Demography of the corkscrew sea anemone *Bartholomea annulata* in the Florida Keys and in laboratory culture: A giant sea anemone under pressure

by

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A thesis submitted to the Graduate Faculty of
Auburn University
in partial fulfillment of the
requirements for the Degree of
Master of Science

Auburn, Alabama
December 12, 2015

Keywords:
Life history, corkscrew sea anemone, Florida Keys, size-based transition matrices,
sea anemone growth, coral reef

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Abstract

The successful management of species requires information on their patterns of distribution, abundance, and population dynamics. Demographic studies are important for gauging how environmental conditions impact populations; individuals in declining populations may experience low viability as revealed by low recruitment and/or high mortality, indicating potential thresholds for population recovery and key parameters to focus on for sustainable management. Giant corkscrew sea anemones *Bartholomea annulata* are common throughout the Caribbean Sea, and also are popular commodities in the ornamental aquarium trade, but almost nothing is known about their population dynamics. The harvest of this anemone for the aquariums is largely uncontrolled in the Florida Keys, and therefore detailed population information is needed to form a scientific basis for effective management. Here, I describe the structure of 6 populations in the Florida Keys, and the dynamics of 2 of these populations over 1 year (May 2014 – May 2015). I also present the dynamics of a population cultured under laboratory conditions, which were examined to determine the maximal growth rates and life-spans in this species under optimal culture conditions.

Study sites were selected in 3 regions of the Florida Keys (Upper, Middle, and Lower), and at 2 levels of human impact within each region. The Upper Keys sites exhibited significantly higher coral cover and anemone abundance, as well as a larger proportion of small, recently-recruited anemones than did sites in the other 2 regions, indicating potentially more stable populations. Low-impact sites also had significantly more coral cover and anemone abundance than did high-impact sites in both the Upper and Middle Keys, but not in the Lower Keys. At the 2 repeat-survey sites, anemone growth rate decreased significantly with body size; small individuals grew 2-2.5x as rapidly as did large individuals in terms of percent growth in tentacle crown surface area (TCSA). In laboratory culture, the percent growth rates of small individuals were even more rapid, up to 15x more than for large anemones. Overall growth was slower in the field than in lab, with individuals growing on average 3-4 cm^2 mo^{-1} TCSA in the field and 7-8 cm^2 mo^{-1} under laboratory conditions. Under both types of conditions, individuals slowed their growth as they neared maximal body sizes of 100 – 150 cm^2 TCSA. Large, relatively old individuals exhibited signs of senescence after they reached peak body size, in terms of shrinkage over several census periods prior to death. Only 33-42% of individuals survived the entire year of study in the field, indicating rapid population turnover of ~1 years, with most mortality occurring in very small or large individuals. Individual lifespans appeared to be longer under laboratory conditions, but still only slightly over half (54%) of individuals survived the entire year of laboratory study.

I conclude that field populations of this sea anemone are highly dynamic in terms of their rates of growth, shrinkage, mortality and recruitment; lifespan is short and population turnover is rapid, on the scale of about a year. Under optimal conditions in the laboratory, this sea anemone has the potential to grow rapidly when small, stops growing after reaching about 100 – 150 cm^2 TCSA, and then gradually shrinks before death; individuals show little to no locomotion under the conditions examined here. Based on these trends, I make the following management recommendations for the harvest of this species: (1) implement a slot limit in which only medium-sized individuals are harvested, (2) limit harvest seasonally to avoid the spawning season each year, and (3) manage marine reserves to protect some populations from harvest.

Acknowledgments

I would like to express my utmost gratitude and appreciation to Dr. Nanette E. Chadwick, first, for the opportunity to study at Auburn and second for her guidance, encouragement, and reassurance throughout my time here. My thesis would not be possible without her advice and dedication to this research and her students. Secondly, I would like to thank my other committee members Dr. Steve Dobson and Dr. Mary Mendonca for their helpful discussions and constructive suggestions to my thesis. I would like to thank Dr. Steve Kempf for his advice and use of his oven.

I would like to thank the members of the Chadwick lab; Jess Gilpin and Mark Stuart for help with field research as well as tolerating my rantings and lab distractions, Matt McVay for thesis discussion, and Channing Cantrell and Bobbie Renfro for all their help in lab. I would like to thank my parents, Patrick and Lynn O‘Reilly for their love, patience, and support throughout my life, as well as my siblings, Colleen, Jack, and Finn for all their support. I would like to thank Jonathan Meador and all my other friends; without their support it would have stretched this out forever.

I want to thank Dr. Bill Fitt of the University of Georgia and the Key Largo Marine Research Laboratory for giving me a place to crash when I made last-minute trips to the Keys because the weather was “right”. I would like to thank the Auburn University Graduate School with their internal grant, as well as the Richard Gilder Graduate School of the American Museum of Natural History, with their Lerner Gray Marine Research Grant, for their monetary support.

Lastly, but most importantly, I want to thank God for the perseverance to finish this project and the strength to ask for help when I needed it.

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List of Abbreviations

TCSA	Tentacle Crown Surface Area
FWC	Florida Fish and Wildlife Conservation Commission
ODD	Oral Disc Diameter
PDD	Pedal Disc Diameter
W_w	Wet Weight
W_d	Dry Weight

Chapter I

Demographic patterns in response to fishing pressure: A look at the corkscrew anemone *Bartholomea annulata*

Changes in the size and structure of organismal populations form the basis for many ecological studies, and can support the understanding of causal factors for past demographic trends, as well as allow the preparation of management plans to address future developments or disturbances in populations (Jackson and Hughes 1985, Ogden 1985, Syms and Jones 2000, Brys et al. 2004, Halford et al. 2004, Smith et al. 2005). Demographic studies also are often used to gauge how environmental conditions and human activity impact populations, and are critical to managing declining populations and potentially in aiding their recovery (Sauvajot et al 1998, Brys et al. 2004, Halford et al. 2004, Babcock et al. 2010). Euler (1760) and Sharpe and Lotka (1911) showed early on that certain life history characteristics are determined by organismal age, thus establishing the importance of determining organismal age in population studies. Patrick Holt Leslie (1945) created a now-classic matrix model to represent change in populations if the ages of individuals are known. Leonard Lefkovitch (1965) modified Leslie's matrix to use life stages to classify populations, instead of equal-length age classes. He found that certain population characteristics could be predicted based on body size class, opening the way for the matrix analysis of organisms for whom age was not easily determined.

The demography of marine invertebrates is often studied using this type of stage- or size-based model, rather than one based on age, because many species lack hard body parts for growth-ring age determination (Sauer and Slade 1986). Especially, in some corals and sea anemones, individuals can shrink, fission, or fusion, resulting in a decoupling of individual size and age (Hughes 1984, Hughes and Jackson 1985, Shick 1991, Hughes and Tanner 2000, Tanner 2001, Chomsky et al. 2004, Nelsen 2008). These events potentially result in some individuals decreasing in size with age (due to fission or shrinkage), or increasing due to factors unrelated to growth rate (fusion of separate individuals), and therefore the need to classify them by size/stage rather than age, because age and size are decoupled.

The corkscrew sea anemone *Bartholomea annulata* is a familiar organism throughout the Caribbean, and like all sea anemones, individuals exhibit body shrinkage so the age of individual cannot be determined from size. They are among the largest Caribbean sea anemones, reaching 30 cm in tentacle crown diameter (Kaplan et al. 1999). This giant anemone is an important species for consideration of demographic patterns, because it contributes to the aesthetic value of reefs for tourism, and also plays a key ecological role in these shallow communities by hosting a number of symbiotic crustaceans. Several species of anemoneshrimps, including *Periclimenes pedersoni,* the major Caribbean cleaner shrimp, associate with *B. annulata* as obligate symbionts (Mahnken 1972, Silbiger and Childress 2008, Briones-Forzan et al. 2012, Mascaro et al. 2012). These giant anemones serve as a visual cue to attract client fishes for cleaning interactions, and thus are essential hubs in the mutualistic network on coral reefs centered around parasite cleaning behavior (Huebner and Chadwick 2012). In Honduras, the body size of *B. annulata* anemones and the number of cleaner shrimps hosted affects the rate of ectoparasite removal from important coral reef fishes such as labrids (wrasses) and serranids (groupers, Titus et al. 2015), so the body size of these anemones is relevant to flow-on ecological processes on coral reefs.

Florida maintains the largest ornamental fishery in the USA, in terms of species and landings (Rhyne et al. 2009). Corkscrew anemones *B. annulata* have become popular organisms in this trade, partly due to their low maintenance needs and low level of aggressive behavior toward other aquarium inhabitants, as well as the generally increasing demand for western Atlantic species (Bruckner 2005). The potential exists for overfishing of targeted reef organisms in this trade, especially as there are few collection limits on season, number, or body size of in Florida. Agencies that control the commercial collection of *B. annulata* have assumed that these anemones have high rates of fecundity and low population turnover, so that intense harvest won't pose a problem (Chiappone et al. 2001, Nelson 2008). However, intensive harvest, even for a short period each year, may not be sustainable for populations of this sea anemone. Jennison (1981) found that individuals are hermaphroditic and reproduce both asexually and sexually; twice each year, they release a large number of small eggs (100-200 μm diameter) and sperm in broadcast spawning for external fertilization. As numbers of these anemones dwindle, the odds of gametes encountering each other for successful external fertilization become slim (Levitan 1992). The resulting planktotrophic planula larvae also are susceptible to high rates of mortality due to predation and starvation. Recruitment rates of *B. annulata* from sexually-produced larvae thus may be low, and are unknown in relation to the contributions from asexually-produced buds. Some populations at St. Thomas may receive fairly high recruitment of 0.17 individuals per square meter per year (Nelsen 2008), but rates are unknown in Florida and other Caribbean regions.

Rates of mortality are high for adult anemones as well; in a one-year study in the U.S. Virgin Islands, mortality was 10-54% per 3 months for individuals of *B. annulata*, with only a 5% survival rate after 2 years (Nelsen 2008). The monitored population had such high turnover of individuals (every 1-2 years) that it depended on frequent recruitment for replenishment. Recruitment appears to be largely local from the natal reef, and thus may be determined mostly by local population density (Nelsen 2008), similar to the dynamics of some acroporid corals (Hughes et al. 2000) and other reef cnidarians and fishes (Jones et al. 1999, Almany et al. 2007, Underwood et al. 2009). If this pattern also occurs for populations in Florida, then intensive ornamental fishing for *B. annulata* could lead to local densities below thresholds for replenishment, resulting in population crashes and local extinctions.

The overall objective of this thesis was to investigate the demographics of corkscrew sea anemones *B. annulata*, including their population size structure and rates of change in body size (growth and shrinkage), recruitment, and mortality, both in field populations in the Florida Keys, and in a laboratory setting.

Chapter II describes the dynamics of 2 populations of *B. annulata* in the Florida Keys that were examined every 2 months for 1 year, plus the static population structure of another 4 populations. Study sites were selected in 3 regions of the Keys (Upper, Middle, and Lower) and at 2 levels of human impact within each region. The populations were divided into 3 size classes and transition matrices were created to determine the relative importance of each cell in the matrix to population size. Growth, recruitment, and mortality rates were determined at the 2 repeat-survey sites, and coral cover, abundance, and size frequency was compared among all 6 field sites.

Chapter III focuses on a population of *B. annulata* individuals that were cultured in a laboratory setting, where they were supplied with high levels of both food and irradiance, and exposed to optimized environmental conditions of temperature, salinity, and water flow. The laboratory population was divided into 4 size classes, in contrast to only 3 in the field, because they reached relatively larger body sizes in the lab. Growth, mortality, and locomotion rates were determined, and evidence of individual senescence was recorded. Relationships among linear measures of body size (1-dimensional length, and in some cases, 2-dimensional area of the oral disk, pedal disk, tentacle crown, and column) and the 3-dimensional measure of body mass (both wet and dry) were established to allow comparisons with measures used in previous studies, and to obtain baseline equations of body size relationships, for future investigations on this anemone species.

Information obtained from both the lab and field populations was compared in both chapters, and synthesized to create a series of recommendations for the sustainable management of populations of this important sea anemone.

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Chapter II

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

Abstract

Giant corkscrew sea anemones *Bartholomea annulata* are common throughout the Caribbean Sea, and are important ecologically as major hosts to cleaner shrimp which remove ectoparasites from diverse reef fishes. These anemones are also popular commodities in the ornamental aquarium trade, but their fishery is largely uncontrolled. Demographic studies are needed to understand how their populations respond to disturbances, and to form a scientific basis for effective species management. I describe here the dynamics of 2 populations of *B. annulata* in the Florida Keys that were examined every 2 months for 1 year, plus the static population structure of another 4 populations. Study sites were selected in 3 regions of the Keys (Upper, Middle, and Lower) and at 2 levels of human impact within each region. The Upper Keys sites had significantly higher coral cover and anemone abundance, as well as a larger proportion of small anemones than did sites in the other 2 regions, indicating potentially more stable populations of sea anemones. Low-impact sites also had significantly more coral cover and anemone abundance than did high-impact sites in both the Upper and Middle Keys, but not in the Lower Keys. At the 2 repeat-survey sites, anemone growth rate decreased with body size; small individuals grew 2-2.5x as rapidly as did large individuals in terms of percent growth in tentacle crown surface area (TCSA). Individuals grew on average 3-4 cm^2 TCSA per month up to

~100 cm^2 TCSA body size, then remained static or shrank. Only about 33-42% of individuals survived the entire year of study, indicating rapid population turnover of ~1 year, with most mortality occurring in very small or very large individuals. Transition matrices and elasticity analysis showed that the status of the largest individuals exerted the most influence on population size. I conclude that field populations of this sea anemone are highly dynamic in terms of their rates of growth, shrinkage, mortality and recruitment; lifespan is short and population turnover is high, on a scale of a about a year. Compared to populations previously surveyed in the U.S. Virgin Islands, anemones in the Florida Keys have higher survivorship and less shrinkage, especially during winter months and in the northern Keys, when and where water temperatures are relatively cool. Based on these trends, management implications for the harvest of this species are discussed.

Introduction

The marine ornamental trade is a multi-million 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. The trade is global and complex, affecting coral reefs in both major biogeographic regions where they occur. Countries in the tropical Indo-Pacific region such as Indonesia, the Philippines, Malaysia and Sri Lanka are the major providers of the 35 million+ fishes and 9-10 million stony corals and other invertebrates (including crabs, shrimps, sea anemones, and echinoderms) that are removed from coral reefs annually (Wabnitz et al. 2003, Bruckner 2005, Rhyne et al. 2012). The majority of these ornamental organisms are shipped to the United States, followed by Europe and Japan as major importing regions (Wabnitz et al. 2003, Rhyne et al. 2012). 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 species, has led to an increase in the ornamental trade in this area (Bruckner 2005, Rhyne et al. 2012).

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 fishery has been managed mainly through input control, in which government agencies have required "trip-ticket" data from commercial landings since 1990. The trip ticket program requires reporting on a trip-by-trip basis for all marine ornamental landings intended for sale. Each trip ticket reports the dealer, harvester, species and number of organisms landed, location harvested, and value of each species (Larkin and Adams 2003, www.myfwc.com/research/saltwater/fishstats/commercial-fisheries/wholesale-retail-dealers/). Recreational harvesting requires no reporting of landings. In contrast to some commercial harvesting of food fishes, little bycatch is produced in this industry because ornamental organisms usually are caught by hand. However, the potential exists for overfishing of the targeted organisms, especially because the Florida ornamental fishery has few limits on season of collection, or on the number or body size of individuals collected.

The marine ornamental trade is an increasing threat to wild populations of coral reef invertebrates; in the Caribbean it has grown steadily as aquarium technology has improved and aquarium ownership has become increasingly popular (Bruckner 2005, Rhyne et al. 2012). In 1998, the State of Florida began to limit the number of commercial permits for ornamental collecting, resulting in a decrease over the past few decades in the number of licensed commercial collectors, from a high of 776 to 160 (Fig. 2.1a). However, the state continues to issue an unlimited number of recreational fishing licenses, which allow collection of a small bag limit of ornamentals for most species (Larkin et al. 2001, Rhyne et al. 2009), with the exception of a few reef fishes, hard corals, conch, and most recently the rosetip anemone *Condylactis gigantea* (www.myfwc.com/fishing/saltwater/recreational/aquarium-species). Even with these changing restrictions in place, pressure from the commercial trade continues to increase, with an average of ~500,000 more individuals of ornamental organisms taken from Florida reefs each year between 1994 and 2007 (Rhyne et al. 2009). The regular and intensive removal of organisms from coral reefs causes loss of biodiversity and habitat, as well as long-term effects on the composition and function of this important marine ecosystem (Roberts 1995, Bruckner 2005, Graham et al. 2011). Unsustainably managed removal can leave reefs more susceptible to and slower to recover from both natural and anthropogenic disturbances, including destructive weather, algal blooms, and disease (Hughes 1994).

The corkscrew sea anemone *Bartholomea annulata* is a common target for Florida's ornamental trade, and is also an important host to diverse obligate symbionts that provide reef services (Briones-Fourzan et al. 2012, Huebner and Chadwick 2012a). Individuals are among the largest Caribbean sea anemones, reaching 30 cm in tentacle crown diameter, and may be common members of Caribbean coral reefs (Kaplan et al. 1999, Fig. 2.2). Commercial fishing data from Florida show a steady decline in the total numbers landed of *B. annulata* over the past decade, even during periods when the number of collecting permits has remained stable (compare Figs. 2.1a, b; www.myfwc.com/research/saltwater/fishstats/commercial-fisheries/landings-in-florida/; pers. comm. Nancy Sheridan & Bill Sharp, Florida Wildlife Commission [FWC]). This type of pattern in a fishery typically indicates declining catch per unit effort, usually due to the increasing scarcity of individuals in the fished populations (Gulland

1964, Maunder et al. 2006). These sea anemones also are in high demand in fisheries in other parts of the Caribbean Sea. In the ornamental trade in Puerto Rico, members of this species rank 7th among the 113 types of invertebrates collected, with 650 individuals collected in the first 6 months of 2002 by a single collector (LeGore et al. 2005).

Abundances of this giant sea anemone are important because they contribute to the aesthetic value of Caribbean reefs for tourism, and also play a key ecological role in hosting a variety of symbiotic crustaceans. Several species of shrimps, including *Ancylomenes* (= *Periclimenes*) *pedersoni*, the major Caribbean cleaner shrimp, associate with *B. annulata* as obligate symbionts (Mahnken 1972, Silbiger and Childress 2008, Briones-Fourzan et al. 2012, Mascaro et al. 2012). Giant anemones such as *B. annulata* serve as a visual cue to attract client fishes for cleaning interactions with the shrimps. In the U.S. Virgin Islands, the number and diversity of fishes cleaned increases with the number of shrimp at each cleaning station, as well as with the size of the host anemone; fishes pose for cleaning only when the anemones are clearly visible (Huebner and Chadwick 2012a,b). In Honduras, the host anemone size and number of cleaner shrimps at each station appears to affect the parasite cleaning rates of important coral reef fishes such as labrids (wrasses) and serranids (groupers, Titus et al. 2015).

Cleaning organisms enhance fish diversity on coral reefs and improve fish health, indirectly affecting the overall ecological condition and ecotourism value of coral reefs (Grutter et al. 2003, Bshary et al. 2007). Cleaners are shown to mediate aggression between piscivorous predatory fish and their potential prey at cleaning stations, creating a possible safe haven for small client fish (Cheney et al. 2008). Studies in the Indo-Pacific region show that when cleaner organisms are removed from reefs, client fishes emigrate from the area (Bshary 2003, Grutter et al. 2003), and recruitment of juvenile fishes declines (Waldie et al. 2011). The loss of herbivorous fishes from reefs can lower coral diversity and lead to phase shifts from healthy reefs to macro-algal dominated states in many regions (Dudgeon et al. 2010, Chadwick and Morrow 2011). In a classic case, uncurbed algal growth in the 1980s in Jamaica due to loss of herbivores led to large-scale reef ecosystem collapse (Sammarco 1982, Hughes et al. 1987, Hughes 1994, Bellwood et al. 2004, Dudgeon et al. 2010).

The shrimp *A. pedersoni*, whose major host is *B. annulata*, cleans members of at least 16 fish families in the Caribbean, including both herbivores and carnivores (Huebner and Chadwick 2012b). Therefore, removal of *B. annulata* sea anemones from coral reefs can have potentially large cascade effects on reef fishes, negatively impacting more than just the targeted anemone populations (Bshary 2003, Grutter et al. 2003, Bshary et al. 2007, Waldie et al. 2011). With significant increases recently in the demand for key reef invertebrates by the aquarium industry (see above), it is becoming urgent to understand the life histories of targeted species and their contribution to the biodiversity on coral reefs, including the sea anemones that host cleaner shrimps. Despite this urgency, little is known about the abundance and distribution of *B. annulata* sea anemones in Florida, or their life history traits such as patterns of growth and mortality (Schuman et al. 2005, Rhyne et al. 2009).

Preliminary data indicate that the mortality rate is high in anemones of this species; in a 1.5-year study in the U.S. Virgin Islands, mortality rates were estimated at 10-54% per 3 months for individuals of *B. annulata*, with a survival rate after 2 years of only 5% of the population (Nelsen 2008). This population had such high turnover (every 1-2 years) that it depends on frequent recruitment. Recruitment appears to be largely local from the natal reef, or the reef of origin where the individuals are produced sexually or asexually by their parents. Thus, recruitment of individuals may be determined mostly by the local population density of adult individuals (Nelsen 2008), similar to the dynamics of some acroporid corals (Hughes et al. 2000) and other reef cnidarians and fishes that self-recruit to their natal reefs (Jones et al. 1999, Almany et al. 2007, Underwood et al. 2009). If this pattern also occurs for populations in Florida, then intensive ornamental fishing for *B. annulata* could lead to local densities below thresholds for replenishment, resulting in population crashes and local extinctions.

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

In size-based population modeling, sensitivity and elasticity analyses can uncover the life stages or sizes that are particularly important to a specific parameter in the model, for example, population growth (Hughes 1984, Gotelli 1991, Pfister 1998, Lirman 2003). Sensitivity analyses reveal how sensitive a parameter (ie: population growth) is to small changes in each of the size classes (due to changes in recruitment, growth, and mortality rates). Elasticity analyses are similar to those for sensitivity in that they estimate changes in population growth with a proportional change in specific vital rates. Elasticities are essentially proportional sensitivities, and are scaled to compare directly the two parameters studied. They are important for inclusion in population studies, because either of these 2 types of analysis can pinpoint the life stages or sizes of organisms on which management strategies should focus (Benton and Grant 1999).

This chapter describes 6 populations of *B. annulata* along the bayside of the Florida Keys, in terms of variation in their population structure among regions of the Keys, and between sites within each region that experience different levels of human impact. Two of the studied sites also were mapped, the anemones tagged, and census information collected every 2 months for a full year, allowing determination of population dynamics over the course of 1 year. Based on the population patterns and processes described here, I discuss the ability of this species to recover from intensive collection in Florida, and recommend a framework for the sustainable harvest of this important coral reef invertebrate.

Materials and Methods

Study sites

The present study was conducted during March 2014 to May 2015 in the Florida Keys, Florida, USA. Two study sites were selected adjacent to shore in each of 3 regions: lower (1 site each at Sugarloaf and Cudjoe Keys), middle (2 sites at Marathon Key), and upper Keys (2 sites at Indian Key, 6 sites total, Fig. 2.3). Within each region, 1 site was selected as a high-impact site, due to easy human access from both the shore and water (ie: adjacent to a public beach with parking, deep enough for boat access, adjacent to a highway, evidence of human use such as abundant lobster traps, etc.), while the other was selected as a low-impact site, because it was less accessible and thus less likely to be impacted by humans (too shallow for boat access, plant growth along the shore too dense for easy shore access, distant from paved roads, etc.). All sites were selected during preliminary observations, based upon the above 2 criteria (region and level of impact), as well as the presence of corkscrew sea anemones *Bartholomea annulata* (N > 40 individuals) that were abundant enough for demographic analyses, but not so abundant as to make re-identification of individuals difficult in future surveys (details below; modified after Sebens 1981a, Hattori 2006, Nelsen 2008).

The 6 examined sites varied somewhat in water depth and shoreline characteristics. The 2 Upper Keys sites, Robbies and Indian Channel, were both very shallow (~1m depth at low tide) and close to Highway 1. The high-impact site, Indian Channel, was located between 2 marinas, and heavy boat traffic was observed throughout the survey. Indian Channel also had a nearby parking shoulder off the highway; 2-6 parked cars were seen in the area during the survey, and people were observed swimming and walking through the study site. The low-impact site Robbies, while also next to the road, had a smaller shoulder and less room for parking. Dense plant growth along the shore also made the water less accessible, and therefore no bathers were seen in the area. In the Middle Keys, the high-impact site Tiki Hut was a frequently-used public boat ramp, with the surveyed area located at ~2-3m deep along the sea wall edge of the boat ramp. People were seen fishing the area and boats were constantly being put in the water at the ramp. The low-impact Quarry site was about 2 m depth, located 2 miles off the highway on a dirt road, in an area prohibited to the public by the Marathon Police Department. However, this site was accessible by boat, and fishing boats were seen in the area occasionally. The Lower Keys low-impact site, Cudjoe, was a former boat ramp, 0.75m deep at low tide. It was too shallow for boats, and the area, while right off the highway, was closed to the public by the Florida State Police. Cudjoe’s high impact counter-part, Bowman’s Channel, was ~1-3m deep, with lots of evidence of human presence; trash along the shore and lobster traps and fishing debris in the water.

In March to July 2014 during the initial visit to each site, surface seawater salinity and temperature were recorded by hand, using a refractometer and digital thermometer. Water temperature and wind speed also were determined from data collected by NOAA buoys in each region of the keys (http://www.ndbc.noaa.gov/), and monthly averages for May 2014 to May 2015 were calculated and compared among regions. Data were analyzed from 1 buoy near the above study sites, in each of the 3 examined regions of the Keys: upper (Buoy LONF1), middle (Buoy VCAF1), and lower (Buoy KYWF1). Also in March 2014, the percent cover of live stony corals at each site was determined by deploying a haphazardly-placed 25-m transect at 1-4 m depth. I visually estimated the percent live coral cover within each 1 m^2 quadrat (divided into 25 smaller quadrats), along both sides of the transect, for a total of 50 m^2 surveyed for live coral cover per site (after Jokiel and Coles 1974).

One-time surveys

Four of the above 6 sites (Robbies, Indian Key, Tiki, and Sugarloaf, Fig. 2.3) were selected for one-time surveys of static population size structure in *B. annulata*, because the individuals at these sites were too sparsely distributed to allow for efficient tagging and repeat monitoring of population change. Beginning in March 2014, preliminary surveys were conducted to determine which sites to use for one-time, static sampling versus repeated, dynamic sampling of the anemone populations. Dynamic sampling at 2 sites was begun in March-May 2014, and repeated bimonthly until May 2015 (see details below), then static surveys were done at the 4 other sites above, in March 2015. In order to compile static survey data for all one-time sites during the same period, at each site in March 2015, a 25-m transect was deployed at least 1 m distant from the coral cover transect described above, and all individuals of *B. annulata* within a 1-m band along the left side of the transect tape were measured. At the end of the transect, the tape was moved one meter to the left and the process repeated until 40-60 anemones were measured, numbers similar to those used in previous studies on the population size structure of sea anemones (Sebens 1981a, Hattori 2002, Mitchell 2003, Chadwick and Arvedlund 2005, Hattori 2006). Because anemone abundance varied widely among the sites, a rectangular area of 4 x 2 m to 200 x 2 m (range of transect areas) was sampled for anemones at each site.

Repeat surveys

The 2 remaining sites (Quarry and Cudjoe, Fig. 2.3) were selected for repeat surveys beginning in March-May 2014, because they contained relatively dense and easily-tagged populations of anemones. Preliminary surveys were made to locate an area within each of these 2 sites that contained dense anemones, and the corners were marked with flagging tape underwater. At the start of each repeat survey, temporary floating buoys were placed at the site corners to easily re-locate the site edges from the water surface. During March 2014, all 50 *B. annulata* individuals within the 50 x 3 m survey area at Cudjoe were marked with an aluminum tag engraved with a number, which was hammered into the substrate adjacent to each anemone (after Porat and Chadwick-Furman 2004, Nelsen 2008, Huebner et al. 2012). A short piece of flagging tape also was attached to each tag to make it more easily visible, and the location of each marked anemone was noted on a site map. During May 2014, 98 anemones were tagged in the 34x2m survey area at the Quarry site, and the same procedures followed as at Cudjoe. SCUBA was used for surveys at the Quarry, and snorkel at Cudjoe, due to the difference in water depth between the sites (see above). Both sites were revisited ~7 times over 1 year, approximately each 2 months (May, July, September, November 2014, January, March, May 2015, except for November 2014 at Cudjoe due to a storm). During each visit, all marked sea anemones were re-measured, and the entire site was examined carefully for new recruits, which also were marked, measured, and mapped (after Chadwick and Arvedlund 2005, Nelsen 2008). Any previously-marked anemones that were not detected in subsequent surveys were considered to be lost to the population.

During each repeat visit to the 2 sites monitored for population change over time (Quarry and Cudjoe), all of the following data were collected for each individual of *B. annulata* in the site, as well as for all individuals observed during the one-time visits in March 2015 at the 4 static sites: tentacle crown length and width in cm (Fig. 2.4, 2.5), orientation (oral disk facing upwards [horizontal] versus sideways [vertical]), microhabitat (anemone tentacle crown contacting live coral, sand, rock, etc.), depth below sea level, number and species of crustacean macrosymbionts, distance to nearest neighbor (up to 2 m), and miscellaneous information (color or anything else of interest, after Chadwick and Arvedlund 2005, Nelsen 2008, Huebner et al. 2012). For each anemone, the longest distance from tentacle tip to tentacle tip across the center of the oral disc was measured as tentacle crown length (L) and then the distance perpendicular to that was measured as tentacle crown width (W). These numbers were used to calculate the tentacle crown surface area (TCSA) using the area equation for an oval, $(L/2*W/2)*\pi$ (after Hirose 1985, Hattori 2002, Chadwick and Arvedlund 2005, Huebner et al. 2012).

Data analysis

Variation in seawater temperature and wind speed were compared across the 3 regions using 1-way ANOVA. Variation in coral cover and abundance between the 6 sites was assessed using nested ANOVA, and 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 χ^2 analysis.

Anemones were divided into 3 size classes by tentacle crown surface area (TCSA): 0-25 cm^2 (I), 25.1-50 cm^2 (II), >50 cm^2 (III). Variation in rates of individual size change were analyzed using a mixed effects linear model in R x64 3.2.0, for the overall population and for each size class. A 1-way ANOVA was used to assess significant differences in rates 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 above size classes, and on the growth or shrinkage of each individual between time points (each 2 months for 1 year, after Nelsen 2008, McVay 2015). Elasticity values were calculated using the Microsoft Excel add-on PopTool 3.2. A value was calculated for each element of each matrix to determine which vital rates were most important for population growth. These population transition matrices did not include the exact effects of sexual and asexual reproduction on population growth (due to unknown fecundity rates), therefore the intrinsic rates of population growth (lambda, λ) potentially could be misrepresented and is not included here.

Individuals of *Bartholomea annulata* on coral reefs mature sexually at medium to large body sizes: ~70 cm^2 TCSA (Jennison 1981 and Chapter III). Thus, we assumed that 70 cm^2 TCSA was the minimum body size at sexual maturity, therefore, only individuals in Size Class III (> 50.1 cm^2 TCSA) likely contributed sexual propagules to recruitment. New individuals that were < 50 cm^2 TCSA were classified as recruits, based on analysis of growth rates of *B. annulata* over 2 months in the laboratory (x + SE = 13.7 + 2.26 cm^2 TCSA per 2 months, range = 9.1-18.2 for individuals in Size Class 1, see Chapter III). New individuals > 50 cm^2 TCSA in each survey were presumed to be immigrants or anemones that had been present but undetected in previous surveys, and were excluded from analysis (0-14 % of the total population at the Quarry, 0-6% of the total population at Cudjoe, depending on survey date, Fig. 2.6). Therefore all recruits < 50 cm^2 contributed to Size Class I and II and were assumed to be produced by Size Class III in the transition matrices.

Recruitment rate was determined as the number of new individuals in the population at each survey. Only individuals < 50 cm^2 were used to determine recruitment rates (see above), however new individuals outside this range were still monitored for growth, shrinkage, and mortality.

Rate of mortality was estimated based on the disappearance of anemones between time points. Anemones that were not relocated for at least 2 time points (4 months total) were considered dead or lost to the population (after Ottaway 1979, Holbrook and Schmitt 2005, Nelsen 2008, McVay 2015). If an individual was not found during one time point, but was found during the next, then the missing measurement was interpolated. However if an individual was missing for more than 2 consecutive time points (4 months), it was considered lost and any anemone found nearby later was classified as an immigrant or recruit. While sea anemones are capable of locomotion, extensive movement is rare; in anemone species with similar-sized individuals, most individuals move < 5 cm over 1-2 years, and the greatest distance moved is ~25-30 cm (Ottaway 1978, Batchelder and Gonor 1981). On coral reefs, other giant sea anemones move so slowly that they can be individually identified even over time scales of a year between surveys (McVay 2015). Also under laboratory conditions, large individuals of *B. annulata* are unlikely to move much once settled, with individuals > 75 cm^2 TCSA not moving at all over 6 weeks (Titus 2011). In my concurrent laboratory study, individuals moved an average of only 2.6 cm/month (Chapter III). Populations of *B. annulata* on Caribbean reefs appear to be more dynamic (Nelsen 2008) than are those of giant anemones on Indo-Pacific coral reefs (McVay 2015), so I surveyed them more frequently. Because my study sites were revisited every 2 months, and change in location by individuals likely was minimal based on the above information, it would have been difficult to confuse one individual with another tagged anemone, at the densities present at these sites.

Life-span was calculated using Kaplan-Meier survival curves. 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 and Jackson 1985), using the following turnover formula:

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

where E = number of deaths during a given period, R = number of recruits, and N = number of total individuals in the population (after Diamond 1969, Hanski, 1999).

All results are reported as means +/- one standard error, unless indicated otherwise.

Results

Site characteristics

Monthly mean seawater temperature and wind speed varied by site during the study year (May 2014 - May 2015) and by region of the Florida Keys (Upper, Middle, and Lower, Figure 2.7a). The Lower Keys experienced more variable and higher maximal seawater temperature than did the other 2 regions, ranging 21.0 - 35.4º C (monthly means, February 2015 and September 2014) compared to only 20.7 - 32.1º C (February 2015 and August 2014) and 20.2 - 31.7 º C (February 2015 and August 2014, in the Middle and Upper Keys, respectively Fig. 2.7a). Wind speed in the Middle Keys (monthly mean = 3.6 m/s, range = 2.2 - 4.7 m/s, N = 12 months) was slower than in the other 2 regions. The Upper Keys had the highest wind speed, with a mean of 5.2 m/s (range = 3.6 - 6.4 m/s), which was not significantly different from that in the Lower Keys (average = 4.8, range = 3.8 – 5.6 m/s, $p = 0.34$, Fig. 2.7b).

During March 2015, all 6 study sites had low percent cover of stony corals (range of means ± SE = 3.4 ± 0.5% to 12.0 ± 1.2%, Fig. 2.8a). Coral cover varied at all 3 levels examined: among 6 sites, 3 regions, and 2 levels of human impact. Both sites in the Lower Keys contained 3x lower coral cover than did the low-impact sites in the Middle and Upper Keys. On average, low-impact sites had about twice the coral cover of high-impact sites (Fig. 2.8a) Cohen's d-effect size calculations suggested a moderate practical significance in the difference of coral cover between the Upper and Lower Keys (d = 0.58), as well as moderate to high practical significance in the differences between the Middle and Lower Keys (d = 0.75), and between the levels of human impact (d = 0.67).

Sea anemone abundance and population structure

The abundance of individuals of *Bartholomea annulata* also varied among sites, from 0.15 individual/m^2 at Bowman's Channel (Lower Keys, high impact), to 5.00 individual/m^2 at Robbies (Upper Keys, low impact, Fig. 2.8b). Sea anemone abundance varied with region, level of human impact, and with site within region. The low-impact site in the Upper Keys (Robbies) had higher anemone abundance than observed at all other sites, with 2-10x more individuals per m^2 than at sites in the Middle Keys, and ~10-25x more than at sites in the Lower Keys (Fig. 2.8b). The Upper Keys region showed high practical significance when comparing anemone abundance to both the Middle Keys (d = 0.67) and the Lower Keys (d = 1.13). Sites with low human impact had about 2 more individuals per m^2 than did sites with high human impact (d = 1.37). The low-impact site in the Middle Keys (Quarry) had ~4-10x more individuals per m^2 than did the remaining sites (all 3 high impact sites and the low impact site in the Lower Keys).

During March 2015, sea anemone population size structure also varied significantly among sites ($\chi^2_{10} = 138.7$, $p < 0.001$, Fig. 2.9) and regions ($\chi^2_4 = 119.7$, $p < 0.001$). Anemone population structure in the Upper Keys differed significantly from that in the other 2 regions, in that it consisted of a relatively high proportion of small individuals (belonging to Size Class I) and a small proportion of large individuals (Size Class III, $p < 0.001$ for both comparisons). Population size structure also varied significantly between sites with different levels of human impact ($\chi^2_2 = 8.07$, $p < 0.05$); high-impact sites had greater proportions of the largest individuals and relatively few small individuals, indicating relatively low recruitment and thus potentially low population stability.

General characteristics of repeat-sampled populations

About half the anemones at both of the repeat-survey sites occupied microhabitats in which their tentacles contacted entirely hard substrate (reef rock, sponge, or coral, 49.7 ± 10.2% of individuals at the Quarry and 44.5 ± 13.8% at Cudjoe, N = 5 and 6 survey periods at Quarry and Cudjoe, respectively). The other half of each population contacted a combination of hard and soft substrate (42.8 ± 7.0% and 50.2 ± 12.7%, respectively). Many of the individuals occurred along the bases and edges of hard substrate areas, at the interface between reef and sand. In contrast, only 7.5 ± 6.3% and 3.8 ± 1.7%, respectively, of individuals occurred with their tentacle crowns entirely surrounded by soft substrate (sand, Fig. 2.10a). The proportion of anemones in each type of microhabitat varied significantly between the 2 sites, during 4 of the 5 survey periods in which microhabitat was recorded at both sites. The Quarry had relatively more anemones touching a combination of hard and soft substrate most months, and Cudjoe site had more touching only hard substrate (May 2014, $\chi^2_2 = 14.6$, $p < 0.001$, July 2014, $\chi^2_2 = 8.0$, $p < 0.05$, January 2015, $\chi^2_2 = 9.7$, $p < 0.01$, March 2015, $\chi^2_2 = 7.4$, $p < 0.05$, May 2015, $\chi^2_2 = 2.5$, $p = 0.29$). Thus, relatively more of the anemones at the Quarry occurred at patch reef edges along the interface between the reef and sand, while more of those at Cudjoe were in the middle of hard reef areas and not near sand.

Most individuals at the Quarry site (77.2 ± 3.7%, N = 5 sample periods, orientation data wasn’t collected in September 2014 due to lack of time) oriented horizontally, with their oral discs facing upwards toward the sea surface. Their body orientations varied somewhat among months, from 69.0% oriented horizontally during November 2014 to 90.0% during March 2015.

A significantly lower proportion (40.8 ± 4.1%, range = 31.0 - 54.8%, in March 2015 and May 2014, respectively) oriented horizontally at Cudjoe during all sample periods, except for the first one (May 2014: $\chi^2{}_2 = 0.002$, $p = 0.96$; July 2014: $\chi^2{}_2 = 34.1$, $p < 0.001$; January 2015: $\chi^2{}_2 = 27.0$, $p < 0.001$; March 2015: $\chi^2{}_2 = 54.1$, $p < 0.001$; May 2015: $\chi^2{}_1 = 20.2$, $p < 0.001$; Fig. 2.10b).

At the beginning of the study in May 2014, total anemone abundance at the Quarry site (1.43 individuals/m^2) was almost 3x that at Cudjoe (0.55 individuals/m^2). During the study year, abundance peaked at the Quarry in November 2014 at 2.60 individuals/m^2 (82% increase over initial abundance) and at 0.70 individuals/m^2 at Cudjoe (26% increase). By the end of the year, abundance had almost doubled (increase of 80.0%) at the Quarry, to 2.57 individuals/m^2 in May 2015, while it decreased by almost a quarter (23.7%) at Cudjoe to only 0.42 individuals/m^2.

The population size structure of *B. annulata* also differed significantly between the 2 sites, but only during the initial survey in May 2014 ($\chi^2{}_2 = 7.45$, $p < 0.05$), and not one year later during the final survey in May 2015 ($\chi^2{}_2 = 4.78$, $p = 0.09$). The initial difference was characterized by a higher percentage of small individuals at the Quarry than at Cudjoe. Individuals in Size Class 1 were twice as abundant as those in other two size classes at the Quarry, while individuals were distributed evenly among all 3 size classes at Cudjoe (Fig. 2.11). By the end of the year, this difference disappeared due to an increased percentage of large individuals at the Quarry site. The two sites differed also in the mean size of individuals at the beginning of the study in May 2104, with significantly larger individuals (43.3 ± 3.5 cm^2 TCSA, N = 62) at Cudjoe than at the Quarry (31.3 ± 2.9 cm^2, N = 97, $t_{157} = 2.61$, $p < 0.01$). However, within 2 months (July 2014), the rapid growth of small individuals at the Quarry led to similar mean anemone body sizes at both sites, a pattern which remained for the rest of the study (Fig. 2.11).

Body growth and shrinkage

Absolute rates of change in body size widely among individuals of *Bartholomea annulata* within each 2-month survey period. The monthly rate of change in body size for all individuals did not differ significantly between the 2 sites examined, and showed an overall pattern of net growth rather than shrinkage (nested ANOVA $F_{1, 306} = 0.824$, $p = 0.37$; Cudjoe = 2.95 ± 0.40 cm^2 mo^{-1} TCSA, Quarry = 4.12 ± 0.40 cm^2 mo^{-1}, N = 6 at the Quarry, N = 5 at Cudjoe. This growth rate varied significantly with size class at both sites (nested ANOVA, $F_{2, 306} = 22.72$, $p < 0.001$). Members of Size Class I grew significantly more rapidly (5.09 ± 0.35 cm^2 mo^{-1} TCSA, N=156 individuals, $p < 0.001$) than did those in Size Class II (3.25 ± 0.39 cm^2 mo^{-1}, N = 121 individuals, $p < 0.001$), which also grew significantly more rapidly than did those in Size Class III (only 1.42 ± 0.44 cm^2 mo^{-1}, N = 111 individuals, $p < 0.01$ for all pairwise comparisons, Fig 2.12a). The Quarry had higher mean growth rates than Cudjoe in Size Class I and II, while Cudjoe had a higher mean growth rate in Size Class III, but none of the between-site values differed significantly (Fig. 2.12b.).

At the Quarry site, absolute growth rate decreased significantly with size class ($F_{2, 212} = 19.46$, $p < 0.001$), and all size classes differed significantly from each other (Fig 2.12b). Individuals in Size Class I grew the most rapidly, at 5.51 ± 0.42 cm^2 mo^{-1} (N =125, $p < 0.001$) those in Size Class II grew at a slower rate (3.47 ± 0.62, N = 86, $p < 0.001$), and those in Size Class III remained relatively stable in body size, with very slow growth of 0.96 ± 0.60 cm^2 mo^{-1}

(N = 86, $p = 0.11$). The mean size of individuals all size classes changed seasonally; with overall body shrinkage in the summer to fall, and growth in the winter to spring (Fig. 2.13, 2.14, 2.15).

At Cudjoe, anemone growth rates also decreased significantly with size class (F = 3.43, d.f. = 2,86, $p < 0.037$), and differed significantly between Size Classes I and III ($p = 0.03$), but not between Size Classes I and II or II and III ($p = 0.32$ and 0.41, respectively, post-hoc pairwise tests, Fig 2.12). Individuals in Size Class I at Cudjoe grew 4.18 ± 0.55 $\text{cm}^2\ \text{mo}^{-1}$ (N = 31, $p < 0.001$), those in Size Class II grew at 3.12 ± 0.46 $\text{cm}^2\ \text{mo}^{-1}$ (N = 35, $p < 0.001$), and those in Size Class III grew at only 2.13 ± 0.62 $\text{cm}^2\ \text{mo}^{-1}$ (N = 25, $p <0.001$). Also similar to anemones at the Quarry site, mean body size within each size class varied seasonally at Cudjoe, with overall growth occurring in the winter to spring and shrinkage in summer to fall, at least for Size Classes II and III (Table 1, Fig. 2.15).

Similar to patterns for absolute change in body size, the percent changes in body size did not differ between the 2 sites. However, overall the Quarry anemones almost doubled in body size on average (87.3 ± 13.7 %) during each 2-month period, while those at Cudjoe grew only 52.1 ± 11.1% ($F_{1,\ 303} = 3.12$, $p = 0.08$). Percent change in body size varied significantly among size classes ($F_{2,\ 303} = 22.47$, $p < 0.001$). Individuals in Size Class I at both sites more than doubled their size every 2 months on average, while those in Size Class III grew an average of only 11-14% per 2-month period. At the Quarry, percent change in body size for members of Size Class I (163.0 ± 25.8% per 2 months) was significantly more rapid than that in both Size Class II (44.1± 9.0%) and III (11.9 ± 5.9%). The same pattern emerged for Cudjoe, with individuals in Size Class I (104.1 ± 27.7%) having significantly more rapid percent change in body size than those in Size Class II (31.4 ± 7.0%) or III (14.6 ± 4.0%).

At both site locations, the mean size of anemones belonging to Size Class III) reached a maximum of ~90 cm^2 TCSA in March 2015 (also during November 2014 at the Quarry site). The Quarry tended to have larger anemones overall, with > 20 individuals reaching sizes greater than 125 cm^2 TCSA, and 7 of these attaining very large body sizes of > 175 cm^2 TCSA. In contrast, at Cudjoe only 9 anemones became larger than 100 cm^2 TCSA, and none grew to > 175 cm^2 TCSA.

Recruitment

Recruitment of new individuals into the anemone populations differed somewhat between sites. The Quarry received 0.22 ± 0.04 recruits/resident and 0.44 ± 0.07 recruits/m^2 during each 2-month survey period. In contrast, the Cudjoe population received only about half as many new recruits on a per-resident basis, 0.13 ± 0.03 recruits/resident, and less than a quarter as many per unit area, 0.08 ± 0.02 recruits/m^2 during each 2-month survey period.

Recruitment rate as a function of number of resident anemones was significantly higher (double the rate) at the Quarry than at Cudjoe during July – September 2014 ($Z = 2.67$, $p < 0.01$), but did not differ significantly during the other 5 sample periods. In contrast, recruitment rate as a function of unit reef area was higher at the Quarry during all sample periods, except for the initial one (May – July 2014: $Z = 1.33$, $p = 0.18$; July – September 2014: $Z = 6.21$, $p < 0.001$; September 2014 – January 2015: $Z = 12.41$, $p < 0.01$; January – March 2015: $Z = 4.89$, $p < 0.001$; March – May 2015: $Z = 5.14$, $p < 0.001$).

Seasonality

The percent of the population that grew, shrank, or remained in the same size class (stasis) did not differ significantly between the winter and summer (Figs. 2.14, 2.15, Table 2.1). The Quarry had relatively high mortality in the winter (34.3% in January 2015), but a pattern of low mortality in September (8.2%) kept the overall mortality for the winter season low. Recruitment rates (per individual) at the Quarry were higher in the winter (0.37 recruits/individual in September and 0.31 recruits/individuals in November 2014), but started decreasing in January (0.16 recruits/individual, Fig. 2.14, 2.15) so the overall recruitment for winter was low. Cudjoe showed recruitment rates that were 3x higher July 2014 – January 2015 than March – May 2015. The orientation of individual anemones showed no patterns of changing with the season.

Mortality and life span

At both the Cudjoe and Quarry sites, the anemones exhibited similar mortality rates of about one-fifth up to about a third of individuals disappearing (dying) every 2 months (Cudjoe: 22.7 ± 8.7% per 2-month period, range = 12.9 – 33.9%, N = 5 periods; Quarry: 21.3 ± 4.3%, range = 8.2 – 34.3%, N=6 periods). Mortality rate did not differ significantly between the 2 sites, except during the final survey period in March to May 2015, when only 18% of the population at Quarry died, while 34% of individuals at Cudjoe died ($Z = 2.25$, $p < 0.05$). The number of deaths varied with season at the Quarry: during winter (3 survey periods, spanning September 2014 – March 2015), a mean of 35 more deaths occurred per 2 month period than during summer (2 survey periods during May – September 2014 and 1 during March - May 2015, t_4= 2.99, p <0.05). Mortality rate did not vary significantly with season at Cudjoe, but the lack of pattern could be due in part to a lack of field data collection in November 2014 because of a storm (see Methods; t_3 = 1.34, p = 0.27).

Dynamic survival curves indicated that overall survival rate was very similar between sites (Fig. 2.16); the survival curve at Cudjoe (y = -0.14ln(x)+0.71 R^2 = 0.97) differed only slightly from that at the Quarry (y = -0.14ln(x)+0.68, R^2 = 0.99). At both sites, only ~30% of the population survived the entire 12 months of the study. About half the population at Cudjoe survived for 6 months, and at the Quarry, half the individuals lasted only 4 months. The survival curves for both sites predicted that only 1% of individuals from the original populations would survive after ~ 60 months (5 years). Similarly, examination of *B. annulata* under laboratory conditions indicated that almost all individuals likely survived less than 4 years or so (Chapter III).

Estimated population turnover times ranged 6.44 – 15.60 months, depending on the 2-month period from which they were calculated. Mean turnover for sea anemones at the Cudjoe site was 10.18 months, while at the Quarry it was slightly shorter at 7.66 months (Table 2.3). During winter, turnover time decreased to only 6.44 months at the Quarry site (November 2014 – January 2015, compared to 15.60 months in May – July 2014). In contrast, a seasonal trend was not observed at Cudjoe, where turnover time decreased throughout the study from 11.02 to 8.31 months, in parallel with increasing mortality over time at this site.

Transition matrices

Similar patterns of transition among size classes were observed at both sites, in terms of the proportions of each size class that remained static, or grew or shrank into other size classes (Table 2.1). Elasticity analyses revealed that during most periods at both sites, the anemones who remained in the largest size class (static in Size Class III) most influenced overall population size (except during May – July 2014 at Cudjoe, when anemones remaining in the smallest size class exerted the most influence). During most periods, static anemones in Size Class III had elasticity values > 0.50 (10 of 12 matrices, 83% of the time, Table 2.2).

Discussion

Overall patterns

This study demonstrates that populations of corkscrew sea anemones are highly dynamic in the Florida Keys, compared to the populations of other coral reef cnidarians that have been examined to date (Hughes and Jackson 1985, Schick 1991, Hughes and Tanner 2000, Holbrook and Schmitt 2005, Edmunds 2010, McVay 2015). The results also reveal potential trends in anemone dynamics with region, level of anthropogenic disturbance, and season. Overall, of the 6 sites examined here, those in the northern Keys and those exposed to low levels of human impact contained the most abundant individuals and the highest proportions of small, recent recruits. These patterns paralleled those in the percent cover of stony corals at each site, indicating overall healthier state of near-shore hard-bottom communities in the northern vs. southern Keys, especially in areas with relatively low exposure to human contact. Examination of dynamics throughout the study year revealed that sea anemone growth, recruitment, and overall abundance are highest in winter vs. summer (Fig. 2.14, 2.15). Populations of this species also experience more rapidly-growing individuals in Florida (present study) than they do further south in the U.S. Virgin Islands (Nelsen 2008). All of these patterns point to both regional and seasonal changes in water temperature as potentially controlling many processes for these anemones, with populations thriving further north and in winter, where and when water temperatures are lowest.

One-time surveys

The observed variation in weather patterns among regions of the Florida Keys, especially the relatively high summer seawater temperatures in the Lower Keys, appear related to the recorded differences in coral cover and anemone abundance by region. Rising sea temperatures worldwide are known to cause reef corals and sea anemones to bleach (Jokiel and Coles 1974, Jokiel and Coles 1990, Brown 1991, Teneva 2012). Rising temperatures are also correlated with slower than normal growth in stony corals, shorter lifespans (Edmunds 2004), and more prevalent diseases (Kuta and Richardson 1996, Kuta and Richardson 2002, Bruno et al. 2007). Relatively still air (low wind speeds) also may lead to higher rates of coral bleaching (Maina et al. 2008). Thus, it is possible that the lower maximal seawater temperatures in the upper Keys in part caused the higher percent coral cover at those sites relative to the Lower Keys (which had higher maximal temperature and lower wind speeds relative to the Middle Keys region). In addition, localized human impacts are known to reduce coral cover, including from the effects of trampling by tourists (Leujak and Ormond 2008, Krieger and Chadwick 2013), point source pollution such as diesel fuel and sewage (Bak 1987, Fabricius 2005), and other disturbances, leading possibly to the lower coral cover at the high vs. low impact sites within each region of the Keys. These patterns of environmental conditions plus human impacts also may have contributed to the patterns of sea anemone abundance and population structure; sites further north and sites with lower human impact having more abundant anemones and relatively more new recruits (small individuals) in their populations.

Repeat surveys

The differences in sea anemone microhabitat use between the 2 repeat-survey sites may have occurred in part because the Cudjoe site had fewer sponges and lower coral cover than the Quarry site, so that individuals occurred on smaller reef rock areas, and more in contact with sand. The overall lack of anemones in contact only with soft substrate (ie: surrounded by sand) may be in part because they are easier prey on sand where they cannot retract into holds surrounded by rock. They also may be more easily removed or damaged by strong currents or wave action during storms, when they are surrounded entirely by shifting, soft substrate (pers. observation), and also likely experience higher sedimentation rates on sand than on the reef.

The higher proportion of horizontal-orienting anemones at the Quarry than at Cudjoe also may relate in part to the difference in their depths below sea level (2.5 vs. 1.0 m). As Cudjoe was so shallow, almost intertidal, the anemones there appeared to experience high levels of water motion, change, and wave action that enhanced sedimentation. The anemone tags were observed to be completely covered with sand and silt during every 2-month survey at Cudjoe, whereas they were not at the Quarry. The shallow nature of this site may have caused the anemones to orient more vertically than in deeper areas, to reduce sedimentation on the tentacle crown, and also reduce extreme irradiance at this shallow depth, as known for some other sea anemones, corallimorpharians, and mobile fungiid corals (Chadwick-Furman and Loya 1992, Kuguru et al. 2010, Dixon et al. 2014).

Body growth and shrinkage

Most previous studies on sea anemone growth have measured either basal diameter (Bucklin 1985, Bucklin 1987, Chomsky et al. 2004a,b), oral diameter (Chia and Spaulding 1972, Chomsky 2004a), or dry weight (Sebens 1981a,b). This makes it difficult to compare their results with growth in tentacle crown surface area (TCSA), in field studies of anemones where the pedal disk is buried deep in holes, such as for *Entacmaea quadricolor* where only the tentacle crown dimensions can be measured (Porat and Chadwick-Furman 2004, McVay 2015), or in cases where the sacrifice of many individuals to assess dry weight is unfeasible. In the present study, TCSA was used as the measure of growth, because the pedal disks of individuals of *Bartholomea annulata* usually were buried under sand, sponges, or in rock crevices. The relationship between pedal disk diameter and TCSA then was determined for individuals cultured under laboratory conditions (Chapter III), so that growth in this anemone species can be compared to that in past studies on this and other types of sea anemones.

Few studies exist on the growth rates of tropical sea anemones (Shick 1991), and even fewer that have followed field populations for more than a few months. The Indo-Pacific giant sea anemone *Heteractis magnifica* was examined for 3 years in the field, and grew an average of 0.75 cm^2 surface area per day with anemonefish present (Holbrook and Schmitt, 2005), an almost 5-fold increase from the 0.14 cm^2 TCSA per day growth rate found here for individuals of *B. annulata* at the Quarry, or the 0.10 cm^2 TCSA per day growth rate at Cudjoe. However, fish symbionts augment growth rates in anemones (Roopin and Chadwick 2009), and the *H. magnifica* individuals without anemonefish grew only ~2x as much, 0.25 cm^2 per day. Because individuals of *H. magnifica* are much larger than those of *B. annulata* (double the body size of the largest individuals in the present study), this more rapid absolute growth rate is not surprising. In terms of percent changes in body size, individuals of *B. annulata* grow more quickly than those of *H. magnifica*, in that they can double their body size (100% size change) in as little as 2 months, depending on initial size, whereas *H. magnifica* takes 12-18 months to do so (with 2 and 1 anemonefish present, respectively). Growth rates in individuals *H. Crispa* which hosts juvenile anemonefish are-0.18 to 0.12 cm^2 per day (or -66.6 to 46.2 cm^2 per year, depending on the size class), and of bulb-tentacle anemones *E. quadricolor,* that host adult anemonefish, are up to-0.30 to 0.27 cm^2 per day (or 111.0 to 100.0 cm^2 per year, McVay 2015). While *E. quadricolor* exhibits almost double the growth rate of *B. annulata* in the field, *H. crispa,* a congener to the corkscrew anemone, is much more comparable.

The decrease in individual growth rates with body size observed here under both Florida field (this chapter) and laboratory conditions (Chapter III) in *B. annulata* is similar to the pattern known for this species at field sites in the USVI (Nelsen 2008). It also parallels the pattern in growth rates observed for other coral reef sea anemones (McVay 2015), the Mediterranean coral *Balanophyllia europaea* (Goffredo et al. 2004), mushroom coral *Fungia granulosa* (Chadwick-Furman et al. 2000), and zooanthid species (Karlson 1988), among other cnidarians. Most organisms invest energy into rapid growth when small, then divert that energy into reproduction after reaching sexual maturity and an adult body size that is safer from predation than are small juveniles. Physiological and biomechanical constraints on maximal body size in *B. annulata* may cause individuals to slow their growth rates when approaching these limits.

The percentage of the *B. annulata* populations that showed body growth (positive size change) was greater in the Florida Keys than for populations examined previously at 2 sites in the U.S. Virgin Islands (USVI, Nelsen 2008). Only 10%-26% of individuals grew over 3 months in the USVI (ie: transitioned into larger size classes), less than half as many compared to the proportion that grew over 2 months in Florida at both the Quarry (39 – 42%) and Cudjoe sites (35-42%, Table 2.1). In addition, body shrinkage rates were higher in the USVI than in Florida, 18-90% compared to 8-21% over 2-3 months, and the rates of stasis (maintenance of stable body size), especially in the larger size classes, were lower. Nelsen (2008) observed highly variable stasis and shrinkage, however some trends emerged; stasis rate decreased as size class increased, and shrinkage rate increased with size class. At both of my study sites in Florida, shrinkage rates also increased with size class, 8-18% at the Quarry and 8-21% at Cudjoe, but unlike the anemones examined by Nelsen (2008), I found that stasis also increased with size, with both sites having ~60% of the largest size class staying within that class over 2 months (Table 2.1). My examination of *B. annulata* individuals under stable laboratory conditions (tank water temperature range = 23.9 to 26.8 ºC) also revealed stasis rates increasing with body size, from 26-73% (smallest to largest size classes, Chapter III). While the present study was conducted using shorter sampling intervals than in the USVI (2 vs. 3 months), the trend of stasis rates increasing with size observed here under both laboratory and field conditions differs markedly from the pattern of low stasis found in the Virgin Islands (Nelsen 2008). In other types of cnidarians, large individuals generally are more stable and less dynamic (more static, less mortality) than are small individuals (Goffredo and Chadwick-Furman 2000, McVay 2015), so the patterns observed here appear to reflect those of healthy cnidarian populations on other types of coral reefs. In contrast, corkscrew anemone populations in the USVI, with their low stability among large individuals, and their low individual growth rates (Nelsen 2008), appear to be under stress.

The high rates of anemone shrinkage and low growth and stasis in the USVI relative to patterns in the Florida Keys and under laboratory conditions may be due to an array of environmental factors. High water flow in the field can damage the soft tissues of anemones, and limit their feeding ability by changing size of the tentacle crown and reducing tentacle expansion (Koehl 1977, Shick 1991). This can divert energy from growth into healing of damaged tissues or into the relatively high energetic costs of remaining expanded in high water flow. Both the Florida Keys sites are on the bayside, receiving both a wind and weather buffer from Atlantic Ocean storms due to being on the leeside of the island keys. Also, both sites were close to shore and were < 2.5 m deep, whereas the two sites in the Nelsen (2008) study were both deeper and farther from shore. One of the USVI sites also had high rates of sedimentation and the other had high water movement, water temperatures are higher on average in the USVI than in Florida, but have cooler summers and warmer winters (27.6 to 30.0 ºC monthly average sea surface temperature, yearly average 28.8 ºC http://www.ndbc.noaa.gov/station_history.php?station=chav3 vs. 26.6, 27.0, and 29.1 ºC yearly average for Upper, Middle, and Lower Keys, respectively), and coral bleaching occurred at one of the USVI sites (Nelson 2008). Thus, high temperatures for longer duration and other factors (such as lower irradiance due to added site depth) may stress both corals and sea anemones at the sites examined in the USVI relative to conditions in the shallow lower Florida Keys. The negative effects of high temperature on body size and growth in these sea anemones also is indicated among anemones in different regions of the Florida Keys, in which more abundant individuals occurred farther north within the Keys than in the south Keys areas. Laboratory populations were maintained at apparently optimal temperatures of only 25ºC, with relatively low water flow and sedimentation, and so more closely mimicked both the environmental conditions and growth rates of Keys anemones, more than they did USVI anemones which appear to be physiologically stressed. I conclude that these anemones grow optimally at relatively low tropical to subtropical temperatures of 24.0 – 27.0 ºC, under low water flow, with low sedimentation, moderate irradiance levels, and ample food supply.

Recruitment

Several studies have described the difficulties of detecting small cnidarian recruits on reef substrates (Chadwick-Furman et al. 2000, Goffredo and Lasker 2008, McVay 2015), therefore it is likely that many of the smallest anemone recruits here were missed during some surveys, leading to underestimates of the abundance of anemones in the smallest size class. However, if they survived until the next survey and remained under 50 cm^2 TCSA, they were included in my recruitment estimates. The much higher number of recruits at the Quarry than at Cudjoe, both in terms of number of residents and reef surface area, could be due in part to the difference in resident anemone abundance between the 2 sites, with Quarry being 4x higher than Cudjoe. Levitan et al. (1992) has shown that a lower abundance of spawning adults in sessile marine invertebrates leads to a lower fertilization success rate. The Quarry had a relatively high number of large individuals, with potentially higher reproductive output (Sebens 1981b, Bucklin 1987, Levitan 1989) than at Cudjoe. Larger individuals also tend to divide more frequently in several anemone species; *Anthopleura elegantissima* (Sebens 1980), *Haliplanella luciae* (Johnson and Shick 1977), *Aiptasia pulchella* (Hunter 1984), and *Metridium senile* (Bucklin 1987). The higher number of large individuals at Quarry could result in higher recruitment, both sexually and asexually. Quarry also had a higher proportion of rocky substrate than Cudjoe and this might lead to a higher level of larval settlement and recruitment numbers.

Mortality and lifespan

Mortality rates for the entire population varied from 8.2-34.3% per 2-month period (Table 2.1, 3.5), comparable to mortality rates found in the Virgin Islands of 10-54% per 3 month period (Nelsen 2008), and slightly lower than 33-39% per 5 week period in the USVI (Titus 2011), and 32-33% mortality rate per 6 weeks in a previous lab study (Titus 2011). The lowest mortality rates observed for *B. annulata* were in my laboratory study, with only 3-26% mortality per 2 months (Chapter III), but maximal mortality values were similar in all of the above studies. Maximum lifespan may be largely determined by senescence processes in this sea anemone, as known for some stony corals (Rinkevich and Loya 1984), and as observed in other studies on this species (Nelsen 2008, Titus 2011).

Mortality rates for this sea anemone were several orders of magnitude higher than for the giant Indo-Pacific sea anemone *Heteractis magnifica* which had only 29% mortality over 3 years (Holbrook and Schmitt 2005), and also are higher than mortality in the related species *H. crispa* (17 to 25% mortality per year) and *E. quadricolor* (11 to 28% per year, McVay 2015). They also are much higher than those of other Caribbean cnidarians examined thus far: the stony corals *Montastrea annularis, Agaricia agaricites,* and *Leptoseris cucullata* from Jamaica have mortality rates of only 16-67%, 57-77%, and 77-96% respectively in 5 years (Hughes and Tanner 2000), and foliaceous corals in two locations at Jamaica over 3 years have only 6-34% and 38-63% morality (Hughes and Jackson 1985). *B. annulata* is smaller in body size than the Indo-Pacific giant sea anemones, and has less soft tissue; this could lead to higher mortality rates. This Caribbean anemone has been shown to have high population turnover of only 1-2 years in both the USVI (Nelsen 2008) and the Florida Keys, and appears to be a weedy anemone species, growing quickly, and reaching reproductive maturity quickly (Chapter III). It is interesting that mortality for this species appears to be somewhat lower in Florida (and in the lab) than in the USVI, indicating that in addition to more rapid growth, the anemones in Florida also have relatively more stable populations than in the USVI, but with similar turnover rates of about 1 year. These regional patterns in addition to seasonal patterns within both regions indicate that relatively low temperatures and possibly other conditions favor the growth and stability of populations of this anemone.

Management implications and conclusions

The results obtained here have implications for the marine ornamental trade, in that the dynamic nature of *B. annulata* populations indicate that they might be suitable for sustainable harvest methods. However, these results also show that they have a short lifespan compared to some other sea anemones (Holbrook and Schmitt 2005, McVay 2015), and therefore require a constant influx of individuals into their populations, to supply the aquarium trade. Field populations thus may grow rapidly due to early reproduction and rapid body growth, but they also can rapidly disappear due to their short lifespans and high rates of mortality.

According to my field data, the largest individuals in the population have the most influence on population growth (Table 2.1, 2.2), therefore restricting the harvest of these individuals may support the stability of populations. Larger anemones, when associated with cleaner shrimp, also receive more client fish visitation for cleaning than do smaller anemones (Huebner and Chadwick 2012a), thus indirectly affecting community health and diversity. Larger anemones also typically have higher gamete production and potentially higher input to recruitment (Sebens, 1981b, Bucklin 1987, Levitan 1989, Kapela and Lasker 1999). Asexual reproduction usually requires a minimum size (Minasian 1982) and there is a minimum size at which *B. annulata* produces gametes (Jennison 1981). By collecting smaller anemones closer to this reproductive cut-off, larger individuals will remain to replenish the population. However, some small individuals need to also remain in each population, so that they can eventually replace large, old individuals near the end of their natural lifespans. Thus, collection of only some mid-size individuals (ie: a slot limit) may best maintain local populations. In landing mostly small to medium-sized individuals, the fishery may affect the population less than if large individuals are collected.

Populations of *B. annulata* can vary in stability depending on the local environment (Nelsen 2008, Titus 2011, Chapter III), therefore management limits on collection need to be tailored on a site by site basis. For example, at high water flow sites, the resident individuals may replace any collected anemones more slowly than do residents at sites that have calmer water conditions; relatively cool-temperature sites also appear to have more stable populations and to suffer less mortality and shrinkage than do areas subject to consistently hotter water temperatures. Designating protected areas for these anemones would allow protected populations to replenish nearby harvested areas. Scott et al. (2011) observed a > 500% increase in abundance of the giant sea anemone *Entacmaea quadriolor* in Australia over 14 years, due in part to long-term protection from harvest. Reserves on the Great Barrier Reef (28% of the local reef area) are known to produce ~50% of all juvenile recruits on both reserve and fished reefs, of important coral reef species such as coral trout (*Plectropomus maculatus)* and stripey snapper (*Lutjanus carponotatus,* Harrison et al. 2012). Reserves in Papua New Guinea also are known to produce ~20% of recruited individuals of squaretail coral grouper *Plectropomus areolatus*, in surrounding fished areas (Almany et al. 2013). In a species of anemone with unknown larval dispersal, the same is possible with *B. annulata.* Protected reserves would allow the survival of individuals, which could then support nearby downstream communities by supplying recruits to area where this species is collected.

Bartholomea annulata is known to spawn twice a year, once around November and once in the spring, around April (Jennison 1981). It is important to support and protect these breeding seasons to maximize reproductive output. A harvest closure of 2-3 months each year would allow the reproducing individuals a chance to spawn before potential collection. This window would also provide time for settlement and growth of new recruits for harvest, thus a window around the predicted November and April spawnings (Jennison 1981) would support population growth and sustainability for *B. annulata*.

Based on the population dynamics of this species in Florida presented here, plus the laboratory dynamics described in Chapter III, in combination with population information from the US Virgin Islands (Nelsen 2008), I recommend the following steps to support the sustainable management of this species: (1) Establish a size limit of *B. annulata* individuals for harvest, which potentially would be a slot limit that allows collection only of individuals in Size Class II (30 - 70 cm^2 TCSA). (2) Designate protected areas to replenish nearby populations on fished and/or degraded reefs, especially those down-current. (3) Seasonally close the fishery during spawning seasons for this anemone, specifically November to March, to allow for gamete output by mature individuals to replenish populations each year.

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Table 2.1. Size-based transition matrices for populations of the corkscrew sea anemone *Bartholomea annulata*, at 2 sites in the Florida Keys, Quarry and Cudjoe. Patterns of individual growth, shrinkage, and stasis are shown for each 2 months over 1 year. Bold numbers indicate within each matrix the transition of highest elasticity, or of multiple transitions that each had elasticity > 0.2, indicating the most influence on population size. If there was no elasticity > 0.2 then the highest elasticity was bolded. q_x = mortality rate, q_x N = number of deaths, and R_n = number of recruits. Recruitment was reported in the matrices, simulating a closed population. The Cudjoe site (Table B) was not surveyed in November 2014 due to a storm, so values in the 2 matrices between Sept. 2014 and Jan. 2015 were interpolated (indicated with **), and both recruitment and mortality were not reported for Nov. 2014 – Jan. 2015.

A. Quarry site

	May – July 2014			July – Sept. 2014			Sept. – Nov. 2014		
	I	**II**	**III**	**I**	**II**	**III**	**I**	**II**	**III**
I	**0.55**	0.24	0.65	0.16	0.00	**1.48**	0.31	0.07	0.66
II	0.19	0.33	0.30	0.41	0.34	0.12	0.22	0.29	0.14
III	0.09	0.38	0.48	0.30	0.62	**0.80**	0.16	0.48	**0.59**
q_x	0.19	0.05	0.04	0.14	0.03	0.04	0.31	0.17	0.25
q_x N	10	1	1	6	1	1	10	7	18
R_n	7	5	1	23	13	21	21	25	20
N	53	21	23	44	29	25	32	42	73

	Nov. 2014 – Jan. 2015			Jan. – Mar. 2015			Mar. – May 2015		
	I	**II**	**III**	**I**	**II**	**III**	**I**	**II**	**III**
I	0.19	0.09	**1.08**	0.23	0.02	0.31	0.38	0.03	0.42
II	0.28	0.13	0.18	0.20	0.18	0.01	0.31	**0.45**	0.08
III	0.17	0.33	**0.41**	0.29	0.38	**0.71**	0.13	0.32	**0.71**
q_x	0.26	0.42	0.33	0.29	0.42	0.26	0.19	0.19	0.17
q_x N	9	23	29	10	19	19	3	6	16
R_n	19	9	7	6	15	15	24	13	10
N	36	55	87	35	45	72	16	31	93

B. Cudjoe site

	May – July 2014			July – Sept. 201			Sept. – Nov. 2014 **		
	I	**II**	**III**	**I**	**II**	**III**	**I**	**II**	**III**
I	**0.63**	0.19	0.86	0.14	0.10	**1.20**	0.38	0.00	0.34
II	0.26	0.43	0.32	0.54	0.33	0.00	0.25	0.59	0.03
III	0.00	0.10	0.32	0.18	0.47	**0.60**	0.00	0.19	**0.89**
q_x	0.11	0.24	0.05	0.11	0.10	0.10	0.38	0.26	0.09
q_x N	2	5	1	3	3	1	6	7	3
R_n	7	5	2	8	4	5	8	4	5
N	19	21	22	28	30	10	16	30	35

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	Nov. 2014 – Jan. 2015**			Jan. – Mar. 2015			Mar. - May 2015		
	I	**II**	**III**	**I**	**II**	**III**	**I**	**II**	**III**
I	0.50	0.14	0.03	0.07	0.00	0.16	0.00	0.00	0.13
II	0.50	**0.57**	0.08	0.33	0.29	0.07	0.67	0.16	0.15
III	0.00	0.29	**0.89**	0.13	0.43	**0.63**	0.00	0.37	**0.55**
q_x	0.00	0.00	0.00	0.47	0.29	0.24	0.33	0.47	0.28
q_x N	0	0	0	7	6	10	1	9	11
R_n	N/A	N/A	N/A	1	4	1	2	2	1
N	6	21	36	15	21	43	3	19	40

Table 2.2. Elasticities calculated based on size-based transition matrices for populations of the corkscrew sea anemone *Bartholomea annulata*, at 2 sites in the Florida Keys, Quarry and Cudjoe. Elasticities are proportional sensitivities based on patterns of individual growth, shrinkage, and stasis, and are shown for each 2 months over 1 year.

A. Quarry

	May – July 2014			July – Sept. 2014			Sept. – Nov. 2014		
	I	**II**	**III**	**I**	**II**	**III**	**I**	**II**	**III**
I	0.19	0.04	0.12	0.03	0.00	0.23	0.08	0.01	0.17
II	0.10	0.09	0.08	0.10	0.04	0.03	0.09	0.06	0.05
III	0.07	0.14	0.18	0.13	0.13	0.31	0.09	0.13	0.32

	Nov. 2014 – Jan. 2015			Jan. – Mar. 2015			Mar. – May 2015		
	I	**II**	**III**	**I**	**II**	**III**	**I**	**II**	**III**
I	0.07	0.02	0.23	0.05	0.00	0.15	0.08	0.01	0.13
II	0.11	0.02	0.05	0.04	0.01	0.01	0.08	0.10	0.03
III	0.14	0.14	0.23	0.11	0.05	0.58	0.05	0.11	0.41

B. Cudjoe

	May – July 2014			July – Sept. 2014			Sept. – Nov. 2014 **		
	I	**II**	**III**	**I**	**II**	**III**	**I**	**II**	**III**
I	0.39	0.08	0.06	0.03	0.02	0.24	0.03	0.00	0.05
II	0.15	0.16	0.02	0.16	0.06	0.00	0.05	0.10	0.01
III	0.00	0.09	0.05	0.09	0.15	0.25	0.00	0.06	0.68

	Nov. 2014 – Jan. 2015			Jan. – Mar. 2015			Mar. – May 2015		
	I	**II**	**III**	**I**	**II**	**III**	**I**	**II**	**III**
I	0.05	0.04	0.02	0.01	0.00	0.09	0.00	0.00	0.07
II	0.05	0.14	0.05	0.06	0.07	0.06	0.07	0.05	0.10
III	0.00	0.07	0.57	0.03	0.12	0.58	0.00	0.17	0.54

Table 2.3. Variation among size classes of the corkscrew sea anemone *Bartholomea annulata*, in the mean percent of individuals (± S.E.M.) that displayed growth, shrinkage, stasis, or mortality (based on TCSA, N/A = not applicable), during 2-month periods (N = 6) over 1 year, at 2 field sites in the Florida Keys.

A. Quarry site	**Size Class I**	**Size Class II**	**Size Class III**
Growth	39.0 ± 8.7%	41.8 ± 4.6%	N/A
Shrinkage	N/A	7.6 ± 3.5%	18.4 ± 5.7%
Stasis	30.3 ± 5.9%	28.7 ± 4.8%	62.0 ± 15.3%
Mortality	22.8 ± 2.8%	21.4 ± 7.0%	18.3 ± 4.9%

B. Cudjoe site	**Size Class I**	**Size Class II**	**Size Class III**
Growth	42.5 ± 8.2%	35.3 ± 6.6%	N/A
Shrinkage	N/A	8.0 ± 3.6%	22.3 ± 9.0%
Stasis	20.6 ± 11.1%	28.6 ± 4.6%	57.0 ± 7.9%
Mortality	24.0 ± 7.0%	27.1 ± 6.0%	21.3 ± 4.4%

Table 2.4. Annual population turnover rates and times of the corkscrew sea anemone *Bartholomea annulata*, calculated from patterns of mortality, recruitment, and abundance, during each 2-month period over 1 year at 2 sites in the Florida Keys. All recruits were used in this table, including those >50 cm^2 TCSA to accurately estimate turnover (see text for details).

A. Quarry site

	Mortality	Recruits	N_i	N_{i+1}	Turnover Rate per 2 month period	Turnover Time (months)
May - July 2014	12	13	97	98	0.13	15.60
July - Sept. 2014	8	57	98	147	0.27	7.54
Sept - Nov. 2014	35	66	147	178	0.31	6.44
Nov. 2014 -Jan. 2015	61	35	178	152	0.29	6.95
Jan. - Mar. 2015	48	36	152	140	0.29	6.95
Mar. - May 2015	25	47	140	162	0.24	8.40
All periods (mean)	31.5	42.3	135.3	146.2	0.26	7.66
All periods (SE)	8.4	7.6	13.1	11.0		

B. Cudjoe site

A.	Mortality	Recruits	N_i	N_{i+1}	Turnover Rate	Turnover Time
May - July 2014	8	14	62	68	0.17	11.82
July - Sept. 2014	7	17	68	78	0.16	12.17
Sept. 2014 - Jan. 2015	16	17	78	79	0.21	9.52
Jan. - Mar. 2015	23	6	79	62	0.21	9.72
Mar. - May 2015	21	5	62	46	0.24	8.31
All periods (mean)	15.0	11.8	69.8	66.6	0.20	10.18
All periods (SE)	3.3	2.6	3.7	6.0		

Figure Legends

Fig. 2.1. A. Numbers of marine life commercial fishing permits issued by the Florida Fishing and Wildlife Conservation Commission (FWC) from 1990 to 2014 to collect corkscrew sea anemones *Bartholomea annulata* (and other non-food fish and invertebrates) for the ornamental aquarium trade, and number of individuals of *B. annulata* landed by commercial fishers from 1994-2014 (2014 data are preliminary; pers. comm. Nancy Sheridan, FWC). Note that a peak of 776 permits were issued in 1997, one year before limits were implemented on the number of permits issued (http://myfwc.com/research/saltwater/fishstats/commercial-fisheries/landings-in-florida/). Each permit allowed the holder to collect up to hundreds of thousands of organisms each year, with no limits set on numbers collected. Data are from the trip ticket program of the Florida Fish and Wildlife Conservation Commission. (http://myfwc.com/research/saltwater/fishstats/commercial-fisheries/landings-in-florida/ and pers. comm. Nancy Sheridan). B. Mean number of *Bartholomea annulata* individuals landed per each marine life commercial fishing permit, 1994-2014. Note that even after the number of issued permits was reduced to a relatively low, stable level in 2006, the number of these anemones collected per permit continued to plummet, reaching an all-time low in 2014.

Fig. 2.2. Expanded individual of the corkscrew sea anemone *Bartholomea annulata* at the Quarry site in the Florida Keys, showing the horizontally-oriented (facing upwards) oral disk and tentacles.

Fig. 2.3. Map of 6 study sites in the Florida Keys: 2 each in the Lower, Middle, and Upper Keys. 1. Cudjoe 2. Bowman's Channel 3. Tiki Hut 4. Quarry 5. Robbie's 6. Indian Channel. Within

each region, the circled number indicates a high-impact site, and the number without a circle indicates a low-impact site (see text for details).

Fig. 2.4. Diagram and photograph taken under laboratory conditions of the corkscrew sea anemone *Bartholomea annulata*, showing a side view of: A. Tentacle crown width, and B. Pedal disc diameter.

Fig. 2.5. Diagram and photograph at Quarry field site (with engraved aluminum tag adjacent) of the corkscrew sea anemone *Bartholomea annulata*, showing a top view of: A. Tentacle crown width, B. Tentacle crown length (both A and B were used to calculate tentacle crown surface area, TCSA), and C. Oral disk diameter.

Fig. 2.6. Population size frequency of new individuals observed to recruit into populations of the corkscrew sea anemone *Bartholomea annulata* during 1 year of surveys every 2 months, at 2 sites in the Florida Keys: A. Quarry, and B. Cudjoe. Note that the majority of new individuals were $< 50\ \text{cm}^2$ Tentacle Crown Surface Area (TCSA) in body size (see text for details).

Fig. 2.7. Regional climate data from NOAA buoys near study sites in the Florida Keys. A. Average monthly temperature (ºC) May 2014 - May 2015 for Upper, Middle, and Lower Keys. Note the high temperature variability in the Lower Keys. B. Average monthly wind speed (m/s) May 2014 - May 2015. Note that the Middle Keys had significantly lower wind speeds on average than the other two regions.

Fig. 2.8. Variation among 6 sites in the Florida Keys, in: A. Percent cover of live stony corals. B. Abundance of the corkscrew sea anemone *Bartholomea annulata*. Bars that have the same letter above them in each graph are not significantly different. Note that high-impact sites had

significantly less coral cover than did low-impact sites, and Lower Keys sites had significantly less coral cover than did sites in the other 2 regions (see statistical tests in the text).

Fig. 2.9. Variation among 6 sites in the Florida Keys, in the population size structure of corkscrew sea anemones *Bartholomea annulata*. Graphs are grouped by region (rows) and level of human impact (columns); and population size structure varied significantly with both factors (see text for details).

Fig. 2.10. Variation in orientation and microhabitat of corkscrew sea anemones *Bartholomea annulata*, between 2 sites in the Florida Keys. A. Proportion of individuals that each contacted hard, soft or both hard and soft substrate. B. Proportion of individuals that oriented their oral disks horizontally or vertically. Note that Cudjoe had significantly more vertically-oriented anemones than did the Quarry site (see text for statistical test).

Fig. 2.11. Variation in the body sizes of all corkscrew sea anemones *Bartholomea annulata*, over 1 year at 2 sites in the Florida Keys. Note that sea anemones at Cudjoe wer significantly larger at the initial time point, but at every other time point, body size did not differ between sites (see text for details of statistical tests).

Fig. 2.12. Variation in absolute growth rates of corkscrew sea anemones *Bartholomea annulata* with size class, at 2 sites in the Florida Keys. Growth rates did not differ significantly between the 2 sites, but varied significantly with size class at the Quarry site (see text for details).

Fig. 2.13. Variation in the initial body sizes of corkscrew sea anemones *Bartholomea annulata* at the beginning of the study in May 2014, with size class at 2 sites in the Florida Keys. A. Quarry. B. Cudjoe.

Fig. 2.14. Demographic rates of corkscrew sea anemones *Bartholomea annulata* at the Quarry site, Florida Keys. A. Proportion of the population exhibiting growth (transition into a larger size class), recruitment (number of recruits/resident), and stasis (remaining within the same size class) over the course of the study. B. Proportion of the population exhibiting shrinkage (transition into a smaller size class) and mortality over the course of the study.

Fig. 2.15. Demographic rates of corkscrew sea anemone, *Bartholomea annulata* at 1 site in the Florida Keys (Cudjoe). A**.** Proportion of the population exhibiting growth (transitions from one size class to a larger one), recruitment (number of recruits/resident), and stasis (remaining within the same size class) over the course of the study. B. Proportion of population exhibiting shrinkage (transitions from one size class to a smaller one) and mortality over the course of the study.

Fig. 2.16. Dynamic survival curves for corkscrew sea anemones *Bartholomea annulata* at 2 sites in the Florida Keys. A. Quarry B. Cudjoe.

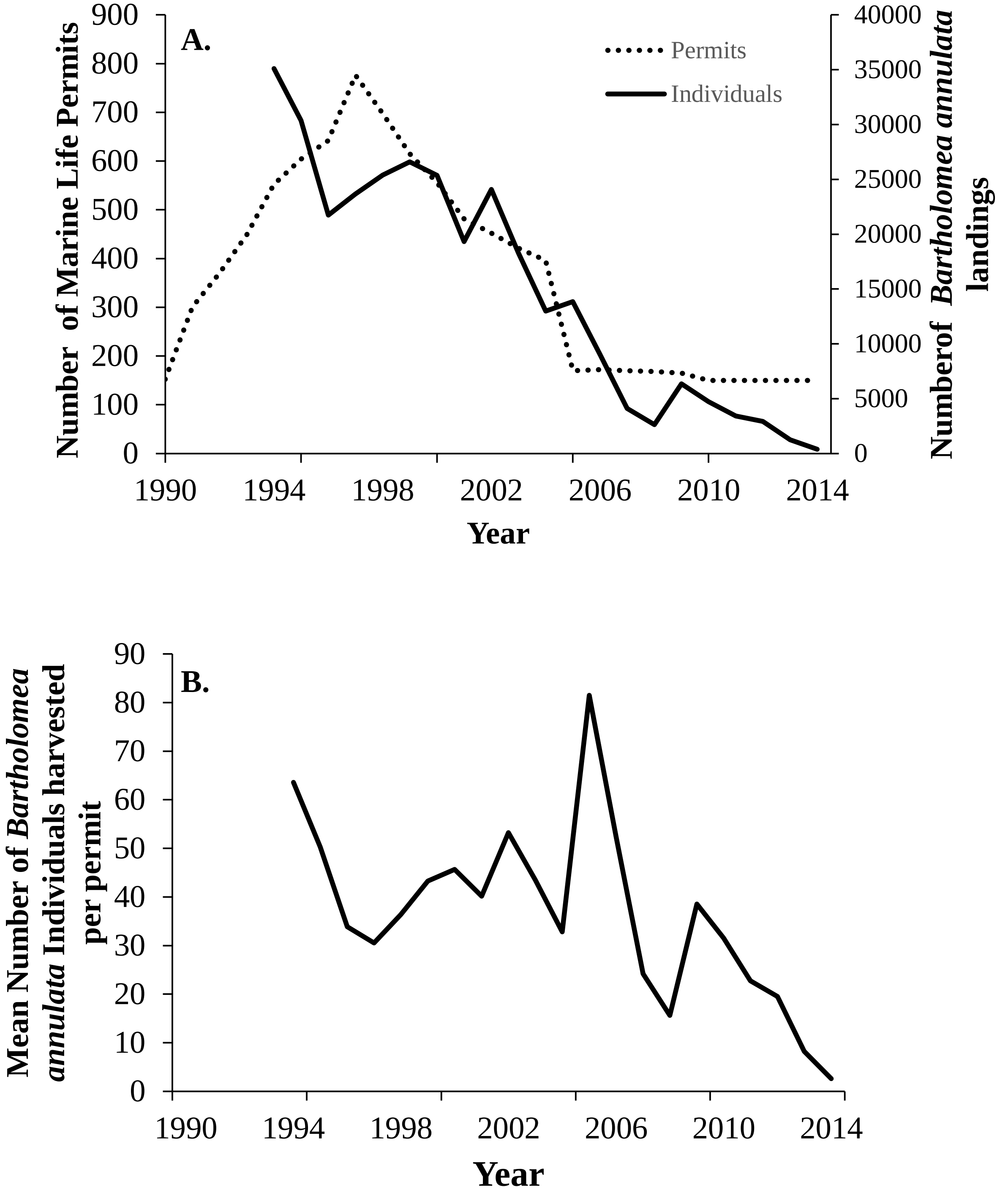
A.
Number of Marine Life Permits
900
800
700
600
500
400
300
200
100
0
Permits
Individuals
40000
35000
30000
25000
20000
15000
10000
5000
0
Numberof *Bartholomea annulata* landings
1990
1994
1998
2002
2006
2010
2014
Year
B.
Mean Number of *Bartholomea annulata* Individuals harvested per permit
90
80
70
60
50
40
30
20
10
0
1990
1994
1998
2002
2006
2010
2014
Year

Fig. 2.1.

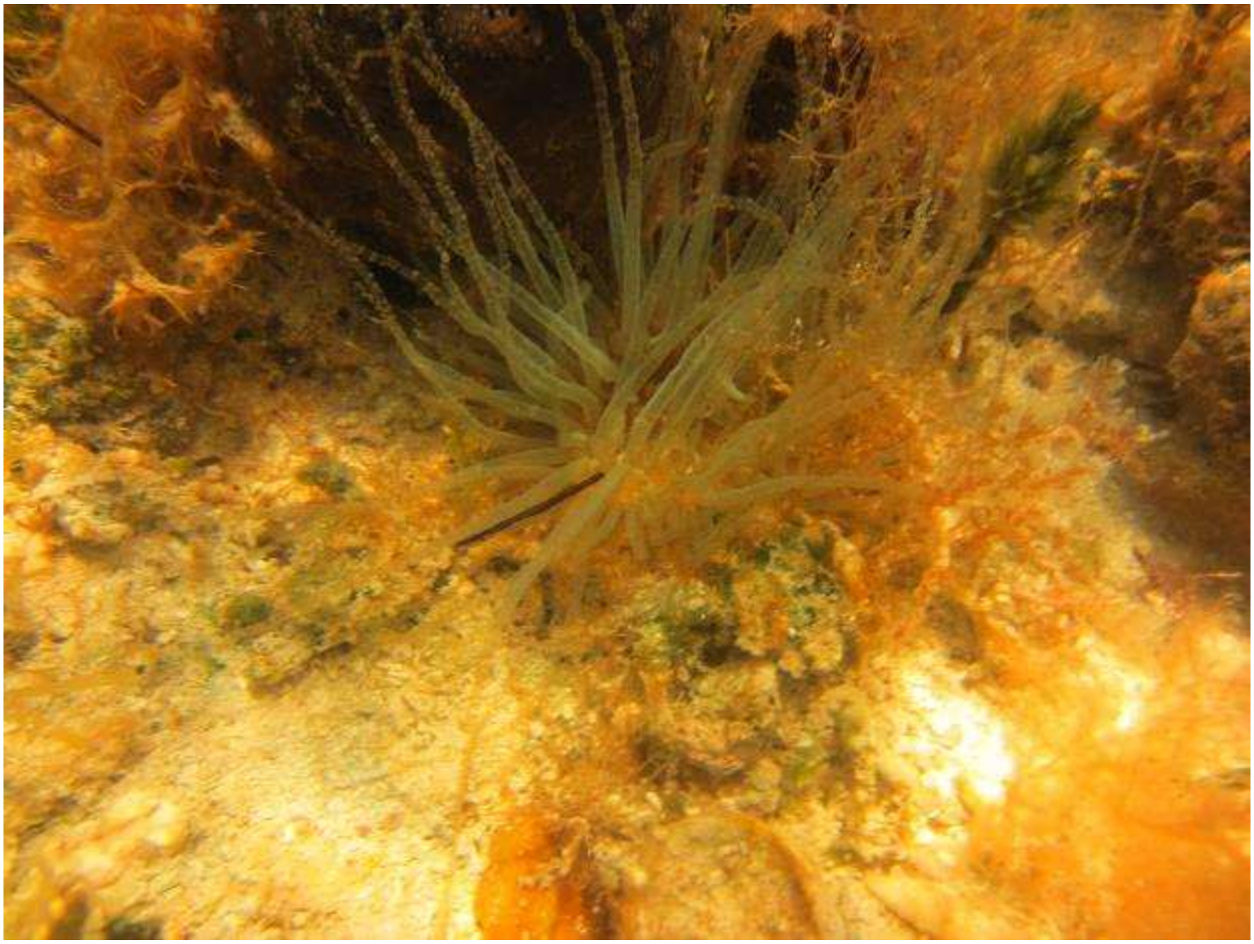

Fig. 2.2.

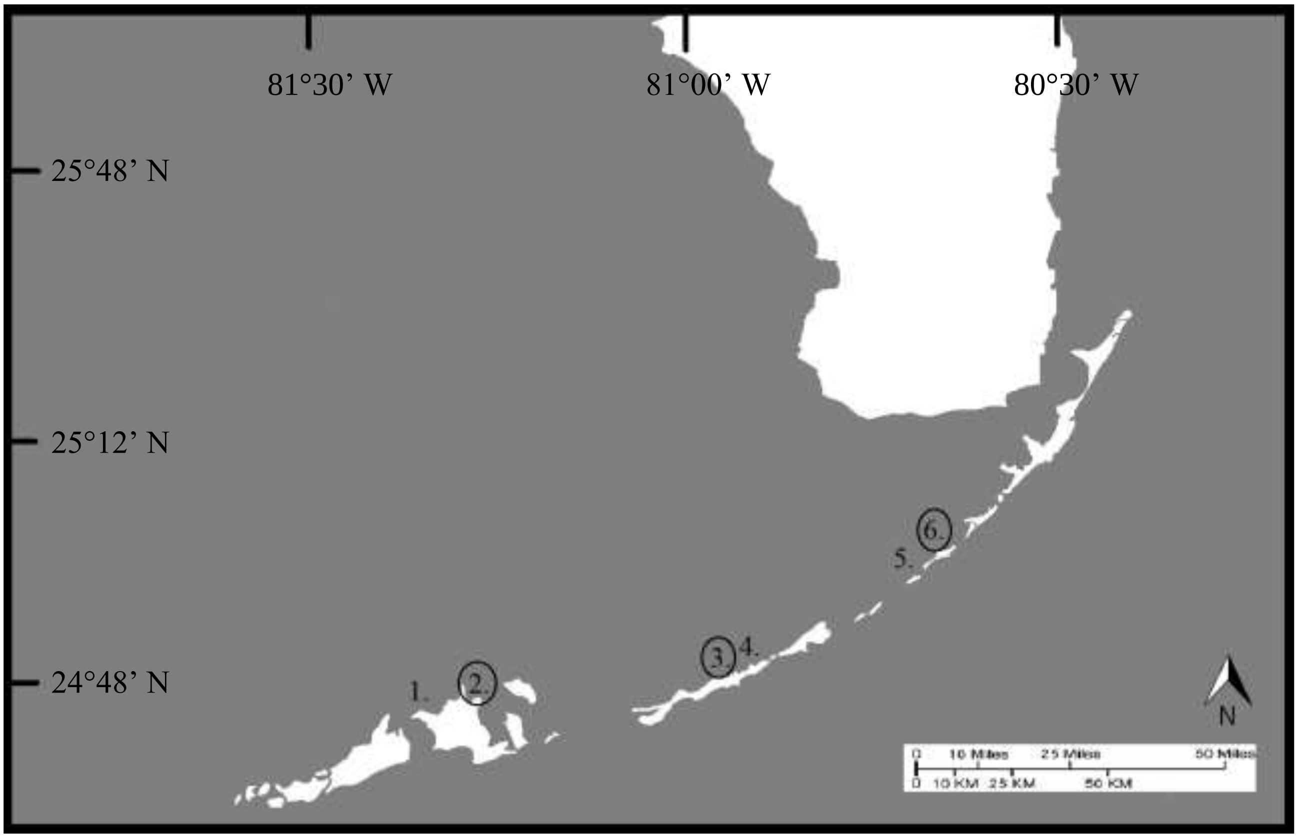
81°30’ W
81°00’ W
80°30’ W
25°48’ N
25°12’ N
24°48’ N
6.
5.
3.
4.
1.
2.
N
0 10 Miles 25 Miles 50 Miles
0 10 KM 25 KM 50 KM

Fig. 2.3.

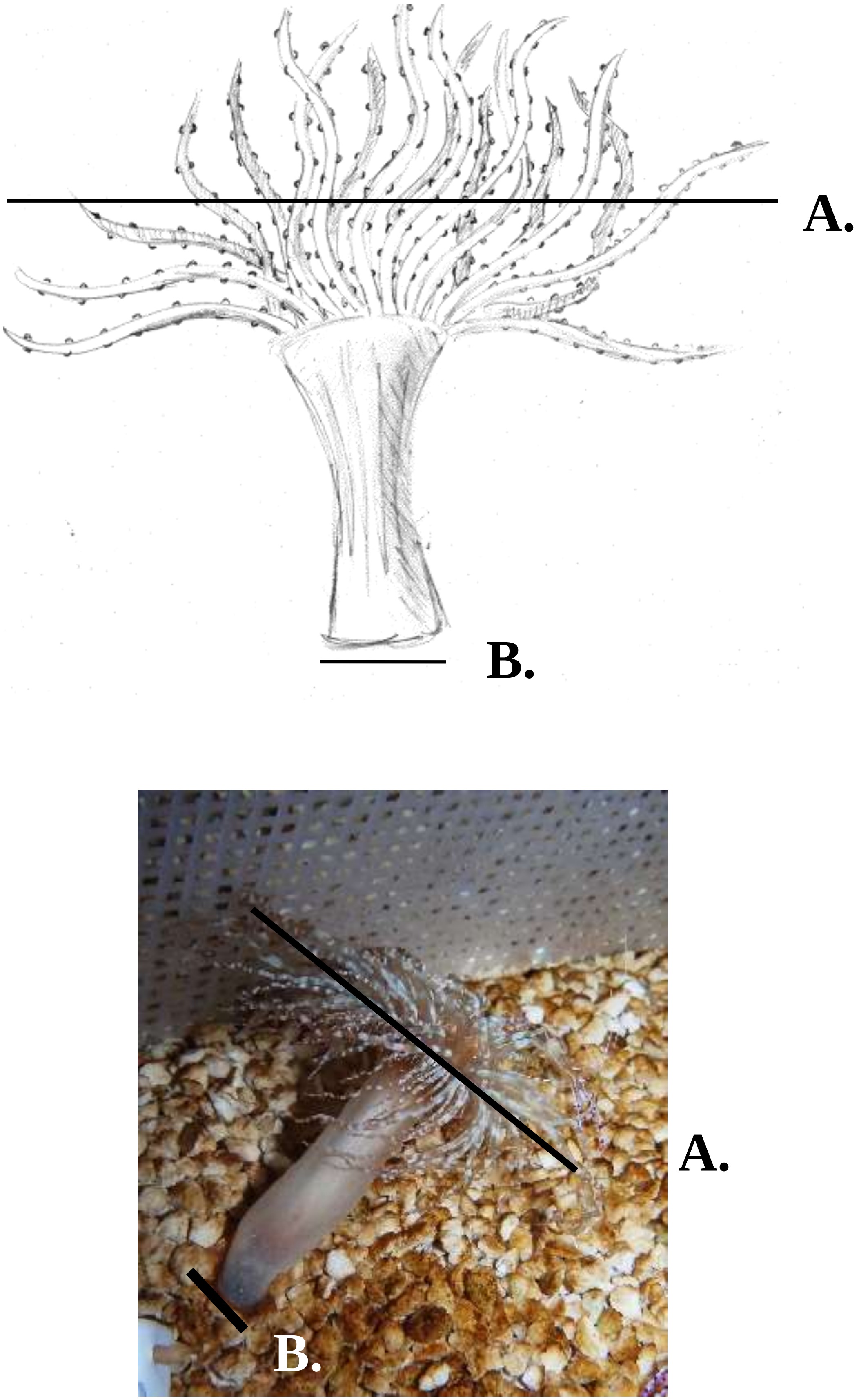

Fig. 2.4.

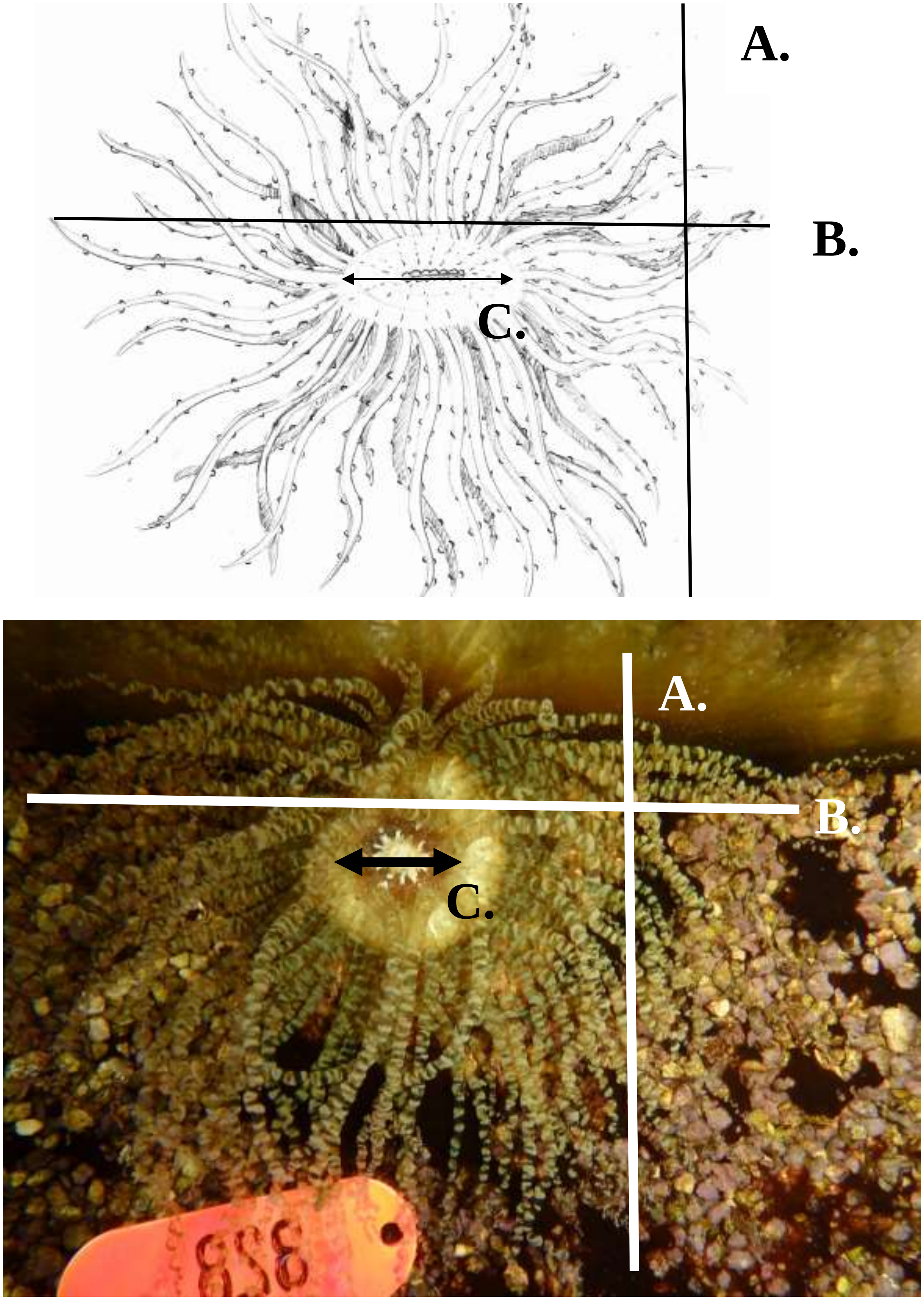

Fig. 2.5.

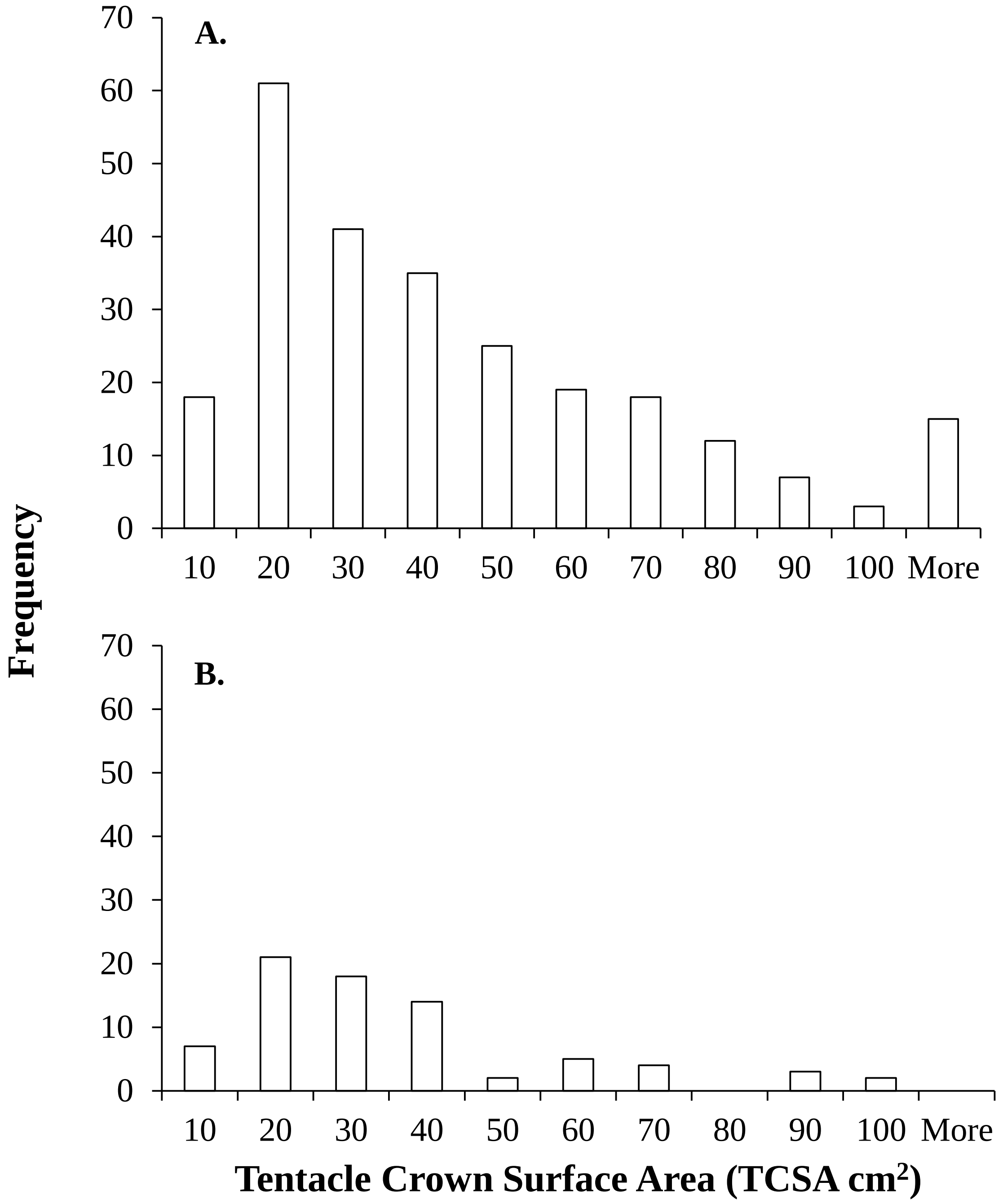
A.
B.
Frequency
0
10
20
30
40
50
60
70
10
20
30
40
50
60
70
80
90
100
More
Tentacle Crown Surface Area (TCSA cm²)

Fig. 2.6.

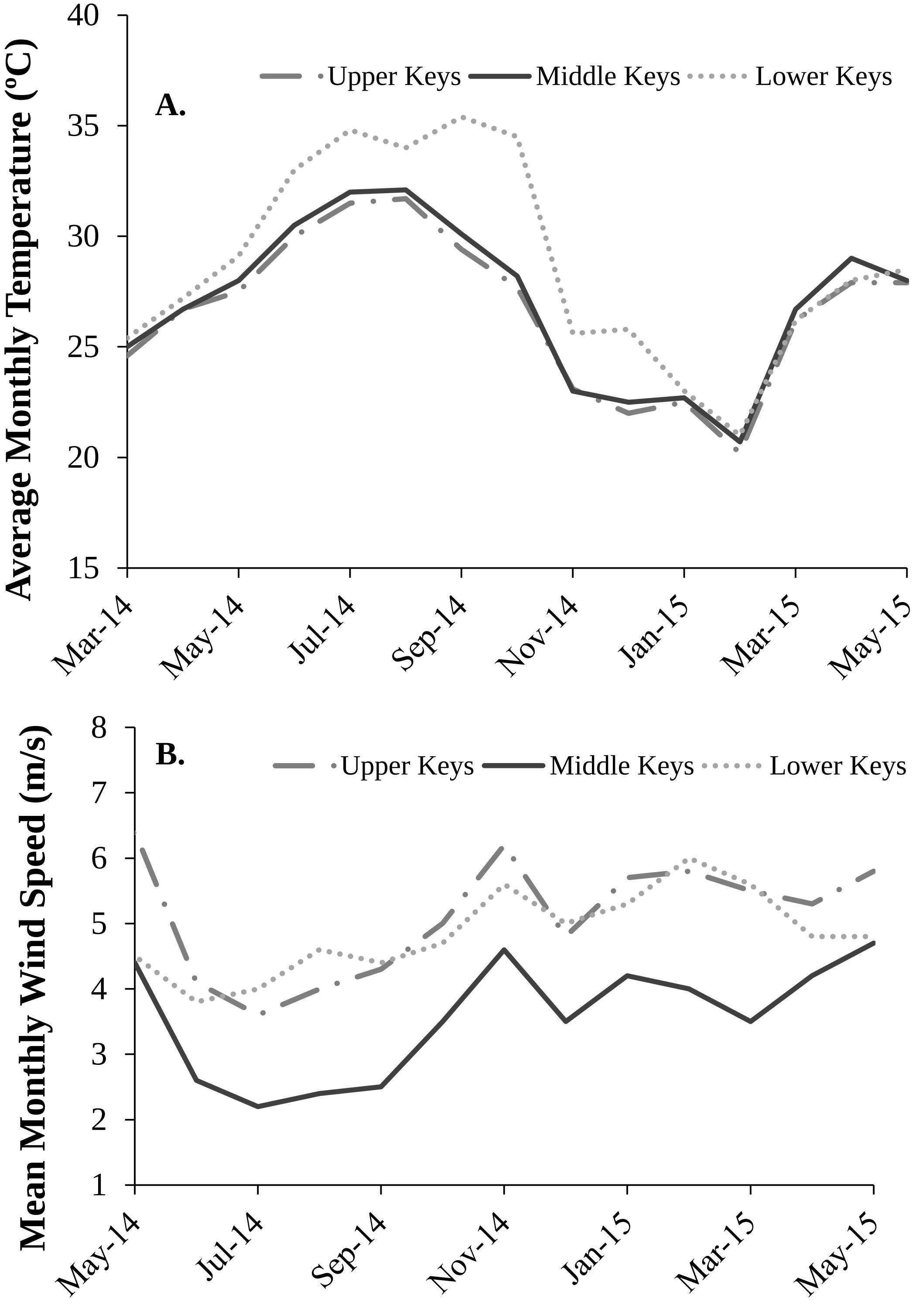
A.
Average Monthly Temperature (ºC)
40
35
30
25
20
15
Upper Keys
Middle Keys
Lower Keys
Mar-14
May-14
Jul-14
Sep-14
Nov-14
Jan-15
Mar-15
May-15
B.
Mean Monthly Wind Speed (m/s)
8
7
6
5
4
3
2
1
Upper Keys
Middle Keys
Lower Keys
May-14
Jul-14
Sep-14
Nov-14
Jan-15
Mar-15
May-15

Fig. 2.7.

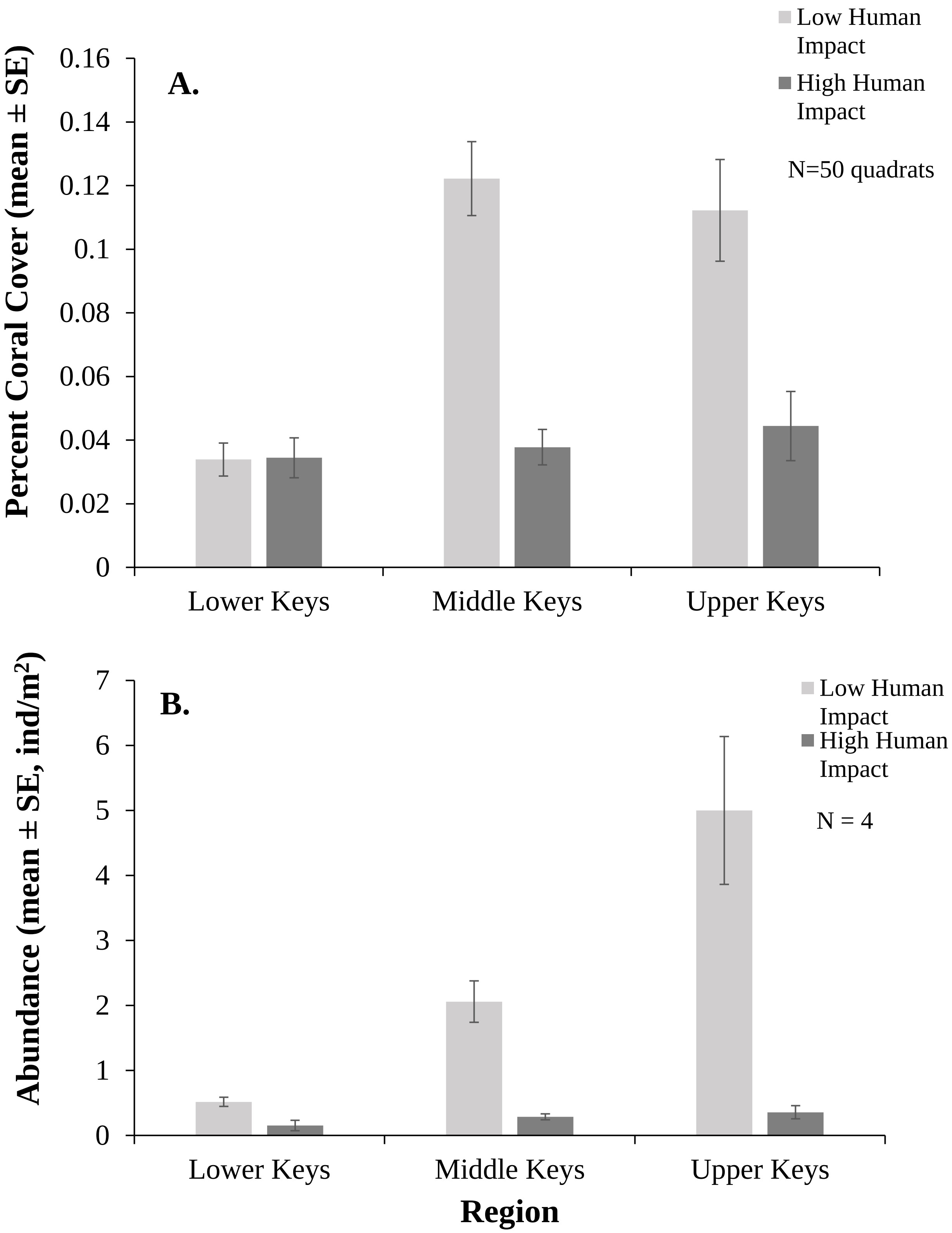
A.
Percent Coral Cover (mean ± SE)
0.16
0.14
0.12
0.1
0.08
0.06
0.04
0.02
0
Lower Keys
Middle Keys
Upper Keys
Low Human Impact
High Human Impact
N=50 quadrats
B.
Abundance (mean ± SE, ind/m^2)
7
6
5
4
3
2
1
0
Lower Keys
Middle Keys
Upper Keys
Region
Low Human Impact
High Human Impact
N = 4

Fig. 2.8.

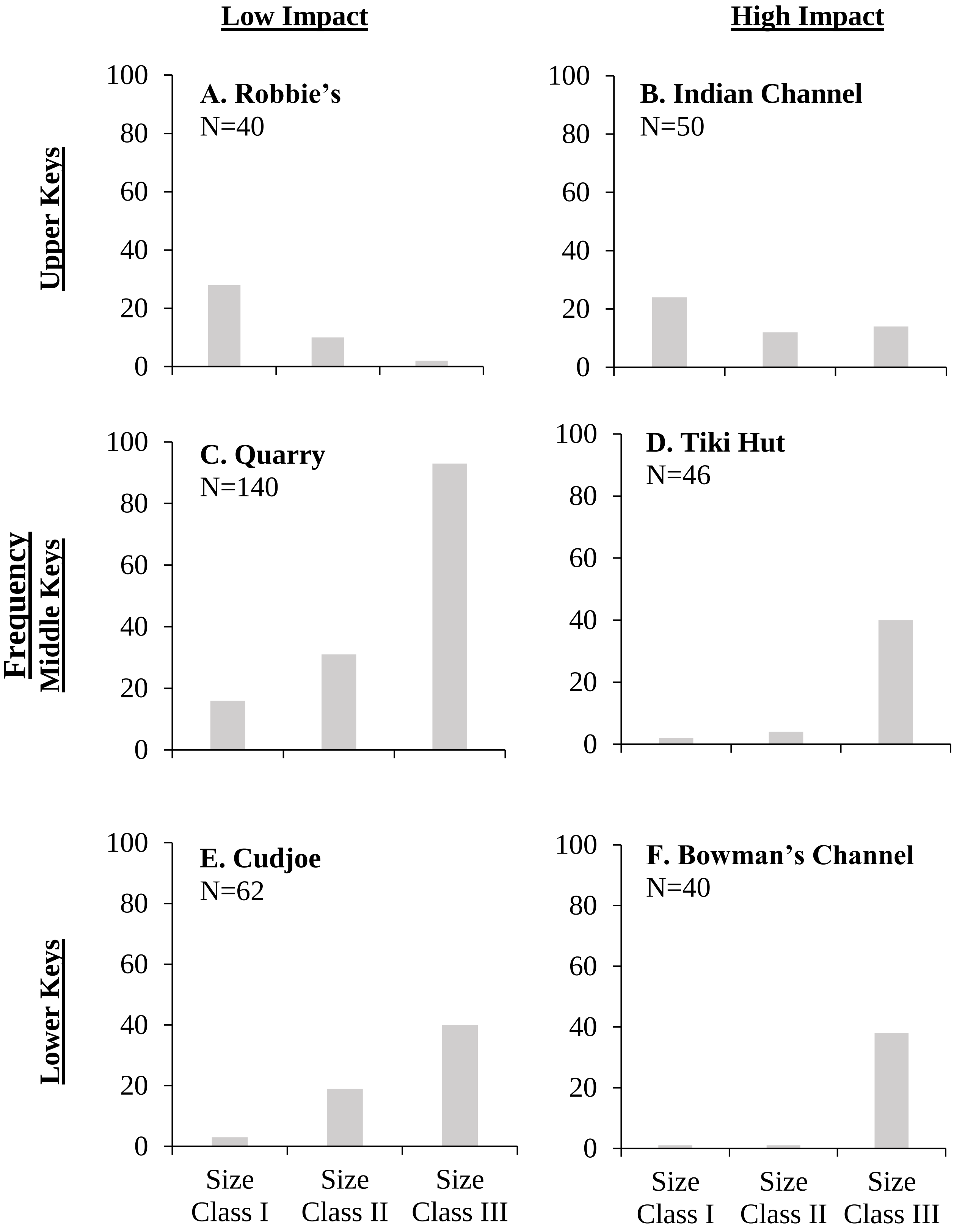
Low Impact
High Impact
Upper Keys
Frequency
Middle Keys
Lower Keys
A. Robbie's
N=40
B. Indian Channel
N=50
C. Quarry
N=140
D. Tiki Hut
N=46
E. Cudjoe
N=62
F. Bowman's Channel
N=40
100
80
60
40
20
0
Size Class I
Size Class II
Size Class III

Fig. 2.9.

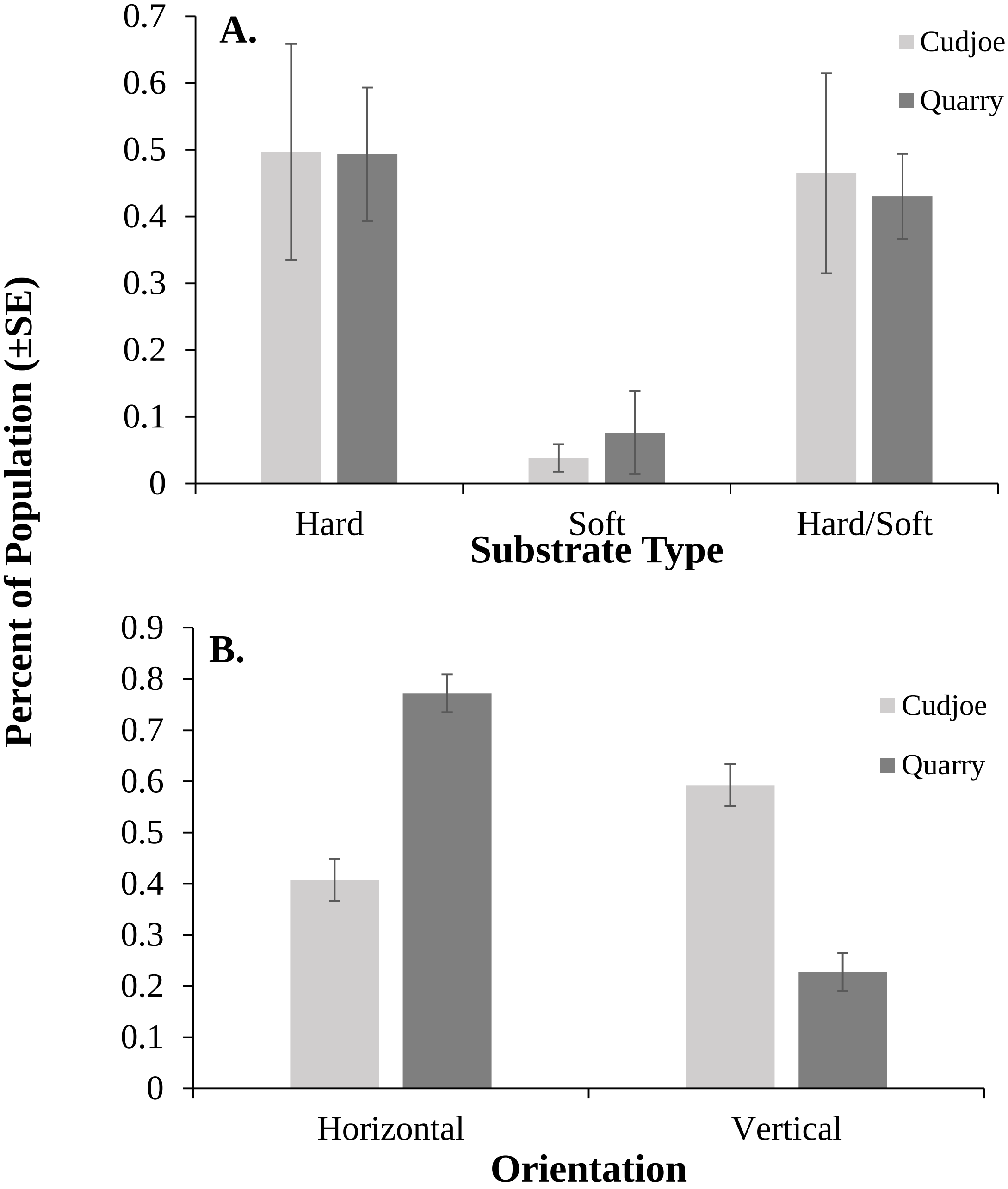
Percent of Population (±SE)
A.
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Cudjoe
Quarry
Hard
Soft
Hard/Soft
Substrate Type
B.
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Cudjoe
Quarry
Horizontal
Vertical
Orientation

Fig. 2.10.

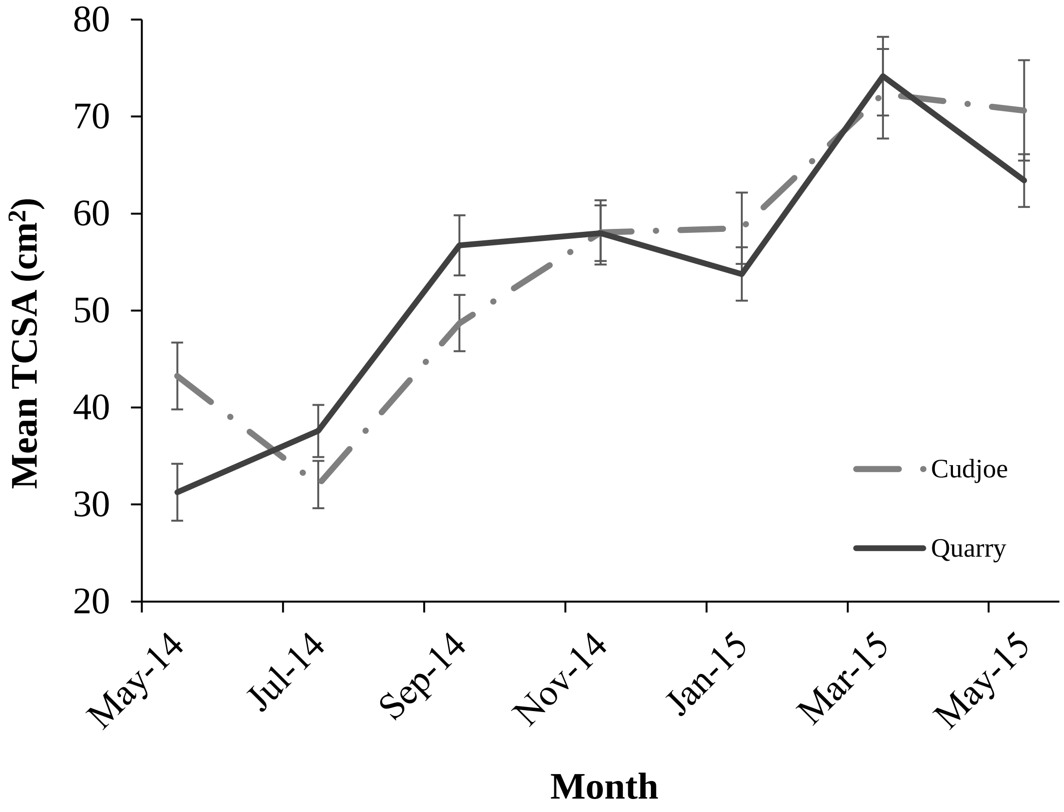
80
70
60
50
40
30
20
Mean TCSA (cm²)
Cudjoe
Quarry
May-14
Jul-14
Sep-14
Nov-14
Jan-15
Mar-15
May-15
Month

Fig. 2.11.

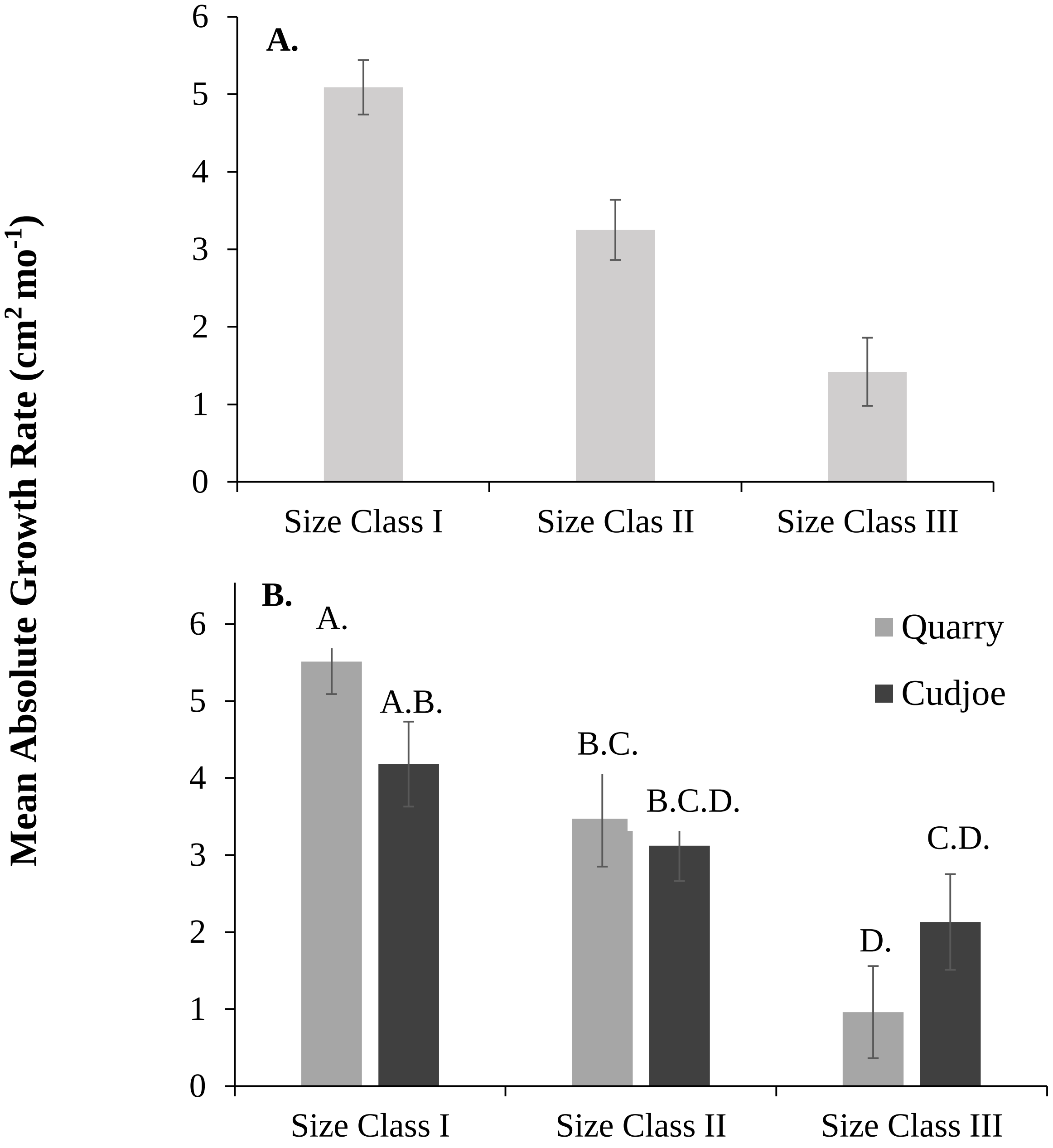
Mean Absolute Growth Rate ($cm^2 mo^{-1}$)
A.
0
1
2
3
4
5
6
Size Class I
Size Clas II
Size Class III
B.
0
1
2
3
4
5
6
A.
A.B.
B.C.
B.C.D.
D.
C.D.
Quarry
Cudjoe
Size Class I
Size Class II
Size Class III

Fig. 2.12.

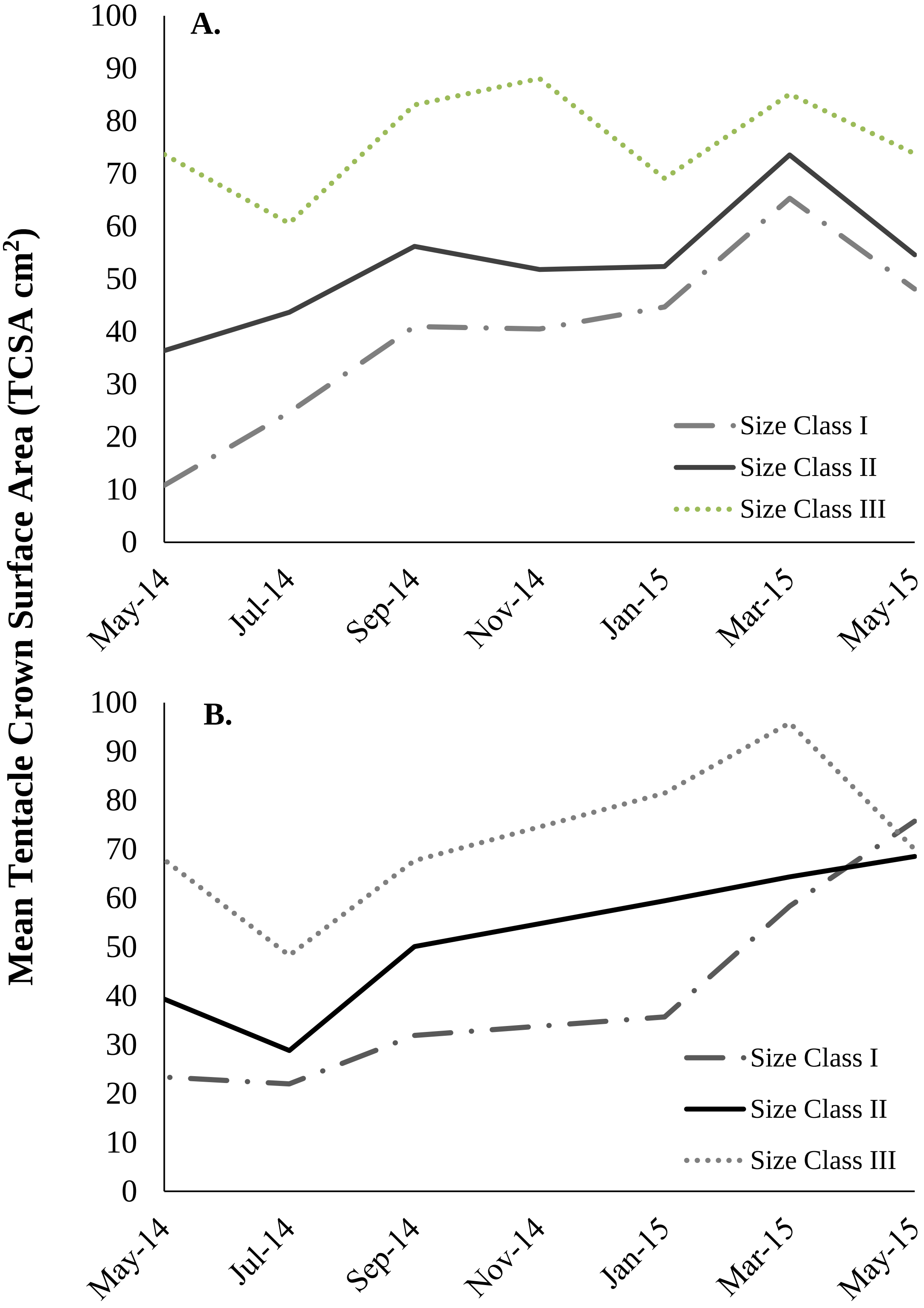
Mean Tentacle Crown Surface Area (TCSA cm^2)
A.
100
90
80
70
60
50
40
30
20
10
0
Size Class I
Size Class II
Size Class III
May-14
Jul-14
Sep-14
Nov-14
Jan-15
Mar-15
May-15
B.
100
90
80
70
60
50
40
30
20
10
0
Size Class I
Size Class II
Size Class III
May-14
Jul-14
Sep-14
Nov-14
Jan-15
Mar-15
May-15
Date

Figure 2.13.

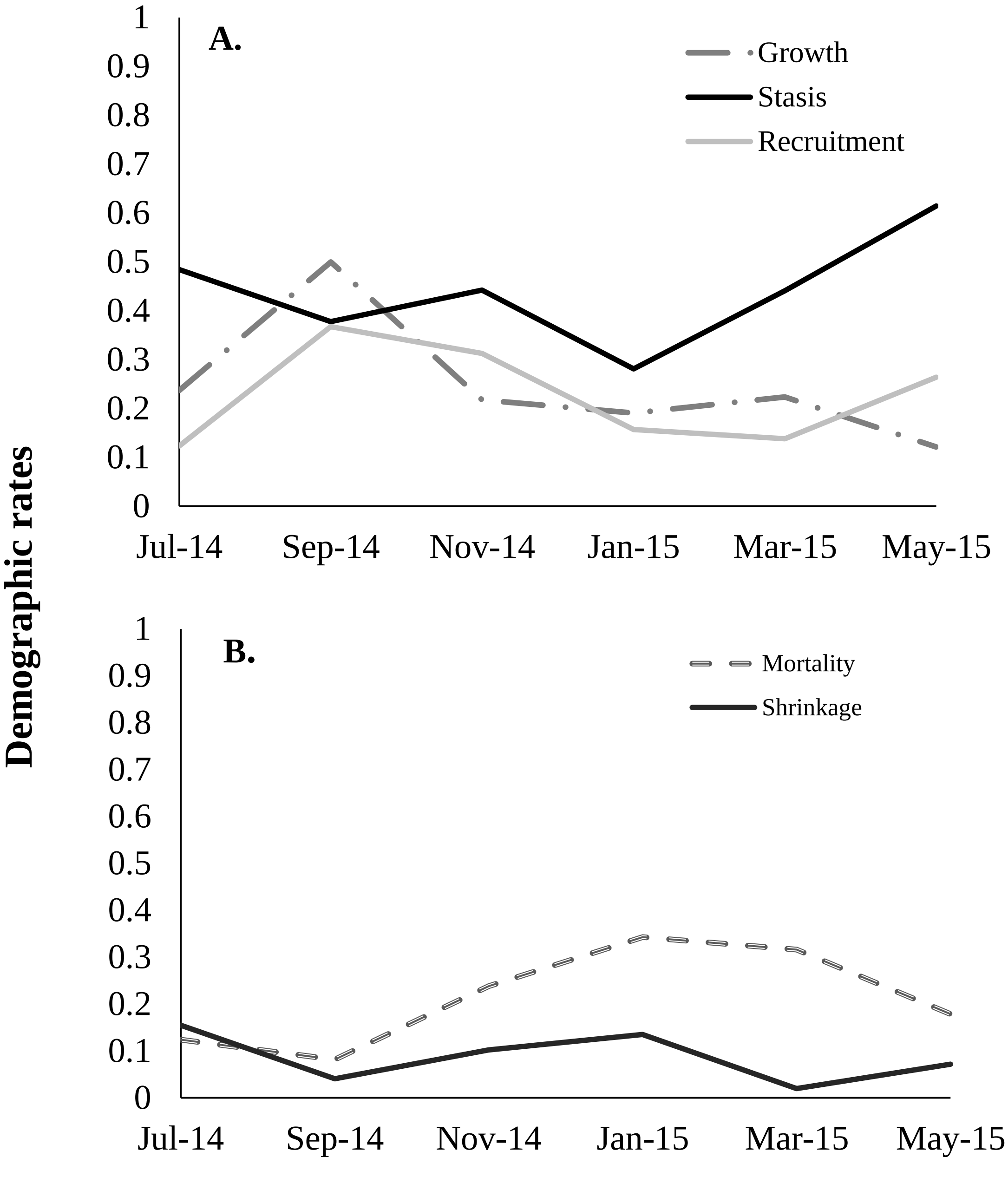
A.
Growth
Stasis
Recruitment
B.
Mortality
Shrinkage
Demographic rates
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Jul-14
Sep-14
Nov-14
Jan-15
Mar-15
May-15

Fig. 2.14.

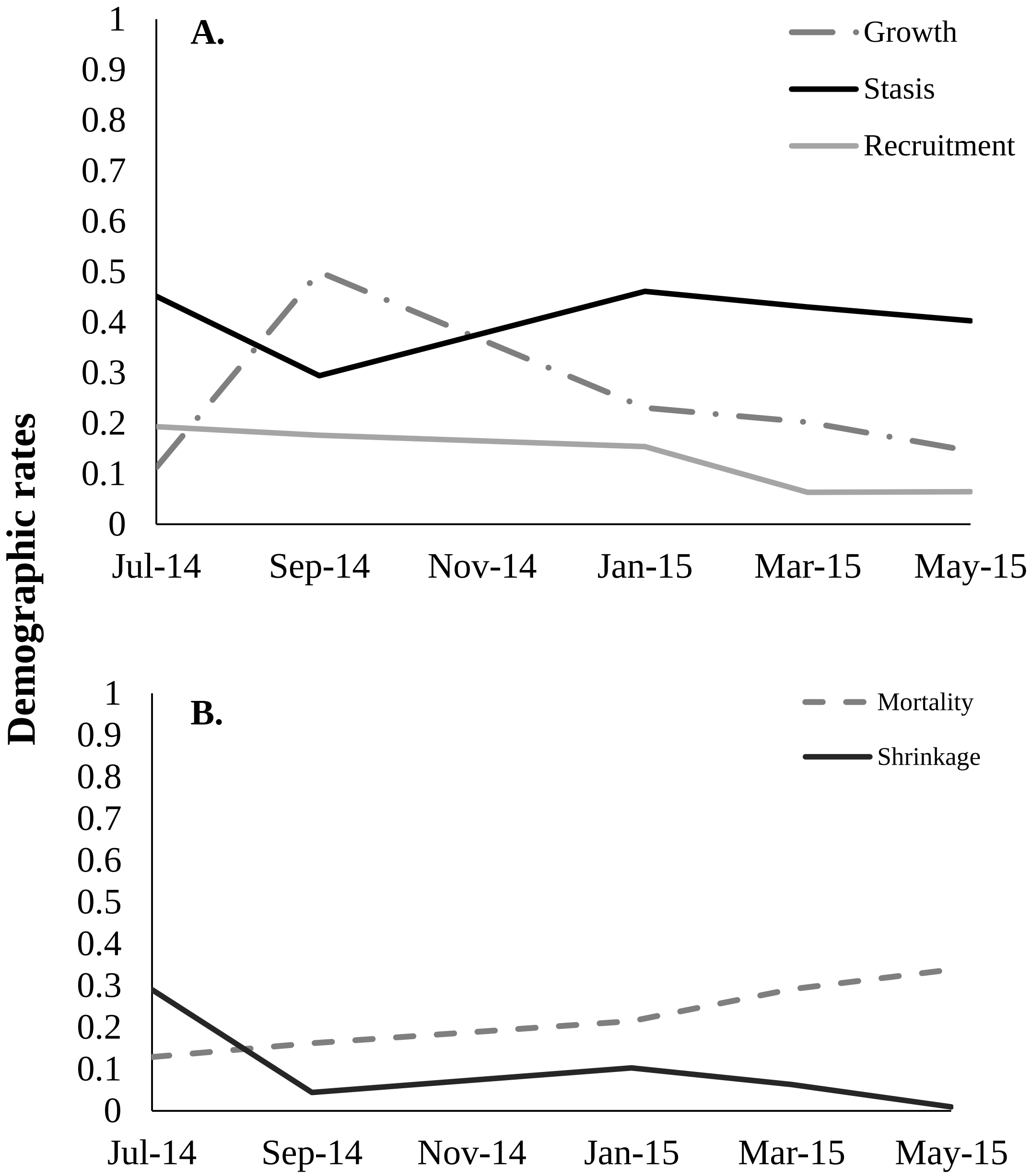
Demographic rates
A.
Growth
Stasis
Recruitment
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Jul-14
Sep-14
Nov-14
Jan-15
Mar-15
May-15
B.
Mortality
Shrinkage
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Jul-14
Sep-14
Nov-14
Jan-15
Mar-15
May-15

Fig. 2.15.

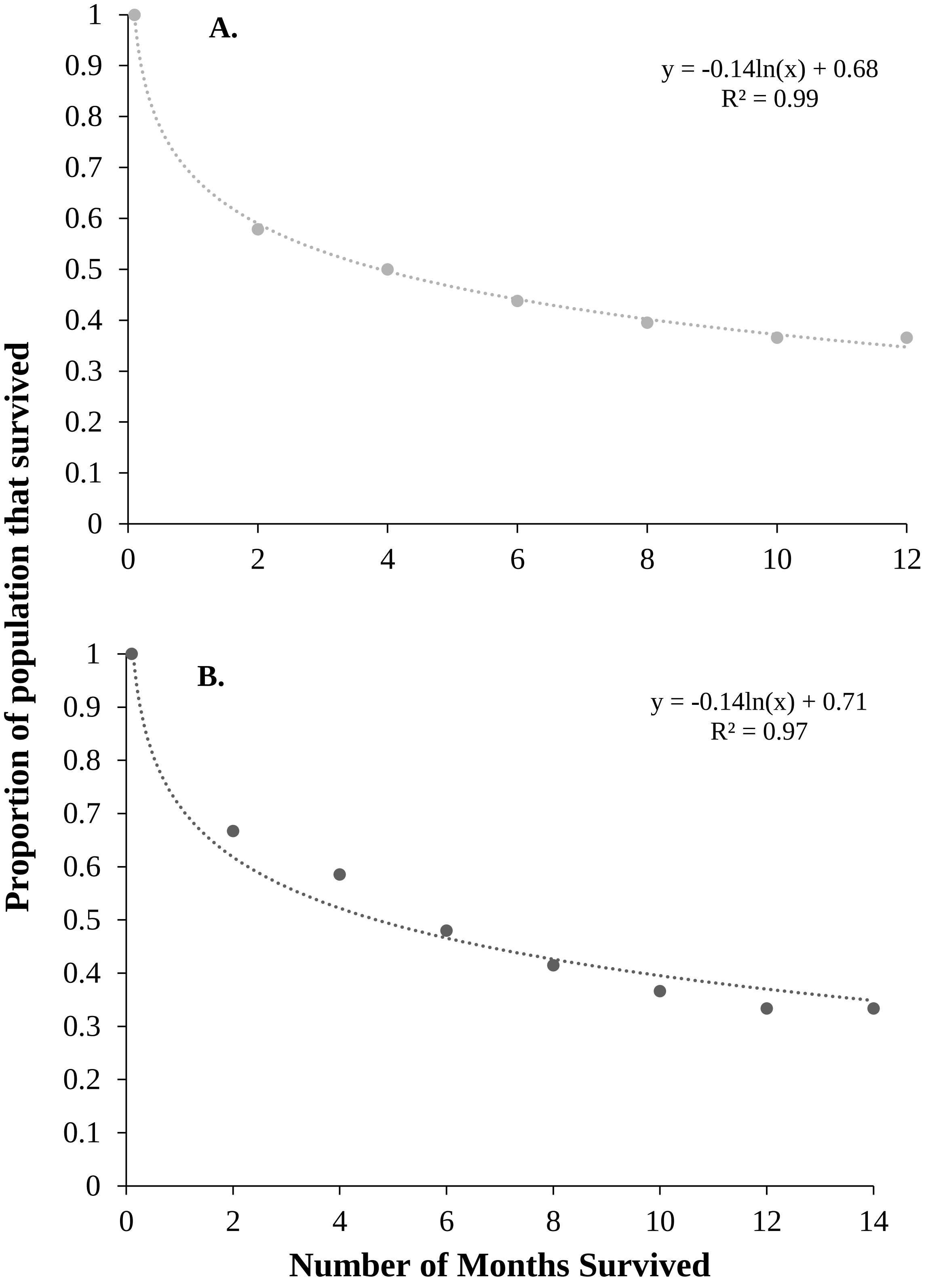
A.
y = -0.14ln(x) + 0.68
R² = 0.99
B.
y = -0.14ln(x) + 0.71
R² = 0.97
Proportion of population that survived
Number of Months Survived
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
0
2
4
6
8
10
12
14

Fig. 2.16.

Chapter III

Population dynamics of the corkscrew sea anemone *Bartholomea annulata* under laboratory conditions

Abstract

Little is known about demographic patterns in organisms with indeterminate growth such as sea anemones, which can both grow and shrink. Giant corkscrew sea anemones *Bartholomea annulata* are common throughout the Caribbean Sea, and form the center of a mutualistic network of obligate exosymbionts, including cleaner shrimp that provide positive cascade effects to diverse coral reef fishes. Individuals of *B. annulata* also are popular commodities in the ornamental aquarium trade, but their fishery is largely uncontrolled. Information on population dynamics of this important sea anemone under controlled conditions is needed to provide understanding of their potential growth rates and lifespans. I report here on the dynamics of individuals over 1 year under optimal laboratory conditions of stable water temperature and water flow, and abundant food supply and irradiance. Anemone growth rate decreased with body size; small individuals grew 2-3x as rapidly as did large individuals, in terms of absolute growth in tentacle crown surface area (TCSA), and > 15x as rapidly in terms of percent body growth. Overall growth rate was about 8 cm^2 per month until individuals reached ~ 150 cm^2 TCSA body size, then they remained static or shrank. Only ~ 50% of individuals survived the year of study; most mortality occurred in very small or large individuals, which shrank for 1-6 months prior to death, indicating possible senescence. Individuals remained mostly stationary with their bases attached to hard substrate, or locomoted slowly across the substratum at ~ 2-3 cm/month. All measures of body size (TCSA, oral and pedal disk diameter, wet and dry weight) were highly correlated, indicating that linear and areal body dimensions infer body mass. I conclude that under optimal conditions, individuals of this sea anemone are able to grow rapidly when small, cease growth at a maximal body size of ~ 150 cm2 TCSA, and then gradually shrink before dying at ~ 1.5 years of age. They attach their bases to hard substratum and then locomote slowly or not at all. These laboratory-based dynamics are compared with those of field populations in the Florida Keys and U.S. Virgin Islands, and management implications are discussed.

Introduction

Demography as a science has been used to manage populations since the times of the ancient Greeks and Romans. Populations change due to the interacting effects of three main processes: birth, death, and migration (Andrewartha and Birch 1954). Rates of individual body growth typically affect birth rates in populations, especially the rates of body growth to maturity and the commencement of sexual reproduction (Murray 1979). Individual growth rates impact rates of mortality, because organisms often reach size refuges from mortality as they grow and age (Murray 1979, Lande 1988). Knowledge of demographic patterns can provide insight into the responses of populations to environmental change, and in turn allow for better population management.

Organisms that exhibit indeterminate growth have the ability to both shrink and grow, and consequently individual age is not tightly linked to body size (Hughes 1984). As a consequence, the population dynamics of indeterminately-growing organisms, such as anthozoans (corals, sea anemones, and their relatives) are more complex to model and predict than are those of organisms with determinate growth such as most vertebrates. In addition, because they often are small in body size, and occupy cryptic or hard to access aquatic habitats, relatively little is known about the demography of sea anemones in particular, and therefore their populations are challenging to manage and potentially protect. Individual anemone size may have a greater impact on their life history traits such as reproduction and mortality, than does individual age. As in most other organisms, body size in sea anemones influences their rates of survival, as well their rates of both sexual and asexual reproduction (Hughes 1984, Shick 1991). Therefore, changes in the size structure of sea anemone populations can lead to large indirect impacts on population dynamics.

Under field conditions, it can be difficult to discern the separate impacts of each of the many environmental variables that influence sea anemone population changes, such as seawater temperature (Chomsky et al. 2004a), food availability (Chomsky et al. 2004b), light (Muller-Parker, 1987), and exosymbiont presence (Porat and Chadwick-Furman 2004, McVay 2015). In addition, the physiologically-maximal rates of growth, reproduction, and lifespan that are possible in a given sea anemone species may not be achieved by individuals in the field. They may however be reached by individuals cultured under optimal conditions in a laboratory setting, with frequent feeding, constant optimal temperature, the absence of predators and competitors, etc. Information from laboratory-cultured populations thus may allow comparison with those under natural conditions in the field, to determine how close the wild individuals come to realizing their potential rates of growth and survival. Thus, it is useful to study the population changes of sea anemones in a controlled environment such as a laboratory setting.

Scant information is available on the demography of the corkscrew sea anemone *Bartholomea annulata*, mostly based on limited study of field populations in Florida (Jennison

1981, Chapter II) and the U.S. Virgin Islands (Nelsen 2008, Titus 2011), but also including preliminary studies on laboratory populations (Titus 2011). These data indicate that individuals of *B. annulata* may grow rapidly and have high mortality rates when small, but that large individuals either remain stable in size or shrink, and have relatively low mortality rates (Chapter II and references therein), similar to patterns known for other corals and sea anemones (Hughes and Jackson 1985, Hughes and Tanner 2000, Nelsen 2008, McVay 2015). The maximum lifespan in the field appears to be about 1-2 years in Florida (Chapter II) and 1.5-2 years in St. Thomas, USVI, depending on microhabitat type (Nelsen 2008), with population turnover times of 1-2 years estimated for both locations. Rates of clonal replication have been reported of 0.39 new budded individuals produced per month per parent individual in the lab, and 0.26 in the field (Titus 2011).

Members of this species are common on Caribbean coral reefs, and are important ecologically as hosts to the main cleaner shrimp in the Caribbean (Mahnken 1972, Silbiger and Childress 2008, Briones-Fourzan et al. 2012, Mascaro et al. 2012). They serve as hubs in a mutualistic network that impacts the dynamics of many coral reef fishes, due to their role as the center of many cleaning stations on coral reefs (Huebner and Chadwick 2012a,b, Titus et al. 2015). Corkscrew sea anemones also are popular organisms in the ornamental aquarium trade (Hardin and LeGore 2005, LeGore et al. 2005, Rhyne et al. 2009). Numbers collected in Florida waters have steadily declined since the mid-1990s, while management tactics have not changed, indicating potentially declining populations and a need for more scientifically-based management to preserve population sizes (Florida Wildlife Commission [FWC] http://myfwc.com/research/saltwater/fishstats/commercial-fisheries/landings-in-florida/, Fig. 2.1, pers. comm. Nancy Sheridan, FWC). More detailed information on their demographics under both field and laboratory conditions would aid in more effective management of this species, to ensure the maintenance of sustainable populations. The present study determined the population dynamics of corkscrew sea anemones *Bartholomea annulata* under laboratory conditions over 1 year. This study is the first long-term, detailed account of population dynamics of this species under laboratory conditions.

Materials and Methods

The present study was conducted at Auburn University during 15 May, 2014 – 17 May, 2015. Individuals of the corkscrew sea anemone *Bartholomea annulata* (N = 33) were collected by hand from nearshore sites at 1 - 2 m depth on Marathon Key, FL, during October 2012 to November 2013. They were transferred to the laboratory within a few days, in plastic bags supplied with seawater and battery-powered aerators. An additional 10 anemones were ordered from a private collector (KP Aquatics, Key Largo, FL) in February 2014. After arrival to the laboratory, all 43 anemones were acclimated to closed-system aquaria supplied with artificial seawater, lighting, heaters, and filters that mimicked coral reef conditions (details of culture conditions in Roopin and Chadwick 2009, Huebner et al. 2012). As of 5 May 2014, 6-8 individuals were cultured in each of 7 80-liter tanks (N = 43), and the following data were collected on each individual: tentacle crown width and length for calculation of tentacle crown surface area (TCSA, after Nelsen 2008, Roopin and Chadwick 2009, Huebner et al. 2012, McVay 2015), oral disc diameter (ODD, longest dimension through the center of the mouth), pedal disc diameter (PDD, longest dimension across pedal disc; not measured in all anemones because some bases were buried in sand at the bottom of the aquaria, see Titus 2011), orientation of the oral disk (horizontal vs. vertical, see Chapter II), nearest neighbor distance, microhabitat type within the tank (base attached beneath sand layer at bottom of the tank, attached to vertical wall of the tank, etc.), and the presence of any macrosymbionts (obligate anemoneshrimps *Periclimenes yucatanicus* and *Ancylomenes pedersoni,* Huebner 2012a,b). These data then were collected monthly for each anemone over 1 year. The body size of each anemone (TCSA, ODD, PDD) was measured with calipers, taking care to avoid contacting or disturbing the anemone body. The number of anemones fluctuated between 3-9 individuals per tank (N = 6 to 9 tanks) over the study year, due to mortality and the addition of anemones to some tanks (see below).

Initially, dyes were applied to individually identify each anemone. In May 2014 after measurement of initial body size, each anemone was carefully removed from its home tank, patted dry, and a small area on the lower column was dyed using tie-dye powder (Tulip, Fresno, CA). The dye was left to absorb into the body wall for 10 minutes in air, then each anemone was placed in a beaker containing seawater for 1 hour to remove any residual dye before being returned to its home tank (modified after Sebens 1976). The dying process appeared to be stressful for the anemones, but none died, and all recovered within 24 hours, as indicated by reattachment to the substrate and complete tentacle re-expansion in their home tanks. Each of 4 dye colors was applied to a different anemone in each of 7 tanks (35 anemones dyed total), plus 1 to 2 anemones were left un-dyed in each tank. Dividers were used to separate anemones in tanks with > 5 individuals, so that colors could be used more than once if necessary. After 5 weeks, the colors faded and disappeared completely. Subsequent monthly re-dyeing likely would have caused stress and alter anemone growth rates, so the body dye method was deemed impractical for this species and was discontinued.

As an alternate method of individual identification, on 14 June 2014, a toothpick with a small numbered plastic tag was inserted into the sandy substrate adjacent to each anemone, with the number visible above the sand surface. This technique of placing numbered tags adjacent to the anemones was effective, and has been employed successfully to monitor this and other anemone species for months to years under both laboratory and field conditions (Nelsen 2008, Titus 2011, Huebner et al. 2012a,b).

Locomotion

Rates of anemone locomotion were monitored daily for the first 7 months (5 May – to 12 December 2014), except for short lapses of 2-3 days each month (and 3 weeks in August, after which minimal movement was observed). The distance of each anemone from its numbered tag was measured each day, and any changes in location were recorded.

A second, overlapping phase of the study was conducted during the final 7 months (11 September 2014 – 30 April 2015). During September, 23 new small anemones (0.19 – 9.42 cm^2 TCSA) were ordered and received from the collector (see above) to replace mortalities, leading to a total sample size of 52 individuals as of September. Due to the highly dynamic nature of the new individuals, as of 11 September 2014, I began to measure them more frequently than monthly; weekly for the first month, and then bimonthly for the following 2 months, to accurately assess their rapid growth rates when small. After 12 December 2014, the individuals from the September cohort were no longer very small or rapidly-growing, so the measurement rate for all individuals was returned to monthly until May 17, 2015. In total, locomotion rates were measured for 7 months (May to Dec 2014), and rates of body size change (growth, shrinkage) and mortality were measured for 12 months (1 year, May 2014 to April 2015), including an intensive period of weekly to bi-monthly measurements of very small individuals for 3 months (September – December 2014).

Body size parameters

At the end of the study, 34 of the remaining individuals were used to measure relationships among body size parameters (TCSA, ODD, PDD, dry weight [W_d], wet weight [W_w]). TCSA, ODD, and PDD were selected as linear measures of body size, because all 3 commonly are used in studies on sea anemones (Chia and Spaulding 1972, Clayton and Lasker, 1985, Bucklin 1987, Chadwick-Furman and Spiegel 2000, Chomsky et al. 2004a,b, Huebner et al. 2012a, Scott et al. 2014, McVay 2015). For *B. annulata*, only PDD has been applied to determine body size at sexual maturity, for individuals collected from reefs in Florida (Jennison 1981; mean PDD of individuals without gonads = 0.74 cm, females = 1.06 cm, males = 1.10 cm, hermaphrodites = 1.42 cm). In the field, these anemones often occupy rocky or sandy crevices near the reef-sand interface (Sebens 1976, Jennison 1981, Briones-Fourzan et al. 2012), with the base attached deep in the crevice or under the sand, making it difficult to accurately measure basal (pedal disk) diameter or even oral disk diameter on live individuals in the field, because only the long tentacles protrude from the crevice (E. O’Reilly and N. E. Chadwick, pers. obs.) As such, I determined the relationships among the other 4 parameters above and TCSA, to facilitate the use of only TCSA as a measure of body size in field studies, and for inference especially of ODD from TCSA in future studies on this species.

I took the 3 linear measures of body size (tentacle crown length and width for calculation of TCSA, ODD [along the long side of the mouth], and PDD, Fig.2.4 and 2.5) 3 times on each individual, with 2-5 minutes between each set of measurements to allow for re-extension of any tentacles that contracted slightly during measurement. These 3 measurements then were averaged for each individual for each parameter, to enhance the accuracy of assessing the dimensions of their highly contractile soft tissues. After completion of linear measurements, each anemone was removed gently from its home aquarium and placed in a beaker with a 1:1 seawater:isotonic $MgCl_2$ solution, to cause them to fully relax their tissues (Sebens 1981a, Jennison 1981). After relaxation was complete (no response to tactile stimuli, about 30 minutes) the individual was removed from the water and patted dry on a paper towel until it was dry enough to stick slightly to the paper towel, then transferred to a labeled piece of aluminum foil and weighed to the nearest 0.001 g for assessment of wet mass. Afterwards, they were transferred in groups of 3-4 individuals to a drying oven, and dried at 80ºC for 24-26 hours, then weighed again to the nearest 0.001 g. One individual did not have PDD measured as it was inaccessible, and 1 individual was missed in the W_w measurement, therefore, N = 33 in for most relationships with PDD or W_W, and N = 32 for the relationship between PDD and W_w..

Data analysis

Anemones were divided into 4 size classes by tentacle crown surface area (TCSA): 0-25 cm^2 (I), 25.1-50 cm^2 (II), 50.1-75 cm^2 (III) and > 75cm^2 (IV). The same size classes were used as for field populations (Chapter II), except that an additional, very large size class IV was added here, because lab anemones became larger than did field anemones. Rates of growth were analyzed using a mixed effects linear model blocking for individuals in R x64 3.2.0, for the overall population and for each size class.

Rates of locomotion were determined by calculating mean monthly locomotion rates for each individual. Kruskal-Wallis tests were applied to assess significant differences in rates among size classes. Covariation between TCSA, ODD, PDD, W_w, and W_d was examined using correlation analysis. All results are reported as mean +/- one standard error, unless indicated otherwise.

Results

Body size parameters

Both one-dimensional measures of body size in *Bartholomea annulata* (oral disc diameter, ODD; pedal disc diameter, PDD) increased in a reverse-exponential fashion with the two-dimensional measure of body size, tentacle crown surface area (TCSA, Figs. 3.1A, 3.2A). For each 1% increase in TCSA, oral disc diameter increased significantly, by 0.49 ± 0.05% ($p < 0.001$, $r^2 = 0.73$, Fig. 3.1A), and pedal disc diameter increased by 0.33 ± 0.07% ($p < 0.001$, $r^2 = 0.39$, Fig. 3.2A). There was a significant linear relationship between the 2 one-dimensional measures of body size, ODD and PDD. For every centimeter increase in pedal disc diameter, there was a 0.84 ± 0.03 cm increase in oral disc diameter ($p < 0.001$, $r^2 = 0.95$, Table 3.1).

The linear measures of ODD, PDD, and TCSA also correlated significantly with the 2 measures of body mass. For each 1% increase in ODD, W_w increased by 1.85 ± 0.41% ($p < 0.001$, $r^2 = 0.40$, Fig. 3.1B) and W_d increased by 1.80 ± 0.38% ($p < 0.001$, $r^2 = 0.41$, Fig. 3.1C).

For each increase in PPD, W_w increased by 2.19 ± 0.40% ($p < 0.001$, $r^2 = 0.50$) and W_d increased by 2.10 ± 0.41% ($p < 0.001$, $r^2 = 0.50$, Figs. 3.2B, C). For each 1% increase in TCSA, there was a 0.96 ± 0.24% ($p < 0.001$, $r^2 = 0.34$) increase in W_w, and a 0.91 ± 0.23% ($p < 0.001$, $r^2 = 0.33$, Figs. 3.3A, B) increase in W_d. Finally, the wet and dry mass of *B. annulata* correlated significantly (Fig. 3.4). For every gram increase in wet mass, there was a 0.16 ± 0.005 g increase in oral disc diameter ($p < 0.001$, $r^2 = 0.97$, Table 3.2).

Individual growth and shrinkage

Rates of body growth and shrinkage varied greatly among individuals, but all individuals increased in body size over the study year, at a mean growth rate of 7.83 ± 1.31 cm^2 TCSA per month. Absolute growth decreased significantly with size class (Kruskal-Wallis, H = 7.6, d.f. = 3, $p < 0.05$); individuals in Size Class I (< 25cm^2 TCSA) grew the most rapidly (Figs. 3.5A, 3.6), at 13.67 ± 2.26 cm^2 ($p < 0.001$), while those in Size Class II and III grew at slower rates (Figs. 3.5B,C) of 4.46 ± 2.93 ($p = 0.13$) and 7.05 ± 1.23 cm^2 per month ($p < 0.001$), respectively. Individuals in Size Class IV remained relatively stable in body size, with individuals occasionally shrinking from one month to the next (Figure 3.5D), but overall they grew 3.88 ± 2.06 cm^2 per month ($p = 0.061$). Absolute growth in Size Class I was significantly different from Size Classes II and IV ($p < 0.05$ for both comparison) but not from Size Class III ($p = 0.09$) (Table 3.3). The very smallest individuals, which were a subset of Size Class I, grew the most rapidly (Figs. 3.7A, B). During the first 3 months of intensive monitoring of these 23 very small individuals (0.19 - 9.42 cm^2 TCSA initial sizes), they grew 17.43 ± 2.68 cm^2 per month ($p < 0.001$).

Changes in individuals belonging to each initial size class followed the same pattern; anemones that began the year in Size Class I grew rapidly, those starting in II and III grew more slowly over the year, and the largest ones in IV grew minimally. Individuals from all 4 initial size classes ceased growth when they reached about 150 cm^2 TCSA (Figure 3.6). After reaching about 100-130 cm^2 TCSA, individuals slowed their growth substantially, then oscillated around a maximum body size of ~ 140-170 cm^2 TCSA. Exceptions were 6 individuals that grew to > 200 cm^2, and 1 individual that grew to an extremely large size of 393 cm^2.

Locomotion

Overall, anemone locomotion rate was slow, only 2.59 ± 0.70 cm/month for the 25 individuals that were followed over the entire 22 weeks (6/14/14 to 12/1/14) of the locomotion study (Fig. 3.8). A similar rate of locomotion (2.47 ± 0.45 cm/month, Fig. 3.9) was obtained from observations made over the entire study year, including partial-year information on individuals that died sometime during the study, plus 19 of the individuals added in September (4 of the smallest individuals often contracted into the sandy substrate and were not visible on a daily basis, so were excluded from locomotion studies). The very small individuals added in September (N=19) locomoted at a slightly (but not significantly, $t = 0.80$ $p = 0.43$) slower rate than did larger individuals over 8 weeks, of 1.76 ± 0.75 cm/month (Fig. 3.10). Locomotion rate did not vary significantly with size class: individuals in Size Class I locomoted 1.84 ± 0.44 cm/month (range = 0.30 - 3.33), those in Size Class II at 1.38 ± 0.23 cm/month (range = 0.56 t-2.00), Size Class III at 2.86 ± 1.22 cm/month (range = 0.00 - 6.67), and the largest individuals in

Size Class IV at 2.68 ± 0.93 cm/month (range = 1.00 - 7.00, H=1.49, d.f. = 3, p = 0.69, Fig. 3.11).

Locomotion varied greatly among individuals, with most individuals (74%, N = 26) moving little (31%, < 1 cm/month) or not at all (43%). In contrast, a few anemones (26%, N = 9) traveled up to 10-25 cm per week. Individuals locomoted at higher rates during the first 1-2 days after monthly measurements of their body sizes, and also after being moved from one tank to another, likely in response to these disturbances. When they were newly added to a tank (upon initial arrival to the laboratory from the field, or following relocation between tanks due to changing densities in tanks from mortality, or tanks needed for other experiments), individuals changed location within the tank several times during the first week, before settling into a space and then remaining mostly fixed. Also, water flow rates varied among tanks and among areas within each tank. In aquarium tanks, anemones that detached from the substrate were carried passively, farther than they would have moved under their own locomotion, because of water flow generated by pumps in the tanks. In some cases, individuals were placed in small glass dishes to facilitate their attachment and settlement into one location, after they had moved all the way across the tank over 1 week without settling.

Mortality and lifespan

Rates of mortality varied significantly with size class. Overall, 29 anemones died during the year (44%, N = 66). Most (72% of the 29 individuals who died) were small, belonging to Size Class I (< 25 cm^2 TCSA), but almost all the rest (21%) were very large, in Size Class 4 (> 75 cm^2 TCSA, but 2 of the large-anemone deaths were due to a temperature spike in the tank,

Fig. 3.12). The remaining 2 deaths were both of medium-sized individuals in Size Class II (25.1-50 cm^2 TCSA). Some variation in the numbers of anemones dying among size classes was because they did not contain equal numbers of individuals (Size Classes I and IV had the most individuals throughout the study, except during the last 4 months when most Size Class I individuals had transitioned to the medium size classes II and III).

On a bimonthly basis, percent mortality rate declined with body size, in that for Size Class I it ranged from 4-83%, for Size Class II from 0 -11%, for Size Class III 0-25%, and for Size Class IV from 0 to only 17% (Table 3.4). As the individuals remained (relatively) the same from time period to time period, it was impossible to statistically compare mortality between groups without committing pseudoreplication.

Before the anemones died, about a third of them (13/29) shrank gradually, for a short (1 wk) to long (6 mo) period, at a shrinkage rate of 5-175 cm^2 TCSA per month (Figs. 3.12, 3.13). In contrast, a few continued to grow until death, at rates of 2-5 cm^2/mo^{-1} TCSA during the final month before death (N = 4). The remaining 9 anemones that died, oscillated in body size at such a slow rate (-10 to +5 cm^2/mo^{-1} TCSA), that it was difficult to determine whether they were growing or shrinking prior to death.

The minimum lifespan of anemones in the laboratory was 12 weeks from the date of initial arrival. Less than half of original population (only 44% of the 43 fairly-large individuals present initially, N=19) survived the full year of study. Of the 23 very small anemones that entered the lab in September, many more (87% N = 20) survived the remaining 8 months and remained alive for at least 3 months after the study ended (Fig. 3.14). The population had a steep die-off in the first 4 months, but this could have been due to in part to beginning the study with many older individuals (some had been in lab ~1 year before the present study began). Overall, mortality rate plateaued after the first 4 months, with few deaths occurring and thus a potential individual lifespan of upwards of 2 years. Because the age at arrival to the laboratory was not known for any individuals, these results do not allow estimation of maximum lifespan, except that it appears to be > 2 yrs. Proportionally, more of the smallest individuals survived to almost 1 year than did the larger and potentially older individuals. As such, more of the larger and older individuals appeared to senesce (shrink) and die during the 1-year study, than did the younger, smaller ones.

Discussion

Body size parameters

The significant relationships among all measures of body size that were observed here for *Bartholomea annulata* were similar to those known for other species of sea anemones (summarized in Table 3.2). They indicate that measurement of any of these parameters allows the inference of body size based on the others, especially the use of linear measures that are easy to obtain from field populations (width and length of the tentacle crown), to infer those that are more difficult to measure (body mass, pedal disk dimensions). The tight correlation of pedal disk diameter (PDD) with body mass may have arisen because the pedal disk area contains most of the mass-dense internal structures (acontia, mesenteries) of the anemones. In contrast, the flared oral disk area is less mass-dense, and the hollow tentacles arise from it, so that oral disk diameter (ODD) was most closely correlated with tentacle crown surface area (TCSA). The glass anemone, *Aiptasia pallida*, [Aiptasiidae], which has similar body shape and is in the same family as *B. annulata*, also exhibits a tightly-correlated relationship between ODD and dry body mass (Clayton and Lasker 1985, Table 3.2), as do Red Sea corallimorpharians *Rhodactis rhodostoma* (Chadwick-Furman et al. 2000), the Pacific Ocean sea anemones *Anthopleura xanthogrammica, A. elegantissima*, and *Metridium senile* (Sebens 1981a), and the Mediterranean Sea anemone *Actinia equina* (Chomsky et al. 2004b, Table 3.2). Thus if morphology is similar, relationships between body parameters across species might also be similar.

Obtaining the oral or pedal disk diameters (ODD, PDD) of *B. annulata* in the field is difficult, because individuals often occur in crevices where the neither the oral disc nor the pedal disc can be seen, or in areas with continuous water flow making them difficult to measure without disturbing the anemones and causing them to contract. Using the equations determined here, the TCSA of *B. annulata* can be used to determine other body parameters such as PDD which is used to assess body size at sexual maturity (Jennison 1981). Cantrell (2014) found a significant relationship between wet mass and TCSA in *B. annulata*, thus justifying the use of TCSA to infer per-gram ammonium uptake rates by individuals. However wet mass isn’t often used or recommended to assess the body mass of marine invertebrates, particularly sea anemones, because the amount of water retained by an individual can vary greatly depending on conditions (Murray et al. 2006). Anemone dry weight is useful in determining feeding rate (Anthony 1997), gonad presence and composition (Francis 1973, Sebens 1981b, Chadwick-Furman et al. 2000), and metabolic cost (Sebens 1981a). If a study needs to keep the organisms alive for further measurements after body sizes are assessed, being able to measure TCSA or other linear dimensions, and to estimate dry mass from those, rather than sacrificing the animals, is useful for long-term studies, and for those that need to follow individuals for their entire natural lifespans (such as the life history studies here).

Jennison (1981) found gonads in individuals of *B. annulata* as small as 1.06 cm PDD, (= 0.89 cm ODD, 68.9 cm^2 TCSA, Table 3.2). Based on a size at maturity of 1.06 cm PDD, about 2/3 of the anemones at the beginning of the present study (67%, N = 21 with PDD measurements in August 2014, range = 0.20 - 238.75 cm^2 TCSA) were sexually mature females, or based only on TCSA, about 1/3 of the anemones (30%, including lab anemones for which PDD couldn't be measured). In terms of the presence of testes, about a quarter of the lab population appeared to be sexually mature males (mean PDD for males = 1.10 cm [Jennison 1981], equivalent to 0.54 cm ODD and 71.9 cm^2 TCSA), and about half potentially possessed both male and female gametes (hermaphrodites, 1.46 cm PDD = 0.74 ODD = 100.2 cm^2 TCSA). Translation of PDD to TCSA for the purpose of determining sexual maturity might cause a slight underestimation of the number of individuals possessing gonads, because sea anemone gonads develop in the column near the pedal disk, so that PDD rather than TCSA may more accurately measure body size for assessment of maturity.

Growth and shrinkage

Little information exists on the growth rates of sea anemones, and often studies have focused on growth in basal diameter (Chia and Spaulding 1972, Bucklin 1985, Bucklin 1987, Chomsky et al. 2004a,b), making them difficult to compare to growth rates obtained from field studies where the anemone pedal disks are buried deep in holes, such as for the giant sea anemone *Entacmaea quadricolor* in which only tentacle crown dimensions can be measured in the field (Porat and Chadwick-Furman 2004, McVay 2015). In the present study, because both basal (pedal) diameter and TCSA were measured, anemone growth rates can be more easily compared to those obtained in past studies.

Growth rate of *B. annulata* measured here under laboratory conditions were slower than those known for other giant sea anemones. The Indo-Pacific giant anemone *Heteractis magnifica* was examined for 3 years in the field and had an average of 0.75 cm^2 surface area growth per day with anemonefish present (Holbrook and Schmitt 2005), however, fish symbionts augment growth rates in anemones (Roopin and Chadwick 2009). The *H. magnifica* individuals without anemonefish grew only 0.25 cm^2 per day. In the Red Sea, the smallest, fastest growing size class of *H. crispa* grew only 0.12 cm^2 per day (McVay 2015). In comparison, *B. annulata* grew 0.10-0.14 cm^2 per day in the field and 0.26 cm^2 under laboratory conditions. In terms of percent changes in body size, individuals of *B. annulata* grow more quickly than those of *H. magnifica*, a much larger anemone, in that they can double their body size (200%) size change in only 1-10 months, depending on initial size, whereas *H. magnifica* takes 12-18 months to do so (with 2 and 1 anemonefish present, respectively, Holbrook and Schmitt 2005, McVay 2015).

Mean absolute growth rate of *B. annulata* in the lab was significantly greater than rates found for two populations in the Florida Keys (Chapter II). The growth rate was ~2-3x greater in lab depending on the site ($p < 0.001$ for both comparisons). Nelsen (2008) examined populations of *B. annulata* at 2 field sites in the U.S. Virgin Islands and found that only 10%-26% of the population showed TCSA growth over 3 months (transitioned into a bigger size class). This is only about half of the proportion of individuals that grew over 2 months in the lab populations, as well as in the Florida Keys (18%-63% grew in lab, 33%-42% grew across 2 field sites, Chapter II). Nelsen found highly variable stasis and shrinkage rates, differing based on size classes, however some trends emerged; stasis rates decreased and shrinkage rates increased with size class. At field sites in Florida, I also found that shrinkage rates increased with anemone body size, but unlike Nelsen (2008), I found that stasis also increased with size (Chapter II). For lab individuals in the present study, shrinkage rates did not vary significantly among size classes, with an mean of 21-27% of the population showing shrinkage ($p = 0.95$) and stasis rates increased with body size, ranging from 26-73% (smallest to largest size classes, Table 3.4). While the present studies observed anemone changes over shorter, 1-2 month periods (compared to each 3 months by Nelsen), the trend of stasis rates increasing with size in the laboratory and field environment is conflicting with the stasis rates found in the Virgin Islands (Nelsen 2008).

Shrinkage rates may be higher and growth and stasis rates lower in the field than in the lab, due to several reasons. Water movement in the field can be extreme and damage the soft tissues of anemones, and it also can limit their feeding ability by changing size of the tentacle crown and reducing the tentacle expansion, thus hindering feeding (Koehl 1977, Shick 1991). This can divert energy from growth into the healing of damaged tissues or into the relatively high energetic costs of remaining expanded in rapid water flow. Other perils are present in the field but absent in lab: predation (Smith 1977, Shick 1991), sedimentation (Rogers 1990, Riegl 1994), lack of nutrition (Chomsky et al. 2004b), as well as extremes of temperature, light, and salinity (Shumway 1978, Chomsky et al. 2004a), and even exposure to toxic pollutants (Ormond and Caldwell 1982), all of which can reduce the feeding abilities of sea anemones, their metabolic rates, and ultimately their growth and body size. The laboratory conditions maintained in the present study included tanks kept at 25 ± 1° C and 35 ppt salinity, lights on a 12-12 cycle, feeding once a week and a water flow rate that was consistent and slow relative to that in many coral reef habitats. As long as the anemones were attached to a substrate, their tentacles remained consistently expanded in the tanks. In addition, they were exposed to neither predators nor competitors that in the field may damage their tissues or remove tissue, causing shrinkage. As such, lab growth rates in an optimized culture system are expected to be more rapid than those under more variable and complex conditions in the field.

Titus (2011) studied *B. annulata* in lab for 6 weeks, looking at effects of feeding on growth and recruitment. He found that on average the fed group increased TCSA by 210.6% while the starved anemones grew an average of 83.4% over 6 weeks. The present study found an mean TCSA increase range from 11-311% per month with an overall mean of 89% increase per month. Like Titus (2011), smaller individuals in this study grew more than did larger ones, while that study found some individuals quadrupled their size over 6 weeks, this study found greater increase; sometimes increasing individual size 29x in a month, with very small individuals increasing TCSA up to 700% in one week (0.2 – 1.58 cm^2 TCSA). This trend of decreasing growth with body size is known also for other anemone species: *Actinia equina* (Chomsky et al. 2004b) *Anthopleura elegantissima* (Sebens 1980a), *Heteractis crispa*, and *Entacmaea quadricolor* (McVay 2015), and is similar to the pattern for many other organisms (vertebrates included), in which small individuals focus on rapid somatic growth while large individuals devote energy to other endeavors such as sexual reproduction (von Bertalanffy 1951).

No recruitment was observed during the present laboratory study. Titus (2011) found that starved anemones produced more pedal lacerates than did fed individuals, so this could explain the lack of asexual reproduction here, as all individuals in the present study were fed. Some other species of anemones produce pedal lacerates during times of stress (Johnson and Shick 1977, Sebens 1980b), and with less stress in the lab environment maintained here, one would expect fewer asexual recruits. There was also no sexual reproduction observed; no spawning or larval stages were seen in this year-long laboratory study, or during the year before in the lab. Jennison

(1981) suggests that sexual reproduction, the development and release of gametes, is seasonal, therefore, with no seasonality in lab (no change in daylight hours and little change in temperature and salinity), it is possible that the stimulus to develop gametes was never received. Additionally, because spawning is a discrete event usually occurring just after dusk in cnidarians (Babcock et al. 1986), it is unlikely to be observed in lab cultures unless caregivers observe the anemones at night.

Locomotion

This study found that on average, *Bartholomea annulata* individuals rarely locomoted long distances and typically remained in one place during the 22-week locomotion study. The rate of locomotion varied with size class (range = 1.84 – 2.86 cm/month mean rate per size class) but not significantly. This contrasts with other studies that observed smaller individuals locomote farther than larger individuals in *B. annulata* (Titus 2011), mobile stony mushroom corals (Chadwick and Loya 1992), and the anemone *Epiactis prolifera* (Dunn 1976). Titus (2011) used different size classes (>50 cm^2 TCSA and <50 cm^2 TCSA), but even with a size class adjustment, no significant difference was found between the 2 groups (p = 0.35). Titus appeared to have higher rates of locomotion; 6 individuals moved over 20 cm during the 6 week study, with one individual moving over 45 cm, while this study found 6 individuals move over 20 cm during the 22 week study and 1 individual (from the anemone population added in September 2014) moved 25 cm over the course of 8 weeks. A complicating factor may be that Titus starved the individuals, which may have stimulated locomotion by the anemones to search for better habitats with more food. The opposite trend occurred in the Pacific sea anemone *Actinia* *tenebrosa,* with the larger adults moving more than smaller juveniles, but this could be due to the high mortality of juveniles, where death occurs before locomotion is observed (Ottaway 1978).

Mortality and lifespan

Mortality rates varied for the laboratory population from 2.6-25.6% of individuals per 2 month period, depending on size class (Table 3.5). This is lower than mortality rates found in the Virgin Islands of 10-54% per 3-month period (Nelsen 2008) and 33-39% per 5 week period (Titus 2011), as well as 18-30% mortality rates in the Florida Keys per 2 month period (Chapter II). It was also lower than the 32-33% mortality rate per 6-week period found in another lab study (Titus 2011). It is an order of magnitude higher than the mortality rate of a giant Indo-Pacific sea anemone; Holbrook and Schmitt (2005) found that *Heteractis magnifica* showed only 29% mortality over their 3 year study. *B. annulata* also showed mortality rates higher than those found in other cnidarians; Hughes and Tanner (2000) found populations of *Montastrea annularis, Agaricia agaricites,* and *Leptoseris cucullata* from Jamaica had mortality rates of 16-67%, 57-77%, and 77-96% respectively for a 5 year period, Hughes and Jackson (1985) found mortality rates of 6-34% and 38-63% for foliaceous corals in two locations over 3 years. Also, McVay (2015) found mortality rates of 18% and 20% per year in Red Sea giant anemones on coral reefs. *B. annulata* is smaller in body size than the Indo-Pacific giant sea anemones and has less soft tissue; this could lead to higher mortality rates. This Caribbean anemone has been shown to have high population turnover in the field (Nelsen 2008, Chapter II) of 1-2 years in the USVI and ~1 year in the Florida Keys, and appears to be a relatively weedy species, growing quickly, and reaching reproductive maturity at small body sizes.

The pattern seen here of mortality rates deceasing with body size (Size Class I having a much higher mortality than the other three, ~ 43% per 2 months compared to 2%, 4%, and 6% for Size Classes II, III, and IV respectively), was similar to that observed by Nelsen (2008) in the field, but this pattern not significant in either study. Two of the field sites that I examined in the Florida Keys also showed the same trends, with mortality rates decreasing with size class from 25-20% at one site, and 30-18% at the other (Chapter II). Lab mortality rates here (Table 3.5) were lower than those observed in the field by Nelsen (2008) of 30-23% in the smallest to largest size classes at one field site, and 54-10% at the other, every 3 months). Smaller individuals may have died more than large ones in lab because they were less able to capture and hold onto food with smaller tentacle crowns, smaller individuals also seemed to be pushed around by current in the tanks more than larger individuals. In the field, where food is scarcer, this pattern might not be as evident.

The pattern of mortality rate being inversely related to body size occurs in many organisms, and is known also for other coral reef sea anemones, and for Caribbean corals over a much longer time scale; Red Sea anemones decrease their mortality rate from 26% in small to only 8% in large individuals (McVay 2015); mounding coral *M. annualaris* mortality rate decreased from 43% in the smallest size class to 3% in the largest size class over five years, lettuce coral, *A. agaricites,* and sunray lettuce coral, *L. cucullata,* had the same pattern with 73-27% and 87-52% respectively, smallest to largest size class over 5 years (Hughes and Tanner 2000). Foliaceous corals also exhibit lower mortality rates in larger than in smaller size classes; 14-27% for the smallest size classes and 0-18% for the larger size classes over 1 year (Hughes and Jackson 1985). Again, smaller individuals may be dying due to the lesser feeding area, because smaller individuals, with a greater surface area to volume ratio, are more susceptible to changes in the environment such as higher temperatures or changes in salinity, and/or because they are more susceptible to total mortality from biological interactions such as disease, predation and competition than are larger individuals. The corals mentioned are all colonial and indicate a benefit for colonial organisms; a larger colony has a higher chance of recovering from partial damage than a smaller colony, and even a small colony might manage damage better than a solitary organism like *B. annulata.* The mortality rates found for solitary individuals of *B. annulata* in lab were an order of magnitude higher than that of the other giant sea anemones and colonial corals, with similar mortality rates over a span of months for the anemone and years for the larger anemones and corals.

Because anemone age was not determined prior to the start of this study, maximum lifespan cannot be determined for the individuals examined here. As 44% of the original population survived the full year of the study, and 87% of the smaller individuals added in September of 2014 survived the remaining 8 months of the study plus an additional 3 months after the study, it appears the maximum lifespan is at least 2 years. This conclusion is similar to the average lifespan estimates from field populations, of 2-3 years in Florida (Chapter II), and in the USVI of 1.5-2 years (Nelsen 2008, Fig. 3.14). That almost half the individuals here died in one year, indicates that life span may be quite short for some anemones of this species, possibly only lasting a few months for many of the small ones, and not much more than a year or two even for those that reach large body size.

In conclusion, individuals of *B. annulata* appear to be short-lived sea anemones that often exhibit senescence in the form of body shrinkage during the 1-6 months prior to death. Individual anemones tended to shrink, sometimes to less half their size, before eventually dying. This could be due to a lesser ability to feed or extend tentacles to the light, as individuals approach death.

Some bryozooans exhibit senescence, with older individuals exhibiting deterioration in feeding and healing abilities (Palumbi and Jackson, 1983). Senescence is hard to observe in the field, however a species of hydromedusae, *Gonionemus vertens*, exhibited senescence as the primary cause of death in these short-lived cnidarians, in that older individuals showed a higher frequency of infection and deterioration (Mills, 1993). Also, senescence is known for some stony corals; individuals of the weedy, short-lived branching coral *Stylophora pistillata* cease sexual reproduction and stop growing, and their exosymbiotic fish and crab symbionts desert them, during the several months prior to colony death (Rinkevich and Loya 1986).

Management implications and conclusions

The laboratory observations obtained here indicate that individuals are able to reach the body size for sexual maturity potentially within only a few months after settlement, and then may continue to grow at rapid rates. Sexual maturity occurs around 1 cm PDD (Jennison 1981), or ~70 cm^2 TCSA, which can be obtained by a much smaller individual (<15cm^2) within a month under laboratory culture. This allows smaller individuals to be harvested and grown in culture to a larger, more desirable, size for sale. Anemone size, when associated with cleaners, is positively correlated with cleaning events (Huebner and Chadwick 2012a), thus indirectly affecting fish health and diversity. Anemone size is also positively correlated with amount of gametes and thus potentially fertilization and recruitment (Sebens, 1981b, Bucklin 1987, Levitan 1989, Kapela and Lasker 1999). Asexual reproduction usually requires a minimum size (Minasian 1982) and there is a minimum size at which *B. annulata* produces gametes (Jennison 1981). By collecting smaller anemones closer to this reproductive cut-off, larger individuals will remain to replenish the population both sexually and asexually as well as maintain ecosystem health through cleaner symbiosis. Thus, collection of small to mid-size individuals may best maintain local populations. In landing small to medium-sized individuals, the fishery will affect the population less; possibly by taking individuals that would've died anyway, or individuals that do not contribute to the population a substantial amount due to less reproductive contribution.

As neither sexual nor asexual recruitment was seen in the laboratory over the year-long study, spawning needs to be protected in the field. There are no studies that describe the frequency of asexual reproduction in *Bartholomea annulata* compared to sexual reproduction, therefore it is important to protect reproduction that promotes the ability to adapt to a changing environment. *B. annulata* is known to spawn only twice a year (Jennison 1981). A harvest closure of 2-3 months each year would allow all reproducing individuals a chance to spawn before potential collection. This window would also provide time for settlement and growth of new recruits for harvest, thus a window around the predicted November and April spawnings (Jennison 1981) would support population growth and sustainability for *B. annulata*.

Based on the laboratory data collected here, I recommend the following: (1) establish a size limit of *B. annulata* individuals for harvest, based on TCSA, and (2) seasonal closing of the fishery during spawning to allow highest gamete output and reproductive success.

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Table 3.1. Relationships between measures of body size in the corkscrew sea anemone *Bartholomea annulata*. TCSA=tentacle Crown Surface Area, ODD=oral disc diameter, PDD=pedal disc diameter, TCD=tentacle crown diameter, W_d= dry weight, W_w =wet weight.

TCSA/TCD Equations	PDD Equations	ODD Equations	r	n	p-value
$TCSA = 62.34(PDD)^{1.17}$	$TCSA = 62.34(PDD)^{1.17}$		0.39	33	<0.001
$TCSA = 64.03(ODD)^{1.51}$		$TCSA = 64.03(ODD)^{1.51}$	0.73	34	<0.001
ODD = 0.84(PDD)	ODD = 0.84(PDD)	ODD = 0.84(PDD)	0.95	33	<0.001
TCD = 7.05(PDD)	TCD = 7.05(PDD)		0.34	33	<0.001
TCD = 8.22(ODD)		TCD = 8.22(ODD)	0.72	34	<0.001
$TCSA = 0.97(PDD)^{1.87}$			0.98	34	<0.001
$W_w = 0.05(TCSA)^{0.97}$			0.34	33	<0.001
$W_d = 0.01(TCSA)^{0.91}$			0.33	34	<0.001
	$W_w = 2.28(ODD)^{1.85}$		0.4	33	<0.001
	$W_d = 0.37(ODD)^{1.80}$		0.41	34	<0.001
		$W_w = 1.32(PDD)^{2.19}$	0.50	32	<0.001
		$W_d = 0.22(PDD)^{2.10}$	0.50	33	<0.001

Table 3.2. Relationships among measures of body size in species of sea anemones. W_d=dry weight, W_w=wet weight, TCSA=tentacle Crown Surface Area, ODD=oral disc diameter, PDD=pedal disc diameter, TCD=tentacle crown diameter.

Species	Wet Weight Equations	Dry Weight Equations	r	n	p-value	Authors
B. annulata	$W_w = 0.05(TCSA)^{0.97}$		0.34	33	<0.001	
		$W_d = 0.01(TCSA)^{0.91}$	0.33	34	<0.001	
	$W_w = 2.28(ODD)^{1.85}$		0.4	33	<0.001	
		$W_d = 0.37(ODD)^{1.80}$	0.41	34	<0.001	
	$W_w = 1.32(PDD)^{2.19}$		0.50	32	<0.001	
		$W_d = 0.22(PDD)^{2.10}$	0.50	33	<0.001	
	$W_d = 0.16(W_w)$	$W_d = 0.16(W_w)$	0.97	33	<0.001	
A. elegantissima		$W_d = 0.019(PDD)^{3.27}$	0.96	38	<0.001	Sebens (1981a)
A. xanthogrammica		$W_d = 0.035(PDD)^{2.67}$	0.94	16	<0.001	Sebens (1981a)
M. senile		$W_d = 0.007(PDD)^{2.78}$	0.88	36	<0.001	Sebens (1981a)
A. pallida		$W_d = 0.18(ODD)^{1.45}$	0.68	66	<0.05	Clayton and Lasker (1985)
A. equina	$W_d = 0.08(W_w) + 0.07$	$W_d = 0.08(W_w) + 0.07$	0.97	20	<0.001	Chomsky et al. (2004b)
A. equina		$W_d = 0.0002(PDD)^{2.47}$	0.98	20	<0.001	Chomsky et al. (2004b)
A. equina	$W_w = 0.0011(PDD)^{2.66}$		0.98	20	<0.001	Chomsky et al. (2004b)
R. rhodostoma	$W_w = 0.06(ODD)^{2.44}$		0.85	96	<0.001	Chadwick-Furman et al. 2000
R. rhodostoma		$W_d = 0.0071(ODD)^{2.54}$	0.94	36	<0.001	Chadwick-Furman et al. 2000

Table 3.3. Variation in absolute growth rates of individuals of *Bartholomea annulata* with size class under laboratory conditions, in cm^2 Tentacle Crown Surface Area (TCSA, mean ± S.E.M.). Shown also are p-values for pairwise comparisons between size classes, as post-hoc Kruskal-Wallis Tests. Note that the growth rate of size class I differs significantly from that in all 3 other size classes, which do not differ from each other. See text for details.

	Size Class I	**Size Class II**	**Size Class III**	**Size Class IV**
Size Class I	**13.67 ±2.26**	*p*=0.03	*p*=0.09	*p*=0.02
Size Class II		**4.46 ±2.93**	*p*=0.70	*p*=0.89
Size Class III			**7.05 ±1.23**	*p*=0.80
Size Class IV				**3.88 ±2.06**

Table 3.4. Variation among size classes of the sea anemone *Bartholomea annulata* under laboratory conditions, in the mean percent of individuals (±S.E.M.) that displayed growth, shrinkage, stasis, or died per 2 month period. Growth, stasis and shrinkage are based on changes in tentacle crown surface area (TCSA), N/A=not applicable.

	Size Class I	**Size Class II**	**Size Class III**	**Size Class IV**
Growth	18.5 ± 8.4%	63.4 ± 10.2%	52.8 ± 10.4	N/A
Stasis	25.6 ± 10.1%	13.4 ± 6.2%	15.3 ± 6.9%	73.2 ± 3.4%
Shrinkage	N/A	21.3 ± 8.4%	26.8 ± 5.9%	20.6 ± 3.1%
Mortality	43.3 ± 14.7%	1.9 ± 1.9%	4.2 ± 4.2%	6.1 ± 3.4%

Table 3.5. Variation in mortality rates per 2 month period for whole populations of the sea anemone *Bartholomea annulata*, with 3 types of environmental conditions: (1) laboratory culture, (2) Middle Florida Keys (Quarry site), and (3) Southern Florida Keys (Cudjoe Key site). Mortality rate for Sept – Nov ’14 at Cudjoe was not recorded due to a storm, then 0.22 mortality rate was observed in the next time period, so mortality was averaged as 0.11 per each 2 months during the Sept ’14 – Jan ’15 period. Note that mortality in lab was lower than at both field sites except during July-Sept 14. During most periods, mortality also was highest at the southern Keys site (Cudjoe). See text for details. Field data from ter II.

Type of environment	May-Jul. '14	Jul.-Sept. '14	Sept.-Nov. '14	Nov. '14-Jan. '15	Jan.-Mar. '15	Mar.-May '15
Laboratory	0.09	0.26	0.08	0.10	0.12	0.03
Quarry field site	0.12	0.08	0.24	0.34	0.32	0.18
Cudjoe field site	0.13	0.16	0.11*	0.11*	0.30	0.34

Figure Legends

Fig. 3.1. Power variation in a 1-dimensional measure of body size in the sea anemone *Bartholomea annulata* (oral disk diameter, ODD), with a 2-dimensional measure: **A.** Tentacle crown surface area (TCSA), and two 3-dimensional measures: **B.** Wet mass. **C.** Dry mass.

Fig. 3.2. Power variation in a 1-dimensional measure of body size in the sea anemone *Bartholomea annulata* (pedal disk diameter, PDD), with a 2-dimensional measure: **A.** Tentacle crown surface area (TCSA), and two 3-dimensional measures: **B.** Wet mass. **C.** Dry mass.

Fig. 3.3. Power variation in a 2-dimensional measure of body size in the sea anemone *Bartholomea annulata* (Tentacle crown surface area, TCSA), and two 3-dimensional measures: **A.** Wet mass. **B.** Dry mass.

Fig. 3.4. Linear variation in wet with dry mass of the sea anemone *Bartholomea annulata.*

Fig. 3.5. Variation in the body size changes of individuals of the sea anemone *Bartholomea annulata* (mean ± S.E.M.), under laboratory conditions over 1 year, with initial size class. **A.** Size Class I (<25 cm^2 TCSA). **B.** Size Class II (25.1-50 cm^2 TCSA). **C.** Size Class III (50.1-75 cm^2 TCSA). **D.** Size Class IV (>75 cm^2 TCSA).

Fig. 3.6. Variation in the mean body size of individuals of the sea anemone *Bartholomea annulata* under laboratory conditions over 1 year, among initial size classes. Note that by the end

of the study, mean body size for all four size classes converged on a maximal size ~150 cm^2 TCSA.

Fig. 3.7. Changes in the body size of very small individuals of the sea anemone *Bartholomea annulata* under laboratory conditions, for individuals that joined the population in Sept. 2014, as measured over 11 weeks. **A.** Size changes for each of N = 23 individuals. **B.** Mean size changes (±S.E.M.).

Fig. 3.8. Locomotion of individuals of the sea anemone *Bartholomea annulata* under laboratory conditions, followed for full 22 week study (N=25). Mean locomotion rate is 2.59 cm/month for these individuals.

Fig. 3.9. Locomotion of total population of the sea anemone *Bartholomea annulata* under laboratory conditions, (N=60) including those that died during the study, mean locomotion rate is 2.47 cm/month.

Fig. 3.10. Locomotion of individuals of the sea anemone *Bartholomea annulata* under laboratory conditions, added 15 weeks into the study (N=19). Mean locomotion rate is 1.87 cm/month.

Fig. 3.11. Mean amount of locomotion of individuals of the sea anemone *Bartholomea annulata* under laboratory conditions, by size class (N=60). There was no significant difference between size classes.

Fig. 3.12. Size of individuals of the sea anemone *Bartholomea annulata* under laboratory conditions, that died during the study (N=29). Some individuals showed shrinkage before death (see text).

Fig. 3.13. Size of individuals of the sea anemone *Bartholomea annulata* under laboratory conditions, that exhibited shrinkage before death, suggesting senescence (N=13).

Fig. 3.14. Kaplan-Meier survival curve for of *Bartholomea annulata,* under laboratory conditions (N=66).

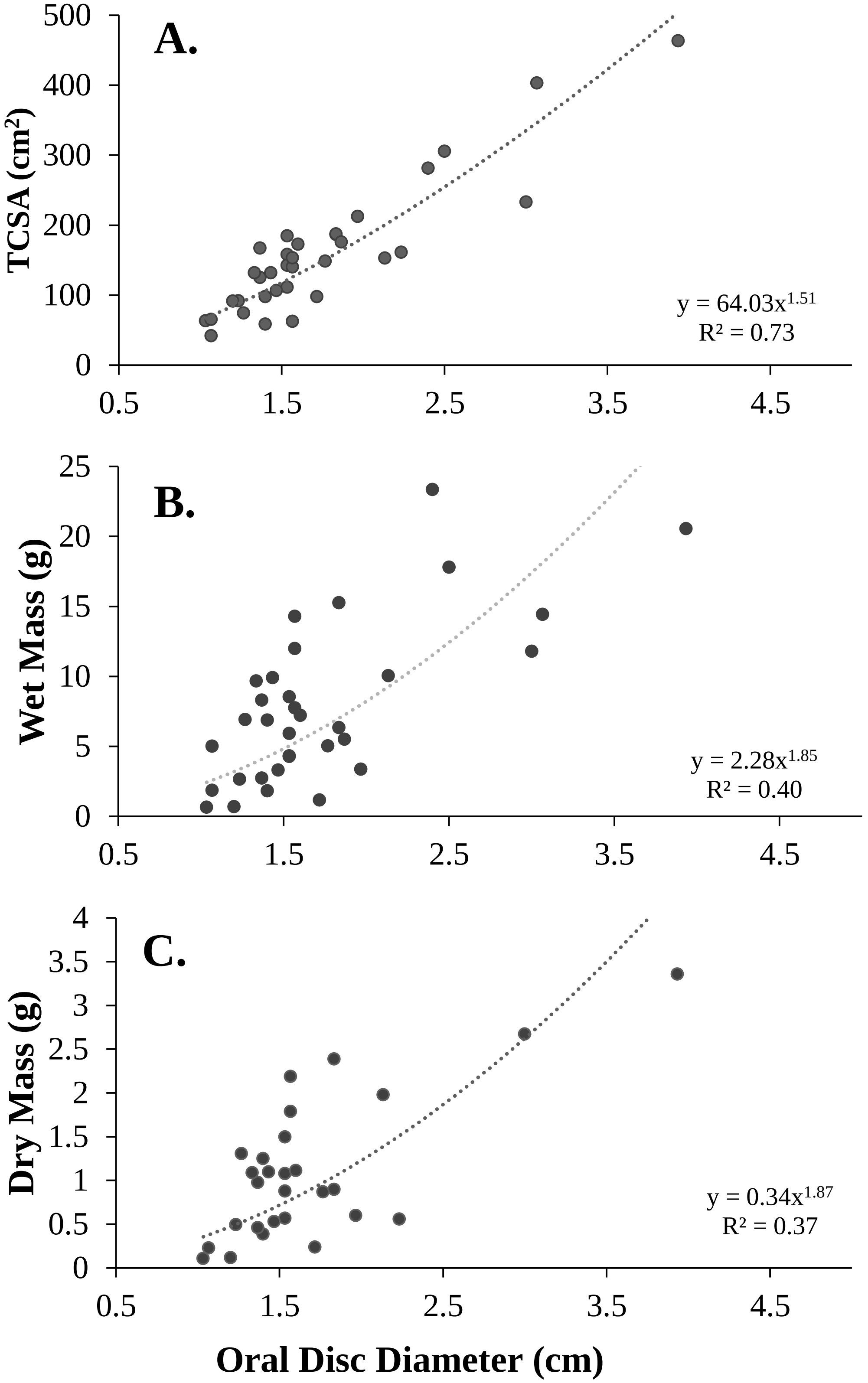

A.
TCSA (cm²)
500
400
300
200
100
0
0.5
1.5
2.5
3.5
4.5
y = 64.03x^1.51
R² = 0.73
B.
Wet Mass (g)
25
20
15
10
5
0
y = 2.28x^1.85
R² = 0.40
C.
Dry Mass (g)
4
3.5
3
2.5
2
1.5
1
0.5
0
y = 0.34x^1.87
R² = 0.37
Oral Disc Diameter (cm)

Fig. 3.1.

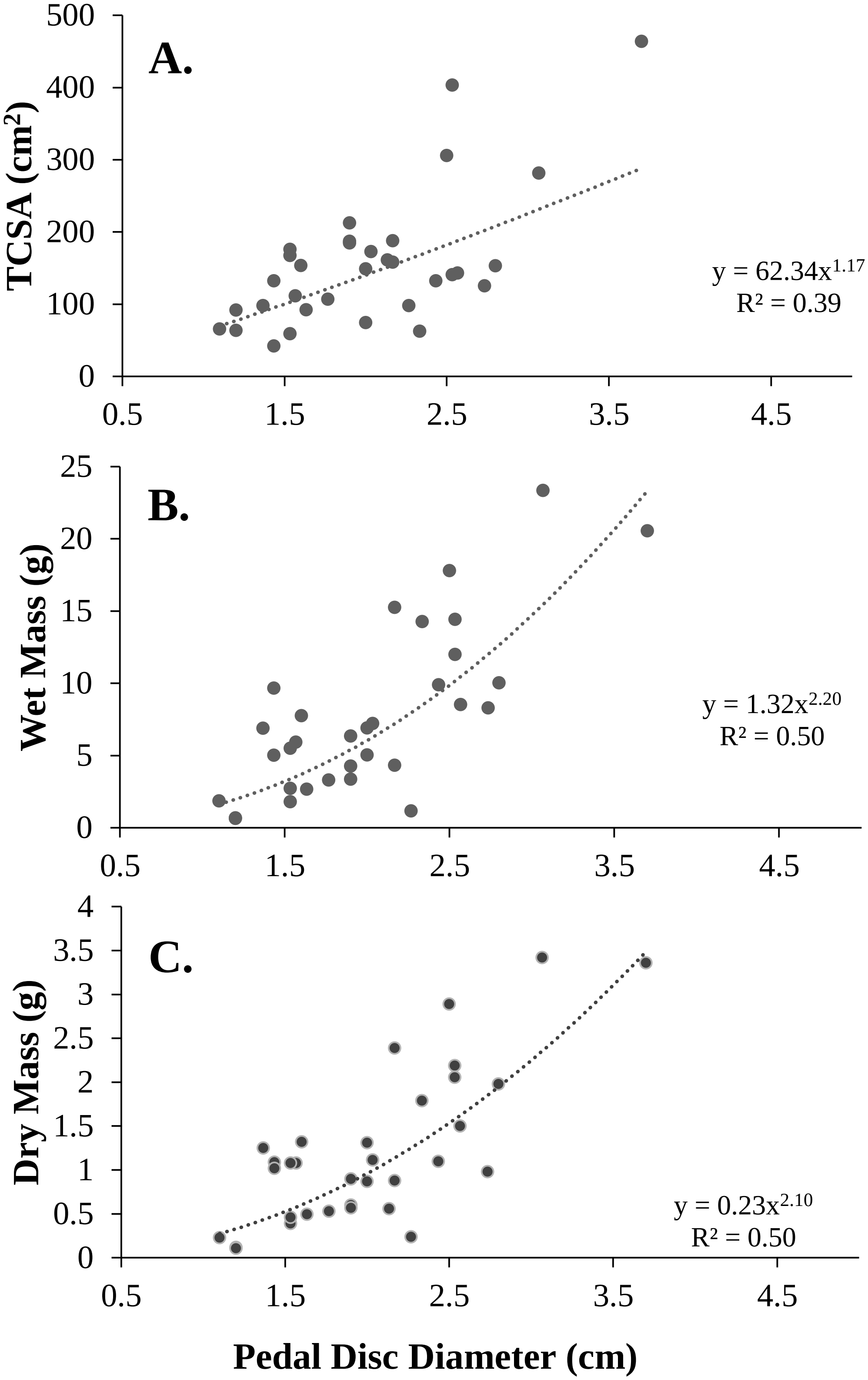

A.
TCSA (cm²)
500
400
300
200
100
0
0.5
1.5
2.5
3.5
4.5
y = 62.34x^1.17
R² = 0.39
B.
Wet Mass (g)
25
20
15
10
5
0
0.5
1.5
2.5
3.5
4.5
y = 1.32x^2.20
R² = 0.50
C.
Dry Mass (g)
4
3.5
3
2.5
2
1.5
1
0.5
0
0.5
1.5
2.5
3.5
4.5
y = 0.23x^2.10
R² = 0.50
Pedal Disc Diameter (cm)

Figure 3.2.

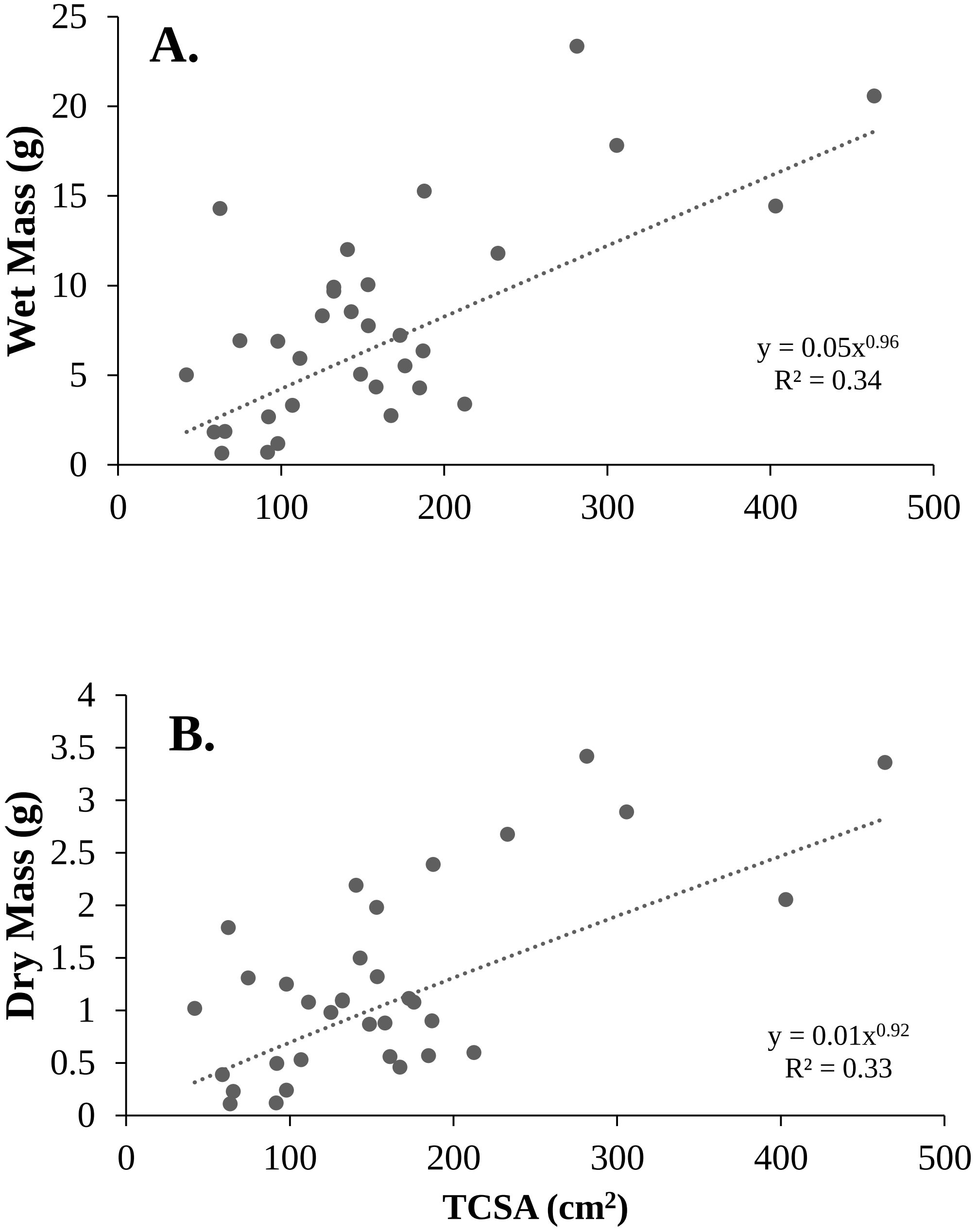
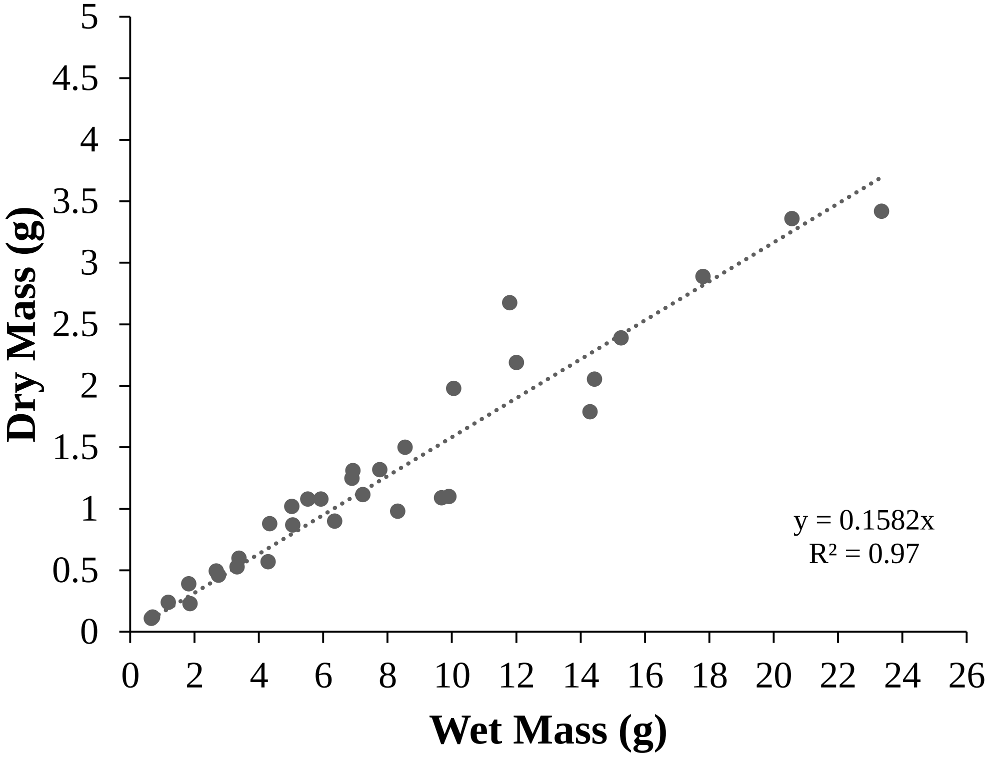

A.
Wet Mass (g)
25
20
15
10
5
0
0
100
200
300
400
500
y = 0.05x^0.96
R² = 0.34
B.
Dry Mass (g)
4
3.5
3
2.5
2
1.5
1
0.5
0
0
100
200
300
400
500
TCSA (cm²)
y = 0.01x^0.92
R² = 0.33

Fig. 3.3.



Dry Mass (g)
5
4.5
4
3.5
3
2.5
2
1.5
1
0.5
0
0
2
4
6
8
10
12
14
16
18
20
22
24
26
Wet Mass (g)
y = 0.1582x
R² = 0.97

Fig. 3.4.

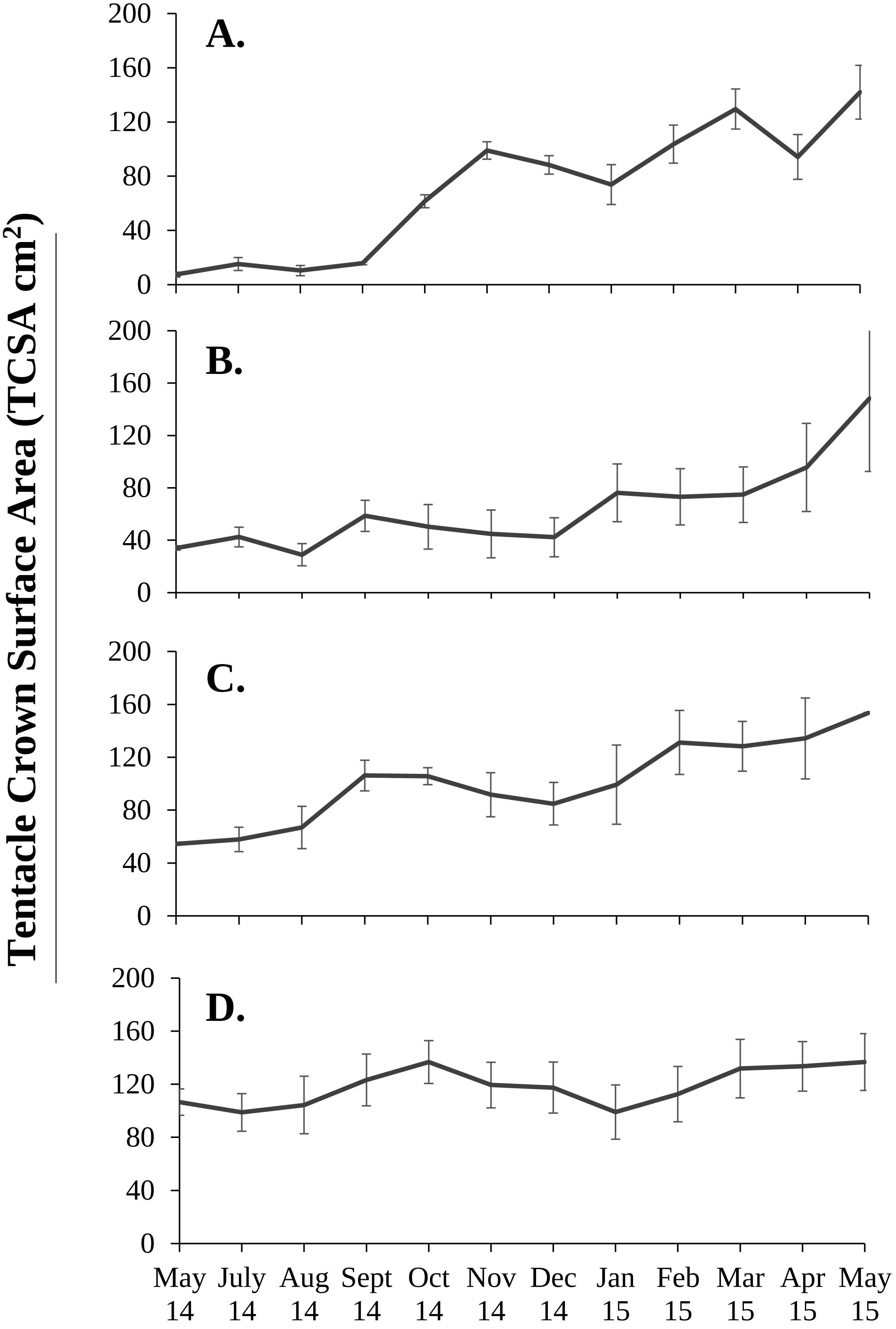

Tentacle Crown Surface Area (TCSA cm2)
A.
B.
C.
D.
0
40
80
120
160
200
May 14
July 14
Aug 14
Sept 14
Oct 14
Nov 14
Dec 14
Jan 15
Feb 15
Mar 15
Apr 15
May 15

Figure 3.5.

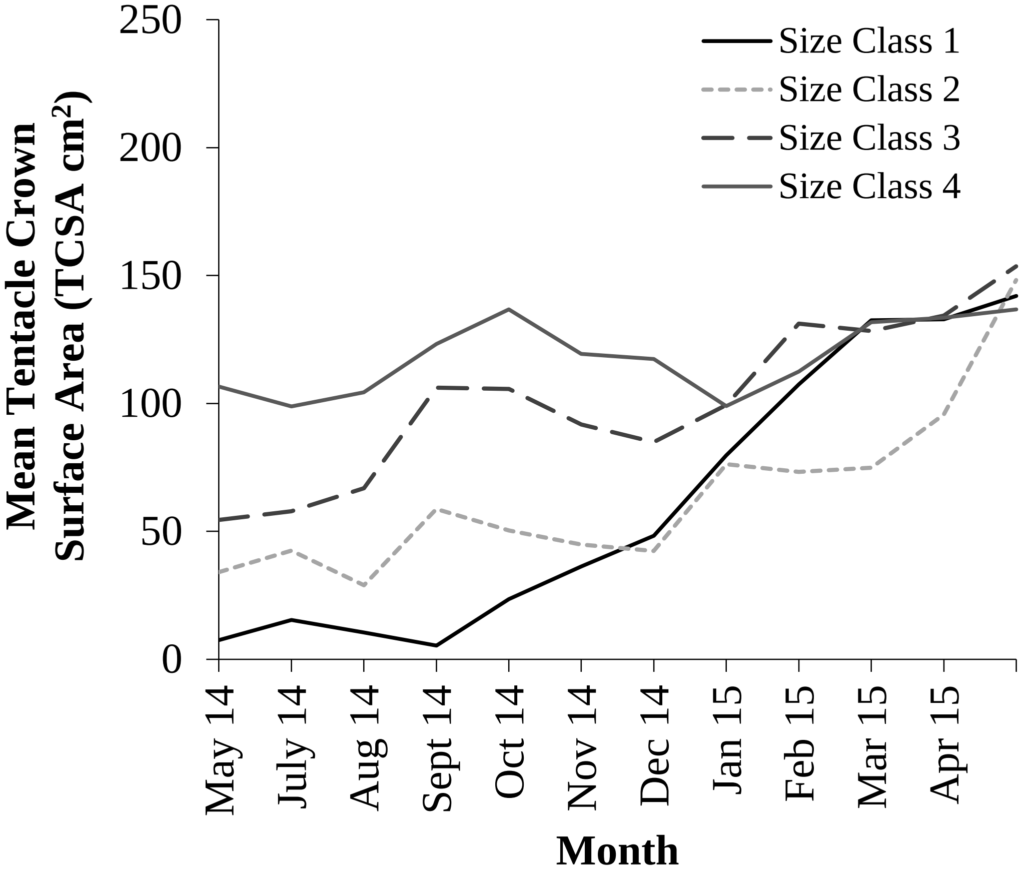

250
200
150
100
50
0
Mean Tentacle Crown Surface Area (TCSA cm²)
Size Class 1
Size Class 2
Size Class 3
Size Class 4
May 14
July 14
Aug 14
Sept 14
Oct 14
Nov 14
Dec 14
Jan 15
Feb 15
Mar 15
Apr 15
Month

Figure 3.6.

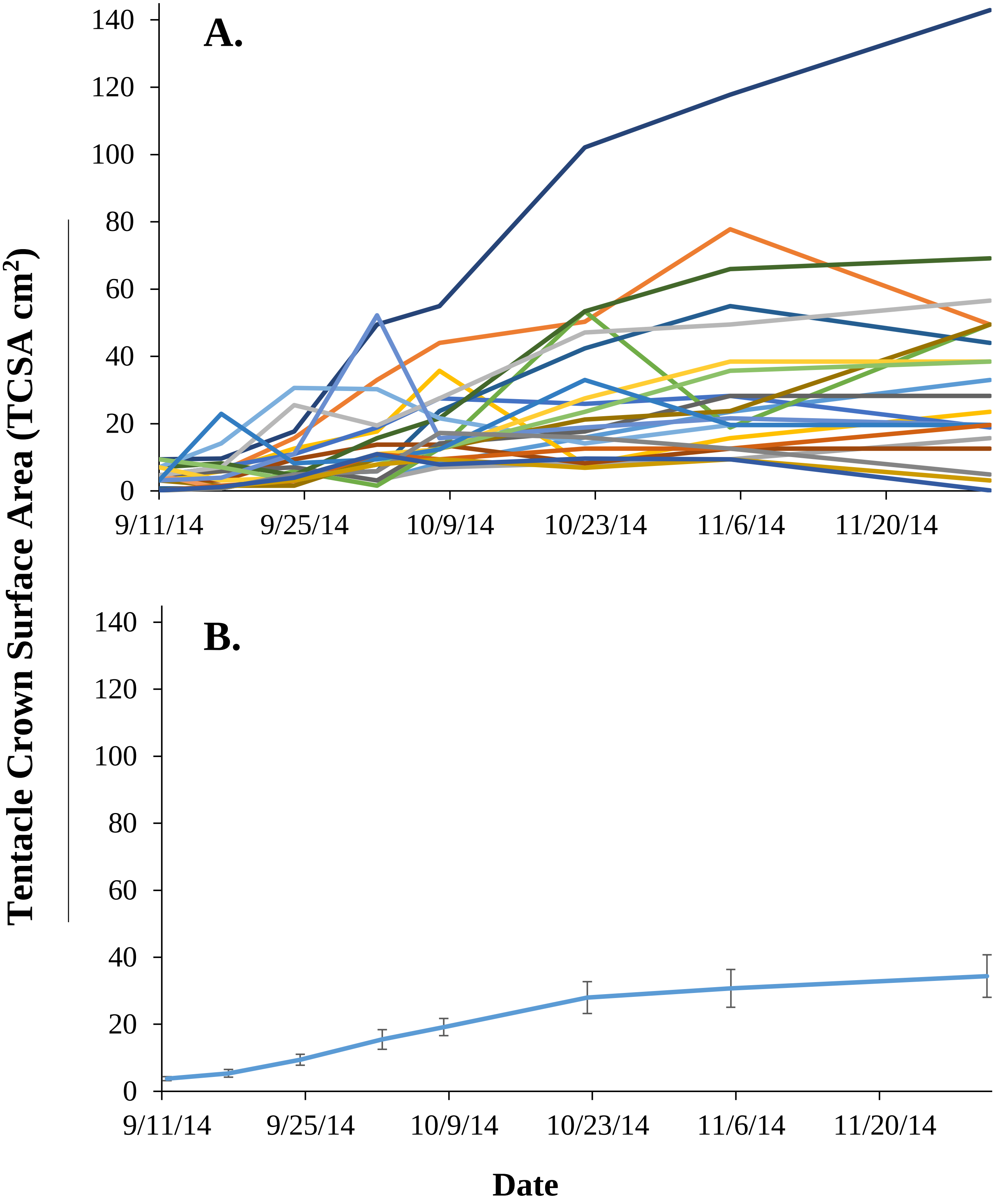

A.
B.
Tentacle Crown Surface Area (TCSA cm^2)
0
20
40
60
80
100
120
140
9/11/14
9/25/14
10/9/14
10/23/14
11/6/14
11/20/14
Date

Figure 3.7.

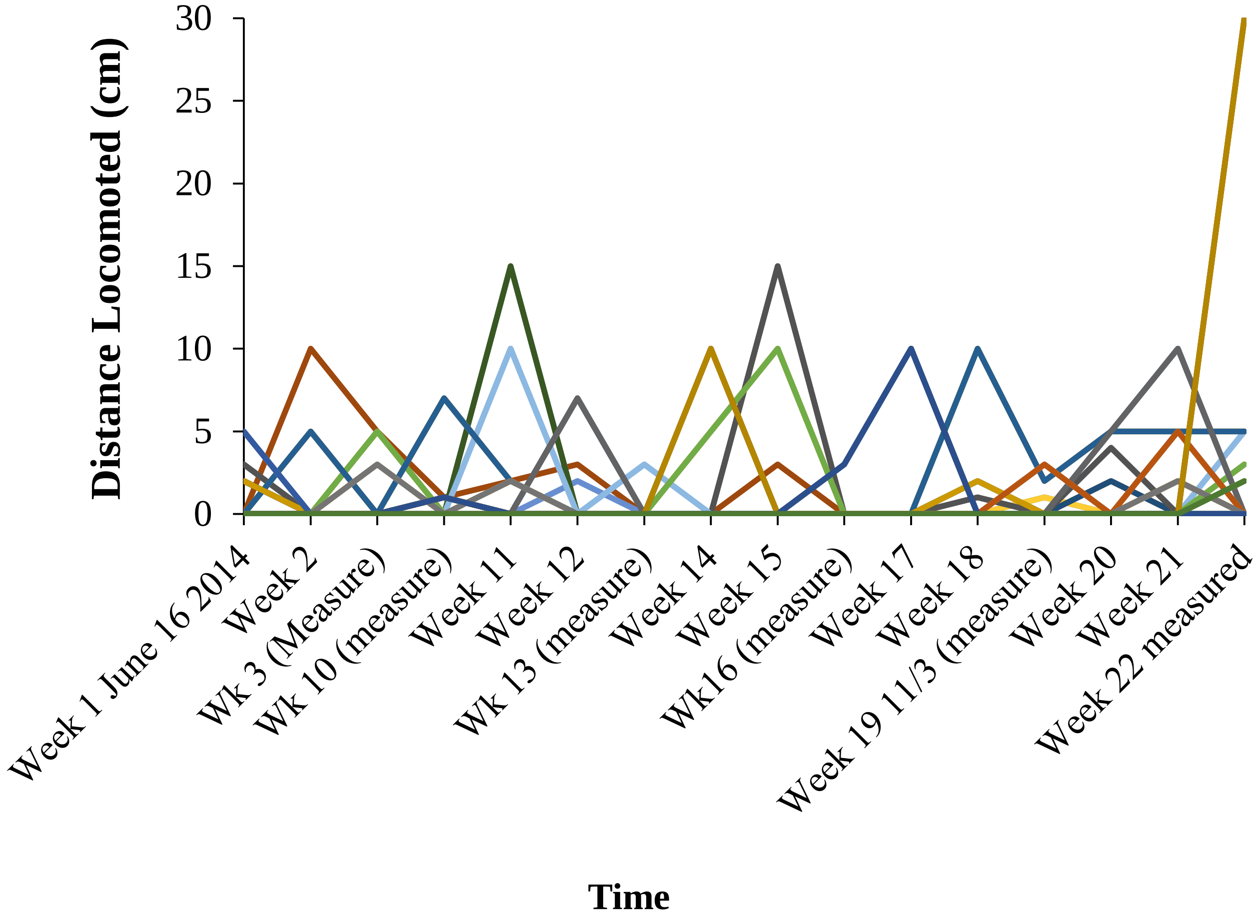
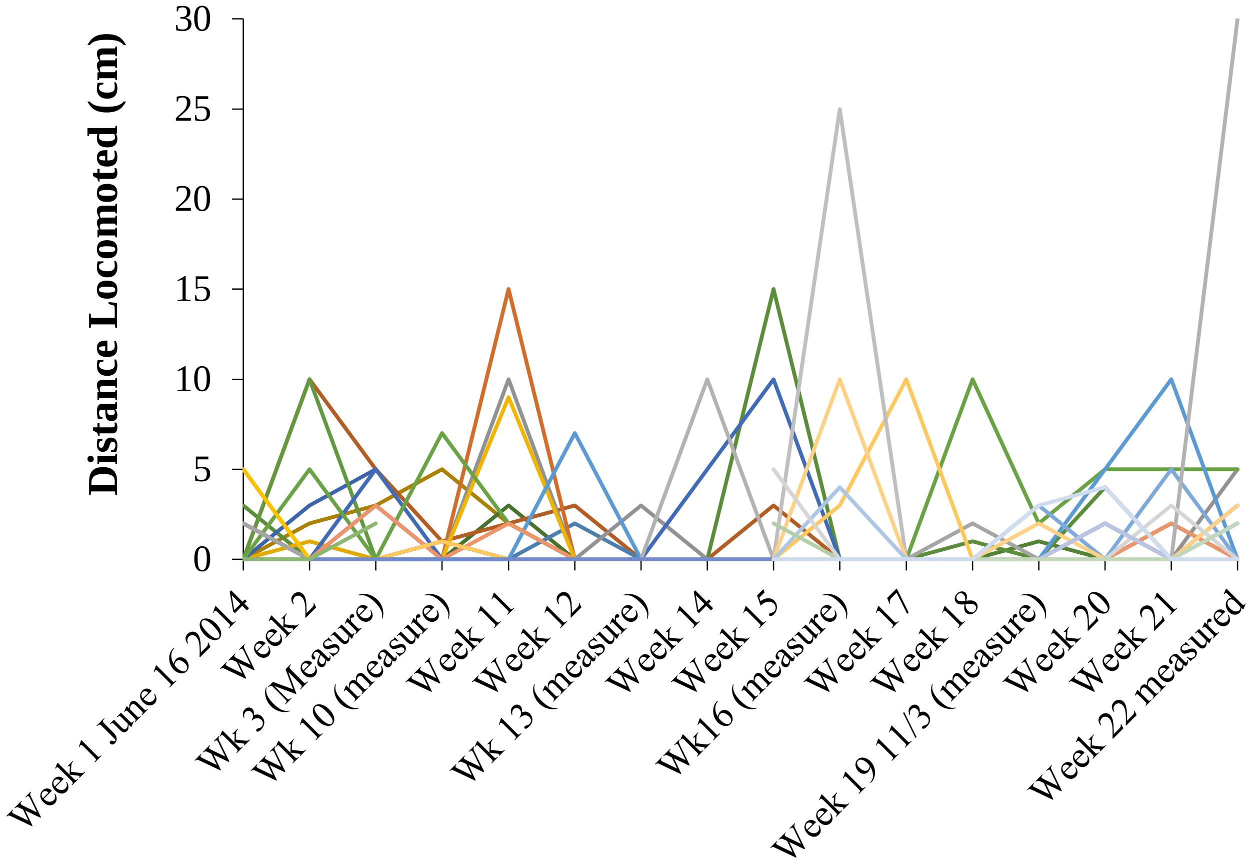

Distance Locomoted (cm)
30
25
20
15
10
5
0
Week 1 June 16 2014
Week 2
Wk 3 (Measure)
Wk 10 (measure)
Week 11
Week 12
Wk 13 (measure)
Week 14
Week 15
Wk16 (measure)
Week 17
Week 18
Week 19 11/3 (measure)
Week 20
Week 21
Week 22 measured
Time

Figure 3.8.



Distance Locomoted (cm)
30
25
20
15
10
5
0
Week 1 June 16 2014
Week 2
Wk 3 (Measure)
Wk 10 (measure)
Week 11
Week 12
Wk 13 (measure)
Week 14
Week 15
Wk16 (measure)
Week 17
Week 18
Week 19 11/3 (measure)
Week 20
Week 21
Week 22 measured
Time

Figure 3.9.

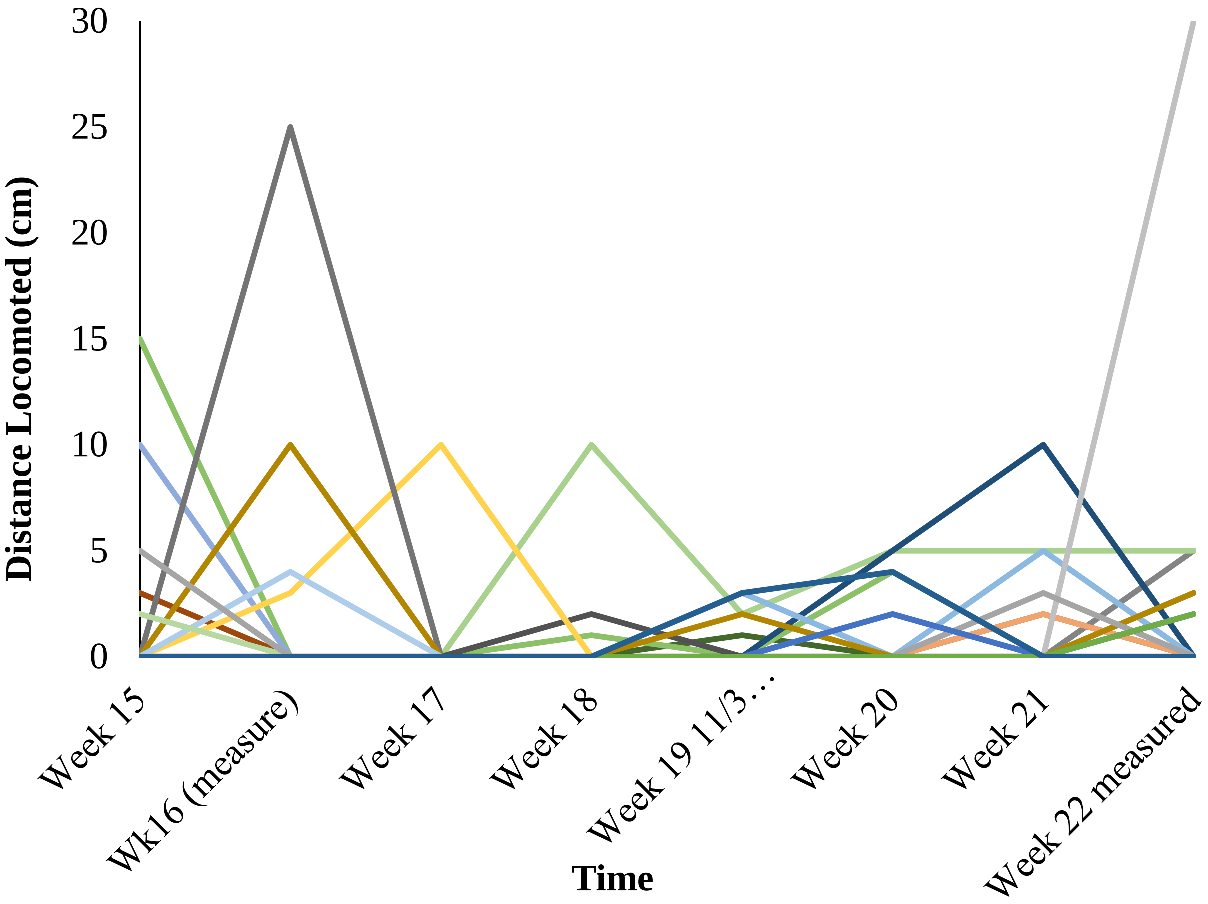

30
25
20
15
10
5
0
Distance Locomoted (cm)
Week 15
Wk16 (measure)
Week 17
Week 18
Week 19 11/3…
Week 20
Week 21
Week 22 measured
Time

Figure 3.10.

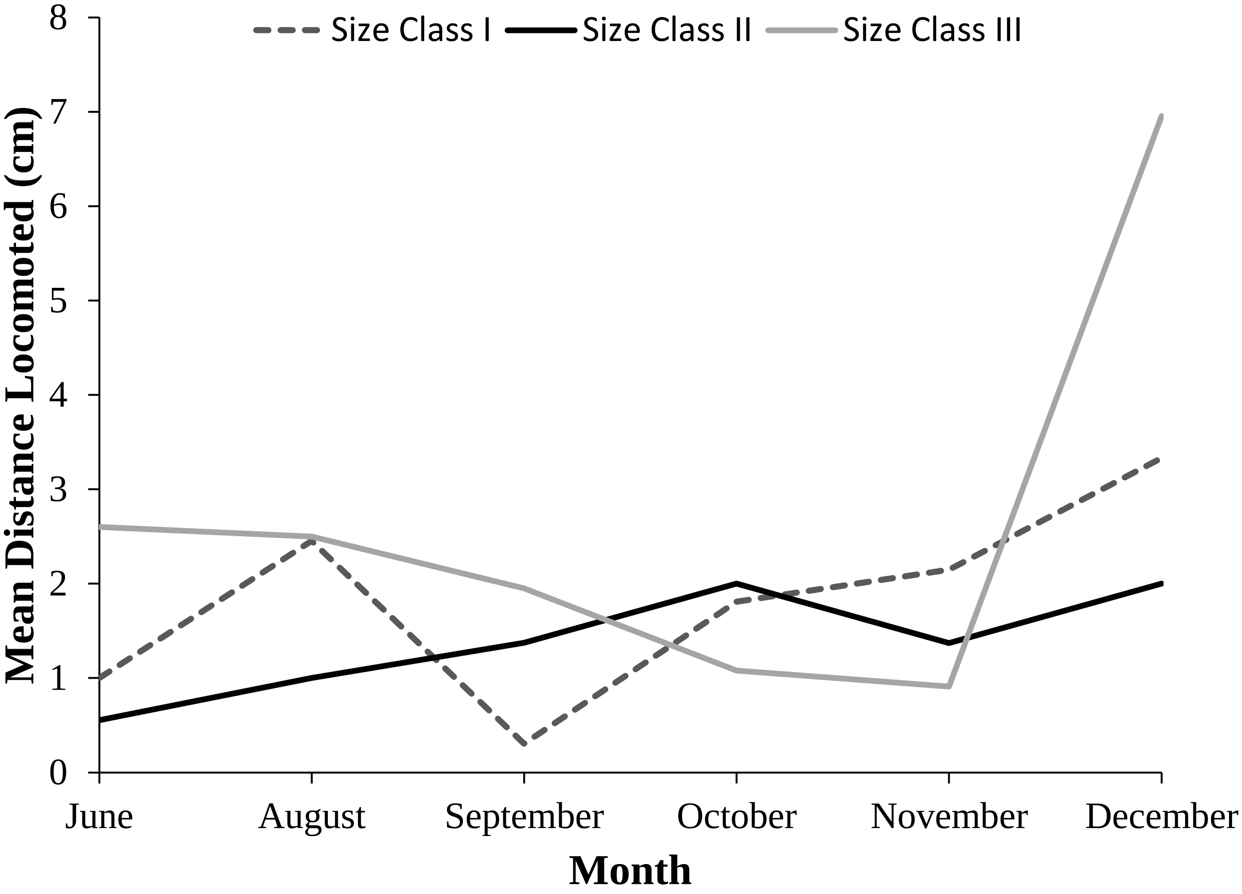

8
7
6
5
4
3
2
1
0
Size Class I
Size Class II
Size Class III
Mean Distance Locomoted (cm)
June
August
September
October
November
December
Month

Figure 3.11.

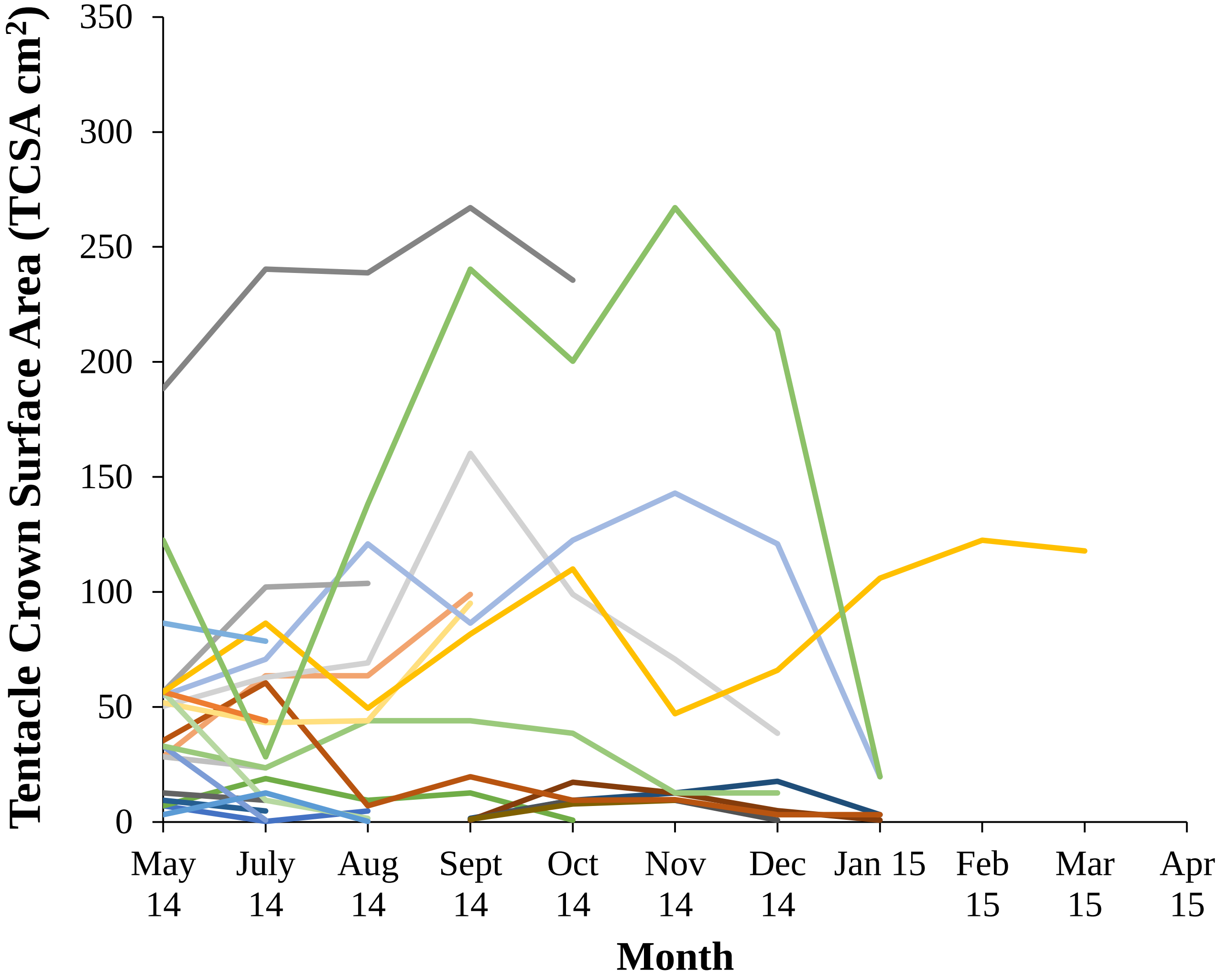
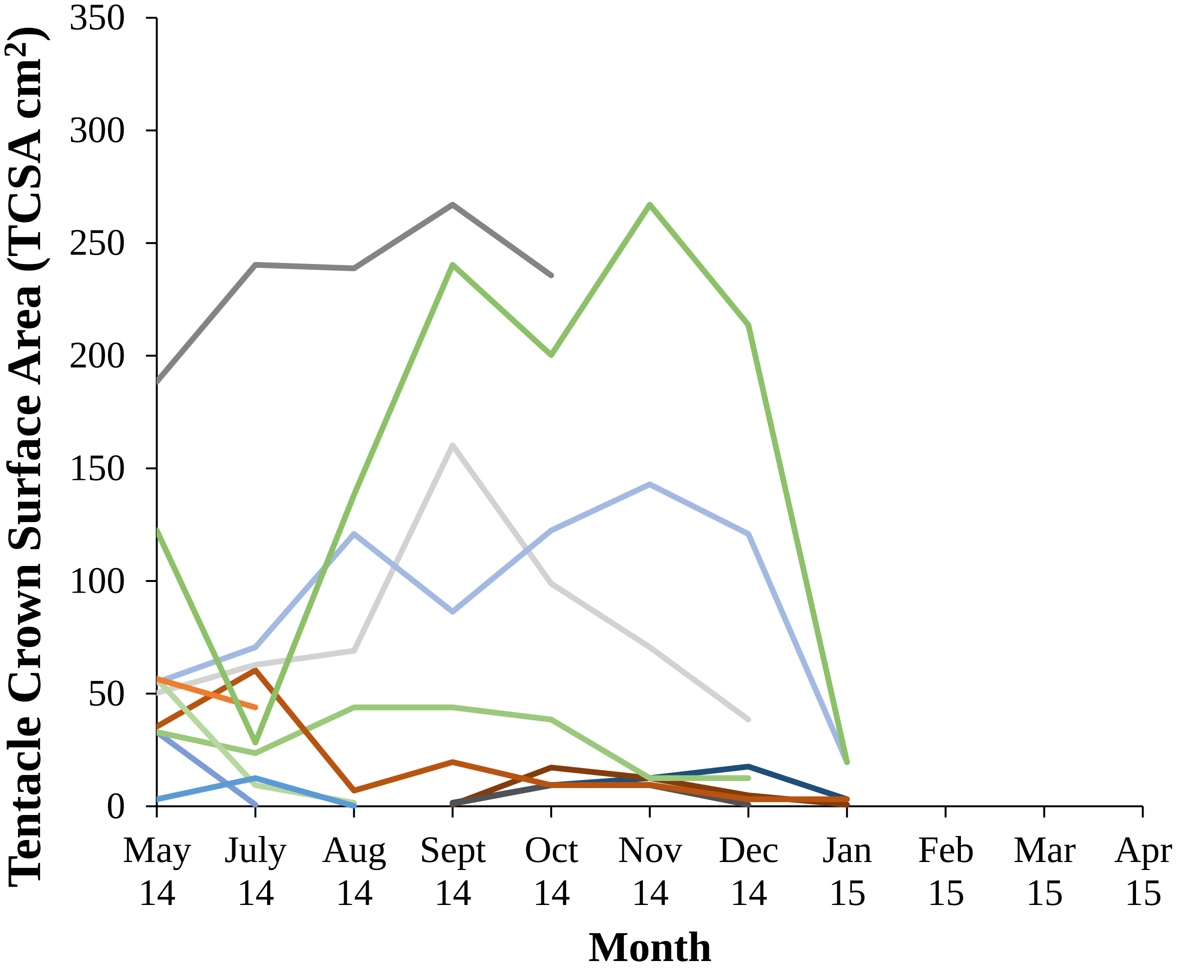
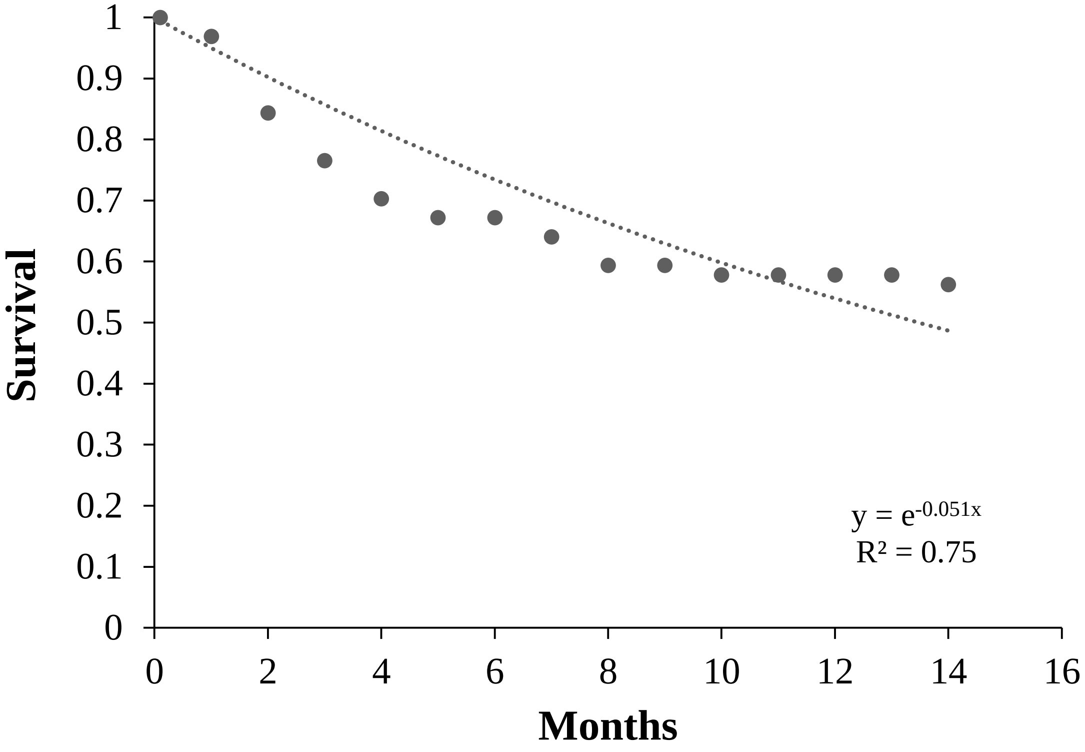

Tentacle Crown Surface Area (TCSA cm^2)
350
300
250
200
150
100
50
0
May 14
July 14
Aug 14
Sept 14
Oct 14
Nov 14
Dec 14
Jan 15
Feb 15
Mar 15
Apr 15
Month

Figure 3.12.



Tentacle Crown Surface Area (TCSA cm²)
350
300
250
200
150
100
50
0
May 14
July 14
Aug 14
Sept 14
Oct 14
Nov 14
Dec 14
Jan 15
Feb 15
Mar 15
Apr 15
Month

Figure 3.13.



1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Survival
0
2
4
6
8
10
12
14
16
Months
y = e^-0.051x
R² = 0.75

Fig. 3.14.