

Occupation dynamics and impacts of damselfish territoriality and gardening activities on recovering populations of the threatened staghorn coral *Acropora cervicornis*

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Abstract

Large-scale coral and coral reef restoration are needed to help recover lost structure and function of degraded coral reef ecosystems. Active coral propagation and reef restoration efforts have scaled up significantly in past decades, particularly for the threatened Caribbean staghorn coral, *Acropora cervicornis*, to the point where 10,000s of nursery-grown staghorn corals are outplanted onto Florida reefs yearly. While we have developed best practices for the propagation and outplanting process, limited attention has been focused on the fate of corals once they are back onto the wild reefs and the factors that influence their growth and survivorship once outplanted. One of the research gaps identified is the role that native predators, such as farming damselfishes, have on the success of coral outplanting and reef restoration.

This is the first study to document the prevalence of resident damselfish and significant negative effects of algal lawns on *A. cervicornis* along the Florida Reef Tract. Impacts of damselfish lawns on *A. cervicornis* colonies were more prevalent than those of other sources of mortality (i.e., disease, predation, and algal/sponge overgrowth), and damselfish activities caused the highest levels of tissue mortality among all the coral stressors evaluated. The presence of a resident damselfish decreased predation by other corallivores, but coral growth rates were significantly lower in colonies with damselfish lawns and the probability of the existence of a damselfish lawn increased as coral colony size and complexity increased. Lower predation by damselfish and other corallivores was documented within protected zones indicating management strategies may alleviate some predation pressure.

While the rates of damselfish occupation and creation of algal lawns observed raise concern for the survival of impacted colonies, the long-term success of active restoration programs designed to enhance staghorn coral populations can drastically increase local populations and may allow *A. cervicornis* to continue to fulfill critical functional roles on local coral reefs. The effects of damselfish predation are, and will continue to be, pervasive, but innovative restoration efforts and strategic outplanting designs may help overcome damselfish damage over time while also providing important information to educate future conservation and management decisions.

Introduction

The cultivation of algal lawns by species of damselfish can have detrimental effects on scleractinian coral colonies (Kaufman 1977; Brawley and Adey 1977; Potts 1977; Williams 1979; Lobel, 1980). Farming damselfish, particularly *Stegastes planifrons*, the threespot damsel, actively establish algal lawns on coral colonies by repeatedly biting away coral tissue allowing lesions to be colonized by turf and filamentous algae (Robertson et al. 1981; Sammarco and Williams 1982; Hixon and Brostoff 1996). Damselfish aggressively defend their algal lawns thereby reducing grazing pressure of herbivorous fish and invertebrates to such an extent that dense mats of filamentous algae develop within their territories (Vine 1974; Belk 1975). Complete colony mortality or metabolic stress may occur as tissues are smothered by algal lawns (Myrberg and Thresher 1974; Sammarco et al. 1986). Additionally, algal overgrowth and increased sedimentation reduces suitable substrate for the settlement of coral larvae (Vine 1974; Potts 1977; Hixon 1997), and lawns provide microhabitat for boring organisms thereby enhancing bioerosion of the coral framework and contributing to overall reef degradation (Risk and Sammarco 1982; Hutchings 1986; Sammarco et al. 1986).

One of the Caribbean's predominant reef building coral genera, *Acropora*, has suffered significant population degradation from multiple biological and anthropogenic stressors (Jaap et al. 1988; Porter and Meier 1992; Bruckner 2002) leading to their inclusion on the Endangered Species List in 2006. The loss of *Acropora*'s high accretion rates and structural complexity guarantees the loss of reef function and structure as acroporid corals are critically important for reef growth, island formation, fisheries habitat, coastal buffering, and biodiversity (Bruckner 2002). The presence of damselfish lawns on *Acropora* has been documented throughout the Caribbean with damselfish territories covering up to 80% of shallow reef habitat (Itzkowitz 1977; Kaufman 1977; Williams 1984; Bruckner 2002; Axline-Minotti 2003; Grober-Dunsmore et al. 2006). In the Bahamas, threespot damselfish were associated with complex *A. cervicornis* colonies 20 times more than with any other microhabitat type (Clarke 1977). However, there is no data on the direct effect of damselfish lawns on the growth and productivity of *A. cervicornis*. With densities of damselfishes along the Florida Reef tract as high as 4.2 fish/m² (Wilkes et al. 2008), the effect of damselfish lawns on benthic community dynamics may be substantial (Fig. 1). In addition to the damage inflicted on adult colonies the presence of damselfish lawns may inhibit the settlement of *Acropora* larvae produced during sexual reproduction, or the attachment of *Acropora* fragments created during asexual fragmentation events (Vine 1974; Potts 1977; Hixon 1997) thereby reducing the success of *Acropora* beyond the direct damage inflicted on the parent colony. As an example, damselfish gardening played an important role in the collapse of staghorn

populations in Jamaica and dramatically slowed the recovery of *A. cervicornis* following Hurricane Allen (Knowlton et al. 1990). In addition, it has been suggested that continued negative effects of damselfish gardening on remnant *A. cervicornis* colonies could devastate existing populations and, therefore, threaten the long-term prospects for population recovery (Roberts 2003). Thus, the significant increase in algal biomass and diversity on coral reefs associated with the formation of damselfish lawns, combined with the absence of grazing urchins and continued fishing pressure of dominant herbivorous fishes in the Caribbean (e.g., parrotfishes, surgeons), may lead to a phase-shift from coral to algal dominance in Caribbean reefs, and more specifically, contribute to the continuous decline of threatened *Acropora* populations.



Figure 1. *Acropora cervicornis* thicket with > 60% mortality due to damselfish algal lawn formation.

With the potential dramatic effect of damselfish lawns on coral reefs, it is important to evaluate the occupation dynamics of damselfish along the Florida Reef Tract, as well as, determine the effect of damselfish predation and formation of algal lawns on the growth and productivity of the threatened Caribbean coral, *A. cervicornis*. This research is especially relevant as this keystone coral species is believed to be in a recovering trend after decades of steady decline and has also become a recent focus of active restoration activities. Information obtained in this study will prove invaluable to reef restoration and rehabilitation efforts, in particular, propagation efforts within in situ coral nurseries designed to provide a sustainable source of healthy corals for use in restoration efforts. Damselfish predation and algal farming has been observed within

coral nurseries in the Florida Keys (K. Nedimyer- personal communication) and the Dominican Republic (algal lawns were present on 33.3% of tagged colonies within the coral nursery resulting in up to 80% colony mortality; V. Galvan, unpublished data) and may have significant consequences on successful propagation of corals for restoration activities and the survival of transplanted colonies on restored reefs.

The three main objectives of this project were to: 1) evaluate the occupation dynamics of damselfishes on *A. cervicornis* colonies along the FRT, 2) determine the impacts of damselfish predation and algal lawn formation on the growth and survivorship of *A. cervicornis*, and 3) identify potential interactions between damselfishes and other *A. cervicornis* predators. The results of this study provide key insights into the dynamic nature of *Acropora*-damselfish interactions and how these relationships may affect the recovery of this threatened coral species.

Methods/Results

Damselfish Occupation and Impacts

Visual surveys were conducted to determine occupational patterns of damselfishes on colonies of *A. cervicornis* on reefs in four regions of the Florida Reef Tract (Miami-Dade County including Biscayne National Park; n=33), Upper Keys (Key Largo; n=9), Middle Keys (Marathon; n=8), and Lower Keys (Looe Key; n=27)). A total of 921 *A. cervicornis* colonies were surveyed including 165 outplanted colonies. All staghorn colonies with living tissue were measured (diameter, height, number of branches, percent live/dead), and assessed for overall condition.

The mean colony size for all colonies surveyed was 43.6 (1.3) cm total linear extension with a mean height of 19.9 (0.4) cm and a mean 35.6 (1.1) branches per colony. Most colonies were “healthy” with a mean 71.4 (1.2) % live tissue and 7.9 (0.7) % predation by snails or fireworms (Fig. 2). Algal or sponge overgrowth was observed on 5.6% of colonies and disease, including Rapid Wasting Disease or Rapid Tissue Loss, was evident on only 1.6% of surveyed colonies. When present, disease caused high tissue mortality within colonies ($32.1 \pm 10.5\%$). Damselfish occupied 285 *A. cervicornis* colonies including 81.9% of colonies with lawns and 22.1% of colonies without lawns. Prevalence of damselfish lawns on *A. cervicornis* colonies (21.9%) was higher than any other source of mortality and caused the highest tissue mortality ($33.4 \pm 2.1\%$; range 5-100%; ANOVA; $p < 0.001$). Three-spot damsels accounted for 42.4% of damselfish occupying colonies with algal lawns followed by cocoa (31.4%), bicolor (16.5%), and dusky (8.2%) damselfish. Prevalence of damselfish bites and chimneys was low (2.7% of colonies), but chimneys were always associated with the presence of a resident damselfish and an algal lawn. The prevalence of corallivore predation was inversely related to the presence of a resident damselfish (Pearson’s

$\chi^2 = 7.61$, $df = 1$, $p = 0.006$), and significantly lower partial tissue mortality due to predation was observed in colonies with algal lawns ($14.8 \pm 2.2\%$) than without ($1.5 \pm 0.4\%$; ANOVA; $p < 0.001$).

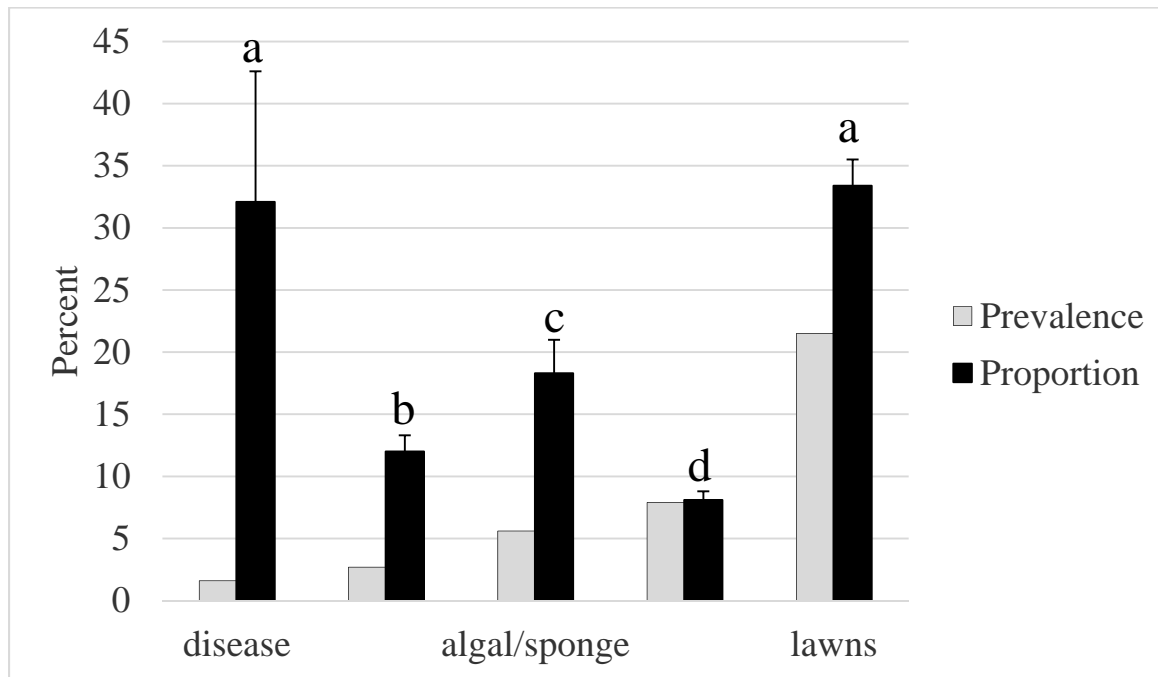
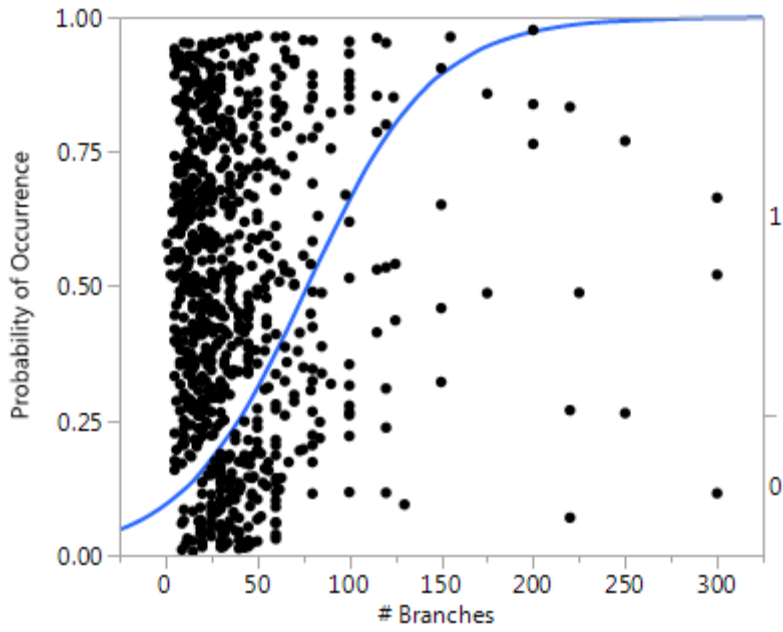
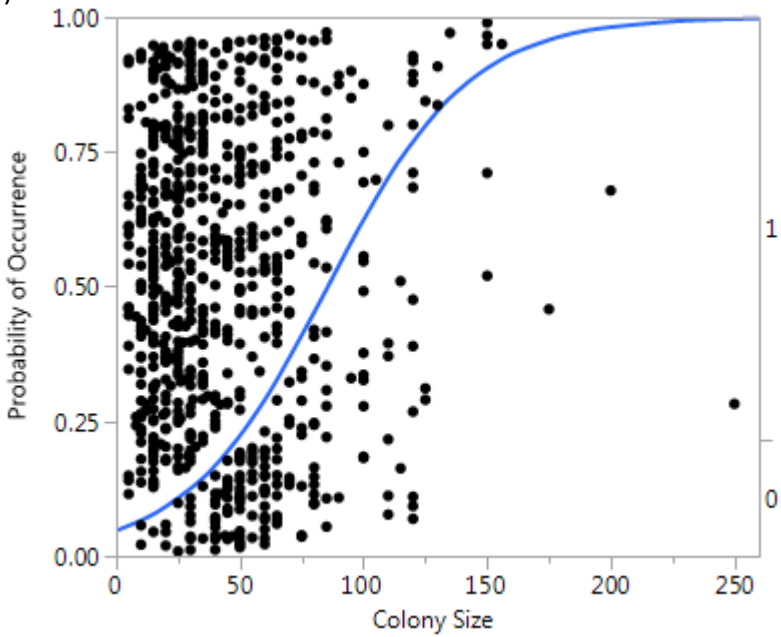


Figure 2. Prevalence of sources of coral mortality (gray bars) and mean percentage of tissue mortality on *A. cervicornis* colonies (black bars \pm SE). Letters reference statistical difference in the mean percentage of tissue mortality of each coral colony affected by mortality between sources (one-way ANOVA; $p < 0.001$).

Mean diameter for all *A. cervicornis* colonies surveyed was 43.6 (SE = ± 1.3) cm with a mean height of 19.9 (0.4) cm and a mean of 35.6 (1.1) branches per colony. Most colonies were “healthy”, with a mean of 71.4 (1.2) % live tissue. The probability of damselfish occupancy (i.e., a colony being used as part of a damselfish territory) increased significantly with staghorn colony size ($p < 0.001$) and number of branches ($p < 0.001$; Fig. 3) based on a logistic regression analysis using damselfish presence-absence data. Thus, larger, more complex staghorn colonies are significantly more likely to be used as damselfish territories than smaller, less complex colonies. Accordingly, colonies with damselfish lawns were significantly larger (max diam; t-test; $p < 0.001$; max height; t-test; $p < 0.001$) and more complex (# of branches; t-test; $p < 0.001$) than colonies without lawns.



a)



b)

Figure 3. Probability of damselfish occupancy and formation of algal lawns based on *Acropora cervicornis* colony size (a) and complexity (# of branches) (b).

To document changes in damselfish lawn presence and size over time, eight *A. cervicornis* colonies with and without damselfish lawns were tagged on three reefs within BNP in 2013 (FRRP 1747, Alina's Reef and Grounding Site). Colonies with and without lawns were of similar size (diameter, One way ANOVA, $p=0.071$) and complexity (# of branches, One way ANOVA, $p=0.165$). Three branches on each tagged colony were marked ~2 cm from the apical tip with small cable ties to document growth rates (Lirman et al., 2010). After one year, percent cover of algal lawns increased 5-10% in three colonies and the percent cover of damselfish bites or chimneys increased by 20% in one colony. Additionally, a new lawn was formed on one colony that, when tagged, did not have an existing lawn. There was a statistical difference in growth between colonies with and without algal lawns. Mean extension rates for branches on colonies with lawns was 8.8 (1.2) cm/yr while rates for branches on colonies without lawns was significantly higher at 12.3 (1.0) cm/yr (t-test; $p=0.024$). Additionally, colonies with damsel lawns had significantly lower evidence of snail and fireworm predation (One way ANOVA; $p=0.001$). Mean snail and fireworm predation was 1.9 (1.4) % on colonies with resident damselfish and 12.0 (1.7) % without lawns thereby indicating that when damselfish defend their territory they significantly reduce predation by other coral predators.

Damselfish occupation rates of outplanted *A. cervicornis* colonies were documented at three non-protected restoration sites (Snapper Ledge, Pickles Reef, and East Patch Looe Key) and three restoration sites within protected areas (Conch Reef, Molasses Reef, and Looe Key ROA). As part of the proposed outplanting design for 2013, 30 colonies of nursery-reared *A. cervicornis* were outplanted in a 5 x 6 grid. Three size classes ($n=10$ corals per size class) were utilized including small (<15 cm max diameter), medium (16-34 cm max diameter), and large (> 35 cm max diameter) colonies to identify potential colony size preferences by damselfish. Five colonies of each size class were tagged and 3 branches were marked with cable ties 2 cm from the apical tip for growth measurements. After one year, no significant differences existed between the Lower Keys and the Upper Keys populations, so data was pooled for analysis. High survivorship of outplants occurred at all sites (89.5%) with higher survival occurring within protected areas (90%) than outside of protected areas (80%). No damsel lawns were formed on outplanted corals at either Lower Keys sites, but five lawns were formed on outplants in the Upper Keys. Lawns were formed on significantly larger (One way ANOVA; $p=0.044$) and more complex (One way ANOVA; $p=0.038$) colonies, and growth rates were significantly lower on colonies with algal lawns (16.7 ± 2.1 cm/yr) than those without (25.8 ± 2.8 cm/yr; One way ANOVA; $p=0.027$). Algal lawns covered a mean 14.0 (2.4) % of the total colony, with 5% of one colony being damaged by damselfish bites or chimneys. Predation was low on all outplants (9.6% of colonies) with snail and fireworm predation covering a mean 14.3 (1.9) % of predated colonies. Predation was significantly lower

on colonies with a resident damselfish than without (One-way ANOVA; $p=0.000$). Protection level did not influence damselfish predation as 80% of the colonies where lawns were formed were located within protected areas in the Upper Keys. In addition, protection level did not influence the overall damage to colonies from predation by snails or fireworms (One way ANOVA; $p=0.329$), but 82.1% of predated colonies were located outside of protected areas.

Based on observations that damselfish lawns are found on larger colonies, additional corals were outplanted to East Patch at Looe Key where many resident three-spot damselfish were observed on the reef. Corals were at least 25 cm in max diameter and 10 corals were placed closely together to form 4 small thickets of at least 60 cm in max diameter. Prior to the completion of the outplanting, three-spot damselfish began to utilize and defend the new territory against divers and other damselfish (Fig. 4). Over 6 months, thickets increased in max diameter by a mean 10% and width by 12%. All thickets were colonized by three-spot damselfish and algal lawns were formed. Algal lawns ranged in size from 20- 45% of the total colony which is a considerable amount of damage to occur over just 6 months (Fig. 5). Similar to trends observed during reef surveys, colonies with damsel lawns had significantly lower occurrence of snail and fireworm predation (t-test, $p = 0.001$).



Figure 4. Three spot damselfish utilizing new territory within outplanted “thicket” at East Patch Looe Key.



Figure 5. Three spot damselfish and algal lawn formed on outplanted thicket at East Patch Looe Key after six months.

Fish Trophic Relationships and Protection Level

To investigate the effect of management strategies on trends in damselfish and predator abundance along the Florida Reef Tract we explored available fish data from NOAA's RVC program covering fish abundance data since 1980 when the SPAs were installed (Smith et al., 2011). Data included surveys within and outside of protected areas from multiple years and reef types for three algal farming damselfish species *Stegastes planifrons*, *S. adustus* and *S. variabilis* and predator species (n= 18) known to predate damselfish including grouper, snapper, and jack species. The mean abundance of predator species (One-way ANOVA, $p=0.003$) and damsel species (One-way ANOVA, $p=0.000$) were significantly different between years and between protection levels (One-way ANOVA, $p=0.000$). For predator species, higher abundance was observed within SPAs (1.55 ± 0.07) than outside (0.91 ± 0.04). However, mean abundance of damselfish also followed a similar pattern with significantly higher abundance within protected areas (4.54 ± 0.21) than outside (1.4 ± 0.04). Protection level significantly affected the abundance of all fish. A trend for decreases in damselfish abundance after increases in predator abundance and vice versa are detectable, particularly within protected areas (Fig. 6) indicating that predator diversity and abundance may play a role in managing damselfish numbers, but this relationship is highly variable both spatially and temporally and, thus, not statistically significant.

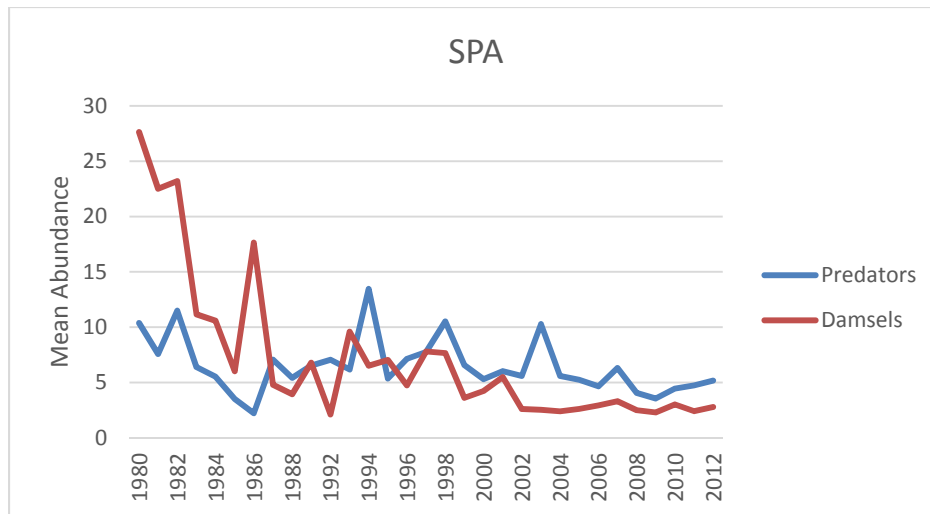


Figure 6. Change in predator and damselfish abundance over time within protected areas along the Florida Reef Tract.

Experimental Damselfish Recruitment

Experimental damselfish habitats were built using healthy *A. cervicornis* colonies from the Coral Reef Foundation coral nursery located in Key Largo (depth = 10 m). The goal of these habitats was to conduct controlled observations of damselfish territorial activities and their behavior in the presence of other predators such as snails and fireworms. Nursery colonies were secured using cable ties to cinderblock platforms with PVC pedestals. Cinderblocks were populated with live corals (n = 12; max diameter >45 cm) or dead coral skeletons (n = 4; controls). Sections of live rock were added to the base of the nursery blocks to provide an initial source of food for the damsels. Platforms were secured with rebar stakes and arranged in a grid pattern using a randomized block design, with each platform separated by 15 m. Platforms were deployed on a large sand patch near the nursery and distanced from any natural reef or source of fish recruitment by 100m (Bohnsack et al., 1994).

Adult three-spot damselfish (> 5cm standard length, n=3) were netted by hand from nearby reefs (Pickles Reef and Snapper Ledge) and netted around treatment platforms for 48 hours to facilitate settlement (Lirman, 1994; Fig. 7). Damselfish (n= 5) were set on nursery block five times. While three damselfish initially recruited to nursery blocks, no damsels remained on the blocks for more than three weeks and no damage from farming was observed on the corals. The lack of successful recruitment was potentially due to rough weather occurring during the winter of 2013/2014 and/or predation. Large schools of jacks and snapper are common in the area and are thought to be the source of damsel predation. Due to the lack of recruitment of damselfish to the experimental blocks, the proposed manipulation experiments designed to investigate

interactions between damselfish and other *Acropora* predators, snails (*Coralliophila*) and fireworms (*Hermodice*) were not completed. However, we were able to still test the hypothesis that damselfish territoriality influenced the impacts of predation by snails and fireworms using our field observations and outplants on wild reefs (see prior section).



Figure 7. Deployment of damselfish on experimental nursery blocks with nets.

Discussion

Damselfishes are important components of coral reefs, and their territorial behavior and gardening activities cause direct mortality to corals (Myrberg and Thresher 1974; Kaufman 1997; Sammarco et al. 1986) and create negative cascading effects by reducing overall grazing on reef macroalgae (Vine 1974; Belk 1975]. In fact, the impacts of damselfish occupation have been recognized as a factor influencing coral reef community dynamics since the Pleistocene (Precht et al. 2010; Lobel 1980; Kaufman 1981; Knowlton 1992). But, the steep decline in coral abundance, especially of those coral species that are commonly used by territorial damselfishes, established the present scenario in which damselfish impacts are now concentrated on a much lower number of coral prey/colonies, thus creating a significant threat to the persistence and recovery of depleted coral populations. Here, we show that territorial damselfishes are a significant source of mortality to recovering and restored populations of the threatened staghorn coral *Acropora cervicornis* along the Florida Reef Tract. Damselfish occupation and impacts are influenced by the size of the staghorn colonies, with larger, more complex colonies having a

higher prevalence of damselfish occupation. Our transplant experiments clearly demonstrated that while staghorn colonies escape damselfish occupation at small sizes, colonies are quickly targeted by damselfishes after colonies reach diameters > 45 cm, and tissue mortality of up to 45% per colony can occur within just six months after damselfish occupation. Moreover, damselfish occupation results in significantly lower coral growth (branch linear extension) in host colonies. The concentration of impacts on remaining small staghorn populations is clearly a source of concern for the recovery of this threatened coral species and should be considered in restoration activities and management strategies. Along the Florida Reef Tract (FRT), the > 900 wild *A. cervicornis* colonies surveyed were generally healthy, with the majority of colonies having > 90% live tissue. However, partial mortality caused by disease, predation, damselfish grazing, and other sources were documented on nearly half of all colonies. Similar to findings by Tunnicliffe (1983), damselfish lawns were the most prevalent source of mortality to *A. cervicornis* and 33.4% of tissue mortality was caused directly by damselfish gardening activities. We documented significantly higher prevalence of damselfish lawns (21.9%) than surveys conducted along the FRT in 2008 (2.2%) (Miller et al. 2008), showing a concerning increase in the occurrence of damselfish occupation over a short time period. In addition to causing immediate tissue mortality (up to 45% tissue mortality within just six months in dense staghorn thickets), damselfish occupation negatively impacted coral growth. Growth rates of *A. cervicornis* were significantly lower in both wild and outplanted colonies with damselfish lawns. While the occupation rate of damselfishes to smaller outplanted colonies was low (5 out of 180 colonies over one year), occupation was clearly size-dependent with the probability of damselfish occupancy increasing as coral colony size and complexity increases. Thus, as colonies become larger and more complex (as shown by the higher occupation rates of the larger wild colonies and dense outplants), damselfish occupation rates will also increase significantly. Considering that small *A. cervicornis* outplants (5 cm total linear extension) can reach colony sizes desirable as damselfish habitat (> 45 cm maximum diameter) within 1-2 years (Lirman et al. 2014; Griffin et al. 2015), reduced growth and productivity as a result of damselfish predation may prevent or delay colonies from reaching a size of sexual maturity. Reduced growth of smaller colonies combined with mortality of larger, more mature (and fecund) *A. cervicornis* colonies may have a significant effect on population dynamics by potentially eliminating important genetic diversity and reducing sexually reproductive populations. In this study, colonies with a resident damselfish exhibited significantly lower predation rates by *Coralliophila* or *Hermodice* and lower partial tissue mortality. Coral predation has been linked to substantial and chronic mortality [55-58], prevention of recovery after acute disturbances such as storms (Knowlton et al. 1990), an increase in coral disease transmission (Williams and Miller 2005; Sutherland et al. 2011), and impairment of propagation and outplanting phases of active *A. cervicornis* restoration projects (Young et al. 2012). Therefore, a reduction in *Coralliophila* and *Hermodice* predation as a result of the presence of a resident damselfish is an important finding of this study and may offset some

of the negative impacts caused by damselfishes. Another potential mechanism for the reduction in damselfish impacts is to reduce the abundance of territorial damselfishes through the increased protection of damselfish fish predators with the establishment of no-take zones. Although some studies documented no relationship between piscivore abundance and damselfish populations (Williams 1978; Precht et al. 2010; Williams 1981), others find damselfish abundance to be negatively correlated with piscivore/predator biomass within protected areas (DeMartini et al. 2008; Vermeij et al. 2015). While the abundance of predatory fish was not directly addressed within our study, focusing *Acropora* population enhancement within areas of potentially higher piscivore biomass, such as within no-take areas, may provide additional protection against damselfish predation and should be considered a priority in the design of restoration strategies.

Gardening damselfishes were only found on *A. cervicornis* colonies with at least some live coral tissue, findings similar to Precht et al. (2010). Few algal lawns were found on colonies devoid of any live tissue and resident farming damselfishes were completely absent in those cases. Only bicolor damselfish, which do not farm lawns and utilize colonies for habitat only, were found on dead colonies (Nemeth, 1998). This observation suggests that direct occupation impacts, as well as reduced growth of the occupied coral, often leads to complete host mortality and that damselfishes may vacate previously occupied colonies shortly thereafter. While the corallivorous snail *C. abbreviata* has been shown to stay on its prey until the tissue is completely consumed (Johnston and Miller 2014), damselfishes, who do not derive a primary dietary benefit from the coral tissue (Lobel 1980; Jones et al. 2006), may be forced to abandon their lawns after colony mortality rather than actively farming their host to death. For example, by eliminating space between coral branches, the amount of available shelter within the colony is reduced when the coral is colonized by algae (Munday 2001) and once algal lawns become too large, damselfishes may not be able to defend them against other herbivores or prevent overgrowth by larger, undesirable macroalgae (Klumpp and Polunin 1989; Foster 1985; Catano et al. 2015). At this point, damselfish may move on to build territories on new, live colonies. Additional studies are needed to investigate such interactive effects between damselfish and their coral hosts to determine potential thresholds for algal farming activities and coral mortality.

The severity of coral predation can change radically depending on the size of the prey population via threshold effects and can strongly influence the potential recovery of depleted coral populations (May 1977). For example, in areas of high staghorn abundance, such as Jamaica or Panama prior to 1980 (Robertson et al. 1981; Tunnicliffe 1983; Goreau 1959; Kinzie 1973), damselfishes and other coral predators had limited effects on coral health as their impacts were distributed across a large population. But, Knowlton et al. (1981; 1990) observed limited declines in coral predator densities after Hurricane Allen and dramatic declines in the abundance of *A. cervicornis*, thus concentrating predator impacts onto small remnant coral populations and

effectively preventing coral recovery. Even at low *A. cervicornis* densities, stable persistence of predators, such as damselfishes, *Coralliophila*, and *Hermodice*, is more likely if predators can occupy nearby, less preferred coral prey (Precht et al. 2010; Knowlton et al. 1990). While *A. cervicornis* is the preferred prey for damselfishes and *Coralliophila* (Johnston and Miller 2014), and thus, is especially vulnerable to intense and focused predator activities, migration by damselfishes, especially threespots, onto less preferred coral hosts as the abundance of preferred prey declines has been observed (Precht et al. 2010). Corals commonly targeted in the absence of *Acropora*, namely species of the boulder genus *Orbicella*, have also experienced drastic declines in abundance and are now listed as threatened under the US Endangered Species Act. In fact, Precht et al. (2010) suggest planting faster-growing, nursery-reared *A. cervicornis* colonies in the vicinity of *Orbicella* colonies to reduce predation potential on the slower growing species while allowing damselfish to return to their preferred prey/habitat. Although damselfish occupation often leads to complete host mortality of *A. cervicornis* and, therefore, would potentially sacrifice some staghorn corals, the ability to rapidly propagate and outplant large numbers of *Acropora* from coral nurseries may serve as a viable option to aid in the recovery of both genera.

This study documents dramatic differences in damselfish occupation rates of *A. cervicornis* based on colony size. As colonies become larger and more complex through high productivity and growth rates or through strategic thicket outplant designs employed during Caribbean restoration efforts, occupation rates also increase. Within very short time scales, outplanted *A. cervicornis* colonies can reach colony sizes targeted as damselfish habitat. Therefore, restoration planting strategies may be modified based on the abundance of coral predators at a given site. However, this may prove to be challenging as damselfish abundances are high throughout the FRT. Faced with the option of transplanting fewer but larger colonies or a greater number of smaller colonies, practitioners may decide to select the latter so that more colonies reach the size where they become desirable habitat to territorial damselfish at roughly the same time, thereby spreading the impacts of damselfishes among a larger number of hosts (assuming a set number of damselfish are available to occupy these colonies). However, transplanting smaller colonies also has disadvantages as both survivorship and reproduction of corals are directly related to size (Hughes and Jackson 1985). The spatial arrangement of colonies within reefs can also influence damselfish impacts and need to be considered in outplanting design. Here, we showed that close spacing of outplants provides immediate habitat for damselfishes and has been shown to be detrimental to coral growth by Griffin et al. (2015). Thus, a wider spacing between colonies may be desired in reefs with higher damselfish abundance. Wider spacing of outplants is also supported by the work of Johnston and Miller (2014) who showed that coral predator impacts are influenced by the composition of the coral neighborhood surrounding targeted species. The combination of high damselfish recruitment and reduced growth rates of closely-spaced colonies, suggests that outplanting staghorn coral in dense aggregations or

thickets may not be suitable for initial recovery of *A. cervicornis* under present conditions. The trade-offs outlined here should be addressed explicitly in future restoration efforts so that science-based recommendations for the active propagation and recovery of threatened coral species can be further refined.

This is the first study, to our knowledge, to evaluate the prevalence of resident damselfishes and significant negative physiological effects of algal lawns on *A. cervicornis* along the FRT. Although damselfishes reduced predation severity by other corallivores, the fast rate of damselfish occupation and subsequent partial coral colony mortality by the creation of algal lawns raise concerns for the success of active restoration programs designed to enhance staghorn coral populations. However, most negative impacts of damselfish identified in this study affected mainly large individual colonies and less than half of the *A. cervicornis* population along the FRT. The remaining wild staghorn population, along with the rapidly increasing restored population, continue to fulfill important functional roles on coral reefs such as providing essential habitat and refuge to other reef organisms. In addition, since damselfishes favor larger colonies, the majority of outplanted colonies, as well as abundant smaller wild colonies, continue to have the opportunity to drastically increase total coral cover through rapid growth and branch expansion. Although the effects of damselfish predation are, and will continue to be, pervasive, strategic outplanting designs may help partly overcome damselfish damage as coral abundance builds over time to the point where damselfish impacts are not overly concentrated.

Education and Outreach

Information collected as part of this study has been included as teaching content within one undergraduate course (MSC 264, Tropical Marine Ecosystem Science) and one graduate course (MBF 615, Tropical Marine Ecology) at the University of Miami to highlight the role that damselfish play in coral reef ecology. The information collected on ways to mitigate the impacts of damselfish on staghorn corals using modified outplanting designs have been incorporated into the “Best Practices” manuals used by our partners in the Dominican Republic (Puntacana Ecological Foundation), the Bahamas (Cape Eleuthera Institute), and the Cayman Islands (Central Caribbean Marine Institute). Our research on the role of damselfishes in coral reef ecology and *Acropora* restoration has been included in lectures and seminars provided during 2014 and 2015 to school groups and summer camps from the following programs: Frost Museum of Science’s Integrated Marine Program and College Training (IMPACT), Upward Bound, YMCA, Junior Scientists in the Sea, MAST academy, CARTHE’s Marine Science Day, and National Park Conservation Association as part of our Rescue A Reef citizen science program (<http://rjd.miami.edu/donate/rescue-a-reef>). These educational activities have reached > 1000 participants. The results of this study were presented at three scientific conferences: 1) National

Center for Coral Reef Research Forum (Miami, FL; 2014), 2) Conference for Ecological and Ecosystem Restoration (New Orleans, LA; 2014), and 3) Coral Reef Foundation Scientific Meeting (Key Largo, FL, Oct 2015).

Publications

Schopmeyer, SA and Lirman, D. 2015. Occupation dynamics and impacts of damselfish territoriality on recovering populations of the threatened staghorn coral, *Acropora cervicornis*. PLoS ONE 10(11): e0141302. doi:10.1371/journal.pone.0141302