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Coral recovery on phase-shifted reefs depend upon the type of macroalgae present

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Coral recovery on phase-shifted reefs depend upon the type of macroalgae present

By

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Abstract

The Florida Keys experienced some of the most drastic transitions from coral to macroalgae dominated states, known as phase-or regime-shifts, of any reefs in the Caribbean. Macroalgae on coral reefs lower coral recruitment by deterring coral settlement either directly through competition or indirectly by changing the chemical environment near the benthos. With evidence of species-specific interactions to coral-macroalgae competition, the type of macroalgae on a phase-shifted coral reef might be more important than just identifying a reef transition. To answer this question, I tested the effect of *Laurencia intricata* (a macroalgae related to the settlement inducing crustose coralline algae) and Dictyotaceae (known for its toxic or allelopathic compounds) on *Porites astreoides* planulae behavior, settlement and choice settlement preference, and post-settlement survival. I found that *P. astreoides* planulae show a positive response to chemical cues released from *L. intricata*, crustose coralline algae, and species in the Dictyotaceae family. However, the positive chemical cue response becomes algal-specific as larvae start probing for settlement substrate. Providing *P. astreoides* larvae with a choice between settlement substrates, revealed that the algal structure caused higher settlement next to *L. intricata*, while Dictyotaceae deterred larval settlement. It may be beneficial for larvae to settle next to *L. intricata* over Dictyotaceae algae. I identified that post-settlement survival was enhanced when *P. astreoides* larvae settled next to *L. intricata* while Dictyotaceae species did not enhance or deter post-settlement survival. These results indicate that coral larvae may be responding differently to a variety of chemical cues. Any chemical or physical cue from a reef may be used by coral larvae to identify and locate settlement substrate on a reef. Once they identify a reef's location, they express a more selective behavior during settlement by avoiding Dictyotaceae macroalgae and favoring *L. intricata*. This suggests that the composition of a phase-shifted reef matters to coral recovery, not only that it has shifted to a dominated macroalgal state.

KEYWORDS: Coral-algae interaction, Larval behavior, Settlement cues, *Laurencia intricata*, *Dictyopteris*, *Dictyota*

Chapter 1: Introduction

1.1 Coral Reef Importance and Phase-shift

Coral reefs are often considered the rainforest of the sea, supporting over a third of known marine species (242,743) (WoRMS Editorial Board 2016) while occupying only 0.2% of the ocean (Costanza *et al.* 1997). The intricate, three-dimensional landscape of coral reefs promote elaborate adaptation and diverse species richness. Estimates suggest at least a million species occupy coral reefs and with 90% of marine species remaining undiscovered this number is likely much higher (Reaka-Kudla 2001). The organisms on coral reefs are a source for anti-cancer and anti-pain compounds and may serve as a rich source for potential life-saving drugs (Bruckner 2002). Coral reefs are an invaluable source of protein, shield thousands of kilometers of coastlines from wave erosion, thus protecting lagoon, seagrass, and mangrove habitats, and provide numerous recreational activities (Costanza *et al.* 1997, Moberg and Folke 1999; Johnson and Marshall 2007). Globally, coral reefs provide an estimated $30 billion of net benefits in goods and services to the world economy (Cesar *et al.* 2003).

With tens of millions of people depending on protein and natural resources from coral reefs, it often leads to their exploitation especially in heavily populated and under regulated areas (Cesar *et al.* 2003). In recent decades, coral reefs experienced some of the highest ecological declines observed among marine ecosystems worldwide (Halpern *et al.* 2008; Schutte *et al.* 2010). The Caribbean basin has experienced some of the most drastic changes in scleractinian coral cover, with average cover being reduced by 80% (Gardner *et al.* 2003; Bellwood *et al.* 2004). Future projections predict this decline will likely continue as sea surface temperatures rise, causing additional stress to corals and triggering massive bleaching (McWilliams *et al.* 2005; Hoegh-Guldberg *et al.* 2007) where their symbiotic algae *Symbiodinium* is expelled (Brown 1996). Other factors contributing to coral reef degradation include natural disasters (i.e. hurricanes) (Rogers and Miller 2006) and anthropogenic stressors (Richmond 1993; McWilliams *et al.* 2005) (i.e. habitat destruction, nutrient loading, and sedimentation). Coral reef degradation often leads to a transition to a macroalgal-dominated state (Hughes 1994; Graham *et al.* 2015) making coral recovery difficult. This transition is known as phase- (Done 1992; Hughes 1994) or regime-shift (Scheffer and Carpenter 2003) with extensive algal

colonization likely (Dudgeon *et al.* 2010). Other phase-shifts can occur to soft coral, sponge, or corallimorpharian, but macroalgal phase-shifts are the most common and detrimental to the ecosystem (Norström *et al.* 2009).

1.2 Causes of Phase-shift

Macroalgal phase-shifts are often caused by anthropogenic activities that alter top-down (herbivory) and bottom-up (nutrient) controls, ultimately impacting an ecosystem's community structure (Dudgeon *et al.* 2010)**.** Anthropogenic activities such as reduced herbivory from overfishing and increased nutrient input from coastal urbanization are the main triggers that cause coral reefs to transition to a macroalgal dominated state (Folke *et al.* 2004). Overfishing in the 1970's reduced the number of competitors and predators of the sea urchin, *Diadema antillarum*, allowing them to reach extremely high densities (Hughes 1994). The abundant *D. antillarum* population controlled macroalgae cover and compensated for the loss of fish herbivores until a mass die-off in 1983 decreased the sea urchin population by 95% (Lessios *et al.* 1984; Hughes 1994). Reduced grazing on reefs resulted in unchecked algal growth, leading to a shift from coral to algal dominated reefs (Hughes 1994). Eutrophication from increased nutrient input prompts algal growth, while simultaneously reducing coral growth through physiological stress, and increases the chances of a coral reef entering a phase-shift (Littler *et al.* 2006). Over the past few decades, anthropogenic activities reduced grazing pressure and eutrophication continue to enhance macroalgal overgrowth making coral reef recovery unlikely (Done 1992; Crosset *et al.* 2004; Hughes 1994).

Herbivory and nutrient concentrations vary among coral reefs and affect the reef's susceptibility to changes in top-down and bottom-up controls differently (Graham *et al.* 2015). For this reason, on some reefs herbivory has a higher impact on macroalgae abundance than nutrient input (McCook 1999; Bellwood *et al.* 2004; Mumby and Steneck 2008), while on other reefs, nutrient input has a higher impact on macroalgae abundance (Lapointe *et al.* 2004; Bell *et al.* 2014). Species of macroalgae also vary in abundance among reefs (Schutte *et al.* 2010) and experience species-specific herbivory and species-specific response to eutrophication (McClanahan *et al.* 2003; Fong 2015), further complicating the impact of top-down and bottom-up controls.

Other factors that influence the susceptibility of a coral reef entering a macroalgal phase-shift include rugosity and depth, as well as larval availability (Chong-Seng *et al.* 2014) and juvenile coral density (Graham *et al.* 2015). Structural complexity is a major contributor to reef diversity and productivity (Graham and Nash 2013). Higher complexity corresponds to increased fish biomass and a healthier, more resilient ecosystem (Rogers *et al.* 2014). Higher fish grazing leads to elevated coral recruitment as they have more substrate (Mumby *et al.* 2007) with settlement facilitator, crustose coralline algae (CCA) (Belliveau and Paul 2002). Deeper reefs are less likely than shallow reefs to undergo a phase-shift due to limited light penetration and algal growth (McCook 1999). Shallower reefs also have a greater risk of recurrent coral bleaching and storm damage, increasing the probability of coral reef degradation (Bridge *et al.* 2013). Reef depth experience a variability in nutrient concentrations (Lapointe 1997). Shallower reefs are exposed to elevated nutrients more than deeper reefs (Bridge et al. 2013) and higher nutrient levels reduce the abundance of CCA, limiting coral settlement substrate and recruitment (Hunte and Wittenberg 1992). Reduced coral recruitment can increase the chances of macroalgal phase-shift (Graham *et al.* 2015), which can even be prevented if recruitment is high enough to replenish colonies lost to mortality events (Gilmour *et al.* 2013). Factoring in spatial variation in herbivory (Hay *et al.* 1983) and nutrient concentration (Fong *et al.* 2001) among reefs, anthropogenic activities affect reefs differently, making it difficult to identify a single factor as the main contributor.

The simple definition of a phase-shift is a taxon that is more numerous or dominant than its competitors (Norström *et al.* 2009). What constitutes a dominant population is rarely defined in scientific literature (Rogers and Miller 2006) and contributes to the misperception on the causes, severity, and generalization of macroalgal phase-shifts (Bruno *et al.* 2009). Traditional examples of phase-shift include a case in Discovery Bay, Jamaica where macroalgal cover was >50% and coral cover was <10% (Dudgeon *et al.* 2010), but such a high percentage of macroalgal cover (only 5.2% of Caribbean reefs) is rarely observed on reefs (Bruno *et al.* 2009; Schutte *et al.* 2010). The entire Caribbean reef basin averages only 15% macroalgal cover (Dudgeon *et al.* 2010) and nearly half (48.9%) of the coral reefs experience higher macroalgal cover than coral cover (Schutte *et al.* 2010). Once a reef has entered a regime-shift, the effects may be permanent. Higher macroalgal abundance threatens adult corals and reduces coral

recruitment, which allows macroalgae to proliferate further, and creates a positive feedback loop that encourages regime-shift persistence (Hughes 1994; Mumby *et al.* 2007; Hughes *et al.* 2010; Bonaldo and Hay 2014). There are only a few case studies of macroalgal phase-shift showing signs of reverting back to a coral dominated state (Myhre and Acevedo-Gutierrez 2007; Stimson and Conklin 2008; Hughes *et al.* 2010), but a complete transformation from a macroalgal to a coral dominated ecosystem has yet to be documented (Rogers and Miller 2006).

1.3 Macroalgae Abundance and Reproduction

Throughout the Caribbean region, the Florida Keys' reef tract experiences some of the highest transitions from a coral to macroalgae-dominated state (Schutte *et al.* 2010). Since the 1970s, coral cover has decreased by 75% (Alevizon and Porter 2015), while macroalgal cover increased by 68% (Lapointe *et al.* 2005; Maliao *et al.* 2008) a change attributed to increased nutrient input (Lapointe *et al.* 2005) and over-fishing (Bohnsack *et al.* 1994). The ability of macroalgae to dominate reef habitat derives from their complex and unique life histories. Their alternation of generations reproductive strategy between haploid and diploid phases allows for the exploitation of different niches during their various life stages, therefore improving survival (Santelices 2004). Another successful reproductive strategy is asexual propagation, such as vegetative fragmentation, enabling them to rapidly expand into new habitats with more favorable conditions (Cecere *et al.* 2011). Macroalgae species exhibit different rates and patterns of vegetative growth and asexual propagation, increasing their capability to colonize and occupy substrate (Santelices 2004). Asexual propagation is highly effective at increasing macroalgal abundance (Herren *et al.* 2013) and distribution on reefs (Yniguez *et al.* 2015).

The rate of space preemption by macroalgae is not only dependent upon species and asexual propagation, but also environmental conditions, e.g. light, nutrients, currents, seasonality (Santelices 2004; Yniguez *et al.* 2010). Environmental conditions and disturbances also change macroalgae morphology improving their ability to adapt to changing environments (Yniguez *et al.* 2010). Many macroalgae species experience seasonal fluctuations in abundance (Jompa and McCook 2003). For example, macroalgal fragment reattachment rates can decrease during the winter months due to high-current

velocity thus reducing abundance (Kilar and McLachlan 1986). South Florida's warm, summer water temperature can weaken macroalgal thalli and enhance fragmentation (Kilar and McLachlan 1986), while increased nutrient run-off from late-summer rains improves fragment survival (Lapointe *et al.* 1992). Seasonal fluctuation of macroalgal abundance and fragmentation rates can alleviate stress to adult coral colonies during population lows, unlike perennial macroalgae where there is constant stress to the adult colony (Jompa and McCook 2003). Any increase in macroalgal abundance on coral reefs is detrimental to corals by physically (Edmunds and Carpenter 2001), chemically (Rasher *et al.* 2011), and physiologically (Morrow *et al.* 2011) affecting adult coral health and simultaneously decreasing coral recruitment.

1.4 Impacts of Macroalgae

1.4.1 Impacts on Adult Corals

Macroalgal structure can physically impact coral health through abrasion and shading (Coyer *et al.* 1993; Edmunds and Carpenter 2001; River and Edmunds 2001; Box and Mumby 2007) and chemically influence coral health by releasing allelopathic compounds (Rasher and Hay 2010; Rasher *et al.* 2011). However, this is dependent upon macroalgae structure and morphology (Rasher *et al.* 2011; Bonaldo and Hay 2014) and the type of chemical compounds released (Rasher and Hay 2014), with some species less hazardous than others. Morphology also affects water motion (River and Edmunds 2001) and reduces flow regimes around adult colonies (Duggins *et al.* 1990), limiting heterotrophic feeding success on particulate matter (Sebens and Johnson 1991; Morrow and Carpenter 2008). Additionally, reduced flow regimes can increase sedimentation rates (Carpenter and Williams 1993), which prevent regrowth of damaged tissue and increase coral stress (Nugues and Roberts 2003).

Corals physically damaged by macroalgae only partly explain the negative impacts associated with phase-shift. Much of the damage to the coral colonies can be attributed to allelopathic compounds released by some macroalgae species (Rasher and Hay 2010; Rasher *et al.* 2011). Allelopathic compounds influence growth, survival, and/or reproduction in corals (Rasher *et al.* 2011). These compounds are found in every aquatic environment and are released not only by macroalgae, but by cyanobacteria, microalgae, and angiosperms (Gross 2003). While positive growth stimulation by

allelopathic compounds can occur (Mohamad 2002), most of these compounds deter or inhibit epiphytic organismal overgrowth, which reduces shading. Macroalgae releases different chemical compounds when exposed to different stressors (Rasher and Hay 2014). Macroalgae discharges allelopathic compounds when subjected to increased abiotic and biotic stressors (Gross 2003) and in response to increased herbivory (Karban *et al.* 1997). On the other hand, the competition for space between macroalgae and corals triggers the release of allelopathic compounds (Gross 2003) that are targeted to decrease coral health rather than deterring herbivory (Rasher and Hay 2014).

Allelopathic compounds weaken coral health by damaging tissue (Rasher and Hay 2010), decrease photosynthesis, cause bleaching (Barott *et al.* 2009; Rasher and Hay 2010; Rasher *et al.* 2011 Shearer *et al.* 2012), trigger tissue necrosis (Shearer *et al.* 2012; Bonaldo and Hay 2014), and reduce fecundity and larval survival in corals (Birrell *et al.* 2008b). These compounds affect coral-associated microbe abundance and concentration (Morrow *et al.* 2011) and alter gene expression in corals and the symbiotic algae living within the coral tissue, *Symbiodinium* (Shearer *et al.* 2014). Alteration in signal transduction can lead to an imbalance between reactive oxidant species production and antioxidant capabilities within the coral holobiont. An imbalance in oxidative regulation can lead to protein damage and tissue apoptosis and/or necrosis (Shearer *et al.* 2012). Coral and *Symbiodinium* gene expression are influenced by species-specific interaction with the allelopathic compounds released from macroalgae, further adding to the complexity of their impact (Shearer *et al.* 2014). In more resilient coral species, their immune response genes are initiated rapidly when exposed to macroalgae, making the coral more equipped to handle microbial fluctuations caused by allelopathic compounds (Shearer *et al.* 2014) and disease-causing pathogens living within macroalgae (Sweet *et al.* 2013).

Furthermore, allelopathic compounds may alter coral physiology and decrease coral health by changing microbe abundance and diversity within the coral (Ritchie 2006; Smith *et al.* 2006; Morrow *et al.* 2011; Morrow *et al.* 2012). Under normal conditions, corals can regulate associated microbes though the release of antimicrobial compounds and enzymes (Krediet *et al.* 2013). Little is known about the relationship coral-associated microbes have with coral physiology, but it is believed to enhance coral pathogen

resistance, nutrient acquisition, and overall health (Krediet *et al.* 2013). An unregulated increase in coral-associated microbes can lead to the development of hypoxic areas and the accumulation of toxins (e.g., secondary metabolites) (Segel and Ducklow 1982; Smith *et al.* 2006; Barott *et al.* 2009). Exudates released by algae cause hypoxic areas to develop at the coral-macroalgal interface, leading to hypoxia-induced coral stress from the microbes consuming organic matter, which increases oxygen demand (Barott *et al.* 2009; Gregg *et al.* 2013; Haas *et al.* 2013). Eventually, weakened coral health can lead to microbial predation on coral tissue and triggering necrosis (Segel and Ducklow 1982; Smith *et al.* 2006; Barott *et al.* 2009). Allelopathic compounds also reduce beneficial microbe abundance, thus decreasing the ability of the coral to defend against invasive microbes. Coral-associated microbes release helpful antibiotics that aid in the battle against invasive microbes (Ritchie 2006). Additionally, when coral health is weakened, some macroalgal species serve as a source for coral disease, increasing the risk of infection. Several species of bacteria inhabiting the surface of macroalgae are associated to some bacteria found in coral disease (Sweet *et al.* 2013).

1.4.2 The Effect of macroalgae on Coral Recruitment

The persistence of phase-shift on coral reefs is credited to macroalgae having a negative effect on coral larvae recruitment (Kuffner *et al.* 2006). Coral sexual reproduction occurs annually, seasonally, or monthly in synchronous events, producing motile coral larvae (i.e., planulae) that eventually settle and metamorphose into a newly settled coral polyp (Richmond and Hunter 1990). The seasonality of coral reproduction also coincides with seasonal increase in several macroalgae species, leading to even higher inhibition of coral recruitment (Yniguez *et al.* 2015). The cause of the low coral recruitment can be attributed to either higher larval-mortality or low settlement due to macroalgal presence (Chong-Seng *et al.* 2014), therefore reducing the chances of phase-shift recovery (Graham *et al.* 2015).

The presence of macroalgae deters coral settlement either directly through competition (Tanner 1995) or indirectly by changing the chemical environment near the benthos (McCook *et al.* 2001). Coral larvae use complex physical and chemical cues to explore the water column and identify appropriate substrate for settlement and metamorphosis (Morse and Morse 1996). Physical cues are used to identify surface

microtopography of the substrate (Whalan *et al.* 2015). Larvae sense pressure depth (Raimondi and Morse 2000; Stake *et al.* 2003), irradiance levels (Mundy and Babcock 1998), salinity levels (Vermeij *et al.* 2006), respond to reef sounds (Vermeij *et al.* 2009), and are attracted to specific colors (Mason *et al.* 2011; Strader *et al.* 2015) to locate suitable substrate. Coral larvae respond to chemical cues that signal suitable substrate; for example, cues released from several species of CCA enhance larval settlement and trigger metamorphosis (Morse and Morse 1991). Macroalgal thalli physically prevent larvae from reaching the substrate (Tanner 1995) and chemically deter planulae through the release of allelopathic compounds (Kuffner *et al.* 2006; Birrell *et al.* 2008b), which change the benthic chemical cues.

Macroalgae increases mortality of recently settled coral polyps through physical abrasion and the chemical release of allelopathic compounds. Macroalgae affects the microbes on the surface of CCA, similar to the way it alters the coral-associated microbes inhabiting corals (Sneed *et al.* 2015). Some bacterial species isolated from the surface of CCA induce coral larvae settlement and play an important role in coral recruitment (Tebben *et al.* 2011). *Halimeda opuntia* and *Dictyota sp*. can shift the bacteria community associated with CCA, possibly affecting strains associated with inducing larval settlement (Sneed *et al.* 2015). Allelopathic compounds released by the Caribbean macroalgae species *Dictyota menstualis* (Kuffner *et al.* 2006), *Dictyota pinnatifida, Dictyota pulchella* (Kuffner *et al.* 2006; Paul *et al.* 2011*)* and *Lobophora variegata* (Kuffner *et al.* 2006) trigger planulae avoidance, thus reducing settlement. Planulae that settle next to macroalgae experience higher mortality through shading and abrasion (Tanner 1995; Box and Mumby 2007). Planulae may have evolved to recognize these harmful compounds, leading to an avoidance behavior. They can distinguish between a healthy and a macroalgae dominated reef (Birrell *et al.* 2008b), which may help explain why less planulae settle around specific algal species and why phase-shifted reefs experience lower coral recruitment (Chong-Seng *et al.* 2014). Phase-shift may reduce the abundance of settlement inducing compounds and increase the amount of allelopathic compounds, which ultimately contribute to macroalgal resilience on coral reefs.

1.5 Florida's Reefs

The Florida Reef Tract experienced coral decline as high as 43.9% in survey areas with 13.2% macroalgae coverage between 1984 to 1991 (Porter and Meier 1992). The northern part of the reef tract experiences seasonal changes in the macroalgal communities. From January to July, macroalgae shows growth when both light and temperature are more favorable. Maximum coverage reached 56.7% in July and dense algal mats covered many corals (Lirman and Biber 2000). During peak cover, more than 50% of coral colonies had their basal perimeter in contact with macroalgae (Lirman and Biber 2000). The high level of contact between corals and macroalgae in the Florida Reef Tract leads to decreased coral survival and growth (Lirman 2001).

Table 1. *Laurencia sp.* survey transects dates from Port Everglades inlet to Dade County line

Month	2005	2006	2007	2008	2009	2011
January			X			
February	X	X	X		X	X
March		X				
April		X	X			
May		X	X	X		
June		X	X			
July		X	X			
August	X	X	X	X		
September		X				
October		X				
November		X				

In the northern section of the Florida Reef Tract, Broward County, corals are at the northern limit of their range and are rarely the dominant reef species. Reef communities typically consist of Caribbean fauna, but vary in composition and density. Here, macroalgae can be seen occupying over half the benthic area (Moyer *et al.* 2003), representing a phase-shifted reef ecosystem. The two dominant genera observed on the Florida Reef Tract are *Halimeda* and *Dictyota*. During the summer, *Dictyota spp.* occupy up to 40% of the reef bottom and exhibits rapid growth and space occupation. *Stypopodium zonalae*, another macroalgae species, shows rapid growth and during blooms, occupies up to 25% of the reef bottom (Lirman and Biber 2000). Another common macroalgae observed in the Florida Reef Tract is *Laurencia spp*. The act of asexual fragmentation allows *Laurencia spp.* to become a dominant organism, especially in shallow habitats and under calm conditions. *Laurencia spp.* has a high fragmentation and reattachment rate, low rate of dispersal, and high post-reattachment survival (Herren *et al.* 2013). *Laurencia spp.* coverage was observed as high as 52% off Broward County. On occasion, average *Laurencia spp.* cover can fluctuate (0 to over 8%) between the nearshore hard-bottom of the Port Everglades inlet to the Miami-Dade County Line (Stacy Prekel, unpublished) (**Fig. 1**).

The Florida Reef Tract has a variety of coral species such as *Diploria strigosa*, *Porites astreoides*, *Orbicella annularis*, *Montastraea cavernosa*, and *Siderastrea siderea* (Moyer *et al.* 2003). The coexistence of corals and high macroalgal cover highlights the importance of identifying the effect phase-shift has on coral planulae.

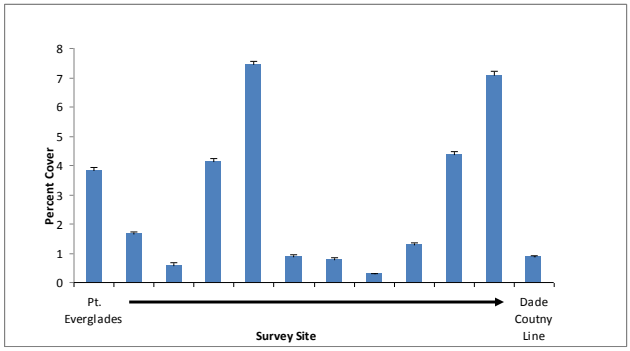

Figure 1. Average *Laurencia spp*. cover in twelve latitudinal transects off Broward County from 2005-2011. (From Port Everglades to Miami-Dade County line) (n=24 surveys per site. Table 1). Transects were conducted within 30m nearshore on hardbottom edge (Stacy Prekel, unpublished). Error bars represent standard error. Data was not collected in 2010.

Laurencia spp. cover was measured along 12 transects between the Port Everglades inlet and the Miami-Dade County line. These same transects were monitored during various months from 2005 to 2011 (**Table 1**), and the average coverage of all transects was 2.73% ± 0.01 SE. *Laurencia spp.* average cover per transect varied from 0.3% to 7.5% (**Fig. 1**) with no observable trends between transects. It should also be noted that all transects experienced some *Laurencia spp.* coverage during observations. Analyzing *Laurencia spp.* cover by month identifies seasonal fluctuations in percent coverage among the twelve transects (**Fig. 2**). There was a noticeable increase in coverage during the summer months and a decrease during the winter months (Stacy Prekel, unpublished). Many macroalgae species experience seasonal increase and decrease in abundance, affecting the spatial spread of benthic organisms (Yniguez *et al.* 2015). The average cover of *Laurencia spp.* in February was almost 3% and continued to rise during spring. The peak percent coverage occurred in May (6%) (Stacy Prekel, unpublished) where a significant decrease (F (10,282) =3.220, p<0.0001)

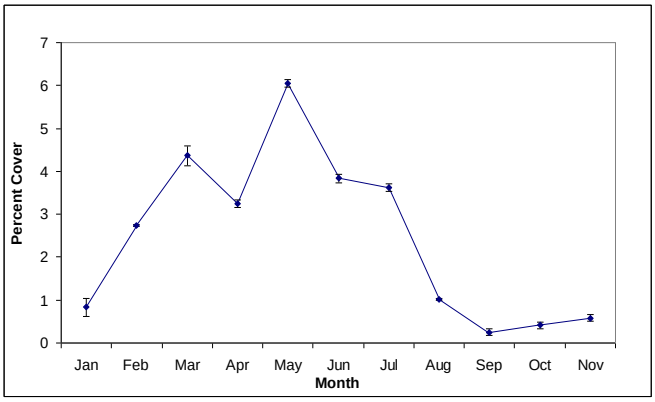

Figure 2. Average *Laurencia spp*. coverage of twelve transects collected from Port Everglades inlet to Dade County line from 2005-2011 divided by month (Stacy Prekel, unpublished). Error bars represent standard error. Data was not collected in the month of December or in the year 2010.

occurred during the months of August (1%), September (0.25%), and October (0.4%) when analyzed in a one-way ANOVA. From September to January, average *Laurencia spp.* coverage remained the same, never exceeding 1% cover. December was the only month that data collection did not occur over the six-year period (Stacy Prekel, unpublished). Overall macroalgal biomass and percent coverage increased from January to July, with a maximum cover greater than 50% and a minimum cover around 25% (Lirman and Biber 2000). Seasonal increases in macroalgal cover occur concurrently with the release of brooding coral *P. astreoides* (Chornesky and Peters 1987), signifying the highest chance of interaction between these seasonally variable macroalgae species and the brooding coral planulae.

1.6 Porites astreoides Reproduction

Porites astreoides is a hermaphroditic coral that release their larvae around the new moon between April and June with a peak in May (Chornesky and Peter 1987; McGuire 1998; Kuffner *et al.* 2006). Brooding corals fertilize their eggs internally and release fully viable competent planulae (Chornesky and Peters 1987). Planula release is associated with the lunar phase, with planulation occurring several days before and after the new moon, depending on water temperature (McGuire 1998). *Porites astreoides* are one of the most abundant coral on South Florida reefs (Chiappone and Sullivan 1996) as they have relatively high fecundity (Chornesky and Peters 1987; McGuire 1998), settle in high densities (Bak and Engel 1979) and planula settlement can occur within a few hours after release (Fadlallah 1983). The rapid growth rate and vigor aided in the increase of *P. astreoides* reef abundance over the past thirty years despite the overall decline in coral cover (Green *et al.* 2008).

1.7 Larval Chemoreception

Marine invertebrate larvae use sensory cells for chemoreception and for processing external metamorphic cues. In many marine invertebrates, the G-protein-coupled receptors (GPCR) facilitate metamorphosis by binding to specific cues in the environment and activating signal transduction pathways inside cells (Gerhart 1999). However, not all marine invertebrate metamorphosis is triggered by GPCR pathway. The coral *Montipora capitata* and *Pocillopora damicornis* larval metamorphosis were not triggered by this pathway (Tran and Hartfield 2012), but may be a factor in other coral

species due to differing receptors and signal pathways among species (Morse *et al.* 1988). Another difference between the larvae of coral species is sensory cell location. Most chemoreception for larval settlement is located on the aboral end of cnidarians (Vandermeulen 1975), however different coral species exhibit variation in the location of these sensory cells within the aboral end. *Montipora capitata* substratum sensory detection is located on the first quarter of the aboral end while *P. damicornis* is located on the second quarter (Tran and Hartfield 2013). Sensory receptor type and location most likely play an important role in why some corals have different responses to specific settlement cues, such as biofilms and crustose coralline algae (CCA).

Biofilms are defined as "matrix-enclosed bacterial populations' adherent to each other and/or to surface or interfaces" (Costerton *et al.* 1995). They provide a stable structure for bacteria to aggregate and function as a community (Costerton *et al.* 1995). Biofilm is a common settlement cue and substrate for many marine invertebrates (Hadfield 2011), and facilitates adhesion of larvae in the process of settling and development into juveniles (Zardus *et al.* 2008). Coral larvae use biofilm and their associated chemical compounds to identify appropriate substrate to settle upon (Sneed *et al.* 2014). Older and more seasoned biofilm increases coral settlement (Webster *et al.* 2004). Specific strains of bacteria associated with biofilms also enhance larval settlement, such as *Roseivivax sp.*, an abundant bacterial group found in the ocean (Sharp *et al.* 2015). Biofilm densities formed by different bacteria influences coral settlement (Tran and Hadfield 2012).

Furthermore, corals are not exclusively attracted to biofilm to identify appropriate substrate; it is most likely a combination of biofilm and CCA. CCA enhances settlement and induces metamorphosis in many coral species (Morse and Morse 1991; Harrington *et al.* 2004; Kitamura *et al.* 2007; Ritson-Williams *et al.* 2009; Price 2010) such as *Agaricia humilis* (Morse and Morse 1991) and *Acropora palmata* (Ritson-Williams *et al.* 2009). Coral larvae increase settlement in response to chemical extracts from certain species of CCA (Harrington *et al.* 2004; Ritson-Williams *et al.* 2009). The exact source of these chemical cues has not been identified, however some studies claim it is the bacteria associated with CCA (Johnson and Sutton 1994; Negri *et al.* 2001) while others identified the CCA tissue as the source (Tebben *et al.* 2015). Unlike allelopathic compounds released by macroalgae, CCA compounds do not cause hypoxic areas or alter coral-

associated microbes within the coral colony, giving CCA the dual benefit of enhancing settlement and not influencing survival (Barott *et al.* 2009; Gregg *et al.* 2013). However, not all CCA species enhance settlement and induce metamorphosis; some species are non-inductive and deter settlement (Morse and Morse 1996; Harrington *et al.* 2004) and eventually decrease post-settlement survival by shedding their surface cell layers to remove newly settled corals (Harrington *et al.* 2004). Additionally, different species of CCA trigger various levels of larval settlement in a variety of coral species (Harrington *et al.* 2004; Ritson-Williams *et al.* 2014).

1.8 Settlement Induction Compounds

Compounds inducing settlement and metamorphosis were identified in both biofilm and CCA. Two compounds, 11-deoxyfistularin-3 (bromotyrosine derivative) and carotenoid fucoxanthinol, isolated from coral rubble with CCA were found to increase coral larvae settlement and induce metamorphosis. Separately, these compounds enhance settlement and metamorphosis, but together their response has a synergistic effect on settlement and metamorphosis (Kitamura *et al.* 2007). Another compound, luminaolide, was isolated from CCA *Hydrolithon reinboldii* and enhanced coral planulae settlement and metamorphosis (Kitamura *et al.* 2009). Researchers have also isolated the compound tetrabromopyrrole (which acts as a metamorphic cue for coral larvae), from bacteria on the surface of the CCA, *Neogoniolithon fosliei* and *Hydrolithon onkodes* (Tebben *et al.* 2011), and from bacteria in a natural biofilm collected off coral reefs (Sneed *et al.* 2014).

1.9 Laurencia and CCA similarities

Compounds isolated from CCA and *Laurencia* are both water soluble and stable for approximately 12 months (Boettcher and Targett 1996). *Laurencia* (Mianmanus 1988) and CCA (Morse and Morse 1984) are both Rhodophytes possessing phycobiliproteins, which are red pigment proteins used during photosynthesis (Duysens 1952). Phycobiliproteins extracted from CCA elicit settlement and help initiate metamorphosis in marine invertebrates, such as the abalone *Haliotis rufescens* (Morse *et al.* 1979; Morse and Morse 1984). When *Strombus gigas* larvae are exposed to phycobiliproteins that are isolated from *Laurencia obtusa,* the larvae initiate metamorphosis earlier, but this does not lead to an overall increase in metamorphosis. The sea hare *Aplysia brasiliana* showed similar results when introduced to

phycobiliproteins; metamorphosis was initiated but did not reach completion (Mianmanus 1988).

Laurencia sp. enhances settlement and induces metamorphosis in a variety of marine invertebrates and several of these invertebrates respond to CCA as well (Boettcher and Targett 1996). *Laurencia obtusa*, *L. papillosa*, and *L. poitei* increase settlement and induce metamorphosis in *A. brasiliana* (Mianmanus 1988) and *S. gigas* (Mianmanus 1988; Davis 1994; Boettcher and Targett 1996). *Strombus gigas* also increases settlement and metamorphosis in the presence of CCA (Boettcher and Targett 1996). Various *Laurencia spp*. enhance larval settlement (Hernkind and Butler 1986; Butler *et al.* 1997) and metamorphosis (Hernkind and Butler 1986; Butler and Hernkind 1991; Butler *et al.* 1997) in the spiny lobster *Panuliris argus*. Some of these compounds isolated form *Laurencia sp.* trigger metamorphosis earlier in *P. argus* larvae than they would have in their absence (Goldstein and Butler 2009). *Laurencia spp.* also induces metamorphosis in echinoderms and mollusks (Boettcher and Targett 1998). The sea urchin, *Strongylocentrotus droebachiensis*, also responds to both CCA (Pearce and Scheibling 1990) and *Laurencia sp.* (Pearce and Scheibling 1994).

Considering that several marine invertebrates respond to *Laurencia* and CCA as a settlement enhancer, may indicate that they are releasing the same or similar chemical cues. However, this does not mean that all marine invertebrates use the same chemical compounds to induce larval settlement and metamorphosis. The CCA compounds that induce metamorphosis in gastropod larvae are different from those that induce *Agaricia* metamorphosis (Morse *et al.* 1988). The neurotransmitter, y-aminobutyric acid (GABA), is found in high concentrations in CCA species (Morse *et al.* 1979) and is a potent settlement and metamorphosis inducer for marine invertebrate larvae (Morse *et al.* 1979; Morse and Morse 1984). The *H. rufescens* (Morse *et al.* 1979) and *S. droebachiensis* (Pearce and Scheibling 1990) displayed a higher proportion of metamorphosis when exposed to GABA. Other invertebrates, such as *S. gigas* (Boettcher and Targett 1998) and *A. brasiliana* (Mianmanus 1988), also responded to GABA, but not as highly as when they were exposed to *Laurencia*. Alternatively, the coral larvae *Agaricia spp.* did not respond to GABA (Morse *et al.* 1988). Taken together, these two rhodophytes

probably release a variety of similar compounds that are species specific settlement cues for marine invertebrates.

Furthermore, coral larvae show a species-specific response to allelopathic compounds (Rasher *et al.* 2011). Coral larvae use chemoreception to identify allelopathic compounds from macroalgae and avoid settling (Kuffner *et al.* 2006). The variety of allelopathic compounds released may be greater than settlement inducers and metamorphosis cues found on the reef. Many of these compounds are polyphenolics, halogenated, phenols, and terpenoids and are used for anti-herbivory and defense mechanisms (Harlin and Rice 1987). The brown alga family Dictyotaceae shows a consistent trend in decreasing coral recruitment. This family is a unique order that is phylogenetically distinct from other brown algae families and includes the genus *Dictyota*, *Lobophora*, *Dictyopteris,* and *Padina* (Lee and Bae, 2002). The genus *Dictyota spp.* (Kuffner *et al.* 2006; Box and Mumby 2007; Diaz-Pulido *et al.* 2010; Paul *et al.* 2011; Olsen *et al.* 2015), *Lobophora sp.* (Kuffner *et al.* 2006; Box and Mumby 2007; Diaz-Pulido *et al.* 2010; Vieira *et al.* 2016), and *Padina sp.* (Birrell *et al*. 2008b) deter settlement and decrease survival in several coral species. The genus *Dictyopteris* and its effect on coral recruitment has not been studied, but *Dictyopteris delicatula* releases chemical compounds to deter herbivory and epiphytic growth similar to other Dictyotaceae species (Hay *et al.* 1988). This indicates a high probability that *Dictyopteris* will deter coral larval settlement and decrease survival.

1.10 Laurencia and Coral Larvae Settlement

The effect of *Laurencia* on coral settlement was only analyzed on the Pacific coral *Platygyra daedalea* (Diaz-Pulido *et al.* 2010). This study identified that *Laurencia intricata,* fleshy algae, and a plastic mimic all inhibited larval settlement, indicating that structure is deterring settlement, rather than the chemical cues from *L. intricata* (Diaz-Pulido *et al.* 2010). However, not all coral species respond the same to macroalga species. *Acropora millepora* larvae experienced higher settlement next to *Lobophora variegata* (Birrell *et al.* 2008b) while *P. astreoides* larvae were deterred (Kuffner *et al.* 2006). There is strong evidence of coral species-specific response to macroalgae (Kuffner *et al.* 2006; Birrell *et al.* 2008b; Diaz-Pulido *et al.* 2010; Denis *et al.* 2014; Olsen *et al.* 2016) and since it was the structure of *L. intricata* that deterred settlement, not the

chemical compounds, it is possible that other coral larvae would have a different response to *L. intricata*.

I hypothesize that *Laurencia* may enhance coral settlement and metamorphosis. *Laurencia* enhancing coral larvae settlement is most likely not an identifier of a suitable location for coral settlement, but instead a trait that both CCA and *Laurencia* share with a common ancestor that remained in the *Laurencia* lineage. Coral larvae may be drawn to the compounds because they are typically released from CCA, signifying a suitable reef substrate with limited macroalgal competition.

1.11 Significance

This is the first study to compare the effect of macroalgae *L. intricata* and a variety of brown macroalgae species in the family Dictyotaceae on *P. astreoides* larval swimming behavior, settlement, and post-settlement survival. If *L. intricata* promotes settlement and survival, this will be the first study to document it. Identifying how macroalgae affects coral behavior may provide insight into new coral reef management techniques.

1.12 Research Objectives

This study examined the effect of the macroalgal species *Laurencia intricata* and several species from the Dictyotaceae family on larval swimming behavior, settlement, and post-settlement survival of the scleractinian coral *Porites astreoides* by addressing the following questions:

1. **Does *L. intricata* and Dictyotaceae impact *P. astreoides* larval swimming behavior?**

   Planulae use chemical cues to identify suitable substrate to settle upon. Attractant cues elicit downward swimming and benthic probing while deterrent cues elicit an avoidance behavior that reduces coral recruitment.

2. **Does *L. intricata* influence *P. astreoides* settlement?**

Exposing coral larvae to different treatments will identify if the chemical cues or algal structure of *L. intricata* affects *P. astreoides* settlement. If settlement is induced, then a comparison to the plastic algal mimic will indicate if the structure or chemical cues are the likely mechanisms. The plastic algal mimic was used as it has the same structure as *L. intricata* but none of the chemical compounds.

3. **Does *L. intricata* have any latent effect on the post-settlement survival of *P. astreoides*?**

Laurencia intricata has a seasonal abundance on South Florida coral reefs. To identify if settling next to *L. intricata* has any lasting impacts on polyp survival after the macroalgal abundance decreases, polyp survival will be observed following the macroalgae removal.

4. **When given a choice of substrates, are *P. astreoides* larvae influenced by the presence of *L. intricata* and Dictyotaceae?**

Providing *P. astreoides* larvae a choice to settle between two macroalgae substrates will determine whether the chemical cues and structure of *L. intricata* and Dictyotaceae are enhancing or deterring coral settlement.

5. **Does *L. intricata* and Dictyotaceae influence the post-settlement survival of *P. astreoides*?**

Determining if *L. intricata* and Dictyotaceae affects newly settled coral post-settlement survival will be tested by exposing them to macroalgae for eight weeks. This will provide the final piece of evidence on how these two influence the early life history stages of *P. astreoides*.

CHAPTER 2

2.1 Introduction

Over the past few decades, the Greater Caribbean basin has suffered on average an 80% decline in scleractinian coral cover (Gardner *et al.* 2003; Bellwood *et al.* 2004). The Florida Keys have experienced some of the highest transitions from a coral to macroalgal dominated state, known as phase-or regime shift (Schutte *et al.* 2010). Coral reefs dominated by macroalgae experience lower juvenile coral density (Chong-Seng *et al.* 2014) by physically (Tanner 1995) or chemically (McCook *et al.* 2001) deterring coral settlement. Coral larvae use complex cues to explore the water column and identify appropriate substrate for settlement and metamorphosis (Morse and Morse 1996). Macroalgae physically prevents larvae from reaching the substrate (Tanner 1995; Kuffner *et al.* 2006) and chemically deters planulae through the release of allelopathic compounds near the benthos (Kuffner *et al.* 2006; Birrell *et al.* 2008b). Planulae that settle next to macroalgae experience higher mortality and more limited growth from shading, abrasion (Tanner 1995; Box and Mumby 2007), and the release of allelopathic chemicals (Kuffner *et al.* 2006; Box and Mumby 2007*;* Birrell *et al.* 2008b; Paul *et al.* 2011; Olsen *et al.* 2015). Low settlement and high coral mortality reduces the ability for a reef to recover from a phase-shift (Graham *et al.* 2015).

The effect of macroalgae on coral larvae depends on the family of macroalgae. The brown algae family Dictyotaceae has consistently shown a trend in reducing coral settlement and survival (Kuffner *et al.* 2006; Diaz-Pulido *et al.* 2010) by releasing allelopathic polyphenolic, phenols, and terpenoids compounds (Harlin and Rice 1987), while red algae, particularly crustose coralline algae (CCA), has facilitated coral recruitment (Morse *et al.* 1988; Morse and Morse 1996; Ritson-Williams *et al.* 2014) by releasing 11-deoxyfistularin-3, carotenoid fucoxanthinol (Kitamura *et al*. 2007), luminaolide (Kitamura *et al*. 2009) and tetrabromopyrrole (Tebben *et al*. 2011). Dictyotaceae is phylogenetically distinct from other brown algae families due to the unique presences of uniflagellate spermatozoids and meiosporangia different from other brown algae and supported by molecular analysis (Lee and Bae, 2002). Genera in this family, including *Dictyota spp.* (Kuffner *et al.* 2006; Box and Mumby 2007; Diaz-Pulido

et al. 2010; Paul *et al.* 2011; Olsen *et al.* 2015), *Lobophora sp.* (Kuffner *et al.* 2006; Box and Mumby 2007; Diaz-Pulido *et al.* 2010; Vieira *et al.* 2015), and *Padina sp.* (Birrell *et al*. 2008b), deter coral larval settlement and decrease coral survival. The genus *Dictyopteris* and its effect on coral recruitment has not been studied, but *Dictyopteris delicatula* releases chemical compounds to deter herbivory and epiphytic growth similar to other Dictyotaceae species (Hay *et al.* 1988), indicating it has the potential to deter coral settlement.

Contrary to brown algae, rhodophytes (red algae), such as the genus *Laurencia* and crustose coralline algae (CCA) are known to trigger settlement and induce metamorphosis in marine invertebrates (Morse *et al.* 1979; Boettcher and Targett 1996). The compounds released by these rhodophytes are water soluble and stable for 12 months (Boettcher and Targett 1996). Two compounds, 11-deoxyfistularin-3 (bromotyrosine derivative) and carotenoid fucoxanthinol, isolated from coral rubble with CCA, increase coral larvae settlement and induce metamorphosis (Kitamura *et al.* 2007). The compounds released by *Laurencia* trigger settlement in lobsters (Hernkind and Butler 1986; Butler and Hernkind 1991; Butler *et al.* 1997), conch (Boettcher and Targett 1996) and sea hares (Mianmanus 1988), but the effect on Caribbean coral larvae is unknown. However, it is possible that *Laurencia* may enhance coral recruitment. If it does, it is likely not because *Laurencia* indicate an appropriate substrate but rather a compound that persisted in the genus from a common ancestor of the algae. Alternatively, *Laurencia* just may not deter settlement because it does not release anti-herbivory, allelopathic compounds.

The larval response to macroalgae may depend on the coral species. *Laurencia intricata* decreased larval settlement in the Pacific coral, *Platygyra daedalea.* All fleshy algae, including the plastic algal mimic, deterred *P. daedalea* larval settlement. This suggests it was the structure of *L. intricata* that deterred settlement not allelopathic compounds (Diaz-Pulido *et al.* 2010). Other coral species may respond positively to the chemical cues released by *Laurencia* as not all coral species exhibit the same response to macroalgae. For example, *Padina sp.* (Dictyotaceae) did not impact *Acropora tenuis* larval settlement (Dixson *et al.* 2014) but decreased settlement in *Acropora millepora* larvae by 30% (Birrell *et al*. 2008b). *Acropora millepora* larvae experienced higher

settlement when exposed to *Lobophora variegata* (Birrell *et al.* 2008b) while *P. astreoides* larvae were deterred by the macroalgae (Kuffner *et al.* 2006). Even settling on the macroalgal surface varies between species; *Acropora palmata* did not settle on *Halimeda opuntia,* but *P. astreoides* experienced a 10% settlement on the algae (Olsen *et al.* 2016).

The variability in coral larval response to different macroalgae (Jompa and McCook 2003) suggests the type of macroalgae on a phase-shifted reef might be as important as algal cover. High Dictyotaceae abundance on a coral reef would negatively impact more coral species than a *Laurencia* dominated reef, further contributing to the macroalgal phase-shift and coral degradation. Our controlled, manipulative experiments tested the effect of *L. intricata* and Dictyotaceae on *P. astreoides* planulae swimming behavior, settlement preference, and post-settlement survival. I hypothesize that *Laurencia* may enhance while Dictyotaceae may decrease coral settlement, metamorphosis, and survival. My research was conducted in the Florida Keys. This was an ideal location to investigate the coral-macroalgae interaction because of the decline in coral cover and the prevalence of macroalgae. This will be the first study to compare the effect of rhodophytes and phaeophytes on coral larval swimming behavior, settlement, and post-settlement survival.

2.2 Methods

2.2.1 Study site

I examined the effect of *Laurencia intricata* on *Porites astreoides* larvae swimming behavior, settlement, and post-settlement survival. This coral species was chosen for its abundance on Florida's reefs and its ease of obtaining larvae. The experiments were conducted at Mote Marine Tropical Research Laboratory (Mote TRL, Summerland Key, FL, USA) May 27-29, 2014, June 24-29, 2014, and April 17-21, 2015 and at Keys Marine Laboratory (KML, Long Key, FL, USA) May 16-20, 2015. I conducted this study in the Florida Keys due to its recent phase-shift from a scleractinian dominated ecosystem to a high macroalgal abundance (Schutte *et al.* 2010) making it ideal for investigating coral-macroalgae interaction.

2.2.2 Collection of Porites astreoides

Seasonal increase in macroalgae coverage occurs simultaneously with the larval release by the coral *P. astreoides* (McGuire 1998), maximizing the chance of interaction between macroalgae and planulae. *Porites astreoides* produce planulae year round; however, they do show some seasonal preference (Chornesky and Peters 1987). Planula release is associated with the new moon between April and June with a peak in May (Chornesky and Peter 1987; Kuffner *et al.* 2006). Collection of *P. astreoides* coral colonies occurred a few days before the new moon. On May 27, 2014 (n=31) and April 17, 2015 (n= 25) coral colonies were collected from Wonderland Reef (24°33.62´N, 81°30.08´W) off Summerland Key, FL. On June 25, 2014, 50 coral colonies were collected from Birthday Reef (24°34.74´N, 81°29.84´W) off Summerland Key, FL. Finally, on May 16, 2015, at KML, 50 colonies of *P. astreoides* were collected at Bridge Rubble #4 and #2 (24°44.023' N, 80°49.770' W). Colonies of *P. astreoides* were collected by chiseling the colony off the substrate with a diameter no larger than 12 cm and then bubble wrapped, moistened with seawater and placed into a cooler for transportation to the research facility. At the facility, corals were maintained in running seawater raceways.

Planulae collection for coral larvae followed the methods described in Kuffner *et al.* (2006). After collection, the colonies were placed into mixing bowls and individually supplied with continuously running seawater. In the mixing bowls, the water flowed over the depressed handle and into a tri-pour beaker fitted with 180 µm Nitex bottom. The Nitex bottom was supported by 1.5 cm diameter PVC 2 cm off the tank bottom. The water level in the collection tank was kept at 15 cm to allow the planulae room to swim but remained in the collection cups. When planulae are released, they travel over the depressed handle and are retained in the Nitex collection cup. At sunrise, larvae were pooled into one container and subsampled for each experiment. Depending on the study, 10-50 larvae were placed into experimental vials for each replicate. Upon completion of planulae collection, healthy colonies were returned to the collection site, and attached with Z-spar A-788 Splash Zone underwater epoxy.

2.2.3 Macroalgae collection

All *Laurencia intricata* and Dictyotaceae species were collected from reefs in Broward County, Florida one to two days before the first experiment. Algal clumps were examined under a dissecting microscope and any foreign organisms or other species of algae were removed. Afterwards, they were maintained in outside tanks before transport to the Florida Keys research facilities for experimentation. *Laurencia intricata* and Dictyotaceae vouchers were placed into 70% ethanol for taxonomic confirmation. *Laurencia intricata* taxonomic identification was confirmed by Dr. Ligia Collado-Vides (FIU), and Dictyotaceae vouchers were identified down to species by Dr. Ana Tronholm (FIU).

Collection of macroalgae occurred in Broward County since macroalgae was easily accessible offshore. The reef communities in Broward County and the Florida Keys exhibited higher macroalgal cover than coral cover (Moyer *et al.* 2003; Beaver *et al.* 2006). In both regions, the macroalgal abundance remains stable over time with seasonal fluctuations, and *Halimeda* and *Dictyota* are the most abundant macroalgae genera (Lirman and Biber 2000; Yniguez *et al.* 2015). The similarity between these regions indicate that macroalgae collected from one area would be similar to the other.

2.2.4 Settlement tile conditioning

Aragonite settlement tiles were used in May 2014, June 2014, April 2015, and May 2015 settlement chambers and in May 2015 larval settlement preference experiments. Ceramic settlement tiles were used in June 2014 and April 2015 larval settlement preference experiments. All settlement tiles were preconditioned on Broward County reefs for at least four weeks to allow a biofilm and CCA to colonize the tile before experimentation. Tiles were maintained in running seawater prior to experimentation and transportation to TRL and KML. Plastic algal mimics, plastic chamber, plastic containers, and vinyl barriers were soaked for at least 24 h prior to experimentation to allow for potentially harmful compounds to leach out.

2.2.5 Experiment 1: Does L. intricata and Dictyotaceae impact P. astreoides larval swimming behavior?

To determine if planulae swimming behavior is altered in the presence of *Laurencia intricata*, a modified version of Gleason *et al.* (2009) experiment was used to observe swimming behavior in response to different algal treatments. Four 500 ml graduated cylinders were filled with 0.2 µm filtered seawater. Ten larvae were added to each graduated cylinder and allowed a 10 min acclimation period before initial data recording. If the larvae were swimming near the treatment, it was deemed a positive response. A negative or neutral response occurred when larvae were distributed evenly throughout the water column. The proportion of larvae observed within the bottom 20% of the graduated cylinder (i.e., showing a positive response to the treatment) was compared among treatments. Experiments conducted in June of 2014, consisted of placing nothing (a blank control), plastic algal mimic, *Laurencia intricata*, or *Dictyota pfaffii-humifusa* complex under a false mesh bottom (180 µm) to prevent contact with algae and avoid losing sight of larvae, but also to allow the dispersal of any chemical cues that may influence behavior. The algal mimic was used for comparison against the control treatment to determine if toxins were released or if larval settlement may be affected in other experiments. *Dictyota pfaffii-humifusa* complex was used as a negative control to compare how larvae responded to deterrent compounds. After the 10 min acclimation period, larval depth was recorded and subsequently every 20 min for 60 min. The four treatments acclimation periods were staggered 5 min apart to allow behavioral observation within the 20 min intervals. The treatments were then replaced with new algae, water, and larvae before another replicate was started. The cylinders were rotated to randomize any biases associated with the cylinders. There was a total of seven replicates during June.

In April, 2015, five treatments were used: a control, a plastic algal mimic, *Laurencia intricata*, an unidentified CCA, and *Dictyopteris justii*. CCA is a known larval attractant and settlement cue and was added to provide a positive cue for comparison. Due to misidentification, *D. justii* was used in place of *D. pfaffii-humifusa* during these trials. Instead of a 20 min interval between treatment observations, it was increased to a 25 min interval to account for the addition of the CCA treatment. This allowed the

acclimation periods to remain staggered every 5 min among the five treatments. There was a total of five replicates in April due to the limited availability of larvae.

2.2.6 Statistical Analysis

A repeated measures ANOVA was used to analyze the proportion of coral larvae swimming within the bottom 20% of the graduated cylinder (i.e., demonstrating a positive response to the treatment). *Porites astreoides* released larvae on multiple sequential days and larval swimming behavior was compared by date, the combination of treatment and date, the combination of time interval and date, and the combination of treatment, time interval, and date. If no significant difference was observed in larval swimming behavior across the combination of treatment, time interval, and date, then swimming behavior was combined by date and compared by the full factorial of treatment and time interval. If no significant difference was observed in larval behavior across different time intervals, and there was no difference between the interaction of time and treatment, the larval response was pooled across time periods and the average proportion of larvae exploring the bottom 20% of the cylinder was compared against algal treatments using a one-way ANOVA.

Dictyota pfaffii-humifusa was used in June 2014 and *D. justii* was used in April, 2015. These two-different species were combined and referred to by their family name, Dictyotaceae. Three other genera in this family are known as coral settlement deterrents, *Dictyota* (Kuffner *et al.* 2006; Box and Mumby 2007; Diaz-Pulido *et al.* 2010; Paul *et al.* 2011; Olsen *et al.* 2015), *Lobophora* (Kuffner *et al.* 2006; Box and Mumby 2007; Diaz-Pulido *et al.* 2010; Vieira *et al.* 2016), and *Padina* (Birrell *et al.* 2008b). Additionally, *Dictyopteris* releases chemical defenses in order to deter herbivory and epiphytic growth, similar too other Dictyotaceae species (Hay *et al.* 1988).

A repeated measures ANOVA was used to compare the proportion of coral larvae swimming at the bottom 20% of the cylinder, by year, treatment x year, time x year, and treatment x time x year interaction. If no significant difference was observed between these interactions, the larval swimming behaviors observed by year was combined. If there were significant differences between groups, subgroup means were compared using post-hoc Tukey-Kramer HSD test. Data that did not adhere to parametric assumptions

were arcsine square-root transformed. All statistical analyses were conducted in JMP 12.0 software.

2.2.7 Experiment 2 Does L. intricata influence P. astreoides settlement?

Planulae settlement was quantified in the presence of *Laurencia intricata*, a blank tile as a control, and a plastic algal mimic that resembled the size, shape, and morphology of *Laurencia intricata* in the absence of chemical compounds. Plastic chambers with Nitex sides were placed on the reef (**Fig. 3**) to test larval settlement preference under more natural conditions (modified from Kuffner *et al.* 2006). The chamber acrylic was 6.4 mm thick to allow solar irradiance with a diameter 10.8 cm and 20.3 cm long. The sides of the chamber were covered by 180 µm mesh Nitex to allow water flow but prevent larvae from escaping. Forty planulae were placed inside the larval chamber containing an aragonite tile with *Laurencia intricata*, an algal mimic, or a blank control. Each treatment was attached with a beaded zip-tie including the control. The circular shape of the larval chamber prevented the tile from sitting flat, but allowed larvae to access all sides of the tile. The three treatment chambers were anchored to rubber mats in a randomized order. Each mat was weighed down with 1.36 kg lead weights and placed 1.5 m apart from each other, and situated parallel to the prevailing current. A total of nine treatment chamber mat replicates were placed in a hard bottom and sparse seagrass community off Summerland Key, Florida at Mote Marine Laboratory at 1 to 1.5 m depth on May 28, 2014 and June 26, 2014. The following year, five treatment chamber mats were placed on the hard bottom in the same location off Summerland Key, FL on April 18, 2015 and May 17, 2015. The larval chambers were left on the hard bottom and sparse seagrass community for 36 h before being analyzed. The number of larvae

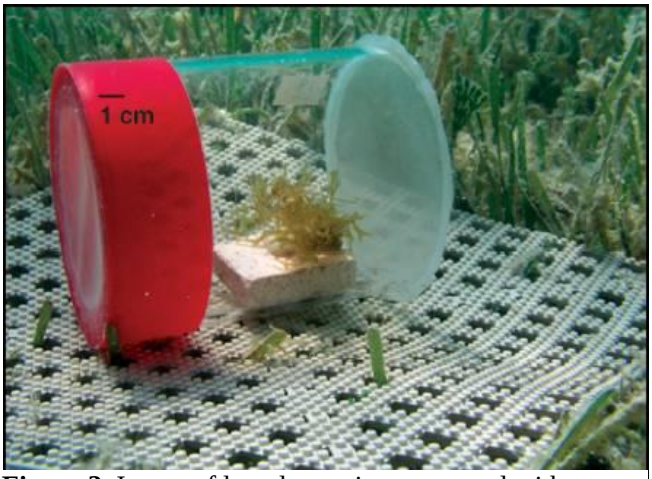

Figure 3. Image of larval containment vessel with macroalgae attached to a ceramic tile connected to a bathmat (Kuffner *et al.* 2006).

swimming, metamorphosed in the water column, settled on chamber/lid, algae/mimic/zip-tie, and settled on the top/bottom/side of the tile were quantified.

2.2.8 Statistical analysis

To determine *L. intricata's* effect on coral larvae settlement, I used a one-way ANOVA to analyze the proportion of coral larvae total settlement (top, side, and bottom of the tile) and to compare across tile treatment, date, and treatment x date interaction. If no significant difference was observed between the interaction of treatment x date, then all treatments by date were combined and analyzed using a one-way ANOVA. A two-way ANOVA was also used to identify the difference in proportion of larvae swimming and metamorphosed in the water column by treatment, date, and treatment x date interaction. To identify if the treatment affected top over bottom settlement, I used a one-way ANOVA to compare top and bottom settlement by treatment. Data that did not adhere to parametric assumptions were transformed into an arcsine square root function prior to analysis. Data that did not meet these assumptions were analyzed in a Wilcoxon non-parametric test. All significantly different results were analyzed with a post-hoc Tukey HSD test to identify significant differences between groups. All statistical analysis was conducted in JMP 12.0 software.

2.2.9 Experiment 3: Does L. intricata have any latent effect on the post-settlement survival of P. astreoides?

After scoring settlement on the reef chamber tiles in May 28, 2014, June 26, 2014, April 18, 2015, and May 17, 2015, *L. intricata* and the plastic algal mimic clumps were removed from each tile and any latent effects on post-settlement survival were reached for each treatment. Latent effects are any impacts on newly settled coral health and survival that occur after *L. intricata* is removed. The tiles were transported in

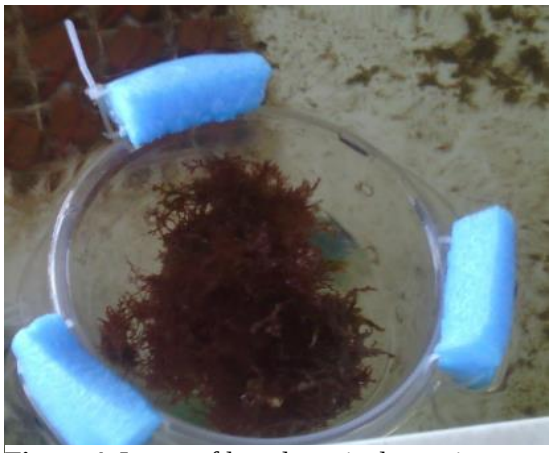

Figure 4. Image of larval survival containment chamber with macroalgae on top of a settlement tile for long-term survival. Treatments were removed for latent survival analysis

seawater from the Florida Keys to Nova Southeastern University Oceanographic Center in a cooler. On May 30, 2014 and June 28, 2014 tiles were placed into 118 ml volume plastic containers with pierced sides to allow water exchange. These containers were set on the bottom of an outside raceway and frequently flipped leading to subsequent mixing of settlement tile. This resulted in a low sample size. In 2015, modifications were made to the containers holding the settlement tiles. These modifications included adding a flotation device to the rim of the container and adding holes on bottom (**Fig. 4**). The containers were scored every week for five weeks to determine potential latent effects.

2.2.10 Statistical analysis

To test any latent effects of macroalgae on coral polyp survival, I used a Kaplan-Meier survival curve for analysis. A Mantel-Haenszel (log rank) test was then used to determine if the survival curves were significantly different between treatments. All statistical analysis was conducted in JMP 12.0 software.

2.2.11 Experiment 4: When given a choice of substrates, are P. astreoides larvae influenced by the presence of L. intricata and Dictyotaceae?

This experiment determined if coral planulae prefer to settle near L*aurencia intricata* or on a control tile (either an algal mimic or a settlement tile without structure) and *Dictyopteris delicatula*. Giving larvae a choice to settle between two different treatments revealed if *Laurencia intricata* increases coral settlement and if *Dictyopteris* deters settlement. Choice chambers were made of plastic 1.89 L containers with the sides replaced with 180 µm Nitex mesh and foam attached around the top edges for flotation **(Fig. 5)**. Two different treatments were attached to preconditioned tiles and added to opposite ends of the chamber. In June 2014,

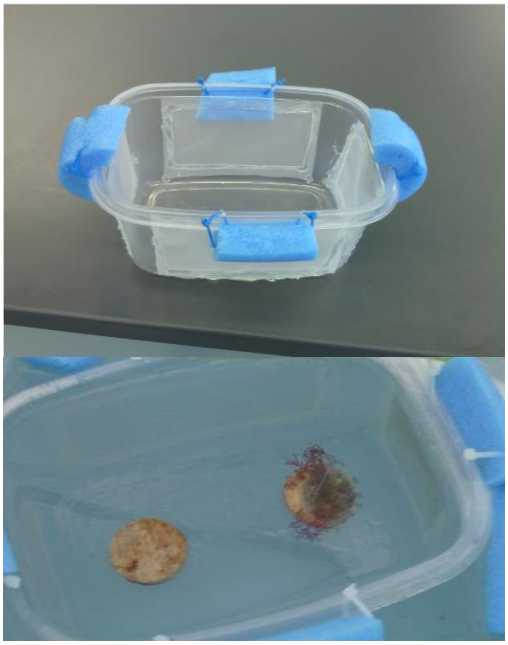

Figure 5. Image of choice experiment containment apparatus with sides fitted with 180 µm Nitex mesh and flotation device

there were three possible pairing combinations between a blank control, plastic algal mimic, and a clump of *Laurencia intricata* treatment. A total of ten replicates of each container combination were used, totaling thirty chambers. In April 2015, a fourth treatment was added, *Dictyopteris justii*. Each treatment, a blank control, plastic algal mimic, *Laurencia intricata,* and *Dictyopteris justii,* was attached to a preconditioned ceramic settlement tile, totaling six possible pairing combinations. Each combination had seven replicates totaling forty-two containers. The final experiment occurred on May 17, 2015 at Keys Marine Lab and used the following treatments attached to a preconditioned aragonite settlement tile, a blank control, a plastic algal mimic, *Laurencia intricata,* and *Dictyopteris delicatula*. Aragonite tiles were used instead of ceramic tiles, due to limited availability of preconditioned tiles. There were five replicates for each of the six possible combinations totaling thirty containers. Fifty *P. astreoides* larvae were added to each chamber and kept in outside raceways for 72 h before scoring. The number of larvae free swimming, metamorphosed in the water column, settled on chamber, algae/mimic/zip-tie, and settled on the top/bottom/side of the tile was quantified.

2.2.12 Statistical analysis

A frequency analysis was used to examine settlement on the tile and on other surfaces between the two choices. I performed a frequency analysis on top, side, and bottom settlement of the paired tiles in each choice container to identify any treatment effect on settlement distribution. Following the frequency analysis, the proportion of larvae settled on each treatment tile was averaged and compared using a one-way ANOVA. If there was not a significant difference in larval settlement observed among choice containers, tile settlement by treatment were then averaged and compared in a one-way ANOVA. Finally, settlement was compared within a treatment among choice containers using a one-way ANOVA. Data that did not adhere to parametric assumptions were transformed into an arcsine square root function prior to analysis. All significantly different results were analyzed with a post-hoc Tukey HSD test to identify significant differences between groups. All statistical analysis was conducted in JMP 12.0 software.

2.2.13 Experiment 5: Does L. intricata and Dictyotaceae influence the post-settlement survival of P. astreoides?

After scoring settlement preference, the same tiles were transported to Nova Southeastern University on June 29, 2014 and May 20, 2015 and placed into individual floating containers with respective treatments placed on top of the tiles (**Fig. 4**). Recruit survival was recorded every seven days for eight weeks. During polyp survival scoring, containers were scrubbed to remove accumulated cyanobacteria, and fouling algal treatments were replaced with newly collected specimens every 7-14 days. In July 13, 2014, three flotation chambers flipped over mixing the treatments, halting observation of those three tiles.

2.2.14 Statistical analysis

To analyze the long-term effects of macroalgae on coral polyp survival, I used a Kaplan-Meier survival curve. A Mantel-Haenszel (log rank) test was then used to determine if the survival curves were significantly different between treatments. All statistical analysis was conducted in JMP 12.0 software.

2.3 Results

2.3.1 Experiment 1: Does L. intricata and Dictyotaceae impact P. astreoides larval swimming behavior?

During June 26-29, 2014, behavior trials consisted of control, mimic, *L. intricata*, and *Dictyota pfaffii-humifusa* complex treatments. The proportion of larvae swimming at the bottom 20% of the cylinder was significantly different by date ($F(3,20)=30.254$, $p=0.001$) but not by the interaction of treatment and date ($F(9,20)=1.240$, $p>0.05$), the interaction between time interval and date($F(9,60)=1.541$, $p>0.05$), or the interaction between treatment, time interval, and date($F(27,60)=0.885$, $p>0.05$). Then, pooling larval swimming behavior trials conducted between 26th through 29th were compared by treatment. The proportion of larvae in the bottom 20% of the graduated cylinder was not significantly different across time (F (3,96) =1.34, p=0.2688), treatment (F (3,32) =1.83, p=0.1435) or the interaction between time and treatment (F (9,96) =1.06, p=0.2351) (**Fig. 6**). However, when pooling observations across time intervals, a significant difference in

larval swimming behavior was seen among treatments. Coral larvae distribution had a significantly higher proportion on the bottom 20% of the cylinder in *L. intricata* treatment compared to the other three treatments ($F(3,140)=6.419$, p=0.001) (**Fig.7**). The planulae may be attracted to the chemical cues released by *L. intricata* causing a higher proportion of coral larvae on the bottom.

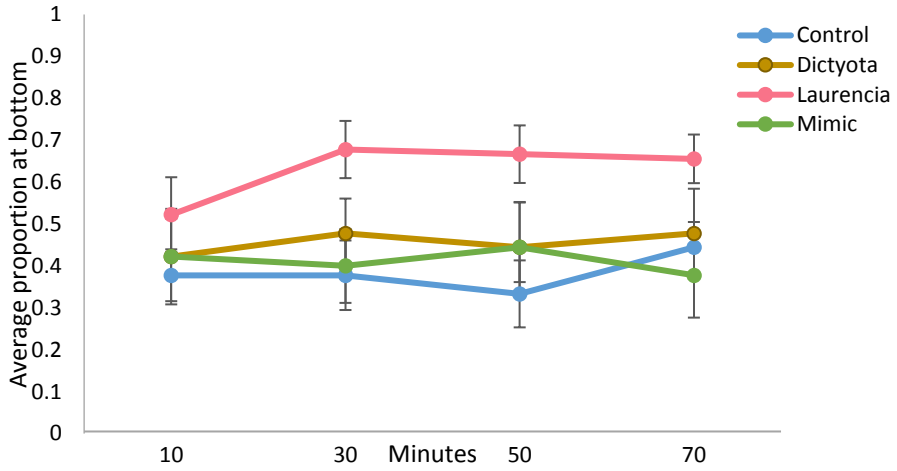

Figure 6. Behavior Experiment 1. Test the hypothesis that *L. intricata* affects coral larval swimming behavior June 26-29, 2014, showing mean (± SE) proportion of larvae at the bottom 120ml of the graduated cylinder (n=7). Larvae were added at time zero and given a 10-minute acclimation period before behavior was recorded every 20 minutes. Larvae responded to *Laurencia* the same as the control, *Dictyota*, and mimic.

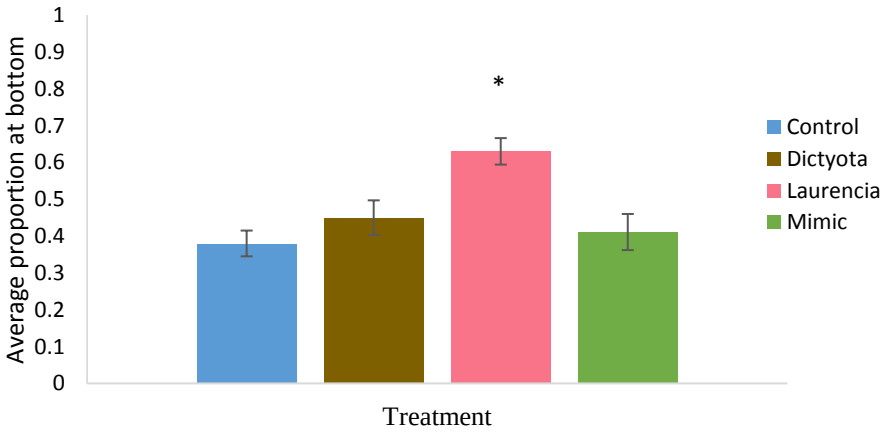

Figure 7. Behavior Expt 1. Test the hypothesis that *L. intricata* affects coral larval swimming behavior June 26-29, 2014, showing mean (±SE) proportion of larvae at the bottom 120ml of the graduated cylinder (n=28). Bars were calculated by treating average value across time periods for each replicate tube as a single data point (* represent significant difference, p-value<0.0001). Larvae were attracted to *Laurencia* over the control, mimic, and *Dictyota*

Table 2. April 19-20, 2015 behavior analysis, Repeated Measures ANOVA of effect on larval swimming behavior by treatment over time ($p<0.05$ is significantly different)

Source	d.f.	SS	***F***	***P***
Treatment	4	12.61	16.26	**<.0001**
Time recorded	3	0.122	0.848	0.473
*Treatment*Time recorded*	12	0.648	0.946	0.510

To discover if larval swimming behavior cue observed from the *L. intricata* treatment was similar to CCA, an unidentified CCA was added in April 19-20, 2015. Additionally, the *Dictyota pfaffii-humifusa* treatment was replaced with *Dictyopteris justii* due to the difficulty in distinguishing between *Dictyota* and *Dictyopteris* species (vouchers of these species were later identified by expert Dr. Ana Tronholm at FIU). First, the two larval swimming behavior dates were compared and similar to June 26-29, 2014, there was a significant difference in the proportion of larvae swimming at the bottom 20% of the cylinder ($F(1,58)=45.978$, $p=0.001$). The interaction between treatment and date also had a significant difference ($F(4,55)=4.658$, $p=0.003$), but not the interaction of time interval and date ($F(3,44)=0.465$, $p>0.05$), or the interaction of treatment, time interval, and date ($F(12,43)=1.081$, $p>0.05$). Combining the observations recorded, the proportion of larvae observed at the bottom 20% of the cylinder was significantly different among treatments ($p=0.001$, **Table 2**). The *Dictyopteris*, unidentified CCA, and *Laurencia* treatment had significantly higher proportion of larvae on the bottom 20% of the cylinder than the control and mimic across time intervals (**Fig. 8**). There were no significant differences between the time intervals recorded and between the interaction of treatment and time intervals recorded ($p>0.05$, **Table 2**). Combining treatments across different time intervals yielded significant differences in mean larvae on the bottom 20% of the cylinder. The treatments with *Dictyopteris*, CCA, and *Laurencia* displayed significantly higher proportion of coral larvae on the bottom 20% of the cylinder compared to the control and mimic treatments ($F(4,95) =32.154$, $p=0.001$) (**Fig. 9**).

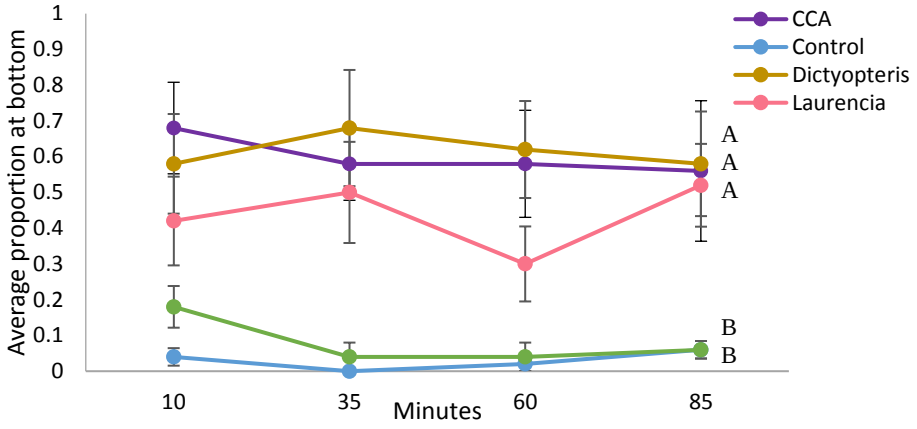

Figure 8. Behavior Expt 1. Test the hypothesis that *L. intricata* affects coral larval swimming behavior April 19-20, 2015, showing mean (±SE) proportion of larvae at the bottom 120ml of the graduated cylinder (n=5). Larvae were added at time zero and given a 10-minute acclimation period before behavior was recorded every 25 minutes (different letters represent significant difference, p-value<0.0001). Larvae were attracted to *Laurencia*, CCA, and *Dictyopteris* over the control and mimic.

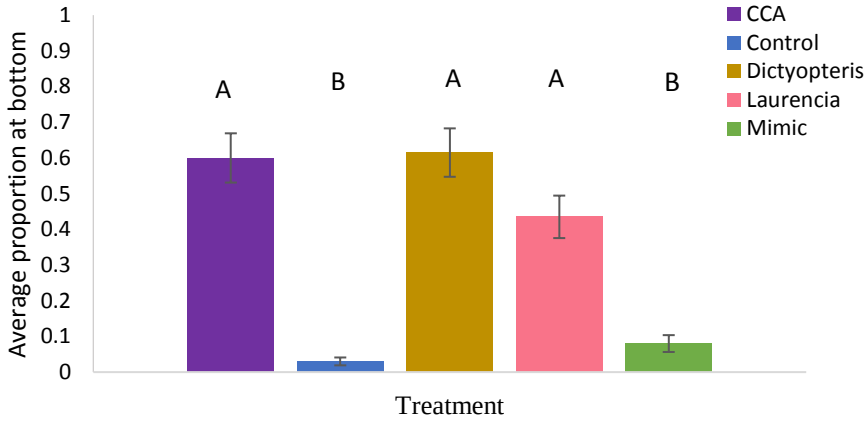

Figure 9. Behavior Expt 1. Test the hypothesis that *L. intricata* affects coral larval swimming behavior April 19-20, 2015, showing mean (±SE) proportion of larvae at the bottom 120ml of the graduated cylinder (n=20). Bars were calculated by treating average value across time periods for each replicate tube as a single data point (different letters represent significant difference, p-value<0.0001). Larvae are attracted to CCA, *Laurencia*, and *Dictyopteris* over the control and mimic.

To identify differences between June 2014 and April 2015 larval swimming behavior, the proportion of larvae at the bottom 20% of the cylinder were compared. The interaction of time intervals and year ($F(3,156)=1.420$, $p=0.239$), the interaction of treatment and year ($F(3,51)=1.655$, $p=0.188$), and the interaction of time intervals, treatment, and year ($F(9,156)=0.756$, $p=0.657$) were not significantly different from each other. June 2014 had a significantly higher proportion of larvae on the bottom when compared to April 2015 ($F(1,51)=8.215$, $p=0.006$). Although June 2014 and April 2015

were significantly different, I was interested in trends across various larval batches, therefore they were combined.

Each day corals released a new batch of larvae that were used to record larval swimming behavior. To determine if there were any differences in larval swimming behavior between the days recorded from June 26-29, 2014, the proportion of larvae at the bottom. The result indicated that a higher proportion of larvae explored the bottom 20% of the cylinder on the 29th when compared to the 26th and 27th (F (3,32) =18.60, p<0.001). The same behavior occurred from April 19-20, 2015, with a higher proportion of larvae exploring the bottom 20% of the cylinder on the 19th compared to the larvae on the 20th (F (1, 23) =27.13, p<0.001). These results suggest that larval swimming behavior varies depending on batch of larvae. It is possible that fewer colonies releasing planulae as larval collection goes on, leading to a higher proportion of larvae from one colony that may show preference towards a downward swimming behavior.

Table 3. June 26-29, 2014 and April 19-20, 2015 behavior. *Dictyota* and *Dictyopteris* treatment combined into Dictyotaceae treatment for analysis. Repeated Measures ANOVA of effect on larval swimming behavior by treatment over time (p<0.05 is significantly different)

Source	d.f.	SS	***F***	***P***
Treatment	3	17.11	5.225	**0.003**
Time recorded	3	0.211	0.873	0.457
*Treatment*Time recorded*	9	0.396	1.640	0.108

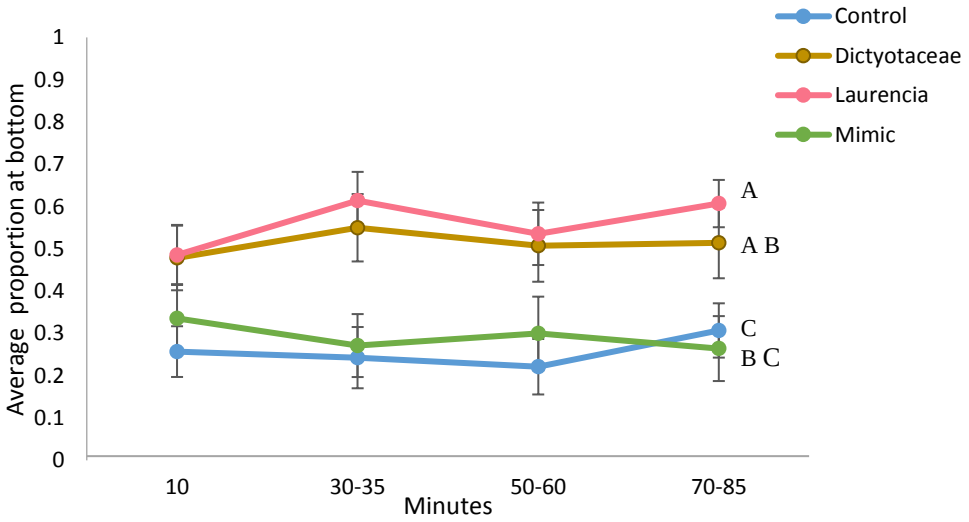

Figure 10. Behavior Expt 1. Test the hypothesis that *L. intricata* affects coral larval swimming behavior combined June 26-29, 2014 and April 19-20, 2015, showing mean (±SE) proportion of larvae at the bottom 120ml of the graduated cylinder (n=12). Larvae were added at time zero and given a 10-minute acclimation period before behavior was recorded every 20-25 minutes (different letters represent significant difference)

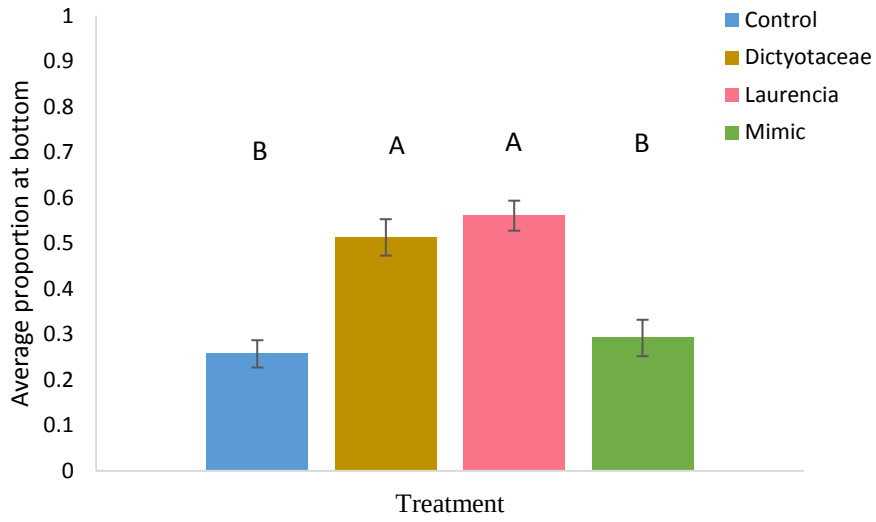

Figure 11. Behavior Expt 1. Test the hypothesis that *L. intricata* affects coral larval swimming behavior June 26-29, 2014 and April 19-20, 2015 combined, showing mean (±SE) proportion of larvae at the bottom 120ml of the graduated cylinder (n=48). Bars were calculated by treating average value across time periods for each replicate tube as a single data point (different letters represent significant difference, p-value<0.0001). Larvae were attracted to *Laurencia,* and *Dictyotaceae* over the control and mimic

Combining June 2014 and April 2015 larval swimming behavior for the control, mimic, *Laurencia,* and the two brown algae, Dictyotaceae, yielded a significant difference between treatments (p=0.003, **Table 3**). My results found *Laurencia* had a higher proportion of larvae on the bottom 20% of the cylinder compared to the mimic and control treatments, but was not significantly different from the Dictyotaceae (**Fig. 10**). These findings are consistent with the hypothesis that coral larvae respond to compounds associated with reefs regardless if they are attractants or deterrents to coral recruitment. There were no significant differences across time, and the interaction of time and treatment was also not significantly different (p>0.05, **Table 3**). After averaging the proportion of coral larvae on the bottom 20% among the different time intervals, a significantly higher proportion of larvae were on the bottom for *Laurencia* and Dictyotaceae when compared to the control and mimic treatments ($F(3,220)= 17.742$, p=0.001) (**Fig. 11**) . This clearly shows that *L. intricata* and Dictyotaceae algae cause a higher proportion of larvae to initiate the downward swimming cue compared to coral larvae that are exposed to an absence of chemical cues seen in the control and mimic treatments.

2.3.2 Experiment 2: Does L. intricata influence P. astreoides settlement?

Reef chambers were placed into the field to expose coral larvae to natural environmental cues while observing their settlement response to *L. intricata*. Chambers were deployed in May 28, 2014, June 26, 2014, April 18, 2015, and May 17, 2015. Settlement by date among different treatments was not significantly different for total ($F(6,72)=0.586$, $p>0.05$), top ($F(6,72)=0.429$, $p>0.05$), side ($F(6,72)=0.610$, $p>0.05$), and bottom ($F(6,72)=0.086$, $p>0.05$) of the tile settlement. This allowed the reef chambers deployed on different dates to be combined for statistical analysis.

To observe if different dates chambers were deployed caused more larvae to remain swimming or metamorphosed in the water column, the proportion of larvae still swimming was compared by the interaction of date and treatment. Larvae swimming by treatment between dates was not significantly different ($F(6,72)=0.377$, $p>0.05$). Analysis of the proportion of larvae metamorphosed in the water column influenced by date suggests there was a significant difference between date and the proportion of metamorphosed larvae in the water column ($F(3,72)=6.115$, $p=0.001$). To determine if there was a difference in the proportion of metamorphosed larvae in the water column varied by date and treatment, the interaction of date and treatment were compared. The proportion of larvae metamorphosed in the water column was not significantly different by date and treatment ($F(6,72)=0.987$, $p>0.05$). For both larval swimming and metamorphosis in the water, the reef chambers deployed on different dates were combined for statistical analysis.

During the various deployment dates, reef chambers experienced relatively similar environmental conditions, except for June 2014. This month experienced unusually high water temperatures with the average water temperature during this time was 30.9º C (averages were taken from NOAA Key West FL Station ID 8724580 field station and likely higher in the shallows where the experiment took place). There was a significantly higher percentage of larvae metamorphosed in the water column in June 26, 2014 (3.0± 0.9%) compared to May 28, 2014 (0.8 ±0.3%), April 18, 2015 (0.2 ±0.1%), and May 17, 2015 (0.8 ±0.4%) (X^2 (3) =15.71, $p=0.0013$). A similar behavior was observed in coral larvae from *Pocillopora damicornis*, and when newly settled larvae became stressed they would release from the substrate and resemble the initial larval

stage with the ability to resettle (Richmond 1985). *Porites astreoides* settled larvae may be trying a similar tactic in response to elevated water temperature, attempting to escape the stressor. Despite larval exposure to these elevated temperatures, the June 26, 2014 settlement did not change the results if included or removed from the analysis. The final analysis included all four deployments in May 28, 2014, June 26, 2014, April 18, 2015, and May17, 2015.

With all dates combined, the proportion of larvae swimming ($F(2,72)=0.131$, $p>0.05$) and larvae metamorphosed in the water column ($F(2,72)=0.332$, $p>0.05$) were not significantly different by treatment. These results suggest that *L. intricata* is not enhancing nor inhibiting the proportion of larvae swimming or the proportion of larvae metamorphosed in the water column.

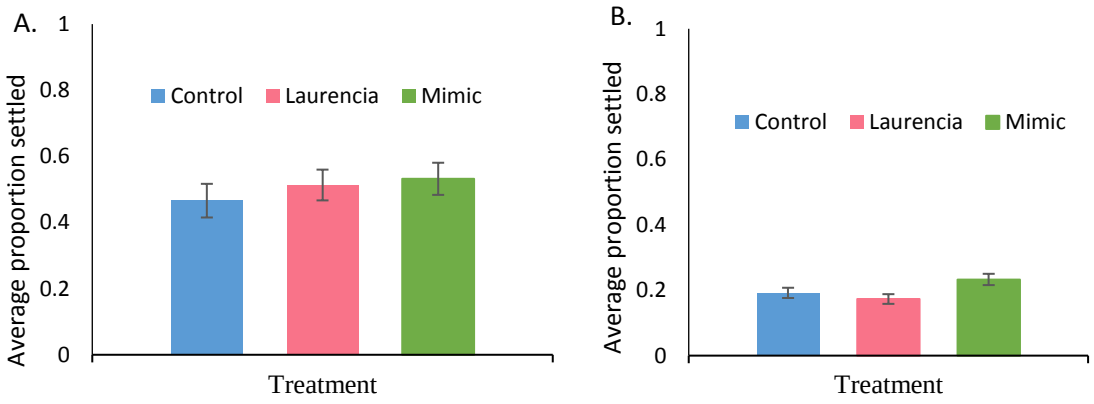

Figure 12. Larval Settlement. Expt 2. Test the hypothesis that *L. intricata* affects coral larvae settlement, showing mean (±SE) proportion of larvae in chambers (n=28) that settled (A) total (top + side + bottom) and (B) top of the tile.

To understand the effect *L. intricata* has on coral larval settlement for all dates, the total proportion of larval settled was compared across treatments. Total settlement included the proportion of larvae settle on top, side, and bottom of the tile. Total settlement experienced no significant differences between the treatments (F (2, 81) =0.30, p=0.5313) (**Fig. 12A**). Treatment attachment occurred on top of the settlement tile for the mimic and *L. intricata* treatments, creating a cryptic environment on top, and the control was left blank, lacking any cryptic habitat. Cryptic environments usually increase coral larvae settlement (Kuffner *et al*. 2006). Contrary to this, there were no significant differences in top settlement between treatments (F (2, 81) =0.63, p=0.3140; **Fig. 12B**). The percentage of larvae settled on the side (F (2, 81) =0.45, $p>0.05$) and bottom (F (2, 81) =0.64, $p>0.05$) of the tile were not significantly different between treatments. Due to

the lack of response observed in larval settlement, it appears that neither *L. intricata* nor the mimic enhanced or deterred settlement. There were also no significant differences between top and bottom settlement among treatments (F (1, 36) =3.18, 0.76, 0.79, p>0.05).

2.2.3 Experiment 3: Does the presence of L. intricata have any latent effects on the post-settlement survival of P. astreoides?

Laurencia experiences seasonal increases and decreases in abundance on the reef (Stacy Prekel, unpublished). To identify if there are any latent effects for coral larvae settling next to *L. intricata* once their abundance decreases, post-settlement survival was observed after the *L. intricata* was removed. After reef chamber settlement was recorded, the treatments were removed from the tiles and post-settlement survival of newly settled coral was observed for five weeks. Latent effects were recorded for all reef chamber treatments except for May 28 and June 26, 2014. These tiles were contaminated with cyanobacteria from overgrowth on the bottom and all containers tipped over, mixing treatments together and preventing further analysis. In April 20 and May 19, 2015, alterations were made to the holding containers to allow them to float, reducing tipping and avoiding cyanobacteria on the bottom. Due to the variability between latent treatment post-settlement survival and a significant difference between survival by month, April 20 and May 19 2015 (X^2(1) =17.78, p<0.001) experiments were not combined for analysis.

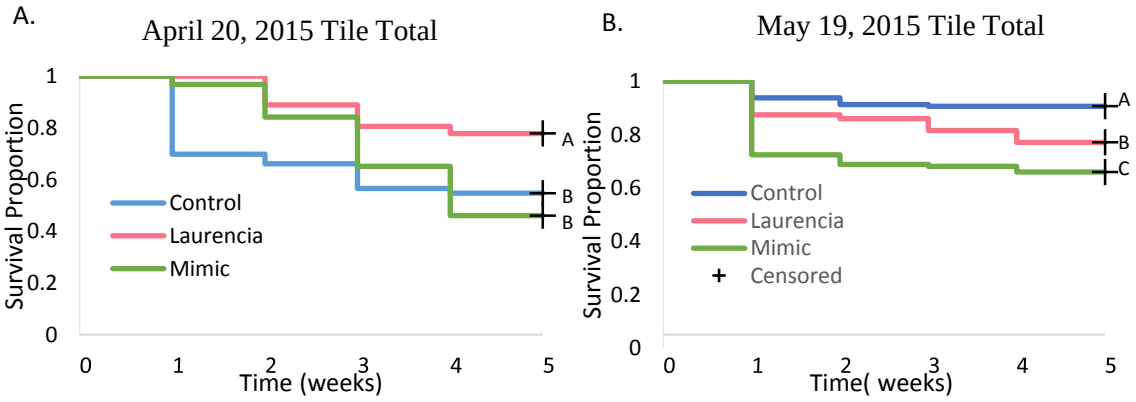

Figure 13. Latent effect on coral larvae post-settlement survival. Expt 3. Test the hypothesis that settling next to *L. intricata* has any latent effects on newly settled coral post-settlement survival, showing survival plots corresponding to proportion survival over five weeks on (A) April 20, 2015 total (top + side + bottom) (different letters correspond to significant difference [p-value=0.0009] between treatments) and (B) May 19, 2015 total (top + side + bottom) (different letters correspond to significant difference between treatments**)**

Differences in spat post-settlement survival were observed among treatments and dates, but it appears that *L. intricata* did not decrease newly settled coral survival. Total survival, including top, side, and bottom of the tile, were significantly different from each treatment in April 20, 2015 (X^2 (2) =14.04, p=0.0009) (**Fig. 13A**). Larvae that settled on the *L. intricata* tile experienced a final proportion of survival at 0.78 ± SE 0.05, which was significantly higher than the control (0.55 ± SE 0.07) and mimic (0.46 ± SE 0.06) treatment. This indicates that latent effects from *L. intricata* promote larval survival, however this trend is not consistent with the May 19, 2015 observations. Total survival for May 19, 2015 was significantly different among treatments (X^2 (2) =27.42, p<0.0001) (**Fig. 13B**). The control had the highest final proportion survive at 0.91 ± SE 0.02 when compared to *L. intricata* (0.77 ± SE 0.04) and the mimic (0.66 ± SE 0.04). *Laurencia intricata* had higher survival over the mimic. This indicates that *L. intricata* is not enhancing survival when compared to the other treatments, but in both April 20, 2015 and May 19, 2015 studies, the latent effect from *L. intricata* is not decreasing survival either. This discrepancy could be due to differences in environmental field conditions, thus impacting coral larvae.

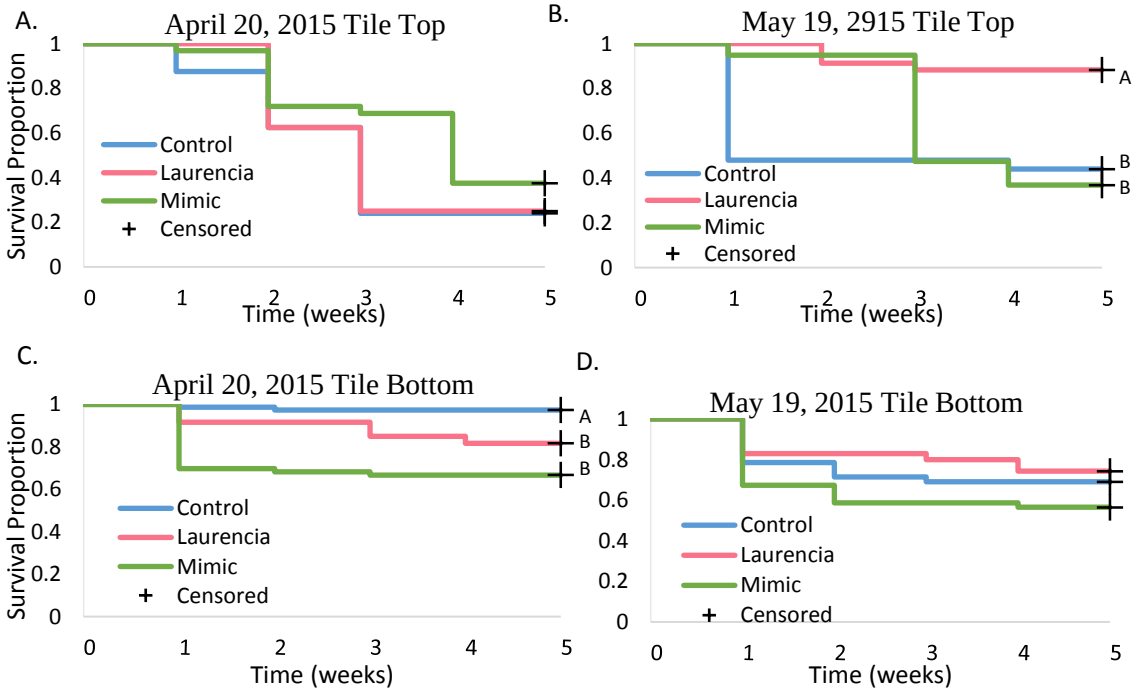

Figure 14. Latent effect on coral larvae survival. Expt 3. Test the hypothesis that settling next to *L. intricata* has any latent effects on newly settled coral post-settlement survival, showing survival plots corresponding to proportion of survival over five weeks on (A) April 20, 2015 top, (B) April 20, 2015 bottom (different letters correspond to significant difference [p-value<0.0001] between treatments), (C) May 19, 2015 top (different letters correspond to significant difference [p-value<0.0001] between survival), and (D) May 19, 2015 bottom of the tile

Settlement location (top, side, and bottom of tile) may affect newly settled coral post-settlement survival. There was a high variance in post-settlement survival between months and locations. All treatments in April 20, 2015 experienced an overall decline in spat top survival and was significantly lower than May 19, 2015 top spat survival (X^2 (1) =44.40, p<0.0001). These results suggest that the environmental factors that spat were exposed to during the experiment may have contributed to the difference in post-settlement survival response between April 20, 2015 and May 19, 2015. Similar conclusions can be made about the variability in treatment survival. Top post-settlement survival by treatment in April 20, 2015 (X^2 (2) =2.61, p=0.2715) (**Fig. 14A**) did not experience a significant difference in the proportion survived, but top post-settlement survival in May 19, 2015 did experience significant difference between treatments (X^2 (2) =23.89, p<0.0001) (**Fig. 14C**).

Both April 20 and May 19, 2015 had no significant difference in side post-settlement survival between treatments (X^2 (2) =0.10, 0.43, p >0.05). Bottom post-settlement survival for April 20, 2015 did have a significant difference in post-settlement survival (X^2 (2) =17.70, p<0.0001). *Laurencia* (0.88 ± 0.06) had significantly higher survival than the control (0.44 ± 0.10) and the mimic (0.37 ± 0.11) treatments (**Fig. 14B**). In May 19, 2015, the proportion on the bottom had no difference in post-settlement survival by treatment (X^2 (2) = 3.24, p=0.1983) (**Fig. 14D**). Due to the variability in latent effect survival, it is not clear if settling next to *L. intricata* had any latent benefits. However, settling near *L. intricata* and then removing it did not trigger any negative latent effects on spat compared to the control and the mimic treatments.

2.2.4 Experiment 4: When given a choice of substrates, are P. astreoides larvae influenced by the presence of L. intricata and Dictyotaceae?

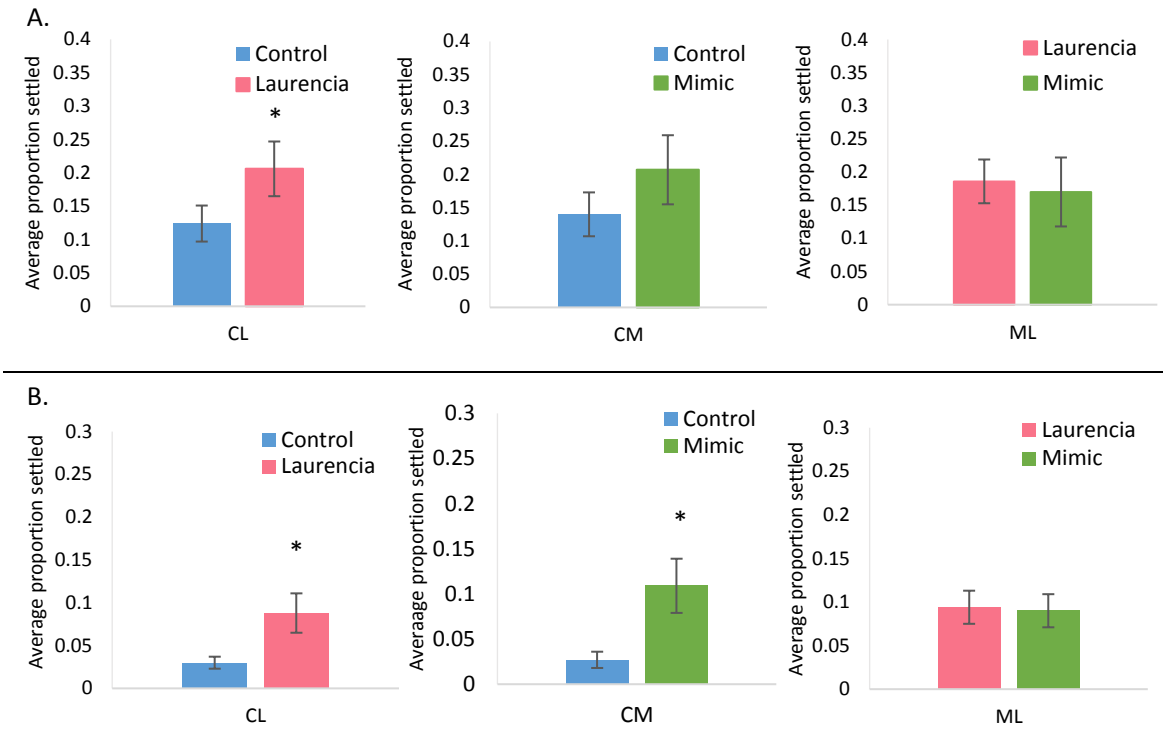

Figure 15. Larval Choice Settlement. Expt 4. Test the hypothesis that providing coral larvae a choice between treatments affect settlement June 26, 2014, showing mean (±SE) proportion of larvae in containers (A) (CL and ML n=10; CM n=9) that total settled (top + side + bottom) (*: significant difference between tiles), (B) (CL and ML n=10; CM n=9) top settled (*: significant difference between tiles)

Table 4. June 26, 2014 choice settlement, frequency analysis of treatment tile effect on settlement distribution by treatment container ($p<0.05$ is significantly different)

Frequency Analysis	d.f.	Chi-Square	***P***
Container CL Control-*Laurencia*	2	0.041	**0.041**
Container CM Control-Mimic	2	24.065	**0.001**
Container ML Mimic-*Laurencia*	2	0.459	0.795

Choice experiments allowed larvae to select which substrate to settle upon and permitted for a more ecologically relevant study. In June 26, 2014, larvae were given an option to settle on three different treatments, each pairwise combinations created three different sets, a control settlement tile and a mimic on a settlement tile (CM), a control

Table 5. June 26, 2014 choice settlement, frequency analysis of treatment tile effect on total tile settlement by treatment container ($p<0.05$ is significantly different)

Frequency Analysis	d.f.	Chi-Square	***P***
Container CL Control-*Laurencia*	1	7.095	**0.008**
Container CM Control-Mimic	1	3.804	0.081
Container ML Mimic-*Laurencia*	1	0.232	0.630

tile and a *L. intricata* on a tile (CL), and a mimic on a tile and a *L. intricata* on a tile (ML). One CM container was removed from the analysis as a larval predator was observed in the container. To determine if larvae prefer to settle next to *L. intricata* over open substrate, *L. intricata* was paired with a blank control tile. Results indicate that coral larvae prefer to settle on top of the *L. intricata* tile rather than on the top of the control tile (**Fig 15B)**. A significantly higher proportion of larvae settled on top of the *Laurencia intricata* treatment when compared to the top of the control tile ($p=0.004$, **Table 4**). Coral larvae were attracted to the chemical cues released by *L. intricata* or by its structure, creating a cryptic habitat and leading to enhanced larval settlement. To determine which of these possibilities was causing the higher *L. intricata* top settlement, a plastic algal mimic resembling *L. intricata's* structure, minus the biological components, was introduced to a control tile. The mimic had a higher proportion of larvae settle on top of the tile over the control treatment ($p=0.001$, **Fig. 15B**, **Table 4**), indicating that coral larvae are attracted to the structure of the algae. There were no significant differences in top settlement when the mimic and *L. intricata* treatments were paired together ($p>0.05$**Fig. 15B, Table 4**). This suggests that the structure of *L. intricata* likely caused higher settlement on the top of the tile, not necessarily the release of chemical cues. Larval settlement preference for the side ($F(1,18) =0.78$, $p>0.05$) and bottom ($F(1,18) =0.74$, $p>0.05$) settlement between pairwise treatments tiles did not differ significantly. This was expected as the algal structure is only present on top of the tile and the side and bottom of the tile are the same for all treatments. To identify any combined effects from settlement location preference, total settlement, including top, side, and bottom of the tile, were compared between treatment tile pairs. Container CL was the only treatment that had a significantly higher proportion of total larval settlement on *L. intricata* treatment over the control treatment ($p=0.008$, **Fig. 15A, Table 5**). In the other two containers, CM

and ML, total settlement was not significantly different between treatments pairs in the proportion of larvae settlement (p>0.05, **Fig. 15A, Table 5)**. Total larval settlement preference for the *L. intricata* tile over the control was most likely driven by the higher top settlement preference for *L. intricata*.

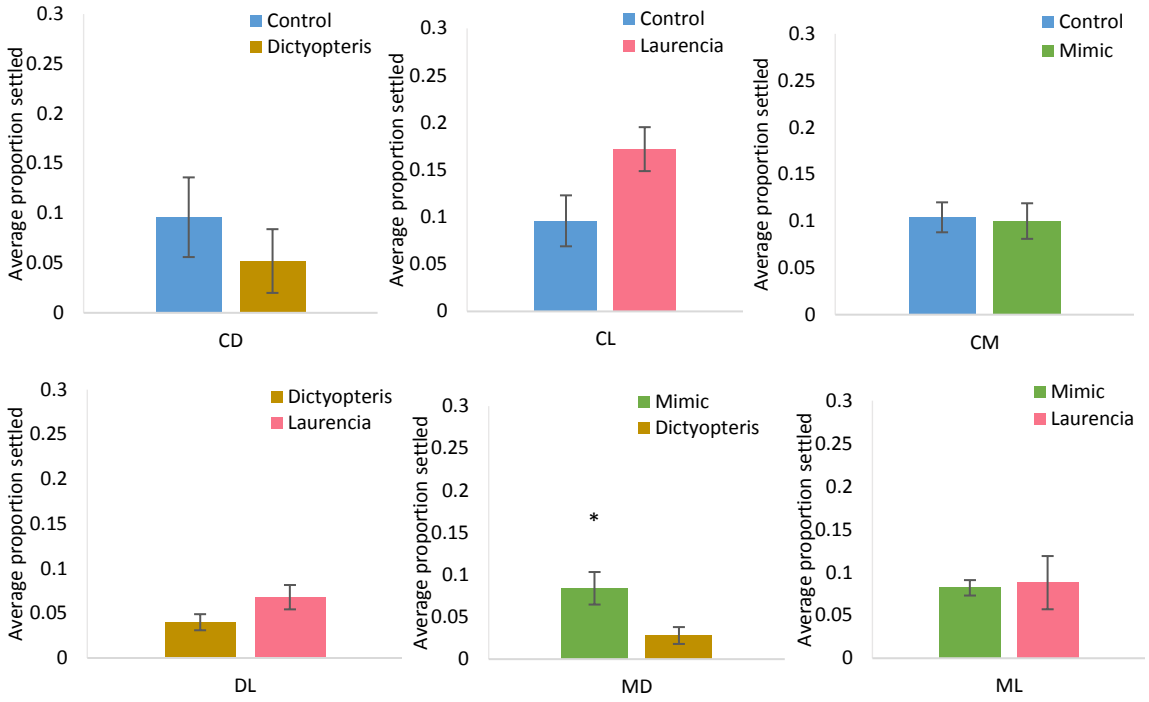

Figure 16. Larval Choice Settlement. Expt 4. Test the hypothesis that providing coral larvae a choice between treatments affect settlement May 17, 2015, showing mean (±SE) proportion of larvae in containers (n=5) top settled (*: significant difference between tiles)

Table 6. May 17, 2015 choice settlement, frequency analysis of treatment tile effect on settlement distribution by treatment container (p<0.05 is significantly different)

Frequency Analysis	d.f.	Chi-Square	***P***
Container CD Control-*Dictyopteris*	2	1.397	0.497
Container CL Control-*Laurencia*	2	3.216	0.200
Container CM Control-Mimic	2	1.926	0.382
Container DL *Dictyopteris-Laurencia*	2	2.434	0.157
Container MD Mimic-*Dictyopteris*	2	6.081	**0.048**
Container ML Mimic-*Laurencia*	2	3.228	0.199

To investigate if algal structure was the only factor to enhance settlement, a macroalgal treatment was added that possessed structure and released deterring compounds. On May 17, 2015, *Dictyopteris delicatula* macroalgae treatment tiles were introduced, bringing the total number of treatments to six: control and *D. delicatula* (CD), control and *L. intricata* (CL), control and mimic (CM), *D. delicatula* and *L. intricata* (DL), *D. delicatula* and mimic (DM), and mimic and *L. intricata* (ML). Top larval settlement preference was significantly higher on the mimic compared to *Dictyopteris* (p=0.048, **Table 6, Fig.16**). All other top larval settlement preferences were not significantly different (p>0.05, **Table 6, Fig. 16**). The choice container housing *Dictyopteris-Laurencia* was the only treatment that experienced a significantly higher frequency settle on the side of the *Dictyopteris* tile when compared to *Laurencia* (X^2 (1)= 13.917, p=0.001). Other settlement distribution by choice container were not significantly different between treatments (X^2 (1)= 3.308, p>0.05). These results suggest that structure is not the only driver for top settlement. The *D. delicatula* has structure on top but lower top settlement, possibly from deterrent chemical cues. It is not clear why only *Dictyopteris* when paired with *Laurencia* resulted in different side settlement. The other treatment combinations did not significantly affect larval settlement preference. The lack in significant difference among tile settlement was most likely a result of the low treatment sample size.

Table 7. May 17, 2015 choice settlement, frequency analysis of treatment tile effect on total tile settlement by treatment container (p<0.05 is significantly different)

Frequency Analysis	d.f.	Chi-Square	**P**
Container CD Control-*Dictyopteris*	1	1.226	0.268
Container CL Control-*Laurencia*	1	0.890	0.346
Container CM Control-Mimic	1	0.011	0.916
Container DL *Dictyopteris-Laurencia*	1	0.127	0.722
Container MD Mimic-*Dictyopteris*	1	1.789	0.181
Container ML Mimic-*Laurencia*	1	1.285	0.257

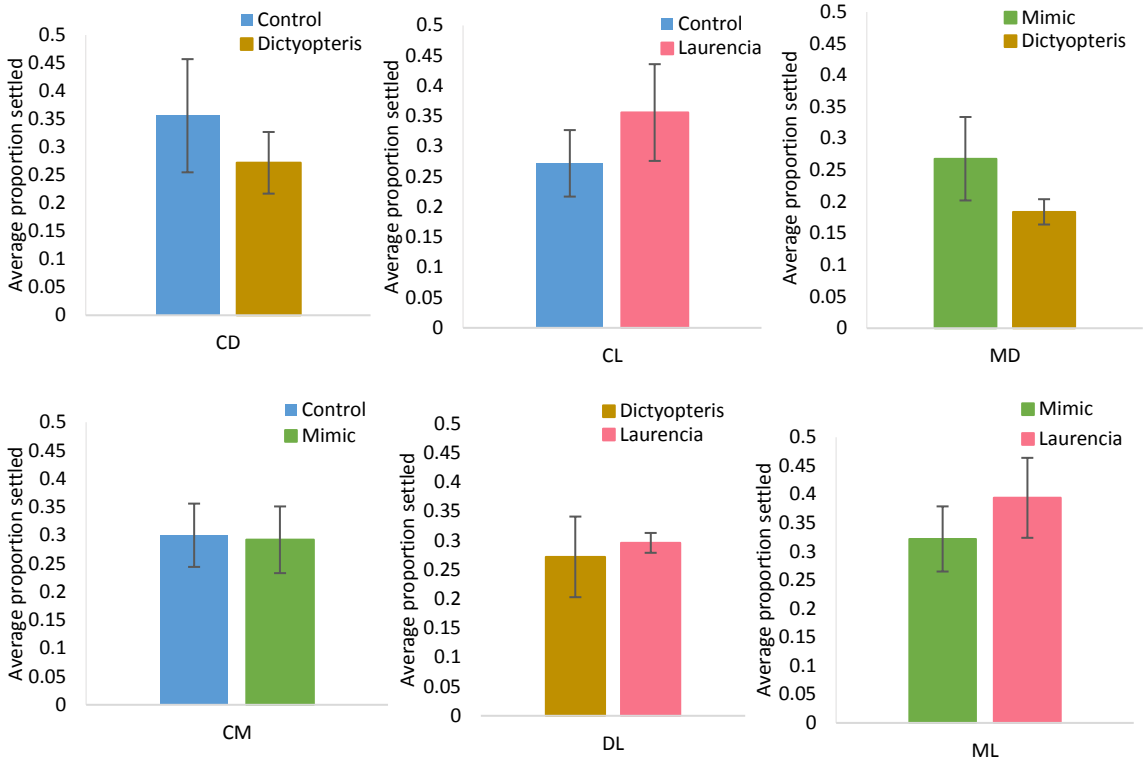

Figure 17. Larval Choice Settlement. Expt 4. Test the hypothesis that providing coral larvae a choice between treatments affect settlement May 17, 2015, showing mean (±SE) proportion of larvae in containers (n=5) total settled (top + side + bottom)

Table 8. May 17, 2015 choice top settlement, One-way ANOVA of effect on treatment tile settlement among different treatment containers ($p < 0.05$ yields significant difference)

Source	d.f.	MS	***F***	***P***
Control	2	0.004	0.227	0.799
Error	12	0.018		
Dictyopteris	2	0.004	0.230	0.798
Error	12	0.017		
Laurencia	2	0.040	4.992	**0.027**
Error	12	0.008		
Mimic	2	0.001	0.326	0.728
Error	12	0.004		

Total settlement did not experience a significant difference among treatment larval settlement preference ($p>0.05$, **Fig. 17, Table 7**). Structure is not the only factor that influences settlement, as allelopathic compounds released from *D. delicatula* are likely deterring settlement.

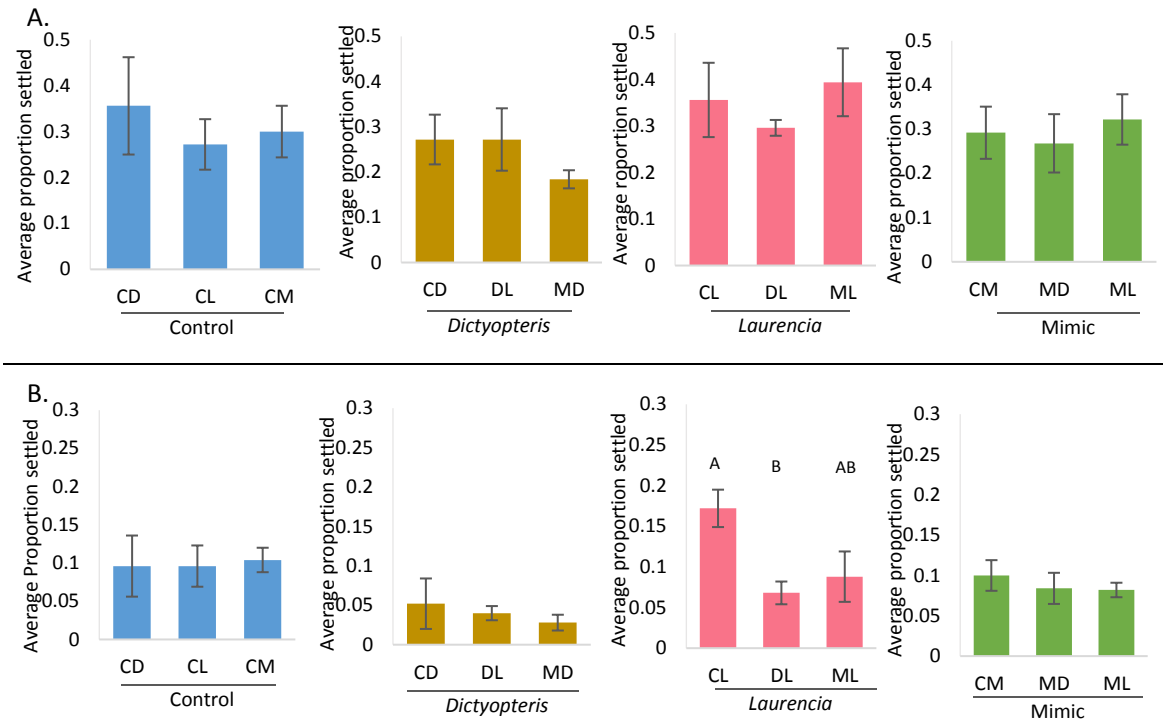

Figure 18. Larval Choice Settlement. Expt 4. Test the hypothesis that providing coral larvae a choice between treatments affects settlement (±SE) proportion of larvae settled on treatment tiles with respect to different treatment containers, May 17, 2015 (A) (n=5) that total settled (top + side + bottom), (B) (n=5) top settled (different letters represent significant difference between tiles)

Table 9. May 17, 2015 choice total settlement, One-way ANOVA of effect on treatment tile settlement among different treatment containers ($p<0.05$ yields significant difference)

Source	d.f.	MS	***F***	***P***
Control	2	0.010	0.269	0.769
Error	12	0.036		
Dictyopteris	2	0.016	0.951	0.414
Error	12	0.017		
Laurencia	2	0.013	0.575	0.577
Error	12	0.022		
Mimic	2	0.005	0.190	0.830
Error	12	0.025		

To determine if *D. delicatula* was affecting larval settlement on the other tile they were paired with, larval settlement by treatment was compared among different containers. Coral larvae top settlement was significantly lower on the *L. intricata* tile when stationed next to *D. delicatula* compared to when the *L. intricata* tile was stationed next to the control treatment. *Laurencia intricata* top settlement when stationed next to the mimic was not significantly different from being paired with the control and *Dictyopteris* treatments ($p=0.027$, **Fig. 18B, Table 8**). The other treatments, control, *D. delicatula*, and

the mimic, did not experience a significant difference in top settlement when paired with the other treatment tiles (p>0.05, **Table 8)**. Total larval settlement was also not influenced by the treatment tile they were paired with (p>0.05, **Fig. 18A, Table 9**). Due to top settlement on the *Laurencia* treatment being statistically similar when paired with the mimic and *Dictyopteris*, it cannot be concluded that *Dictyopteris* is affecting settlement on the *Laurencia* treatment tile through the release of allelopathic compounds.

2.2.5 Experiment 5: Does L. intricata and Dictyotaceae influence the post-settlement survival of P. astreoides?

Previously, any latent effect from *L. intricata* did not negatively influence newly settled coral post-settlement survival. To determine any effect a consistent presence of *L. intricata* has on newly settled coral post-settlement survival, choice containers tiles were separated into individual containers and the treatments remained on the tile for long-term analysis. June 29, 2014 bottom($X^2(2) = 3.498$, p-value>0.05) and side ($X^2(2) = 0.989$, p-value>0.05) post-settlement survival had no significant difference between treatments. Total tile post-settlement survival for the control, *L. intricata*, and the mimic also did not experience significant difference between treatments (p>0.05, **Fig. 20A, Table 10**). Top survival by treatment was the only location that experienced a significant difference between treatments (p=0.015, **Table 10**). *Laurencia intricata* (0.55 ± 0.05) and the mimic (0.54 ± 0.05) top post-settlement survival were significantly higher than the control's (0.36 ± 0.07) survival (**Fig. 20B**). These results indicate that settlement location may play an important role in newly settled coral survival and more importantly, in the presence of structure

A. B.

Table 10. Long-term survival, Kaplan-Meier Survival Curve of treatment tiles over eight-week period (p<0.05 yields significant difference)

Log-Rank Test	d.f.	Chi-Square	***P***
June 29, 2014 Total Survival Treatment	2	0.800	0.670
June 29, 2014 Top Survival Treatment	2	8.385	**0.015**
May 20, 2015 Total Survival Treatment	3	7.301	0.063
May 20, 2015 Top Survival Treatment	3	7.988	**0.046**
May 20, 2015 Total Minus Dictyotaceae Treatment	2	7.241	**0.027**
May 20, 2015 Top Minus Dictyotaceae Treatment	2	4.717	0.095

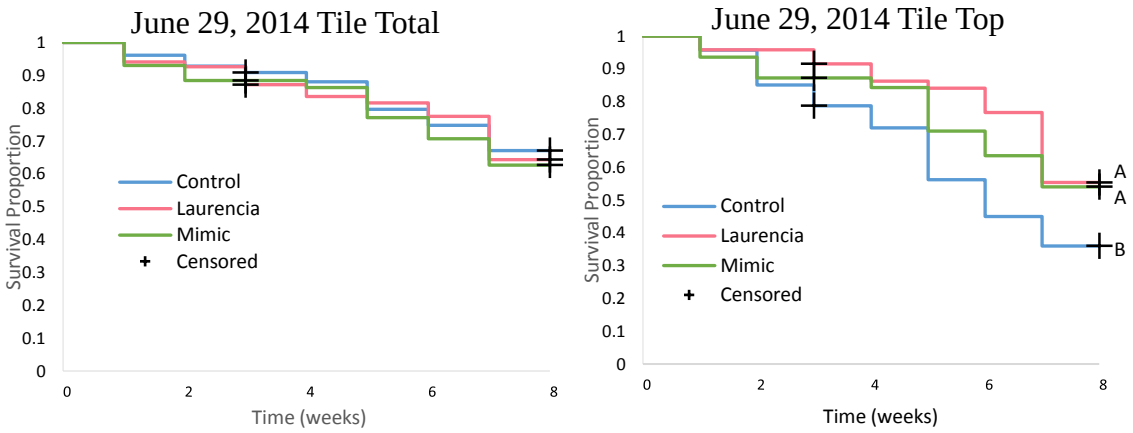

Figure 19. Larvae post-settlement survival. Expt 5. Test the hypothesis that settling next to *L. intricata* affects newly settled coral post-settlement survival with long term exposure, showing survival plots corresponding to proportion survive June 29, 2014 (A) total (top + side + bottom) and (B) top (different letters correspond to significant difference between treatments) of the tile

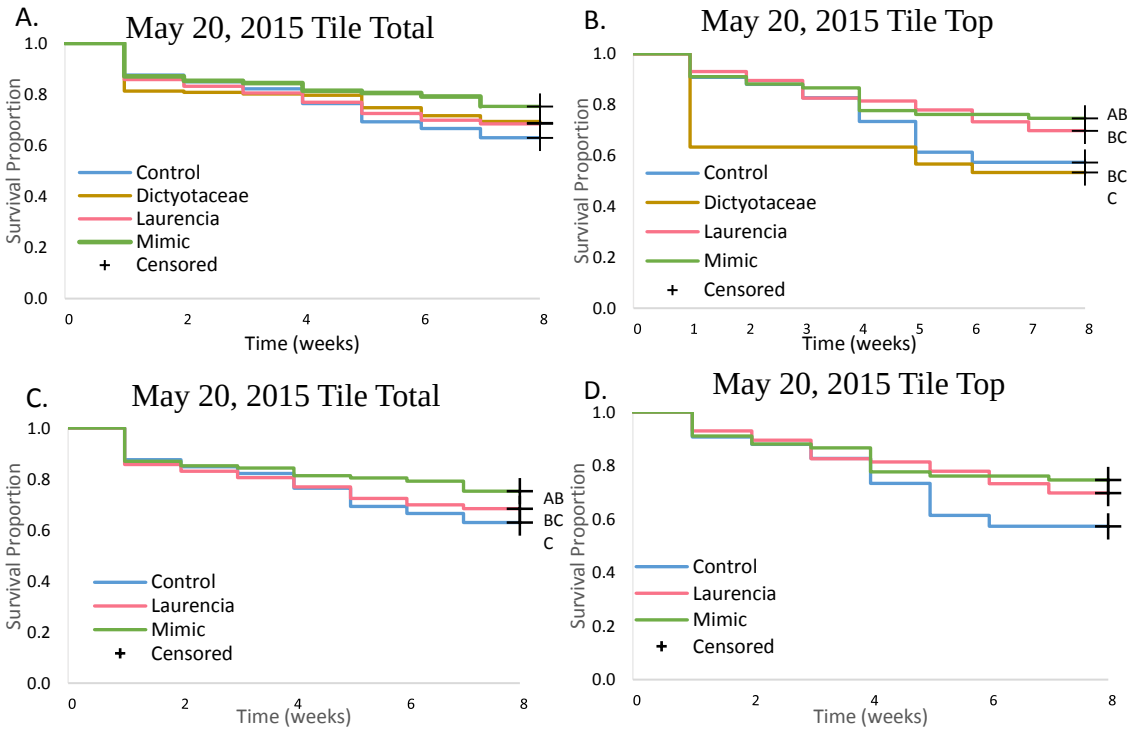

Figure 20. Larvae post-settlement survival. Expt 5. Test the hypothesis that settling next to *L. intricata* affects newly settled coral post-settlement survival with long term exposure, showing survival plots corresponding to proportion survive May 20, 2015 (A) total (top + side + bottom), (B) top (different letters correspond to significant difference between treatments), (C) total (top + side + bottom) without Dictyotaceae (different letters correspond to significant difference between treatments), and (D) top of the tile without Dictyotaceae

In May 2015, the post-settlement survival added the *D. delicatula* treatment. During weekly replacements, different genera of the brown alga family Dictyotaceae were used due to the difficulty of field identification therefore I will refer to these species collectively by their family name, Dictyotaceae. Total survival by treatment did not

experience a significant difference in post-settlement survival (p>0.05, **Fig. 21A, Table 10).** Due to the inconsistencies in the Dictyotaceae species used, this treatment was removed from the analysis and compared. Without Dictyotaceae, total settlement survival was significantly different between treatments (p=0.027, **Table 10**). The control tile had the lowest proportion survive at 0.63 ± 0.03 compared to the mimic, 0.75 ± 0.03 (**Fig. 21C)**. *Laurencia intricata* (0.68 ± 0.03) was not significantly different from the control or mimic tiles (**Fig. 21C**). These findings support the results identified in June 2014 of enhanced coral post-settlement survival with algal structure compared to settling without.

Looking at settlement tile spat survival by location (side, bottom, and top) showed similar trends observed in June 2014. Side (X^2(3,2) = 3.235, 2.496, p-value>0.05) and bottom (X^2(3,2) =2.082, 2.034, p-value>0.05) post-settlement survival by treatment were not significantly different in survival with or without Dictyotaceae. Top spat survival was significantly different between treatments with Dictyotaceae (p=0.046, **Table 10**). The mimic (0.75 ± SE 0.05) was the only treatment that had significantly higher post-settlement survival than the Dictyotaceae treatment (0.53 ± SE 0.09) (p=0.046, **Fig. 21B**). *Laurencia intricata* (0.70 ± SE 0.05) top post-settlement survival was not significantly different from Dictyotaceae (0.53 ± SE 0.09) (p>0.05, **Fig. 21B**). The mimic (0.75 ± SE 0.05) was not significantly different from the control (0.57 ± SE 0.06) in newly settled coral top survival (p>0.05, **Fig. 21B**). The mimic and *L. intricata* did not have significantly different top post-settlement survival, nor did the control and Dictyotaceae (p>0.05, **Fig. 21B**). Finally, the control and *L. intricata* top post-settlement survival was not significantly different (p>0.05, **Fig. 21B**). Low sample size might explain why there is not a distinct difference between the treatments like in June 29, 2014. Removing Dictyotaceae treatments from top post-settlement survival analysis yielded no significant differences in survival (p>0.05, **Fig. 21D, Table 10**). Algal structure exhibits a trend of improving newly settled coral post-settlement survival, except for the Dictyotaceae treatment. Dictyotaceae post-settlement survival is similar to the control treatment without structure. This may be from allelopathic compounds decreasing coral fitness as Dictyotaceae provides structure but lowers survival. This may also be due to Dictyotaceae morphology leading to decreased survival. There was a drastic decline where survival dropped by 37% after the first week. The species on the tile during the decline was *D. delicatula*, the same species that deterred settlement. There is a high

probability that this species is releasing allelopathic compounds that are harmful to corals. This data supports that *L. intricata* is not decreasing newly settled coral post-settlement survival, but rather is most likely increasing newly settled coral survival through the advantages of a creating a cryptic habitat.

Table11. Summary of experimental findings, (+) positive response, (-) negative response, (NE) No effect, and blank cells represent a treatment that was not present

Experimental Objectives	Dictyotaceae	*Laurencia intricata*	Mimic
Expt. 1. Larval swimming behavior in Water column	*Dictyota* (-) *Dictyopteris* (+)	+	NE
Expt. 2. Reef chamber settlement		NE	NE
Expt. 3. Latent effect on post-settlement survival		NE	NE
Expt. 4. Larval settlement preference	-	+	+
Expt. 5. Long-term post-settlement survival	NE	+	+

2.4 Discussion

In this study, I tested if red algal species, *L. intricata,* and several species from the brown algal family Dictyotaceae influence *P. astreoides* larval swimming behavior, settlement, and post-settlement survival. My findings identified a hierarchy of cues that can be divided into two categories, chemical and physical. Algal chemical cues regardless, if they were settlement attractants or deterrents, elicited positive geotaxis behavior while larvae were in the water column. During settlement, the Dictyotaceae species deterred settlement and *L intricata* enhanced settlement. This provides evidence that coral larvae respond to most coral reef chemical cues while in the water column but become more selective and demonstrate a species-specific response to algae when probing the bottom. My results are the first to show that macroalgal species, *L. intricata,* enhances coral settlement and increases coral spat survival. I also demonstrated two different responses to macroalgae species, one species facilitated settlement, while another inhibited it. This indicates that the abundance of certain macroalgal species may be more harmful to coral recovery than other macroalgal species.

Chemical and physical cues most likely contributed to the differences observed in coral larval settlement between *Laurenica* and D*ictyopteris.* It appears that *L. intricata* releases chemical compounds that trigger larval swimming behavior but it is uncertain if those chemicals enhance settlement and trigger metamorphosis, similar to CCA. It is clear, however, that *L. intricata* does not release chemicals that deter larval settlement. All of the tiles were conditioned for at least four weeks and were colonies by biofilm and some CCA, a settlement enhancer (Morse and Morse 1996). Based on my results it appears that *L. intricata* is not releasing additional chemical cues that enhance larval settlement. This would explain why settlement was the same across all treatments for the reef chambers. The chemical cues from CCA were the dominant cue causing similar settlement trends across the control, mimic, and *L. intricata* treatments.

Coral larvae can sense light irradiance to find shaded habitat (Fadlallah 1983; Mundy and Babcock 1998; Raimondi and Morse 2000) and use microtopography of the substrate to settle in cryptic locations (Whalan *et al.* 2015). Algal structure provides a refuge from predation and this may explain why coral prefer settlement under some structure types despite negative impacts from shading or abrasion (Venera-Ponton *et al.* 2011). Macroalgal morphology can also deter coral settlement, with some species occupying more of the substrate preventing coral larvae from settling (Box and Mumby 2007). Here, when providing larvae a choice between settlement substrate, the structure played a factor in determining larval settlement. *Porites astreoides* larvae preferred to settle under the structure of *L. intricata* or the mimic, but not *Dictyopteris,* which seems to have an unfavorable structure and/or releases allelopathic chemicals to deter settlement. The mimic used in this study was representative of *Laurencia*'s morphology indicating that larvae may prefer the round branching structure over the flat, broad structure of *Dictyopteris*. This may also play a role in identifying structure of the macroalgae, eventually leading to decreased settlement next to *Dictyopteris* or increased settlement next to *Laurencia*. The morphology of the mimic may dictate the larval response. If it occupies more space on the substrate, it may prevent larval settlement rather than creating beneficial habitat (Diaz-Pulido *et al.* 2010). This may explain why other studies found coral settlement was not enhanced by algal structure (Tanner 1995), but instead it occupied more of the substrate preventing larval settlement rather than creating a refuge (Diaz-Pulido *et al.* 2010).

Although it appears that the physical cue of the macroalgae influences settlement, the release of chemical compounds that enhance or deter settlement and survival cannot be dismissed. Along with the unfavorable algal morphology, the allelopathic compounds released by *Dictyopteris* (Hay *et al.* 1988) may explain the reduced larval settlement. The chemical cues released by *Laurenica* may be promoting coral settlement in conjunction with the favorable structure of *Laurencia*. This combination of chemical and physical cues may potentially increase coral settlement on a phase-shifted reef dominated by *L. intricata* and decrease coral settlement on a *D. delicatula* dominated reef. Although the mimic and *L. intricata* enhanced settlement due to their structure, *L. intricata* had the added benefit of releasing chemical cues to initiate the downward swimming motion, drawing larvae to the substrate for settlement. Dictyotaceae also triggered coral larval downward swimming, but decreases coral larval settlement. The positive effect of *Laurenica* and the negative effect of Dictyotaceae on coral settlement is amplified by their influence on coral spat post-settlement survival.

Coral larvae that settle next to *L. intricata* did not experience decreased post-settlement survival, but Dictyotaceae decreased spat survival. Macroalgal structure is documented to decrease survival from shading and abrasion (Rivers and Edmunds 2001; Box and Mumby 2007). Macroalgae morphology could explain the difference in these findings; broader and flatter thalli morphology, characteristics of Dictyotaceae, shield more sunlight and have more surface area to catch the wave action, increasing abrasion (Box and Mumby 2007). However, allelopathic compounds cannot be ruled out as the culprit for decreased coral post-settlement survival. *Laurencia intricata's* morphology is quite different from the macroalgae used in these studies. The thalli are round and blunt resulting in more light penetration and less abrasion due to rounded thallus catching less wave action (Box and Mumby 2007). Macroalgae morphology may explain the species specific survival differences on coral larvae, but it does not explain why larval survival in the control treatment was lower. However, when the structure is absent on the control treatments, which leads to higher exposure to sunlight and ultraviolet radiation (UV). Increased UV exposure may also explain the variability observed during latent post-settlement survival were the control experienced higher survival than the structured treatments. The structure was removed exposing coral spats to higher UV decreasing their survival. Sunlight is important for photosynthesis and coral calcification, but too

much can cause photoinhibition, requiring more energy for photosynthesis and eventually decreasing survival (Hoogenboom *et al.* 2006). Larvae show a preference to settle under lower UV exposure to increase survival, suggesting that too much UV can cause mortality (Gleason *et al.* 2005).

My findings demonstrate that *L. intricata* is not decreasing and Dictyotaceae is decreasing the preferred habitat for *P. astreoides* larvae on South Florida reefs. This is particularly helpful as *Laurencia* (Stacy Prekel, unpublished) and Dictyotaceae (Lirman and Biber 2000) show seasonal fluctuation on South Florida reefs which coincide with peak planular release of *P. astreoides* (Chornesky and Peter 1987; McGuire 1998; Kuffner *et al.* 2006). A Dictyotaceae phase-shift could be more detrimental to coral reef recovery than a *Laurenica* dominated reef. *Laurencia* may benefit coral recruitment on Florida reefs by not hindering coral settlement or survival like Dictyotaceae. It should be noted that other phase-shift organismal states, e.g. soft coral, sponge, and corallimorpharian, may have differing effects on coral reef recovery as well. Soft corals and sponges quickly colonize reefs after coral decline, with sponges rapidly overgrowing the remaining coral colonies, but corallimorpharian transition is a slower and less drastic transition (Norström *et al.* 2009). The same can be expected by different macroalgae species dominating the substrate. I identified differing coral settlement cues in two common macroalgae species associated with macroalgal phase-shifts. This suggests that coral recovery is not just dependent upon reducing macroalgal growth but specific macroalgal species. Ultimately, more investigation into how different species of macroalgae affect coral larvae recruitment is vital for a comprehensive understanding of the coral reef community and conservation.

CHAPTER 3: DISCUSSION

3.1 *Results overview*

The red macroalga, *Laurencia intricata,* either enhanced or had a neutral effect on larval swimming behavior, settlement, and post-settlement survival. Prior to coming into contact with the substrate, it appears that coral planulae exhibit the same behavior when exposed to *L. intricata*, CCA, and *Dictyopteris justii*. However, *D. delicatula* was identified as a coral larval deterrent. Coral larvae may be initially attracted to compounds that both facilitate and inhibit larval settlement and survival because they signal the presences of a coral reef. My results suggest the structure instead of the chemical cues released by *L. intricata* cause higher larval settlement and most likely enhances survival. Coral larvae prefer to settle in cryptic environments, and the algal structure may serve as a refuge from grazing, predation, and UV radiation.

3.2 Experimental Obstacles

In my June 26, 2014 reef settlement experiment, there were a significantly higher number of metamorphosed larvae in the water column than other months. An increase in metamorphosed larvae in the water column may be a response to stress associated with elevated water temperatures. The water temperature from June 26-28, 2014, was 30.9º C when the settlement chambers were in the field, which was unusually high for that time of year. Similarly, this was also observed with coral larvae from *Pocillopora damicornis.* When newly settled larvae became stressed, they would release from the substrate, resembling their initial larval stage with the ability to resettle (Richmond 1985). *Porites astreoides* larvae exposed to elevated temperatures experience premature metamorphosis and a decrease in photosynthetic ability, leading to increased mortality (Edmunds *et al.* 2001). The increase in metamorphosed larvae in the water column may eventually lead to lower coral recruitment as it is unknown whether or not *P. astreoides* re-attached. Although high-water temperatures are known to decreases *P. astreoides* larval settlement (Olsen *et al.* 2015), the temperature in June 2014 did not affect overall coral larval settlement. Ocean temperatures are predicted to increase due to global climate change; coral cover and recruitment will most likely continue to decline as water temperatures continue to rise (Baker *et al.* 2008).

Coral larval settlement preference in April 2015 experienced decreased settlement compared to June 2014; most likely due to overgrowth by cyanobacteria. Coral larvae experience decreased settlement and survival next to cyanobacteria (Kuffner and Paul 2004; Kuffner *et al.* 2006; Paul *et al.* 2005; Morrow *et al.* 2011) and the same results were observed during the April 2015 larval settlement preference. Overgrowth occurred at the treatment attachment interface. The algal treatments, *L. intricata* and *D. justii*, experienced the highest number of tiles overgrown. *Dictyopteris justii* treatments had zero top settlement, and *L. intricata* experienced an average top settlement less than 1%. This data was removed from my final analysis due to the impact of cyanobacteria's effect on settlement. Cyanobacteria decreased top recruitment for *P. astreoides* larvae to under 5% (Kuffner *et al.* 2006) and my results were drastically lower, which might be attributed to cyanobacteria-macroalgae competition for space causing both organisms to chemically defend against one another. Different abiotic and biotic stressors can influence the abundance and compound structure of the chemical defense released by macroalgae (Gross 2003). Coral larvae respond to a complex combination of chemical cues for recruitment (Morse and Morse 1996) and may respond to these new combinations of compounds differently than they would if exposed to them separately. It has been identified that corals respond synergistically to two compounds released from CCA than they would to each compound separately (Kitamura *et al.* 2007). Coral larvae respond synergistically to deterrent stressors, such as allelopathic chemicals from cyanobacteria and higher ocean temperatures. Together, these stressors drastically decrease coral settlement (Ritson-Williams *et al.* 2016). It is conceivable that deterrence compounds from two different sources may have a combined effect on coral larvae. Further investigation is required to identify how competition between macrophytes affect allelopathic compounds and their effect on coral settlement and survival.

3.4 Larvae Behavior in Water Column

Contrary to the hypothesis that allelopathic compounds deter coral larvae, the larvae were attracted to *Dictyopteris* when exposed to chemical cues from the algae. Larval swimming behavior remained the same in the presence of *Dictyopteris justii*, *L. intricata* and unidentified CCA. These results were surprising since *Dictyopteris delicatula* release chemical compounds to deter herbivory and epiphytic growth, compounds known to deter coral larvae settlement in other macroalgal species (Hay *et al.*

1988). *Porites astreoides* larval settlement response to *L. intricata* was unknown until this study identified that *L. intricata* does not deter settlement, but rather enhances coral settlement by releasing chemical cues and providing amenable structure Initially, coral larvae may respond to chemical cues from the reef habitat as they identified where settlement substrate is located, and then became more selective when deciding where to permanently settle. Gleason *et al.* (2009) found that water collected from a healthy reef and a macroalgae phase-shifted reef both resulted in more coral larvae at the bottom, than water collected from the open ocean: suggesting that coral larvae respond to the presence of the reef, regardless of its state.

Dictyota pfaffii-humifusa complex did not attract coral larvae to the bottom, contradicting the previous hypothesis that all chemical cues from the reef habitat identify where substrate is located. Prior to this study, it was unknown how coral larvae react to *D. pfaffii-humifusa* complex, although it has strong antifouling and inhibitory compounds (Stirk *et al.* 2007) suggest it would be harmful to corals. Since larval swimming behavior for the control, mimic, and *D. pfaffii-humifusa* complex were similiar, coral larvae may respond to deterrent cues similarly to the absence of chemical cues. Another explanation may be that *P. astreoides* larvae do not respond to the chemical cues released by *D. pfaffii-humifusa* complex. This may indicate that there are some compounds from coral reefs that do not trigger the downward larval swimming behavior. Coral species are known to respond differently to various macroalgae species (Diaz-Pulido *et al*. 2010) and *P. astreoides* larvae may respond differently to *D. pfaffii-humifusa* complex.

Since *D. pfaffii-humifusa* complex and *D. justii* are part of the Dictyotaceae family and similarly deter coral settlement between species of this family, the *D. pfaffii-humifusa* complex and *D. justii* treatments were combined. *Laurencia intricata* and Dictyotaceae treatments resulted in a higher proportion of larvae at the bottom of the cylinders when compared to the control. These results further support the hypothesis that coral larvae are attracted to chemical cues from any reefs, regardless if it is degraded or dominated by algae. Coral-macroalgae interactions are species-specific, (Birrell *et al*. 2008b; Diaz-Pulido *et al.* 2010; Paul *et al.* 2011; Denis *et al.* 2014; Olsen *et al.* 2016) and identifying which positive and negative cues trigger larval swimming behavior will require more investigation.

After larvae find a reef habitat, their search for substrate is more selective. Larvae avoid allelopathic compounds when selecting substrate (Birrell *et al.* 2008b). I found that coral larvae avoided *D. delicatula* and settled on other substrates. Coral larvae can distinguish between macroalgae and CCA (Dixson *et al.* 2014), even between different CCA species, with certain species preferred over others (Ritson-Williams *et al.* 2009). Increased selectiveness is advantageous to corals, especially since corals are influenced by the surrounding organisms, and where they settle ultimately determines the coral larvae's success (Bak and Engel 1979). Coral-macroalgae interactions are species-specific for both algae and corals (Birrell *et al.* 2008b; Denis *et al.* 2014; Diaz-Pulido *et al.* 2010; Olsen *et al.* 2016; Paul *et al.* 2011) and identifying *P. astreoides* larval response to attractant and deterrent cues will require more investigation.

3.5 Macroalgae Structure and Coral Larvae Settlement

Porites astreoides larvae preferred to settle under algal structure, either *L. intricata* or the mimic, affecting settlement location when provided a choice between substrate. This is most likely due to shading and the creation of a cryptic habitat by the algal structure increasing top settlement, since this is where the structure is located. Algal structure also provides the added benefit of creating a refuge from predation and increased survival (Venera-Ponton *et al.* 2011). Most coral larvae prefer to recruit to low irradiance and shaded habitats (Fadlallah 1983; Mundy and Babcock 1998; Raimondi and Morse 2000). Macroalgae morphology not only affects the level of irradiance, shading, and protection, but also causes tissue damage from abrasion, reducing coral recruitment (Jompa and McCook 2003). Despite the negative effect associated with settling next to macroalgal structure, I observed enhanced settlement when sufficient substrate was available.

Contrary to larval settlement preference, when one settlement substrate was presented to *P. astreoides* larvae in the field, I observed that settlement location was not altered. This could be a result of limited settlement substrate, requiring recruitment to occur in unfavorable locations, i.e. substrate without shading. Another reason may be that CCA is a potent settlement enhancer (Morse and Morse 1996) and that the chemical cues from CCA were the dominant factors that caused the same settlement across the control, mimic, and *L. intricata* treatments even though the control lacked any top structure. The

percentage of *P. astreoides* settled on the control treatments (46.6 ± SE 5.1%) was similar to comparable studies on macroalgae's effect on larval settlement (Kuffner *et al.* 2006; Paul *et al.* 2011). Therefore, the conditioned substrate offered to *P. astreoides* larvae was suitable for settlement and did not alter the results. Other studies found no influence on settlement when comparing the control (Paul *et al.* 2011), plastic mimic, and some macroalgae treatments (Nugues and Szmant 2006; Paul *et al.* 2011; Olsen *et al.* 2016). Another study identified that the plastic mimic increased top recruitment when compared to the blank control and macroalgae treatments (Kuffner *et al.* 2006). This may be from the various coral species responding to macroalgae morphology and structure differently.

When providing larva a choice between settlement substrate, I found the structure played a larger factor in determining larval settlement. My findings are the first to identify a macroalgae species that increased coral recruitment. In June 2014, I observed *L. intricata* promoting coral settlement by creating a desirable cryptic habitat with its structure. This was not consistently observed between June 2014 and May 2015 trials. May 2015 larval settlement preference had a lower sample size and this may have resulted in the inability of *L. intricata* to enhance top settlement in the same treatment pairing. I hypothesize that the structure of *L. intricata* is enhancing recruitment due to the similar morphology the mimic shares with *L. intricata*. Depending on the mimic morphology, this could lead to the development of a less cryptic habitat (Diaz-Pulido *et al.* 2010). This may also explain why some mimics do not increase settlement in other experiments, but instead the mimic may occupy more space during settlement, decreasing coral recruitment (Tanner 1995).

Macroalgae morphology may explain why settlement was deterred by *D. delicatula*, although the presence of allelopathic compounds cannot be ruled out. *Dictyopteris delicatula* morphology is similar to many *Dictyota spp.*, possessing almost ribbon-like, flattened thallus branches. This morphology tends to oscillate more due to its broader shaped thalli, leading to higher abrasion (Box and Mumby 2007). Larvae may have developed an ability to recognize compounds released by macroalgae that have high abrasion capability and established an avoidance behavior. The effect the genus *Dictyopteris* has on coral settlement was not investigated prior to my research, but other

genera in the family Dictyotaceae have, (Kuffner *et al.* 2006; Box and Mumby 2007; Diaz-Pulido *et al.* 2010) and were identified to deter settlement and decrease survival of corals. *Dictyopteris delicatula* releases chemical defenses to deter herbivory and epiphytic growth, similar to other macroalgal species that deter larval settlement (Hay *et al.* 1988). Taken together, there is reason to believe that *Dictyopteris* might also release compounds that deter settlement and help explain the results in this study.

3.6 Latent and Long-term Polyp Survival

I observed stark differences between spat post-settlement survival. The latent post-settlement survival showed no true pattern between treatments and long-term post-settlement survival showed clear and consistent patterns among treatments. Latent post-settlement survival (exposed to macroalgae during settlement only) varied between location and months, while long-term macroalgal exposure did not vary. Removing the macroalgae reduces shading and increases UV exposure to the coral spat and this may contribute to decreased survival (Gleason *et al.* 2005; Hoogenboom *et al.* 2006) and to the variability observed. The larvae used in latent post-settlement survival experiment were also placed into the field for settlement, exposing them to an array of environmental factors (Gleason and Hofmann 2011) that were not experienced by the coral in the long-term exposure experiment. In April 2015 during the latent experiment, survival on the top of tiles was 50% lower than May 2015. It is not clear why there is a drastic difference between these two months. One possibility is that the parent corals were collected from different reefs separated by 70 km and could have variability in fitness and environmental stress. The exposure to environmental conditions can explain the variability in post-settlement survival (Vermeij *et al.* 2006). The one takeaway from the latent research is that recruiting next to *L. intricata* is no more harmful to newly settled coral survival than the plastic mimic or the control.

Surprisingly, in the long-term exposure experiment survival next to the plastic mimic or *L. intricata* showed a clear advantage. One study showed macroalgae benefits coral larval survival by providing a refuge from herbivory outweighing the negative effects associated with algae (Venera-Ponton *et al.* 2011). Usually, macroalgal structure leads to decreased survival from shading and abrasion (Rivers and Edmunds 2001; Box and Mumby 2007), but macroalgal morphology is an overlooked factor that influences

the structure's impact on coral spat survival. Broader and flatter thalli tend to shield more sunlight and provide more surface area to catch the wave action to increase abrasion (Box and Mumby 2007). *Laurencia intricata's* morphology is quite different from the macroalgae used in these studies. The thalli of *L. intricata* are round and blunt, resulting in more light penetration and less abrasion, possibly due to the rounded thallus moving less in high energy environments. Other macroalgae morphology used in studies were flat, with wide branching thalli, blocking more light and moving more in high energy environments. The algal mimic resembles *L. intricata's* morphology, but the plastic is more rigid than the microalgae, potentially causing less damage to corals from abrasion because the individual branches did not move (Rivers and Edmunds 2001; Box and Mumby 2007). This more rigid structure could explain why survival was higher on the mimic than *L. intricata*. However, this does not explain why the control treatment survival was lower. Structure was absent on the blank control treatments perhaps leading to higher exposure to ultraviolet radiation (UV). Sunlight is important for photosynthesis and coral calcification, but too much can cause photoinhibition, requiring more energy for photosynthesis and eventually decreasing survival (Hoogenboom *et al.* 2006). Larvae show a preference to settle under lower UV exposure to increase survival, indicating that too much UV can cause mortality (Gleason *et al.* 2005). Although anecdotal during post-settlement survival treatment tiles developed a cyanobacteria film that appeared to be more frequent on the control tiles than the other treatments. Cyanobacteria decreases coral larvae survival (Kuffner *et al.* 2004; Kuffner *et al.* 2006) and higher light exposure can enhance cyanobacteria's growth (Reuter and Müller 1993) contributing to lower survival of the control treatments.

During long-term post-settlement survival, the macroalgae was replaced when their health started to degrade. The *D. delicatula* was not consistently the same species during the experiment due to the difficulty identifying Dictyotaceae in the field. There was a total of three different species used during the 8-week study and the exact impact of these species remains unknown. The overall trend of these brown algae decreased *P. astreoides* survival when compared to the plastic mimic. The brown algae used during this experiment shared similar morphology and was the reason for misidentifying these species as each other. There was a sharp decline of 40% survival during the first week next to *D. delicatula*. This could be a result of allelopathic compounds or abrasion and

shading by the macroalgae thalli. The morphology of *D. delicatula* has the characteristics of high abrasion and blocking sunlight (Rivers and Edmunds 2001). If the morphology was to blame for the decreased survival, then the other species would likely cause decreased survival as well. Larvae were exposed again to *D. delicatula* during week five, but was mixed with *Canistrocarpus cervicornis* and contributed to a decrease in post-settlement survival. I propose that *D. delicatula* is the main driver causing the mortality of newly settled polyps, possibly from allelopathic compounds. *Canistrocarpus cervicornis* effect on coral larvae is unknown. The other macroalgae used here, *Dictyota cf. pulchella,* was not included in my larval manipulation experiments, but did not affect survival in other studies (Kuffner *et al.* 2006).

3.7 Unanticipated Findings

For the first time this study found that *D. delicatula,* and possibly the genera *Dictyopteris*, negatively affected coral larvae recruitment. This genus is rarely reported on, but a couple of coral reef studies have documented the genus as a dominant macroalgae (Cole *et al.* 2008; Downie *et al.* 2013) indicating that *Dictyopteris* has the potential to interact with corals. I provided evidence that *D. delicatula* deterred *P. astreoides* settlement and is potentially decreased post-settlement survival. The mechanisms at which this macroalgae is affecting coral larvae was not determined within the scope of this research, but is likely from allelopathic compounds or physical interference. Pairing *Dictyopteris* with *Laurencia* resulted in lower settlement on *Laurencia* compared to when *Laurencia* paired with the control. This may be due to compounds released by *Dictyopteris,* but cannot be confirmed as the mimic paring with *Laurencia* did not differ from the either paired treatments. Additionally, all other treatments paired with *Dictyopteris* experienced no difference in larval settlement. There may be an interaction between the compounds released by *Laurencia* and *Dictyopteris* that could be affecting larval settlement similarly as the April 2015 cyanobacteria invasion of macroalgal treatments resulted in lower settlement than cyanobacteria alone (Kuffner *et al.* 2006). A similar response was observed by exposing the coral larvae to allelopathic compounds and increased temperature, which lead to a drastic reduction in coral larvae settlement compared to each stressor individually (Ritson-Williams *et al.* 2016). Although no study observed two macroalgae species and their combined effect on

larval settlement, it is conceivable that larvae change their behavior when two different chemical cues are present. This could help to explain why the side of the tile settlement was higher on the *Dictyopteris* treatment when paired with *Laurencia* and was not observed in any other treatment pairing.

Habitat selection is critical to subsequent survival of the coral into adulthood, since the location determines the environmental conditions experienced throughout its life history (Baird *et al.* 2003). Our knowledge of the complexity and selectiveness of coral larval choice in habitat selection continues to expand, as it is becoming more apparent that coral species and other sessile marine invertebrate larvae respond differently (Walters *et al.* 1996). For example, *Padina sp* enhances *Acropora muricata* (Denis *et al.* 2014) and *Acropora tenuis* (Dixson *et al.* 2014) larval settlement, but *Acropora millepora* is deterred by this macroalgae (Birrell *et al.* 2008b). *Sargassum muricatum* increases settlement of *A. millepora* (Denis *et al.* 2014), but deterred *Platygyra daedalea* (Pulido-Diaz *et al.* 2010). *Acropora. millepora* enhances settlement when exposed to *L. variegata* (Birrell *et al.* 2008b) but *P. astreoides* (Kuffner *et al.* 2006) and *P. daedalea* (Diaz-Pulido *et al.* 2010) are deterred by the macroalgae. Diaz-Pulido *et al.* (2010) found that all fleshy algae they exposed *P. daedalea* larvae to were deterred by the algae, including the plastic mimic. Some coral species are deterred from settling by algal structure while other species prefer structure depending on the macroalgae species (Birrell *et al.* 2008b). *Platygyra daedalea* was deterred by *L. intricata*'s structure (Diaz-Pulido *et al.* 2010), but I found that *P. astreoides* larvae preferred *L. intricata*'s structure leading to increased settlement on the top of the tile. At least one species was shown to settle on the algal structure over the substrate. Olsen *et al.* (2016) identified that neither *P. astreoides* nor *Acropora palmata* larvae were deterred or enhanced by *Halimeda opuntia*, but a significant amount of *P. astreoides* larvae chose to settle on the surface of the macroalga, eventually leading to coral mortality as the macroalga grows (Nugues and Szmant 2006; Olsen *et al.* 2016). It is not surprising that coral species are selective when it comes to habitat choice, coral recruitment location is species-specific and corals are particularly tuned to a preferred habitat (Baird *et al.* 2003).

Finally, identifying that larval swimming behavior varies depending on when they are released was not expected. The results indicated that a higher proportion of larvae

explored the bottom four days after coral colony collection when compared to one and two days after collection in June and similar variation occurred in April 2015, with a higher proportion of larvae exploring the bottom the first day after collection compared to larvae two days after collection. Larvae vary in their susceptibly to environmental stressors by their day released (Cumbo *et al.* 2013). Larval swimming behavior may also vary between coral larvae and the day they are released. It is possible that fewer colonies releasing planulae as larval collection goes on, leading to a higher proportion of larvae from one colony that may show preference towards a downward swimming behavior.

3.8 *Macroalgae Impact on Coral Reefs*

I further demonstrated that *L. intricata* is not decreasing and Dictyotaceae is decreasing the preferred habitat for *P. astreoides* larvae on South Florida reefs. This is particularly important because *Laurencia* (Stacy Prekel, unpublished) and some species from the family Dictyotaceae (Lirman and Biber 2000) show seasonal fluctuation on South Florida reefs coinciding with peak planula release of *P. astreoides* (Chornesky and Peter 1987; McGuire 1998; Kuffner *et al.* 2006). A high *Laurencia* abundance could result in higher recruitment of corals to Florida reefs and improve juvenile coral survival. Unlike *Laurencia*, Dictyotaceae macroalgae occurring during peak planular release would negatively affect *P. astreoides* larval recruitment, reducing settlement and polyp survival. *Laurencia spp.* cover was observed as high as 52% (Stacy Prekel, unpublished) and *Dictyota spp.*, Dictyotaceae family, cover was observed as high as 40%. Both percent covers were high enough to influence coral recruitment. If Dictyotaceae algae have higher cover than *Laurencia* during *P. astreoides* settlement, any benefit of *Laurencia* could be negated.

The final benefit gained by larvae settling next to *Laurencia* may improve survival during bleaching. Shading by macroalgae during mass bleaching has been shown to increase survival in juvenile corals, but this is usually viewed as short-term benefit due to the negative impacts associated with macroalgae (Birrell 2003). Because *L. intricata* did not decrease *P. astreoides* polyp survival, there would be no long-term impacts correlated to settling next to the algae. Shading by Dictyotaceae during bleaching events is viewed as a short-term benefit due to the allelopathic compounds released by several species in this family (Kuffner *et al.* 2006; Box and Mumby 2007; Paul *et al.* 2011). This

becomes particularly important as the frequency of mass bleaching events increases due to rising ocean temperatures, contributing to coral decline (Hoegh-Guldberg *et al.* 2007; McWilliams *et al.* 2005). Dictyotaceae phase-shift is more detrimental to coral reef recovery than a *Laurencia* dominated reef.

3.9 Conclusion

Overall, this study is the first to reveal the macroalgae, *L. intricata*, to enhance settlement and survival of *P. astreoides* larvae. Additionally, myresults imply that *P. astreoides* larval swimming behavior shows a preference to both attractant and deterrent chemical cues when trying to locate a coral reef. Furthermore, *D. delicatula* was identified as a deterrent to coral settlement and survival that warrants further study. *Laurencia intricata* seasonal increase coinciding with *P. astreoides* planular release has the potential to enhance coral recruitment and may counter some of the negative effects of macroalgae phase-shift and aid in coral reef recovery. Investigating other coral species' recruitment success next to *L. intricata* will ultimately determine its ecological impact to phase-shifted reefs.

Appendix

Taxonomic identification of Dictyotaceae voucher specimens collected off Broward County, along with their corresponding week introduced to survival treatments and date collected

Choice Voucher Species Identification	Week Replaced
Dictyopteris delicatula	1
Dictyota cf. pulchella	4
Pool: *Dictyopteris delicatula, Canistrocarpus cervicornis*	5
Canistrocarpus cervicornis	6
Dictyota cf. pulchella	7
Dictyota cf. pulchella	7

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