95″N, 64° 58′ 42.41″W) and Flat Cay (FC: 18° 19′ N, 64° 59′ W). BB was a small inshore (200 m from shore) patch reef in a partially-enclosed bay (described in Huebner and Chadwick, 2012a, 2012b), while FC was an offshore (2.2 km from shore) fringing reef. The sites were near each other (~2 km distant) at similar depth below sea surface (6–10 m). At each site, the following five major habitat characteristics were quantified to determine how they varied between the sites: % cover of live stony corals, downwelling intensity of photosynthetically active radiation (PAR, μE m−2 s−1), sedimentation rate (after Gilmour, 2002), and two relative measures of water motion level (sediment grain size and cld card dissolution rate, Jokiel and Morrissey, 1993; for details on measurement of physical parameters, see Nelsen, 2008). Percent coral cover was determined using photoquadrats (N = 20) placed at random intervals (via random number generator) along a 50-m transect tape located haphazardly on the coral reef in each site, and quantified using a grid of 25 randomly-generated points superimposed over each photograph, following Walker et al. (2007). Significant differences in habitat characteristics between the 2 sites were assessed using independent two-sample t-tests in SAS v. 9.1 (SAS Institute Corp., 2005).

The sites were established along coral reef margins, because *B. annulata* abundance peaked in these areas of intermixed coral patches, rubble, and sand (Briones-Fourzná et al., 2012; Mahenke, 1972). An area of 47 × 6 m was monitored at BB (282 m²), and 70 × 11 m plus 73 × 5 m at FC (1135 m², details in Nelsen, 2008), both with long axis parallel to the reef edge. A larger reef area was examined at FC than BB to include enough individuals for population dynamic monitoring at both sites (after Hattori, 2002; Hirose, 1985; Dixon et al., 2017), because the anemones occurred in lower abundance at FC (N = 53) than at BB (N = 107, assessed in March 2007). The body size of each *B. annulata* was measured as the length (L) and width (W) of the fully extended tentacle crown, to calculate tentacle crown surface area (TCSA = [L/2] * [W/2] + π, Briones-Fourzná et al., 2012; Hattori, 2002; O'Reilly and Chadwick, 2017). Contracted anemones were returned to later in the survey to obtain measurements. The few anemones that remained contracted for the entire 1-wk survey during each 3-mo period (0–1.4% of individuals depending on the period, see below) were removed from population analyses for that period, leading
to slight variation in sample sizes between periods. TCSA was used because it is the only major body dimension measurable in these anemones that extend their tentacle crowns out of reef holes, and because it correlates significantly with other size parameters (pedal and oral disk diameter, wet and dry mass, Cantrell et al., 2015; Dixon et al., 2017; O’Reilly, 2015). Each individual was mapped and tagged with an aluminum oval tag engraved with an ID number, attached to adjacent reef substrate using a stainless steel nail. This tagging method is reliable because most coral reef anemones, including _B. annulata_, attach their bases deep within reef holes and crevices, and do not locomote substantially across the substratum (Dixon et al., 2017; Hattori, 2006; O’Reilly and Chadwick, 2017). Sand often surrounds these crevices, so _B. annulata_ are unlikely to locomote among them as they are not known to move across sand.

Field data were collected during a 1-wk period at the start of each 3-mo sampling period (first week of the month in March 2007, June 2007, Sept 2007, Dec 2007, March 2008). During the five sequential population surveys, rates of recruitment, growth, and mortality were determined based on the presence and body size of individuals. All new anemones were recorded and tagged when they recruited to the reef (newly appeared in sites), to determine recruitment rate as well as potential lifespan. Most sea anemones and corals have planktonic durations of only a few days to weeks before they settle on the benthos (Strathmann, 1987) therefore the age (within a few weeks) of each anemone that was followed post-recruitment is known. Anemones that disappeared between sample periods were considered to have been lost to the population and were recorded as a mortality event (after Dixon et al., 2017; O’Reilly and Chadwick, 2017).

Anemones from BB and FC were not genotyped prior to the present study, because suitable population-level markers did not exist at the time. However, more recent genetic data for _B. annulata_ show only weak population genetic structure across the entire Caribbean, and do not show any population genetic differentiation between BB and FC (Titus, 2017). Thus, we can largely reject the hypothesis that locally adapted genotypes drive any observed differentiation between the two sites (Strathmann, 1987) therefore the age (within a few weeks) of each anemone that was followed post-recruitment is known. Anemones that disappeared between sample periods were considered to have been lost to the population and were recorded as a mortality event (after Dixon et al., 2017; O’Reilly and Chadwick, 2017).

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We used Chi-squared tests to test the null hypothesis of no difference in sea anemone population size structure between the 2 sites during each sample period. Two-sample tests were employed to test the null hypotheses that anemone body sizes and recruitment rates did not differ between the sites throughout the study, performed in SAS/STAT v. 9.1 (SAS Institute Inc., 2004).

### 2.2. Stage-based population dynamic modeling

Population dynamics were analyzed using a stage-based model, because this type of modeling can elucidate the extent to which populations maintain demographic stability (after Hughes, 1984; Lirman, 2003; O’Reilly and Chadwick, 2017). Transition matrices were created based on three body size classes (TCSA, 0.1–25.0 cm² [I], 25.1–50.0 cm² [II], and > 50.0 cm² [III]) and showed the proportion of each population that exhibited growth or shrinkage (after Dixon et al., 2017; Edmunds, 2010; Hughes and Jackson, 1985). Size class limits were chosen so that each size class contained at least 10 individuals during the initial survey in March 2007 at BB; however, FC exhibited lower abundance and significantly smaller individuals, so did not contain as many individuals in size classes II and III (see section 3.1). Each matrix showed the proportion of individuals that exhibited growth into a larger size class (I-II, I-III, II-III), stasis in the same size class (I-I, II-II, III-III), or shrinkage into a smaller size class (II-I, III-II, III-I) between surveys. For each transition matrix, the dominant eigenvalue (λ), damping ratio (ρ), and elasticity were determined (Caswell, 2001). All population parameters were calculated using the Microsoft Excel add-on PopTools 3.2 (www.poptools.org). The transition matrices did not include the effects of reproduction on population growth, due to undetermined fecundity rates. Therefore, rates of population change (λ) reported here represent rates calculated without reproductive contribution. Elasticity analyses estimated the effect of a proportional change in the vital rates on population change (λ), and revealed life stages or sizes classes that were particularly influential to a specific parameter in the model, such as λ. These values were calculated for each element in the matrix, to determine the vital rates that were most important for population growth. Transition probabilities were bootstrapped 1000 times to obtain confidence intervals for λ and damping ratios (ρ (after Bierzychudek, 1999; Edmunds, 2010).

### 2.3. Field experiments

Two 4.5 mo reciprocal transplant experiments were conducted during March–July and July–November 2009, in which anemones were transplanted between the inshore (BB) vs. offshore (FC) sites to examine the impacts of coral reef habitat type on anemone phenotypic plasticity, in terms of recruitment, growth, and mortality. Two experiments were performed to increase the experimental sample size, because time constraints limited the number of anemones that could be manipulated during each field experimental period. Prior to initial transplantation in March 2009, anemones were selected that occurred on a piece of small movable substrate (conch shell, coral rubble; 24 at BB and 22 at FC) near to but outside of the mapped areas described in section 2.1, and then tagged, measured, and mapped. Ten tagged anemones were assigned randomly at each site to a control group of no transplantation between sites, and the remainder (14 at BB and 12 at FC) to a treatment group of reciprocal transplantation between the sites. To control for effects of manipulation disturbance, all anemones were collected and then either reciprocally transplanted or returned to their original site. All anemones on the experimental substrates were surrounded entirely by sand, ensuring that any missing anemones were the result of mortality rather than locomotion across hard substrate (see section 2.1). They were monitored after 1 mo and 4.5 mos for recruitment of adjacent new individuals to the same experimental substrate (conch shell or coral rubble), changes in body size, and mortality. Tagged substrates that could not be re-located after 1 or 4.5 mos were excluded from analyses due to the uncertainty of anemone survival.

This field experiment was repeated during July–November 2009 using an additional 24 anemones at BB and 22 at FC. Rates of anemone recruitment, growth, and mortality did not differ significantly between the two experiments, so the data were pooled for statistical analyses (total N = 48 at BB and 44 at FC). The null hypothesis of no significant difference in initial body size between the treatment and control groups within each site was analyzed using Mann-Whitney U tests. Growth rate data were log-transformed to meet assumptions of normality, and the null hypothesis of no difference in growth rate between BB and FC was analyzed using 2-way Analysis of Variance (ANOVA). Significant differences in anemone mortality between treatments and sites were analyzed using chi-squared tests of independence in SYSTAT v13.0 (2010). All results are presented as means ± one standard deviation unless otherwise indicated.

### 3. Results

#### 3.1. Field population monitoring

The offshore site at FC exhibited significantly higher levels of live stony coral cover, irradiance (a measure of water clarity), and sediment grain size and clod card mass (both measures of water motion level), than did the inshore site at BB; the two sites did not differ significantly in sedimentation rate (Table 1).

At the beginning of the study in March 2007, _B. annulata_ abundance was almost 10-fold greater at BB (0.38 individuals m⁻²; _N_ = 107 in 282 m² area) than at FC (0.05 m⁻²; _N_ = 53 in 1135 m²). By March 2008, anemone abundance had increased by ~15% at BB (to 0.44 m⁻²; _N_ = 122) and ~45% at FC (0.07 m⁻²; _N_ = 77). Initial population size structure differed significantly between the two sites (Chi-squared test,
Variation in habitat characteristics between two coral reef sites: Brewers Bay (BB) and Flat Cay (FC), at St. Thomas, US Virgin Islands. Data are presented as means ± SD, numbers of replicates examined at each site are shown as sample sizes (df = degrees of freedom), and statistical results of 2-tailed t-tests are indicated as t- and p-values. PAR = photosynthetically-active radiation at the sea floor (6–10 m depth). Sediment grain size refers to the grain sizes (mm diameter) of bottom sediments collected from the reef-sand interface at each site, and sedimentation rate refers to the dry mass (g) of suspended sediments that settled per unit area per day into sediment traps; both plus clod card dissolution rate are measures of water motion level. See Nelsen (2008) for methods details.

### Table 1

<table>
<thead>
<tr>
<th>Coral reef site</th>
<th>% cover of stony corals</th>
<th>PAR at midday (µE m(^{-2}) s(^{-1}))</th>
<th>Sedimentation rate (g 125 cm(^2) d(^{-1}))</th>
<th>Bottom sediment grain size (mm)</th>
<th>Clod card dissolution rate (% loss of clod card mass, g d(^{-1}))</th>
</tr>
</thead>
<tbody>
<tr>
<td>Brewers bay</td>
<td>15.2 ± 15.3</td>
<td>59.2 ± 3.3</td>
<td>0.06 ± 0.02</td>
<td>0.53 ± 0.04</td>
<td>19.1 ± 0.9</td>
</tr>
<tr>
<td>Flat cay</td>
<td>31.0 ± 19.3</td>
<td>194.6 ± 8.8</td>
<td>0.06 ± 0.06</td>
<td>0.75 ± 0.04</td>
<td>20.8 ± 1.1</td>
</tr>
<tr>
<td>Sample size (df)</td>
<td>20 (19)</td>
<td>40 (39)</td>
<td>3 (2)</td>
<td>3 (2)</td>
<td>10 (9)</td>
</tr>
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</table>

Mar 07, \(\chi^2 = 31.14, p < 0.001\), Fig. 1) and remained significantly different throughout the study (Jun 07, \(\chi^2 = 38.25\); Sep 07, \(\chi^2 = 31.15\); Dec 07, \(\chi^2 = 51.22\); Mar 08, \(\chi^2 = 48.32, p < 0.001\)). At BB, individuals ranged 0.8–451.6 TCSA cm\(^2\), while at FC they ranged only 1.6–98.9 cm\(^2\). At BB, <50% of the anemones occupied the smallest size class, while at FC almost 70% were in the smallest size class, and no individuals at FC reached 100 cm\(^2\) TCSA during the study. Consequently, individuals were significantly larger at BB than at FC, both at the beginning of the study in March 2007 (2-tailed test, \(t_{60} = 2.88, p < 0.01\)) and at the end of the study (March 2008: \(t_{197} = 4.07, p < 0.0001\)).

Recruitment was significantly more frequent at BB than at FC, in terms of the number of new individuals observed per unit area (BB = 0.17 ± 0.03 recruits m\(^{-2}\) per 3 mos; FC = 0.04 ± 0.01 recruits m\(^{-2}\) per 3 mos; \(N = 4\) 3-mo periods examined; \(t_{6} = 7.13, p < 0.001\)). Recruitment was high during both spring and summer at BB compared to fall and winter, while at FC it was relatively high only during spring (row \(R_{n}\) in Table 2).

The percent of individuals within each size class that grew (transitioned into larger size classes) ranged from 11 to 35% at BB and 3–33% at FC during each 3-mo period (lower left proportions within each period in Table 2; transitions I-II, I-III, II-III). For all size classes combined, during spring (Mar-Jun) about the same percentage of individuals grew at both sites (BB: 18%, \(N = 107\); FC: 19%, \(N = 53\)). Then during summer (Jun-Sep) the percent of individuals that grew peaked at BB (22%, \(N = 127\)) while it decreased at FC (to only 10%, \(N = 86\)), and remained higher at BB than at FC for the rest of the year (Sep-Dec BB: 9%, \(N = 147\); FC: 3%, \(N = 72\); Dec-Mar BB: 14%, \(N = 136\); FC: 10%, \(N = 71\), Table 2). Stasis rates of individuals in each size class (percent remaining in the same size class) similarly ranged widely within each site (11–59% at BB and 0–43% at FC) but generally were higher at BB than at FC, especially for the largest size class (diagonal proportions within each period in Table 2; I-I, II-II, III-III). The percent of individuals in each size class that shrank (transitioned to a smaller size class) also ranged widely both at BB (4–26%) and FC (0–60%) during each 3-mo period (upper right proportions within each period in Table 2; II-I, III-II, III-I). For all individuals combined, rates of shrinkage were low (BB 9–11% during the year, FC 5–24%) compared to rates of stasis or growth. Shrinkage rates were identical at both sites in spring (Mar-Jun); 9% at both BB and FC, then became higher at BB (10%) than at FC (5%) in summer (Jun-Sep). They peaked in the fall (Sep-Dec) when the percent of individuals that shrank more than quadrupled at FC to 24% (compared to only 11% at BB), then returned to lower levels in winter at both sites (Dec-Mar BB: 11%, FC 7%). Rates of growth, stasis, and shrinkage overall were highly variable, with most polyps remaining static during each 3-mo period at both sites (Table 2).

The percent of individuals in each size class that died ranged widely from 14 to 42% at BB and 12–60% at FC during each 3-mo period (mortality rates; row \(q_{k}\) in Table 2). During spring (Mar-Jun), total mortality for all size classes combined was lower at BB (28%) than at FC (41%), then in summer (Jun-Sep) it remained constant at BB (31%) but rose to a peak at FC of 64%, and returned to lower levels at both sites during fall (Sep-Dec; BB: 34%, FC: 43%) and spring (Dec-Mar; BB: 40%, FC: 42%). Overall mortality was higher at FC than BB during all 4 census periods. During most periods at both sites, individuals in the smallest size class (I) exhibited the highest mortality (Table 2). Dynamic survival curves for both populations showed that <25% of the original anemones remained after 12 mos (Fig. 2).

### 3.2. Stage-based population dynamic modeling

Matrix models reflected the temporally variable nature of B. annulata populations at both sites, as evidenced by reliance on a steady supply of recruits to maintain population size, rapid rates of transition among size classes, and high mortality (Table 2). The population at BB showed greater decline during winter (Sep-Mar) than summer (Jun-Sep), while FC exhibited the opposite pattern. Elasticity analyses at BB indicated that stasis in the smallest and largest size classes exerted the largest effect on population growth rate; in 2 of the 4 censuses, these matrix elements possessed the two highest elasticity values (Table 3). Results were less consistent at FC, but revealed that the stasis of small anemones was the most influential contributor to population growth during fall and winter.

Rates of intrinsic population change (dominant eigenvalues, \(\lambda\)) at BB and FC were < 1 when input from reproduction was not included, indicating a decrease in population size during each period (Table 4). During all periods, \(\lambda\) values were within the 95% confidence intervals of values obtained through bootstrap resampling. The damping ratio (\(\rho\)) varied among sample periods (Table 4), indicating a variable rate of convergence to a stable size distribution. Flat Cay showed lower \(\lambda\) and \(\rho\) in summer and fall than during winter to spring, while Brewer's Bay
Table 2

Transition matrices of *Bartholomea annulata* over 12 mos at two coral reef sites on St. Thomas, U. S. Virgin Islands (Brewers Bay and Flat Cay), based on three size classes: I (0.1–25 cm² tentacle crown surface area), II (25.1–50.0 cm²), and III (> 50 cm²). Columns refer to the proportion of individuals in each size class that transitioned to other size classes (rows) during each transition period. Bold cells represent parameters with highest elasticity for each year (see Table S1). $q_x$ = mortality rate (proportion of individuals that died during each transition period), $q_N$ = number of individuals that died, $R_n$ = number of recruits (those in the largest size class were excluded from recruitment analyses, see Methods), $N$ = number of individuals present at the beginning of each transition period (two individuals that remained contracted during the Sep 2007 survey at FC and the Dec 2007 survey at BB were excluded from analysis, leading to variation in sample sizes among periods). Survey data were collected during the first week of the month in each of 5 mos: Mar 2007, Jun 2007, Sep 2007, Dec 2007, and Mar 2008. The initial 3-mo transition period thus extended from ~1 Mar – 1 Jun 2007, the second period extended ~1 Jun – 1 Sep 2007, etc. Note that these data are from 3-mo censuses, in contrast to Table 1 in O’Reilly and Chadwick (2017) that reports data in similar format, from 2-mo censuses in Florida for this species.

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<tbody>
<tr>
<td></td>
<td>I</td>
<td>II</td>
<td>III</td>
<td>I</td>
</tr>
<tr>
<td>Brewers Bay</td>
<td>0.50</td>
<td>0.13</td>
<td>0.04</td>
<td>0.40</td>
</tr>
<tr>
<td>II</td>
<td>0.11</td>
<td>0.26</td>
<td>0.23</td>
<td>0.21</td>
</tr>
<tr>
<td>III</td>
<td>0.04</td>
<td>0.35</td>
<td>0.59</td>
<td>0.07</td>
</tr>
<tr>
<td>Flat Cay</td>
<td>0.35</td>
<td>0.26</td>
<td>0.14</td>
<td>0.32</td>
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<tr>
<td>N</td>
<td>19</td>
<td>8</td>
<td>3</td>
<td>22</td>
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<td>54</td>
<td>31</td>
<td>22</td>
<td>68</td>
<td>30</td>
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3.3. Field experiments

In the field experiments, seven recruits appeared on experimental substrates at BB after 1 mo, while only one recruit appeared at FC. By 4.5 mos, this number had grown to a total of 12 recruits at BB, but remained only one at FC. Newly-recruited anemones formed small aggregations of 2–4 individuals together with the original anemone on each tagged substrate. Recruits were small, ranging only 7.85–61.26 TCSA cm² (26.31 ± 14.55 cm², N = 13).

The initial TCSA of anemones did not differ significantly between the control and treatment groups at either BB or FC (Mann-Whitney U Tests, U = 101, p = 0.20 at BB; U = 76.5, p = 0.14 at FC). However, anemones at BB initially were significantly larger than those at FC, because individuals in the source population at BB were larger on average than those at FC (Section 3.1; Fig. 1). The growth rate of small anemones was highly variable, with individuals ranging from 90% shrinkage to > 100% growth after only 1 mo. Although growth varied considerably within site, across all size classes the anemones at BB grew significantly more and shrank less than did those at FC, regardless of the site of origin (Fig. 3). After 1 mo, the percent change in anemone body size varied significantly with the site of destination (two-way ANOVA, $F_{1,90} = 14.94, p < 0.001$; Fig. 3a), but not site of origin ($F_{1,90} = 0.22, p = 0.64$), and there was no interaction effect ($F_{1,90} = 0.28, p = 0.60$). In terms of positive versus negative changes in body size (growth versus shrinkage), after 1 mo, 11 of 24 surviving anemones (46%) exhibited positive growth at BB while significantly fewer anemones (only 3 of 25 surviving individuals, 12%) exhibited positive growth at FC (test of independence, $\chi^2 = 6.86, p < 0.01$). The impact of destination site on anemone size change did not persist after 4.5 mos ($F_{1,90} = 0.72, p = 0.40$; Fig. 3b), nor did the effect of site of origin ($F_{1,90} = 0.24, p = 0.63$; no interaction effect, $F_{1,90} = 0.48, p = 0.49$), possibly due to low anemone survival after 4.5 mos (see below). Between-site differences in positive versus negative growth were not significant at 4.5 mos ($\chi^2 = 2.73, p = 0.09$).

Rates of anemone mortality were high, and did not differ
Table 3

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<thead>
<tr>
<th>Site</th>
<th>Period</th>
<th>$\lambda$</th>
<th>$\rho$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$\lambda_{1000}$</td>
<td>$\lambda_{sample}$</td>
<td>$\rho_{1000}$</td>
</tr>
<tr>
<td>A. Brewers Bay</td>
<td>Mar – Jun 2007</td>
<td>0.76 (0.40–1.16)</td>
<td>0.78</td>
</tr>
<tr>
<td></td>
<td>Jun – Sep 2007</td>
<td>0.80 (0.50–1.11)</td>
<td>0.72</td>
</tr>
<tr>
<td></td>
<td>Sep – Dec 2007</td>
<td>0.67 (0.32–1.06)</td>
<td>0.66</td>
</tr>
<tr>
<td></td>
<td>Dec 2007 – Mar 2008</td>
<td>0.61 (0.37–0.90)</td>
<td>0.61</td>
</tr>
<tr>
<td>B. Flat Cay</td>
<td>Mar – Jun 2007</td>
<td>0.65 (0.33–1.03)</td>
<td>0.71</td>
</tr>
<tr>
<td></td>
<td>Jun – Sep 2007</td>
<td>0.42 (0.23–0.56)</td>
<td>0.43</td>
</tr>
<tr>
<td></td>
<td>Sep – Dec 2007</td>
<td>0.65 (0.31–0.99)</td>
<td>0.48</td>
</tr>
<tr>
<td></td>
<td>Dec 2007 – Mar 2008</td>
<td>0.64 (0.32–0.99)</td>
<td>0.61</td>
</tr>
</tbody>
</table>

Table 4

Demographic characteristics of *Bartholomea annulata* at 2 coral reef sites (Brewers Bay and Flat Cay) on St. Thomas, U. S. Virgin Islands, each 3 mos during March 2007 – March 2008. Size-based transition matrices were used to calculate $\lambda$, the intrinsic rate of population change and $\rho$, the damping ratio. Transition matrices and therefore $\lambda$ analysis did not include effects of recruitment, thus $\lambda$ values < 1 indicated declining populations without recruitment. Transition probabilities were bootstrapped 1000 times to create confidence intervals for $\lambda$ and $\rho$. $\lambda_{1000}$ and $\rho_{1000}$ show mean values based on the bootstrapped transition matrices (95% CI); $\lambda_{sample}$ and $\rho_{sample}$ show values from the transition matrices based on the population data.

Fig. 3. Variation in percent change in *Bartholomea annulata* body size, comparing transplanted and non-transplanted individuals. Change in body size (TCSA = tentacle crown surface area in cm², ± SD) of corkscrew sea anemones *Bartholomea annulata* with site of origin versus site of destination, at (A) 1 mo and (B) 4.5 mo after reciprocal transplantation between 2 coral reef sites on St. Thomas, U.S. Virgin Islands: BB = Brewers Bay and FC = Flat Cay. Sample sizes are shown in parentheses. Note that all anemones showed net shrinkage at FC, regardless of timescale or site of origin.

4. Discussion

4.1. General comments

This study demonstrates that individuals of *Bartholomea annulata* exhibit high levels of turnover under both experimental and natural conditions. Rapid recruitment and growth, high mortality, and short lifespan are shown to be inherent life history characteristics of this species, contravening expectations that symbiotic hosts in general, and tropical sea anemones specifically, are necessarily long-lived with static populations. These data place *B. annulata* among the fastest-growing and shortest-lived tropical sea anemones on record, as observed...
recently for this species in the Florida Keys (O’Reilly and Chadwick, 2017). These findings have important implications for symbionts of *B. annulata*, both microalgae and crustaceans, as well as for reef fishes that use these anemones as cleaning stations (reviewed in Cantrell et al., 2015, Huebner and Chadwick, 2012a, 2012b). Three major implications are: (1) Crustacean symbionts of *B. annulata*, especially obligate associates, are likely to have short lifespans and to mature quickly. The degree to which these small crustaceans are mobile also will determine the extent to which *B. annulata* influences symbiotic crustacean life histories. (2) Cleaning stations centered around *B. annulata* function as short-lived features of Caribbean coral reefs; reef fishes thus must frequently search for new cleaning stations that they locate using visual cues transmitted by the anemones (Huebner and Chadwick, 2012a). (3) Any process that disrupts recruitment likely leads to rapid population decline of *B. annulata*, and subsequently affects the demography of crustacean symbionts and the ability of reef fish assemblages to engage in symbiotic interactions with cleaner shrimp. Conversely, because these anemones exhibit rapid recruitment, their populations potentially could recover quickly from disturbance events at some reef sites.

### 4.2. Recruitment, growth, and mortality

Rates of recruitment, growth, and mortality varied somewhat between the sites examined here, but overall trends suggest that these traits are largely dependent on anemone body size and age. These findings demonstrate that populations are heavily reliant on regular recruitment to maintain population size, and can experience 100% turnover of individuals within 12–24 mos.

Recruitment rates vary widely for these anemones between sites within region (two sites each within the USVI and Florida) that are only ~ 2 km apart, and between regions (USVI vs. Florida, ~1800 km apart, O’Reilly and Chadwick, 2017, present study). A combination of anemone body size, abundance, and local environmental conditions may contribute to this variation. In particular, small anemones under laboratory conditions produce recruits via pedal laceration, but only when starved, suggesting that nutritional limitation may trigger clonal replication in this species (Titus, 2011). Local abundance also could enhance recruitment (O’Reilly and Chadwick, 2017), with populations that contain the highest abundance receiving the most recruits. Recruits likely are produced by both sexual and asexual processes, although a genetic study by Titus et al. (2017) indicated that populations in both the USVI and Florida rely primarily on sexual reproduction. Long-lived genets or ramets of some cnidarians may occupy the same locations on coral reefs over long time spans (Bythell et al., 2018), but this likely is rare for *B. annulata* and other sea anemones (Dixon et al., 2017; O’Reilly and Chadwick, 2017; present study).

Dispersal ability and the degree to which *B. annulata* larval self-recruit to their home reefs remain unknown, but recent evidence suggests weak genetic structure and moderate gene flow across large spatial scales (Titus, 2017). This species may rely primarily on sexual reproduction via broadcast spawning (Titus et al., 2017), and the subsequent recruits may be attracted to parent populations, similar to scleractinian corals in which the planktonic larvae are attracted to conspecifics (Bramanti and Edmunds, 2016) and often self-recruit to parent populations (Figueiredo et al., 2013; Swearer et al., 2002). The pattern of significantly higher recruitment observed here per unit reef area at a site that contained relatively more abundant anemones, in addition to similar patterns observed between sites examined in Florida (O’Reilly and Chadwick, 2017) support the hypothesis that these larvae may self-recruit to parental reef areas.

Individual growth rates in this species are inversely proportional to body size, with small anemones growing 2-3× faster than large ones. The growth rate of *B. annulata* under laboratory conditions (Titus, 2011; O’Reilly, 2015) generally outpaces that under field conditions, as measured in both the USVI (present study) and Florida (O’Reilly and Chadwick, 2017), but the smallest individuals grow the fastest in all studies thus far. Anemones may grow more slowly in the field vs. laboratory due to a range of environmental stressors that are present on coral reefs (e.g., partial predation, pollution, sedimentation, extreme temperatures) but absent in laboratory tanks. The degree to which individuals of *B. annulata* rely on their endosymbiotic algae for nutrition remains unknown. However, high rates of water flow in the field potentially damage the soft tissues of delicate-bodied sea anemones such as *B. annulata* and limit both their heterotrophic feeding ability and exposure of their microalgae to sunlight, by changing the size of the tentacle crown and reducing tentacle expansion (Koehl, 1977; Shick, 1991). This process could contribute to the low abundance of *B. annulata* at reef sites with relatively high water motion (Colombara et al., 2017). Exposure to more rapid rates of water flow on coral reefs than in laboratory tanks thus may cause these anemones to redirect energy from growth into tissue regeneration, or into the relatively high energetic costs of remaining expanded in rapidly-moving water (O’Reilly and Chadwick, 2017). Water flow and food availability may work in concert to partially drive patterns of local abundance and recruitment, as both were higher at the inshore site (BB) that exhibited lower water motion and higher suspended particulate matter (Table 1) than did the offshore site (FC). Comparison of anemone transition rates in all five types of studies conducted to date for this species indicate that they vary, in terms of positive or neutral transitions (growth/stasis) versus negative ones (shrinkage/death), between studies conducted at northern vs. southern sites, at inshore vs. offshore sites, and under laboratory vs. field conditions (Fig. 4). Individuals exhibit a higher proportion of positive transitions at calm-water, high-nutrient, cooler sites, than at rough-water, low-nutrient, relatively warm sites. Additionally, the growth and survival rates of these anemones vary temporally, and are higher in the field during winter periods with relatively cool temperatures, than during summer when temperatures are warmer (O’Reilly and Chadwick, 2017; present study). Recent experimental laboratory data indicate that the optimal temperature for this species is ~ 24°C (similar to temperatures in the laboratory and in the northern Florida Keys during winter), with body shrinkage occurring when temperatures are substantially higher (as in the USVI or in the southern USVI site exhibited the lowest growth.
Florida Keys during summer) or lower (as during low-temperature laboratory experiments, A. Colombara and N. Chadwick, unpublished data).

The patterns observed here of decreasing growth rate with body size parallel those known for other coral reef cnidarians with indeterminate body size, including sea anemones (Chomsky et al., 2004; Dixon et al., 2017; Sebens, 1980), mushroom corals (Chadwick-Furman et al., 2000), cup corals (Goffredo et al., 2004), and zoanthids (Karlson, 1988). The upper limit of body size for many marine invertebrates may be set by current environmental conditions rather than by pre-determined limits imposed by genotype (Sebens, 1980). Further, large individuals require less energy per unit mass to meet metabolic requirements than do small individuals, and can allocate more energy toward reproduction (Sebens, 1982). Organisms must thus invest more energy into growth and metabolic requirements than into reproduction, when relatively small. The interplay of these factors may partially explain the patterns observed for B. annulata at FC, where relatively high water flow may act to limit body size well below biomechanical or genetic restrictions, whereas calmer and higher nutrient conditions at BB may allow individuals to reach body sizes closer to their physical maxima. However, the present study did not include replicate analyses at the site level, so definite conclusions about effects of physical or biological variables on anemone demography in the field cannot yet be made.

The inverse relationship observed here between body size and mortality rate is similar to that recorded for field populations in Florida (O’Reilly and Chadwick, 2017), as well as for other sea anemones and corals that die over decadal time scales (Goffredo and Chadwick-Furman, 2000; Hughes and Tanner, 2000; Dixon et al., 2017). Small anemones likely face high rates of predation and impacts from other types of biological interactions, as well as enhanced sensitivity to changes in physical factors such as temperature and water flow compared to large individuals, as known for other reef cnidarians (Shick, 1991).

Turnover rates were high at both sites examined here, indicating that population abundances may fluctuate rapidly and rely heavily on frequent recruitment. The similar turnover rates at all sites examined thus far, with < 25% of populations surviving 12 mos, and complete population turnover in < 24 mos (O’Reilly and Chadwick, 2017; present study), together indicate that short lifespan likely is an inherent feature of this species. Some large, old laboratory individuals have been observed to senesce (shrink) prior death (O’Reilly, 2015), as also observed at field sites in Florida (O’Reilly and Chadwick, 2017). While cnidarians have been thought not to age or senesce (Comfort, 1979; Finch, 1991; Kirkland, 1989), senescence and limited lifespan (< 10 yrs) have been documented for large Indo-Pacific sea anemones (Dixon et al., 2017; McVay, 2015). Individuals of the short-lived branching coral Stylphora pistillata cease sexual reproduction and stop growing, and their exosymbiotic fish and crab symbionts desert them, over several months prior to colony death (Rinkevich and Loya, 1986; Wolodarsky, 1979). Senescence likewise has been reported for hydro-medusae Gonionemus vertens, in which old individuals exhibit a higher frequency of infection and deterioration than do young ones (Mills, 1993). Genetically-programmed senescence could be a common feature of old age in some cnidarians, but may be detected rarely due to a lack of frequent monitoring near the end of individual lifespans. Estimates for B. annulata reveal that this species is the shortest-lived sea anemone on record, with lifespans much shorter than those quantified for the few other tropical (Dixon et al., 2017) and temperate sea anemones (Ottaway, 1980; Sebens, 1983) that have been examined to date.

4.3. Conceptual framework for the symbiosis

These findings have important implications for population dynamics of the crustaceans that form exosymbiotic associations with B. annulata. While our data contravenes expectations that tropical anemones live for several decades, members of this species might have extensive enough lifespans to serve as effective hosts for many types of associated decapod crustaceans. Anemone shrimps reach sexual maturity within a few months (Knowlton, 1980) and live < 2 yrs. (Gilpin and Chadwick, 2017; Spotte and Bubuic, 1997). Thus, juvenile crustaceans that recruit to newly-settled sea anemones may acquire hosts that live the 6 + mos needed for the crustaceans to produce several generations of offspring. Early sexual maturity and short lifespan thus could be a universal feature of tropical anemone-associated crustaceans (Chace Jr. and Bruce, 1993). Although the abundance of associated crustaceans may increase with anemone body size (Briones-Fourzán et al., 2012), there is no evidence that B. annulata needs to meet a certain size threshold before hosting symbionts. Crustaceans recruit to B. annulata when the hosts are still quite small (Gilpin and Chadwick, 2017; S. Ratchford and N. Chadwick, unpublished data). As such, relative to the apparent biology of their symbionts, these anemones appear to be static enough to mediate multiple generations of crustaceans.

Shrimp migration among anemones could limit the impact of B. annulata on crustacean lifespans. Sexually mature A. armatus move up to 4 m from their anemones at night, to forage and colonize new, possibly younger hosts (Knowlton, 1980). Likewise, the anemone shrimps A. pedersoni and P. yucatanicus are host generalists and can reside on a variety of large tropical anemone species (Briones-Fourzán et al., 2012; Titus and Daly, 2017), although their rates of among-host migration remain unknown. The closely-related cleaner shrimp Periclimenes longicarpus on Indo-Pacific reefs migrates frequently among anemones nocturnally (Chadwick et al., 2008). Because some of these associated crustaceans provide behavioral and physiological benefits to anemones (Cantrell et al., 2015; McCammon and Brooks, 2014), future studies are warranted to examine how crustacean symbionts impact the hosts at the level of population dynamics.

It is concluded that B. annulata displays far more rapid turnover of individuals than would be expected for a symbiotic host species. For the large assemblage of fishes that relies on this symbiosis for ectoparasite removal services, these anemone-based cleaning stations thus are transient, short-lived features of coral reefs. The reef fishes in > 20 common families that regularly visit A. pedersoni cleaning stations (Huebner and Chadwick, 2012a) must frequently search for recently-recruited anemones, as the older ones senesce and die. In Florida and Puerto Rico, these anemones and symbiotic crustaceans are harvested for the ornamental aquarium trade, and are listed as a species of conservation concern (Legore et al., 2005; Rhyne et al., 2009). The short lifespans (compared to that of some other cnidarians) of these animals and their reliance on frequent reproduction (Titus et al., 2017) suggest that, while this symbiotic system may be stable where populations are abundant, overharvesting could lead to an almost immediate population crash of both anemones and crustaceans. Given the ecological importance of these symbioses as cleaning stations for reef fishes, there could be immediate, radiating effects of either anemone or cleaner shrimp removal from coral reef ecosystems.

Declarations of interest

None.

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References


Titus, B.M., Daly, M., 2017. Specialist and generalist symbionts show counterintuitive levels of genetic diversity and idiosyncratic expansion events along the Florida Reef Tract. Coral Reefs 36, 339–354.


Erratum for:

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