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

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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, 2000; 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., anemonefishes) 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

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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 guest 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 (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; Szczebak 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-Fourzán et al., 2012; Colombara et al., 2017; Herrnkind 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-Fourzán et al., 2012; Jennison, 1981; Sebens, 1976). Food is acquired through both heterotrophy, and autotrophy in which *B. annulata* associates with several species of microalgae *Symbiodinium* (Grajales et al., 2016), similar to most other coral reef anemones (Baker, 2003; Rowan, 1998). Individuals reproduce sexually twice each year through broadcast spawning (Jennison, 1981) and clonally year-round via pedal laceration (Cary, 1911), occurring as single individuals or small aggregations that may or may not comprise asexual clones (Titus et al., 2017). This is a model system to test expectations about the stability of sea anemone hosts and the maintenance of crustacean symbioses, because the population dynamics and life history of *B. annulata* likely exert a major influence over many crustaceans in terms of their abundance, inter- and intraspecific group sizes, mobility, reproductive opportunities, and lifespan.

An initial field study indicated that populations of *B. annulata* may exhibit high turnover (O'Reilly and Chadwick, 2017), but was conducted in Florida Bay where seasonal sea surface temperatures can vary by 10 °C, representing atypical conditions compared with more stable environments in the Greater Caribbean (Bramanti and Edmunds, 2016; Briones-Fourzán et al., 2012), so may not be directly generalizable across the entire species range. Here, the findings of O'Reilly and Chadwick (2017) are compared with those obtained at other coral reef locations, to test the hypothesis that large sea anemones are long-lived with stable population structure as a prerequisite for supporting assemblages of ectosymbionts. Findings are presented from monitoring and modeling of *B. annulata* populations at two Caribbean reef sites and from experimental field manipulations, to determine the extent to which these sea anemones adapt to specific sites. Conclusions then are made about the impacts of anemone life history patterns on the dynamics of crustacean symbionts and cleaning stations, 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 clod 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-Fourzán et al., 2012; Mahnken, 1972). An area of 47 × 6 m was monitored at BB (282 m^2), and 70 × 11 m plus 73 × 5 m at FC (1135 m^2, 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-Fourzán 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