Coral Reefs (2013) 32:597–601
DOI 10.1007/s00338-012-1001-1

NOTE

Effects of predator exclusion on recruit survivorship in an octocoral (*Briareum asbestinum*) and a scleractinian coral (*Porites astreoides*)

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Received: 6 February 2012 / Accepted: 14 December 2012 / Published online: 10 January 2013

Abstract Recruits of the Caribbean scleractinian coral *Porites astreoides* and the octocoral *Briareum asbestinum* were established on artificial substrata and reared on a reef in cages designed to exclude various classes of organisms known to feed on corals. Post-settlement survivorship of recruits was measured for periods of 2 weeks (*B. asbestinum*) and 1 month (*P. astreoides*) on East Turtle Reef in the Florida Keys during May and June 2010. Predator exclusion did not affect survivorship among *P. astreoides* recruits during the study. Recruits of *B. asbestinum* experienced lower survivorship in treatments that allowed access by fish compared with fish exclusion treatments. The results indicate that predation may be an important determinant of post-settlement mortality among *B. asbestinum* recruits, and fishes are the primary contributors to predation-induced mortality. *B. asbestinum* recruit survivorship differed by an order of magnitude between recruits in the control condition and those in the predator exclusion (0.087 and 0.372, respectively). The findings illustrate the need to consider the effects of interactions early in life on the survival, propagation, and recovery of coral populations.

Keywords Coral · Recruit · Survivorship · Predation

Communicated by Biology Editor Dr. Mark Vermeij

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Introduction

Predation can be an important factor in determining the growth and abundance of populations (Peckarsky 1993; Hik 1995), as well as the structure of communities (Paine 1974). For species with multiple life history phases, the significance of predation may vary across stages, and predation during a single stage can have great effects on population dynamics and community structure (Louda 1982; Paine and Beck 2007; Denham 2008). As the primary biogenic constructors of reefs, corals' role as ecosystem engineers make their population dynamics critically important to the health and biodiversity of reef communities, and the effects of predation on their populations could affect the entire reef ecosystem. Due to the dramatic degradation of reefs worldwide (Hughes and Tanner 2000; Bruno and Selig 2007; Thompson and Dolman 2010), understanding the relative importance and effects of the factors that structure coral assemblages is imperative to formulating effective protection and recovery strategies for these ecosystems.

Predation on early life stages can play a major role in shaping community assemblages of plants, fish, and marine invertebrates (Ostfeld et al. 1997; Osman and Whitlatch 2004; Almany and Webster 2006; Bologna 2007) and is an important process in determining the survival of recruits in both terrestrial and marine systems (Carr and Hixon 1995; Paine and Beck 2007; Denham 2008; Naddafi et al. 2010). In the case of coral recruits, the effect of grazing can be ecologically equivalent to a predation event. Even a selective grazer "sampling" a single polyp is likely to result in the mortality of that individual. Thus, while many species are chemically and structurally defended (Harvell and Fenical 1989), the effectiveness of these defenses is mitigated early in life by recruits' small size.

The goal of this study was to assess the impact of early life history predation on coral populations, by examining the effects of predator exclusion on survivorship immediately following settlement in two common constituents of inshore Caribbean coral reefs—the octocoral *Briareum asbestinum* and the scleractinian coral *Porites astreoides*. Common reef inhabitants, such as the flamingo tongue snail (*Cyphoma gibbosum*) (Harvell 1983; Gerhart 1986; Lasker et al. 1988), bearded fireworm (*Hermodice carunculata*) (Ott 1972; Vreeland and Lasker 1989), and chaetodontid (Lasker 1983, 1985) and scarid fishes (Rotjan and Lewis 2005, 2009; Mumby 2009) all graze/browse adult scleractinian and/or octocoral colonies and are potential predators of coral recruits. Coral predators were broadly segregated into two classes, benthic invertebrates and reef fishes. The goal of the study was to quantify the overall importance of predation on survival in the first weeks after settlement and assess the contributions of each predator guild.

Methods

Porites astreoides larvae were obtained from 30 colonies of 10–30 cm diameter, which were collected in early May 2010 from concrete construction debris at a site in the Florida Keys (known locally as “Rubble Pile”, 24° 44.016′N, 80° 49.590′W) and maintained at the Keys Marine Laboratory in flow through seawater tables (61 × 244 × 41 cm deep). Planulae were collected as they were released as described in Kuffner et al. (2006). *B. asbestinum* surface broods and larvae were collected from the surface of 20 encrusting-morph colonies in Florida Bay (24°49.942′N, 80°48.622′W) in May 2010 using a 50-ml syringe.

Planulae were combined for each species and maintained at room temperature in 6-L plastic containers. After 3 days, 100 *P. astreoides* planulae were transferred into each of thirty five, 1 L “deli containers” containing 500 ml of seawater and a single Plexiglas settling plate, which had been seasoned at 2 m depth at Craig Key during March and April 2010. Turf algae were scrubbed from the seasoned plates prior to use. *B. asbestinum* were transferred to deli containers, and a 38-L aquarium containing 8–12 cm cleaned, dead gorgonian branches at a density of 100 planulae per branch. Numbers of larvae and settlement rates were low; therefore, only plates and branches with at least 30 settled recruits were used in the experiments.

One week old, settled recruits were placed into one of five treatments (Table 1) on the reef at East Turtle Reef (24°43.501′N, 80°55.120′W) at a depth of 6 m. Plates and branches in treatments on the substratum (control, substratum partial, substratum caged) were attached to the vertical sides of cinder blocks in order to minimize sedimentation. Cages (15 × 15 × 15 cm) were constructed out of 0.6-cm mesh galvanized hardware cloth. They were comprised of four sides and a roof and had tabs extending from the base of each corner for attachment flush with the cinder block. Partial cages on the substratum (SP) included a 2.5 cm gap between the bottom of the cage and surface of the cinder blocks. Floated treatments (floated caged and floated exposed) were suspended approximately 1 m above the substratum with a Styrofoam float and were anchored to cinder blocks by monofilament, which benthic grazers and predators cannot climb. Floated cages (FC) were complete 15 × 15 × 15 cm cubes, with vertically oriented plates. A single cinder block contained one replicate of each of the five treatments for *P. astreoides* and three treatments (Ctrl, SC, FE) for *B. asbestinum* (see below). Blocks were arranged on clear horizontal areas of the reef, taking care to randomize light exposure to the different treatments. Differences in water flow created by the cages were assessed by comparing the dissolution of hemispheres of dental plaster (Jokiel and Morrissey 1993) in cages to those outside of the cages.

To test the effectiveness of the cage design at excluding potential predators, carrageenan strips flavored with squid (Harvell et al. 1988) were placed in both substrata and floated cages prior to the introduction of settled recruits. Strips were also left exposed on the cinder blocks. The exposed carrageenan strips were all consumed during a single 95-min dive, while the strips in each cage were intact. The presence of potential predators at the study site was assessed by seven stationary fish surveys (as in Bohnsack and Bannerot 1986) and five belt transect surveys for invertebrates. Invertebrate surveys used 25-m transects laid out at random across the reef, with two divers identifying and counting any invertebrate visible within 1 m of either side of the transect.

Seven replicates of each of the five treatments were set on the reef for *P. astreoides* on 20 May 2010 and six replicates of the control (Ctrl), substratum-cage (SC), and floated-exposed (FE) treatments for *B. asbestinum* on 14 June 2010. The number of replicates was determined by the availability of settled larvae. The number of *P. astreoides* and *B. asbestinum* individuals on each plate/branch were counted visually upon placement onto the reef, and every third day for 1 month and 2 weeks, respectively. When necessary, plates and branches were removed from cages for counting. During each census, cages were cleaned of algae and other fouling debris using a toothbrush. The final survivorship of recruits was compared between treatments, using a one-way ANOVA and Scheffe contrast tests between specific treatments. Test statistics with probabilities <0.05 were considered significant.

Results and discussion

Twelve species of benthic invertebrates and 27 fish species were identified in the surveys. The snail *Cyphoma gibbosum*

Table 1 Treatments used in the predator exclusion experiments

Name	Treatment	Groups excluded
Control (Ctrl)	Exposed plates and branches on the substratum	None
Substratum-partial cage (SP)	Plates and branches on the substratum enclosed by a raised cage	Fishes
Substratum caged (SC)	Plates and branches on the substratum completely surrounded by a mesh cage	Fishes and benthic invertebrates >0.6 cm diameter
Floated exposed (FE)	Exposed plates and branches floated above the substratum	Benthic invertebrates
Floated caged (FC)	Plates and branches floated above the substratum completely surrounded by a wire mesh enclosure	All grazers and predators

and urchin *Eucidaris tribuloides* were the most common benthic invertebrates and the fishes included butterflyfish (*Chaetodon* spp.), parrotfishes (*Scarus* spp.), and wrasses (*Thalassoma* spp.). No significant differences in dissolution were detected among plaster half-spheres in the different treatment groups ($F_{3,8} = 1.400$, $p = 0.319$).

In all survivorship comparisons for both *Briareum asbestinum* and *Porites astreoides* recruits, the first count after introduction to the reef was used as the initial number of individuals. Large decreases between the initial number of recruits and the number counted at the first census were seen in all treatments for both species. This initial decrease was likely due to the loss of weakly attached recruits and stress associated with the altered environment, and therefore not indicative of predation-induced mortality. Exclusion of either the first set of counts or the first two counts had no effect on the results of the statistical analysis (ANOVA results not shown).

Predator exclusion had a significant effect on survivorship of the *B. asbestinum* recruits (Fig. 1). Survivorship of *B. asbestinum* recruits in the substratum-caged (SC) condition was significantly higher than those exposed in the control (Fig. 1, SC vs. Ctrl) as well as those floated and exposed (FE) (Fig. 1, SC vs. FE). *P. astreoides* recruits had high survivorship during the experiment, with no significant differences in final mean survivorship between treatments (Fig. 1).

The significant effects of predator exclusion on the survivorship of *B. asbestinum* indicate that predation limited recruit survival. The lack of difference between the floated and substrate exposed treatments suggests that grazing by fish accounted for the observed mortality. Fishes such as chaetodons and wrasses are likely predators of polyps in both settings. However, feeding by benthic predators coupled with reduced fish predation in the substrate exposed treatment could also explain the observed mortality.

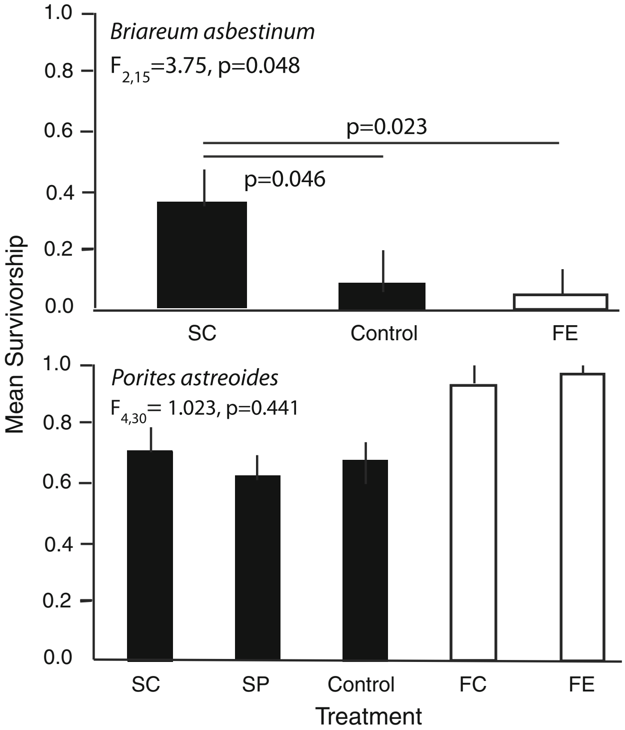

Fig. 1 Mean survivorship of *B. asbestinum* and *P. astreoides* recruits from 6 to 7 replicates in each treatment after 10 and 22 days, respectively. Standard *error bars* and results of analysis of variance shown. *Lines* between treatments and *p* values indicate significant post hoc pairwise *t* tests. *SC* substratum caged, *SP* substratum partial, *Ctrl* control, *FE* floated exposed, *FC* floated caged

The relatively greater effects of grazing by fish compared to invertebrates are surprising given that *B. asbestinum* larvae and juveniles (Harvell et al. 1996) contain defensive compounds that minimize predation by fishes (Harvell et al. 1988; West 1998) and are less effective against the gastropod *Cyphoma gibbosum* (Vrolijck and Targett 1992). However, the small size of single *B. asbestinum* recruits likely minimizes the effects of chemical defenses. A grazer that indiscriminately scraped off a polyp or a browser that "sampled" a recruit would inevitably kill the single polyp individual.

The relatively lower predation-induced mortality of *P. astreoides* recruits compared to *B. asbestinum* may be attributable to differences in morphology between the two species. *P. astreoides* recruits were broader and flatter, had the beginnings of a calcified skeleton, and commonly settled in relatively sheltered areas between ridges that were present on the plates (see also Lasker et al. 1998). In contrast, *B. asbestinum* recruits were globular, fleshy polyps, which were visually conspicuous and exposed on the smooth pieces of gorgonian axis. These differences may reflect similar patterns that occur naturally, as *P. astreoides* characteristically settle on rocky substrata encrusted with coralline algae, and the encrusting form of *B. asbestinum* routinely settles on gorgonian branches (Bayer 1961). However, the gorgonian branches that *B. asbestinum* larvae normally settle on also have live gorgonian tissue and/or other epibionts. In this case, newly settled recruits might not be as conspicuous to visual predators as in our experiments, creating the potential to overestimate mortality.

Briareum asbestinum polyps persist in a “recruit-like” stage ($\ll$5 cm) for several months (H. Lasker, pers. obs.). Two week recruit survival from the control (0.087) and substratum-caged (0.372) treatments differ by four orders of magnitude when extrapolated to 2 months (1.9×10^{-2} vs. 2.6×10^{-6}), suggesting that predation may have a large effect on recruit survival. However, if mortality is density dependent, then a large numerical effect will not necessarily mean predation regulates recruit abundance (Penin et al. 2011).

The effect of predation on coral recruit survivorship may have significant implications for reef management, especially when considering the top–down trophic regulation of corallivorous organisms. *C. gibbosum* abundance has been observed to increase an order of magnitude in the absence of predatory fishes (Burkepile and Hay 2007), and areas in the Florida Keys that are open to fishing have higher densities of *C. gibbosum* (Chiappone et al. 2003). Similarly, the loss of large predatory fishes from reefs may release smaller corallivorous fishes, such as chaetodons and labrids from predation pressure (Jennings and Polunin 1997; Carr and Hixon 1995).

Processes affecting recruit survival, along with local dispersal patterns, will determine the ability of increasingly damaged and degrading reefs to persist and recover. The results presented here suggest the need for a comprehensive approach to reef management, which considers a wide range of trophic interactions in maintaining and increasing coral abundance.

Acknowledgments This work would not have been possible without the staff at Keys Marine Laboratory, who provided all the logistical support as well as assistance in the field. We also thank E. Joseph, N. Leigh, and P. Marcum for their help in the field. The research was supported by NSF grants OCE 0825625 (HRL) and OCE-0926822 (MAC) and was conducted under permit FKNMS-2010-039.

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