

**UNDERSTANDING ABUNDANCE, BEHAVIOR, AND TROPHIC POSITION
OF MESOPREDATORY REEF FISH: CASE STUDIES FROM THE
WESTERN PACIFIC AND CARIBBEAN OCEANS**

by

Lane Nicole Johnston

A thesis submitted to the Faculty of the University of Delaware in partial
fulfillment of the requirements for the degree of Master of Science in Marine Studies

Summer 2018

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ACKNOWLEDGMENTS

I would like to thank my advisor Dr. Danielle Dixson for providing me with this opportunity and support throughout my time at University of Delaware. Also, thank you to my committee for their help on this project and during my graduate experience. Thank you Dr. Pat Gaffney for the numerous conversations about statistical analysis, Dr. Doug Miller for additional help with statistics and ecological background, and Dr. Julia Spät for help with the original proposed project on elasmobranchs and continued support as the research changed.

I would also like to thank the entire Dixson Lab for their amazing support and collaboration. In particular, thank you to my work-wife Molly Ashur for all brainstorming, editing, feedback, friendship, and support, without whom I would not have been able to successfully complete my degree. I am also incredibly thankful for all the guidance and mentorship provided by Dr. Rohan Brooker. And to the entire close-knit family that has become the Dixson Lab: Jen, Paul, Emily, Taylor, and Zara, thank you for all your help in the field and lab, as well as the dear friendships that we have formed.

Thank you to my parents for constantly supporting me even from 3,000 miles away. Their love and encouragement has been ceaseless and I am so thankful for everything they have done for me. Thank you to all the friends that I have made during my time in Delaware. The close community of graduate students has made my time in Lewes an incredible experience, and I could not imagine going through this process without those close friends I have made here.

Lastly, I would like to dedicate this to Frank. Your light has consistently supported me through my many endeavors and has given me confidence when I needed it most. I know you would be proud of everything I have accomplished.

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ABSTRACT

Predator – prey dynamics are fundamental drivers of population structure, diversity, and behavior of organisms in all natural ecosystems. With the reduction of apex predators from human activities in almost every ecosystem, including terrestrial and aquatic, lower trophic level predators are becoming increasingly important in the Anthropocene. Understanding the behavioral traits of mesopredators is required for a better understanding of the relationships between predation and vulnerable life history stages for prey. Coral reefs are ideal model systems to examine the relationships mesopredators have with their environment and the communities of organisms they influence. Here, I conducted two experiments investigating the behavior of mesopredator reef fish in the Indo-Pacific and Caribbean Oceans. The arc-eye hawkfish, *Paracirrhites arcatus*, is a common fish found in the tropical waters of the Pacific Ocean. My findings demonstrate a strong preference for the branching Scleractinian coral, *Pocillopora eydouxi*, by *P. arcatus* on the reefs around Moorea, French Polynesia. Abundance of this preferred substrate explained the density and territory size for *P. arcatus*.

Habitat appears to be an important factor in determining behavioral characteristics of mesopredators worldwide. On the Mesoamerican Barrier Reef System, the common mesopredator *Halichoeres bivittatus*, the slippery dick wrasse was also influenced by habitat, most notably through diet, determined by stable isotope analysis, and density. These findings indicated that *H. bivittatus* individuals are site-attached, despite being found in both rubble and seagrass habitats. Findings

from this study demonstrated variation in diet, not only based on fish size, but also by habitat.

Understanding the behavior of these organisms in coral reef environments can better inform scientists about the ecological influence mesopredators have on population structures, particularly resulting from predation on the early life history stages of other coral reef fishes.

Chapter 1

PREFERRED CORAL DETERMINES TERRITORY SIZE, BEHAVIOR, AND DENSITY OF *PARACIRRHITES ARCATUS* ON MOOREAN REEFS

This chapter is in prep for submission to the journal Coral Reefs.

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1.1 Introduction

Predator-prey interactions are a fundamental exchange in natural ecosystems, driving factors such as species distribution, community composition, ecosystem resilience, and biodiversity (Duffy 2002; Jackson et al. 2001; Myers et al. 2007). The ecological importance of apex predators, such as wolves, lions, and sharks, is well understood, exerting top-down control on ecosystem structure and population dynamics (Heithaus et al. 2008; Myers et al. 2007; Pace et al. 1999; Schmitz et al. 2000). However, secondary predatory species, i.e. mesopredators, also play key ecological roles, for instance mediating the populations of smaller prey through both direct and non-consumptive effects (Brook et al. 2012; Schmitt et al. 2009).

Understanding the ecological role of mesopredators is especially important given the

declines of apex predators occurring globally (Jackson et al. 2001). The mesopredator release theory suggests that, as top predators are removed, intermediate predators will flourish, resulting in higher predation rates on smaller prey organisms (Prugh et al. 2009). In contrast to apex predators that are often highly mobile, requiring large areas of space to hunt to meet energetic requirements, mesopredators are relatively sedentary, relying on the habitat available within small territories for food and resources (Feeney et al. 2012; Gordon et al. 2015; McNab 1963; Palacios et al. 2016). As most species exist within heterogeneous environments, understanding how smaller mesopredators select, and interact with, their habitat can provide further information on their ecology, and the impacts of mid-level predation within an ecosystem.

An ideal model system for examining these relationships is found on coral reefs. These ecosystems rank among the most biodiverse on earth, with a myriad of trophic levels and species occurring in relatively small finite locations at high densities (Davidson 1998; Knowlton 2001). This diversity is, in part, linked to the habitat and trophic diversity that coral reefs provide. While the role of large predators, and apex predator declines, on coral reefs has been well studied (Jackson et al. 2001; Heithaus et al. 2008, Myers et al. 2007), the role of smaller reef-associated mesopredators is less understood despite their ecological importance (Almany and Webster 2006). Nonetheless, coral reefs are home to a high diverse assemblage of small predators from a variety of taxa, including many fishes and crustaceans. Some evidence indicates that these species can exert strong control over small prey populations with

important ecological consequences. For instance, the presence of small, predatory fishes can influence patterns of larval fish settlement and post-settlement survival, with subsequent wide-ranging effects on recruitment, population structure, and replenishment (Almany 2003, 2004; Vail and McCormick 2011; Dixon et al. 2012). As mesopredators, with low trophic level status, have the potential to impact key ecological processes that affect resilience, understanding their behavior is essential.

Small, predatory reef fishes are often highly specialized, frequently relying on reef-forming Scleractinian corals for habitat. The structural complexity that these corals provide is essential for these species, both providing shelter from larger predators and increasing refuge for mid-trophic level predators (Beukers and Jones 1998; Graham and Nash 2013). While the importance of live corals for fishes is well established, many species display strong species level preferences for corals, with the underlying drivers for this behavior often unclear. However, as corals continue to decline worldwide, determining the effects of changing coral communities on small, predatory reef fishes is increasingly critical to the understanding of how these ecosystems will respond to future conditions (Wilson et al. 2006). For instance, patterns of habitat use, feeding modes, periodicity in activity level, and other types of behaviors by mesopredators may influence similar patterns in prey species. Examining habitat use and species interactions in areas with different levels of coral coverage can provide evidence for how shifting benthic communities will impact associated organisms and processes.

An excellent model for examining coral-mesopredator interactions is the hawkfish (Cirrhitidae) due to their prevalence on all Moorean reefs. These fishes are common mesopredators on coral reefs worldwide, often associated with Scleractinian corals (DeMartini 1996; Kane et al. 2009; Coker et al. 2015). As they lack swim bladders, hawkfish spend most of their time perched, hawk-like, on coral branches and rubble, only swimming over the substrate in short bursts (DeMartini 1996; Randall 1963). From these perches, hawkfish can monitor their surroundings for potential prey, striking at small fishes and invertebrates (Hiatt and Strasburg 1960, Leray et al. 2012). Some hawkfishes display preferences for specific coral habitats; however, what drives these preferences, and if they influence subsequent behavior, remains largely unknown. For instance, in Moorea, French Polynesia, the arc-eye hawkfish, *Paracirrhites arcatus*, often occupies *Pocillopora* corals (Leray et al. 2012). Although this preference likely reflects the advantage this coral habitat provides, it is not known if *P. arcatus* distinguishes between *Pocillopora* species, and if preferred coral availability impacts hawkfish density, alters the hawkfish behavior or the resident prey. To this end, I examined if a) *P. arcatus* exhibited species-level coral preferences, and if so does preferred coral availability correspond with differences in b) *P. arcatus* abundance or c) spatial or temporal variation in behavior.

1.2 Methods

1.2.1 Habitat preferences of *P. arcatus* and effects of preferred coral on abundance

Observational transects were conducted on the reef at two sites surrounding Moorea Island (Figure 1.1; Temae - 17°29'52"S, 149°45'14"W and Vaipahu - 17°28'52"S, 149°51'20"W), during January and February 2016, to determine if coral habitat influences abundance of *P. arcatus*. Temae is located on the northeastern side of the island, within the reef crest, and is characterized as a lagoon habitat. Vaipahu is located on the north side of the island, beyond the reef crest, and is characterized as an outer-slope habitat. At Temae, twenty 25 × 2m transects were run perpendicular to the island. At Vaipahu, fifteen transects were conducted; five 25 × 2m and ten 13 × 2m. Overall, a total of 750 m² of reef was surveyed at Temae and 486 m² reef was observed at Vaipahu. For each transect, the total number of *P. arcatus* was recorded along with the substrate composition upon which they were found. Additionally, a note was made if the substrate was shared with another hawkfish, of the same species or otherwise (*Neocirrhites armatus* were also present but less abundant on Moorean reefs). Total substrate composition along transects was also estimated visually into the following categories: *P. eydouxi*, *Porites* sp., other hard coral, rock and algae. As *P. eydouxi* was the preferred habitat utilized by *P. arcatus* (chi-squared test), coverage of this coral species (over total coral coverage, *Porites* sp., etc.) was used in additional analysis for this study, as the focal species was most closely associated with this specific coral habitat.



Figure 1.1: Island of Moorea, French Polynesia. Study sites are indicated in yellow. Vaipahu is located on the outer slope of the reef crest and Temae is in the lagoon inside the reef crest.

1.2.2 Effects of preferred coral abundance on *P. arcatus* behavior

To measure if the behavior of *P. arcatus* varies spatially or temporally, and if this reflects differences in coral abundance or composition, observations were conducted at both sites during three distinct time periods, morning 0800–1100, midday 1100–1400, and afternoon 1400–1700. For each time period at each site, minimums of five *P. arcatus* were observed for 40–65 minutes (mean time = 60 min, ± 6 SE), (Temae: 0800–1100 $n = 5$, 1100–1400 $n = 6$, 1400–1700 $n = 9$; Vaipahu: 0800–1100 $n = 5$, 1100–1400 $n = 5$, 1400–1700 $n = 8$). Fish were observed on snorkel at Temae and on SCUBA at Vaipahu from a distance of 2 m to ensure that observer presence did not

affect behavior (as per Sweatman 1984). During the observation period, each type of substrate used by *P. arcatus* as a perch, the number of moves between perches, the number of feeding strikes taken, and any intra or interspecific interactions with non-prey fish were recorded. When possible, feeding strike success was also noted based on swallowing motions or if food was visible in the mouth of the fish. The total length of the focal fish was estimated by noting where the tip of the head and tail were relative to points on the substrate, then the distance between these points was measured to the nearest 5 millimeters (Sweatman 1984). Following the completion of each observational period, the territory size (the polygon of area used by the focal individual during the trial period) to the nearest 0.5m was measured by transect-tape. The observer then visually estimated substrate composition within the territory.

1.2.3 Statistical analysis

Statistical analyses were conducted in R v3.4.4 (R Core Team 2018).

Difference in *P. eydouxii* coverage between sites was tested using a Wilcoxon rank sum test. A chi-squared test was used to determine if fish selectively spent more time on *P. eydouxii* than would be expected given its abundance. To investigate if site or *P. eydouxii* coverage explained variation in *P. arcatus* density, a stepwise model selection approach for a generalized linear model (GLM) using a poisson family and log link function was used. The model was run on the density of *P. arcatus* per m² between sites and against *P. eydouxii* coral coverage within each transect.

On examination of the territory data, one fish exhibited an exceptionally large territory (24 m²). Using the Grubbs' test for outliers ($p < 0.05$) this individual was considered an outlier and was removed from all tests that included territory size. With the outlier removed, territory size was log-transformed based on a Box Cox test. Using a stepwise model selection approach, a GLM tested for the effect of *P. eydouxii* coverage, site, time of day and fish size on territory size. To assess the effect of time of day, *P. eydouxii* coverage, site, and fish size on the total number of strikes and number of successful strikes, separate negative binomial GLMs with a log link function were used, as residuals were non-normal. Models were simplified using a stepwise model selection approach. Residuals for models that required normal distribution of residuals were tested for normality using the Shapiro-Wilks test.

1.3 Results

1.3.1 Habitat preferences of *P. arcatus* and effects of preferred coral on abundance

Paracirrhites arcatus preferentially selected *P. eydouxii* as habitat at both locations (Temae: $\chi^2=1645.6$, $p<0.001$; Vaipahu $\chi^2=216$, $p<0.001$). Of the 100 fish recorded, only 3 *P. arcatus* were observed on substrate other than *P. eydouxii*; all 3 were from the less *P. eydouxii*-dense location (Temae), and were either found on rock (n=2) or *Porites spp.* (n=1). Both site (Figure 1.2A; GLM) and percent *P. eydouxii*

coverage (Figure 1.2B; GLM) significantly impacted hawkfish density; however, there were no interactive effects between these variables (Table 1.1).

Table 1.1: Results of GLM evaluating effects to density of *P. arcatus*

	Estimate	Z-score	p-value
Location	1.190	2.607	<0.01
% <i>P. eydouxi</i> coverage	3.327	2.249	<0.05

P. eydouxi cover was lower at the Temae site, which corresponded with lower hawkfish density, averaging 1 hawkfish 41m⁻². In comparison, *P. eydouxi* coral coverage was significantly higher at the Vaipahu outer slope site (Figure 1.3, Wilcoxon rank sum test: $df = 1, p < 0.001$), corresponding with significantly higher hawkfish density, averaging 1 hawkfish 7.14m⁻² (Table 1.2).

Table 1.2: *Pocillopora eydouxi* coverage and *Paracirrhites arcatus* density between study sites.

	Temae	Vaipahu
<i>P. eydouxi</i> percent coverage ($\pm$ SE)	0.63 $\pm$ 0.05	25.00 $\pm$ 2.72
<i>P. arcatus</i> m ⁻² ($\pm$ SE)	0.02 $\pm$ 0.003	0.14 $\pm$ 0.019 SE

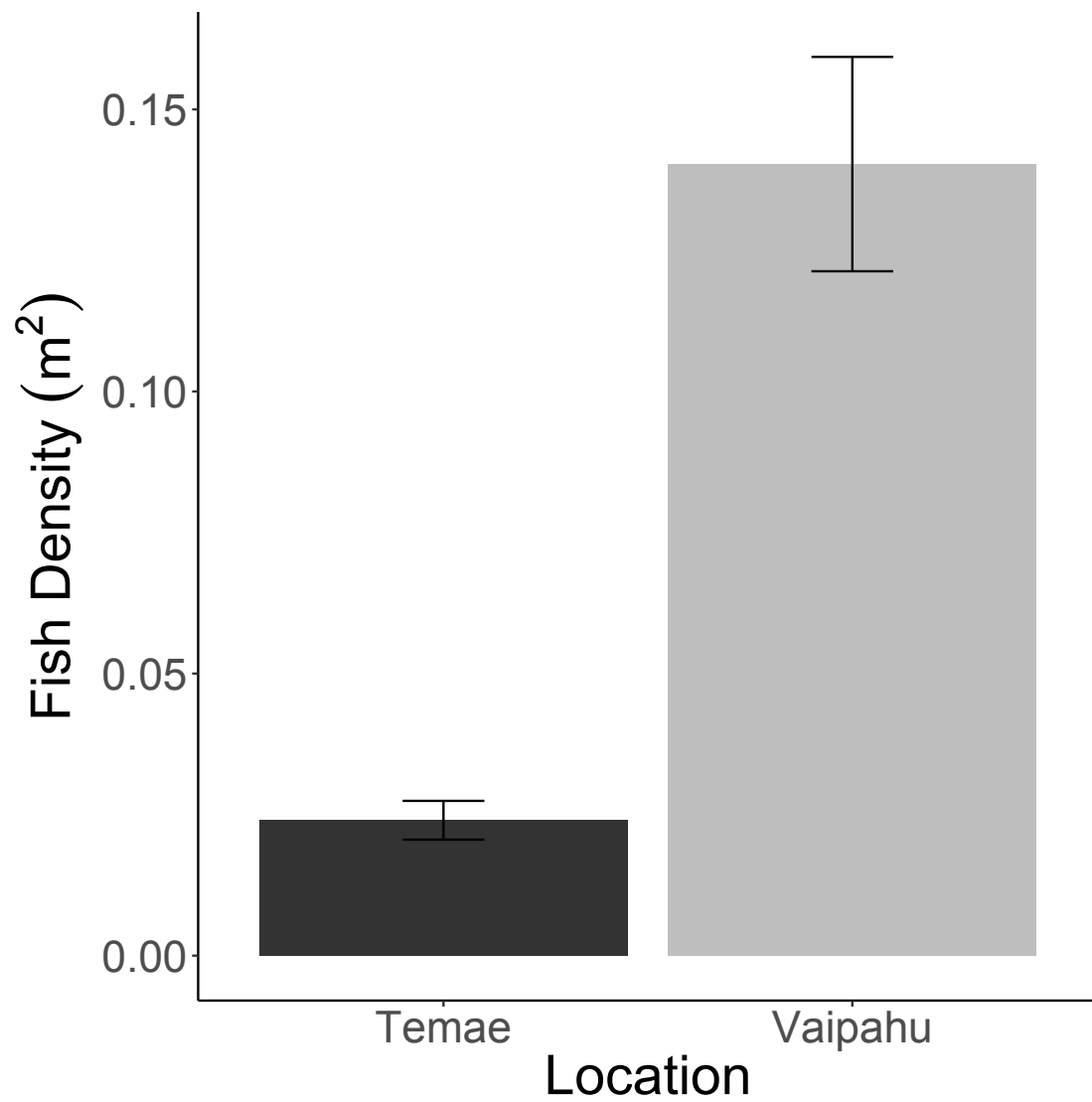


Figure 1.2A: Fish density significantly differed between locations (GLM; $p < 0.001$).
At Temae, mean *P. arcatus* $\text{m}^{-2} = 0.024 \pm 0.003$ SE and at Vaipahu mean *P. arcatus* $\text{m}^{-2} = 0.14 \pm 0.019$ SE.

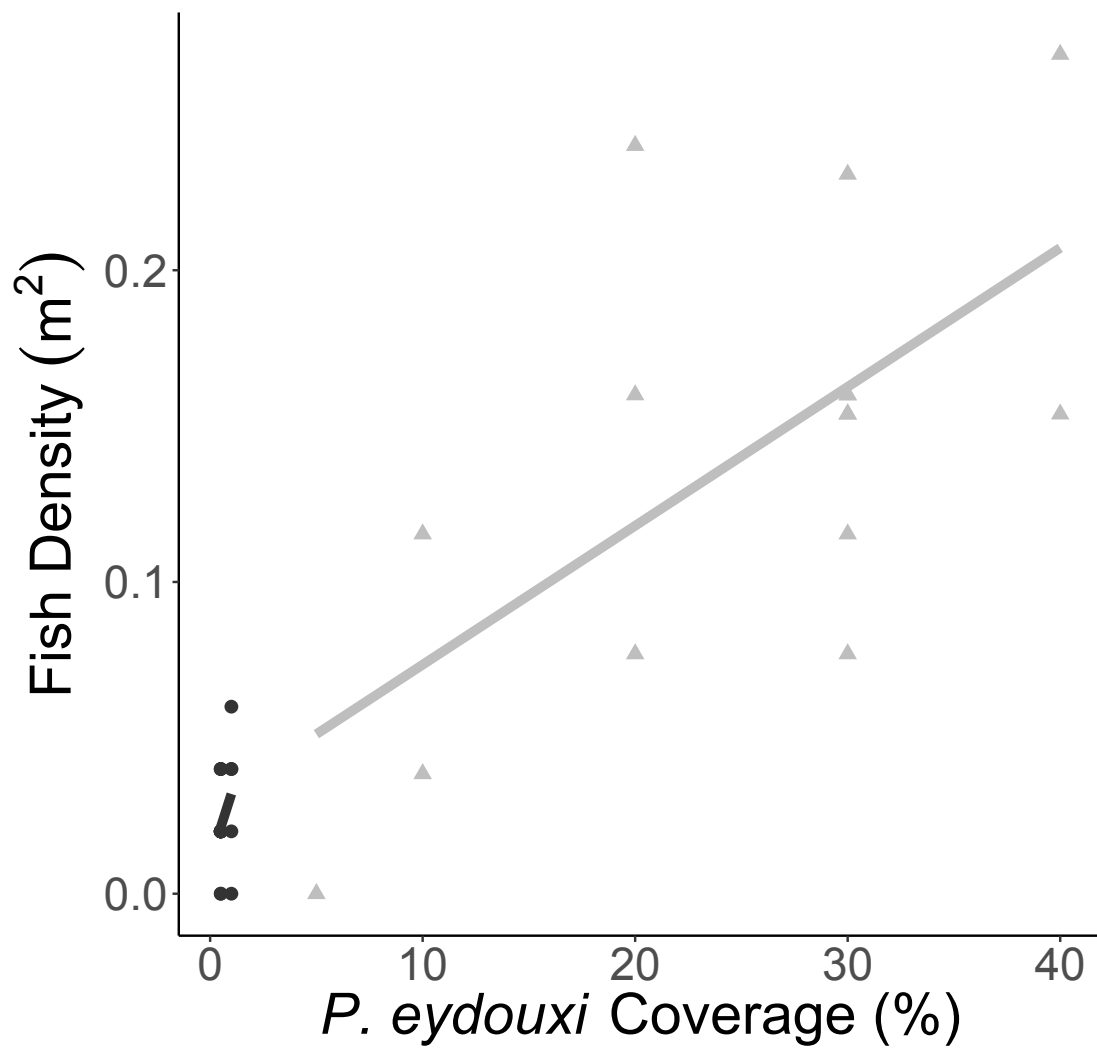


Figure 1.2B: *P. arcatus* density significantly increased with *P. eydouxi* coverage (GLM; $p < 0.05$). Temae had low *P. eydouxi* coverage while Vaipahu had more varied coverage.

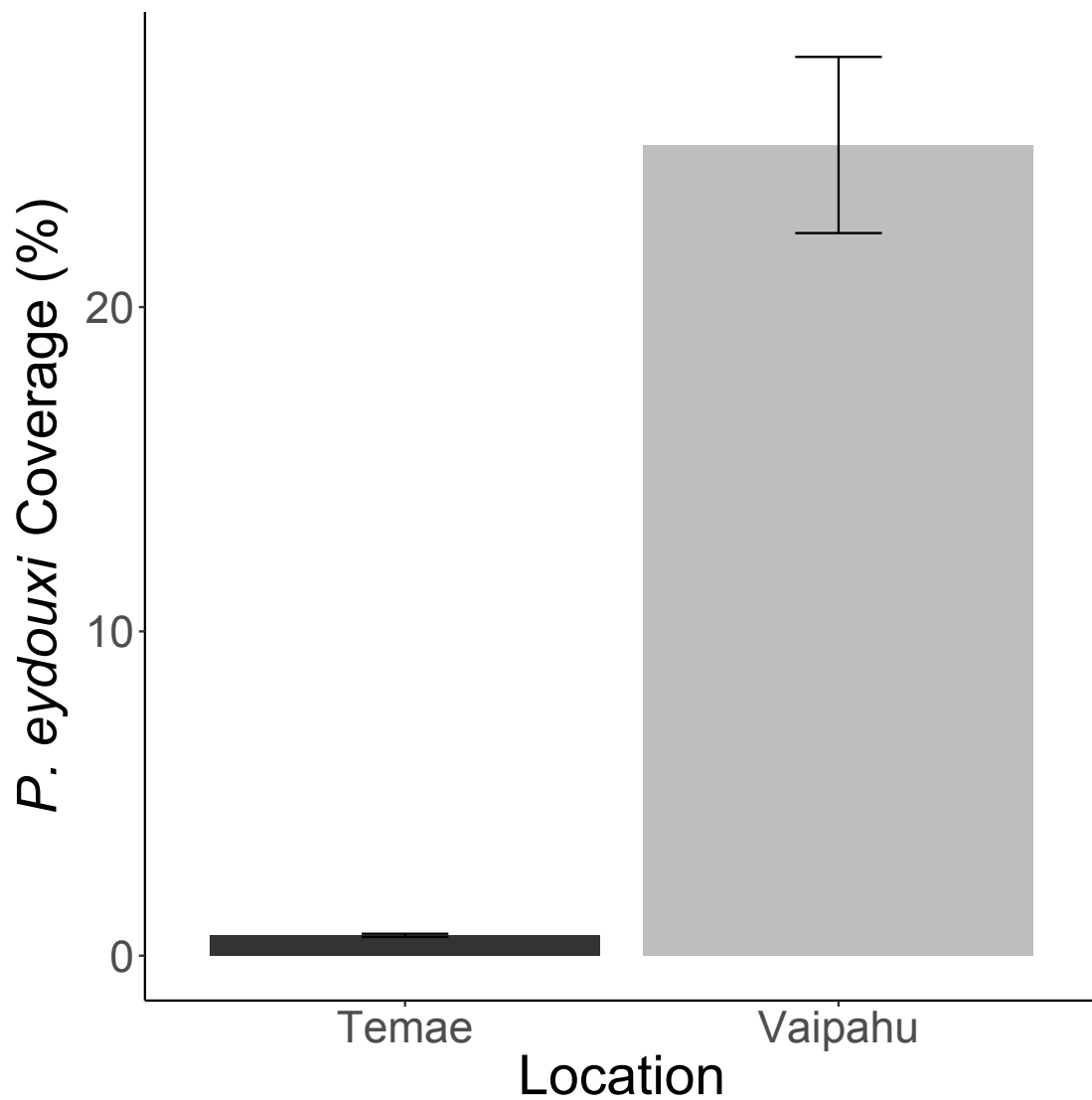


Figure 1.3: *P. eydouxi* coverage differed significantly between habitats (Wilcoxon rank sum test; $p < 0.001$).

1.3.2 Effects of preferred coral abundance on *P. arcatus* behavior

Territory size differed significantly between the two sites (GLM, $p = 0.004$), with the mean size of lagoon territories significantly larger ($3.2 \text{ m}^2 \pm 0.63 \text{ SE}$) than outer slope territories ($2.1 \text{ m}^2 \pm 0.45 \text{ SE}$). Time of day had no effect on territory size,

however across both sites, territory size decreased with increasing *P. eydouxi* coverage (Figure 1.4) and increased with fish size (Figure 1.5) (Table 1.3). There were no interactive effects of variables on the territory size of *P. arcatus* and thus were removed from the final model.

Table 1.3: Effects of main factors on territory size of *P. arcatus*.

	F-value	<i>df</i>	<i>p</i>
Location	9.98	1	0.004
Time of day	1.52	2	0.24
<i>P. eydouxi</i> coverage	48.44	1	<0.001
Fish size	6.64	1	0.01

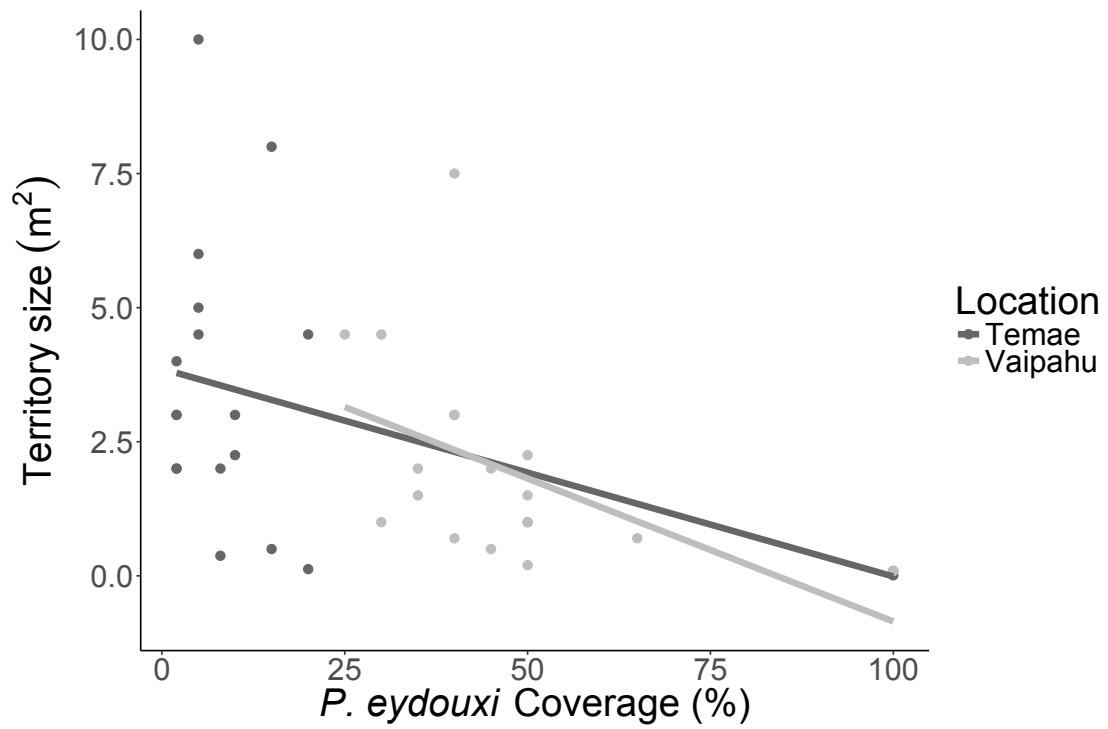


Figure 1.4: Territory size (m²) decreased with *P. eydouxi* coverage; GLM $p < 0.001$.

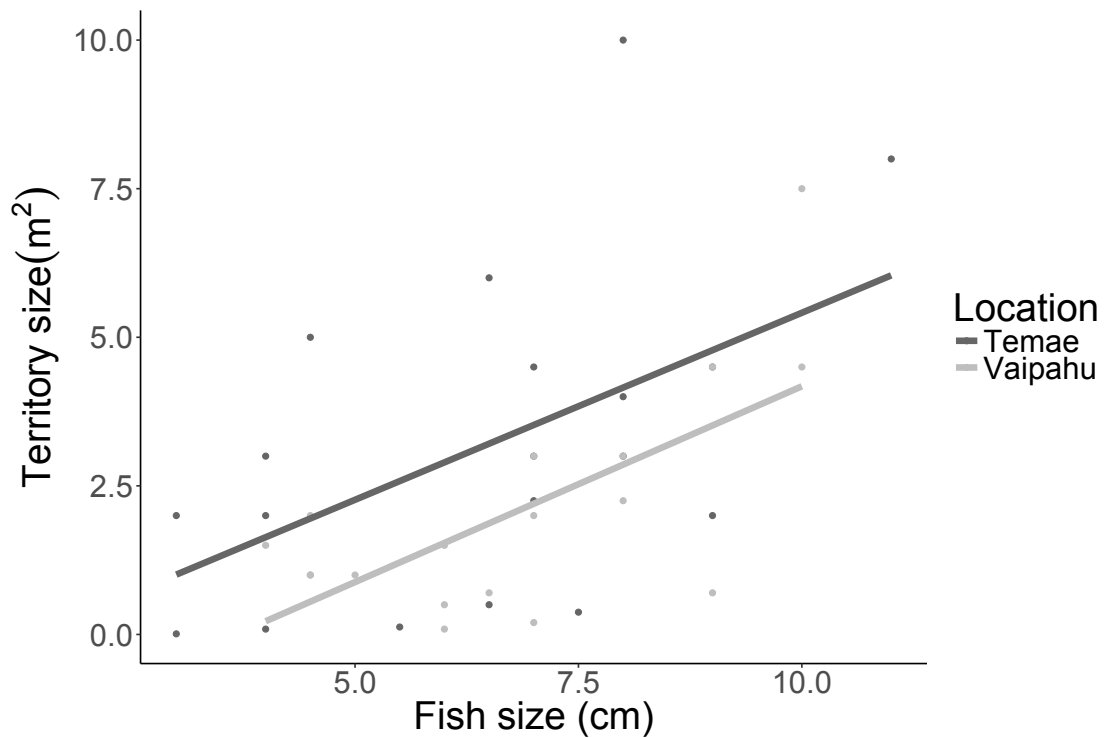


Figure 1.5: Larger fish patrol larger territories. Territory size significantly increased at both sites with an increase in fish size (Table 1.3).

There was no effect of site, observation time (morning, midday, or afternoon) or any interaction between these variables on the strike rates by *P. arcatus*. However, there was a significant effect of *P. eydouxii* abundance on strike rates (Figure 1.6; Estimate= -1.380, Z-score = -2.244, $p < 0.05$) with fish occupying territories with a greater density of *P. eydouxii* striking less. In addition, there was no significant effect of *P. eydouxii* density, location, observation time, or fish size on feeding strike success (Table 1.4). For this reason, data were pooled; fish observed had an average hourly feeding rate of 0.313 strikes $\pm$ 0.06 SE.

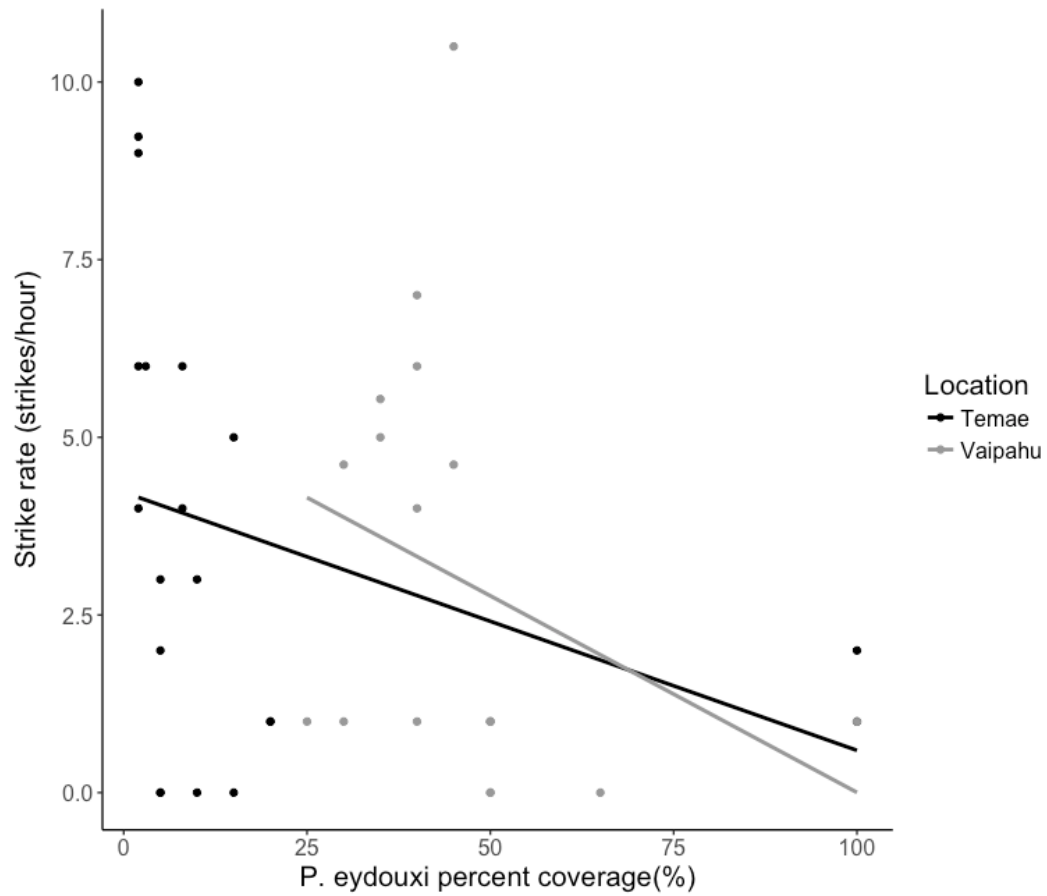


Figure 1.6: Strike rate decreased significantly with *P. eydouxi* coverage. Negative binomial GLM; $p < 0.05$.

Table 1.4: Results of effects to feeding strike success by *P. arcatus* (Negative binomial GLM).

	Estimate	SE	p-value
Location	-0.21	0.43	0.63
<i>P. eydouxi</i> coverage	-0.98	0.78	0.21
Fish size	-0.03	0.08	0.72
Trial length	0.02	0.05	0.68

1.4 Discussion

In Moorea, patterns of habitat use by *P. arcatus* were closely related to the abundance of *P. eydouxi* coral. *P. arcatus* associated with *P. eydouxi* more than expected given availability, indicating a preference for this coral species. Other studies on this species have also shown preference for Pocilloporidae (DeMartini 1996; DeMartini and Donaldson 1996; Beukers and Jones 1998; Kane et al. 2009; Shima et al. 2008; Schmitt et al. 2009; Coker et al. 2015). This preference reflected abundance, with the lagoon site, Temae, characterized by both low *P. eydouxi* coverage and *P. arcatus* abundance, and the outer slope site, Vaipahu, characterized by both high *P. eydouxi* coverage and *P. arcatus* abundance. Fish movement also reflected preferred coral availability, with *P. eydouxi* coverage inversely related to territory size, suggesting that, where access to this coral is limited, fish must patrol a greater area (Figure 1.4). Together, these findings suggest that the availability of *Pocillopora* coral is a critical factor in the ecology of *P. arcatus*. Due to a number of historic bleaching events in French Polynesia, there are limited species of coral that are present on the reefs (Pratchett et al. 2013). *Pocillopora* spp. are considered thermally-tolerant corals that have outcompeted other, more vulnerable branching coral species on these reefs (Pratchett et al. 2013). Thus as one of the few branching corals available on the reefs of Moorea, it is an ideal microhabitat utilized by *P. arcatus*. The structural complexity provided by *P. eydouxi* provides shelter from larger fish, hosts and attracts abundant prey, and provides a good perch for hunting for this mesopredatory fish (Beukers and Jones 1998). For *P. arcatus*, many of the recruiting fish that form a primary prey

source use live coral as habitat, making preferred corals indirectly essential for providing food.

The strong relationship between territory size and preferred habitat availability is similar to what has been seen in various other coral-associated fishes. For instance, obligate corallivorous fishes often display preferences for corals at the genus or species level (Berumen and Pratchett 2006; Brooker et al. 2013), and will utilize smaller territories when preferred coral availability is high, but patrol larger territories when availability is low (Kokita and Nakazono 2001). For coral-dependent species such as corallivores, the need to search farther and longer for sufficient prey, or defend a larger area from other individuals, can result in weakened physiological condition, growth, and reproductive potential (Jones 1986; Kerrigan 1997; Pratchett et al. 2004).

Habitat availability is a limited resource on coral reefs. Not only does conspecific competition for space occur, but for favorable microhabitats, intraspecies competition can also arise (Schmitt et al. 2009). In addition to impacting the distribution of predators, the strong relationship between preferred corals and coral-associated predators will likely effect small coral-associated prey, as the presence of resident predators on substrate can displace prey fish that utilize the same microhabitat (Holbrook et al. 2011). For example, on the reefs of Moorea, larger *Pocillopora* heads will host either *P. arcatus* or colonies of damselfish, but not both (Holbrook et al. 2011). This effect can subsequently reduce coral skeletal growth as nitrogenous waste availability is reduced when larger colonies of fish are unable to occupy a coral

(Holbrook et al. 2011). Predation can also have indirect effects on prey recruitment if it prevents populations of older conspecifics from occupying a coral, as conspecific presence has shown to increase recruitment (Steele 1997; Sweatman 1983, 1985).

The effects of changing habitat abundance and quality on larval fishes and recruitment are well studied (Bonin et al. 2009; Syms and Jones 2000); however, it is equally important to understand how their primary predators will respond to future conditions on coral reefs. This is especially important for habitat specialists, as these species are likely to be more vulnerable than co-occurring habitat generalists (Munday 2004; Sale 1975). From this study, and others (see DeMartini 1996 and Kane et al. 2009) *P. arcatus* appear to be non-obligate habitat specialists, choosing to spend the majority of their time on coral heads of the branching species *P. eydouxi*. As climate change is expected to reduce coral cover, diversity, and topographic complexity, in particular through coral bleaching and mortality, predicting how predatory and prey habitat specialists will be influenced will help elucidate future dynamics of coral reefs (Munday 2004; Munday et al. 2008).

While this initial study investigated how the abundance of preferred coral habitat influences the distribution and behavior of an abundant mesopredatory fish, the results have relevance for understanding the role that these mesopredators play on Moorean reefs. Many studies on coral reef fish populations look at the influences on recruit abundance and behavior (Almany and Webster 2006; Bonin et al. 2009; Dixon et al. 2012; Holbrook and Schmitt 1997; Sweatman 1985), and my findings indicate

that the behavior of the predators that are consuming larval and newly recruited fish is an equally important story, and the pressure they exert can vary greatly as reef composition varies. Future studies should continue to investigate the role of mesopredators in marine ecosystems and how shifts in preferred habitat influence all trophic levels of marine food webs.

1.5 Acknowledgements

I thank Dr. Marc Besson, and Dr. Zoe Pratte for assistance with fieldwork and for the support from Dr. David Lecchini and the staff at the Centre de Recherches Insulaires et Observatoire de l'Environnement, Moorea. Thank you to Dr. Patrick Gaffney for help with statistical analysis. Funding for this project came from Dr. Dixon's start-up. This study was conducted under the guidelines of Institutional Animal Care and Use Committee, and the University of Delaware's animal ethics committee approved the project. (IACUC No. 1297).

Chapter 2

VARIATION OF PREDATION PRESSURE IN TWO TROPICAL MARINE HABITATS BY A COMMON CARIBBEAN WRASSE

2.1 Introduction

Population structures of coral reefs are controlled by a number of factors including recruitment, habitat availability, ecological disturbances, and predation (Connell 1978; Hixon and Beets 1993; Syms and Jones 2000). Many studies focus on the drivers of prey populations through larval settlement and recruit survival, in particular how habitat availability or predator presence can influence these key life history stages (Beukers and Jones 1998; Bonin et al. 2009; Munday et al. 2008; Steele 1999). Predators can have both direct and indirect effects on prey populations of fish. Direct effects of consumption by predators can negatively influence abundance, species richness and diversity of recruit fish populations (Caley 1993; Carr and Hixon 1995; Beukers and Jones 1998; Eggleston et al. 1997). For example, as many as 56% of taxonomically diverse juvenile coral reef fishes are estimated to be consumed within 1-2 days of settlement (Almany and Webster 2006). Indirectly, predator presence can suppress recruit settlement by the release of chemical cues by predators used by recruiting fish to avoid ‘risky’ areas during habitat selection (Dixon et al. 2012; Vail and McCormick 2011). Predator presence is one of the biggest threats to the early life stages of coral reef fish, and thus is important to examine in order to better understand population dynamics (Almany 2004; Carr and Hixson 1995; Shulman and Ogden 1987; Webster 2002).

Globally, apex predators are being lost at a dramatic rate in marine ecosystems through overfishing and other anthropogenic activities (Estes et al. 1998; Jackson et al. 2001; Myers et al. 2007). The mesopredator release theory, reviewed by Prugh et al. (2009), states that as apex predators are removed, the intermediate predator populations will increase, resulting in higher predation rates on the smaller prey organisms. For small recruit fish populations, these smaller abundant mesopredators are the biggest threats to their survival (Carr and Hixon 1995; Connell 1998; Feeney et al. 2012; Holbrook and Schmitt 2002). Small predatory piscivores fill a different trophic niche than large apex predators, with many mesopredator species considered resident, gape-limited predators (Carr and Hixon 1995; Feeney et al. 2012; Holbrook and Schmitt 2002). Understanding the behavior of mesopredators can provide insight on how early life history stages of reef fish populations are impacted.

Within tropical ecosystems, a number of different habitats are present, with some fish species utilizing multiple habitats such as seagrass beds, mangrove swamps, coral reefs and rubble habitat. Wrasses (*Labridae*) are an abundant mesopredatory fish found in most tropical and subtropical ecosystems (Nelson 1994). Several species of wrasses found on the Mesoamerican Barrier Reef are found in a number of habitats within the region, including coral reefs, seagrass beds, rocky/rubble habitat, and mangrove swamps (Rocha et al. 2015; Sayer et al. 1993; Victor 1982). While some labrids, such as *Xyrichtys martinicensis*, are found only in a specific tropical habitat and are highly site-attached, other species of labrids can be found in multiple distinct habitats within a region (Rocha et al. 2005; Victor 1987). *Halichoeres bivittatus* is a common wrasse that can be found in seagrass beds, rubble areas, and coral reefs of the Western Atlantic and Caribbean (Robins and Ray 1986). As this species is known to

feed on reef fishes, understanding variation in morphology and behavior of *H. bivittatus* related to the habitat where individuals are found can aid understanding their impact on recruit populations (Böhlke and Chaplin 1993). This study examined *H. bivittatus* found in Belize, including variation in density and morphology in groups from seagrass beds and rubble habitat. Additionally, I determined dietary differences based on size class and collection location. Lastly, I estimated predation on a model recruit fish species, *Stegastes partitus* and investigated whether larger *H. bivittatus* will consume larger individuals of the same prey species (*S. partitus*). Findings from this study illuminate the variable role *H. bivittatus* likely plays in population dynamics in the different habitats found in the Mesoamerican Barrier Reef System.

2.2 Materials and Methods

2.2.1 Study Site

This study was conducted in the habitats surrounding Carrie Bow Cay, located on the Mesoamerican Barrier Reef off the coast of Belize (16° 48'9.70"N, 88° 4'55.42"W) between July and October of 2018. Carrie Bow Cay is uniquely situated in close proximity to a number of tropical ecosystems, including coral reefs, seagrass beds, rubble scapes, and mangrove swamps. Here, I compared differences in the behavior of a common mesopredator fish found primarily in two habitats, seagrass beds and rubble scapes. Rubble areas used in this study were on the edge of reef and coral dominated areas. Seagrass beds were dominated by turtlegrass (*Thalassia testudinum*), and sparse growth of both manatee grass (*Syringodium filiforme*) and shoal grass (*Halodule wrightii*). Seagrass beds are interspersed with sandy patches.

The majority of the sampling efforts took place in a large 10×10 m sand patch surrounded by seagrass on all sides and with sparse coverage of seagrass within the patch.

2.2.2 Study Species

Halichoeres bivittatus, the slippery dick, a common wrasse found throughout the Caribbean and Western Atlantic is found in shallow waters of reef and rocky habitat, and less commonly in seagrass beds (Cervigón 1993; Robins and Ray 1986). As voracious predators, they are gregarious and often will aggregate into groups to feed when rocks are turned over (Böhlke and Chaplin 1993). *H. bivittatus* are protogynous hermaphrodites that undergo sex change with corresponding color change, transitioning from white with a beige-brown stripe in the juvenile and intermediate stages, to a green and pastel color terminal phase (Figure 2.1, Allsop and West 2003; Roede 1972). Due to their abundance and predatory nature, this species was selected to gain a better understanding of its influence on the ecosystem around Carrie Bow Cay, and likely to the greater Mesoamerican Barrier Reef.

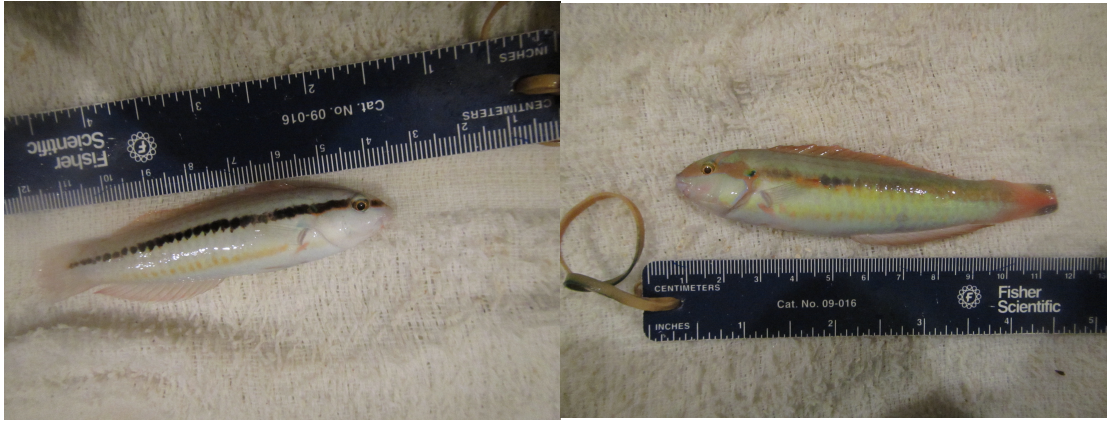


Figure 2.1 Intermediate and terminal phase *H. bivittatus* specimens

2.2.3 Transects

To determine difference in the density of *H. bivittatus* found in seagrass beds or reef/rubble areas, 20 × 2 m belt transects (n=16 in seagrass, n=10 in rubble/reef) were conducted. In the seagrass bed (depth = 7 m), transects were conducted on SCUBA, and in rubble areas (depth < 1 m), transects were conducted on snorkel. Transects were video recorded (GroPro Hero 4) when transect tapes were deployed to ensure researchers did not scare focal fish from transects. Videos were analyzed, recording the number of adult and juvenile *H. bivittatus* per 40m surveyed. A Wilcoxon rank sum test was used to determine statistical difference between the densities of *H. bivittatus* in the two habitats surveyed.

2.2.4 Samples for stable isotope analysis

To investigate if there are discrete groups of *H. bivittatus* living in the seagrass and rubble areas surveyed, samples were taken for stable isotope analysis. White muscle tissue samples from *H. bivittatus* (small: n=12, medium: n=12, large from the

seagrass: n=10, large from the rubble: n=10), ten *Xyrichtys martinicensis* (Rosy Razorfish), and ten *Thalassoma bifasciatum* (Bluehead Wrasse) were placed in 100% high-grade ethanol after removal with a scalpel. *Xyrichtys martinicensis* and *T. bifasciatum* were selected as comparative wrasses found in each habitat exclusively (seagrass and rubble respectively). Following return to University of Delaware, samples were removed from ethanol and placed in the drying oven at 60°C.

Samples were ground into a fine powder with a ceramic mortar and pestle and aliquotted into tin capsules using a Sartorius microbalance. Animal tissue was weighed into 1 ± 0.15 mg samples. All samples were sent to the Cornell Stable Isotope Laboratory (Ithaca, New York) to be analyzed for $\delta^{15}\text{N}$, $\delta^{13}\text{C}$, fractional total nitrogen, and fractional total carbon. Analyses were performed on a Thermo Delta V isotope ratio mass spectrometer interfaced to a NC2500 elemental analyzer. Instrument calibration was repeated every ten samples and used four standards, one chemical (Methionine) and three in-house ('CBT', 'KCRN', 'Deer'). The chemical and in-house standards had the following mean and standard deviations for $\delta^{13}\text{C}$: Methionine = $-25.10\text{‰} \pm 0.31$, CBT = $-25.66\text{‰} \pm 0.05$, KCRN = $-13.12\text{‰} \pm 0.04$, Deer = $-20.11\text{‰} \pm 0.05$. The chemical and in-house standards had the following mean and standard deviations for $\delta^{15}\text{N}$: Methionine = $-1.26\text{‰} \pm 0.26$, CBT = $17.55\text{‰} \pm 0.09$, KCRN = $1.32\text{‰} \pm 0.07$, Deer = $6.28\text{‰} \pm 0.06$. Isotope corrections were performed using a two-point normalization (linear regression) of all $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data using two in-house standards (CBT and KCRN).

Preserving samples in ethanol for stable isotopic analysis was thought to be appropriate given that other studies have done so (see Hempson et al. 2017); however upon further literature review, contradicting studies demonstrate preservation may influence stable isotope analysis (Arrington and Winemiller 2002; Jacobs et al. 2005; Kelly et al. 2006). To determine the influence ethanol preservation has on $\delta^{15}\text{N}$, $\delta^{13}\text{C}$, %N and %C in tissue samples, additional 20 samples of *H. bivittatus* are being tested. Part of the collected tissue sample will be dried fresh, and part will be preserved in ethanol before preparation for stable isotope analysis. Differences in isotopic analysis will be calculated and used to normalize original samples. To ensure bias was not introduced by lipid content in the stable isotope analysis, C:N ratios for animal tissue were analyzed. For the focal species, *H. bivittatus*, and comparative wrasses, *X. martinicensis* and *T. bifasciatum*, low lipid content, around 5% lipid (C:N <3.5), indicated there was no bias resulting from lipid content (Post et al. 2007).

To examine variation in trophic level, $\delta^{15}\text{N}$ values were used and for carbon-source (food source) $\delta^{13}\text{C}$ values were used. Welch's two sample t-tests tested for variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ between large *H. bivittatus* individuals from the two habitats. T-tests for each isotope were used to compare wrasses from the same habitat (i.e. from the seagrass: large *H. bivittatus* vs. *X. martinicensis*, and from the rubble: large *H. bivittatus* vs. *T. bifasciatum*). Ontogenetic variations in stable isotope ratios for *H. bivittatus* from the seagrass bed were tested using two linear regressions for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$.

2.2.5 Samples for otolith analysis

To verify size measurements were indicative of fish age, a subset of individuals collected for morphological measurements were euthanized according IACUC regulations for otolith removal. Otoliths of 25 individuals (small: 6, medium: 10, large: 9) were removed and an age analysis was conducted at the University of Delaware. Due to the size of *H. bivittatus* otoliths, specimens could not be sectioned and were analyzed whole (see Victor 1982). Otoliths were prepared by first cleaning and then set into Crystalbond adhesive on microscope slides. Otoliths were examined under a compound microscope at magnifications from 400 to 1000X. Using a mounted AxioCam ERc and the photo program AxioVision (Special Edition 64, version 4.9.1), color balance adjustments and photos of otoliths were taken for age analysis (Figure 2.2). Age indicated by growth marks were grouped into the following ages: 0+, 1+, 2+, 3+, with the + indicating growth beyond the final growth ring. There appeared to be no individuals sampled >4 years as there were never more than 3 sagittal growth rings observed. A Kruskal Wallis rank sum test was used to test if the length of *H. bivittatus* varied with age, namely if older fish were longer.

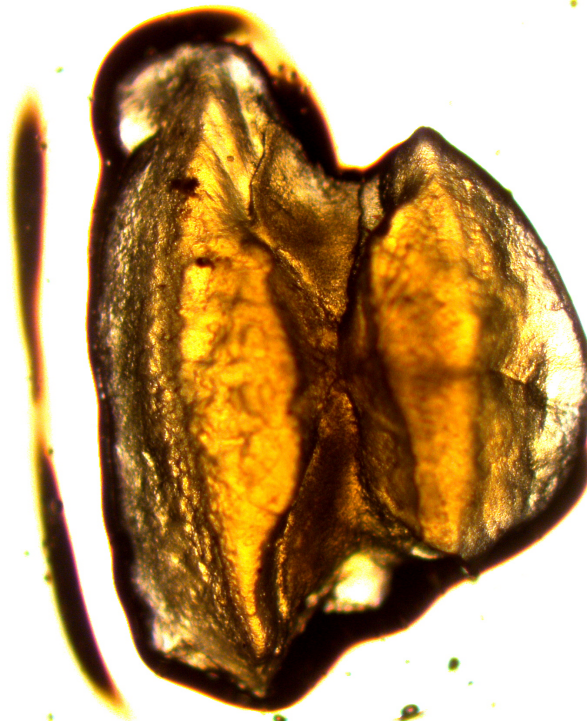


Figure 2.2: Sagittal otolith from a 135 mm TL *H. bivittatus* (2 growth rings visible).

2.2.6 Samples for morphological comparison

It is unknown if *H. bivittatus* utilize different habitats during different life stages or benefit differently from when living in one habitat compared to the other. To determine this, the relationships between the length and weight of *H. bivittatus* collected from either location were compared. Fish were collected using hand nets and measured to the nearest mm, lightly dried with a towel and weighed to the nearest gram. To ensure a range of different sizes were collected, fish were grouped into three size classes based on total length (TL): small (39 - 64mm, mean = 54.33mm $\pm$ 1.83 SE), medium (65 - 99mm, mean = 78.31mm $\pm$ 1.46 SE), and large (100-142mm,

mean= 122.23mm $\pm$ 2.14 SE). From the seagrass bed site, 34 individuals were analyzed (12 small, 12 medium, and 10 large), and from the rubble/reef site, 63 individuals were analyzed (12 small, 30 medium, and 21 large). Length data were transformed using a natural log and generalized linear model (GLM) was used to determine statistical difference in morphological measurements between habitats. An outlier identified through residual plot analysis was removed from the model; residuals from the new model were tested for normality using the Shapiro-Wilks test.

2.2.7 Feeding rate and prey-size preference experiments

The maximum feeding rate for *H. bivittatus* were tested by placing individuals into a 37-liter aquaria with three recruit *Stegastes partitus* (a common recruit fish found in rubble and seagrass habitats) with mean total length = 14.6 $\pm$ 0.41 SE. Trials began at 1900hr and ended 24-hours later. Approximately every 3 hours fish were checked and prey fish that were consumed were replaced, meaning for the majority of the trial there were three *S. partitus* available as prey. Initial trials indicated that *H. bivittatus* are not nocturnally active, and therefore prey replacement stopped at 2200hr and commenced at 0700hr. Two pieces of 1" PVC corners were placed in the bucket to provide prey fish with shelter. *H. bivittatus* were starved for 24hrs before the experiment was initiated and were weighed prior to and after the feeding rate experiment. Total counts for prey fish consumed were tallied for each individual.

Prey size selection can differ between species, with some mesopredators selecting a majority of small-sized prey, others selecting a majority of large-sized prey populations, and other predators not selecting based on prey size (Holmes and McCormick 2010). To determine if larger predators fed on larger prey fish, *H.*

bivittatus individuals of each size class (10 small, 12 medium, 15 large) were placed in 37-liter aquaria for 24hrs with 3 different size classes of *S. partitus* (Figure 2.3).

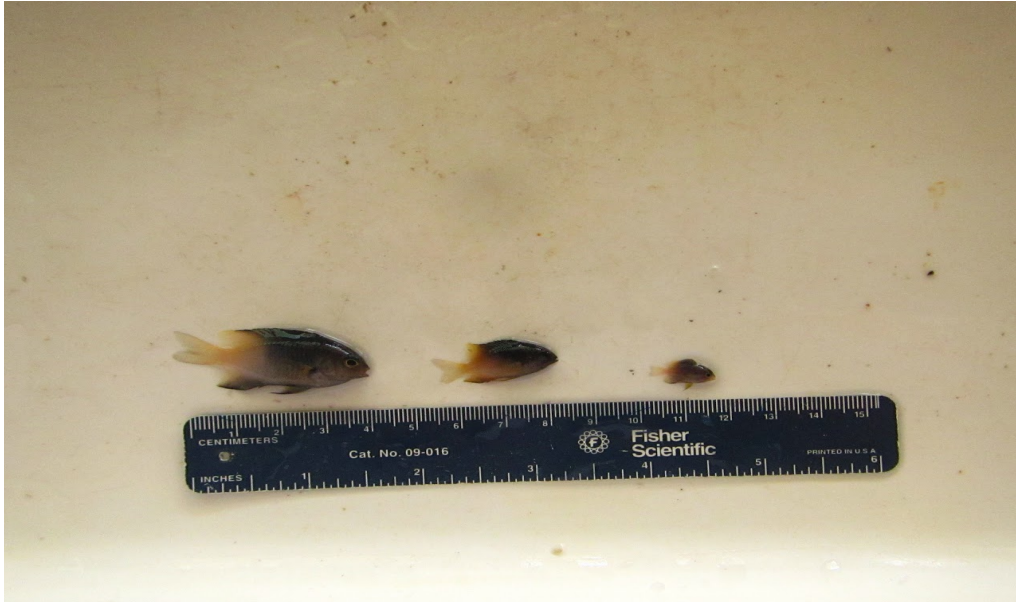


Figure 2.3: Prey *S. partitus* of 3 different size classes: small, medium and large.

Large *S. partitus* were small adults (mean TL $41.89\text{mm} \pm 6.15$ SD), medium *S. partitus* were juveniles (mean TL $28.65\text{mm} \pm 2.12$ SD) and small *S. partitus* were newly settled recruits (mean TL $14.64\text{mm} \pm 1.36$ SD); prey was collected with hand nets from the rubble. Prey *S. partitus* were not replaced during these trials to determine if predators would eat prey of various sizes. Total counts for prey fish consumed were tallied for each individual; some partial prey were found at the conclusion of the trial and were counted as eaten because prey fish were killed and partially consumed; and including these partially eaten dead individuals ensured a more conservative estimate of predation based on size. *H. bivittatus* were starved for

24 hours prior to the start of the experiment, and following the 24 hour trial individuals were weighed, and measured for TL. As a possible driver of prey-size preference, gape size was measured to determine if fish with larger gapes were foraging for a larger, more nutritionally dense food. Gape size was measured by opening mouth of *H. bivittatus* with forceps and measuring the vertical gape to the nearest mm. A linear regression was conducted to analyze how the vertical gape size varied with fish total length. A prey index was used to test if fish size predicted the prey size that individuals were targeting (Table 2.1). No large prey *S. partitus* were consumed by any size predator and thus were not included in the exact Jonckheere-Terpstra trend test for significance (analysis conducted using StatXact (Cytel, Inc.)).

Table 2.1: Prey index used to test predation by different sized *H. bivittatus*.

Index	Prey ingested
0	No fish consumed
1	Small <i>S. partitus</i> consumed
2	Medium <i>S. partitus</i> consumed
3	Small and medium <i>S. partitus</i> consumed

2.3 Results

2.3.1 Transects

From transect surveys, densities of *H. bivittatus* varied between seagrass and rubble habitats (Figure 2.4; Wilcoxon rank sum test, $p < 0.001$). In the rubble, transect

data indicated that there is approximately 1 fish per 1.04 m² ($\pm$ 1.79 SE) compared to 1 fish per 6.45 m² ($\pm$ 6.25 SE) in the seagrass bed.

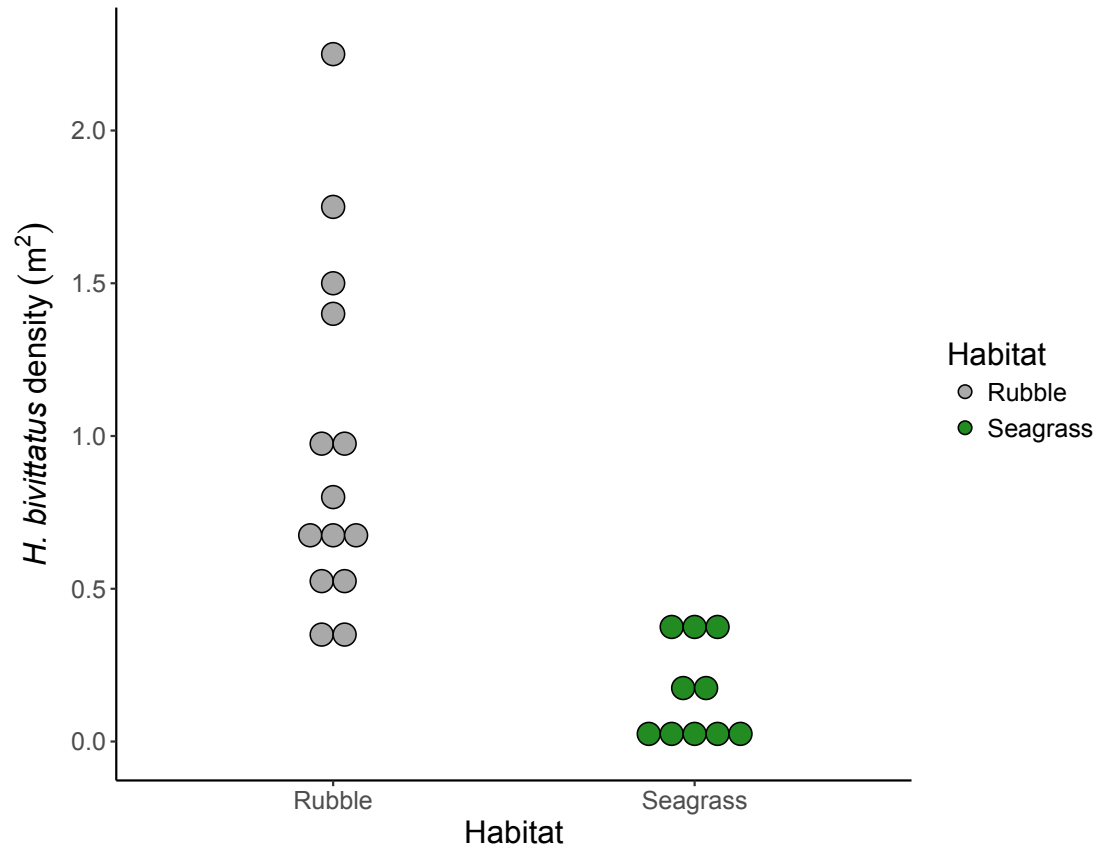


Figure 2.4: Density of *H. bivittatus*/m² differed in habitats surveyed, with higher density of individuals found in the rubble habitat. (Wilcoxon rank sum test, $p < 0.001$).

2.3.2 Stable isotope analysis

This study suggests there may be discrete groups of *H. bivittatus* living in the seagrass and rubble areas surveyed. $\delta^{15}\text{N}$ for populations of large *H. bivittatus* differed significantly between seagrass and rubble habitat, but did not differ for $\delta^{13}\text{C}$ (Figure

2.5; Table 2.2). Because $\delta^{15}\text{N}$ isotopic signatures vary between individuals of the same size class (large) from the two distinct habitats, there is evidence that the same species is consuming different diets as a result of the environment where individuals are found.

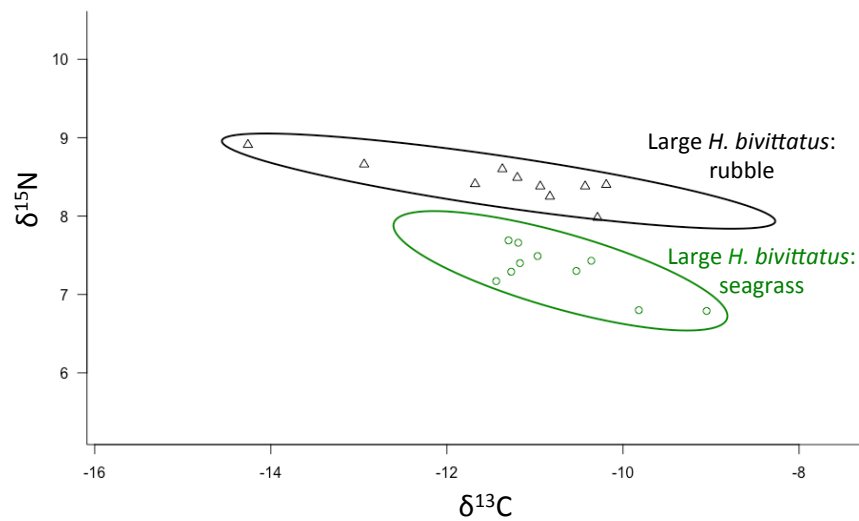


Figure 2.5: $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios with 95% confidence ellipse for large *H. bivittatus* from rubble (black triangle) and seagrass (green circle) habitats. (Separate Welch's two sample t-tests: $\delta^{13}\text{C}$ $p=0.16$; $\delta^{15}\text{N}$ $p<0.001$). Differing $\delta^{15}\text{N}$ ratios indicate individuals are feeding on distinct diets in the two different habitats.

Stable isotope values indicated that wrasse species (large *X. martinicensis* and large *H. bivittatus*) found in the seagrass had diets differing significantly in terms of trophic level ($\delta^{15}\text{N}$) and carbon source ($\delta^{13}\text{C}$) (Figure 2.6; Table 2.2). In the rubble,

stable isotope analysis from wrasses (large *T. bifasciatum* and large *H. bivittatus*)

differed significantly only by $\delta^{15}\text{N}$ (Figure 2.6; Table 2.2).

Table 2.2: Differences in stable isotope values for large wrasse populations. (Welch's two sample t-tests used to test for significance.)

	$\delta^{15}\text{N}$			$\delta^{13}\text{C}$		
	<i>t</i>	<i>df</i>	<i>p</i>	<i>t</i>	<i>df</i>	<i>p</i>
Within species (<i>H. bivittatus</i>) seagrass vs rubble	9.09	17.15	<0.001	-1.48	14.79	0.16
Between species (seagrass) <i>X. martinicensis</i> vs <i>H. bivittatus</i>	3.02	19.88	<0.001	5.95	19.05	<0.001
Between species (rubble) <i>T. bifasciatum</i> vs. <i>H. bivittatus</i>	4.52	14.48	<0.001	2.06	13.47	0.06

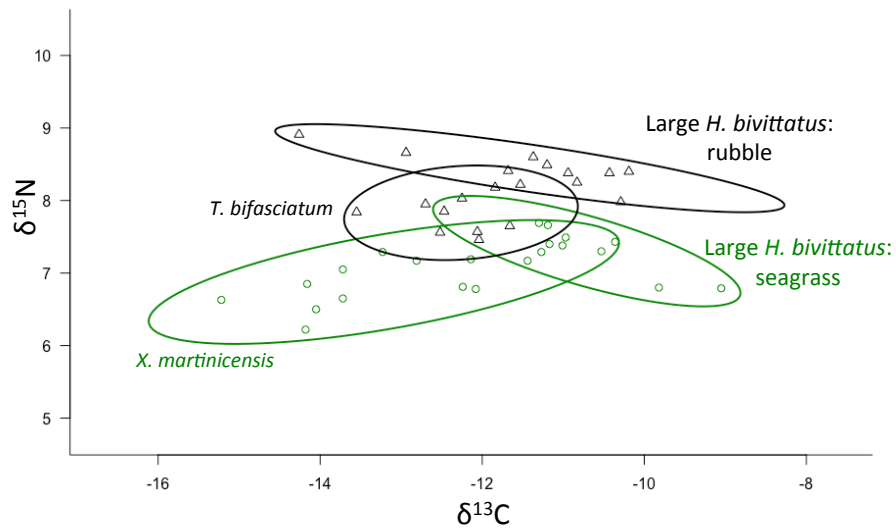


Figure 2.6: Comparative wrasse species from the seagrass (green circles) and rubble (black triangles). Welch's two sample t-tests indicate in the seagrass, between species varied significantly by $\delta^{15}\text{N}$ ($p < 0.001$) and $\delta^{13}\text{C}$ ($p < 0.001$). In the rubble, species varied significantly by $\delta^{15}\text{N}$ ($p < 0.001$) but did not by $\delta^{13}\text{C}$ ($p = 0.06$).

Within the seagrass bed, $\delta^{15}\text{N}$ values varied significantly with size (Figure 2.7), as did $\delta^{13}\text{C}$ values (Figure 2.8), indicating that as individuals grow their diets are composed of organisms from higher trophic levels and with different carbon sources.

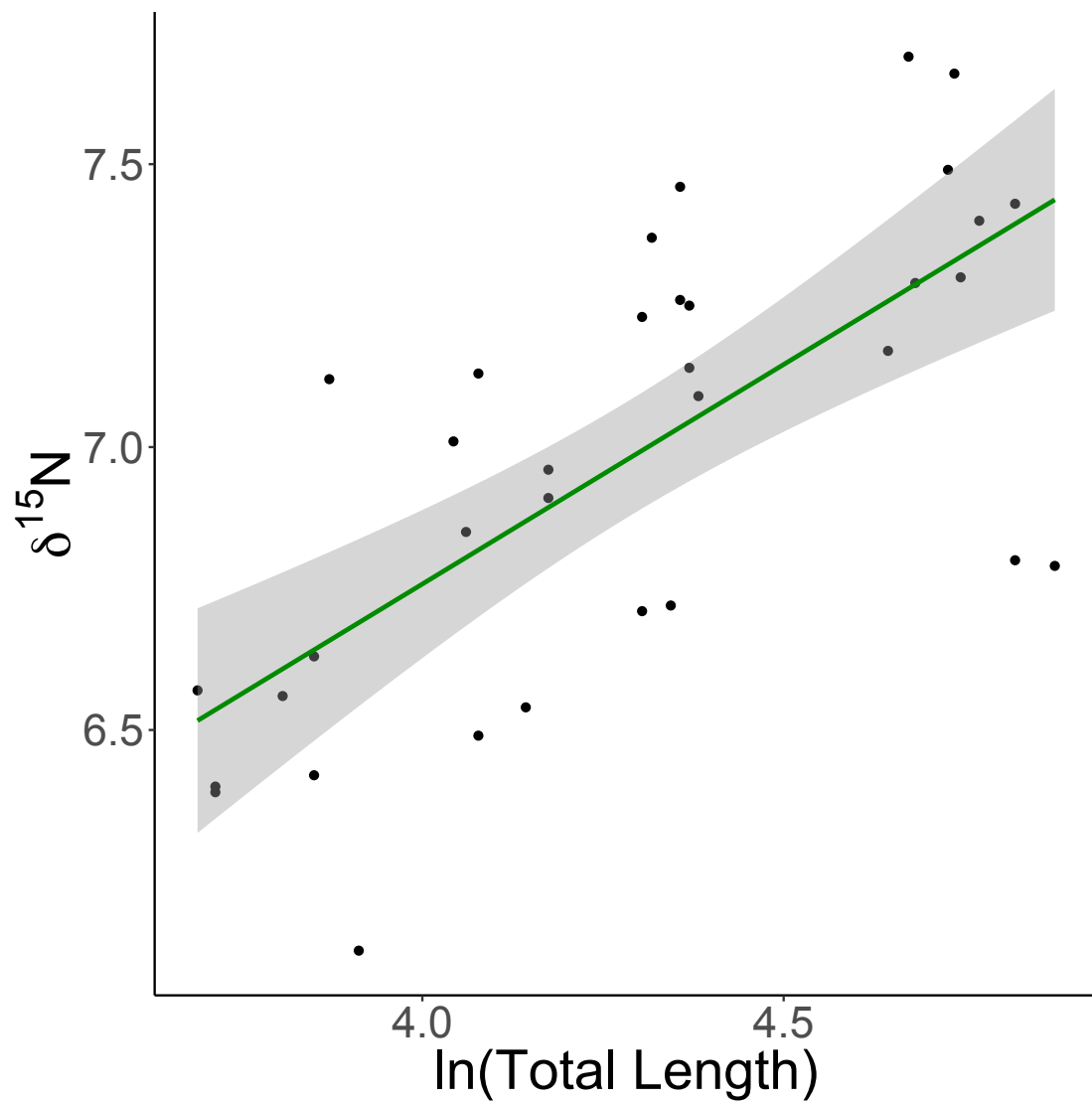


Figure 2.7: $\delta^{15}\text{N}$ values for differing lengths of *H. bivittatus* from the seagrass bed.
 Linear regression; $p < 0.001$, $\delta^{15}\text{N} = 0.78 * \ln(\text{TL}) + 3.65$ (95% confidence interval indicated by shading).

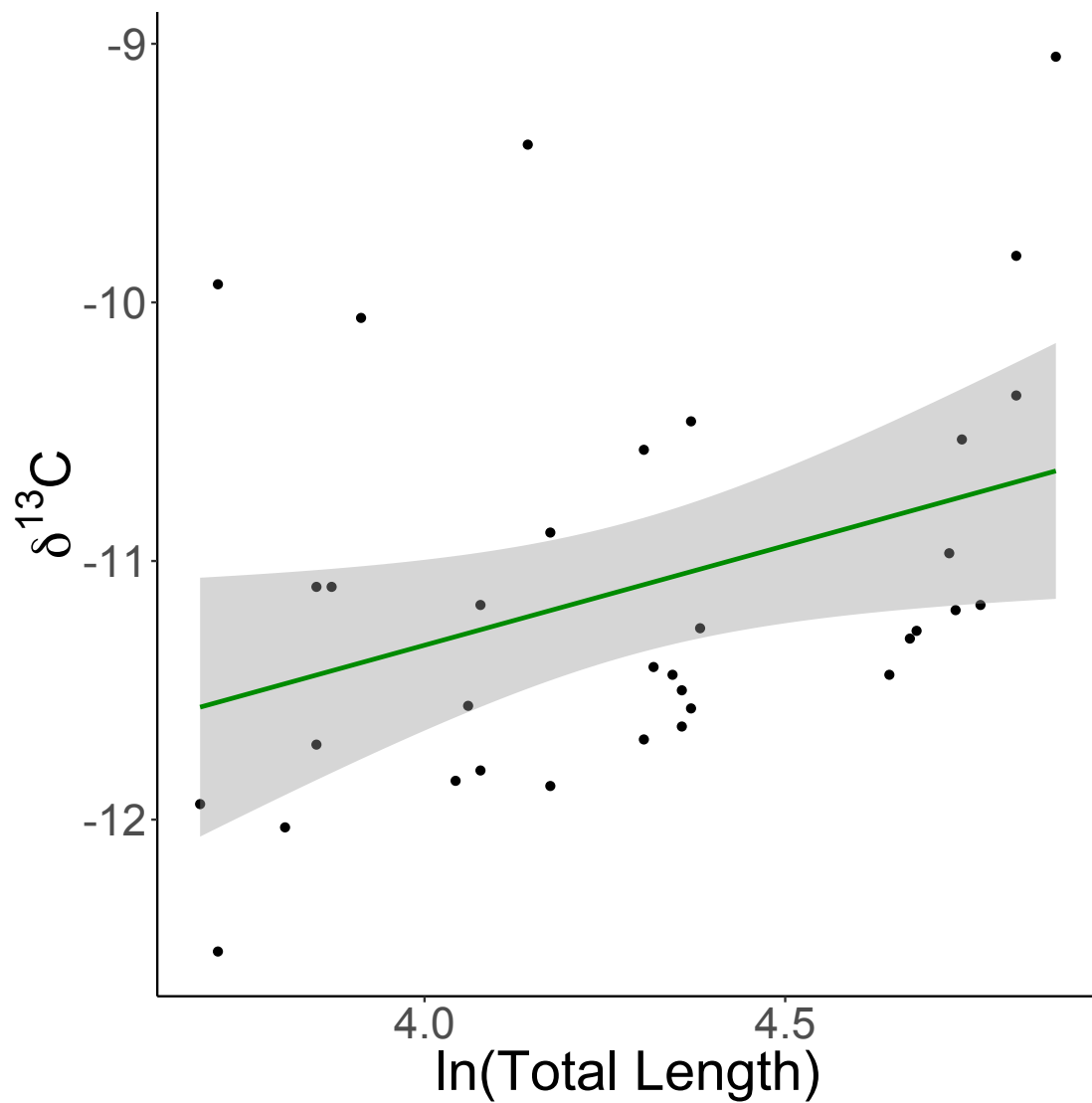


Figure 2.8: $\delta^{13}\text{C}$ values for differing lengths of *H. bivittatus* from the seagrass bed. Linear regression; $p=0.04$, $\delta^{13}\text{C}=0.77 * \ln(\text{TL}) - 14.41$ (95% confidence interval indicated by shading).

2.3.3 Otolith analysis

Otolith verification analysis indicated that group (small, medium, large)

average length is related to fish age (Kruskal Wallis test $\chi^2 = 16.36$, $p < 0.001$). Total

fish length increased with age as indicated by growth marks in sagittal otoliths (Figure 2.10).

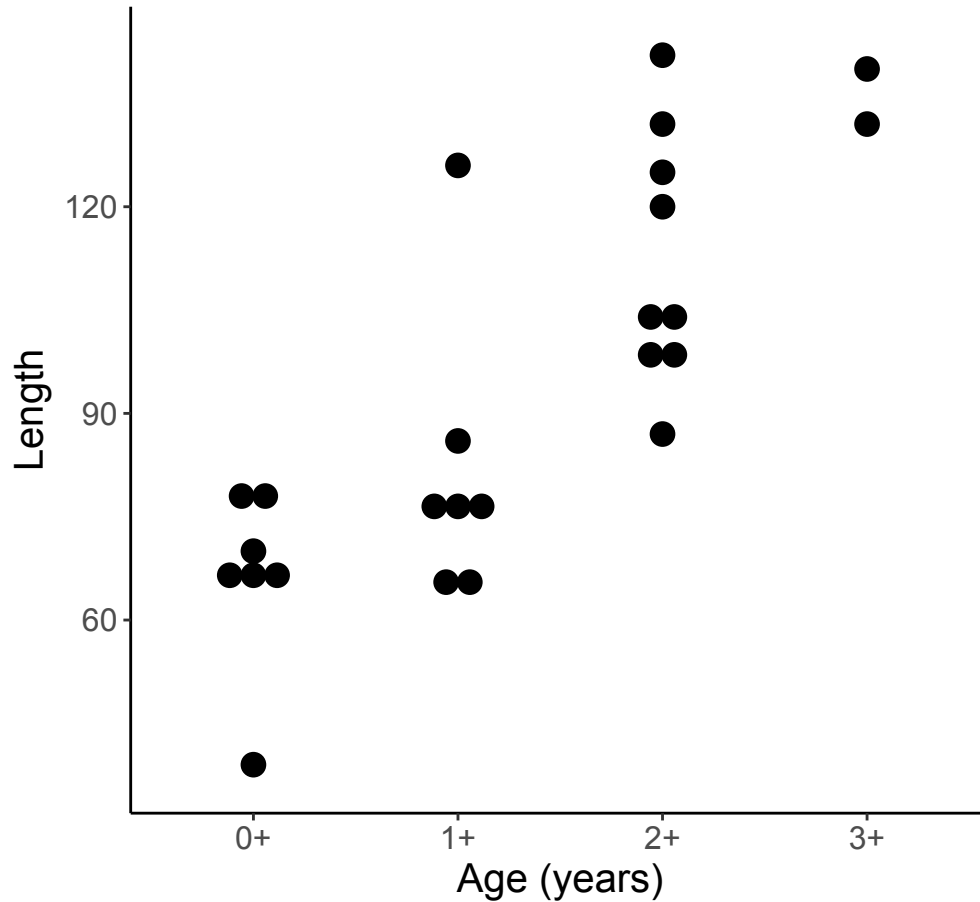


Figure 2.10: Total length of *H. bivittatus* significantly increased with otolith age estimates. Kruskal-Wallis rank sum test; $\chi^2 = 16.35$, $p < 0.001$.

2.3.4 Morphological comparisons

Length to weight relationships also varied between habitats and there was an interactive effect of length and habitat on weight (Table 2.3, Figure 2.9). For small individuals, *H. bivittatus* from the seagrass have smaller length to weight ratios than

their rubble counterparts, indicating that small fish from the seagrass are heavier than fish of the same length from the rubble. For example, small fish (mean = 54.33mm $\pm$ 1.83 SE) weighed 22% more if they were from the seagrass compared to the rubble. The length to weight ratios converged towards the upper end of *H. bivittatus* maximum size; large fish (mean= 122.23mm $\pm$ 2.14 SE) from the reef weighed only 5% more than fish of the same length from the seagrass bed.

Table 2.3 Morphological comparisons of *H. bivittatus* between habitats (GLM)

	F-value	<i>df</i>	<i>p</i>
Total Length (ln)	17983.89	1	<0.001
Habitat	27.42	1	<0.001
Length x Habitat	24.97	1	<0.001

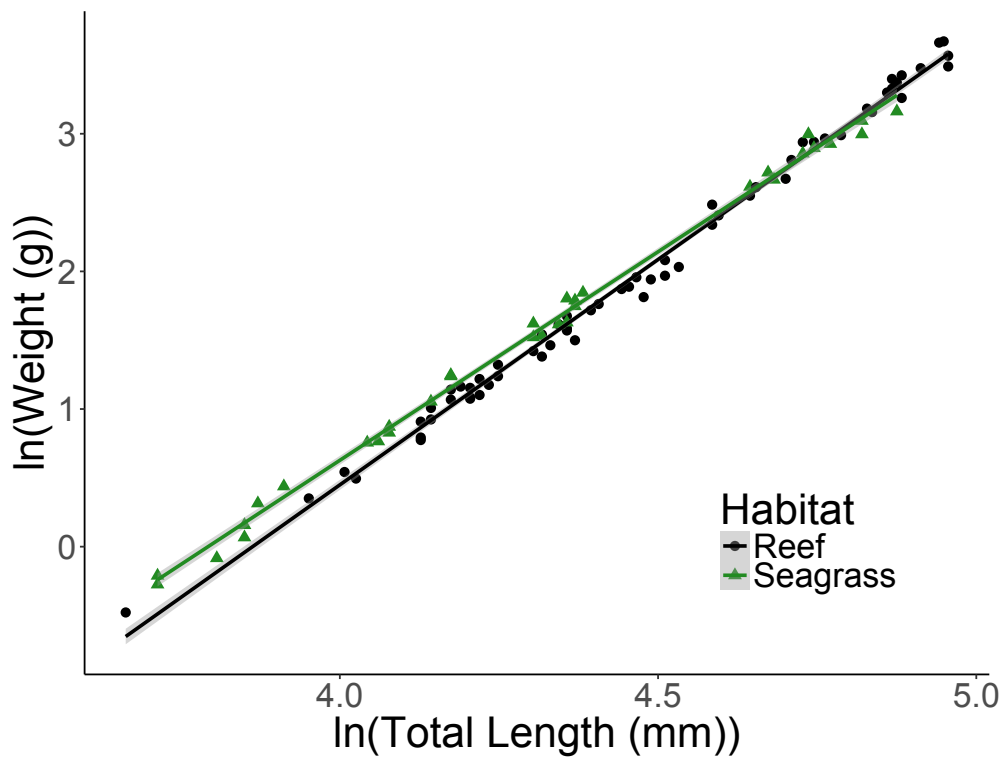


Figure 2.9: Length and weight regression lines of *H. bivittatus* populations from seagrass and rubble habitats.

2.3.5 Feeding rate and prey size preference

The mean feeding rate of *H. bivittatus* on recruit *S. partitus* was $1.85 \text{ fish} \pm 0.54$ per 24 hours. Since fish were replaced when consumed, this is likely an estimate of the upper end of their feeding rate. No significant relationship of prey size and predator size was found ($J-T = -1.52$ $p = 0.065$). Gape size and fish total length were significantly correlated (Figure 2.11; linear regression: $F_{(1, 35)} = 423.7$, $p < 0.001$), therefore as predator size did not predict size of prey consumed, gape may not be a limiting factor for *H. bivittatus*.

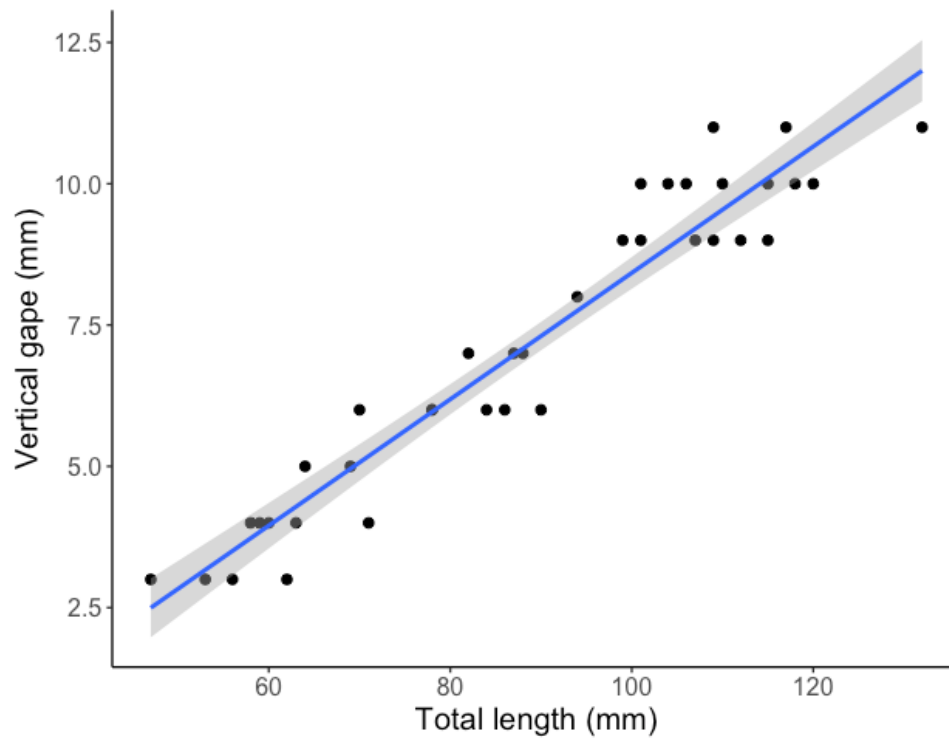


Figure 2.11: Gape significantly correlates to total length of *H. bivittatus* fish. GLM; $p < 0.0001$, Vertical gape (mm) = $0.11(\text{TL}) - 2.76$.

2.4 Discussion

My findings suggest that *H. bivittatus* is a site-attached mesopredator with significant differences between individuals found in the seagrass beds compared to those found in rubble habitats. Not only is abundance of *H. bivittatus* higher in the rubble areas, but also these two groups vary morphologically and by stable isotope content. There were individuals present in the seagrass, but the length to weight ratio (heavier fish of the same size in the seagrass than rubble) and differing levels of $\delta^{15}\text{N}$ (*H. bivittatus* from the rubble found higher on the trophic scale than those from the seagrass) suggest that *H. bivittatus* from the rubble are consuming higher on the food

chain, but small and young *H. bivittatus* from the seagrass are consuming more.

Increased weight of fish is often used in fisheries science as a measure of physiological condition and can result from diets with higher lipid content, increasing not only fitness but also reproductive potential and recruitment of new generations of fish (Adams 1999; Bolger and Connolly 1989; Chauyapechara et al. 2003). While this study did not specifically look at lipid variation between individuals from the two habitats, findings suggest that food availability and food quality variation between seagrass and rubble may explain differences for the focal study species.

Ontogenetic changes in diet for morphologically similar labrids has been well studied, indicating that larger fish consume more and larger prey (Roede 1972; Wainwright 1988). Similarly, Martha and Jones (2002) found ontogenetic variations in behavior of six similar labrid species, with juvenile *H. bivittatus* exhibiting more hovering and searching behaviors than their conspecific intermediate and terminal phase adults. Decreased searching and swimming alone more often, in adult *H. bivittatus*, may indicate that these individuals are more efficient at hunting and feeding. My findings of increasing $\delta^{15}\text{N}$ for larger size *H. bivittatus* in the seagrass (Figure 2.7) demonstrate that as these fish become larger, they are able to eat organisms found on higher trophic levels (Peterson and Fry 1987). Similar trends found in $\delta^{13}\text{C}$ values show that the carbon source of smaller *H. bivittatus* represents a more pelagic than benthic source (Hempson et al. 2017; Peterson and Fry 1987). Furthermore, while non-significant the laboratory feeding experiment demonstrated a trend towards larger fish consuming larger prey, but also being more effective hunters

of small prey fish. Other studies have highlighted the omnivorous tendencies of *H. bivittatus*, particularly their consumption of crustaceans, molluscs, and echinoderms, and ontogenetic variation exhibited in the diets of *H. bivittatus* for these prey with older fish consuming larger individuals of these phylum (Roede 1972; Wainwright 1988). This transition between the type of prey, as well as increased efficacy in foraging for *H. bivittatus* may be the mechanisms behind the variation for different sizes of this mesopredator.

In the context of broader ecological implications, variations found between different sizes (and age as confirmed by otolith analysis) of *H. bivittatus* found in either seagrass or rubble habitat, indirectly suggest that predation pressure varies across the *H. bivittatus* population. This is important because mesopredators, like *H. bivittatus*, are known to impact populations of larval and recruit fishes (Almany 2003, 2004; Vail and McCormick 2011; Dixon et al. 2012). While my results indicate larger fish exert predation pressure higher on the food chain through the stable isotope results, the prey-size preference feeding experiment did not demonstrate a significant relationship between predator and prey size.

For most prey, the bigger-is-better strategy is expected, as larger individuals will discourage predation by their consumers (Rice et al. 1993; Wang et al. 2007). The optimal foraging theory predicts that prey is not always protected at bigger sizes because predators will preferentially select prey of a certain size that gains them the most food for a given amount of energy expended during foraging (Hughes 1980; MacArthur and Pianka 1966). Similar to findings by Holmes and McCormick (2010),

I found that for *H. bivittatus* size classes (and likely gape-limitation, as these two morphological measurements are highly correlated) do not significantly discriminate based on prey size, and thus do not have an optimal prey size during the in-lab experiment. Rather than exhibiting a foraging strategy of higher reward with higher payout by consuming large *S. partitus*, larger *H. bivittatus* seemed more efficient at foraging overall, but not necessarily on large prey. Dietary niche based on ontogeny may be more discrete than what was captured in the experiment, with smaller *H. bivittatus* consuming invertebrates rather than recruit fish (Roede 1972; Werner and Gilliam 1984).

Despite some of the variation in predation patterns found for *H. bivittatus*, mesopredators are known to be extremely influential on recruit fish populations (Schmitt et al. 2009; Vail and McCormick 2011). Recruit fishes were seen in both seagrass and rubble habitats, but a further analysis of the transect data counting the number of recruits in each location will likely show that a greater number and species richness of fishes recruit to rubble habitats compared to seagrass, unless they are seagrass-specific species (additional transect analysis for recruit populations in prep). Jones (2005) found that several Caribbean wrasses, including *H. bivittatus*, utilized home ranges relative to their body size, but spent the majority (~50%) of their time in core activity centers that were a fraction of the total size of the home range (13-24% of total home range). Small core activity areas may explain the different groups of *H. bivittatus* found in separate habitats. Reflected in their diets through stable isotope analysis, these groups appear to live amongst their primary food source. Dissimilar to

species like roving parrotfish that can cover thousands of m² of reef, *H. bivittatus* seem to exert their functional role as a mesopredator over a smaller spatial scale (Welsh and Bellwood 2012). Understanding these behavioral patterns is useful in determining the influence this prevalent mesopredator has on the ecosystem as a whole. Of particular interests to ecologists is how population structures are formed, and one key influence to population structure is predation pressure at bottleneck points, such as larval settlement and recruit survival (Hixon and Beets 1993). *H. bivittatus* will consume recruit fish, but this study suggests that there are significant differences in the predation pressure they exert based on differing sizes and habitats where they are found.

2.5 Acknowledgements

I would like to thank Jen Joseph, Molly Ashur, Dr. Rohan Brooker, and Dr. Tiffany Sih for their assistance in data collection for this project. Additionally, I thank Jordan Zimmerman, Jake Matthews and Cameron Day for their help with otolith analysis. Thank you to Dr. Aaron Carlisle at UD and Dr. Kim Sparks at the Cornell Stable Isotopes Laboratory for assistance with stable isotope analysis and funding for this portion of the study provided by the UD Starves Howe Memorial Grant. This study was conducted under the guidelines of Institutional Animal Care and Use Committee, and the University of Delaware's animal ethics committee approved this project. (IACUC No. 1313).

CONCLUSION

For the two mesopredator species studied here, habitat was a key factor in determining behavioral patterns and impacts within their respective ecosystems. The findings from my first study indicated that the preferred coral of *Paracirrhites arcatus*, *Pocillopora eydouxi*, greatly influenced not only presence and abundance of this mesopredator, but also the territory size that individuals patrolled. With higher *P. eydouxi* coverage, fish had smaller territories, indicating that they may not have to travel as far to find sufficient resources. Similarly, my second study found that although *Halichoeres bivittatus* is present in both seagrass and rubble habitats in Belize, groups of individuals found in these respective habitats appeared to vary from one another. *H. bivittatus* from the seagrass had different isotopic signatures and length to weight ratios from those of the same size found in the reef area, indicating that these groups have different diets reflecting their habitat. Both these studies indicate that mesopredators can be highly site attached, leading to variances in behavior and diet given the environment in which they are found.

Population structures for coral reefs are controlled by a number of effects but predation is a major driver. As a result, mesopredators are known to be immensely important on coral reefs (Beukers-Stewart et al. 2011; Carr and Hixon 1995; Feeney et al. 2012; Holbrook and Schmitt 2002; Holmes and McCormick 2010). In particular, they can suppress populations, particularly during vulnerable larval, recruit, and juvenile stages (Almany and Webster 2006). Larval settlement and recruit survival are well studied, but my findings indicate that understanding both sides of the

relationship, influences to predator behavior and influences to prey behavior, can be informative when describing predator-prey relationships on coral reefs.

As habitat loss and overfishing continues to increase, mesopredators will undoubtedly be affected (Jackson et al. 2001; Munday 2004). Not only do my studies demonstrate that habitat loss could negatively affect, or at least change, behavior of mesopredators, loss of apex predators from overfishing could also lead to a mesopredator release (Prugh et al. 2009). Understanding fixed differences in mesopredator behavior is important as we see shifting baselines already occurring for our marine ecosystems (Knowlton and Jackson 2008). Future studies should continue to look at influences to mesopredator behavior and investigate how predator-prey interactions are integrated across multiple trophic levels.

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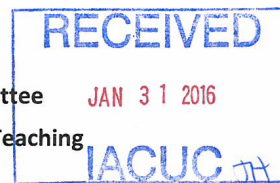
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Appendix

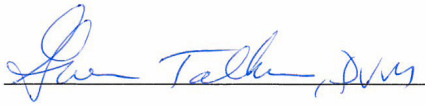
STATEMENT OF ETHICS

The studies were conducted under the under the guidelines of Institutional Animal Care and Use Committee, and the experiments were approved by the University of Delaware's animal ethics committee; IACUC Numbers: 1297 & 1313.

University of Delaware
Institutional Animal Care and Use Committee
Application to Use Animals in Research and Teaching



Title of Protocol: Determining the predatory role of arc-eye hawkfish on coral reefs of Moorea, French Polynesia													
AUP Number: 1297-2016-0	← (4 digits only — if new, leave blank)												
Principal Investigator: Danielle Dixson													
Common Name: Arc-eye hawkfish													
Genus Species: Paracirrhites arcatus													
Pain Category: (please mark one)													
<table border="1" style="width: 100%; border-collapse: collapse;"> <thead> <tr> <th colspan="2" style="text-align: left; padding: 2px;">USDA PAIN CATEGORY: (Note change of categories from previous form)</th> </tr> <tr> <th style="width: 15%; padding: 2px;">Category</th> <th style="padding: 2px;">Description</th> </tr> </thead> <tbody> <tr> <td style="text-align: center; padding: 2px;">☐ B</td> <td style="padding: 2px;">Breeding or holding where NO research is conducted</td> </tr> <tr> <td style="text-align: center; padding: 2px;">☐ C</td> <td style="padding: 2px;">Procedure involving momentary or no pain or distress</td> </tr> <tr> <td style="text-align: center; padding: 2px;">☒ D</td> <td style="padding: 2px;">Procedure where pain or distress is alleviated by appropriate means (analgesics, tranquilizers, euthanasia etc.)</td> </tr> <tr> <td style="text-align: center; padding: 2px;">☐ E</td> <td style="padding: 2px;">Procedure where pain or distress cannot be alleviated, as this would adversely affect the procedures, results or interpretation</td> </tr> </tbody> </table>		USDA PAIN CATEGORY: (Note change of categories from previous form)		Category	Description	☐ B	Breeding or holding where NO research is conducted	☐ C	Procedure involving momentary or no pain or distress	☒ D	Procedure where pain or distress is alleviated by appropriate means (analgesics, tranquilizers, euthanasia etc.)	☐ E	Procedure where pain or distress cannot be alleviated, as this would adversely affect the procedures, results or interpretation
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IACUC Approval Signature: <u></u>
Date of Approval: <u>2/2/16</u>

University of Delaware
Institutional Animal Care and Use Committee
Request to Amend an Animal Use Protocol

RECEIVED
APR 09 2018
IACUC

Title of Protocol: Understanding chemical cues in settlement site selection on coral reefs could lead to more effective marine management	
AUP Number: 1313-2018-A	← (4 digits only)
Principal Investigator: Danielle Dixon	
Requested Changes I am requesting a change to: (Check <u>all</u> that apply) ☐ Animal Species (Complete Section 1) ☐ Animal Numbers (Complete Section 2) ☐ Animal Procedures (Complete Section 3) ☐ Therapeutic or Experimental Agents (Complete Section 4) ☐ Pain Category (Complete Section 5) ☐ Use of Biological Material, Hazardous Agents or Radiation (Complete Sections 4 & 6) ☐ Other (Specify) Click here to enter text. (Complete Section 7)	
Changes MUST NOT be initiated until IACUC approval is granted	

Official Use Only IACUC Approval Signature: <u>Shirley T. Talley, DVM</u> Date of Approval: <u>4/18/18</u>
