

# Population dynamics of corkscrew sea anemones *Bartholomea annulata* in the Florida Keys

Erin E. O'Reilly, Nanette E. Chadwick\*

Department of Biological Sciences, 101 Rouse Life Science Building, Auburn University, Auburn, Alabama 36849, USA

**ABSTRACT:** Corkscrew sea anemones *Bartholomea annulata* are important ecologically as hubs of a mutualistic network involving cleaner shrimps and client fishes on Caribbean reefs. They also are collected for the ornamental aquarium trade, but little is known about their population dynamics to support conservation management. We quantified variation in population structure among regions of the Florida Keys and levels of human impact within region. The Upper Keys and low-impact sites supported higher population abundance and proportions of small anemones than the Lower Keys and high-impact sites. At 2 sites where we monitored anemone dynamics every 2 mo for 1 yr, individuals recruited frequently and grew rapidly to maximum body size and then remained static or shrank. Fewer than half the individuals survived all year, indicating rapid population turnover, with mortality occurring mostly among small individuals or large ones that appeared to senesce beforehand. Stasis of large individuals (or lack thereof) exerted the most influence on population size. We conclude that in Florida, corkscrew anemones experience relatively high recruitment and survival at sites with low human impact and in the Upper Keys, where summer water temperatures are cooler than in the Lower Keys. Populations are highly dynamic and appear to rely on frequent recruitment, potentially linked to the presence of resident adults at high enough abundances for fertilization of broadcast propagules. The ephemeral nature of these anemones has important implications for the dynamics of their anemoneshrimp symbionts, for reef fishes that utilize them as parasite cleaning stations, and for the conservation management of their populations.

**KEY WORDS:** Sea anemone · Demography · Recruitment · Mortality · Coral reef · Size-based transition matrix

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## INTRODUCTION

The marine ornamental trade is a multimillion-dollar industry involving over 45 countries on 6 continents, yet little is known about the life histories of many ornamental organisms to support sustainable harvest practices (LeGore et al. 2005, Shuman et al. 2005, Rhyne et al. 2009, 2012). The trade is global and complex, affecting coral reefs in the major biogeographic regions of both the Caribbean and the tropical Indo-Pacific. While coral reefs in the Caribbean Sea supply a relatively small percentage of the global trade compared to the Indo-Pacific, the demand for new taxa, specifically western Atlantic spe-

cies, has led to an increase in the ornamental trade in this region (Bruckner 2005, Rhyne et al. 2012, Mazza et al. 2015). Florida maintains the largest ornamental fishery in the USA, in terms of numbers of species and landings, and its reefs have become degraded in part due to this fishery (Rhyne et al. 2009). The marine ornamental trade in the Caribbean has grown steadily as aquarium technology has improved and aquarium ownership has become increasingly popular (Bruckner 2005, Rhyne et al. 2012, Erni Cassola et al. 2016). This intensive removal of organisms causes loss of biodiversity and habitat, as well as long-term effects on the composition and function of reefs (Roberts 1995, Bruckner 2005, Graham et al. 2011),

\*Corresponding author: chadwick@auburn.edu

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<sup>§</sup>Corrections were made to Fig. 3 after publication. For details see [www.int-res.com/abstracts/meps/v567/c\\_p109-123](http://www.int-res.com/abstracts/meps/v567/c_p109-123)  
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leaving them more susceptible to and slower to recover from both natural and anthropogenic disturbances, including destructive weather, algal blooms, and disease (Hughes 1994).

Corkscrew sea anemones *Bartholomea annulata* have been a common target for the ornamental trade in Florida as well as in other parts of the Caribbean (LeGore et al. 2005, Rhyne et al. 2009). Numbers of *B. annulata* landed in Florida have declined steadily over the past decade, even while the number of collecting permits has remained stable (Fig. 1). This type of pattern may indicate either reduced catch per unit effort or a change in consumer demand (Gulland 1964, Maunder et al. 2006). Individuals of *B. annulata* are among the largest, most common Caribbean sea

anemones, reaching 30 cm in tentacle crown diameter (Kaplan et al. 1999, O'Reilly 2015). In Florida, they reproduce sexually by broadcasting gametes during November and April each year and also replicate clonally via pedal laceration (Jennison 1981). These anemones host not only the major Caribbean cleaner shrimp *Ancylomenes* (= *Periclimenes*) *pedersoni* (Mahnken 1972) but also several other species of crustacean associates (Mahnken 1972, Silbiger & Childress 2008, Briones-Fourzán et al. 2012, Mascaro et al. 2012). Individuals function as visual cues that attract client fishes for cleaning interactions; the number and diversity of fishes that their resident shrimp clean both increase with anemone size, as fishes pose for cleaning only when the host anemones are visible (Huebner & Chadwick 2012a,b). The body size of anemones and number of cleaner shrimps at each station affect the parasite cleaning rates of coral reef fishes (Titus et al. 2015). Therefore, the removal of large *B. annulata* sea anemones from coral reefs, together with their shrimp symbionts, can have potentially negative effects on reef fishes, as known from cleaner removal experiments in other reef systems (Bshary 2003, Grutter et al. 2003, Bshary et al. 2007, Waldie et al. 2011). With recent increases in the demand for key reef invertebrates by the aquarium industry, it is becoming urgent to understand the life histories of targeted species and their dynamics on coral reefs, including the sea anemones that host cleaner shrimps.

Sea anemones are capable of both growing and shrinking throughout their lifetimes, and because they possess only soft tissues, they leave no indication of previous body size (Hughes 1984, Hughes & Jackson 1985, Chomsky et al. 2004a). Therefore, it is difficult to determine their size–age relationships and to apply age-based demographic models such as the classic Leslie model (Leslie 1945). Population changes in anemones and related organisms such as some stony corals thus are most appropriately analyzed using a size-based model (Hughes 1984).

We describe variation in the population structure of *B. annulata* among regions of the Florida Keys and between sites within each region that experience different levels of human impact. We also employ a size-based transition model to assess the dynamics of 2 populations in which individuals were mapped and examined every 2 mo for 1 yr. We then discuss the ecological and conservation management implications of demographic patterns in this species. This is the first published description of population dynamics in a Caribbean sea anemone.

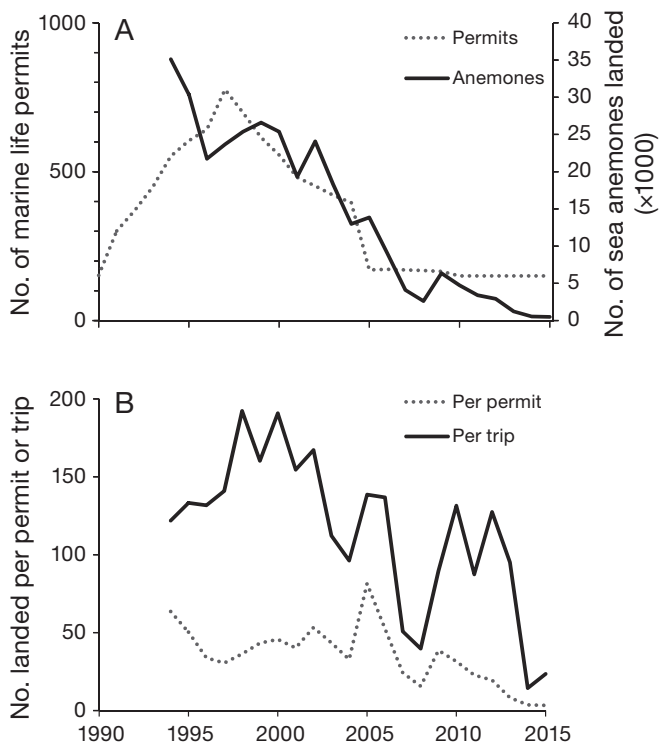


Fig. 1. (A) Numbers of marine life commercial fishing permits issued by the Florida Fish and Wildlife Conservation Commission (FWC) during 1990 to 2015 to collect *Bartholomea annulata* for the ornamental aquarium trade, and number of individuals of *B. annulata* landed by commercial fishers during 1994 to 2015 (not assessed prior to 1994; N. Sheridan pers. comm.). Note that a peak of 776 permits were issued in 1997, 1 yr before limits were placed on permit number. Source: Trip ticket program of FWC (<http://myfwc.com/research/saltwater/fishstats/commercial-fisheries/landings-in-florida/> and N. Sheridan, FWC, pers. comm.). (B) Mean number of *B. annulata* individuals landed per marine life commercial fishing permit and per commercial ornamental fishing boat trip during 1994 to 2015. Note that even after the number of issued permits was greatly reduced in 2006, the number of anemones collected per permit continued to decrease

## MATERIALS AND METHODS

### Study sites

The present study was conducted from May 2014 to May 2015 in the Florida Keys, Florida, USA. Two study sites were selected adjacent to shore at 0.5 to 3 m depth (all water depths given at low tide) in each of 3 regions: Upper Keys (Indian Channel [24° 53' 24" N, 80° 39' 36" W] and Robbies [24° 52' 48" N, 80° 42' 00" W], both on Indian Key), Middle Keys (Tiki Hut [24° 43' 48" N, 81° 01' 12" W] and Quarry [24° 45' 00" N, 80° 58' 48" W], both on Marathon Key), and Lower Keys (Bowman's Channel [24° 39' 36" N, 81° 30' 36" W] on Sugarloaf Key and Cudjoe [24° 39' 00" N, 81° 33' 00" W] on Cudjoe Key) (6 sites total; see site map Fig. S1 in the Supplement, at [www.int-res.com/articles/suppl/m567p109\\_supp.pdf](http://www.int-res.com/articles/suppl/m567p109_supp.pdf)). Within each region, we selected 1 high-impact site that appeared to be easily accessible by humans from both the shore and water (i.e. adjacent to a public beach with parking, deep enough for boat access, adjacent to Interstate Highway 1, and/or evidence of frequent human visitation as indicated by abundant lobster traps, waste, etc.) and 1 low-impact site that appeared to be less accessible and thus less likely to be impacted by humans (i.e. too shallow for boat access, plant growth along the shore too dense for easy shore access, distant from paved roads, little or no evidence of visitation). We defined high-human-impact sites as exposed to the effects of human activities in the form of potential chemical disturbance to sea anemones, such as pollution from boat fuels or automobile engine oils (Ormond & Caldwell 1982, Samiullah 1985) and/or physical disturbance including tissue abrasion or enhanced sedimentation caused by swimmers and snorkelers (Krieger & Chadwick 2013). Low-human-impact sites were defined as experiencing a relative absence of human activities in close proximity to the study site. All sites were selected based on the 2 criteria described in this paragraph (region and level of impact), as well as the presence of high enough abundances of *Bartholomea annulata* for demographic analyses (>40 ind. per 400 m<sup>2</sup> area, details in next subsection). Sites consisted of small patch reefs, coral rubble, or rocky boulders.

Sea anemone population parameters such as growth rates and body size are known to vary with temperature (Chomsky et al. 2004a), so we assessed variation in mean monthly seawater temperature during May 2014 to May 2015, as calculated from 1 NOAA weather buoy located in each of the 3 regions

that contained our study sites ([www.ndbc.noaa.gov/](http://www.ndbc.noaa.gov/); Fig. S1 in the Supplement).

We also assessed stony coral percent cover at each site because corals are close relatives of sea anemones, and variation in their percent cover may reveal the general effects of both natural and anthropogenic variation among sites that also impact sea anemones. In March 2015, live stony coral percent cover was determined by deploying a haphazardly placed 25 m belt transect at 1 to 3 m depth at each site. We visually estimated the percent live cover of stony corals within each of 25 sub-squares (20 × 20 cm each) created by string that subdivided each 1 m<sup>2</sup> quadrat frame, which we deployed along both sides of the transect, for a total of 50 m<sup>2</sup> surveyed for live coral cover at each of the 6 study sites (N = 1 transect per site, N = 50 quadrats per transect; after Jokiel & Coles 1974, Nadon & Stirling 2006).

### Population surveys

During March 2015, a 25 m transect was deployed at least 1 m distant from the coral cover transect described in the previous paragraph for each site, and all individuals of *B. annulata* within a 1 m band along the left side of the transect tape were measured (details in the following paragraphs). The tape then was moved and the process repeated until 40 to 60 anemones were measured, numbers similar to those used in previous studies on the population size structure of sea anemones (Sebens 1981a, Hattori 2002, 2006, Mitchell 2003, Chadwick & Arvedlund 2005). The abundance of sea anemones varied widely among sites, so we sampled different transect dimensions to reach ~40 to 60 anemones sampled per site (range of transect areas sampled = 1 × 8 m [i.e. only part of 1 transect was sampled] to 25 × 8 m [i.e. 8 transects sampled, each 25 × 1 m], N = 6 sites). We recorded both the total number of anemones per transect (N = 1 transect per site) and the number per 4 quadrat areas within each transect (quadrat areas = 2–50 m<sup>2</sup> each, depending on the total transect area sampled).

Two sites (Quarry and Cudjoe) also were selected for repeat surveys that began in May 2014 because they contained populations of sea anemones that were dense enough for ease of tagging and mapping but not so dense as to prevent clear identification of each individual among survey dates. At each of the 2 repeat-survey sites, an area containing 50 to 100 anemones was marked at the corners with plastic flagging tape attached to coral rubble (34 × 2 m at

Quarry and 50 × 3 m at Cudjoe). At the beginning of each repeat survey, temporary floating buoys were placed at the site corners to easily relocate the site edges from the water surface. In May 2014, all *B. annulata* individuals were marked with an aluminum tag engraved with a number, which was hammered into the dead coral substrate adjacent to each anemone (after Porat & Chadwick-Furman 2004, Huebner et al. 2012, Hobbs et al. 2013). A short piece of flagging tape was attached to each tag to make it easily visible, and the location of each marked anemone was noted on a site map. SCUBA was used for surveys at the Quarry (3 m depth), and snorkel was used at Cudjoe (0.5 m depth), due to the different water depth at each site. Both sites were revisited ~7 times over 1 yr, approximately each 2 mo (May, July, September, November 2014 and January, March, May 2015, except for November 2014 at Cudjoe due to a storm). This sampling frequency was based on the highly dynamic nature of individuals of this species, as previously observed in the US Virgin Islands (USVI) (Nelsen 2008). During each visit, all marked sea anemones were remeasured, and the entire site was examined carefully for new recruits, which also were marked, measured, and mapped (after Chadwick & Arvedlund 2005). Any previously marked anemones that were not detected in subsequent surveys were considered lost to the population.

During each visit, the following data were collected for each observed individual: tentacle crown length and width, depth below sea level, and miscellaneous information (color, substrate type, and distance and direction to other close individuals for reidentification, after Chadwick & Arvedlund 2005, Huebner et al. 2012). The longest distance from tentacle tip to tentacle tip across the center of the oral disc was measured as tentacle crown length ( $L$ ), and the distance perpendicular was measured as tentacle crown width ( $W$ ), used to calculate tentacle crown surface area (TCSA =  $[L/2 \times W/2] \times \pi$ ; after Hirose 1985, Hattori 2002, Chadwick & Arvedlund 2005, Huebner et al. 2012). TCSA is an ecologically relevant measure of body size because it quantifies the area occupied by the anemone on the substrate and is accurate in that it correlates significantly with all other measures of body size in this species (O'Reilly 2015).

### Statistical analysis

Variation in mean monthly seawater temperature was compared among the 3 regions for the periods of both maximum (July–September 2014) and mini-

imum temperatures (December 2014–February 2015) during the study year using a 2-way ANOVA ( $N = 3$  mo examined in each of 3 regions during 2 periods). Based on the values obtained from each transect as a whole, variation in coral cover and sea anemone abundance among the 6 sites was assessed using Cohen's  $d$  effect statistic (Cohen 1988). With such a small sample size ( $N = 1$  transect per site), a significant difference between variables (high impact vs. low impact and Upper, Middle, and Lower Keys) was unlikely to be accurate; therefore, the effect size between sites was reported. ANOVA also was performed, based on variation in coral cover among the fifty 1 m<sup>2</sup> quadrats examined within each band transect per site and among the 4 quadrats (2–50 m<sup>2</sup> each) within each band transect examined for anemone abundances. For both analyses, post hoc pairwise comparisons between high- and low-impact sites within each region, as well as among regions, were performed. Variation in the population size structure of anemones among the 6 sites was assessed using  $\chi^2$  analysis.

Sea anemones were divided into 3 size classes by TCSA: 0 to 25 cm<sup>2</sup> (I), 25.1 to 50 cm<sup>2</sup> (II), and >50 cm<sup>2</sup> (III). Size classes were selected based on those used previously for this species (Nelsen 2008) and because our initial survey results in Florida also revealed that they yielded approximately equal numbers of individuals per size class. Variation in rates of individual size change were analyzed using a mixed effects linear model in R x64 3.2.0 with a blocking variable for individual, for the whole population at each of the 2 repeat-survey sites, and for each size class within a site. A 1-way ANOVA was used to assess significant differences in rates of body size change among size classes.

Population dynamics were analyzed using a size-based model (after Hughes 1984, Gotelli 1991, Lirman 2003). Transition matrices were created based on the 3 body size classes described in the previous paragraph and on the growth or shrinkage of each individual between time points (each 2 mo for 1 yr). Elasticity values were calculated using the Microsoft Excel add-on PopTools 3.2. A value was calculated for each element of each matrix to determine which vital rates were most important for population growth. The transition matrices did not include the effects of sexual and asexual reproduction on population growth, due to unknown fecundity rates; therefore, the intrinsic rates of population change ( $\lambda$ ) reported here represent rates calculated without input from reproduction. Transition probabilities were bootstrapped 1000 times to obtain confidence

intervals for  $\lambda$  and damping ratios  $\rho$  (after Bierzychudek 1999, Edmunds 2010).

Recruitment rate was determined as the number of new individuals in the population at each survey date. New individuals  $< 50 \text{ cm}^2$  TCSA were classified as recruits, based on analysis of growth rates of *B. annulata* under laboratory conditions (mean  $\pm$  SE:  $13.7 \pm 2.3 \text{ cm}^2$  TCSA per 2 mo, range: 9.1–18.2 for individuals in Size Class 1; O'Reilly 2015). New individuals  $> 50 \text{ cm}^2$  TCSA at each survey date were presumed to be immigrants or anemones that had been present but undetected in previous surveys and, as such, were excluded from recruitment analyses but were included in estimates of growth, shrinkage, and mortality (0–14% of individuals at the Quarry, 0–6% at Cudjoe, depending on survey date, Fig. S2 in the Supplement). We used  $50 \text{ cm}^2$  TCSA as a cutoff size because (1) fast-growing recruits potentially could reach this body size within ~2 to 4 mo (see this paragraph), and (2) previous studies used size at sexual maturity as a cut-off for classification of sea anemone recruits (Sebens 1981b,c, 1982), which in *B. annulata* occurs at ~0.74 cm pedal disc diameter (Jennison 1981), equivalent to ~43.8  $\text{cm}^2$  TCSA (O'Reilly 2015).

Mortality rates were estimated based on the disappearance of anemones between survey dates. Anemones that were not relocated for at least 2 survey periods (4 mo total) were considered dead or lost to the population (after Ottaway 1979, Holbrook & Schmitt 2005). If a mapped individual was not located during 1 survey but was found during the next, then the missing measurement was interpolated. However, if an individual was missing for more than 2 consecutive surveys (4 mo), it was considered lost, and any anemone found nearby later was classified as an immigrant or recruit. We used this process because sea anemones occasionally contracted into their reef holes and thus may have avoided detection during a given survey but were unlikely to remain contracted for long periods due to their requirement of light exposure for photosynthesis by their endosymbiotic microalgae (Pearse 1974, Sebens & DeRiemer 1977). Sea anemones are capable of locomotion but appear to move only short distances, if at all, over rocky substrate ( $< 5 \text{ cm}$  over 1–2 yr, with greatest distance moved  $< 1 \text{ m}$ , Ottaway 1978, Batchelder & Gonor 1981, Mitchell 2003, Holbrook & Schmitt 2005, Hattori 2006). Measured rates of locomotion for *B. annulata* under laboratory conditions are  $< 3 \text{ cm mo}^{-1}$  (O'Reilly 2015). Thus, it would have been difficult to confuse individually identified anemones based on their locations at the abundances recorded at our repeat-survey sites (0.5–2.1 ind.  $\text{m}^{-2}$ , see 'Results').

Maximum lifespans were calculated using Kaplan-Meier survival curves (Kaplan & Meier 1958, Zaragoza et al. 2014). Population turnover time was calculated as the time required for the complete replacement of individuals, which was the reciprocal of the turnover rate (Hughes 1984, Hughes & Jackson 1985), according to the turnover ( $T$ ) formula:

$$T = \frac{(E + R)}{(N_i + N_{i+1})} \quad (1)$$

where  $E$  = number of deaths during a given period,  $R$  = number of recruits, and  $N_i$  = number of individuals in the population (after Diamond 1969, Hanski 1999). All results are reported as mean  $\pm$  1 standard error, unless indicated otherwise.

## RESULTS

### Site characteristics

Mean monthly surface seawater temperatures did not vary significantly with region or time of year (2-way ANOVA,  $F_{2,11} = 2.43$ ,  $p = 0.13$ ) due to high variation within both season and region (Fig. S3 in the Supplement). However, during peak temperatures in late summer (July–September), the Lower Keys experienced somewhat higher seawater temperatures (32.0–33.5°C) than the Middle (30.1–32.1°C) and Upper Keys (29.4–31.7°C). During minimum temperatures in late winter (December 2014–February 2015), seawater temperatures were very similar among the 3 regions (21.0–23.0, 20.7–22.5, and 20.2–22.0°C for the Lower, Middle, and Upper Keys, respectively).

All sites contained a low percent cover of live stony corals (range =  $3.4 \pm 0.5$  to  $12.0 \pm 1.2\%$ ), which varied with both region and level of human impact. Coral cover varied significantly at all 3 levels examined: among sites, among regions, and between some sites that differed in the level of human impact (nested ANOVA,  $F_{2,294} = 9.76$ , 13.37, and 38.50, respectively,  $p < 0.001$  for all, Fig. 2A). Both sites in the Lower Keys contained 3 $\times$  less coral cover than at low-impact sites in the Middle and Upper Keys. Low-impact sites in the Upper and Middle Keys contained ~2 $\times$  the coral cover of high-impact sites (Fig. 2A). Cohen's  $d$  effect size indicated (1) moderate practical significance in the difference of coral cover between the Upper and Lower Keys ( $d = 0.58$ ), (2) moderate to high practical significance in the coral cover difference between the Middle and Lower Keys ( $d = 0.75$ ), and (3) moderate practical

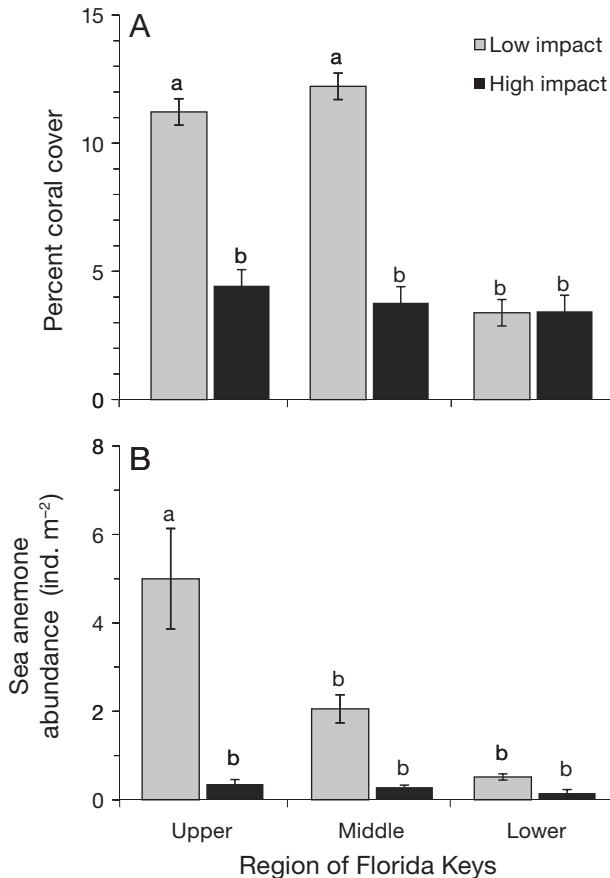


Fig. 2. Variation among sites in the Florida Keys in (A) percent cover of live stony corals (N = fifty 1 m<sup>2</sup> quadrats per site), and (B) abundance of *Bartholomea annulata* (N = 4 quadrats per site; quadrat dimensions varied with local anemone abundance). Mean ± SE. Bars with the same letter are not significantly different

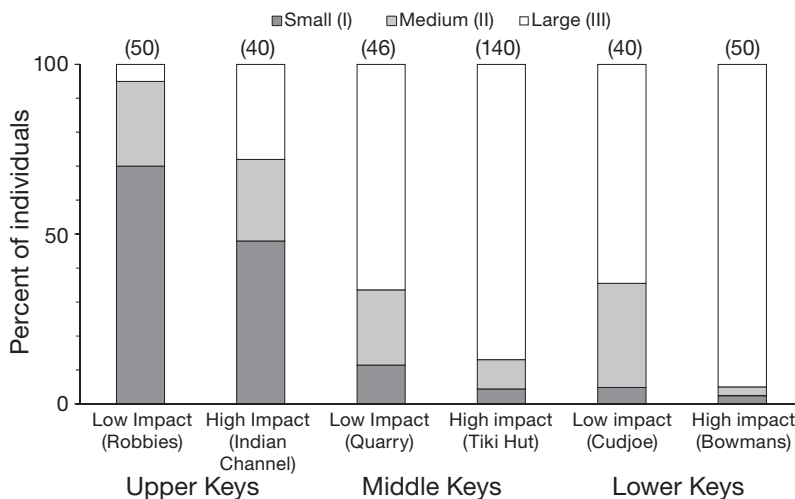


Fig. 3. Variation in the population size structure of *Bartholomea annulata* among 3 regions of the Florida Keys (Upper, Middle, Lower) and between sites within each region that were exposed to high versus low human impact. Numbers in parentheses indicate sample size

significance in the coral cover difference between sites with high vs. low human impact ( $d = 0.67$ ).

### Sea anemone abundance and population structure

The abundance of *Bartholomea annulata* also varied with both region and level of human impact, from only 0.15 ind. m<sup>-2</sup> at Bowman’s Channel (Lower Keys, high impact) to 5.00 ind. m<sup>-2</sup> at Robbies (Upper Keys, low impact, Fig. 2B). Sea anemone abundance varied significantly with region (ANOVA,  $F_{2,18} = 11.72$ ,  $p < 0.001$ ), level of human impact ( $F_{1,18} = 26.28$ ,  $p < 0.001$ ), and site within region ( $F_{2,18} = 13.12$ ,  $p < 0.001$ ). Robbies contained higher anemone abundance than all other sites examined, with 2 to 10× more ind. m<sup>-2</sup> than at sites in the Middle Keys and ~10 to 25× more than in the Lower Keys (Fig. 2). The Upper Keys showed high Cohen’s  $d$  practical significance for the difference in anemone abundance compared to both the Middle ( $d = 0.67$ ) and Lower Keys ( $d = 1.13$ ).

Sea anemone population size structure varied significantly with level of human impact ( $\chi^2 = 8.07$ ,  $p < 0.05$ ), in that low-impact sites contained a much higher proportion of small individuals (Size Class I, 4.0–70.0% of the population) than did high-impact sites (2.5–48.0%). Population size structure also varied significantly with region ( $\chi^2 = 119.7$ ,  $p < 0.001$ ), in that it consisted of a relatively high proportion of small individuals in the Upper Keys relative to both the Middle and Lower Keys ( $p < 0.001$  for both comparisons, Fig. 3).

### Repeat-sampled populations

In May 2014, sea anemone abundance at the Quarry (1.43 ind. m<sup>-2</sup>) was almost 3× that at Cudjoe (0.55 ind. m<sup>-2</sup>). During the study year, abundance peaked at the Quarry in November 2014 at 2.60 ind. m<sup>-2</sup> (82% increase over initial abundance) and at 0.71 ind. m<sup>-2</sup> at Cudjoe (26% increase, January 2015). By May 2015, abundance had almost doubled (increase of 80.0%) at the Quarry, to 2.57 ind. m<sup>-2</sup>, while it decreased by a fourth (25.4%) at Cudjoe, to 0.41 m<sup>-2</sup>.

Similar patterns of body size transition occurred at both sites (Table 1). During most periods at both sites, anemones that remained in the largest

size class (i.e. static in Size Class III) were the most elastic (Tables S1 in the Supplement), with elasticity values  $>0.50$  (except during May–July 2014 at Cudjoe, when anemones remaining in the smallest size class were most elastic). Initial population size structure differed significantly between the 2 sites ( $\chi^2 = 7.45$ ,  $p < 0.05$ ), when a higher percentage of small individuals occurred at the Quarry than at Cudjoe. By the end of the study year, this difference disappeared due to an increased percentage of large individuals at the Quarry (Table 1). Rates of intrinsic population change ( $\lambda$ ) indicated that when input from recruitment was not included, both populations declined during all periods, especially during the winter months (September 2014–March 2015, Table S2 in the Supplement). During most periods,  $\lambda$  values obtained through standard analysis were within the 95% confidence intervals of values obtained through  $\rho$  bootstrap resampling (Table S2 in the Supplement). The damping ratio ( $\rho$ ) varied widely among sample periods (Table S2 in the Supplement) but declined over time with both the standard analysis as well as the bootstrap analysis, indicating a slowing of the rate of convergence to a stable size distribution. This trend was explained in part by the mortality rates,

which increased with time (over the winter), leading to increasingly altered size distributions near the end of the study (Table 1).

### Recruitment

The Quarry site received 12 to 46 recruits total each 2 mo (Table 1), or  $0.22 \pm 0.04$  recruits per resident anemone ( $= 0.44 \pm 0.07$  recruits  $m^{-2}$ ). In contrast, Cudjoe received only about half as many recruits per resident ( $0.13 \pm 0.03$ ) and, due to relatively low population abundance, less than a quarter as many recruits per square meter ( $0.08 \pm 0.02$ , or only 4 to 12 recruits total per 2 mo). On a seasonal basis, recruitment per individual at the Quarry was relatively high in the late summer to fall ( $0.37$  recruits  $ind.^{-1}$  in September and  $0.31$  in November 2014) but declined in January ( $0.16$  recruits  $ind.^{-1}$ ) before increasing slowly throughout the spring ( $0.24$  recruits  $ind.^{-1}$  in March and  $0.26$  recruits  $ind.^{-1}$  in May). At Cudjoe, recruitment rate was  $3\times$  higher during the summer to winter (July 2014–January 2015,  $0.15$ – $0.19$  recruits  $ind.^{-1}$  per 2 mo) than during the spring ( $0.06$  recruits  $ind.^{-1}$  per 2 mo for both March and May 2015).

Table 1. Transition matrices of *Bartholomea annulata* over 1 yr at 2 sites in the Florida Keys (Quarry and Cudjoe) based on 3 size classes: I (1–25  $cm^2$  tentacle crown surface area), II (25.1–50.0  $cm^2$ ), and III ( $>50$   $cm^2$ ). Columns refer to the proportion of individuals in each size class that transitioned to other size classes (rows) during the transition period. Values in **bold** represent parameters with highest elasticity for each year. Cudjoe was not surveyed in Nov 2014 due to a storm; transition values between Sep 2014 and Jan 2015 were interpolated, and recruitment and mortality rates were not reported.  $q_x$ : mortality rate (proportion of individuals that died);  $q_x N$ : number of individuals that died;  $R_n$ : number of recruits (those in the largest size class were excluded from recruitment analyses, see 'Materials and methods' and Fig. 2); N: sample size

	May–Jul 2014			Jul–Sep 2014			Sep–Nov 2014			Nov 2014– Jan 2015			Jan–Mar 2015			Mar–May 2015		
	I	II	III	I	II	III	I	II	III	I	II	III	I	II	III	I	II	III
Quarry																		
I	0.54	0.24	0.17	0.16	0.00	0.04	0.31	0.07	0.03	0.22	0.09	0.03	0.23	0.02	0.01	0.38	0.03	0.02
II	0.18	0.33	0.31	0.41	0.35	0.12	0.22	0.28	0.14	0.31	0.16	0.19	0.20	0.18	0.02	0.31	0.45	0.08
III	0.09	0.38	<b>0.48</b>	0.29	0.62	<b>0.80</b>	0.16	0.48	<b>0.59</b>	0.16	0.33	<b>0.45</b>	0.29	0.38	<b>0.71</b>	0.13	0.32	<b>0.71</b>
$q_x$	0.19	0.05	0.04	0.14	0.03	0.04	0.31	0.17	0.24	0.31	0.42	0.33	0.28	0.42	0.26	0.18	0.20	0.19
$q_x N$	10	1	1	6	1	1	10	7	18	11	23	29	10	19	19	3	6	18
$R_n$	7	5	1	23	13	21	21	25	20	19	9	7	6	15	15	24	13	10
N	53	21	23	44	29	25	32	42	73	36	55	87	35	45	72	16	31	93
Cudjoe																		
I	<b>0.63</b>	0.19	0.32	0.18	0.10	0.00	0.38	0.00	0.00	0.50	0.14	0.03	0.07	0.00	0.04	0.00	0.00	0.03
II	0.26	0.48	0.32	0.53	0.33	0.00	0.25	0.57	0.03	0.50	0.57	0.08	0.33	0.29	0.07	0.67	0.16	0.15
III	0.00	0.09	0.32	0.18	0.47	<b>0.90</b>	0.00	0.18	<b>0.89</b>	0.00	0.29	<b>0.89</b>	0.13	0.43	<b>0.65</b>	0.00	0.37	<b>0.55</b>
$q_x$	0.11	0.24	0.04	0.11	0.10	0.10	0.37	0.25	0.08	0.00	0.00	0.00	0.47	0.28	0.24	0.33	0.47	0.27
$q_x N$	2	5	1	3	3	1	6	7	3	0	0	0	7	6	10	1	9	11
$R_n$	7	5	2	8	4	5	8	4	5	N/A	N/A	N/A	1	4	1	2	2	1
N	19	21	22	28	30	10	16	28	35	6	21	36	15	21	43	3	19	40

### Body growth and shrinkage

Overall, anemone growth rates did not vary significantly between the 2 sites examined (nested ANOVA  $F_{1,306} = 0.824$ ,  $p = 0.37$ ; Cudjoe =  $2.95 \pm 0.40 \text{ cm}^2 \text{ mo}^{-1}$  TCSA; Quarry =  $4.12 \pm 0.40 \text{ cm}^2 \text{ mo}^{-1}$ , Fig. 4). At the Quarry, absolute growth decreased significantly with body size ( $F_{2,212} = 19.46$ ,  $p < 0.001$ ), and all size classes differed significantly from each other (pairwise comparisons,  $p < 0.001$ , Fig. 4). Individuals in Size Class I grew the most rapidly ( $5.51 \pm 0.42 \text{ cm}^2 \text{ mo}^{-1}$ ,  $N = 125$ ), those in Size Class II grew more slowly ( $3.47 \pm 0.62 \text{ cm}^2 \text{ mo}^{-1}$ ,  $N = 86$ ), and those in Size Class III remained relatively stable in size ( $0.96 \pm 0.60 \text{ cm}^2 \text{ mo}^{-1}$ ,  $N = 86$ ). The mean size of individuals changed seasonally, with the body shrinkage of initially large anemones during March to July (warmer months) and growth during July to March (cooler months, Fig. 5 and Fig. S3 in the Supplement).

At Cudjoe, anemone growth rates also decreased significantly with size class (ANOVA,  $F_{2,86} = 3.43$ ,  $p < 0.05$ ) and differed significantly between Size Classes I and III ( $p < 0.05$ ) but not between Size Classes I and II or II and III ( $p = 0.32$  and  $0.41$ , respectively, post

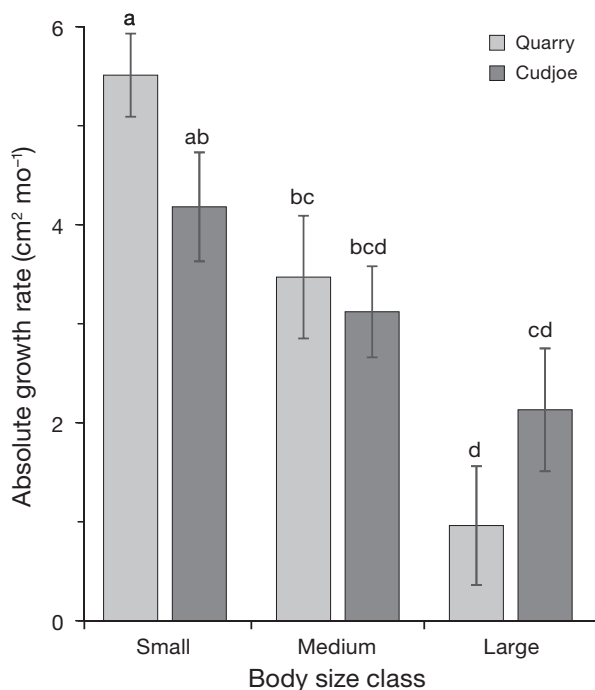


Fig. 4. Variation in absolute growth rates (mean  $\pm$  SE) among 3 size classes of *Bartholomea annulata* at 2 sites in the Florida Keys (Quarry and Cudjoe). Each individual was assigned to a body size class when it initially appeared at the site, and its growth during the entire period that it remained present was used to calculate a monthly growth rate. Bars with the same letter are not significantly different

hoc pairwise tests, Fig. 4). Individuals in Size Class I at Cudjoe grew  $4.18 \pm 0.55 \text{ cm}^2 \text{ mo}^{-1}$  ( $N = 31$ ), those in Size Class II grew  $3.12 \pm 0.46 \text{ cm}^2 \text{ mo}^{-1}$  ( $N = 35$ ), and those in Size Class III grew at only  $2.13 \pm 0.62 \text{ cm}^2 \text{ mo}^{-1}$  ( $N = 25$ ). Similar to the Quarry site, the mean body size of initially large individuals changed seasonally at Cudjoe, with stasis or growth occurring during the cooler months (July–March) and shrinkage occurring during the warmer ones (March–July, Figs. 5 & S3 in the Supplement).

Percent changes in body size likewise did not vary significantly with site but varied significantly among size classes (ANOVA,  $F_{2,303} = 22.47$ ,  $p < 0.001$ ). Individuals in Size Class I at both sites more than doubled their size every 2 mo on average, while those in Size Class III grew only ~11 to 14 % per 2 mo. At the Quarry, percent change in body size for members of Size Class I ( $163.0 \pm 25.8\%$  per 2 mo) was significantly more rapid than that in both Size Class II ( $44.1 \pm 9.0\%$ ) and Size Class III ( $11.9 \pm 5.9\%$ , pairwise comparisons,  $p < 0.05$ ). The same pattern emerged for Cudjoe, with Size Class I ( $104.1 \pm 27.7\%$ ) having significantly more rapid percent growth than Size Class II ( $31.4 \pm 7.0\%$ ) or Size Class III ( $14.6 \pm 4.0\%$ ,  $p < 0.05$ ). Anemones in Size Class III reached a maximum of ~90 cm<sup>2</sup> TCSA in March 2015 at both sites and also in November 2014 at the Quarry (Fig. 5). The Quarry contained larger anemones overall, with >20 individuals that reached >125 cm<sup>2</sup> and 7 of these attaining very large size of >175 cm<sup>2</sup> TCSA. In contrast, at Cudjoe, only 9 anemones became >100 cm<sup>2</sup> TCSA, and all remained <175 cm<sup>2</sup>. Anemones from all 3 initial size classes converged by the end of the year on the largest size class (Fig. 5).

### Mortality and life span

Mortality rates were high at ~20 to 30 % each 2 mo (Cudjoe:  $22.7 \pm 8.7\%$  per 2 mo, range = 12.9–33.9%; Quarry:  $21.3 \pm 4.3\%$  per 2 mo, range = 8.2–34.3%) and did not vary significantly with site except during the final period ending in May 2015, when 18% of individuals at the Quarry and 34% at Cudjoe died ( $Z = 2.25$ ,  $p < 0.05$ ). Mortality rate varied significantly with season at the Quarry (during winter [September–March], ~35 more deaths occurred per 2 mo than during summer [March–September],  $t_4 = 2.99$ ,  $p < 0.05$ ) but not at Cudjoe ( $t_3 = 1.34$ ,  $p = 0.27$ ; potentially caused by lack of field data in November 2014 because of a storm, see 'Materials and methods').

At both sites, only ~30 to 40 % of individuals survived the entire year of study (Fig. 6). At Cudjoe,



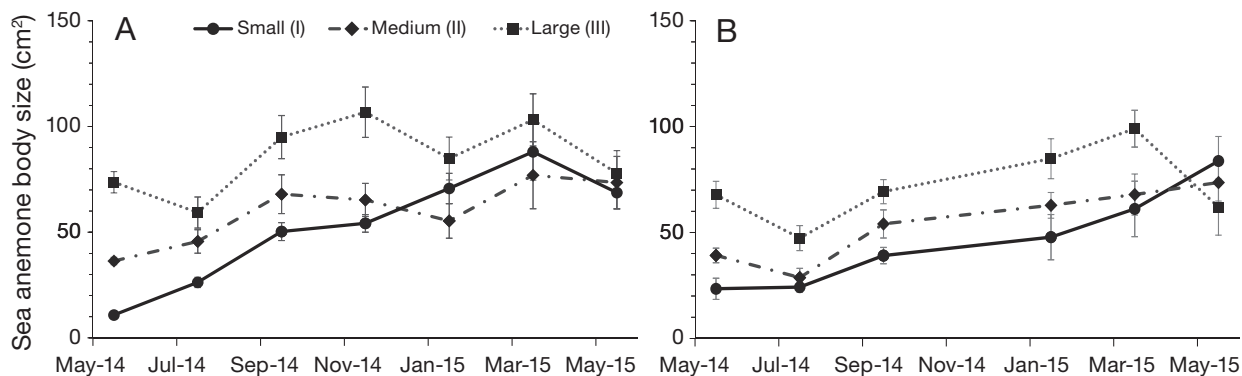


Fig. 5. Variation over 1 yr in the mean body sizes ( $\pm$  SE) of *Bartholomea annulata* from each of 3 initial size classes at 2 sites in the Florida Keys: (A) Quarry, (B) Cudjoe. Data are shown as anemone body sizes during May 2014 in each size class (sample sizes given in Table 1) and how the body sizes of the anemones from those initial groups changed during the study year

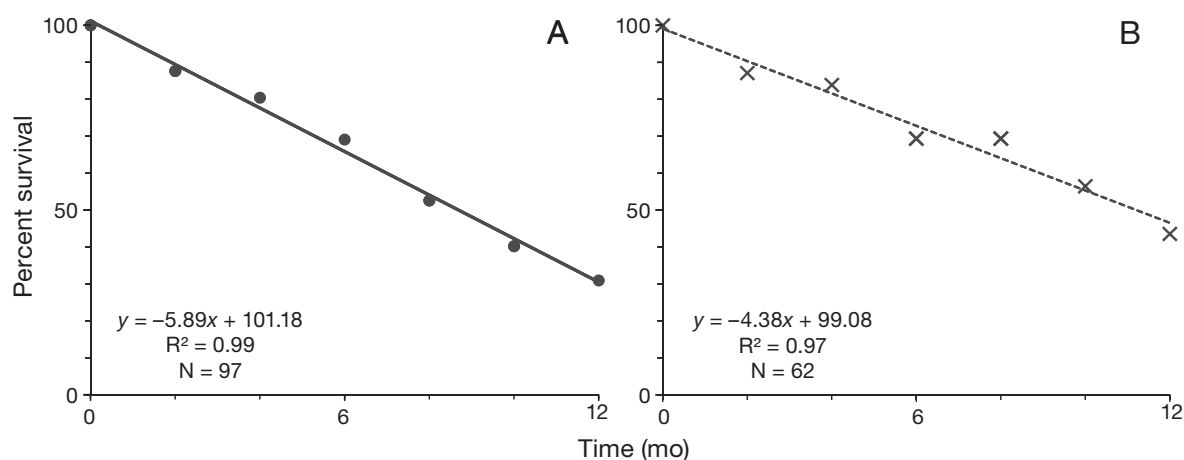


Fig. 6. Dynamic survival curves of corkscrew sea anemones *Bartholomea annulata* at 2 sites in the Florida Keys: (A) Quarry, (B) Cudjoe

about half the population survived for 10 mo; at the Quarry, for only 8 mo. Approximately 1% of individuals from both original populations were projected to survive after ~20 mo. Estimated population turnover times were 6.4 to 15.6 mo, depending on the 2 mo period from which they were calculated. The mean turnover time for sea anemones was 10.3 mo at Cudjoe and only 8.6 mo at the Quarry (Table S3 in the Supplement). During the winter, turnover time decreased to 6.4 mo at the Quarry (November 2014–January 2015), compared to 15.6 mo in summer (May–July 2014). A seasonal pattern did not emerge at Cudjoe, where turnover time decreased throughout the study from 11.0 to 8.3 mo, in parallel with increasing mortality over time at this site.

## DISCUSSION

### Overall patterns

*Bartholomea annulata* appear to be more dynamic than all other populations of coral reef cnidarians examined to date, including stony corals (Hughes & Jackson 1985, Hughes & Tanner 2000, Edmunds 2010), soft corals (Lasker 1990), and other species of sea anemones (Shick 1991, Holbrook & Schmitt 2005, McVay 2015). Our results indicate that they have short lifespans and an individual turnover time of only ~1 yr, with rapid growth to large body size during this short period. These anemones appear to thrive in the northern Keys and at sites with low human impact, where they are abundant and popu-

lations contain high proportions of small individuals, indicating potential recent recruitment, relative to the southern Keys and high-human-impact sites. Furthermore, their rates of dynamic recruitment and body growth are higher in the Middle than in the Lower Keys and in winter vs. summer. Further south in the USVI, these anemones grow more slowly and have higher mortality than in Florida (Nelsen 2008, O'Reilly 2015). These spatial and temporal patterns support the idea that environmental conditions in the northern Caribbean, especially during winter, may enhance the recruitment, growth, and survival of *B. annulata*.

Localized human impacts may cause reductions in coral cover, including from the effects of trampling by tourists (Leujak & Ormond 2008, Krieger & Chadwick 2013), point source pollution such as diesel fuel and sewage (Ormond & Caldwell 1982, Samiullah 1985, Bak 1987, Fabricius 2005), and other anthropogenic disturbances that impact nearshore communities, leading possibly to the observed low coral cover and anemone abundances at high-impact sites in the Keys.

### Recruitment

The rapid recruitment observed at the Quarry relative to the Cudjoe site, in terms of both number of residents and reef surface area, may have been caused in part by the much higher (4×) abundance of resident sea anemones at the Quarry. In terms of recruitment of sexual propagules, the low abundance of spawning adults in the Cudjoe population may lead to both sperm dilution and low fertilization success rate (Levitan et al. 1992), as well as low egg output by the small individuals at that site, as known for other sessile marine invertebrates (Sebens 1981b, Bucklin 1987, Levitan 1989). Clonal replication appears to be uncommon but occurs in *B. annulata* (Jennison 1981, Titus et al. 2015) and correlates with body size in sea anemones (Johnson & Shick 1977, Sebens 1980, Hunter 1984, Bucklin 1987). Thus, the preponderance of large individuals at the Quarry could in part cause higher recruitment at that site relative to Cudjoe, in terms of both sexual and clonal mechanisms. The recruitment rates reported here, as well as abundances of individuals in the smallest anemone size class, both represent low estimates, due to the difficulty of detecting very small cnidarian recruits on rocky substrates (Chadwick-Furman et al. 2000, Goffredo & Lasker 2008, McVay 2015). Many cnidarians self-recruit to coral reefs, causing the local

abundance of large spawning adults to be particularly important to recruitment (Black et al. 1991, Swearer et al. 2002). This may be especially true for highly dynamic sea anemones such as *B. annulata*, in which calculated rates of intrinsic population change ( $\lambda$ ) indicate that their populations may decline rapidly in the absence of local recruitment.

### Body growth and shrinkage

Few studies exist on the growth rates of tropical sea anemones (Shick 1991), and even fewer have examined field populations for more than a few months. Individuals of *B. annulata* exhibit high percent growth relative to other tropical sea anemones but low absolute growth rates. In Moorea, giant sea anemones *Heteractis magnifica* grow  $\sim 0.75$  cm<sup>2</sup> surface area d<sup>-1</sup> with anemonefish present (Holbrook & Schmitt 2005), almost 5× more rapidly than the 0.10 to 14 cm<sup>2</sup> TCSA d<sup>-1</sup> reported here for *B. annulata*. However, fish symbionts augment growth rates in sea anemones (Roopin & Chadwick 2009), and *H. magnifica* without anemonefish grow only  $\sim 2\times$  as rapidly, 0.25 cm<sup>2</sup> d<sup>-1</sup>. In terms of percent change in body size, individuals of *B. annulata* grow more quickly than those of *H. magnifica*, in that they can double their size in <2 mo, depending on initial size, whereas *H. magnifica* requires 12 to 18 mo to do so, possibly because they reach a much larger maximum body size ( $\sim 2\times$  as large as *B. annulata*). In the Red Sea, bulb-tentacle anemones *Entacmaea quadricolor* that host adult anemonefish can grow  $\sim 0.27$  cm<sup>2</sup> TCSA d<sup>-1</sup>, but leathery anemones *H. crispa* that host juvenile anemonefish grow only  $\sim 0.12$  cm<sup>2</sup> TCSA d<sup>-1</sup> (McVay 2015), comparable to growth rates exhibited here by *B. annulata*.

The decrease in growth rate of *B. annulata* with body size observed here under field conditions in Florida is similar to the pattern known for this species at field sites in the USVI and under laboratory conditions (Nelsen 2008, O'Reilly 2015). It also parallels the pattern of decreasing growth with body size in other coral reef sea anemones (McVay 2015) and solitary stony corals (Chadwick-Furman et al. 2000, Goffredo et al. 2004). The percent of individuals that grew in Florida was about twice as high (35–42% per 2 mo) as that in the USVI (10–26% per 3 mo, Nelsen 2008). Conversely, the percent of individuals that shrank was much lower in Florida, only 8 to 21% compared to 18 to 90% per 2 to 3 mo in the USVI (Nelsen 2008). In Florida, rates of stasis (maintenance of stable body size) increased with body size, with

both sites having ~60% of the largest size class remaining within that class over 2 mo, similar to the pattern under laboratory conditions (O'Reilly 2015). In other types of cnidarians, large individuals generally are more stable than are small individuals (Goffredo & Chadwick-Furman 2000, McVay 2015), so the patterns observed here for Florida appear to reflect those of healthy cnidarian populations on coral reefs. In contrast, *B. annulata* populations in the USVI, with their low stability of large individuals as well as low individual growth rates (Nelsen 2008), appear to be occupying less optimal habitat.

Variation in patterns of growth, stasis, and shrinkage in *B. annulata* among the environments examined thus far may be due to several factors. High rates of water flow ( $>10 \text{ cm s}^{-1}$ ) and wave action can damage or dislodge sea anemones and limit their feeding ability by reducing tentacle expansion (Koehl 1977, Shick 1991), causing them to divert energy from growth into healing damaged tissues or into maintaining tentacle expansion in high water flow. However, high water flow also may enhance rates of feeding, waste removal (Koehl 1977, Anthony 1997), and gas exchange in sea anemones (Szczebak et al. 2013). Polyps of *B. annulata* exhibit long, thin tentacles that are more easily deformed by moving water than are the more robust tentacles of some other cnidarians such as *Alcyonium siderium*, which thrive in high-flow and wave-prone environments ( $12\text{--}35 \text{ cm s}^{-1}$ , Sebens 1984), or *Anthopleura* spp., which are also known to thrive in high-flow environments (Koehl 1984). Exposure to relatively low water flow may enhance the ability of *B. annulata* to attain large body size, as observed at the sites examined here, which experienced a wind buffer from Atlantic Ocean storms due to their inshore positions on the leeward side of the Florida Keys. In contrast, smaller individuals have been reported at offshore reefs in the USVI, which experienced high water flow relative to inshore reefs (water flow levels quantified as relative rather than absolute values, Nelsen 2008). Conditions in the laboratory where these anemones exhibit their most rapid growth and largest body sizes include low water flow ( $<2 \text{ cm s}^{-1}$ ) and no wave action (O'Reilly 2015). High seawater temperatures also cause stress in sea anemones and reduce their growth rates (Chomsky et al. 2004a). Growth rates of *B. annulata* correlate negatively with seawater temperatures in the environments examined to date (most rapid growth in the laboratory at  $23.9\text{--}26.8^\circ\text{C}$ , slower growth in Florida at  $26.6\text{--}28.3^\circ\text{C}$  yearly averages, and slowest in the USVI at  $27.6\text{--}31.0^\circ\text{C}$  monthly averages, yearly average  $28.8^\circ\text{C}$

[www.ndbc.noaa.gov/station\\_history.php?station=chav3](http://www.ndbc.noaa.gov/station_history.php?station=chav3)). Finally, these anemones grow more rapidly when fed at least once per week than when starved (O'Reilly 2015), as known for other sea anemones (reviewed in Chomsky et al. 2004b). We conclude that these anemones appear to grow most rapidly under conditions of low water flow, low tropical to subtropical seawater temperatures, and ample food supply.

### Mortality and lifespan

Mortality rates of *B. annulata* observed here (8–34% per 2 mo) were similar to those in the USVI (10–54% per 3 mo, Nelsen 2008) but somewhat higher than under laboratory conditions (3–26% per 2 mo, O'Reilly 2015). These mortality rates are the highest known for a sea anemone, several orders of magnitude greater than for other coral reef anemones (*H. magnifica*: 29% per 3 yr, Holbrook & Schmitt 2005; *H. crispa*:  $17\text{--}25\% \text{ yr}^{-1}$ , *E. quadricolor*:  $11\text{--}28\% \text{ yr}^{-1}$ , McVay 2015). Based on their rapid rates of recruitment and mortality in both types of field environments examined thus far (Florida and USVI), as well as rapid mortality in laboratory culture (O'Reilly 2015), we conclude that *B. annulata* exhibit high rates of population turnover of ~1 to 2 yr and thus appear to be weedy anemones. The weedy nature of this anemone may relate in part to its small body size relative to the other coral reef anemones for which mortality has been assessed (see this paragraph). Laboratory cultures reveal that lifespan in this species may be determined in part by internally controlled senescence, in that individuals undergo gradual shrinkage prior to death (O'Reilly 2015), similar to the process of senescence in some weedy corals (Rinkevich & Loya 1986).

### Management implications and conclusions

The dynamic nature of *B. annulata* populations indicates that they may be suitable for sustained harvest, in that high rates of recruitment allow some populations to recover rapidly from the loss of individuals. However, because they have short lifespans, their populations require a frequent influx of recruits to maintain population size, as indicated by values of  $\lambda < 1$  that reveal population decline during all examined periods when recruitment is not included. Field populations thus may grow rapidly due to rapid recruitment and body growth (present study) and

attainment of sexual maturity at small body size (Jennison 1981), but they also can rapidly decline due to the short lifespans of individuals and subsequently high mortality.

Stasis of the largest individuals exerts the most influence on population growth, so restrictions on the harvest of large individuals could support the stability of populations. Larger anemones, when associated with cleaner shrimp, also receive more client fish visitation than do smaller anemones (Huebner & Chadwick 2012a), thus contributing to enhancement of fish health and diversity on reefs. Large anemones typically produce more sexual propagules than do small ones and potentially contribute to high local recruitment (Sebens 1981b, Bucklin 1987, Levitan 1989, Kapela & Lasker 1999). Asexual reproduction usually requires a minimum body size in sea anemones (Minasian 1982). However, small individuals are also needed to eventually attain reproductive size and replace large, old individuals that are near the end of their natural lifespans. Collection of only a portion of medium-sized anemones above the size at sexual maturity but not near maximum body size (i.e. a slot limit) would allow both the smallest and largest individuals to remain and replenish populations. This type of slot limit has been applied to the management of some fish populations (Eder 1984, Kurzawski & Durocher 1993, Wilde 1997). Because the dynamics of *B. annulata* populations vary with environmental conditions (see this and previous paragraph), management of collection for the ornamental trade ideally should be tailored on a site-by-site basis. For example, at sites with high water flow, resident polyps may replace collected anemones more slowly than do residents at sites with calmer water conditions; relatively cool-temperature sites also may support more stable populations and suffer less mortality and shrinkage than do areas subject to high temperature spikes.

Designating protected areas for these anemones would allow protected populations to replenish nearby harvested areas. Scott et al. (2011) observed a >500% increase in the abundance of giant sea anemones *E. quadricolor* in Australia over 14 yr, due in part to long-term protection from harvest. Non-fished reserves on the Great Barrier Reef (Harrison et al. 2012) and in Papua New Guinea (Almany et al. 2013) produce up to 50% of the recruits of important species on both reserve and fished reefs. Strategically located reserves would allow the survival of large anemones to support nearby downstream communities by supplying recruits to areas where this species is collected.

A seasonal harvest closure of 2 to 3 mo yr<sup>-1</sup> also would allow reproducing individuals of this species to spawn annually before collection. Individuals of *B. annulata* spawn twice each year in Florida, in November and April (Jennison 1981). Protection of these breeding seasons would maximize reproductive output by this species and provide a window of time for the settlement and growth of new recruits.

The highly dynamic nature of individuals of *B. annulata* has important implications for the mutualistic network in which this anemone is a hub (Cantrell et al. 2015). The crustacean associates of *B. annulata* are expected to be highly dynamic in terms of migration among host anemones (as known for anemone-shrimps in other systems, Chadwick et al. 2008) as they depart from senescing individuals and colonize recently recruited hosts on the reef. The client fishes that visit these cleaning stations likewise are expected to be flexible behaviorally in terms of where they search for cleaner shrimps associated with this ephemeral host.

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#### LITERATURE CITED

- ✦ Almany GR, Hamilton RJ, Bode M, Matawai M and others (2013) Dispersal of grouper larvae drives local resource sharing in a coral reef fishery. *Curr Biol* 23:626–630
- ✦ Anthony KRN (1997) Prey capture by the sea anemone *Metridium senile* (L.): effects of body size, flow regime, and upstream neighbors. *Biol Bull* 192:73–86
- ✦ Bak RPM (1987) Effects of chronic oil pollution on a Caribbean coral reef. *Mar Pollut Bull* 18:534–539
- ✦ Batchelder HP, Gonor JJ (1981) Population characteristics of the intertidal green sea anemone *Anthopleura xanthogrammica* on the Oregon coast. *Estuar Coast Shelf Sci* 13: 235–245
- ✦ Bierzychudek P (1999) Looking backwards: assessing the projections of a transition matrix model. *Ecol Appl* 9: 1278–1287

- Black KP, Moran PJ, Hammond LS (1991) Numerical models show coral reefs can be self-seeding. *Mar Ecol Prog Ser* 74:1–11
- Briones-Fourzán P, Pérez-Ortiz M, Negrete-Soto F, Barradas-Ortiz C, Lozano-Álvarez E (2012) Ecological traits of Caribbean sea anemones and symbiotic crustaceans. *Mar Ecol Prog Ser* 470:55–68
- Bruckner AW (2005) The importance of the marine ornamental reef fish trade in the wider Caribbean. *Rev Biol Trop* 53:127–137
- Bshary R (2003) The cleaner wrasse, *Labroides dimidiatus*, is a key organism for reef fish diversity at Ras Mohammed National Park, Egypt. *J Anim Ecol* 72:169–176
- Bshary R, Oliveira RF, Oliveira TSF, Canário AVM (2007) Do cleaning organisms reduce the stress response of client reef fish? *Front Zool* 4:21
- Bucklin A (1987) Adaptive advantages of patterns of growth and asexual reproduction of the sea anemone *Metridium senile* (L.) in intertidal and submerged populations. *J Exp Mar Biol Ecol* 110:225–243
- Cantrill CE, Henry RP, Chadwick NE (2015) Nitrogen transfer in a Caribbean mutualistic network. *Mar Biol* 162:2327–2338
- Chadwick NE, Arvedlund M (2005) Abundance of giant sea anemones and patterns of association with anemonefish in the northern Red Sea. *J Mar Biol Assoc UK* 85:1287–1292
- Chadwick NE, Đuriš Z, Horká I (2008) Biodiversity and behavior of shrimps and fishes symbiotic with sea anemones in the Gulf of Aqaba, northern Red Sea. In: Por FD (ed) *Aqaba- Eilat, the improbable gulf: environment, biodiversity and preservation*. The Hebrew University Magnes Press, Jerusalem, p 209–223
- Chadwick-Furman NE, Goffredo S, Loya Y (2000) Growth and population dynamic model of the reef coral *Fungia granulosa* (Klunzinger, 1879) at Eilat, northern Red Sea. *J Exp Mar Biol Ecol* 249:199–218
- Chomsky O, Kamenir Y, Hyams M, Dubinsky Z, Chadwick-Furman NE (2004a) Effects of temperature on growth rate and body size in the Mediterranean Sea anemone *Actinia equina*. *J Exp Mar Biol Ecol* 313:63–73
- Chomsky O, Kamenir Y, Hyams M, Dubinsky Z, Chadwick-Furman NE (2004b) Effects of feeding regime on growth rate in the Mediterranean Sea anemone *Actinia equina* (Linnaeus). *J Exp Mar Biol Ecol* 299:217–229
- Cohen J (1988) *Statistical power analysis for the behavioral sciences*, 2nd edn. Lawrence Erlbaum Associates, Hillsdale, NJ
- Diamond JM (1969) Avifaunal equilibria and species turnover rates on the Channel Islands of California. *Proc Natl Acad Sci USA* 64:57–63
- Eder S (1984) Effectiveness of an imposed slot length limit of 12.0–14.9 inches on largemouth bass. *N Am J Fish Manage* 4:469–478
- Edmunds PJ (2010) Population biology of *Porites astreoides* and *Diploria strigosa* on a shallow Caribbean reef. *Mar Ecol Prog Ser* 418:87–104
- Erni Cassola G, Pacheco MSC, Barbosa MC, Hansen DM, Ferreira CEL (2016) Decline in abundance and health state of an Atlantic subtropical gorgonian population. *Mar Pollut Bull* 104:329–334
- Fabricius KE (2005) Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. *Mar Pollut Bull* 50:125–146
- Goffredo S, Chadwick-Furman NE (2000) Abundance and distribution of mushroom corals (Scleractinia: Fungiidae) on a coral reef at Eilat, northern Red Sea. *Bull Mar Sci* 66:241–254
- Goffredo S, Lasker HR (2008) An adaptive management approach to an octocoral fishery based on Beverton-Holt model. *Coral Reefs* 27:751–761
- Goffredo S, Mattioli G, Zaccanti F (2004) Growth and population dynamics model of the Mediterranean solitary coral *Balanophyllia europaea* (Scleractinia, Dendrophylliidae). *Coral Reefs* 23:433–443
- Gotelli NJ (1991) Demographic models for *Leptogorgia virgulata*, a shallow-water gorgonian. *Ecology* 72:457–467
- Graham NAJ, Ainsworth TD, Baird AH, Ban NC and others (2011) From microbes to people: tractable benefits of no-take areas for coral reefs. *Oceanogr Mar Biol Annu Rev* 49:117–148
- Grutter AS, Murphy JM, Choat JH (2003) Cleaner fish drives local fish diversity on coral reefs. *Curr Biol* 13:64–67
- Gulland JA (1964) Catch per unit effort as a measure of abundance. *Rapp P-V Reun Cons Int Explor Mer* 155:8–14
- Hanski I (1999) *Metapopulation ecology*. Oxford University Press, New York, NY
- Harrison HB, Williamson DH, Evans RD, Almany GR and others (2012) Larval export from marine reserves and the recruitment benefit for fish and fisheries. *Curr Biol* 22:1023–1028
- Hattori A (2002) Small and large anemonefishes can coexist using the same patchy resources on a coral reef before habitat destruction. *J Anim Ecol* 71:824–831
- Hattori A (2006) Vertical and horizontal distribution patterns of the giant sea anemone *Heteractis crispata* with symbiotic anemonefish on a fringing coral reef. *J Ethol* 24:51–57
- Hirose Y (1985) Habitat, distribution and abundance of coral reef sea-anemones (Actiniidae and Stichodactylidae) in Sesoko Island, Okinawa, with notes on expansion and contraction behavior. *Galaxea* 4:113–127
- Hobbs JPA, Frisch AJ, Ford BM, Thums M, Saenz-Agudelo P, Furby KA, Berumen ML (2013) Taxonomic, spatial and temporal patterns of bleaching in anemones inhabited by anemonefishes. *PLOS ONE* 8:e70966
- Holbrook SJ, Schmitt RJ (2005) Growth, reproduction and survival of a tropical sea anemone (Actinaria): benefits of hosting anemonefish. *Coral Reefs* 24:67–73
- Huebner LK, Chadwick NE (2012a) Reef fishes use sea anemones as visual cues for cleaning interactions with shrimp. *J Exp Mar Biol Ecol* 416–417:237–242
- Huebner LK, Chadwick NE (2012b) Patterns of cleaning behavior on coral reef fish by the anemoneshrimp *Ancylomenes pedersoni*. *J Mar Biol Assoc UK* 92:1557–1562
- Huebner LK, Dailey B, Titus BM, Khalaf M, Chadwick NE (2012) Host preference and habitat segregation among Red Sea anemonefish: effects of sea anemone traits and fish life stages. *Mar Ecol Prog Ser* 464:1–15
- Hughes TP (1984) Population dynamics based on individual size rather than age: a general model with a coral reef example. *Am Nat* 123:778–795
- Hughes TP (1994) Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265:1547–1551
- Hughes TP, Jackson JBC (1985) Population dynamics and life histories of foliaceous corals. *Ecol Monogr* 55:141–166
- Hughes TP, Tanner JE (2000) Recruitment failure life histories and long-term decline of Caribbean corals. *Ecology* 81:2250–2263

- Hunter T (1984) The energetics of asexual reproduction: pedal laceration in the symbiotic sea anemone *Aiptasia pulchella* (Carlgren 1943). *J Exp Mar Biol Ecol* 83: 127–147
- Jennison BL (1981) Reproduction in three species of sea anemones from Key West, Florida. *Can J Zool* 59: 1708–1719
- Johnson LJ, Shick JM (1977) Effects of fluctuating temperature and immersion on asexual reproduction in the intertidal sea anemone *Haliplanella luciae* (Verrill) in laboratory culture. *J Exp Mar Biol Ecol* 28:141–149
- Jokiel PL, Coles SL (1974) Effects of heated effluent on hermatypic corals at Kahoe Point, Oahu. *Pac Sci* 28:1–18
- Kapela W, Lasker HR (1999) Size-dependent reproduction in the Caribbean gorgonian *Pseudoplexaura porosa*. *Mar Biol* 135:107–114
- Kaplan EL, Meier P (1958) Nonparametric estimation from incomplete observations. *J Am Stat Assoc* 53:457–481
- Kaplan E, Peterson R, Kaplan S (1999) A field guide to coral reefs: Caribbean and Florida. Houghton Mifflin Harcourt, New York, NY
- Koehl MAR (1977) Effects of sea anemones on the flow forces they encounter. *J Exp Biol* 69:87–105
- Koehl MAR (1984) How do benthic organisms withstand moving water? *Am Zool* 24:57–70
- Krieger JR, Chadwick NE (2013) Recreational diving impacts and the use of pre-dive briefings as a management strategy on Florida coral reefs. *J Coast Conserv* 17:179–189
- Kurzawski KF, Durocher PP (1993) Effects of a slot length limit on largemouth bass in a newly-opened Texas reservoir. *Proc Annu Conf Southeast Assoc Fish Wildl Agen* 47:711–719
- Lasker HR (1990) Clonal propagation and population dynamics of a gorgonian coral. *Ecology* 71:1578–1589
- LeGore RS, Hardin MP, Ter-Ghazaryan D (2005) Organization and operation of the marine ornamental fish and invertebrate export fishery in Puerto Rico. *Rev Biol Trop* 53:145–153
- Leslie PH (1945) On the use of matrices in certain population mathematics. *Biometrika* 33:183–212
- Leujak W, Ormond RFG (2008) Reef walking on Red Sea reef flats—quantifying impacts and identifying motives. *Ocean Coast Manage* 51:755–762
- Levitan DR (1989) Density-dependent size regulation in *Diadema antillarum*: effects on fecundity and survivorship. *Ecology* 70:1414–1424
- Levitan DR, Sewell MA, Chia FS (1992) How distribution and abundance influence fertilization success in the sea urchin *Strongylocentrotus franciscanus*. *Ecology* 73:248–254
- Lirman D (2003) A simulation model of the population dynamics of the branching coral *Acropora palmate*. Effects of storm intensity and frequency. *Ecol Modell* 161:169–182
- Mahnken C (1972) Observations on cleaner shrimps of the genus *Periclimenes*. *Sci Bull Nat Hist Mus Los Angeles County* 14:71–83
- Mascaro M, Rodriguez-Pestana L, Chiappa-Carrara X, Simoes N (2012) Host selection by the cleaner shrimp *Ancylomenes pedersoni*: Do anemone host species prior experience or the presence of conspecific shrimp matter? *J Exp Mar Biol Ecol* 413:87–93
- Maunder MN, Sibert JR, Fonteneau A, Hampton J, Kleiber P, Harley SJ (2006) Interpreting catch per unit effort data to assess the status of individual stocks and communities. *ICES J Mar Sci* 63:1373–1385
- Mazza G, Aquiloni L, Inghilesi AF, Giuliani C and others (2015) Aliens just a click away: the online aquarium trade in Italy. *Manage Biol Invasions* 6:253–261
- McVay MJ (2015) Population dynamics of clownfish sea anemones: patterns of decline, symbiosis with anemonefish, and management for sustainability. MSc thesis, Auburn University, AL
- Minasian LL (1982) The relationship of size and biomass to fission rate in a clone of the sea anemone *Haliplanella luciae* (Verrill). *J Exp Mar Biol Ecol* 58:151–162
- Mitchell JS (2003) Mobility of *Stichodactyla gigantea* sea anemones and implications for resident false clown anemonefish *Amphiprion ocellaris*. *Environ Biol Fishes* 66:85–90
- Nadon MO, Stirling G (2006) Field and simulation analyses of visual methods for sampling coral cover. *Coral Reefs* 25:177–185
- Nelsen M (2008) Population dynamic modeling of the corkscrew sea anemone *Bartholomea annulata* on Caribbean coral reefs. MS thesis, Auburn University, AL
- O'Reilly E (2015) Demography of the corkscrew sea anemone *Bartholomea annulata* in the Florida Keys and in laboratory culture: a giant sea anemone under pressure. MSc thesis, Auburn University, AL
- Ormond RFG, Caldwell S (1982) The effect of oil pollution on the reproduction and feeding behavior of the sea anemone *Actinia equina*. *Mar Pollut Bull* 13:118–122
- Ottaway JR (1978) Population ecology of the intertidal anemone *Actinia tenebrosa*. I. Pedal locomotion and intraspecific aggression. *Mar Freshw Res* 29:787–802
- Ottaway JR (1979) Population ecology of the intertidal anemone *Actinia tenebrosa*. III. Dynamics and environmental factors. *Mar Freshw Res* 30:41–62
- Pearse VB (1974) Modification of sea anemone behavior by symbiotic zooxanthellae: expansion and contraction. *Biol Bull* 147:641–651
- Porat D, Chadwick-Furman NE (2004) Effects of anemonefish on giant sea anemones: expansion behavior growth and survival. *Hydrobiologia* 530-531:513–520
- Rhyne A, Rotjan R, Bruckner A, Thusty M (2009) Crawling to collapse: ecologically unsound ornamental invertebrate fisheries. *PLOS ONE* 412:e8413
- Rhyne AL, Thusty MF, Schofield PJ, Kaufman L, Morris JA Jr, Bruckner AW (2012) Revealing the appetite of the marine aquarium fish trade: the volume and biodiversity of fish imported into the United States. *PLOS ONE* 75: e35808
- Rinkevich B, Loya Y (1986) Senescence and dying signals in a reef building coral. *Experientia* 42:320–322
- Roberts CM (1995) Effects of fishing on the ecosystem structure of coral reefs. *Conserv Biol* 9:988–995
- Roopin M, Chadwick NE (2009) Benefits to host sea anemones from ammonia contributions of resident anemonefish. *J Exp Mar Biol Ecol* 370:27–34
- Samiullah Y (1985) Biological effects of marine oil pollution. *Oil Petrochem Poll* 2:235–264
- Shuman CS, Hodgson G, Ambrose RF (2005) Population impacts of collecting sea anemones and anemonefish for the marine aquarium trade in the Philippines. *Coral Reefs* 24:564–573
- Scott A, Malcolm HA, Damiano C, Richardson DL (2011) Long-term increases in abundance of anemonefish and their host sea anemones in an Australian marine protected area. *Mar Freshw Res* 62:187–196
- Sebens KP (1980) The regulation of asexual reproduction

- and indeterminate body size in the sea anemone *Anthopleura elegantissima* (Brandt). *Biol Bull* 158:370–382
- ✦ Sebens KP (1981a) The allometry of feeding energetics and body size in three sea anemone species. *Biol Bull* 161: 152–171
- ✦ Sebens KP (1981b) Reproductive ecology of the intertidal sea anemones *Anthopleura xanthogrammica* (Brandt) and *A. elegantissima* (Brandt): body size, habitat, and sexual reproduction. *J Exp Mar Biol Ecol* 54:225–250
- ✦ Sebens KP (1981c) Recruitment in a sea anemone population: juvenile substrate becomes adult prey. *Science* 213: 785–787
- ✦ Sebens KP (1982) Recruitment and habitat selection in the intertidal sea anemones, *Anthopleura elegantissima* (Brandt) and *A. xanthogrammica* (Brandt). *J Exp Mar Biol Ecol* 59:103–124
- ✦ Sebens KP (1984) Water flow and coral colony size: inter-habitat comparisons of the octocoral *Alcyonium siderium*. *Proc Natl Acad Sci USA* 81:5473–5477
- ✦ Sebens KP, DeRiemer K (1977) Diel cycles of expansion and contraction in coral reef anthozoans. *Mar Biol* 43: 247–256
- Shick JM (1991) A functional biology of sea anemones. Chapman & Hall, London
- Silbiger NJ, Childress MJ (2008) Interspecific variation in anemone shrimp distribution and host selection in the Florida Keys (USA): implications for marine conservation. *Bull Mar Sci* 83:329–345
- Swearer SE, Shima JS, Hellberg ME, Thorrold SR and others (2002) Evidence of self-recruitment in demersal marine populations. *Bull Mar Sci* 70:251–271
- ✦ Szczebak JT, Henry RP, Al-Horani FA, Chadwick NE (2013) Anemonefish oxygenate their anemone hosts at night. *J Exp Biol* 216:970–976
- ✦ Titus BM, Daly M, Exton DA (2015) Temporal patterns of Pederson shrimp (*Ancylomenes pedersoni* Chace 1958) cleaning interactions on Caribbean coral reefs. *Mar Biol* 162:1651–1664
- ✦ Waldie PA, Blomberg SP, Cheney KL, Goldizen AW, Grutter AS (2011) Long-term effects of the cleaner fish *Labroides dimidiatus* on coral reef fish communities. *PLOS ONE* 6: e21201
- ✦ Wilde GR (1997) Largemouth bass fishery responses to length limits. *Fisheries* 22:14–23
- ✦ Zaragoza WJ, Krediet CJ, Meyer JL, Canas G, Ritchie KB, Teplitski M (2014) Outcomes of infections of sea anemone *Aiptasia pallida* with *Vibrio* spp. pathogenic to corals. *Microb Ecol* 68:388–396

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