Running Head: Octocoral recruitment and survival

Title: Species level identification of *Antillogorgia* spp. recruits identifies multiple pathways of octocoral success on Caribbean reefs

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Abstract

Successful recruitment is critical to the maintenance and resilience of populations and may be at the core of the transition from scleractinian to octocoral dominated faunas on some Caribbean reefs. For sessile invertebrates, recruitment incorporates the composite effects of larval supply, settlement and survival. The relative success of these processes differs between species and successful recruitment may be achieved through different life history strategies. Recruitment of six abundant and widespread *Antillogorgia* spp. was assessed at six sites on Little Bahama Bank from 2009–2012. Identification of recruits to species level, based on microsatellite analyses, revealed differences in recruitment and survival between species, sites and years. The broadcast spawning species, *A. americana* and *A. acerosa* had low rates of early recruitment and post-settlement survival. Higher levels of recruitment success were achieved among brooding and surface brooding species following somewhat different patterns of early recruitment and survival. The internal brooder *Antillogorgia hystrix* had the highest recruitment at five of the sites but low survival dramatically reduced its abundance and after a year it had similar densities as the surface brooding species, *A. elisabethae* and *A. bipinnata*. The brooders have smaller colonies and will produce fewer larvae than the broadcast spawning species, but they release competent larvae which probably accounts for their higher recruitment rates. The *Antillogorgia* illustrate the diversity of successful reproductive strategies exhibited by octocorals.and differences in the life history strategies among these congeners are best characterized by their mode of larval development.

Keywords: gorgonian, coral reef, recruitment, post-settlement mortality, *Antillogorgia,* Bahamas, life history

Introduction

Marine communities are populated by species, which commonly have life histories involving a larval stage that disperses from its natal population. In these systems maintenance of the community is not necessarily determined by whether individuals reproduce successfully, but rather by whether larvae successfully recruit to that site. Historically, recruitment was not considered an important component of community dynamics (Thorson 1946) but it has become clear that in some settings recruitment is critical to the dynamics of populations and community structure (Gaines and Roughgarden 1985; Connolly and Roughgarden 1999). On coral reefs, where the density and diversity of organisms has historically been great, density dependent regulation has often modulated the effects of recruitment (Tanner 1999; Tanner et al. 2009; Bramanti and Edmunds 2016; Edmunds et al. 2018). However, coral reef communities in general (Connell 1997; De'ath et al. 2012; Edmunds et al. 2014)and Caribbean coral reefs in particular (Connell 1997; Gardner et al. 2003; Côté et al. 2005; Gardner et al. 2005; Roff and Mumby 2012) have experienced precipitous declines through the direct, indirect and perhaps synergistic effects of hurricanes, overexploitation, disease and climate driven changes in water temperature. These effects are expected to grow over the next century (Hughes et al. 2017), and predictions for the future of coral reefs are dire (Hoegh-Guldberg et al. 2017). While amelioration of conditions is essential to the future success of reefs, the resilience of existing populations and the establishment and reestablishment of populations in suitable habitats will be dependent on recruitment.

Over a half century of ecological research has explicitly contrasted species that rely on high levels of reproduction and dispersal for persistence versus those that have lower reproductive output coupled with higher individual survival (MacArthur and Wilson 1967, and

100s of references thereafter). Many benthic marine invertebrates have bipartite life histories in which gametes and larvae disperse. In these species, the contrast in life history strategies has often been between species with high vs low levels of recruitment, where recruitment is the number of individuals arriving in a population over an arbitrarily selected time interval. Thus, recruitment incorporates the composite effect of the production of larvae, supply of larvae to a specific site, settlement and then survival between settlement and the time at which the population is censused. Each of these processes can differ between species, locations and over time. Some marine species have life histories that make it possible to conduct censuses within days of settlement (c.f., Minchinton and Scheibling 1991), and success at multiple stages of the life history can be assessed. This is not the case when settlement is less predictable, occurs at low density and/or when the newly settled recruits are difficult to discover. In those cases, census data incorporate an element of post-settlement survival. Furthermore, the difficulty of identifying early life history stages of many benthic species has led to studies that are often limited to the level of families or genera. Such analyses conceal potentially important differences in the settlement and survival of different species which may have important effects on the assembly and maintenance of communities. In this study we used species specific estimates of recruitment at six-month time intervals over four years to identify differences in settlement and post-settlement survival.

The recruitment dynamics of reefal species is essential to our understanding of reef futures, and recruitment of species that appear to be maintaining populations in the midst of overall reef decline is particularly important. In the Caribbean, a number of “alternative” communities have been observed to develop as scleractinians decline (Norstrom et al. 2009) and increased abundance of octocorals have been reported at many sites (Ruzicka et al. 2013; Lenz et al. 2015; Tsounis and Edmunds 2017; Sanchez et al. 2019). To the extent that a transition in community structure has occurred at those sites, there has not been a monotonic increase in octocoral abundances. Octocorals at those sites have undergone declines in abundance but have recovered, leading to net increases in overall abundance (Florida Keys, (Ruzicka et al. 2013); St John, Virgin Islands, (Lenz et al. 2015; Tsounis and Edmunds 2017). Increasing numbers of colonies requires recruitment, and thus, recovery of octocorals at those sites has been dependent on recruitment. The observed resilience further emphasizes the importance of recruitment (also see Lasker et al. 2020).

Studies of octocorals that have quantified recruitment at the level of species have most commonly focused on a single species (*Muricea californica and M. fruitcosa* (Grigg 1977), *Leptogorgia virgulata*, (Gotelli 1988), *Plexaura kuna (Lasker 1990; Lasker et al. 1998)* and *Antillogorgia elisabethae (Lasker 2013)* or single genus (*Antillogorgia* spp.(Yoshioka 1994). Broader surveys have distinguished among genera in the Florida Keys (Bartlett et al. 2018) among a mix of general and species in Puerto Rico (Yoshioka 1996), between species of *Antillogorgia* in The Bahamas (Lasker and Jamison 2006) and between species in Eastern Pacific reefs in Panama (Gomez et al. 2014). Both single species and community level analyses have documented high levels of variability over time as well as highly heterogeneous recruitment both between and within sites.

Antillogorgia spp., the focal species of this study, are among the most widespread and abundant of the Caribbean reef octocorals. They range from the coast of South America to Bermuda (Bayer 1961; Lasker and Coffroth 1983; Lasker 1990) and are common at virtually every site that has been characterized (Goldberg 1973; Kinzie 1973; Lasker and Coffroth 1983; Yoshioka and Yoshioka 1987; Jordan-Dahlgren 2002; Lenz et al. 2015). In The Bahamas, *Antillogorgia* spp. are abundant across a wide array of habitats; 8 of the 11 currently recognized species have been observed at sites ranging from San Salvador to the Great Bahama Bank (unpublished data). During the period of 2009 to 2012 an extensive research program was conducted to characterize the populations, dynamics and genetic structure of *Antillogorgia elisabethae* in the northern Bahamas (Lasker 2013; Smilansky and Lasker 2014; Lasker and Porto-Hannes 2015). In this report we consider recruitment and survival of the six most common *Antillogorgia* spp., supplementing data on recruitment of *A. elisabethae,* with data on the recruitment and survival of *A. americana, A. acerosa, A. bipinnata, A. hystrix* and *A. rigida*.

Comparison of recruitment of these *Antillogorgia* spp. provides opportunity to evaluate differences in recruitment across life history strategies in a group of closely related species. All six species are gonochoric. *A. americana* broadcast spawns in spawning events, which in The Bahamas are believed to occur November and/or December (based on studies in the Florida Keys (Fitzsimmons-Sosa et al. 2004; Coelho and Lasker 2016)). *A. elisabethae*, *A. bipinnata* and *A. hystrix* exhibit similar timing, spawning in November/December. *A. elisabethae* and *A. bipinnata* surface brood (Gutiérrez-Rodríguez and Lasker 2004). *A. hystrix* is a true brooder and releases planulae that are already infected with Symbiodiniaceae (formerly *Symbiodinium* spp. (LaJeunesse et al. 2018) symbionts (Coelho and Lasker 2014). *A. acerosa* is believed to broadcast spawn (Yoshioka 1979). The reproductive mode of *A. rigida* is unknown.

Methods

The research was conducted at six sites along the southern edge of the Little Bahama Bank in The Bahamas. The research sites (ESM Table 1, ESM Figure 1) were initially chosen to study the dynamics of *A. elisabethae* populations (Lasker 2013; Lasker and Porto-Hannes 2015).

Those sites were selected because they had previously been subject to harvests of *A. elisabethae*. In the context of this study their selection can be characterized as arbitrary, but all six sites had diverse octocoral communities with many colonies of other *Antillogorgia* spp. The octocoral communities at the sites are similar to gorgoniid dominated communities that have been reported from forereefs throughout the Caribbean (Goldberg 1973; Kinzie 1973; Lasker and Coffroth 1983; Yoshioka and Yoshioka 1989; Sánchez et al. 1997; Etnoyer et al. 2010).

The sites have been described in Lasker (2013) and are depicted in ESM Fig. 1. At each site, a center point was arbitrarily selected and then four 20m transects were established using random headings and random distances (1-40m) from the center point to define the starting point of the transect. The transects were then laid out on random headings from that start point. The start and end of the transects were permanently marked with steel rods. Five points were randomly selected on each transect and at each point a 3.5 x 1 m band was marked which was subdivided in to 6 sampling areas, three 1x1 m quadrats that were used for annual censuses of all colonies and three 0.25 x 1 m quadrats that were used for censuses of recruits. Quadrats were marked with masonry nails. The layout of the quadrats is depicted in Fig. 1.

Census and Sampling Protocols. Recruits were censused (counts of all recruits present within each quadrat during the visit) and collections made from specific quadrats based on age/size of the recruits. The censuses and collections were made biannually between January 2009 and June 2012. Winter censuses and collections were made in January (2009, 2011 and 2012) or February (2010) (henceforth all are referred to as January censuses and collections) with a summer census and collection in June of each year. Collections of recruits in the three different quadrats were designed to characterize numbers of recruits in each year's cohort that were present 1-2 months, 6-7 and 13-14 months after spawning. During every January sample, all single polyp, 1-2 month old recruits from the November/December spawning events present in quadrat #12 were collected (Fig. 1). The presence of recruits in the #12 plots in June collections indicates that not all of the one polyp recruits had been collected in the previous January collection. Thus, in order to fully characterize the earliest estimate of recruitment, recruits present in the #12 quadrat in June were also collected and January recruitment was calculated as the number of recruits found in the #12 plots in January plus the number found in the #12 plots found in June. This is an underestimate of the number of recruits present at 1-2 months as some of the recruits that escaped detection in Jan/Feb would have died before June. In the following January sample, the surviving 13-14 month old recruits, which could be distinguished by their 3-5 cm height, were collected from quadrat #13. The fates of individual recruits cannot be followed in this sampling scheme, but the censuses track the number of recruits still present, i.e., surviving, in each year's cohort. Numbers of adults (colonies ≥ 20 cm height) were counted in quadrats 1, 2 and 3 (Fig. 1) in 2012.

Species Identification. Recruits that were collected were measured after each dive and preserved in 95% ethanol. Upon return to the University at Buffalo recruits were identified to species on the basis of amplification of two microsatellite loci (Pel-19 and Pel-32) that had previously been shown to distinguish the species of *Antillogorgia* present at these sites in The Bahamas (Jamison and Lasker 2008). All procedures followed those in Jamison and Lasker (2008) and Lasker and Porto-Hannes (2015). More recruits were obtained in each collection than could be analyzed prior to the next collection and the species level identification was limited to subsets of the collected recruits. A total of 4,990 recruits were collected across the three years and six sites and of those 2,456 were analyzed and identified to species using the two microsatellite markers. The number of recruits collected varied between sites, and many more one-month and six- month old recruits were collected than 13-month old recruits. In order to maximize the accuracy of the relative abundance estimates greater proportions of samples were analyzed from collections with fewer recruits (ESM Table 2). The proportions of the different species at the different sites and ages were used to calculate species specific recruitment rates. Abundances of the six species among the recruits were calculated in two ways. At the three Cross Harbour sites, where 100s of recruits were sampled, year specific values were calculated using the relative frequencies of the analyzed samples for each year. Due to the relatively small number of recruits from some of the sites, collections were pooled over years. Thus, differences in proportions of species recruiting in the different years cannot be discerned for all of the sites.

Statistical analyses were all conducted using SPSS v. 25. As a wide variety of tests were employed with the different data sets they are noted in the presentation of the results for each type of data.

RESULTS

Recruitment. Numbers of recruits censused at the different sites and at different quadrats within the sites differed dramatically, with some quadrats never yielding a recruit while hundreds might be censused in an adjacent quadrat. The number of recruits censused in the individual $0.25m^2$ quadrats in a single census ranged from 0 to 274. Quadrats with large amounts of sand or surfaces with sediment and turf algae had few recruits, but there were no obvious associations between recruitment and crustose coralline algae nor the presence or absence of specific scleractinian or octocoral species. When data from January censuses (i.e., counts of new recruits in quadrats 11, 12 and 13) from all sites are pooled, the frequency distribution (ESM Figure 2A) has dramatically more cases of empty quadrats than would be expected from a Poisson distribution (Kolmogorov-Smirnov Test, $p<0.001$). At the level of the individual sites the frequency distribution from Cross Harbour Ridge (ESM Figure 2B) fits an exponential distribution (Kolmogorov-Smirnov Test of fit to normal, binomial and Poisson distributions, each $p<0.001$; test of fit to exponential distribution, $p=0.134$). Frequency distributions from Cross Harbour Slope and Cross Harbour Patch had multimodal distributions (data not shown). The numbers of recruits at the other three sites were low, and the frequency distributions contained a preponderance of zero values (data not shown).

January recruitment rates for *Antillogorgia* spp., i.e., all species combined, are depicted in Figure 2. There were significant differences in numbers of recruits between Sites, Quadrats, and Years by Sites (Generalized Linear Model [GLM]- Site, Year*Site, Quadrats, all $p<0.001$; Year, $p=0.029$; SPSS v 25). Estimated marginal means for Sites and Years are included in ESM Table 3. As is evident in Figure 2 the three Cross Harbour sites, and Cross Harbour Ridge in particular, had greater recruitment than the other sites. Recruitment at the sites with the highest value (Cross Harbour Ridge, 2009) and lowest (Gorda Patch, 2011) differed by almost 2 orders of magnitude. Recruitment was lowest in 2010 at five of the six sites. Comparison of estimated marginal means (ESM Table 3) indicate that recruitment in 2010 and 2011 was lower than 2009 and 2012, but as the significant Site by Year interaction suggests, those difference were not uniform across all six sites, with overall recruitment in 2010 being lower than 2012 only at three of the sites.

The proportions of the six different species in the collections differed between sites and as a function of recruit age (ESM Table 2). The general trend was *A. elisabethae*, and to a lesser extent *A. bipinnata*, increased in relative abundance between one and seven months and *A.*

hystrix declined in relative abundance as the recruits aged. However, that pattern varied between sites. *A. hystrix* was proportionately most abundant among the one month recruits at the three Cross Harbour sites, rare at Sandy Point and was not present in the samples from the other three sites. The large number of recruits in collections from the Cross Harbour sites made it possible to compare recruitment among years as well as sites. The calculated species specific recruitment rates from the January censuses differed between Species, Sites and Years (GLM with gamma distribution, all p <0.001, ESM Table 4). All interactions were significant. The overall pattern reflected in the estimated marginal means were that ordered recruitment rates were *A. hystrix* >> *A. elisabethae* > *A. bipinnata* > *A. americana* > *A. acerosa* > *A. rigida* (ESM Table 4). Among years, overall recruitment rates were greatest in 2009 > 2012 > 2011 > 2010. However, as all of the interaction terms were significant those patterns did not apply uniformly across Sites, Years and Species.

In order to calculate species specific rates for all sites a second analysis was conducted in which the extrapolated species-specific abundances were calculated pooling data across years, which was necessary due to the low numbers of recruits collected from the non-Cross Harbour sites. Abundances for all species at all sites are shown in Figure 3. Statistical modeling of these data (GLM) did not include a Year x Species nor the 3-way interactions as proportions of the different species were based on identifications that were pooled over years. All main effects and interactions were significant (ESM Table 5). Estimated marginal means indicate that recruitment rates of the species were *A. hystrix*>*A. elisabethae*>*A. bipinnata*>*A. americana* = *A. acerosa* > *A. rigida*. As suggested by the interaction terms *A. hystrix* had the highest recruitment rates at the three Cross Harbour sites, and *A. elisabethae* disproportionately greater recruitment at Cross

Harbour Ridge and Cross Harbour Slope. The greater high recruitment rates at the Cross Harbour sites were primarily a function of the recruitment of *A. hystrix* and *A. elisabethae*.

The relationship between recruitment at each site in each of the four years and adult abundances, which were assessed in 2012 is presented in Fig. 4A. Correlations with adult abundance were slightly greater when abundance was calculated as the sum of colony heights (Fig. 4B), a measure that incorporates colony size into the estimate of adult abundance. Significant correlations between adult abundance (summed colony heights) and recruitment were observed for *A. acerosa*, *A. bipinnata, A. elisabethae, and A. hystrix.* (r= 0.991, 0.994, 0.997, 0.992, all p<0.001). There were no significant correlations between adult and recruit abundance for *A. americana* (r=0.662, p=0.45), nor *A. rigida* (r= -0.244, p=0.64).

Mortality. The number of recruits surviving to 6-7 months was calculated as the number of recruits found in the #11 quadrats in the June samples, and the number surviving to 13-14 months was calculated as the number of larger (i.e. 1-5 cm) colonies collected in the #13 quadrats in January. The frequency distribution of numbers of recruits in quadrats was extraordinarily variable, and adjacent quadrats did not start with the same number of recruits. Numbers of recruits observed in a quadrat 1-2 months after settlement were sometimes lower than the number of recruits in the adjacent quadrat 6-7 months later. Thus, quadrat and transect specific estimates of survivorship are not reported. Instead, average values for each site and year were calculated (ESM Table 6). In two cases, Gorda Patch in 2011 and Cross Harbour Patch in 2009, the average number of recruits in quadrats censused 13 months after spawning exceeded the number in the quadrats that were sampled at 7 months. Both cases were at sites and years in which fewer than 10 recruits were found, making survival calculations very sensitive to random variation in the numbers of recruits found. The plot of numbers of recruits from each site over

13 months (Figure 5A, ESM Table 6) again illustrates the differences in recruitment at the sites. The slopes of the lines suggest differences in mortality between sites and relatively little difference in mortality between the two time periods. However, as evident in Figure 2, the relative abundances of the species among the recruits differed between sites and analyses that differentiated among the species identified a more complex result.

Substantial numbers of recruits of *A. bipinnata, A. elisabethae* and *A. hystrix* were found at the three Cross Harbour sites and statistical analysis of mortality rates for those species and sites (Figure 5B, ESM Table 7) identified significant differences between Species ($p=0.004$), Site ($p<0.001$) and Age ($p=0.019$), as well as significant interactions between Species x Age ($p=0.004$), Site x Age ($p<0.001$) and Species x Site x Age ($p=0.028$). Post-hoc Scheffe tests and comparisons of estimated marginal means for the interactions indicated that mortality was greater in the first 7 months post-settlement, that *A. hystrix* had higher mortality than either *A. elisabethae* or *A. bipinnata,* that mortality was greater at the Cross Harbour Patch site than the other two Cross Harbour sites and that 1-7 month mortality of *A. hystrix* did not differ between sites, and that 7-13 month mortality of *A. hystrix* was greater at the Cross Harbour Patch site.

Comparisons of mortality and survivorship among all six species must be interpreted cautiously as density estimates for *A. acerosa, A. americana* and *A. rigida* are based on small numbers of individuals. Survivorship to the two ages and across species are presented in ESM Table 8. The species fall into two groups. *A. bipinnata and A. elisabethae* had relatively high survival during the first seven months (51 and 33%, respectively) and reduced mortality and thus high survivorship after 13 months (48 and 39%). (The estimate of survivorship of *A. elisabethae* was greater after 13 months than seven months, which illustrates the variability inherent with the census approach to estimating survival.) In contrast, *A. acerosa, A. americana* and *A. hystrix*, all had low survival during the first 7 months and 13 month survivorship was <10%. *A. rigida*, for which the fewest number of recruits were found, was intermediate to the two groups. Five of the six species exhibited higher mortality during the first seven months after recruitment than in the subsequent six months.

There was no evidence of density dependent survival of the recruits as either a function of the number of adult colonies (r=-0.34, p=0.11) nor with the number of recruits initially found at the site (p= 0.15, p=0.49). Survival of *A. elisabethae* and *A. hystrix* at the Cross Harbour sites when plotted against the number of same species recruits (ESM Figure 3) has an appearance of density dependence, but neither species exhibits such a correlation (*A. elisabethae*, r= -0.44, p= 0.18; *A hystrix*, r= 0.20, p= 0.55; ESM Figure 3B), nor was there a correlation when total *Antillogorgia* spp. survival and density were compared (r=0.14, p=0.24; ESM Figure 3A).

DISCUSSION

Characterizations of the life histories of marine species typically focus on reproductive modes, such as broadcast spawning versus brooding and number of oocytes or larvae generated (c.f., Thorson 1950; Vance 1973; Strathmann 1977; Hadfield and Strathmann 1996; Hart 2002; Kahng et al. 2011). Reef anthozoans tend to broadcast large numbers of eggs that disperse well but have low probabilities of survival and settlement or brood eggs and produce fewer larvae which do not disperse great distances (Szmant 1986). The species level analyses coupled with censuses that differentiated between settlement/early recruitment and post-settlement mortality reported here also suggest a set of life history strategies that are best distinguished on the basis of developmental mode with a suite of associated characteristics that affect adult survival.

Reproductive Effort. While there are differences in numbers of gametes produced by individual polyps the factor that most affects reproductive output is the number of polyps in the colony, i.e., size of the colony. Although colonial taxa such as octocorals are often portrayed as having indeterminate growth (Sebens 1987), species have different maximum sizes (Bayer 1961) and Goffredo and Lasker (2005) found growth of *A. elisabethae* follows a von Bertalannfy growth curve. Thus, the colonies of species that grow to large size will generate substantially larger numbers of eggs and presumably larvae than species with smaller colonies as has been characterized for *Eunicea flexuosa* (Beiring and Lasker 2000). As colonies approach full size there may be an increase in individual polyp fecundity (Beiring and Lasker 2000), suggesting a change in resource allocation, but the effects of colony size, i.e., numbers of polyps, dominate variance in whole colony fecundity. Thus, colony size and reproductive effort are linked traits.

Settlement and post settlement survival. Increasing dispersal will inevitably carry larvae to inhospitable habitats. Thus, the number of larvae that successfully settle should be inversely related to the time spent in the water column. Assuming they are immediately competent, a greater proportion of brooded larvae will settle than for broadcast spawning species where larvae spend several days in the water column as they develop and then remain competent up to several weeks (c.f., Coelho and Lasker 2016). In addition, larvae that do not immediately settle use greater proportions of their energy stores which should affect their survival once they do settle and metamorphose.

The recruitment patterns observed among the *Antillogorgia* spp., follow the generalized model described above. *Antillogorgia bipinnata* and *A. elisabethae*, which surface brood had among the higher recruitment rates observed in the study and for both species recruitment was correlated with abundances of adult colonies. The data for *A. elisabethae* support similar patterns observed at these same sites in 2004-2007 (Lasker 2013) and genetic data suggest the dispersal kernel for *A. elisabethae* is less than 1 km (Lasker and Porto-Hannes 2015). Similarly, *A. hystrix*, which broods its larvae releasing competent, negatively buoyant larvae that contain Symbiodiniaceae symbionts (Coelho and Lasker 2014), also had high recruitment when recruitment was assessed 1-2 months after spawning. In contrast *A. americana* broadcast spawns and had recruitment rates that were dramatically lower than the brooder and surface brooders, and recruitment was not correlated with adult abundance. This is consistent with the larval behavior of *A. americana* (Coelho and Lasker 2016) and with a biophysical model of dispersion of *A. americana* that shows limited self-seeding of *A. americana* populations in The Bahamas (Coelho 2018). Recruitment of *A. acerosa*, which broadcast spawns were also low, but were correlated with adult abundance. This latter result points to the inherent difficulty in differentiating whether adult-recruit correlations are reflective of recruitment driving adult abundance or adult abundance driving recruitment.

The one exception to the expected patterns was the post-settlement survivorship of *A. hystrix* recruits. Over the four years of this study we observed dramatically more recruits of *A. hystrix* than any other *Antillogorgia* spp., but after a year *A. hystrix* were no more abundant than recruits of *A. bipinnata* and *A. elisabethae*. Survivorship of *A. hystrix* recruits was only 0.09 after 6-7 months compared to 0.48 and 0.33 for *A. bipinnata* and *A. elisabethae*, respectively. The difference in survival is striking. While size is not a clear indicator of provisioning the egg with nutrients, there is not an obvious difference in provisioning as *A. elisabethae* and *A. hystrix* have similar size eggs (Gutiérrez-Rodríguez and Lasker 2004; Coelho and Lasker 2014). Furthermore, *A. hystrix* larvae already have Symbiodiniaceae symbionts, which would seemingly enhance survival (but see Hartmann et al. 2019). It is likely that secondary compounds present in both *A. elisabethae* and *A. bipinnata* eggs deter predators as the developing larvae cover the surface of colonies after spawning and are not actively consumed by fishes such as *Chaetodon* spp. or wrasses. Chemical defense of larvae has been demonstrated for another surface brooding octocoral, *Briareum asbestinum* (Harvell 1989; Harvell et al. 1996). In contrast, feeding on the broadcast spawning octocoral *Plexaura kuna* by *Chaetodon capistratus* increases immediately before spawning, when the polyps are filled with eggs (Lasker 1985), suggesting they are poorly defended. Thus, differences in the presence or absence of secondary compounds with antipredator or antibiotic properties may contribute to the differences in recruit survival, but this remains to be tested for *Antillogorgia* spp. There may be a tradeoff in chemical and structural defenses in Caribbean octocorals (Pawlik et al. 1987), but the manner in which predator defense partitions in a life history context is unclear.

Density dependent survival of scleractinian recruits has been observed in an experimental setting (Doropoulos et al. 2017), but there was no evidence of such an effect at our sites in The Bahamas. However, the recruit densities reported here were based on counts over a 0.25 m^2 area, which masks the within quadrat variability that was often observed when collecting the recruits. Density at the millimeter and centimeter scale over which recruits probably interact may have affected survival of *Antillogorgia* recruits.

Mortality in colonial species in general and octocorals in particular is characterized as size dependent (Lasker 1990; Yoshioka 1994), with the greatest mortality occurring among the smallest colonies. That pattern was evident in this study as mortality from months 7 to 13 was lower than the preceding six months. The mortality reported here varied between species but all of the mortality rates are within the wide range of mortality rates reported in the literature. Lasker et al. (1998) reported 100% mortality after 3 months for *Plexaura kuna* planulae that had been settled on artificial substrates and then returned to the reef and Evans et al. (2013) in a similar experiment report over 90% mortality of newly settled *Briareum asbestinum* recruits after only 2 weeks. Yoshioka (1996) suggested that mortality immediately after settlement approaches 80% at the Puerto Rico sites that he monitored, but in an earlier study reported mortality of < 6 cm height *Antillogorgia* colonies that ranged from 15-47% (Yoshioka 1994). The lower mortality among *Antillogorgia* reported by Yoshioka may relate to the larger sizes of colonies in his < 6 cm class compared to the single polyp recruits that were collected in this study, or to species differences, as *A. americana* dominated at his study sites.

Studies of recruitment inevitably incorporate early post-settlement mortality that occurs between settlement and the time at which recruitment in assessed. Thus, measures of recruitment and post-settlement/post-recruitment mortality are sensitive to timing of the observations. Studies that census recruitment shortly after reproduction and settlement will report higher recruitment and, when it is monitored, higher post-recruitment mortality. Studies that report data summed across multiple species will be biased by the recruitment of those species that had spawned and settled closest to the census dates. For instance, Yoshioka (1994) reports recruitment rates of *Antillogorgia* spp. along the southern shore of Puerto Rico which are lower than the Bahamas data reported here. However, his data come from “spring” monitoring, which would have incorporated more post-settlement mortality than the January data from The Bahamas. In this study, recruitment in 2010 was lower than the other years (ESM Table 2), but those data were collected in February which would have incorporated 2-3 additional weeks of mortality than the other censuses. Alternatively, the difference may reflect supply and it is noteworthy that sea surface temperature preceding that year’s spawning was anomalously high (ESM Figure 4).

In this study four species dominated the recruitment data, and the data were collected within two months of their known spawning. Had the data been collected just ahead of spawning, the "recruitment failure" of *A. hystrix*, not its post-settlement mortality, would have been a primary discussion point. To the extent that the reproductive cycles are known, Caribbean octocorals appear to have two spawning patterns, with many plexaurid species spawning in summer and gorgoniids spawning in late Fall/early Winter (Kahng et al. 2011). However, there is variation in those patterns between species and localities (c.f., Yoshioka 1979; Kapela and Lasker 1999; Fitzsimmons-Sosa et al. 2004; Bastidas et al. 2005; Coelho and Lasker 2016), and mixing data from species with different reproductive cycles will confound estimates of recruitment and survival.

Recruitment has been an essential component of the resilience of octocorals on Caribbean reefs (c.f., Lasker et al. 2020). The *Antillogorgia* illustrate the diversity of successful reproductive strategies exhibited by octocorals. However, it is unclear how those reproductive traits interact with adult colony survival. Octocorals have been more resistant to environmental stressors such as temperature that have had such dramatic effects on scleractinians. However, octocorals are not immune to those stresses (Lasker et al. 1984; Lasker 2005; Prada et al. 2010), and conditions on Caribbean reefs are likely to become more stressful. A more complete understanding of the species level reproductive biology and its relationship with adult survivorship will be necessary to predicting the future of these octocoral communities.

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Conflict of Interests

On behalf of all authors, the corresponding author states that there is no conflict of interest.

Literature Cited

Bartlett LA, Brinkhuis VIP, Ruzicka RR, Colella MA, Lunz KS, Leone EH, Hallock P (2018) Dynamics of stony coral and octocoral juvenile assemblages following disturbance on patch reefs of the Florida reef tract. In: Duque C, Camacho ET (eds) Corals in a Changing World. IntechOpen, pp99-120

Bastidas C, Croquer A, Zubillaga AL, Ramos R, Kortnik V, Weinberger C, Marquez LM (2005) Coral mass- and split-spawning at a coastal and an offshore Venezuelan reefs, southern Caribbean. Hydrobiologia 541:101-106

Bayer FM (1961) The Shallow Water Octocorallia of the West Indian region. Martinus Nijhoff, The Hague.

Beiring EA, Lasker HR (2000) Egg production by colonies of a gorgonian coral. Marine Ecology-Progress Series 196:169-177

Bramanti L, Edmunds PJ (2016) Density-associated recruitment mediates coral population dynamics on a coral reef. Coral Reefs 35:543-553

Coelho MAG (2018) Life History Traits of Caribbean Octocorals of the Genus Antillogorgia and Their Implications for Larval Dispersal. University at Buffalo, State University of New York,

Coelho MAG, Lasker HR (2014) Reproductive biology of the Caribbean brooding octocoral *Antillogorgia hystrix*. Invertebrate Biology 133:299-313

Coelho MAG, Lasker HR (2016) Larval behavior and settlement dynamics of a ubiquitous Caribbean octocoral and its implications for dispersal. Marine Ecology Progress Series 561:109-121

Connell JH (1997) Disturbance and recovery of coral assemblages. Coral Reefs 16:S101-S113

Connolly SR, Roughgarden J (1999) Theory of marine communities: Competition, predation, and recruitment-dependent interaction strength. Ecological Monographs 69:277-296

Côté IM, Gill JA, Gardner TA, Watkinson AR (2005) Measuring coral reef decline through meta-analyses. Philosophical Transactions of the Royal Society B-Biological Sciences 360:385-395

De'ath G, Fabricius KE, Sweatman H, Puotinen M (2012) The 27-year decline of coral cover on the Great Barrier Reef and its causes. Proc Natl Acad Sci U S A 109:17995-17999

Doropoulos C, Evensen NR, Gomez-Lemos LA, Babcock RC (2017) Density-dependent coral recruitment displays divergent responses during distinct early life-history stages. Royal Society Open Science 4

Edmunds PJ, Nelson HR, Bramanti L (2018) Density-dependence mediates coral assemblage structure. Ecology 99:2605-2613

Edmunds PJ, Adjeroud M, Baskett ML, Baums IB, Budd AF, Carpenter RC, Fabina NS, Fan TY, Franklin EC, Gross K, Han XY, Jacobson L, Klaus JS, McClanahan TR, O'Leary JK, van

Oppen MJH, Pochon X, Putnam HM, Smith TB, Stat M, Sweatman H, van Woesik R, Gates RD (2014) Persistence and Change in Community Composition of Reef Corals through Present, Past, and Future Climates. Plos One 9

Etnoyer PJ, Wirshing HH, Sanchez JA (2010) Rapid Assessment of Octocoral Diversity and Habitat on Saba Bank, Netherlands Antilles. Plos One 5

Evans MJ, Coffroth MA, Lasker HR (2013) Effects of predator exclusion on recruit survivorship in an octocoral (Briareum asbestinum) and a scleractinian coral (Porites astreoides). Coral Reefs 32:597-601

Fitzsimmons-Sosa K, Hallock P, Wheaton J, Hackett KE, Callahan MK (2004) Annual cycles of gonadal development of six common Gorgonians from Biscayne National Park, Florida, USA. Caribbean Journal of Science 40:144-150

Gaines S, Roughgarden J (1985) Larval settlement rate: a leading determinant of structure in an ecological community of the marine intertidal zone. Proc Natl Acad Sci 82:3707-3711.

Gardner TA, Côté IM, Gill JA, Grant A, Watkinson AR (2003) Long-term region-wide declines in Caribbean corals. Science 301:958-960

Gardner TA, Côté IM, Gill JA, Grant A, Watkinson AR (2005) Hurricanes and Caribbean coral reefs: Impacts, recovery patterns, and role in long-term decline. Ecology 86:174-184

Goffredo S, Lasker HR (2005) Modular growth of a gorgonian coral generates predictable patterns of colony and population growth. Integrative and Comparative Biology 45:1003-1003

Goldberg WM (1973) Ecology Of Coral-Octocoral Communities Off Southeast Florida Coast - Geomorphology, Species Composition, And Zonation. Bulletin Of Marine Science 23:465-488

Gomez CG, Guzman HM, Gonzalez A, Breedy O (2014) Survival, growth, and recruitment of octocoral species (Coelenterata: Octocorallia) in Coiba National Park, Pacific Panama. Bulletin of Marine Science 90:623-650

Gotelli NJ (1988) Determinants of recruitment, juvenile growth, and spatial distribution of a shallow water gorgonian. Ecology 69:157-166.

Grigg RW (1977) Population dynamics of two gorgonian corals. Ecology, 58:278-290.

Gutiérrez-Rodríguez C, Lasker HR (2004) Reproductive biology, development, and planula behavior in the Caribbean gorgonian *Pseudopterogorgia elisabethae*. Invertebrate Biology 123:54-67

Hadfield MG, Strathmann MF (1996) Variability, flexibility and plasticity in life histories of marine invertebrates. Oceanologica Acta 19:323-334

Hart MW (2002) Life history evolution and comparative developmental biology of echinoderms. Evolution & Development 4:62-71

Hartmann AC, Marhaver KL, Klueter A, Lovci MT, Closek CJ, Diaz E, Chamberland VF, Archer FI, Deheyn DD, Vermeij MJA, Medina M (2019) Acquisition of obligate mutualist symbionts during the larval stage is not beneficial for a coral host. Molecular Ecology 28:141-155

Harvell CD (1989) Chemical and structural defenses of Caribbean gorgonians (Pseudopterogorgia spp.): Intracolony localization of defenses. Limnol, Oceanogr 34:380-387

Harvell CD, West JM, Griggs C (1996) Chemical defense of embryos and larvae of a West Indian gorgonian coral, Briareum asbestinum. Invertebrate Reproduction & Development 30:239-247

Hoegh-Guldberg O, Poloczanska ES, Skirving W, Dove S (2017) Coral Reef Ecosystems under Climate Change and Ocean Acidification. Frontiers in Marine Science 4

Hughes TP, Barnes ML, Bellwood DR, Cinner JE, Cumming GS, Jackson JBC, Kleypas J, van de Leemput IA, Lough JM, Morrison TH, Palumbi SR, van Nes EH, Scheffer M (2017) Coral reefs in the Anthropocene. Nature 546:82-90

Jamison JL, Lasker HR (2008) Identification of octocoral recruits using microsatellite primers: Relationships between recruitment and adult distribution of Pseudopterogorgia spp. Limnology and Oceanography 53:1963-1972

Jordan-Dahlgren E (2002) Gorgonian distribution patterns in coral reef environments of the Gulf of Mexico: evidence of sporadic ecological connectivity? Coral Reefs 21:205-215

Kahng SE, Benayahu Y, Lasker HR (2011) Sexual reproduction in octocorals. Marine Ecology Progress Series 443:265-283

Kapela W, Lasker HR (1999) Size-dependent reproduction in the Caribbean gorgonian Pseudoplexaura porosa. Marine Biology 135:107-114

Kinzie RAI (1973) The zonation of West Indian gorgonians. Bull Mar Sci 23:93-155.

LaJeunesse TC, Parkinson JE, Gabrielson PW, Jeong HJ, Reimer JD, Voolstra CR, Santos SR (2018) Systematic Revision of Symbiodiniaceae Highlights the Antiquity and Diversity of Coral Endosymbionts. Current Biology 28:2570-2580.e2576

Lasker HR (1985) Prey Preferences and Browsing Pressure of the Butterflyfish Chaetodon-Capistratus on Caribbean Gorgonians. Marine Ecology-Progress Series 21:213-220

Lasker HR (1990) Clonal propagation and population dynamics of a gorgonian coral. Ecology 71:1578-1589

Lasker HR (2005) Gorgonian mortality during a thermal event in the Bahamas. Bulletin of Marine Science 76:155-162

Lasker HR (2013) Recruitment and Resilience of a Harvested Caribbean Octocoral. Plos One 8

Lasker HR, Coffroth MA (1983) Octocoral Distributions at Carrie Bow Cay, Belize. Marine Ecology-Progress Series 13:21-28

Lasker HR, Jamison JL (2006) Relationships between recruitment and adult distribution among Pseudopterogorgia spp. on the little bahama bank. Integrative and Comparative Biology 46:E81-E81

Lasker HR, Porto-Hannes I (2015) Population structure among octocoral adults and recruits identifies scale dependent patterns of population isolation in The Bahamas. Peerj 3:29

Lasker HR, Peters EC, Coffroth MA (1984) Bleaching of Reef Coelenterates in the San-Blas Islands, Panama. Coral Reefs 3:183-190

Lasker HR, Kim K, Coffroth MA (1998) Production, settlement, and survival of plexaurid gorgonian recruits. Marine Ecology-Progress Series 162:111-123

Lasker HR, Martínez-Quintana Á, Bramanti L, Edmunds PJ (2020) Resilience of Octocoral Forests to Catastrophic Storms. Scientific Reports 10:4286

Lenz EA, Bramanti L, Lasker H, Edmunds PJ (2015) Long-term variation of octocoral populations in St. John, US Virgin Islands. Coral Reefs 34:1-11

MacArthur RH, Wilson EO (1967) The theory of island biogeography. . Princeton University Press, Princeton, NJ

Minchinton TE, Scheibling RE (1991) The influence of larval supply and settlement on the population structure of barnacles. Ecology 72:1867-1879

Norstrom AV, Nystrom M, Lokrantz J, Folke C (2009) Alternative states on coral reefs: beyond coral-macroalgal phase shifts. Marine Ecology Progress Series 376:295-306

Pawlik JR, Burch MT, Fenical W (1987) Patterns Of Chemical Defense Among Caribbean Gorgonian Corals - A Preliminary Survey. Journal Of Experimental Marine Biology And Ecology 108:55-66

Prada C, Weil E, Yoshioka PM (2010) Octocoral bleaching during unusual thermal stress. Coral Reefs 29:41-45

Roff G, Mumby PJ (2012) Global disparity in the resilience of coral reefs. Trends in Ecology & Evolution 27:404-413

Ruzicka RR, Colella MA, Porter JW, Morrison JM, Kidney JA, Brinkhuis V, Lunz KS, Macaulay KA, Bartlett LA, Meyers MK, Colee J (2013) Temporal changes in benthic assemblages on Florida Keys reefs 11 years after the 1997/1998 El Nino. Marine Ecology Progress Series 489:125-141

Sanchez JA, Gomez-Corrales M, Gutierrez-Cala L, Vergara DC, Roa P, Gonzalez-Zapata FL, Gnecco M, Puerto N, Neira L, Sarmiento A (2019) Steady Decline of Corals and Other Benthic Organisms in the SeaFlower Biosphere Reserve (Southwestern Caribbean). Frontiers in Marine Science 6

Sánchez JA, Zea S, Diaz JM (1997) Gorgonian communities of two contrasting environments from oceanic Caribbean atolls. Bulletin of Marine Science 61:453-465

Sebens KP (1987) The ecology of indeterminate growth in animals. Ann Rev Ecol Syst, 18:371-407.

Smilansky V, Lasker HR (2014) Fine-scale genetic structure in the surface brooding Caribbean octocoral, Antillogorgia elisabethae. Marine Biology 161:853-861

Strathmann RR (1977) Egg size, larval development, and juvenile size in benthic marine invertebrates. American Naturalist 111:373-376

Szmant AM (1986) Reproductive ecology of Caribbean reef corals. Coral Reefs 5:43-53.

Tanner JE (1999) Density-dependent population dynamics in clonal organisms: a modelling approach. Journal of Animal Ecology 68:390-399

Tanner JE, Hughes TP, Connell JH (2009) Community-level density dependence: an example from a shallow coral assemblage. Ecology 90:506-516

Thorson G (1946) Reproduction and larval development of Danish marine bottom invertebrates, with special reference to the planktonic larvae in the sound (Oresund). Medd Komm Danmarks Fisk Havund Ser:Plankton 4:1-519.

Thorson G (1950) Reproductive and larval ecology of marine bottom invertebrates. Biological Reviews of the Cambridge Philosophical Society 25:1-45

Tsounis G, Edmunds PJ (2017) Three decades of coral reef community dynamics in St. John, USVI: a contrast of scleractinians and octocorals. Ecosphere 8

Vance RR (1973) More on reproductive strategies in marine benthic invertebrates. American Naturalist 107:353-361

Yoshioka BB (1979) Aspects of the ecology of *Pseudopterogorgia americana* and *Pseudopterogorgia acerosa*., University of Puerto Rico, Mayaguez, p69

Yoshioka PM (1994) Size-specific life-history pattern of a shallow-water gorgonian. Journal of Experimental Marine Biology and Ecology 184:111-122

Yoshioka PM (1996) Variable recruitment and its effects on the population and community structure of shallow-water gorgonians. Bulletin of Marine Science 59:433-443

Yoshioka PM, Yoshioka BB (1987) Variable effects of Hurricane David on the shallow water gorgonians of Puerto Rico. Bulletin of Marine Science 40:132-144

Yoshioka PM, Yoshioka BB (1989) Effects of wave energy, topographic relief and sediment transport on the distribution of shallow-water gorgonians of Puerto Rico. Coral Reefs 8:145-152

FIGURE LEGENDS

Figure 1.

Diagram showing the layout of the three 0.25 x 1 m quadrats sampled to assess recruitment. Recruits were collected from quadrats labelled 11, 12 and 13 at three different ages post-spawning events. Numbers of recruits in 1 x 1 m quadrats labelled 1, 2 and 3 were monitored and those data have been reported in Lasker (2013). Adult censuses were from quadrats 1, 2 and 3. Photos correspond to 1 (C), 6 (B) and 13 (A) month old recruits. Scale for the 13 month recruits is approximately 3x that of the 6 month recruit. Photo credits: C, T. Higgs; A-B, H.R. Lasker.

Figure 2. *Antillogorgia* spp. recruitment rates to 0.25 m^2 quadrats at six sites on the Little Bahamas Bank. See text for methodology of calculating recruitment rate. Logarithmic scale used in order to visualize recruitment at the sites with averaged recruitment <1 recruits per quadrat. Values are means of approximately 20 quadrats. Error bars are standard errors.

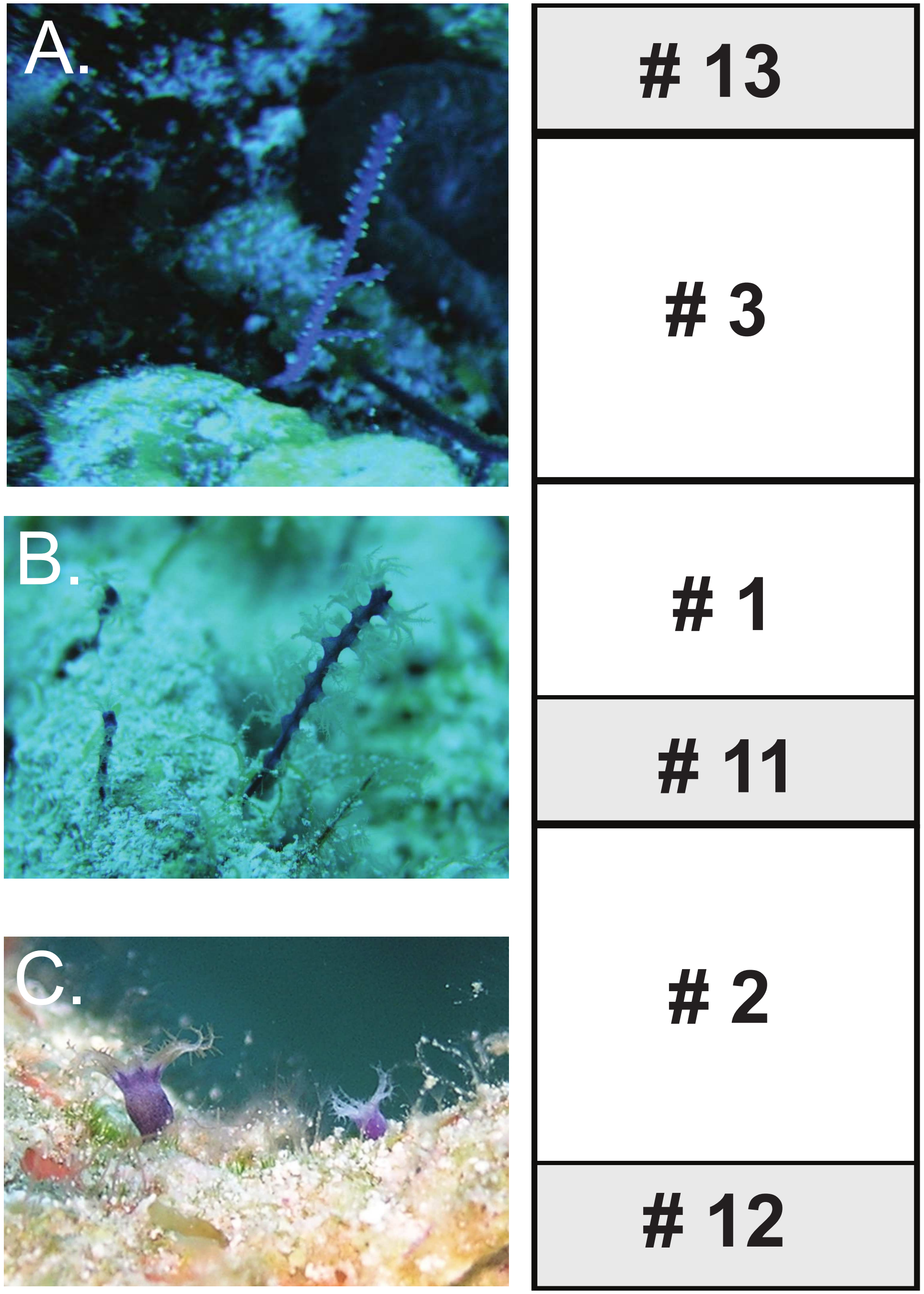
Figure 3. Recruitment of six *Antillogorgia* spp. to sites on the Little Bahama Bank. Recruitment was assessed 1-2 months following spawning and species abundance of the recruits based on censuses of 20 0.25 m^2 quadrats at each site and molecular identification of approximately half of the recruits.

Figure 4. Relationship between *Antillogorgia* spp. recruitment and adult colony abundance at six sites on the Little Bahama Bank. A, adult abundance as numbers of colonies; B, adult abundance as the sum of the colony heights. Significant results are noted in bold $p<0.01$.

Figure 5. A, Survival of *Antillogorgia* spp. at six sites on the Little Bahama Bank. B, Estimated marginal mean mortality of 3 *Antillogorgia* spp. at three sites in Cross Harbour, Abaco, The Bahamas. Values are means with 95% confidence intervals.

Figure 1

Recruit Collections



13-14 months old -
All 3-5 cm height
recruits collected
each January

7-8 months old -
All recruits collected
each June

1-2 months old -
All recruits collected
each January

Figure 2

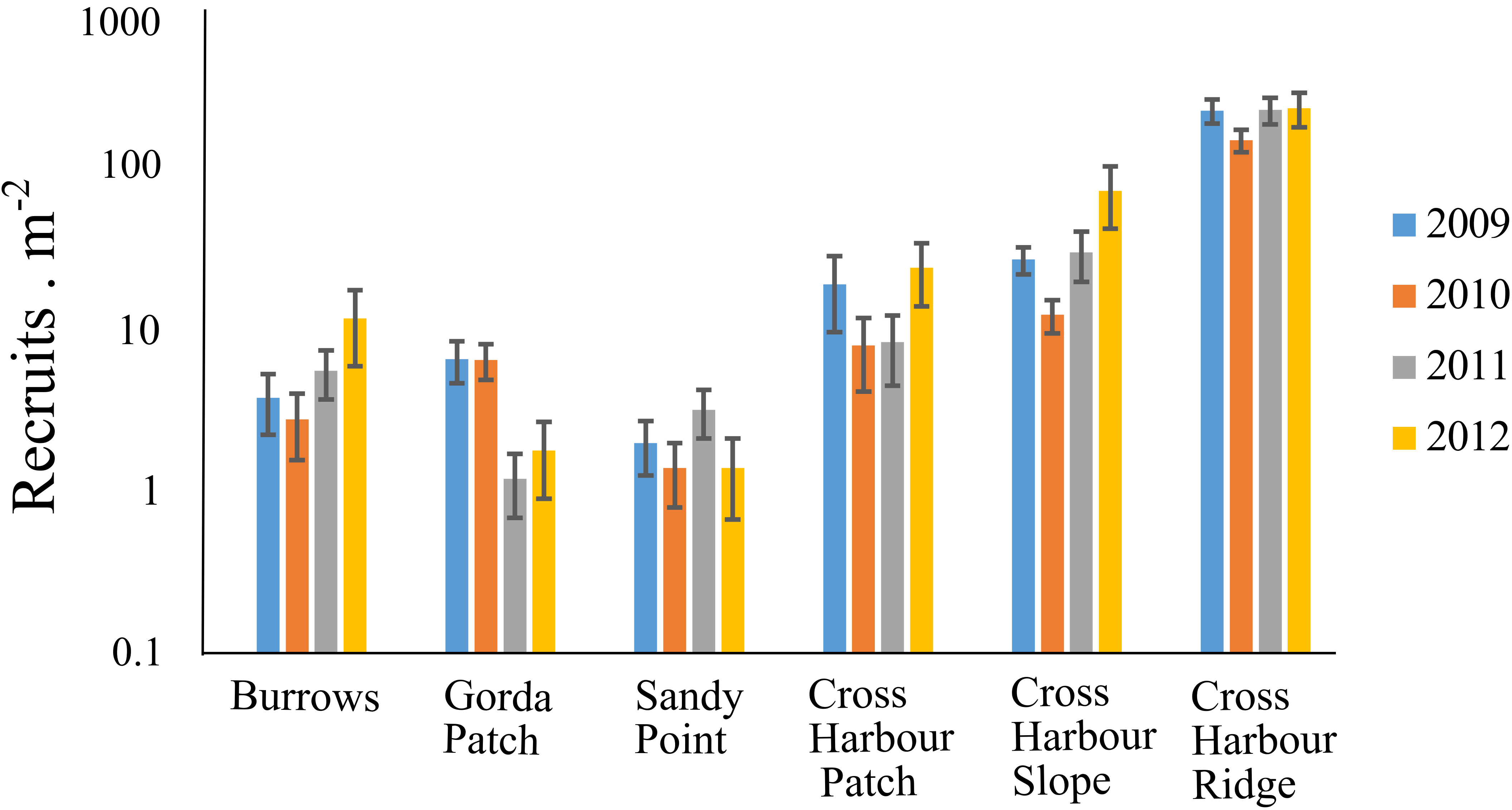

Recruits . m^{-2}
1000
100
10
1
0.1
Burrows
Gorda Patch
Sandy Point
Cross Harbour Patch
Cross Harbour Slope
Cross Harbour Ridge
2009
2010
2011
2012

Figure 3

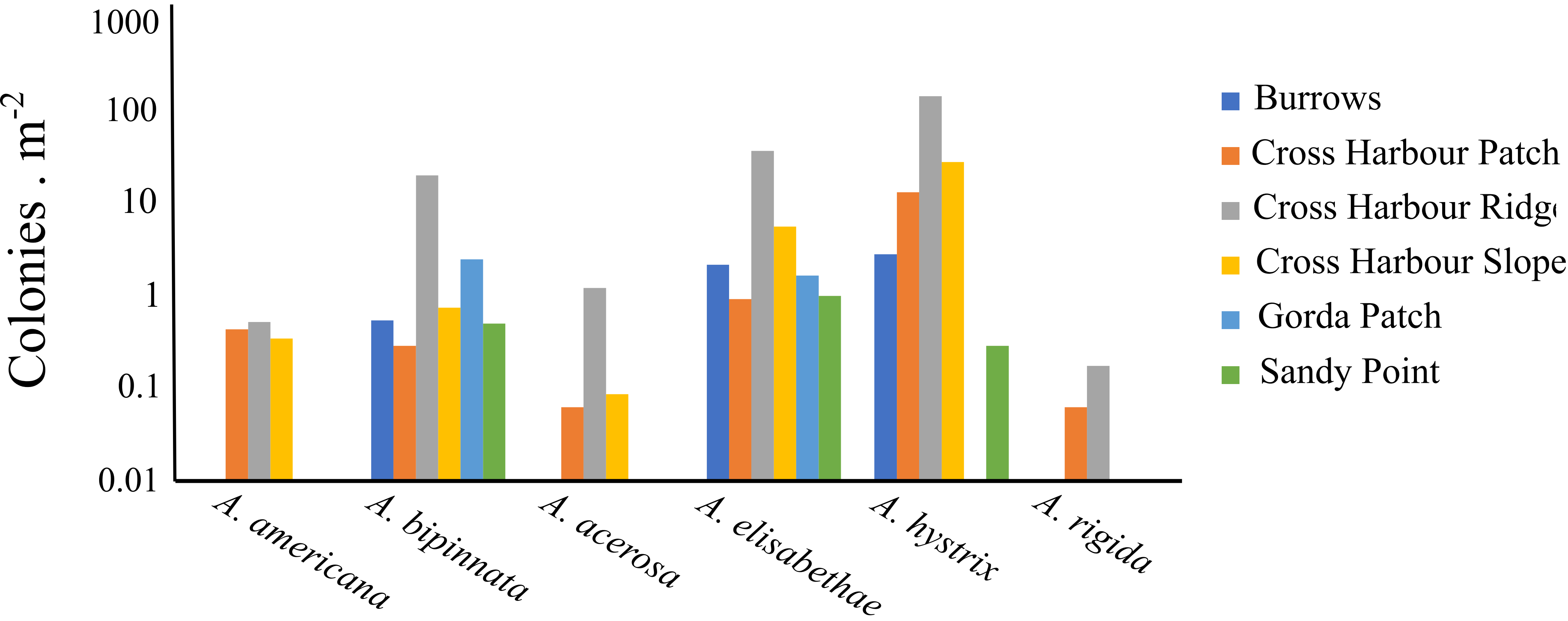

Colonies . m^{-2}
1000
100
10
1
0.1
0.01
A. americana
A. bipinnata
A. acerosa
A. elisabethae
A. hystrix
A. rigida
Burrows
Cross Harbour Patch
Cross Harbour Ridg
Cross Harbour Slope
Gorda Patch
Sandy Point

Figure 4

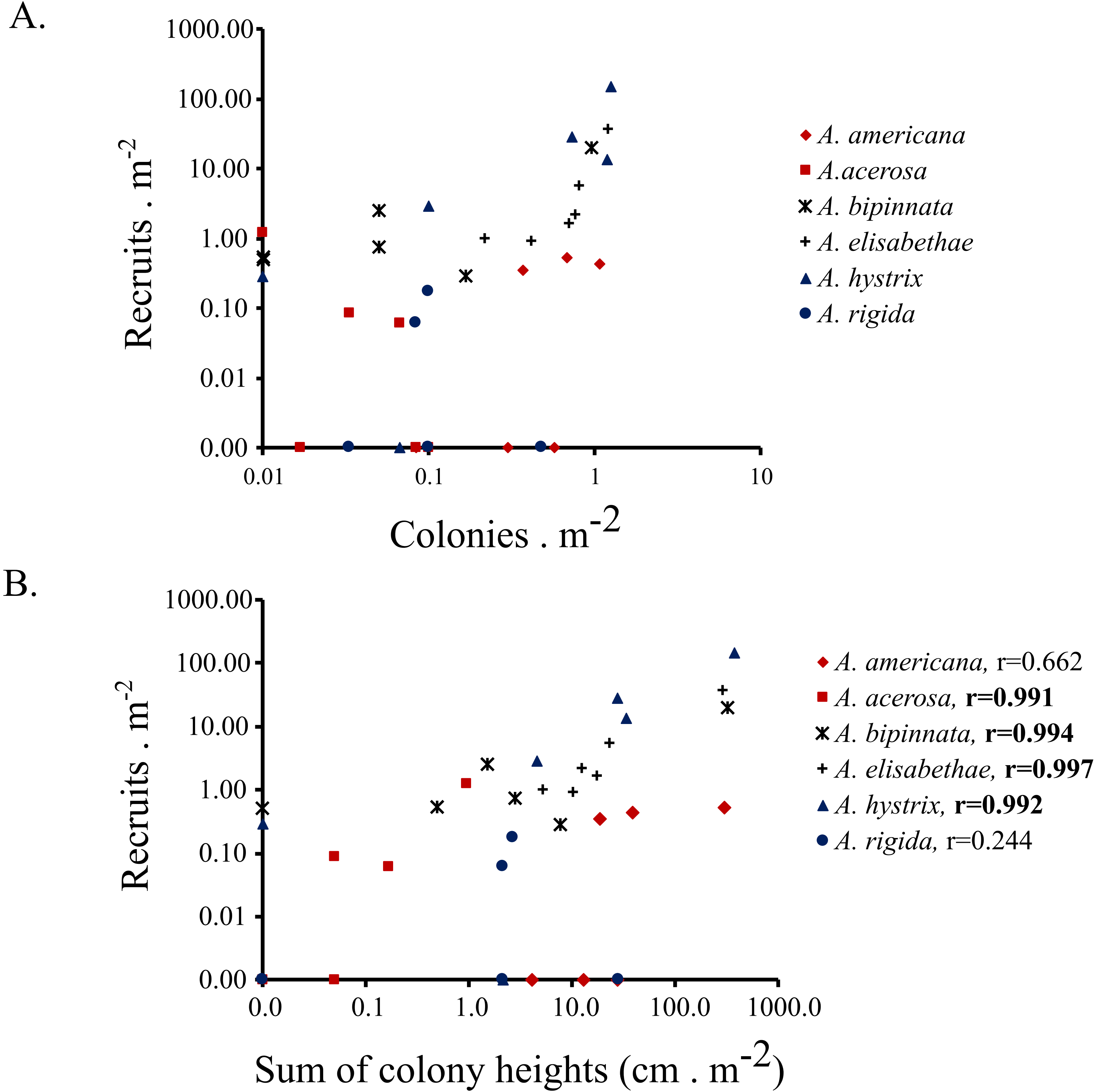
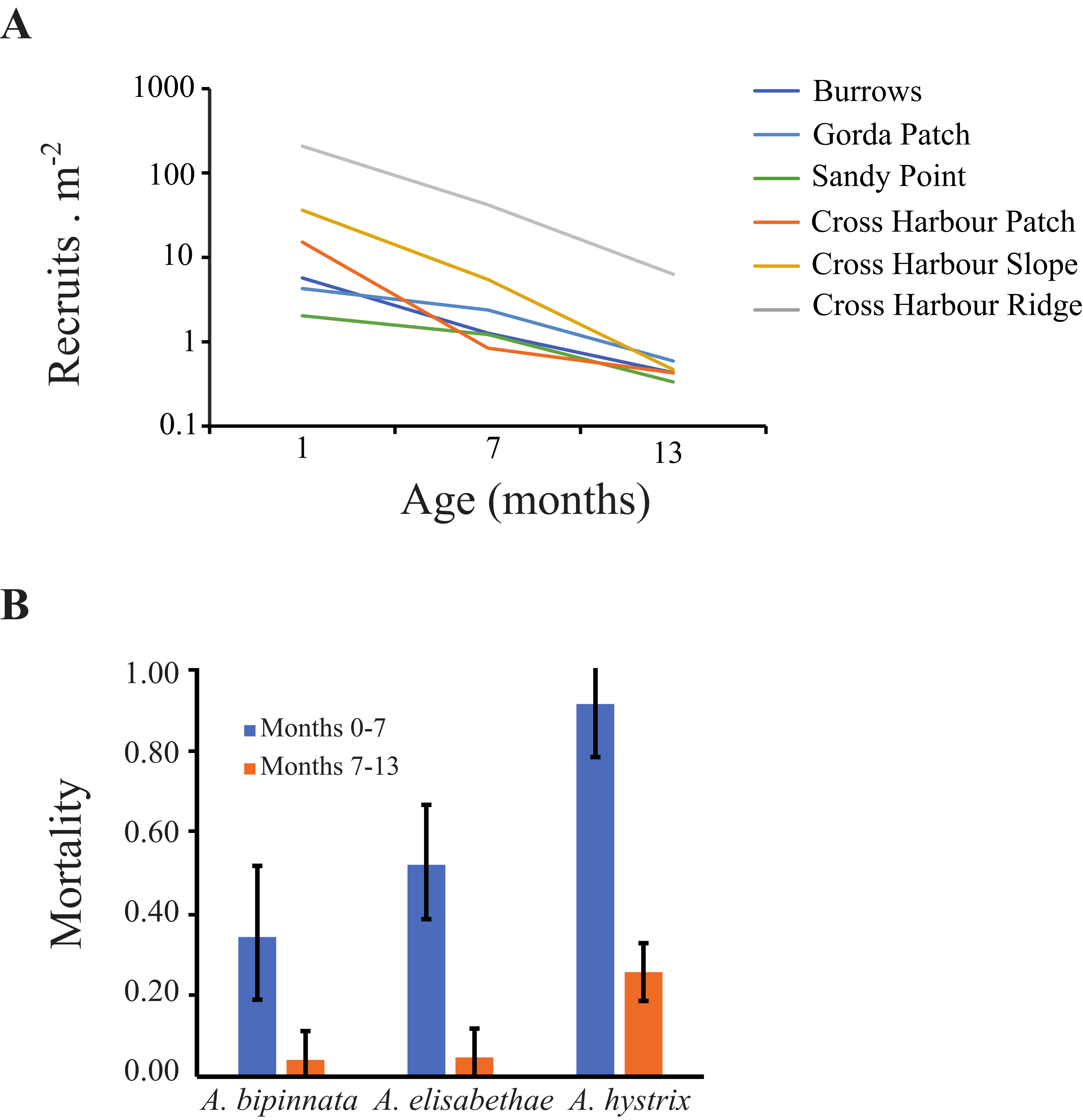

A.
1000.00
100.00
10.00
1.00
0.10
0.01
0.00
0.01
0.1
1
10
Recruits . m^{-2}
Colonies . m^{-2}
◆ *A. americana*
■ *A.acerosa*
✱ *A. bipinnata*
+ *A. elisabethae*
▲ *A. hystrix*
● *A. rigida*
B.
1000.00
100.00
10.00
1.00
0.10
0.01
0.00
0.0
0.1
1.0
10.0
100.0
1000.0
Recruits . m^{-2}
Sum of colony heights (cm . m^{-2})
◆ *A. americana,* r=0.662
■ *A. acerosa,* **r=0.991**
✱ *A. bipinnata,* **r=0.994**
+ *A. elisabethae,* **r=0.997**
▲ *A. hystrix,* **r=0.992**
● *A. rigida,* r=0.244

Figure 5


A
1000
100
10
1
0.1
Recruits . m^{-2}
1
7
13
Age (months)
Burrows
Gorda Patch
Sandy Point
Cross Harbour Patch
Cross Harbour Slope
Cross Harbour Ridge
B
1.00
0.80
0.60
0.40
0.20
0.00
Mortality
Months 0-7
Months 7-13
A. bipinnata
A. elisabethae
A. hystrix