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Physical and Biological Drivers of Juvenile Fish Distributions in Unstructured Shallow Tropical Nearshore Habitats

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PHYSICAL AND BIOLOGICAL DRIVERS OF JUVENILE FISH DISTRIBUTIONS IN UNSTRUCTURED SHALLOW TROPICAL NEARSHORE HABITATS

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ABSTRACT

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MAY 2019

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The structural complexity of aquatic habitats can influence the ecological processes that occur within them, as fine-scale topographic features act as refugia for small fishes, buffering the effects of environmental stressors. Accordingly, the habitat requirements of juvenile demersal fishes in shallow littoral zones are often defined by their associations with distinct benthic microhabitats, such as densely vegetated substrates. However, an array of ecologically-important juvenile fishes also associate with topographically-homogeneous, sparsely-vegetated substrata. Absent the benefits offered by structural refugia, such fishes may be more affected by environmental variability and may have evolved distinct strategies for coping with stressors. I examined this hypothesis by assessing the factors shaping juvenile fish assemblages across the littoral zones of a subtropical island, where I predicted that flow-related stress and positive social interactions would be influential in governing the distributions of species occupying open, unstructured habitats. Spatio-temporal variability in the strength of wave-and tide-driven water movement were among the principal drivers of habitat use for a variety of juvenile fishes, exerting the most pronounced effects on species with an aversion to dense

benthic vegetation (i.e., *Bothus* spp., and *Albula vulpes*), with little impact on species

inhabiting seagrass (*Haemulon* spp. and *Halichoeres bivittatus*). Spatial segregation

between *A. vulpes* and its cryptic congener *Albula goreensis* was unrelated to benthic

habitat characteristics but well-explained by differential relationships with wave

exposure, suggesting that niche partitioning between these functionally-indistinct species

was mediated by flow. After accounting for phenotypic clustering caused by an

extensive suite of environmental filters, residual correlations in species abundance were

dominated by strongly- asymmetric positive associations, primarily between soft-bottom

benthivores and *Eucinostomu*s spp. Interspecific relationships were weak among

seagrass-associated taxa. Disparities in the foraging behaviors and putative vigilance-

keeping abilities of *Eucinostomus* spp. and its associate *A. vulpes* implied that the large

organizational influence of eucinostomids could be explained by their capacity for

producing risk-related information, which more vulnerable species exploited.

Collectively, these findings support the hypothesis that fishes using unstructured habitats

are more exposed to flow-related stress than those occupying complex habitats, and

likewise that they employ alternative antipredator strategies, relying on social

mechanisms to reduce predation risk.

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CHAPTER 1

GENERAL INTRODUCTION

1.1 Juvenile habitats and structural complexity

Establishing the biotic and abiotic factors that drive animal distributions is integral to determining species' ecological requirements and to predicting the ways their communities will respond in the event of natural and human-induced disturbance or environmental change, two fundamental goals of conservation science. However, the preconditions for growth and survival can differ substantially over the lifetime of an organism, with the most pronounced variability occurring during early life stages when growth and associated developmental changes tend to progress at an accelerated rate. Demersal marine fishes are characterized by a bipartite life history that begins with a highly mobile pelagic-planktonic larval stage, followed by settlement into coastal habitats and a subsequent transition into a more bottom-associated existence. For most species, this post-settlement demersal phase involves at least one, and frequently several ontogenetic shifts in habitat utilization (McCormick and Makey 1997, Hylkema et al. 2015), as early pressure to maximize survival via the use of low-risk habitats is eventually mitigated by increases in size and performance (Sogard 1997, Gibb et al. 2006), favoring the exploitation of more productive habitats which, despite harboring higher densities of predators, are conducive to more rapid growth (Werner and Hall 1988, Dahlgren and Eggleston 2000, Kimirei et al. 2013). As such, the early life stages of most demersal fishes commonly rely upon multiple distinct yet interconnected habitats prior to recruitment into adult populations (Parrish 1989, Adams and Ebersole 2009, Nagelkerken et al. 2015).

In temperate and tropical regions, these habitats occur principally within highly productive, shallow nearshore environments including estuaries, lagoons, and back-reef zones, leading to the recognition of these systems as "nurseries" which support a diverse array of species (Adams et al. 2006, Nagelkerken et al. 2015, Sheaves et al. 2015). Yet the relatively enclosed nature of these waters and their close proximity to heavily-developed coastlines expose them to a variety of anthropogenic stressors (Kennish 2002, Dahlgren and Marr 2004, Kennish et al. 2014). At the same time, the limited mobility, narrow niche breadth, and generally strict ecological requirements of juvenile fishes (Wilson et al. 2008, Nash et al. 2015) suggest that this life stage may be particularly susceptible to the negative effects of environmental degradation and habitat loss that often accompany human activities (Wilson et al. 2010, van der Lee and Koops 2015), creating a precarious situation with potentially serious ramifications for population replenishment. Indeed, when larval supply is not limiting and adult habitat is plentiful, juvenile habitat can be the limiting factor in determining adult population sizes (Halpern et al. 2005), and it is thus not surprising that low juvenile habitat availability is routinely linked with reduced adult abundance (Nagelkerken et al. 2002, Mumby et al. 2004, Fodrie and Levin 2008, Sundblad et al. 2014).

As such, the early developmental stages of marine demersal fishes are often considered among the most critical from the perspective of conservation (Levin and Stunz 2005). However, practical and logistical considerations often preclude the implementation of habitat preservation or restoration efforts at lagoon- or estuary-wide scales, instead requiring that they are enacted at the level of smaller, discrete subregions. Accordingly, there has been great interest in assessing the relative value or "nursery

function" of distinct habitats or spatial units within the larger nearshore systems they comprise, permitting their prioritization (Beck et al. 2001, Dahlgren et al. 2006).

In tropical environments, research evaluating the nursery function of distinct habitats within back-reef or lagoonal systems has focused overwhelmingly on the role of structurally-complex habitats such as seagrass or macroalgal beds and fringing mangroves, which are generally thought to provide refuge from larger piscivorous predators while also harboring high densities of prey, ultimately permitting higher rates of survival among juvenile fishes (Heck et al. 2003, Gillanders 2006, Nagelkerken 2009). Moreover, these works have almost exclusively addressed the role of such habitats as nurseries for coral reef fishes, whose later life stages are often relatively sedentary and are themselves strongly associated with physical structure (Friedlander and Parrish 1998a, Graham and Nash 2013). Accordingly, along with basic physio-chemical covariates such as turbidity, temperature, and salinity, studies relating juvenile fish distributions to environmental variation in tropical nearshore systems have concentrated principally on benthic habitat characteristics, and the environmental requirements of juveniles are routinely framed in terms of their associations with certain microhabitats (Jenkins and Wheatley 1998, Dahlgren and Eggleston 2001, Gratwicke et al. 2006). While this focus on benthic microhabitat association has expanded in recent decades to consider landscape metrics that reflect variation in the arrangement of habitats at broader spatial scales (Kendall et al. 2003, Drew and Eggleston 2008), these measures remain primarily oriented toward structural features of the benthic environment.

While it is without question that benthic habitat characteristics are an important driver of distributions among species that exploit more complex or densely-vegetated

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habitats, relationships with the benthos may be less efficacious for explaining patterns of habitat use among species that utilize the comparatively unstructured, homogenous and unvegetated substrates that can comprise the dominant areal fraction of back-reef or lagoonal (tropical near-shore) systems. The spatial distribution of benthic vegetation such as seagrasses and macroalgae is itself strongly regulated by environmental factors such as bathymetry, incident wave energy, temperature, salinity, turbidity and nutrient availability (Duarte 1991, Koch et al. 2006), typically limiting the areal coverage of these habitats to a relatively small fraction of nearshore systems. In contrast, sandy, unvegetated or sparsely-vegetated habitats exist across a comparatively vast range of physio-chemical environmental conditions, from sheltered mangrove creeks to exposed, high-energy beaches, and are often considered to represent the relatively inhospitable matrix within which patches of more productive vegetated habitats are situated. Accordingly, large differences in the relative abundance or availability of these general habitat types, and in the degree to which their distributions are tied to gradients in other (i.e., physio-chemical) environmental parameters, dictate that the discriminatory value of benthic habitat association should be considerably lesser in unvegetated habitats, particularly from the perspective of conservation, where areal coverage is among the principal considerations (Beck et al. 2001, Dahlgren et al. 2006).

Furthermore, obvious discrepancies in the physical or topographic complexity of densely-vegetated versus relatively unvegetated habitats may have ramifications for the extent to which other biotic and abiotic factors influence distributions, and the manner in which they act to do so. As previously discussed, the microhabitats or physical refugia created by structurally-complex habitats can serve to mediate the effects of both

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biological and physical stressors, from mitigating predation risk (Beukers and Jones 1998) to ameliorating hydrodynamic stress (Johansen et al. 2008), with sweeping implications for individual behavior and species interactions (Crowder and Cooper 1982, Nunes et al. 2015). In the absence of the advantages offered by topographically-complex benthic habitats, bottom-associated fishes inhabiting relatively unstructured surroundings may thus be more heavily impacted by certain environmental parameters or may have evolved fundamentally distinct strategies for coping with ambient stresses.

    Many juvenile fishes associate with benthic habitats of limited topographic complexity, exploiting sparsely-vegetated and relatively homogenous environments that, although typically fostering less-diverse assemblages, are nonetheless essential to a distinct array of functionally, ecologically, and economically important fishes (Edgar et al. 1994, Lara and González 1998, Layman and Silliman 2002). For these fishes, it seems likely that the principal drivers behind the use of space use may differ inherently from those of taxa utilizing more complex benthic habitats. In the preliminary stages of my research, I was confronted with the obvious inadequacy of benthic habitat characteristics and traditional environmental covariates (i.e., temperature, salinity, turbidity) for explaining observed patterns of abundance among several species of fishes occupying relatively homogenous and unvegetated shallow littoral habitats in The Bahamas. Nonetheless, conspicuous patterns emerged over the course of early sampling efforts: (1) a strong relationship between the abundance of several juvenile fishes and the relative scale, morphology, and degree of sheltering that characterized embayments that held sampling sites, alluding to the importance of hydrodynamic or flow-related variables; and (2) exceedingly high rates of co-occurrence among certain species at very fine scales (i.e.,

the level of individual seine hauls), potentially evidencing positive interspecific

associations. Consequently, the direction of my research evolved towards investigating

the roles of these fundamental yet seldom-considered factors in governing the

distributions of juvenile fishes inhabiting relatively unstructured benthic environments,

while likewise attempting to shed light on the mechanisms underlying their influence.

1.2 Species distributions and community assembly

Following the niche theory of community assembly (Weiher and Keddy 1995,

Webb et al. 2002), species distributions can be thought of as arising through two

fundamentally distinct but complementary processes: (1) environmental (or habitat)

filtering; and (2) biotic interactions. The concept of environmental filtering holds that a

species' fitness, or ability to persist, under a given set of ambient conditions is a function

of its combined traits (Keddy 1992). Accordingly, environmental gradients act as a

screen, narrowing the potential species pool to those organisms whose phenotypes are

compatible with local parameters. While environmental filtering is often associated with

abiotic factors that vary over relatively broad geographic scales (i.e., temperature or

salinity), biotic factors that are integral to defining fundamental aspects of the physical

environment, such as structure-creating organism (i.e., corals, seagrasses or mangroves),

may likewise be considered to act as filters. Meanwhile, at the finer scales where

individuals interact directly or indirectly, the distribution of fishes in space and time is

thought to reflect species' interrelationships (Jackson 2001). For example, predator

distributions may be driven largely by those of their prey, while prey may seek to occupy

habitats that minimize their rate of encounter with predators (Sih 1984, Rose and Leggett

1990). Likewise, potential competitors may partition habitats in such a way as to

minimize redundancy in resource utilization (Werner and Hall 1979).

Although the niche theory of assemblage has broad support in freshwater

communities (Poff 1997, Jackson et al. 2001), the more open nature of marine habitats,

greater dispersal potential of marine fish larvae, and correspondingly more dynamic

character of recruitment variability among marine fishes has led to the proposal of

alternative theories of assembly (Gravel et al. 2006) which seek to incorporate the greater

stochasticity inherent in these systems (Lasker 1981, Siegel et al. 2008). Yet, while the

aspect of random chance may manifest itself in the form of "competitive lotteries" for

space (Sale 1978) or priority effects (Shulman et al. 1983, Munday 2004) in early post-

settlement stages, long-term patterns of juvenile survivorship and abundance are often

relatively uniform across cohorts despite pronounced inter-cohort variability in larval

influx (Sale and Ferrell 1988, Forrester 1990), and are better predicted by habitat

characteristics (Wilson et al. 2017), suggesting that the influence of recruitment volatility

is limited by stabilizing post-settlement processes such as environmental filtering and

density-dependent competition and/or predation (Hixon and Webster 2002, Hixon and

Jones 2005). Moreover, the consistency of species-environment relationships over both

time and space provides further evidence of the non-random nature of assemblages

(Richardson et al. 2017, Ahmadia et al. 2018)

Therefore, while stochasticity certainly makes a limited contribution to producing

observed patterns of abundance, I assume going forward that the distributions of post-

settlement juvenile fishes can be explained primarily by deterministic mechanisms akin

to those operating in freshwater environments, consistent with niche theory (Mouillot et al. 2007, Yeager et al. 2011, Pereira et al. 2015).

1.3 Flow-related stress as an environmental filter

In lotic freshwater systems, the characteristics of ambient water movement are generally considered to be among the most fundamental environmental filters affecting fish assemblages (Lewis 1969), acting hierarchically over a broad range of scales to determine species distributions (Poff 1997, Jackson et al. 2001, Biggs et al. 2005). Of the various mechanisms through which flow-related stress can influence animals (reviewed by Hart and Finelli (1999)), its direct implications for station-holding, locomotion, and accompanying metabolic costs have received the greatest attention in the case of lotic fishes, evidenced by a large body of research relating habitat use to swimming performance (Peake et al. 1997, Nelson et al. 2003) and energetic constraints (Rosenfeld and Boss 2001, Rosenfeld and Taylor 2009). This has in turn enabled a largely mechanistic understanding of the ways that different traits interact with streamflow to govern habitat utilization in lotic environments (Leavy and Bonner 2009, Sagnes and Statzner 2009), permitting eco-mechanical predictions of the flow-related habitat requirements of juvenile fishes (Wolter and Arlinghaus 2003, Del Signore et al. 2014).

In light of their well-demonstrated importance in freshwater habitats, one might expect that flow-related limitations on habitat utilization would be given similar attention in hydrodynamically-complex coastal marine environments. However, while fish-flow relationships have been studied extensively within certain groups of reef-associated fishes, i.e., the Labridae (Bellwood and Wainwright 2001, Fulton et al. 2001, Fulton et al. 2005), the recognition of flow as a fundamental environmental filter has not proliferated

widely across studies of marine fishes. Nonetheless, observations in marine coral reef habitats parallel those in freshwater habitats, indicating that water movement, associated primarily with waves, is among the principal factors structuring coral reef fish assemblages (Friedlander et al. 2003, Bejarano et al. 2017), acting primarily through its interaction with swimming performance (Bellwood and Wainwright 2001, Fulton et al. 2001) to affect the distributions of distinct species at varying spatial and temporal scales (Friedlander and Parrish 1998b). Although few works have focused specifically on juvenile life-stages, several have noted that juveniles or smaller individuals are more constrained by flow than their adult counterparts (Depczynski and Bellwood 2005, Nunes et al. 2013) suggesting that ontogeny plays a role in mediating fish-flow relationships (Fulton and Bellwood 2002).

While the limited exposure to wave energy in physically-sheltered environments has long been thought to contribute to value of estuaries or lagoons as nurseries for juvenile fishes (Blaber and Blaber 1980), surprisingly little effort has been directed towards quantifying the relationship between wave or tide-related water movement and habitat use by juvenile fishes in these systems. Several studies examining the structure of fish communities in temperate coastal embayments and shallow surf zones have demonstrated significant effects of both spatial (Romer 1990, Clark 1997, Layman 2000) and temporal (Lasiak 1984, Clark et al. 1996) variability in hydrodynamic conditions, but few have attempted to relate species distributions directly to physically-relevant characteristics of incident flow. Maxwell et al. (2009) found that bed stress from tidal currents was negatively related to the abundance of juveniles of several benthic fishes in shallow coastal habitats. Jordaan (2010) likewise demonstrated that potential wave

energy acted on multiple scales to determine the distribution of a variety of demersal juvenile fishes. Trimoreau et al. (2013) showed that mean significant wave height limited the distribution of juveniles of flatfishes (*P. platessa and S. solea*) in shallow soft-bottom littoral habitats. A handful of these works have measured flow in terms of velocities that can be related directly to swimming performance; for example, Watt-Pringle and Strydom (2003) observed that the abundance of early juveniles was negatively correlated with maximum wave-induced water velocity, with significantly greater numbers of individuals present in sheltered trough habitats characterized by mean velocities of 18 cm s^{-1} than in more open habitats where velocities averaged 30 cm s^{-1}. Similarly, Druon et al. (2015) found that juvenile Hake (*Merluccius merluccius*) in the Mediterranean Sea were primarily restricted to regions with depressed bottom current velocities, of 3.4 cm s^{-1} or less.

1.4 Species interactions among juvenile fishes

The scientific dialog with regard to biotic interactions and their role in regulating species distributions has been overwhelmingly focused on competition, which, through the principle of limiting similarity (Macarthur and Levins 1967) should preclude the co-existence of ecologically-equivalent species, driving ecological character displacement and ultimately niche differentiation (Dayan and Simberloff 2005). Tropical marine fishes present no exception to this trend (reviewed by Bonin et al. (2015)), and although mortality in early life stages is commonly attributed to predation (Carr and Hixon 1995, Almany and Webster 2006), there is general agreement that predators merely act as the ultimate vehicles of demise, and that density-dependent competition, predominantly for space, is the principal factor underlying juvenile survival (Hixon and Jones 2005, Bonin

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et al. 2009). However, there is increasing recognition that other forms of biotic

interactions, including positive relationships such as commensalism and mutualism, can

also have important implications for species distributions and community assemblage

(Bertness and Callaway 1994, Bruno et al. 2003). While classic examples of mutualism

typically involve ecologically disparate taxa and "ecosystem engineers" or "foundation

species" which do not compete for resources (Stachowicz 2001), positive interactions can

also occur between potential competitors or mutual guild members, where they can serve

to help buffer physical and biological stressors and/or mitigate the effects of competition,

facilitating coexistence and leading to positive interspecific associations (Gross 2008).

Positive interspecific relationships between potential competitors are not unheard

of among fishes. Commonly referred to as "heterospecific foraging associations"

(reviewed by Lukoschek and McCormick (2000)), but often classified as cases of social

or aggressive mimicry (Sikkel and Hardison 1992, Sazima 2002), these relationships are

typically thought to be motivated by direct food-related benefits, obtained by one or both

participating species (Ormond 1980, Sazima et al. 2006). However recent work in coral

reef habitats suggests that alternative mechanisms may be at work in driving interspecific

sociality among fishes (Gil & Hein 2017), paralleling a growing consensus among studies

of mixed-species bird flocks which suggest that interspecific information transfer, and

associated antipredator benefits, play a central role in driving heterospecific associations

(Sridhar et al. 2012).

1.5 Hypothesis and objectives

In the chapters that follow, I explore the overarching hypothesis that the principal

biotic and abiotic factors driving the distributions of juvenile fishes in shallow nearshore

environments should differ among species occupying habitats characterized by contrasting levels of structural complexity. I expect that while the traditional notion of benthic microhabitat association may apply to the distribution of species that exploit topographically-complex densely-vegetated habitats, it will be superseded by other factors in the case of species that utilize sparsely-vegetated and comparatively unstructured habitats. Specifically, I predict that hydrodynamic stress associated with waves and tides will act strongly to regulate the habitat use of fishes that associate with open, unvegetated substrates. Likewise, I expect that positive interspecific associations will be influential in determining the distributions of fishes that inhabit low-complexity environments.

The first two data chapters focus on the role of hydrodynamic stress as an environmental filter. In Chapter 2, I employ numerical hydrodynamic models to approximate spatial gradients and temporal fluctuations in the strength of wave and tide-driven water velocities across the littoral zones of a subtropical island. I then relate these parameters to the distribution of *Albula vulpes* juveniles, as estimated by beach seine sampling over the course of roughly one year, in order to assess the role of flow-related variables in shaping patterns of habitat use. Then, in Chapter 3, I combine hydrodynamic variables with stable isotope analyses to evaluate whether species-specific differences in response to spatio-temporal variation in the intensity of wave-driven flow can serve to explain niche partitioning between *Albula vulpes* and its morphologically indistinct congener, *Albula goreensis.*

Conversely, the latter two data chapters (4 and 5) center primarily on species interrelationships. In Chapter 4, I apply a joint species distribution model to identify

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"residual" correlations in species abundance while explicitly controlling for the effects of environmental filtering, permitting inferences as to nature and strength of putative species interactions, and likewise the importance of distinct taxa in shaping observed assemblages (notably, this analysis also entails a community-wide assessment of species responses to hydrodynamic variables). Subsequently, in Chapter 5, I employ quantitative behavioral analyses in conjunction with stable isotope-based estimates of niche overlap to elucidate the likely mechanisms underlying the strong positive interspecific associations revealed by Chapter 4.

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CHAPTER 2

WAVE AND TIDE-DRIVEN FLOW ACT ON MULTIPLE SCALES TO SHAPE THE DISTRIBUTION OF A JUVENILE FISH (*ALBULA VULPES*) IN SHALLOW NEARSHORE HABITATS

2.1 Abstract

Environmental stress associated with incident flow is among the most fundamental physical factors structuring fish distributions. In shallow marine habitats, flow-related stress arises through several distinct processes, yet their combined ramifications for habitat utilization by fishes are rarely evaluated concurrently. We used hydrodynamic models to resolve spatial and temporal variability in wave- and tide-driven water velocities across the littoral zone of a subtropical island, and related these, along with other environmental predictors, to patterns in the abundance of a juvenile fish (*Albula vulpes*) as determined by 785 beach-seine samples. Exerting universally negative effects on abundance, flow-related predictors were among the most influential drivers of habitat use, particularly at landscape scales where contrasts were most apparent. Spatial gradients in the strength of wave-induced and tide-driven flow were pronounced and varied inversely across the study area, applying contradictory constraints on *A. vulpes* distributions and limiting juveniles to the small subset of habitats where near-maximal wave and tide-driven water velocities were mutually depressed over the long term. Meanwhile, within the few embayments where *A. vulpes* occurred with regularity,

abundance was inversely related to short-term fluctuations in wave-driven water velocity, evidencing fine-scale movements as fish presumably sought reduced rates of flow. Juveniles were consistently absent from the remaining majority of stations regardless of temporal variability, indicating that they were unable to exploit these areas even during periods of calm. Collectively, these observations are consistent with the hypothesis that spatial and temporal variability in incident flow act simultaneously at distinct scales to structure motile fish distributions.

2.2 Introduction

The physical stress imposed by the movement of water can have profound effects on organisms in aquatic environments, from freshwater streams (Statzner et al. 1988; Nikora 2010) to rocky intertidal (Denny 2006; Burrows et al. 2008) and coral reef habitats (Dollar 1982; Harborne et al. 2006). For fishes, flow-related environmental stress can impact the performance of basic ecological functions such as locomotion (Pavlov et al. 2000; Lupandin 2005) and resource acquisition (Schaefer et al. 1999; Asaeda et al. 2005) while concurrently regulating the energetic expenditures associated with these activities (Facey and Grossman 1990; Boisclair and Tang 1993; Enders et al. 2003). As such, incident flow is among the most fundamental physical factors governing habitat utilization by fishes across a variety of freshwater (Lewis 1969; Poff and Allan 1995) and marine systems (Friedlander et al. 2003; Fulton et al. 2005).

Ambient flow is likely to have even greater ramifications for the distribution of small-bodied fishes such as juveniles, for whom habitat use is already constrained by relatively strict ecological requirements and low mobility compared to more advanced ontogenetic stages (Wilson 2008; Nash et al. 2013; Welsh et al. 2013). Small fishes

achieve lower absolute swimming speeds than larger-bodied individuals, limiting the water velocities they are capable of negotiating (Brett 1965; Beamish 1978), and are subject to disturbance by a broader range of turbulence scales, increasing their susceptibility to the destabilizing effects of unsteady flows (Lupandin 2005; Webb et al. 2010). It is not surprising then that juvenile fishes exposed to elevated flow velocities exhibit comparatively large reductions in prey capture success (Flore and Keckeis 1998), greater rates of flow refuging (Fulton and Bellwood 2002; Johansen et al. 2008), and can be disproportionately affected by extreme flow events (Lassig 1983; Del Signore et al. 2014). Collectively, these impacts may lead to the exclusion of smaller fishes from wave- or current-swept environments (Sagnes et al. 1997; Depczynski and Bellwood 2005; Eggertsen et al. 2016), placing major constraints on habitat utilization. While juvenile fishes should occupy relatively low-flow environments compared to adults (Blaber and Blaber 1980; Sagnes et al. 1997; Fulton and Bellwood 2002), the varying abilities of fishes to contend with moving water should nonetheless give rise to distinctive patterns of habitat use across species, (Bellwood et al. 2002; Fulton et al. 2005; Leavy and Bonner 2009), constituting a fundamental niche difference. Yet, despite the considerable attention it has received in lotic freshwater habitats, the "hydrodynamic niche" of a species is rarely included among the environmental factors used to define the essential habitat requirements of juvenile marine fishes.

Studies linking wave-driven flow to the distributions of marine organisms almost universally employ the concept of "wave exposure," an abstraction that is seldom well defined or evaluated in a quantitative manner (Lindegarth and Gamfeldt 2005). Denny (1995) defines wave exposure as an "integrated index of the severity of the

hydrodynamic environment." Interpreted in this way, wave exposure is largely a function of coastal geomorphology, bathymetry, and prevailing climatic patterns and is thus a temporally invariant property of a point in space, giving rise to geographically varying "exposure gradients." However, in coastal marine habitats, hydrodynamic conditions at a given location are often dynamic, dependent not only upon the relatively fixed seascape characteristics that govern wave development or dissipation but also upon temporal variability in remote and local wind forcing (Denny and Gaines 1990). While short-term fluctuations in flow-related stress may have little effect on the distributions of sessile organisms such as those found in rocky intertidal zones (Denny et al. 1985), they may nevertheless have important implications for habitat utilization by motile organisms, which can modify their position in response to changing environmental conditions (Menge and Sutherland 1987, Friedlander and Parrish 1998). Accordingly, several works examining the temporal dynamics of fish communities have linked fish abundance, diversity, and assemblage structure with changes in wave height or tidal current speed on hourly or daily scales (Lasiak 1984, Clark et al. 1996, Eggertsen et al. 2016), suggesting that fish do in fact undertake movements in response to temporally varying hydrodynamic conditions.

Although the distributions of motile organisms can be influenced by ambient flow on multiple scales (Denny et al. 2004), few studies have attempted to document directly how spatial and temporal variation in flow-related stress act together to influence habitat utilization by marine fishes (but see Friedlander and Parrish 1998). Likewise, because of the logistical challenges involved with characterizing incident flow at ecologically-relevant scales, such works rarely quantify hydrodynamic stress in physically-meaningful

terms, instead employing categorical classifications or proxies such as wind speed or wave height, which can hinder mechanistic interpretation and limit the transferability of results (Lindegarth and Gamfeldt 2005; Denny and Gaines 2007). Furthermore, most research has focused on adult fishes in topographically complex coral reef habitats, where individuals exploit fine-scale structural refugia or steep bathymetric gradients to mitigate the adversity imposed by high-flow environments (Fulton and Bellwood 2002; Johansen et al. 2008; Eggertsen et al. 2016), likely buffering the observable effects of hydrodynamic stress on distributions.

During their early ontogenetic stages, many species of tropical fish are associated with relatively unstructured shallow littoral habitats (Dahlgren and Marr 2004; Dominici-Arosemena and Wolff 2006). Littoral zone waters are hydrodynamically heterogeneous, subject to flows driven by remote swell, local wind forcing, and tidal fluctuations (Dean and Dalrymple 2004; Lowe et al. 2009), and the depth-limited shorelines that juvenile fishes often exploit as predation refugia (Paterson and Whitfield 2000) can be subject to some of the greatest wave-related stresses (Denny 2006; Webb et al. 2010). Yet, compared to coral reefs, the surf zones, tidal flats, and lagoons that make up much of tropical nearshore systems are characterized by low topographic complexity and homogeneous water depths, providing little in the way of shelter from wave- or current-induced flow. As such, hydrodynamic stress arising due to waves or tides should have substantial implications for patterns of habitat use among juvenile fishes that occupy these waters.

The present study examined the role of flow-related stress, as measured by ambient water velocity, on the distribution of juvenile *Albula vulpes*, an abundant,

mobile, and ecologically important inhabitant of shallow nearshore environments. To achieve this, we employed high-resolution hydrodynamic models to estimate spatiotemporal variation in the wave-generated and tidally-driven water velocities experienced across the shallow littoral zones of a subtropical island for an extended period. We then related these factors, in conjunction with other covariates, to observed patterns in the abundance of juvenile *A. vulpes* as determined by beach-seine sampling over the course of roughly one year. Specifically, we evaluated contrasts in the relative abundance of *A. vulpes* juveniles in response to: (1) spatial gradients in long-term mean and maxima of wave-induced water velocities (akin to the traditional interpretation of "wave exposure"); (2) short-term temporal fluctuations in wave-induced water velocities, as reflected by the mean conditions in the 24 h preceding each sampling event; and (3) persistent spatial gradients in tide-induced water velocity.

2.3 Methods

2.3.1 Study area

Located on the eastern edge of the Bahamas archipelago, the island of Eleuthera borders the Atlantic Ocean, spanning approximately 120 km from northwest to southeast with an average width of 3 km (Figure 2.1). Easterly Tradewinds prevail in this region, with a greater northerly component during the dry season (November–April) and southerly component during the wet season (May–October). In the winter and early spring, approaching continental air masses can generate periods of strong westerly and northerly winds (Sealey 2006). The windward coast is characterized by a steep depth gradient and wind-fetch exceeding 6000 km, yielding a wave regime dominated by long-period oceanic swells. In contrast, the leeward coast abuts the shallow Bahamas banks

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and fetch is largely restricted to less than 200 km, limiting wave development to locally generated wind-swell. The waters of the region are microtidal, with a mean tidal range of approximately 1 m and a maximum close to 1.2 m, leading to generally mild inshore tidal currents (Gonzalez and Eberli 1997). Differential exposure to wind and waves coupled with markedly distinct bathymetry give rise to divergent nearshore habitats on the windward and leeward coasts. With the exception of several sheltered sounds, the windward shore comprises primarily exposed sandy beaches and semi-exposed bays, while shallow flats, mangrove creek systems, and lower energy beaches predominate to leeward.

2.3.2 Study species

Adult A. vulpes exploit a mosaic of relatively open, shallow-water habitats including reef crests, lagoons, tidal flats, and mangrove creeks, where they forage primarily on benthic invertebrates, often in large conspecific schools (Colton and Alevizon 1983; Humston et al. 2005; Murchie et al. 2013). Juveniles (< 150 mm fork length (FL)), however, are conspicuously absent from these groups, and although the habitats they occupy are not well described, evidence suggests that juveniles utilize similarly unstructured, shallow, and sparsely vegetated soft-bottom littoral zones, typically within lagoonal environments (Layman and Silliman 2002; Nero and Sealey 2006; Snodgrass et al. 2008). While A. vulpes adults can display a high degree of site fidelity, they are also highly mobile, commonly undertaking tide-related movements on the order of several kilometers (Humston et al. 2005; Murchie et al. 2013), and capable of traveling more than 100 km over a period of just a few days in spawning-related migrations (Haley 2009; Danylchuk et al. 2011). Given this mobility and apparent lack

of structural association, and furthermore considering that the shallow littoral zones they frequent are susceptible to strong wave-driven currents, A. vulpes presents a fine model species for examining the effects of flow on juvenile distributions.

2.3.3 Fish sampling

Twenty-one sites spanning approximately 40 km along the windward and leeward coasts of Eleuthera were selected to represent a broad spectrum of littoral zone habitats characterized by diverse flow regimes. Stratified random sampling was conducted at intervals year-round, between January 2012 and April 2013, encompassing both the wet (May–October) and dry (November–April) seasons. During each sampling period, stations were visited consecutively in random order over the course of roughly 5 d. Unless precluded by logistical considerations, a minimum of three seine hauls representing a range of water depths were carried out at each station.

Sampling was conducted with a 15.2 m × 1.2 m, 3.2 mm mesh bagless beach seine. The seine was set perpendicular to shore, pulled roughly parallel to shore for 20 m, closed, and then hauled out, encompassing a total area of approximately 210 m^2 per sample. Over the duration of each seine haul, the composition and density of benthic vegetation (primarily *Thalassia testudinum*) was visually assessed, and at the conclusion, the proportional coverage of medium-to-dense benthic vegetation vs. unvegetated or sparsely-vegetated bottom was estimated and recorded. Following Harborne et al. (2008), medium-to-dense vegetation was defined as seagrass standing crop densities corresponding to category 3 or greater on the visual scale described by Mumby et al. (1997). The minimum and maximum depths encountered in each haul were noted, and the approximate geographic centroid of the sampled area was recorded with a handheld

global positioning system receiver. Fish specimens captured in each haul were identified to the lowest possible taxon (genus or species) and enumerated before being released. A representative subsample of individuals (up to 30 of each species) were sacrificed and retained on ice for detailed measurements and further analyses, except for large individuals (obviously exceeding 150 mm FL), which were measured on-site and released. All fish sampling for this study was approved by the University of Massachusetts Amherst Institutional Animal Care and Use Committee (protocol 2010-0005).

2.3.4 Hydrodynamic models

Wave- and tide-driven flow characteristics were estimated independently via discrete numerical models to manage computational demands. While this decoupling precluded the evaluation of wave–tide interactions, their omission likely had little influence on estimated hydrodynamic parameters in our study area, where small tidal ranges, mild tide-induced currents, and a generally inverse relationship between the strength of wave- and tide-driven forcing would have limited the strength of such interactions, which furthermore tend to be localized (Davis and Fox 1981). The fine-scale complexity of coastal features in the vicinity of sampling sites required that models were supplied with high-resolution bathymetric and coastline data. Accordingly, water depths in shallow nearshore regions of Eleuthera (< 6 m deep) were derived from multispectral satellite imagery (following Stumpf et al. 2003) at a horizontal resolution of 9.6 m and combined with existing lower resolution bathymetric data for deeper waters to produce a digital elevation model (DEM) of the seabed in the study area. The resulting DEM was subsequently utilized in the generation of meshes for the wave and tide model

domains. Production of the bathymetric dataset is described in greater detail in Appendix 2A.

2.3.4.1 Wave model

The small water depths and incident long-period swell that typify littoral zones within the study area necessitated the consideration of shallow-water processes such as wave shoaling, refraction, and depth-limited breaking, precluding the use of less computationally demanding fetch-based models (Sundblad et al. 2014; Callaghan et al. 2015). Therefore, the properties of wave-driven flow were obtained from a simulated wave field generated with SWAN (Booij et al. 1999), a third-generation phase-averaged numerical wave model, the accuracy of which has been verified in environments characterized by similar fetches, depths, and wave climates (Lowe et al. 2009; Mariotti and Fagherazzi 2013). To accommodate the large model domain while maintaining the fine spatial resolutions required to resolve these processes accurately, an unstructured grid was employed, ranging in resolution from 15 km at the open boundaries to less than 25 m in coastal zones. Given the large problem size, forward integration of the model over a multiyear period was not a computationally feasible alternative. Instead, a surrogate model was developed, approximating the response surface relating wind or swell forcing with hydrodynamic conditions experienced at each mesh node based on an intelligently reduced set of high-fidelity simulations (Box and Draper 1987; Queipo et al. 2005).

The range of input parameters evaluated by response surface models was determined based on frequency distributions comprising 4 years of meteorological and oceanographic observations from two nearby National Oceanic and Atmospheric

Administration (NOAA) National Buoy Data Center (NBDC) stations; station SPGF1 in

Grand Bahama (located approximately 300 km northwest of the study area), and Sta.

41047 (approximately 500 km east-northeast of the study area) for wind and swell data,

respectively. For the wind-driven model, five wind speeds from 2.5 to 20 m s^{-1} were

evaluated for every 15 of wind angle ($n = 24$ directions), representing a total of 120 input

parameter sets. In the case of remote swell, early process studies revealed that due to

sheltering by adjacent islands and the northern extent of Eleuthera itself, swells

originating from 180–360 and 0–30 (from south clockwise through to north-northeast) did

not have a substantive impact on the study area, thus allowing the range of incoming

swell directions to be truncated. Accordingly, the swell-driven model incorporated three

input parameters; five swell heights (from 0.5 to 4.5 m), each with four dominant periods

(from 5.5 to 14.5 s) were evaluated for every 15 of dominant swell direction between 30

and 180 inclusive ($n = 11$ directions), for a total of 220 parameter combinations. Model

outputs included significant wave height, peak period, peak bottom period, bottom orbital

velocity, and energy flux. Additional details on the wave model, including validation, are

available in Appendix 2B.

2.3.4.2 Tide model

    Tidal current velocities were estimated using the opensource software package

Finite-Volume Coastal Ocean Model (Chen et al. 2006), on an unstructured mesh similar

to that of the wave model but encompassing an altered spatial domain that maintained

deep water where the tidal harmonics used to force the simulation were most reliable.

The depth-averaged tidal model was forced at the open boundaries with sea surface

elevation generated using the nine principal regional tidal harmonics (M_2, S_2, N_2, K_2, K_1,

O_1, P_1, Q_1, and M_4), the amplitude and phase of which were derived from the TPX08 1/30

tidal atlas (Egbert and Erofeeva 2002). The model was forward integrated for 50 d with a

time step of $\Delta t = 0.1$ s, and vertically averaged velocity components were archived hourly

for each model control volume. Flow velocity at a fixed height above the substrate was

estimated by reconstructing the inertial sublayer using the universal logarithmic profile,

and the bed stress was extracted from depth-averaged simulations with hydraulic

roughness set to a constant value appropriate for the prevailing substrates in the model

domain. For further specifics on the production and validation of the tidal model, please

see Appendix 2C.

2.3.5 Data analyses

2.3.5.1 Hydrodynamic predictors

Predictor variables derived from hydrodynamic models included both wave- and

tide-driven water velocities, reflecting different distributional characteristics over distinct

temporal scales (summarized in Table 2.1). Maximum bottom orbital velocity, defined as

the near-bed wave-induced water velocity parallel to the seafloor in the direction of

dominant flow, was selected as an appropriate metric for quantifying hydrodynamic

stress associated with waves. This measure provides a widely transferable, physically

interpretable representation of the wave-driven water movement experienced by bottom-

associated fishes in shallow habitats and has been employed in both field and

experimental studies (Fulton and Bellwood 2005; Gabel et al. 2011; Anton et al. 2014).

To approximate spatial gradients in wave-related stress integrated over extended

timescales (akin to the common interpretation of wave exposure), long-term mean (U_{mean})

and 99th quantile (U_{max}) bottom orbital velocity at each mesh node was estimated by

interrogating the wind and swell-driven response surface models with hourly histories of forcing parameters recorded at the respective NOAA NBDC station over a 4 yr time period from 01 January 2010 to 2014, and then calculating the statistics of interest from the resulting distributions. Model outputs were then extracted at the site of each seine haul, taking the greater of wind or swell-forced velocities. Near-maximal (99th quantile) velocity was chosen over the absolute maximum to omit the most anomalous events, limiting consideration to those likely to occur on an annual basis.

To capture temporal variability in remote and local forcing, and resultant short-term fluctuations in flow-related stress, we approximated the wave-induced water velocity experienced at each seine haul location proximal to the moment of sampling. Instantaneous bottom orbital velocity (U_{inst24}) was estimated by interrogating the response surface models with the mean forcing parameters recorded at NBDC stations in the 24 h preceding each sampling event, using the greater of wind and swell-forced outputs. Twenty-four hours was selected as an appropriate temporal window because wave conditions do not develop nor moderate immediately in response to changing winds, but rather on the scale of several hours to days, and remote swell originating from NBDC Sta. 41047 would require many hours to reach the study area (approximately 11 h for the median wave period of 8.5 s). Moreover, we assumed that a substantial time lag is likely to be associated with the relocation of animals in response to environmental change, a conclusion supported by observations of Lasiak (1984) who found that wind speed averaged over a window of 12–48 h was a better predictor of surf-zone fish abundance than that recorded at the moment of sampling. Data exploration revealed that U_{inst24} was strongly correlated with U_{mean} and U_{max}. Therefore, to preclude potential problems with

multicollinearity, U_{anom24} was defined as the difference between U_{inst24} and U_{mean}. The resulting variable may be considered a measure of temporal wave anomaly, reflecting the departure from long-term mean conditions at a given location in the 24 h preceding a sampling event, with positive values indicating above-average water velocities.

Because most temporal variation in tide-driven flow occurs on relatively fine and predictable (semidiurnal) scales, we did not evaluate short-term fluctuations in tidal currents, but focused instead on persistent geographic gradients in the strength of tide-driven flow. Hydrodynamic stress generated by tidal exchange (U_{tide}) was quantified using the maximum current velocity associated with the M_2 (principal lunar semidiurnal) tidal component, as this reflects the typical velocities encountered on a day-to-day (6.21 h) basis at any given location (Maxwell et al. 2009). Tidal current velocities were estimated at a height of 5 cm above the substrate, to best reflect conditions experienced by bottom-associated fishes such as *A. vulpes* (McMahon and Hartman 1989).

2.3.5.2 Biotic predictors

In addition to hydrodynamic variables, biotic habitat characteristics recorded at the time of sampling were integrated as predictors to increase model accuracy. Given the previously described benthic habitat associations of *A. vulpes* juveniles (Layman and Silliman 2002; Nero and Sealey 2006; Snodgrass et al. 2008), the proportion of sampled seabed area categorized as having medium-to-dense benthic vegetation coverage (as defined above) was incorporated as a covariate. Likewise, considering the relationship between water depth and relative predation risk in habitats akin to those studied here (Rypel et al. 2007), we included the mean water depth sampled by each seine haul

(estimated by averaging the minimum and maximum depths encountered) as an explanatory variable.

Recent works have highlighted the value of taking into account biotic interactions such as competitive or facilitative relationships when modeling species distributions (Guisan and Thuiller 2005, Elith and Leathwick 2009). Using the presence or abundance of an interacting species as a predictor can improve explanatory power, (see Wisz et al. [2013] for a review), provided that its distribution is "unlinked" or independent of the focal species (Anderson 2017). Pilot sampling conducted the year prior to the present work revealed that the relatively infrequent occurrence of *A. vulpes* juveniles coincided almost exclusively with the presence of more commonly occurring mojarras (*Eucinostomus* spp.) of similar size. In remote underwater video surveys undertaken to explore this phenomenon, *A. vulpes* juveniles were observed only in the presence of and commingled within larger shoals of like-sized mojarras, among which they actively foraged. Further details on these findings are available in Appendix 2D.

The close affiliation of *A. vulpes* with eucinostomids parallels a relationship described for *Centropomus* spp., juveniles of which are thought to benefit from increased foraging efficiency and reduced predation risk as a result of associating with eucinostomid shoals (Sazima 2002). Given *A. vulpes*' rarity and nominal relative abundance among the much more numerous and widely distributed *Eucinostomus* spp., it seems likely that while eucinostomids exert a measurable effect on the distribution of *A. vulpes*, the reciprocal effect of *A. vulpes* on *Eucinostomus* spp. is comparatively negligible. Following the reasonable assumption that its relationship with *A. vulpes* was effectively unidirectional (i.e., that the distribution of *A. vulpes* did not have a meaningful

influence on that of *Eucinostomus* spp.), the log-transformed abundance of *Eucinostomus* spp. in each seine haul was considered as an additional biotic predictor. Statistical model

The observed abundance of *A. vulpes* juveniles was related to predictors using a generalized linear mixed modeling (GLMM) framework, employing a negative binomial error distribution with the NB1 Parameterization (Cameron and Trivedi 1986) and a log link function. To manage model complexity given the relatively sparse nature of the observed abundance data, and furthermore to facilitate interpretation of results, we opted not to consider interaction terms. A random intercept was included for the factor "station" to account for the potential interdependency of observations within sampling locales arising from unmeasured environmental variation. Explanatory variables were inspected for outliers, collinearity, and variance inflation, and continuous predictors were standardized to improve model-fitting stability and interpretability of results. Covariates in the form of count data were log-transformed to reduce residual heterogeneity. The significance of fixed effects was assessed using likelihood ratio tests, and 95% confidence intervals (CI) for fixed effect coefficients were obtained via likelihood profiling. Residuals were inspected for indications of bias and heteroscedasticity and closely examined for any evidence of spatial and/or temporal autocorrelation. Model validation was carried out following methods described in Zuur et al. 2009, and posterior predictive simulations were employed to further assess model fit and to verify that distributional assumptions were met. Analyses were completed in R version 3.4.0 (R Core Team, 2017), employing the package "glmmTMB" (Brooks et al. 2017) and replicated using "glmmADMB" (Fournier et al. 2012; Skaug et al. 2016).

2.4 Results

2.4.1 Fish sampling

Between January 2012 and April 2013, 785 seine hauls were conducted across the 21 stations. A total of 205 juvenile *A. vulpes* (verified by genetic analyses) were collected in 57 distinct sampling events (7% of all seine hauls) and ranged from 30 to 149 mm FL with a mean length (± SD) of 58 ± 25 mm. When *A. vulpes* were present in seine hauls, their abundance ranged from 1 to 23 individuals, with a mean of 3.6 (± 3.8). Except for a single individual, *A. vulpes* collections were limited to just six stations (1, 2, 6, 17, 18, and 19), located entirely within three embayments (Figure 2.1). Biotic habitat variables associated with each seine haul varied primarily within but also among stations (Appendix 2E, Table 2E-1). *Eucinostomus* spp. were present in 482 seine hauls (61%), occurring at every station and totaling 33,147 individuals. When eucinostomids were present, there was a mean of 69 (± 149) individuals per haul, with an average length of 50 (± 19) mm FL. Eucinostomids occurred in 56 of the 57 seine hauls that contained *A. vulpes* juveniles (> 98%), accounting for 204 of the total 205 *A. vulpes* juveniles collected (> 99%). Conversely, *A. vulpes* were present in fewer than 12% of seine hauls capturing *Eucinostomus* spp. When these taxa co-occurred, *A. vulpes* typically comprised a small fraction of individuals, constituting on average less than 1% of combined total abundance.

2.4.2 Hydrodynamic models

Modeled estimates of wave-induced bottom velocities and tidal current velocities (summarized in Table 2.2) compared closely with in situ observations recorded by others in similar habitats and water depths (Hine et al. 1981; Fulton and Bellwood 2005;

Eckman et al. 2008). Remotely generated long-period swell dominated the wave regime

at windward stations, producing the maximum wave heights and bottom velocities at all

but the most sheltered sites, but had little effect on leeward stations, where locally

generated wind-waves predominated (Figure 2.2). Estimates of long-term mean bottom

orbital velocity, U_{mean}, at seine haul locations ranged from 1.1 to 42.6 cm s^{-1} with a mean

($\pm$ SD) of 9.4 ($\pm$ 7.8) cm s^{-1}, and varied significantly across stations (Kruskal Wallis $\chi^2 =$

637.4, df = 20, $p \leq 0.0001$), with the greatest velocities occurring at windward sites

exposed to remote swell (e.g., Sta. 4, 7, and 8) and the lowest occurring in tidal creeks or

sounds with limited fetch (e.g., 2, 9, 11, 12, and 19) (Appendix 2E, Table 2E-2). Long-

term near-maximal bottom velocity, U_{max}, ranged from 6.7 to 59.8 cm s^{-1}, with a mean of

25.3 ($\pm$ 8.9) cm s^{-1}, and also differed significantly among stations (Kruskal Wallis $\chi^2 =$

656.75, df = 20, $p \leq 0.0001$), again with the greatest velocities occurring at windward

stations subject to remote swell (e.g., 4, 7 and 8) but also at leeward-side beaches with

relatively uninterrupted westward fetch and minimal sheltering by reefs (e.g., 20 and 21)

(Figure 2.3). The overwhelming majority of variation in both U_{mean} and U_{max} occurred

between stations, with comparatively little intra-station variance (Figure 2.4).

Instantaneous bottom velocity proximal to the time of sampling, U_{inst24}, ranged from 0 to

56.2 cm s^{-1}, with a mean of 8.9 ($\pm$ 10.2) cm s^{-1}, and varied significantly between stations

(Kruskal Wallis $\chi^2 = 440.75$, df = 20, $p \leq 0.0001$), displaying inter-station variability of

similar magnitude to U_{max}. Corresponding instantaneous departures from long-term

mean bottom velocity, U_{anom24}, ranged from -16.7 to $+30.6$ cm s^{-1}, with a mean of 0.5 ($\pm$

5.9) cm s^{-1}. While significant differences in U_{anom24} were detected among stations

(Kruskal Wallis $\chi^2 = 104.69$, df = 20, $p \leq 0.0001$), the magnitude of these differences was small compared to that of intra-station variability (Figure 2.5).

Consistent with the microtidal nature of the study area, estimated tidal currents were generally mild, with maximum near-bed velocity, U_{tide}, averaging 3.7 ($\pm$ 4.9) cm s^{-1}. Nonetheless, prominent spatial gradients existed (Figure 2.3), with velocities ranging from 0.1 to 28.9 cm s^{-1}. Mean values within stations ranged from effectively zero to upward of 18 cm s^{-1}, with the fastest currents typically occurring at stations proximal to flow obstructions or constrictions such as the mouths of creeks or sounds (e.g., 9 and 10), and near-zero velocities occurring along open shorelines or beaches within protected basins or embayments. The majority of this variation occurred at broad spatial scales, leading to large and significant differences between stations (Kruskal Wallis $\chi^2 = 700$, df = 20, $p \leq 0.0001$) (Figure 2.4). In general, persistent gradients in tidal current strength were inversely related to corresponding gradients in the intensity of wave-driven flow (Appendix 2E, Table 2E-3), with the strongest negative correlation occurring between U_{tide} and U_{max} (Spearman's rank order correlation, $\rho = -0.387$, $p \leq 0.0001$).

2.4.3 Relationships between *A. vulpes* and flow

Wave-induced 24-h mean bottom velocities (U_{inst24}) coinciding with *A. vulpes* collections averaged 4.4 ($\pm$ 5.2) cm s^{-1} and ranged from 0 to 24.2 cm s^{-1} (Table 2.3); however, the vast majority (97%) of individuals were collected in samples with $U_{inst24} <$ 12 cm s^{-1}. Corresponding 24-h anomalies from long-term mean velocities (U_{anom24}) ranged from -7.4 to 3.3 cm s^{-1}, with a mean of -1.8 ($\pm$ 2.6) cm s^{-1}; 93% of individuals occurred when departures were no greater than 2 cm s^{-1} above the long-term average at a site. Near-maximal long-term wave-driven water velocities (U_{max}) estimated at locations

where *A. vulpes* occurred ranged from 10.4 up to 30.1 cm s^{-1}, with a mean of 20.5 ($\pm$ 4.1) cm s^{-1}, and 95% of individuals occurred at sites with $U_{max} < 24.2$ cm s^{-1}. Tidally driven flow velocities (U_{tide}) associated with *A. vulpes* occurrences were mild and typically represented a small fraction of corresponding wave-driven velocities at a given location, averaging only 1.1 ($\pm$ 1.3) cm s^{-1}. Except for a single outlying individual, *A. vulpes* juveniles were limited to locations where maximum tidal current velocity (U_{tide}) did not exceed 3.2 cm s^{-1}.

In the reduced GLMM, the abundance of *A. vulpes* juveniles was inversely correlated with both spatial and temporal variation in the strength of wave-driven flow (Table 2.4). Although U_{mean} was not significantly linked, both U_{max} and U_{anom24} exerted roughly equivalent negative effects on abundance per unit (i.e., cm s^{-1}) increase in flow velocity, evidenced by their similar raw regression coefficients. However, the standardized effect of long-term near-maximal velocity (U_{max}) on *A. vulpes* abundance was nearly twice that of 24-h departure from long-term mean velocity (U_{anom24}), attributable to the markedly greater variability of U_{max}. Despite its much lower magnitudes, tidal flow velocity (U_{tide}) exerted a significant negative effect on abundance approximately four times that of an equivalent per unit increase in U_{max} or U_{anom24}, with a standardized effect comparable to that of both wave-related metrics (U_{max} and U_{anom24}) combined.

Spatial gradients in long-term wave-induced flow maxima (U_{max}) were coarse grained, varying at broad scales consistent with the dominant features of coastal geomorphology, consequently driving patterns of abundance at the level of distinct embayments or water bodies (i.e., between stations or groups of adjacent stations). In

contrast, as one might expect, temporal departures from long-term mean velocities (U_{anom24}) differed relatively little between stations but exhibited substantial variation within them, influencing abundance at finer spatial scales (i.e., within stations or clusters of stations). Notably, only 11 stations (2, 3, 5, 6, 9, 11, 12, 14, 17, 18, and 19) were characterized by mean near-maximal wave-induced water velocities (U_{max}) equal to or less than the maximum instantaneous velocity that coincided with the occurrence of *A. vulpes* juveniles over the course of the study period ($U_{inst24} = 24.2$ cm s^{-1}). Due to the inverse relationship between the magnitudes of U_{max} and U_{tide}, the spatial constraints placed on *A. vulpes* distributions by fixed gradients in tidal flow were largely at odds with those imposed by wave-driven flow; just 11 stations (1, 2, 4, 6, 7, 8, 15, 17, 18, 19, and 21) experienced mean peak tidal current velocities equal to or below the maximum tidal current velocity associated with the presence of juvenile *A. vulpes* during the study ($U_{tide} = 3.2$ cm s^{-1}, excluding the single, far-outlying individual). Accordingly, when constraints imposed by U_{max} and U_{tide} were considered concurrently just five stations representing the intersection of the two aforementioned subsets (2, 6, 17, 18, and 19) were distinguished by mean long-term hydrodynamic conditions within the above-defined limits. Altogether, these five stations produced more than 93% of *A. vulpes* juveniles collected.

2.5 Discussion

Using physical models to resolve spatial gradients and temporal fluctuations in the wave- and tide-induced water velocities likely to be experienced by fishes over broad geographic extents and a prolonged time period, we were able to elucidate, quantitatively, the impacts of distinct flow types on the observed abundance of *A. vulpes* juveniles.

Hydrodynamic variables were among the most influential environmental predictors, particularly at the landscape scale (i.e., between embayments) where differences were most consistent and pronounced, exerting universally negative effects on abundance and limiting *A. vulpes* to a small subset of habitats distinguished by depressed rates of flow. The lack of similar negative relationships among juveniles of other demersal fishes collected by the same sampling efforts demonstrates that the inverse correlation between *A. vulpes* abundance and ambient water velocity was not an artifact of declining gear efficiency but rather reflected true decreases in abundance.

Spatial and temporal variation in wave-related environmental stress likely act in concert to control the distribution of many fishes, yet prior to our study these factors were rarely investigated in parallel, nor measured in a consistent and physically meaningful way. By disentangling the effects of persistent geographic gradients and short-term volatility in wave forcing, we showed that incident waves act on multiple, distinct scales to regulate habitat use by *A. vulpes* juveniles. The greater predictive power of U_{max} as compared to U_{mean} suggests that relatively rare but extreme events may delimit the boundaries of habitats used by *A. vulpes* juveniles at broad scales (i.e., among embayments), a finding consistent with observations by others that maxima are often more relevant than means when relating organismal distributions to wave-induced stresses (Denny and Gaines 1990; Gaines and Denny 1993; Denny et al. 2009). Concurrently, within stations or embayments that were habitable from the perspective of long-term maxima (U_{max}), the perceived abundance of *A. vulpes* declined in response to momentary increases in wave-driven water velocity, signaling that juveniles undertook fine-scale long-shore or cross-shore movements, presumably seeking reduced flow

velocities (Friedlander and Parrish 1998; Layman 2000). Conversely, *A. vulpes* were

consistently absent from stations subject to elevated long-term flow maxima regardless of

temporal fluctuations, evidencing that fish were unable to exploit these areas even during

periods of relative calm.

This multiscale relationship can be explained as a logical outcome for animals

with finite mobility. For sessile, site-attached organisms, the hydrodynamic suitability of

a given location is effectively static, determined by the likelihood of encountering flow-

related stresses that exceed one's tolerances over extended timescales, on the order of a

reproductive lifetime or more (Denny et al. 1985; Denny and Gaines 1990; Denny et al.

2004). In contrast, highly mobile organisms can respond to adverse ambient conditions

by seeking more favorable environments, in which case the habitability of a location may

be dynamic, a product of flow variability on finer temporal scales (Menge and Sutherland

1987). Most demersal fishes fall somewhere between these extremes, demonstrating

mobility but also bounded by varying degrees of site fidelity or home range limitation

(Chapman and Kramer 2000; Fetterplace et al. 2016) that constrain the distances they

may reasonably relocate in response to time-varying conditions (Friedlander and Parrish

1998). Such limitations on mobility and their consequences for habitat use should be

particularly evident in the case of juveniles, whose truncated home ranges (Jones 2005;

Nash et al. 2015; Welsh et al. 2013) correlate with the prolonged occupancy of nursery

areas before recruitment to adult habitats (Robertson and Duke 1990; Smith and

Sinerchia 2004).

Thus, for motile juvenile fishes, the hydrodynamic suitability of a habitat should

be a function of both fixed spatial gradients and temporal fluctuations in flow, with the

relative importance of these factors, and the respective scales at which they operate, mediated by mobility. At distances that fall within an individual's mobility constraints, habitat use is likely to be driven by short-term temporal variability in flow as fishes move dynamically to locate optimal conditions. Correspondingly, at scales exceeding the distance one can effectively relocate, habitat use should be governed by persistent geographic gradients in ambient flow intensity, as individuals occupy areas where the risk of encountering hydrodynamic extremes is minimized over their residency (i.e., the duration of the juvenile ontogenetic stage). The patterns in the distribution of *A. vulpes* elucidated here were consistent with this expectation, implying that while juveniles may have undertaken movements between stations within embayments (on the order of hundreds of meters to a few kilometers), mobility limitations likely precluded migration beyond the confines of a given embayment.

The influence of cyclical variations in tidal flow on the migratory patterns (Gibson 2003; Bretsch and Allen 2006) and fine–scale-habitat utilization (Auster 1987; Eggertsen et al. 2016) of fishes have been widely examined, but the implications of persistent spatial gradients in the strength of tidal currents have received relatively little attention (but see Thresher 1983). While some juvenile fishes exploit the predictable oscillations in water velocity associated with tidal exchange (Weihs 1978; Gibson 2003), tidal flows can also inflict energetic costs and limit foraging opportunities, particularly for smaller fishes that do not employ refuging behavior or cannot profit from the enhanced delivery of planktonic prey in moving water (Hobson and Chess 1978; Auster 1987; Eggertsen et al. 2016). Accordingly, the chronic, diel stresses that accompany the occupation of habitats subject to strong tidal flows may lead some fish to avoid such

areas altogether. The strong negative relationship we observed between maximum tide-driven water velocity (U_{tide}) and juvenile *A. vulpes* abundance implies that despite its comparatively low magnitude when juxtaposed with wave-driven flow, the costs of negotiating tidal currents may nonetheless present a significant obstacle to habitat utilization by *A. vulpes* juveniles.

Per unit increase in water velocity, spatial gradients in tidally-driven flow (U_{tide}) exerted a much greater negative influence on the abundance of *A. vulpes* than corresponding gradients in wave-driven flow (U_{max}). This apparent discrepancy may be explained by the differing frequency or regularity with which individuals should theoretically experience the conditions reflected by these metrics. In the case of U_{max}, estimated velocities represent only potential maxima that fishes are likely to encounter over an extended residency period, and thus there is a substantial component of chance in this metric; for a given individual, velocities approaching U_{max} may never arise, or may occur for only a brief total duration, on the order of hours to days. In contrast, for U_{tide}, this aspect of probability is absent; at any location, tidal flow velocities approaching U_{tide} will occur with certainty on a diel basis, lasting on the order of many minutes to hours at a time. Thus, considered over the entire term that an individual occupies a habitat, the aggregate cost incurred by a given increase in U_{tide} tide may far exceed that of an equivalent change in U_{max}, making locations characterized by even moderate tide-driven flow velocities less sustainable.

Due to the inherently different ways that wave- and tide-induced flows are altered by variation in coastal morphology and bathymetric topography, gradients in wave- and tide-driven water velocity were inversely related across the study area, a phenomenon

that had important implications for *A. vulpes* distributions. Gradual depth-shoaling and shoreline constrictions tend to amplify tidal current velocities locally through the effects of continuity, whereas these same topographic characteristics tend to diminish the intensity of wave-driven flow through damping and sheltering (Dean and Dalrymple 2004). In contrast, steeply sloping bathymetric features such as the fringing coral reefs that parallel exposed coastlines can have the opposite effect, intensifying wave-driven forcing at the seabed via wave transformation and breaking yet contributing little to the amplification of tidal currents. As such, while gradients in long-term wave-induced flow maxima (U_{max}) acted to restrict juveniles to sheltered, enclosed environments, corresponding gradients in tidal flow velocity (U_{tide}) had the opposite effect, limiting *A. vulpes* to more open bodies of water. Together, these contradictory controls excluded juveniles from the dominant fraction of littoral zone habitats in the study area, confining *A. vulpes* juveniles to meso-scale embayments where local geomorphological characteristics served to limit wave exposure without considerably magnifying tidal currents.

Biotic variables appear to have played a limited role in shaping *A. vulpes* distributions at broad spatial scales (i.e., between embayments) where contrasts in abundance were most evident. Both *Eucinostomus* spp. and the sparse vegetation with which *A. vulpes* was associated were common throughout the study area and varied primarily at the intrastation level, reflecting fine-scale spatial patchiness in their distributions. Even so, the strong predictive power of *Eucinostomus* spp. abundance suggests the relationship of *A. vulpes* with this taxon merits further investigation. Notably, *A. vulpes* juveniles were absent from the overwhelming majority (88%) of

Eucinostomus spp. occurrences, consistent with the results of pilot sampling and indicating that the distribution of eucinostomids was largely independent from that of *A. vulpes*. Furthermore, when both species co-occurred, *A. vulpes* comprised a nominal proportion of total individuals, supporting the assumption that the presence of *A. vulpes* did not exert an ecologically meaningful effect on *Eucinostomus* spp. at the individual level. Collectively, these findings offer strong evidence that the inclusion of *Eucinostomus* spp. count as a covariate was appropriate.

2.5.1 Likely mechanisms behind observed fish-flow relationships

The inverse correlation we detected between the abundance of *A. vulpes* and ambient flow intensity is consistent with relationships documented among juveniles of other bottom-associated fishes (Maxwell et al. 2009; Trimoreau et al. 2013; Druon et al. 2015) and can be attributed to several possible mechanisms through which hydrodynamic stress acts to influence the habitat use of aquatic organisms (Hart and Finelli 1999; Denny 2006; Webb et al. 2010). Most directly, this negative relationship may reflect limitations of *A. vulpes*' swimming performance, a key determinant of the flow environments that fish are able to accommodate (Bellwood and Wainwright 2001; Fulton et al. 2001, 2005). The oscillatory nature of wave-driven flows makes them intrinsically unsteady, and this irregularity is amplified by turbulent eddies associated with wave-breaking in the shallow littoral zones where *A. vulpes* juveniles reside (Webb et al. 2010; Denny 2014). Likewise, in the near-bed depth strata occupied by *A. vulpes*, even relatively unidirectional (e.g., tidal) flows can be complex and turbulent due to benthic boundary layer effects (Hart et al. 1996; Carlson and Lauder 2011; Meyers and Belk 2014). The negotiation of such turbulent or unsteady flows is inherently tied to maneuverability and

stability (Liao 2007; Webb et al. 2010); yet, the streamlined fusiform body, fin arrangement, and dominant body-caudal-fin or subcarangiform swimming mode that characterize *A. vulpes* are traits thought to sacrifice stability and maneuverability (i.e., unsteady swimming performance) in exchange for optimized straight-line cruising efficiency (i.e., steady swimming performance) (Webb 1984; Blake 2004; Langerhans and Reznick 2010). Accordingly, the ability of *A. vulpes* juveniles to efficiently surmount high unsteady water velocities associated with waves or near-bed flows is probably limited.

Considering these limitations, *A. vulpes* juveniles may incur substantial costs when confronted with elevated unsteady flow velocities. Perhaps most acutely, strong wave-driven currents can displace juvenile fishes such as *A. vulpes* from the shallow littoral margins they exploit as predation refugia (Wolter and Arlinghaus 2003; Kucera-Hirzinger et al. 2008; Schludermann et al. 2013), disorienting individuals and placing them at heightened risk of mortality (Paterson and Whitfield 2000; Rypel et al. 2007). Likewise, chronic energetic outlays required to counter the perturbations caused by unsteady flows (Webb 2002; Enders et al. 2003; Roche et al. 2014) may reduce the metabolic resources available to *A. vulpes* for growth, likely translating to diminished survival among juveniles, for whom rapid growth is often critical (Anderson 1988; Sogard 1997). Growth and survival may also be adversely affected by reductions in foraging efficiency brought about by elevated rates of flow (Flore and Keckeis 1998; Schaefer et al. 1999; Gabel et al. 2011) and associated increases in turbidity (Ljunggren and Sandström 2007; Sweka and Hartman 2001; Johansen and Jones 2013), which can be of particular consequence for visually oriented predators like *A. vulpes* (Hannan et al.

2015; Higham et al. 2015; Taylor et al. 2015). Taken together, these immediate and longer-term fitness ramifications may make the occupancy of wave or current-swept environments untenable.

By quantifying hydrodynamic stresses in physically meaningful terms (i.e., water velocities), we were able to evaluate them within the context of animal performance (i.e., swimming speeds), permitting a degree of biomechanical inference regarding the mechanisms through which distinct flow types acted to influence habitat utilization by *A. vulpes* juveniles. Critical speed (U_{crit}) is a measure of swimming performance that reflects the ability of fishes to negotiate flow (Brett 1964; Plaut 2001) and has thus been adopted to predict the "critical" water velocities likely to displace juvenile fishes from shallow littoral zone habitats (Wolter and Arlinghaus 2003; Wolter et al. 2004; Kucera-Hirzinger et al. 2008). Among small juveniles, U_{crit} is closely related to body length and varies little across species sharing similar morphologies and swimming modes (Brett 1964; Flore and Keckeis 1998; Wolter and Arlinghaus 2003). As adults, *A. vulpes* achieve high critical speeds comparable to those of like-sized rheophilic salmonids (Nowell et al. 2015), with whom they share a similar fusiform morphology and subcarangiform mode of propulsion. Assuming that the performance of juvenile *A. vulpes* is likewise comparable, a reasonable approximation of U_{crit} for individuals of the mean size captured here (58 mm FL) would fall in the vicinity of 40 cm s^{-1} (Brett and Glass 1973; Flore and Keckeis 1998; Wolter and Arlinghaus 2003).

Considered in the context of likely swimming performance, the mean instantaneous wave-driven water velocity associated with *A. vulpes* occurrence (U_{inst24} = 4.4 cm s^{-1}) seems negligible, representing a small fraction of critical speed. However, if

limitations on mobility make habitat suitability a function of hydrodynamic extremes likely to be experienced over an extended period, long-term near-maximal wave-driven velocity (U_{max}) should provide a more meaningful point of comparison. In this case, the mean and maximum U_{max} coinciding with *A. vulpes* occurrences (20.5 and 30.1 cm s^{-1}, respectively) correspond much more closely with predicted swimming performance, particularly when one considers the reduction of U_{crit} in unsteady or turbulent flows such as those associated with waves (Pavlov et al. 2000; Lupandin 2005). It is also noteworthy that the maximum U_{inst24} associated with the presence of *A. vulpes* (24.2 cm s^{-1}) correlated well with these values. Collectively, these observations appear to support the hypothesis that broad-scale distributional constraints are set largely by the probability of confronting acute hydrodynamic stresses produced by infrequent but extreme events. Conversely, declines in the abundance of *A. vulpes* in response to comparatively minor increases in U_{tide} and U_{anom24} (relative to U_{crit}) may signal that more chronic flow-related stresses, such as increased energetic costs or diminishing foraging efficiency, may be the principal drivers of observed negative relationships with these variables.

Incident flow may also have acted in more circuitous manners to regulate the distribution of *A. vulpes* via its effects on other organisms or the broader benthic environment. Spatiotemporal variability in wave-driven flow can have implications for the distribution and behavior of benthic invertebrates (Fenwick 1976; Bishop 2008; Gabel et al. 2008), potentially modulating the availability of *A. vulpes'* prey and consequently the value of distinct flow environments as foraging grounds. Less directly, ambient flow may have affected *A. vulpes* abundance through its role in defining basic characteristics of benthic habitats, such as the distribution of vegetation or sediments,

which can affect utilization by fishes and invertebrates through a variety of mechanisms (Snelgrove and Butman 1994; Boström et al. 2006; Santin and Willis 2007).

Alternatively, environmental factors causally unrelated to flow, but nonetheless characteristic of high-flow habitats, may have acted to exaggerate the perceived negative relationship between hydrodynamic variables and *A. vulpes* abundance. For example, stations situated in mangrove creek systems (which consistently exhibited high tidal current velocities) were typified by expansive shallow intertidal zones that dried during low tide, leaving only small channelized regions submersed throughout the tidal cycle. Thus, to remain in the shallow littoral margins they appeared to prefer, *A. vulpes* juveniles would be required to undertake substantial horizontal migrations, often on the order of hundreds of meters to kilometers, several times a day, constituting a considerable energetic burden which may ultimately reduce the utility of creek habitats. Moreover, the drastic reduction in wetted area during low tide would likely serve to concentrate nekton, leading to increased encounter rates with the predatory piscivores that are abundant in tidal creeks (Rypel et al. 2007; Murchie et al. 2015; Harborne et al. 2016) further inflating the costs of occupying these systems.

2.5.2 Conclusion

Broadly, this work demonstrates the fundamental yet often disregarded importance of ambient flow, or an individual's "hydrodynamic niche" in shaping habitat use by juvenile fish in coastal marine environments, mirroring observations in lotic freshwater habitats. The simultaneous consideration of stress associated with both wave and tide-driven water movement revealed that distinct flow types, and the divergent ways they are altered by coastal morphology, can act to magnify the restrictions placed on

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habitat utilization by hydrodynamic constraints. Furthermore, by evaluating gradients in

flow over an extended spatiotemporal domain and at distinct scales, we were able to

elucidate relationships that would not have been detectable using in situ observations

acquired at the times of sampling, providing insights on the likely role of mobility in

mediating the relationship between water movement and habitat use. Moreover, by

defining flow-related stresses explicitly and in physically relevant terms, we were able to

place them within the context of organismal performance, permitting additional

inferences about the mechanisms underlying observed fish-flow relationships.

From the perspective of conservation, our findings indicate that low-flow habitats

are a fundamental ecological requirement of *A. vulpes* juveniles, and may, given the

apparent rarity of hydrodynamically-compatible environments within our study area,

constitute a critical limiting factor for the replenishment of this economically valuable

species. The seemingly low probability of long-distance (i.e., inter-embayment)

migration by post-settlement juveniles, and their sporadic, isolated occurrence in higher-

flow habitats suggest that observed distributions may reflect the results of differential

post-settlement mortality. However, similar distributional patterns noted among

settlement-stage *A. vulpes* larvae over the course of this study imply that habitat selection

during settlement may also have played a role in determining distributions. The results of

this research can be easily extended to predict suitable habitats for *A. vulpes* juveniles in

other domains where appropriate hydrodynamic data is available.

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2.7 Tables

Table 2.1 Hydrodynamic variable definitions

Hydrodynamic variables	
U_{mean}	Long-term (~4 yr) mean wave-driven bottom orbital velocity; the greater of wind and swell.
U_{max}	Long-term (~4 yr) near-maximal (99th quantile) wave-driven bottom orbital velocity; the greater of wind and swell.
U_{inst24}	Instantaneous wave-driven bottom orbital velocity at the time of sampling, estimated based on wind and swell conditions averaged over the 24 hr period preceding a sampling event.
U_{anom24}	Wave-driven bottom velocity anomaly, reflecting the instantaneous departure from long-term mean conditions (U_{mean}) at the time of sampling (i.e., U_{inst24} - U_{mean})
U_{tide}	Maximum tidal flow velocity associated with the M_2 (principal diurnal) tidal constituent, at a height of 5 cm above the seabed, reflecting the typical maximum velocity experienced on diel timescales.

Table 2.2 Minimum, maximum, and mean (±1 SD) values of environmental predictors across the entire spatio-temporal domain of the present study. Refer to Table 2.1 for definitions of variables.

	Min	Max	Mean (±1 SD)
U_{mean} (cm s^{-1})	1.1	42.6	9.5±7.9
U_{max} (cm s^{-1})	6.7	59.7	24.9±8.9
U_{inst24} (cm s^{-1})	0	56.2	9.0±10.2
U_{anom24} (cm s^{-1})	-16.6	30.6	-0.5±5.9
U_{tide} (cm s^{-1})	0.1	28.9	3.7±5
Mean Depth (cm)	8	107	46±23
Benthic Vegetation (% cover)	0	100	25±39
Eucinostomus spp. (# indivs)	0	1000	42±122

Table 2.3 Range and mean (±1 SD) of hydrodynamic variables (in cm s^{-1}) for seine haul samples with *A. vulpes* juveniles present. Refer to Table 2.1 for definitions of variables.

	Min.	Max.	Mean (±1 SD)
U_{mean}	1.9	25.1	6.2±4.5
U_{max}	10.4	30.1	20.5±4.1
U_{inst24}	0.0	24.2	4.4±5.2
U_{anom24}	-7.4	3.3	-1.8±2.6
U_{tide}	0.2	10.3	1.1±1.3

Table 2.4 Summary of fixed effects coefficients estimated from the reduced Generalized Linear Mixed Model (GLMM) relating environmental covariates to the observed abundance of *Albula vulpes* juveniles. Ninety-five percent confidence intervals were obtained from likelihood profiles, and p-values were determined via likelihood ratio tests.

Predictor Variable	Coefficient			χ^2	p
	Estimate (standardized)	95% C.I. (standardized)	Estimate (raw)		
(Intercept)	-5.16	-6.5 – -4.08	-0.23	-	-
U_{max}	-1.45	-2.02 – -0.9	-16.42	16.54	<0.0001
U_{anom24}	-0.76	-1.21 – -0.34	-13.02	13.26	<0.001
U_{tide}	-2.85	-4.65 – -1.55	-57.48	16.9	<0.0001
Vegetation cover	-0.54	-0.97 – -0.18	-1.37	9.13	<0.01
Eucinostomus spp.	1.65	1.35 – 1.96	0.87	98.71	<0.00001

2.8 Figures
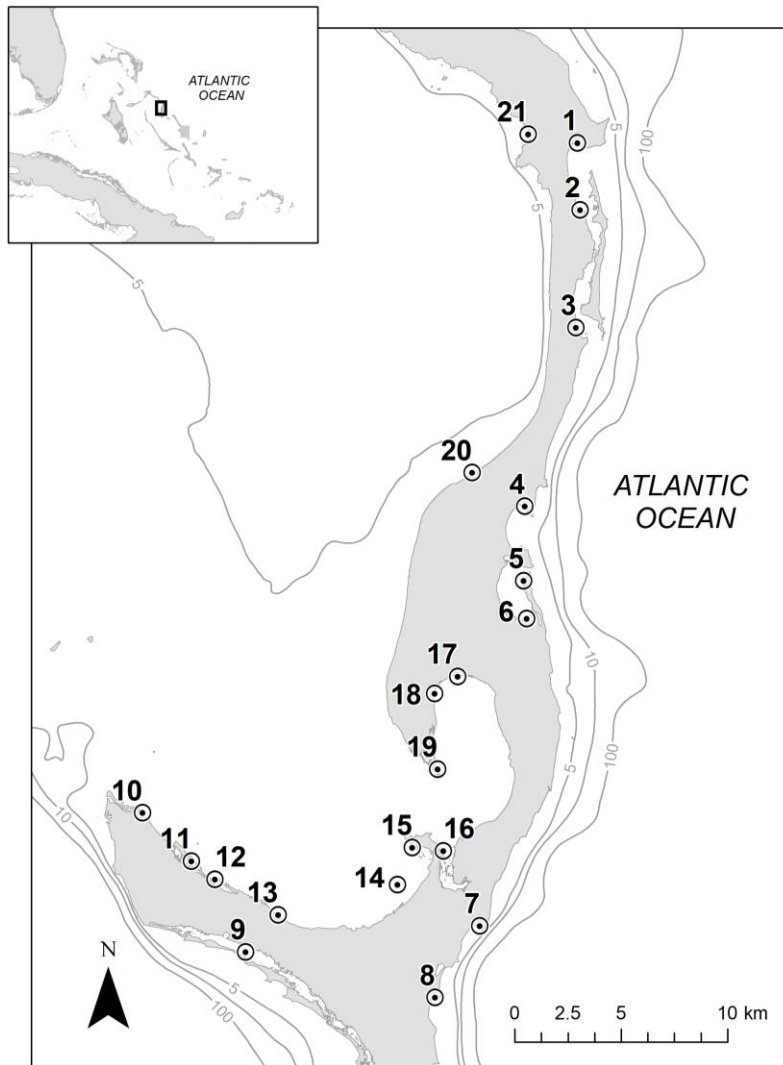
Figure 2.1 Map of study area depicting the location of sampling stations. Bathymetric contours reflect water depth in meters.
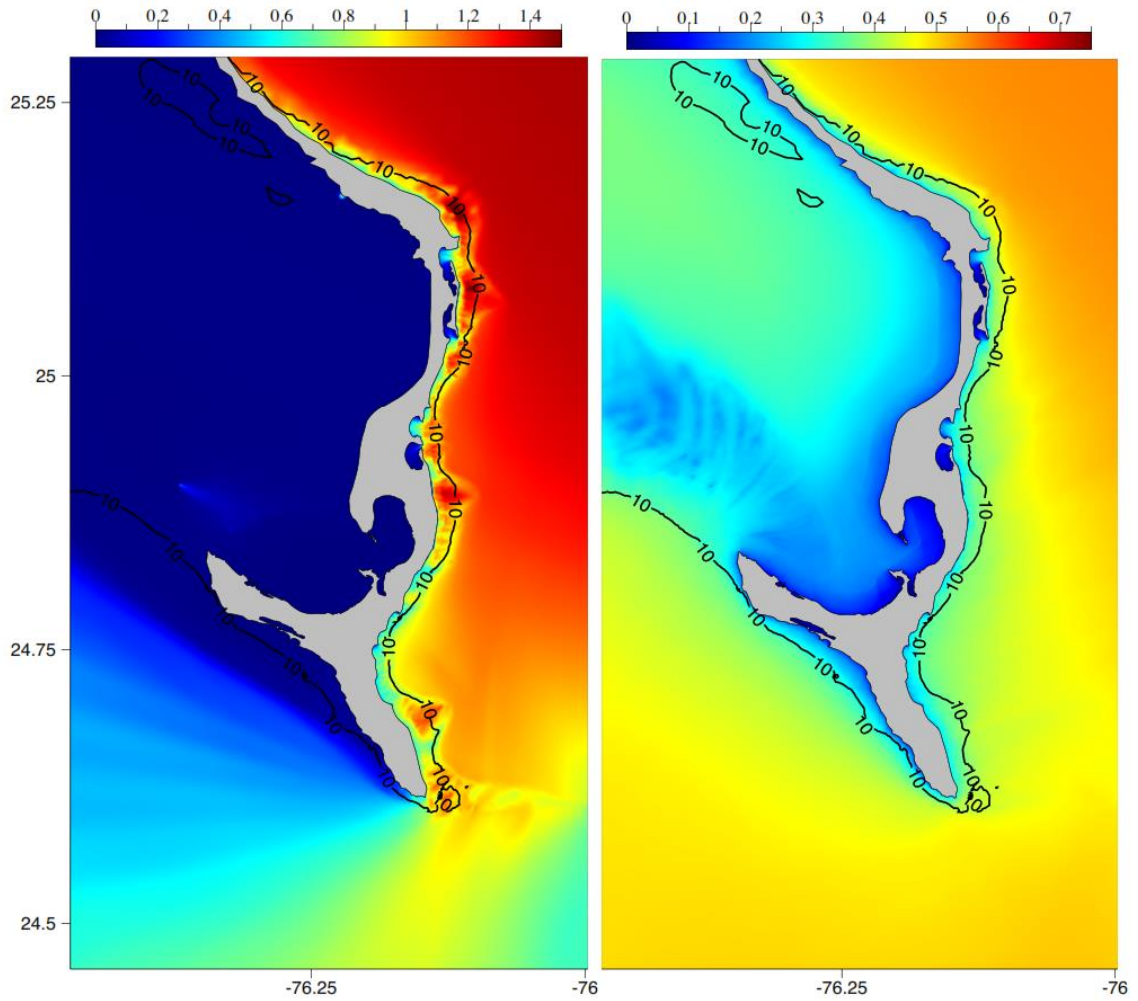
Figure 2.2 Mean significant wave heights (in meters) for remote swell (left panel) and wind-driven (right panel) waves within the study area, based on simulated wave fields computed using SWAN. The 10 m isobath is shown for reference. Note the difference in the range of wave height scales depicted in the color gradient ramps.
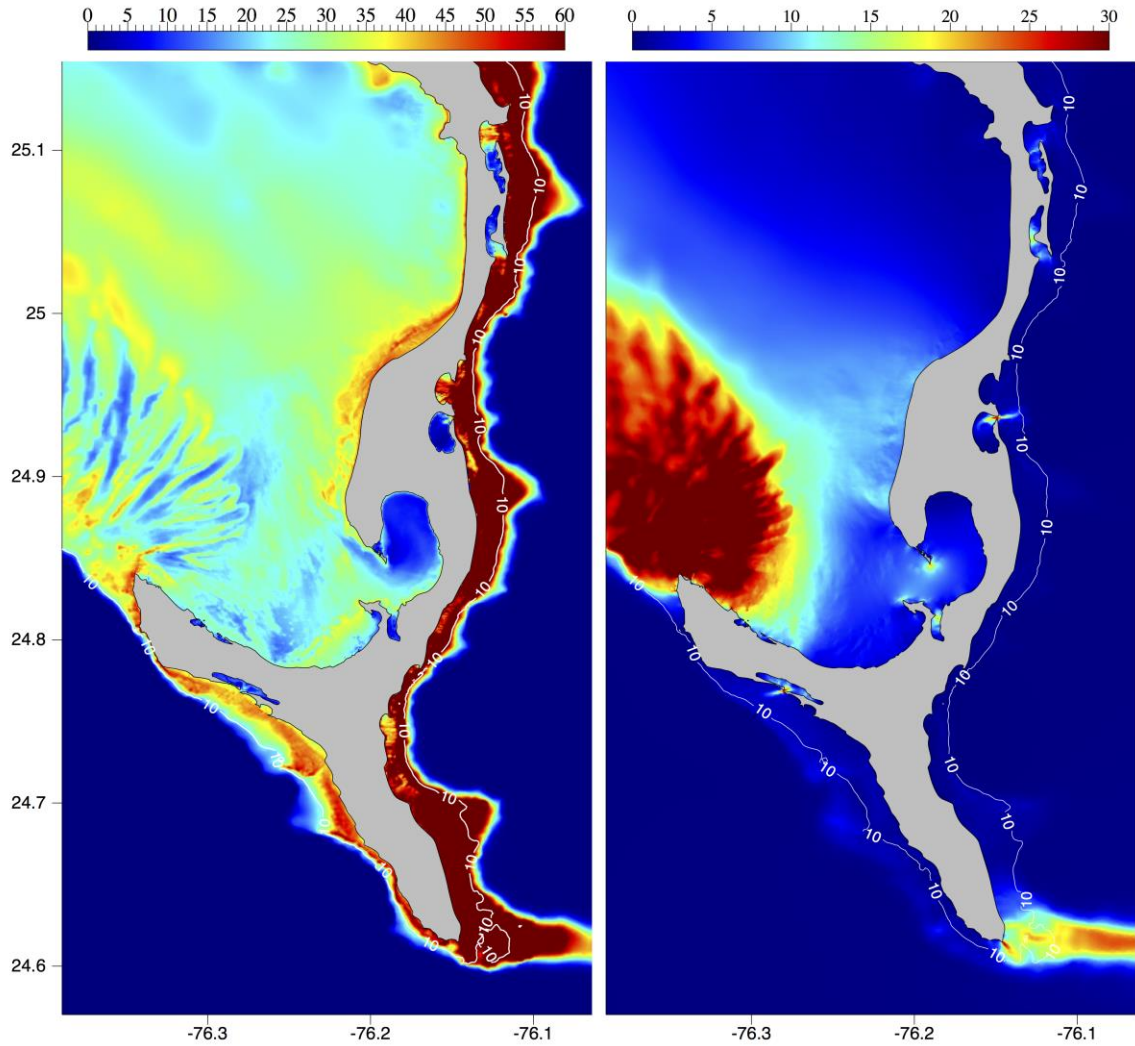
Figure 2.3 Near-maximal (99th quantile) wave-induced bottom orbital velocity for wind and swell combined, termed U_{max} (left panel), and maximum tidal current velocities associated with the M_2 (principal lunar semidiurnal) constituent at a height of 5 cm above the substrate, termed U_{tide}, (right panel), as estimated by hydrodynamic models. To better depict variability within areas of interest (i.e., at sampling stations), maximum values depicted by the color gradient ramps have been truncated to 60 cm s^{-1} and 30 cm s^{-1} for U_{max} and U_{tide} respectively. The 10 m isobath is shown for reference.
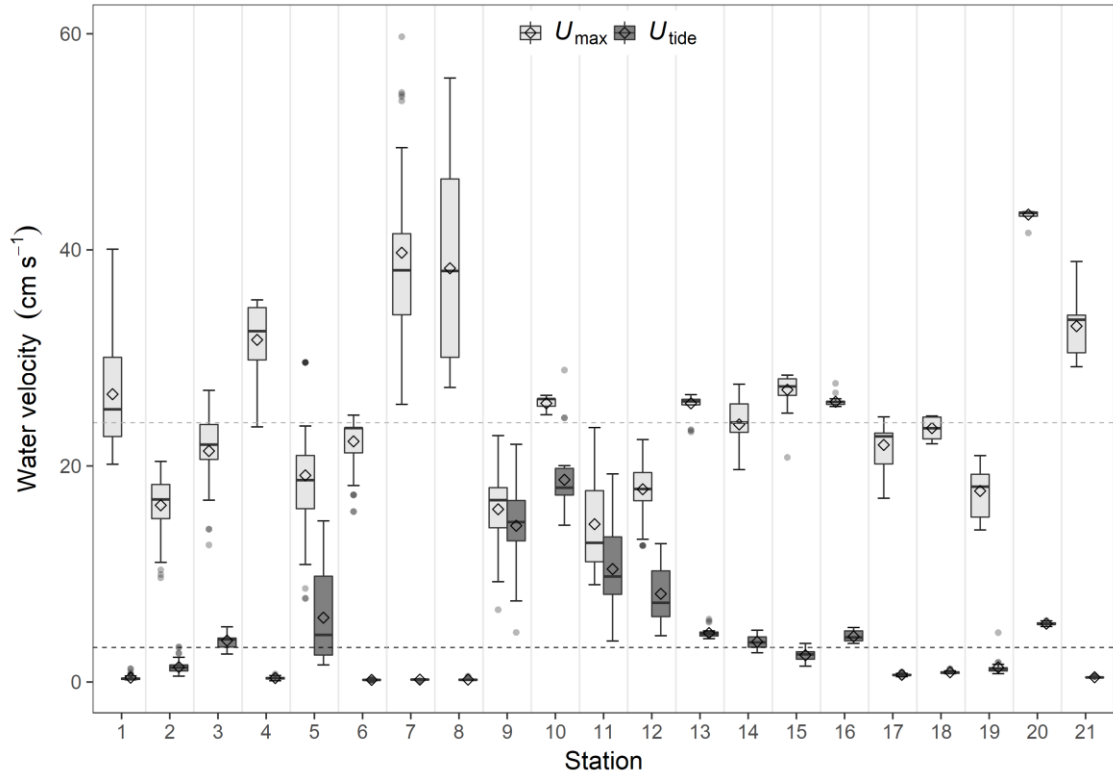
Figure 2.4 Boxplots of near-maximum wave-driven (U_{max}, with light grey fill) and tide-driven (U_{tide}, in dark grey fill) near-bed water velocities at sampling locations, grouped by station. Diamonds indicate means; dots signify outliers.
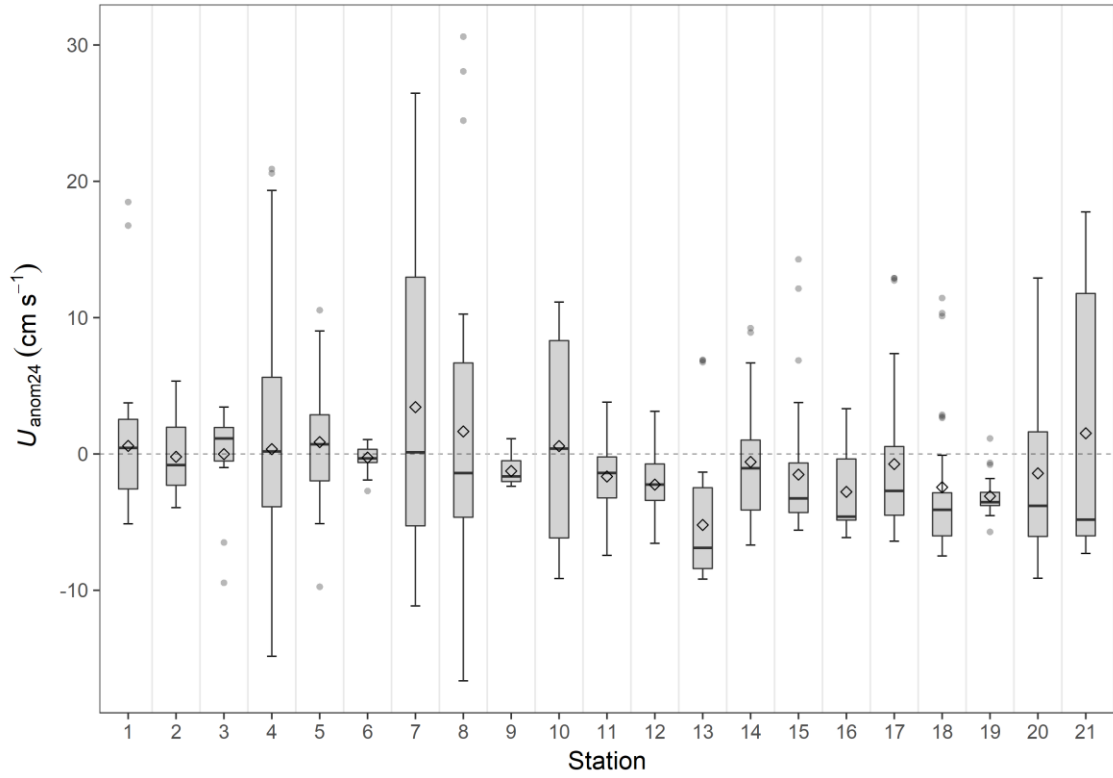
Figure 2.5 Boxplot of 24-hour wave-driven bottom velocity anomaly, (U_{anom24}) estimated to occur at sampling locations, grouped by station. Diamonds indicate means; dots signify outliers.

2.9 Appendix 2A: Bathymetric Model

Model production

Shallow-water bathymetry (<6 m depth) for the immediate study area was derived

from 4.8 m spatial resolution, 10-bit Quickbird multispectral satellite imagery using the

"ratio transform" method of Stumpf and Holdereid (2003). This approach exploits the

differential absorption of visible light spectra in seawater to infer relative differences in

water depth from the ratio of reflectance between distinct color bands (i.e., blue and

green) in remotely sensed imagery. Relative bathymetry was then calibrated to absolute

depths based on ground-truth data obtained from nautical charts and manually-recorded

depths throughout the study area. Each of 5 distinct Quickbird scenes was processed

independently to account for variation in oceanographic, atmospheric, and astronomic

conditions at the time of image capture. Estimated water depths were then corrected for

tidal height at the time of image capture, calibrated to mean tide level (MTL) and finally

merged into a single continuous raster at 9.6 m spatial resolution. Deep-water

bathymetry (>4 m) surrounding the immediate study area was produced using a

triangulated irregular network (TIN) mesh incorporating a combination of hydrographic

point soundings and depth contours acquired from multiple sources including NOAA and

Garmin electronic navigational charts (ENCs). The deep-water TIN was interpolated to a

9.6 m resolution raster and then merged with the shallow-water bathymetry, employing a

blend between 4 m and 6 m depth. For the remainder of the extended model domain, the

General Bathymetric Chart of the Oceans (GEBCO) 2014 30 arc-second grid (Weatherall

et al. 2015) was utilized, with the exception of some regions of the Bahama Banks, where

a shallow-water TIN was generated from additional ENC-derived point soundings and

depth contours in order to address deficiencies in the shallower regions of the GEBCO

dataset. High-resolution shoreline contours for the immediate study area were extracted

from the infrared bands of the Quickbird imagery, and then manually corrected as

necessary based on visible spectra. Coarser shoreline data for the remainder of the model

domain were obtained from the NOAA world vector shoreline (US Defense Mapping

Agency 2005) database. The final, combined bathymetric dataset extended from roughly

23.5° to 26° latitude and -78° to -75° longitude.

Validation

The accuracy of the image-derived bathymetric model was evaluated by comparing

predicted water depths with field-surveyed depths along two transects encompassing

variable bottom types within an embayment where sampling stations 5 & 6 were situated

(Fig. 2A-1). Transect A comprised 29 points spanning 1200 m from west to east, while

Transect B included 15 points stretching approximately 350 m from north to south.

Surveyed depths were recorded with a lead line and corrected for tidal height at the time

of measurement to obtain depth at MTL. Bathymetric profiles were well-resolved by the

model for both transects (Fig. 2A-2). Image-derived water depths corresponded closely

with surveyed depths, with a total root-mean-squared-deviation (RMSD) of 0.37 m across

all 44 points, and a regression slope of 0.95 (Fig 2A-3).

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Figures
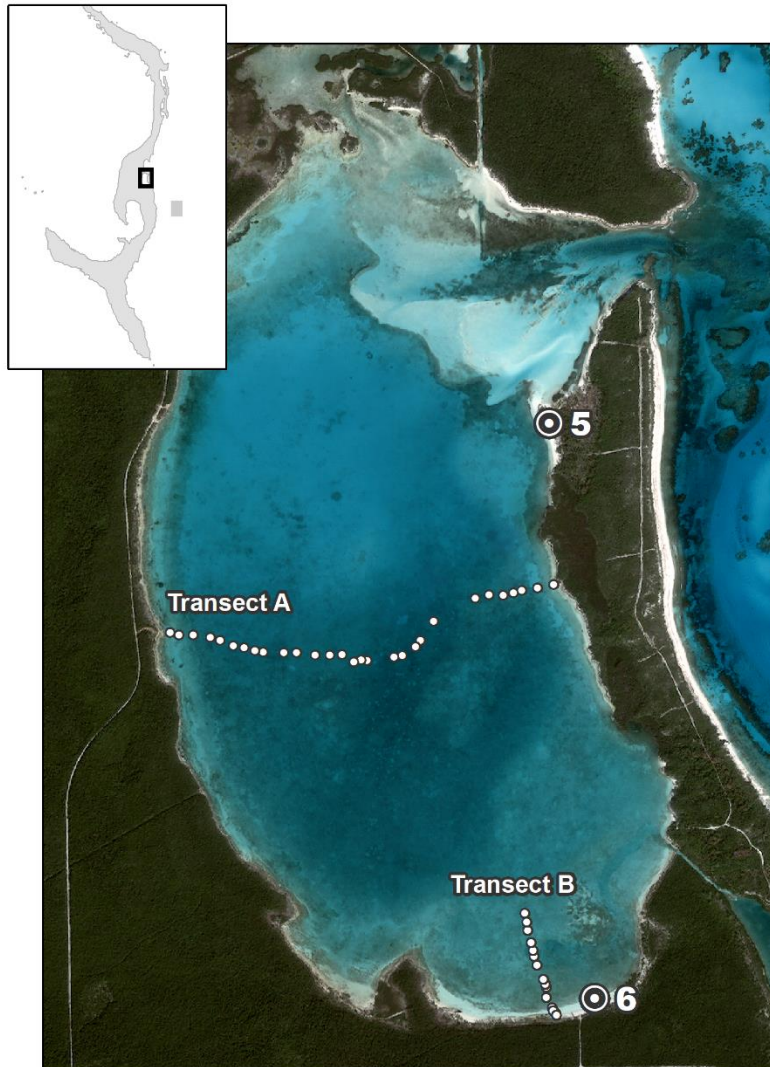
Figure 2A-1. Satellite image depicting the locations of depth survey points along two transects ("A" & "B") used for validation of the image-derived bathymetric data. The locations of sampling stations 5 & 6 are also displayed for reference.

Transect A.
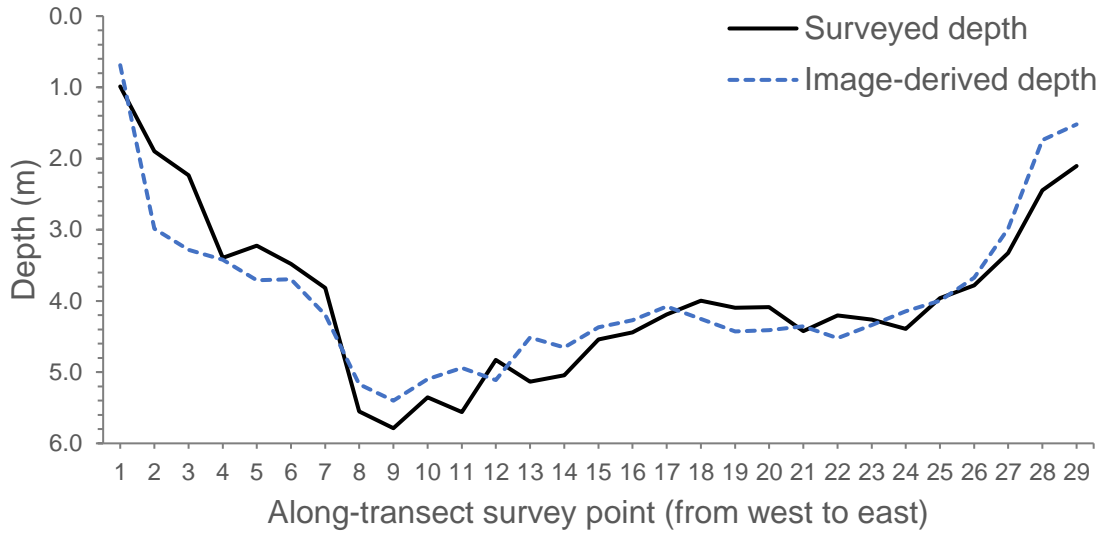
Transect B.
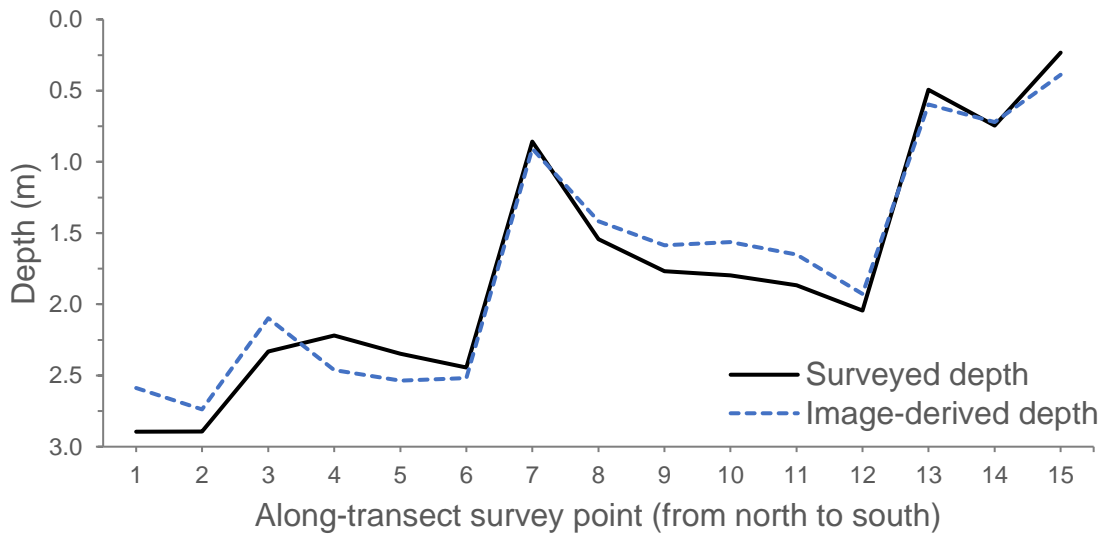
Figure 2A-2. Image derived and field-surveyed bathymetric profiles corresponding to two transects located in the embayment where stations 5 & 6 were situated (see Fig. 2A-1 for the exact locations of transects).
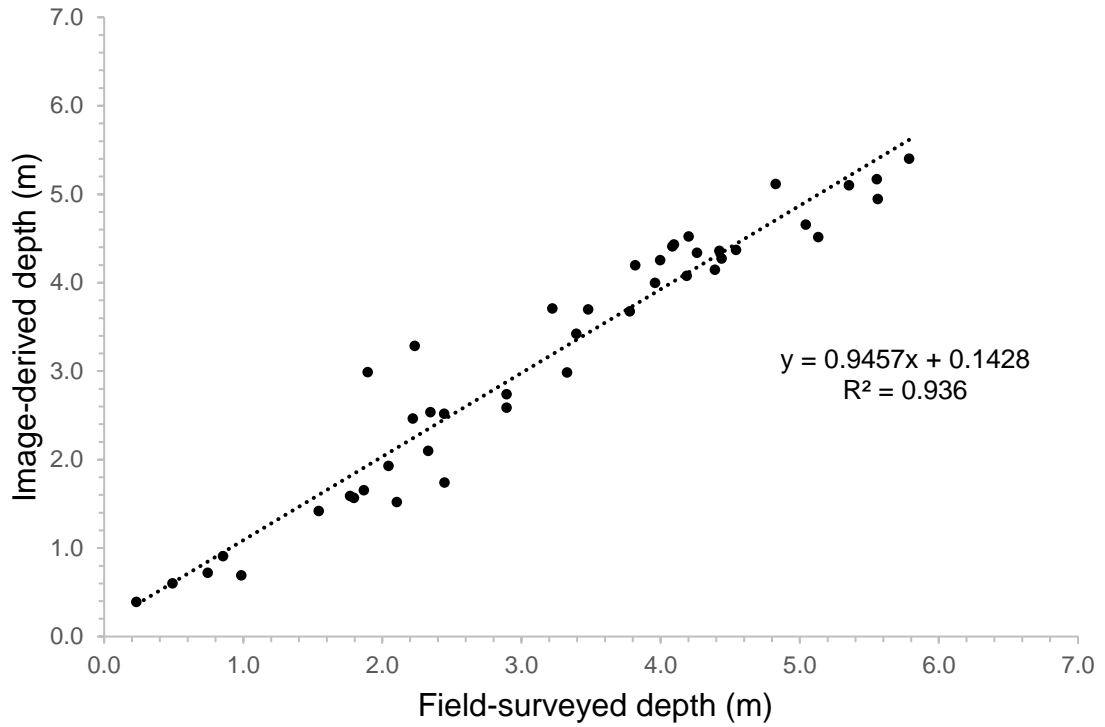
Figure 2A-3. Regression of field-surveyed and image-derived depths recorded at points (n=44) along two transects located in the embayment where stations 5 & 6 were situated (see Fig. 2A-1 for the exact locations of transects).

2.10 Appendix 2B: Wave Model

Wave model setup

To estimate the wave characteristics in the vicinity of Eleuthera Island, a regional setup of the third generation phase-averaged wave model SWAN (v41.01) (Booij et al. 1999) was used. Due to the large range of spatial scales, computations were carried out on an unstructured grid. Meshes were generated with the open source software *gmsh* (Geuzaine and Remacle 2009). The mesh used for production runs is comprised of 318K vertices and edge lengths range from 15 km at the open boundary to 25 m along the portion of the Eleuthera coast containing the sampling sites. Mesh resolution on adjacent islands was set to 1000 m. The bathymetry and coastline were derived from a composite product developed in the present work and described in detail in Appendix 2A. Maximum depth in the computational wave domain was truncated to 1000 m. Wave direction was discretized in 10° increments and wave frequency was discretized using 31 frequencies spaced logarithmically between 0.0521 Hz and 1.0 Hz. The wave model domain and bathymetry are shown in Fig. 2B-1.

To quantify the impact of waves at the sampling sites, it was necessary to consider several years of wind and swell forcing to be able to include seasonal variability and reduce the impact of inter-annual variation and extreme events. Given the relatively large problem size and constraints due to limited computational resources it was not feasible to integrate the model forward over the complete multi-year time period. The approach in the present work was to employ response models known as surrogates to develop, discretely, the relationship between the wave forcing and the wave impact characteristics at the sites of interest. Here the influence of wind (local forcing) and swell

(remote forcing) were considered separately to reduce the number of combinations necessary to capture the variability of the true forcing. For the wind-driven surrogate model five wind speeds (U_{10} [ms^{-1}]=[2.5, 5, 10, 15, 20]) were considered for every 15° of wind angle for a total of 120 parameter sets. The values for U_{10} were selected using the frequency distribution of wind speeds from NOAA station SPGF1 located on Settlement Point on Grand Bahama. For the swell response model, combinations of three parameters were used. These were: wave heights H_s [m]=[.5, 1.5, 2.5, 3.5,4.5], dominant period T_p [s]=[5.5, 8.5, 11.5, 14.5], and dominant direction θ_p = [120°-270°] in increments of 15°. Combined, the swell response model required wave solutions from a total of 5×4×11 = 220 forcing parameter sets. The parameter ranges for H_s and T_p were selected from frequency distributions of wave observations from NDBC buoy 41047. The truncated range of wave direction was established by conducting process studies using a coarser model. Remote swell in the range 0° - 120° and 270° - 360° was not found to have any significant impact in the sampling areas, primarily due to sheltering by the Exuma Cays to the west and Cat Island to the south and thus swell forcing from these directions was not considered in the response model. It should be noted that while extreme combinations of the three swell parameters are rare in the observations (e.g. highest waves at shortest period), the establishment of a regular lattice in parameter space enabled more efficient and more accurate interpolation during post-processing. Thus all combinations of the triplets were considered. The wave model was forced using each of the 120 wind-forced and 220 swell-forced parameter sets until a steady state convergence was obtained, requiring approximately 16 core-hours of compute time per condition. To build the two surrogate models required a total of approximately 5500 core-hours of compute time.

Four wave metrics were selected for the study. These were: (1) the amplitude of bottom wave orbital velocity (w_{bot} [ms^{-1}]), (2) the significant wave height (H_s [m]), (3) the flux of wave energy in the dominant wave direction (*Pow* [Wm^{-1}]), and (4) the bed stress due to waves (τ_{bw} [Nm^{-2}]). The first three metrics are computed directly by SWAN. The wave-induced bed stress τ_{bw} was derived from the archived SWAN output using the method of Soulsby (1997). This approach includes the influence of bottom roughness in a wave friction factor f_w which depends on the median grain size D_{50}. For the present work, we employed a constant median grain size $D_{50} = 0.5$ mm ($\varphi=1$) as it is representative of the characteristic sediments in the region (Gardner 1993).

The wind response was constructed by interrogating the wind surrogate model with wind speed and direction from NOAA station SPGF1 for the period Jan 1, 2010 - Jan 1, 2014. The swell response was constructed using wave direction, significant height, and dominant period from NOAA NDBC 41047 located 500 km NE of Eleuthera over the period Jan 1, 2012 - Jan 1, 2015. Computations of the mean, maximum, and 99th percentile values for each impact variable were computed at each of the model vertices.

Validation

A low resolution setup of the wave model was constructed to validate the physics parameterization. This model was integrated over a period coinciding with the placement of NOAA NDBC buoy 41016. The 41016 buoy is situation at the northern end of Exuma sound (Fig. 2B-1) and is significantly sheltered from remote swell by Eleuthera, the Exuma Cays, and Cat Island. Buoy measurements included wind speed and direction, dominant wave period, and significant wave height from July 27, 1992 to Jan 27, 1993. The low resolution model was forced by instantaneous wind speed and direction from the

41016 buoy and the model-computed wave field at the buoy location was archived for skill assessment. Comparison of observed and model-computed time series for significant wave height H_s and dominant period *DPD* at the 41016 site are shown in Fig. 2B-2. The model captures well both small and large events. A quantiles (Q-Q) plot of the two time series is shown in Fig. 2B-3. The slope of the regression for H_s is 1.06 and for DPD is 0.92. The root-mean square deviation for H_s is 0.12 m and for DPD is 0.55 s.

Regional waves

The remote ocean swell produces significant wave heights of $H_s \sim 1$ m incident on the exposed coastline of eastern Eleuthera (Fig. 2B-4 [left panel]). The swell has negligible influence on western Eleuthera due to sheltering. The local wind-driven response produces smaller significant wave heights of $H_s \sim 0.5$ m along eastern Eleuthera compared with the swell response (Fig. 2B-4 [right panel]). However, on the southern and western coastlines of Eleuthera, the local wind-driven response dominates the wave field, producing significant wave heights in the range of 0.2 - 0.4 m.

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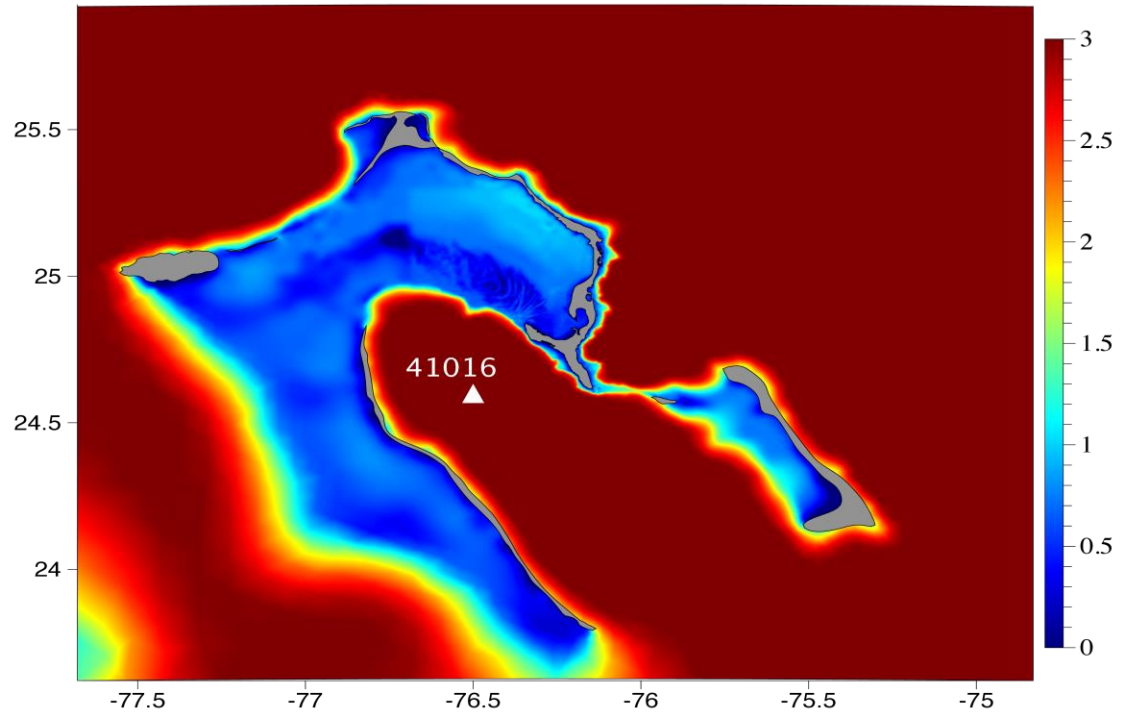
Figure 2B-1. Wave model domain and bathymetry $\log_{10}(h)$ [m] with location of NDBC 41016.
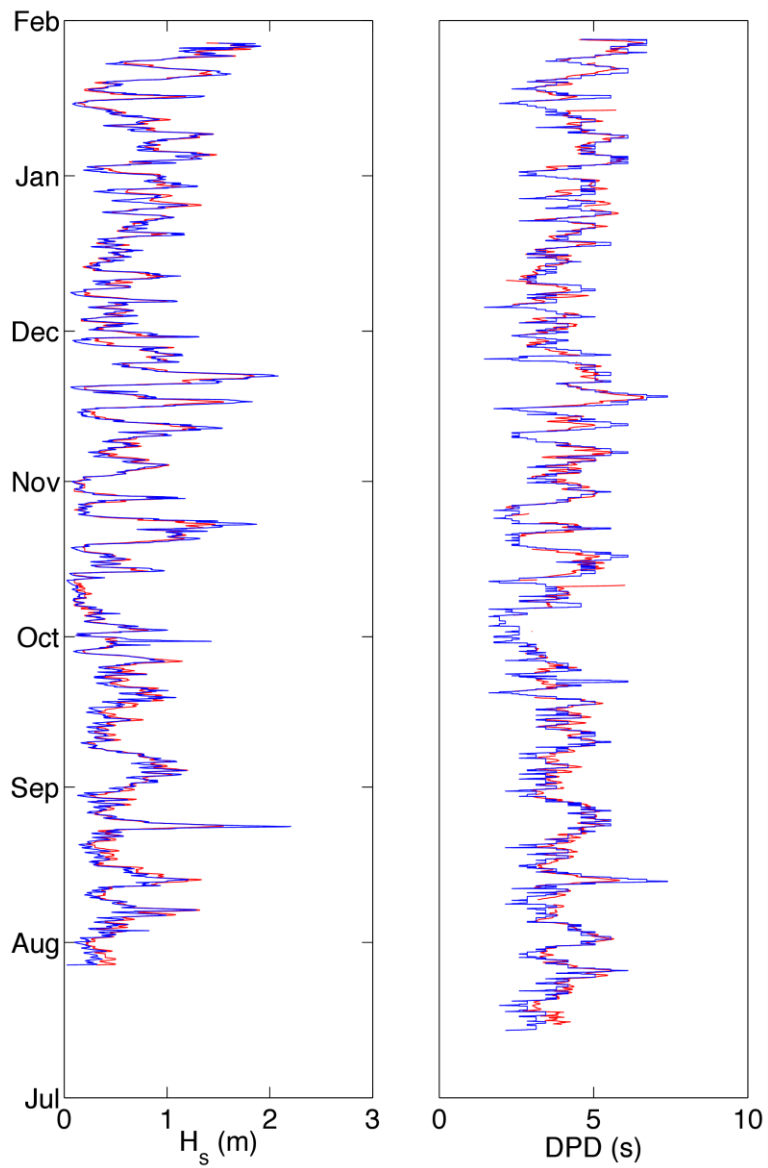
Figure 2B-2. Time series of observed (red line) and model-computed (blue-line) significant wave height (left) and dominant period (right) at the NDBC 41016 buoy during the period July 27, 1992 - Jan 27, 1993
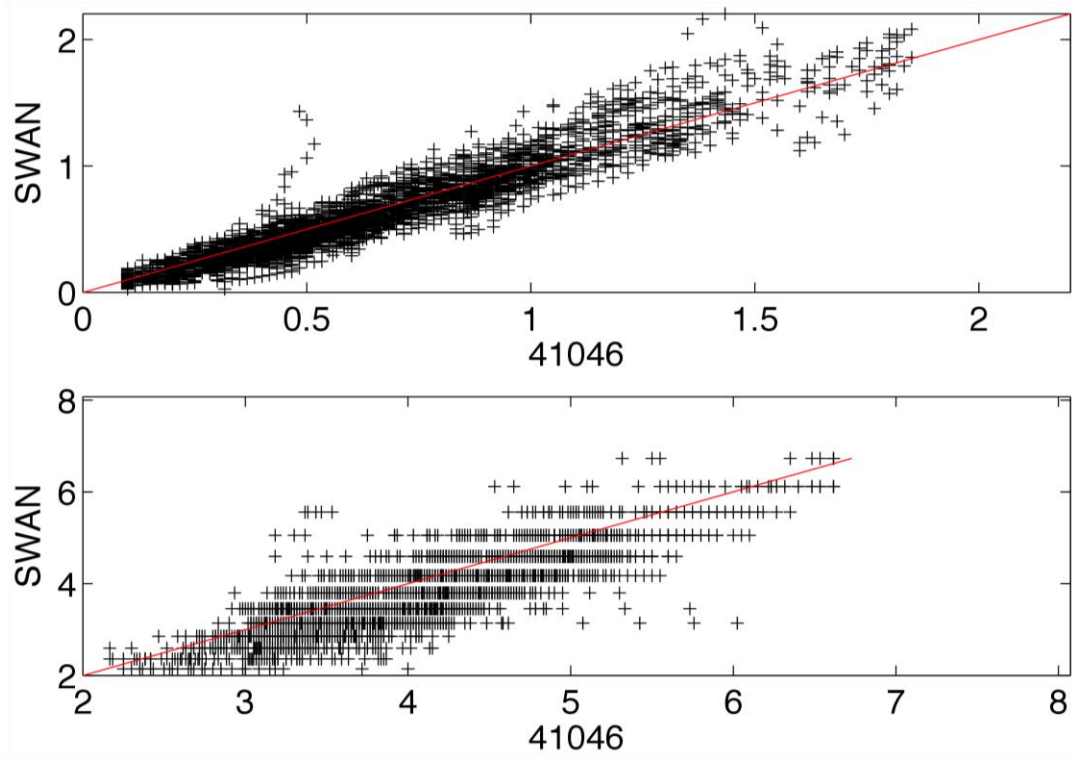
Figure 2B-3. Q-Q plot for H_s [m] (upper panel) and dominant period DPD [s] (lower panel)
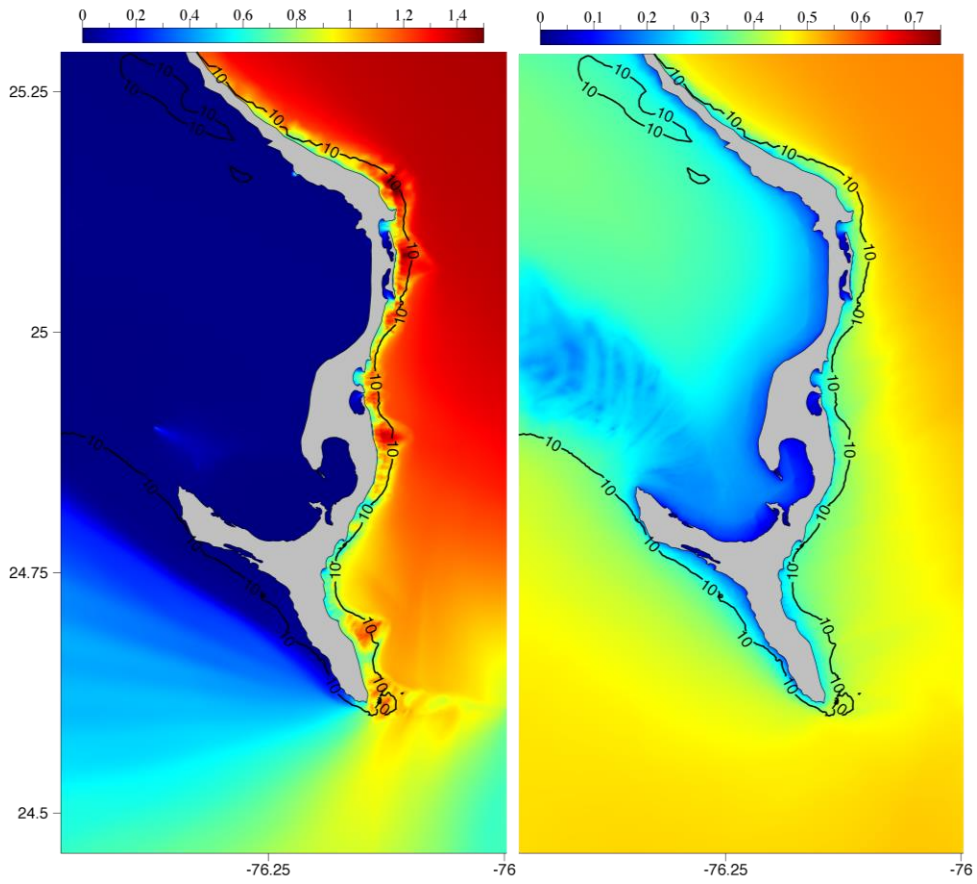
Figure 2B-4. Mean significant wave height H_s [m] due to remote swell (left) and local wind (right). 10-m isobath shown for reference.

2.11 Appendix 2C: Tidal Model

Tide model setup

A two-dimensional depth-averaged tidal model was developed to estimate the spatial distribution of tidal velocity around Eleuthera Island. This model was constructed using the shallow water equation solver of the Finite-Volume Community Ocean Model (FVCOM). FVCOM is an open source software package for the simulation of ocean processes in coastal regions (Chen et al. 2006) on unstructured triangular grids. The model is parallelized for execution and scales well on modern distributed network machines (Cowles 2008). The unstructured mesh used for Eleuthera contains 707,554 elements and 357,427 vertices. Horizontal resolution ranges from 25 m along the coast and in the embayments of southern Eleuthera to 15 km at the open boundary. The resolution along outlying islands is 1500 m and in the northern section of the Exuma Cays is 250 m. The bathymetry and coastline were derived from a composite product developed in the present work and described in detail in Appendix 2A (Fig. 2C-1). The irregular shape of the domain maintains deep water along the open boundary to ensure the harmonics used to force the simulation are reliable. The model was driven at the boundary with sea surface elevation generated using the nine principal regional tidal harmonics (M_2,S_2,N_2,K_2,K_1,O_1,P_1,Q_1,M_4). The amplitude and phase (°G) for these harmonics were derived from the TPX08 1/30° tidal atlas (Egbert and Svetlana 2002; 2016). Bottom friction was set using the Strickler-Manning formulation with a Manning coefficient n=0.02. The depth-averaged FVCOM tidal model was integrated for 50 d at a time step of Δt=0.1s and velocity components and sea surface height were archived hourly. The archived fields were used to compute a maximum and mean velocity at each

model control volume. The model run required approximately 10,000 core-hours of computational time on six 24-core nodes for a total of 72 h of walltime.

Validation

The tidal model was validated through comparison with measurements of sea surface elevation and bottom velocities. There are two fixed observation stations providing tidal elevation for Eleuthera. The first is on the west side of the island (NOAA TEC4625) and the other on the east side (NOAA TEC4627) (Fig. 2C-2). At these stations, the observed height and time of high and low tides are generated using adjustments from a nearby reference station (Settlement Point, Grand Bahama Island NOAA Station: 9710441). The error for these predictions is not reported. Comparison of the model-computed sea surface elevation with high and low tide heights from these stations is shown in Fig. 2C-3. The model captures well the spring-neap variability and the diurnal inequality at both sites. The RMSE of the model at the time of high and low tide from the observations at west Eleuthera is 0.047 m and at the east Eleuthera site is 0.031 m.

In addition to the fixed sites, eight short duration records of bottom pressure and near-bottom velocities were available from a prior study of predatory fishes in patch reefs around Eleuthera (Harborne et al. 2017). The timeframe of this study was Feb 28, 2015 to March 9, 2015. The observations were made using two sets of instruments, each set containing a bottom-mounted pressure sensor and a bottom-mounted Lowell Instruments TCM-1 tilt current meter. Both sets were moved four times during the two-week study period for a total of eight observation locations AH1-AH8 (Fig. 2C-2, lower panel). Comparison of the model-computed elevations with elevations derived from the pressure

sensors is shown in Figure 2C-4. The RMSE for model-computed sea surface elevation at sites AH1-AH4 (Fig. 2C-4, upper panel) is 0.055 m and at sites AH5-AH6 (Fig. 2C-4, lower panel) is 0.049 m. To compare model-computed velocities with values recorded by the tilt-meters, the model velocities were reconstructed using the logarithmic law of the wall to a fixed height. The tilt-meters are within the bottom boundary layer of the tidal flow and do not measure the velocity at a fixed height above the bed. Rather, a fixed function is used to transform the tilt angle from the vertical to a characteristic bottom velocity. In the present work, the model-computed velocities are reconstructed to a height of 0.5 m above the bed. This produces good agreement with the tilt-meters at all sites, including both the low and high velocity sites as shown in Fig. 2C-5. Ellipticity of the tidal currents is small and the model captures the local direction of tidal velocities well (Fig. 2C-6) at all sites with the exception of AH7 where the compass on the tilt current meter was suspected to have experienced magnetic interference.

Regional tides

In the deep waters surrounding the island, the tidal characteristics are slowly varying. The amplitude of the M_2 constituent is approximately 0.36 m and strength of the first harmonic is relatively small ($M_4 \sim 0.002$ m). As the Kelvin wave approaches Eleuthera from the west, the shallow waters of the Marker Bars transform the tidal characteristics considerably. A delay of approximately 2.5 h is imparted on the M_2 component (Fig. 2C-7a) and the M_2 amplitude on the western shore is enhanced by approximately 0.01 m relative to shore of eastern Eleuthera (Fig. 2C-7b). The friction increases the nonlinearity of the tide ($M_4 \sim 0.02$ m). The relative phase $2M_2 - M_4$ ranges from 0 °G in the deep water to 80 °G along western Eleuthera, indicating a slight flood

dominance (Fig. 2C-7c). The mean annual magnitude of the model-computed vertically-averaged tidal currents range from ~0.01 ms^{-1} in the deep water to ~0.65 ms^{-1} near the tip of Cape Eleuthera. This value reaches ~0.15 ms^{-1} in the entrance to Rock Sound, and as high as 0.35 ms^{-1} in the narrow channel leading to Half Bay (Fig. 2C-7d).

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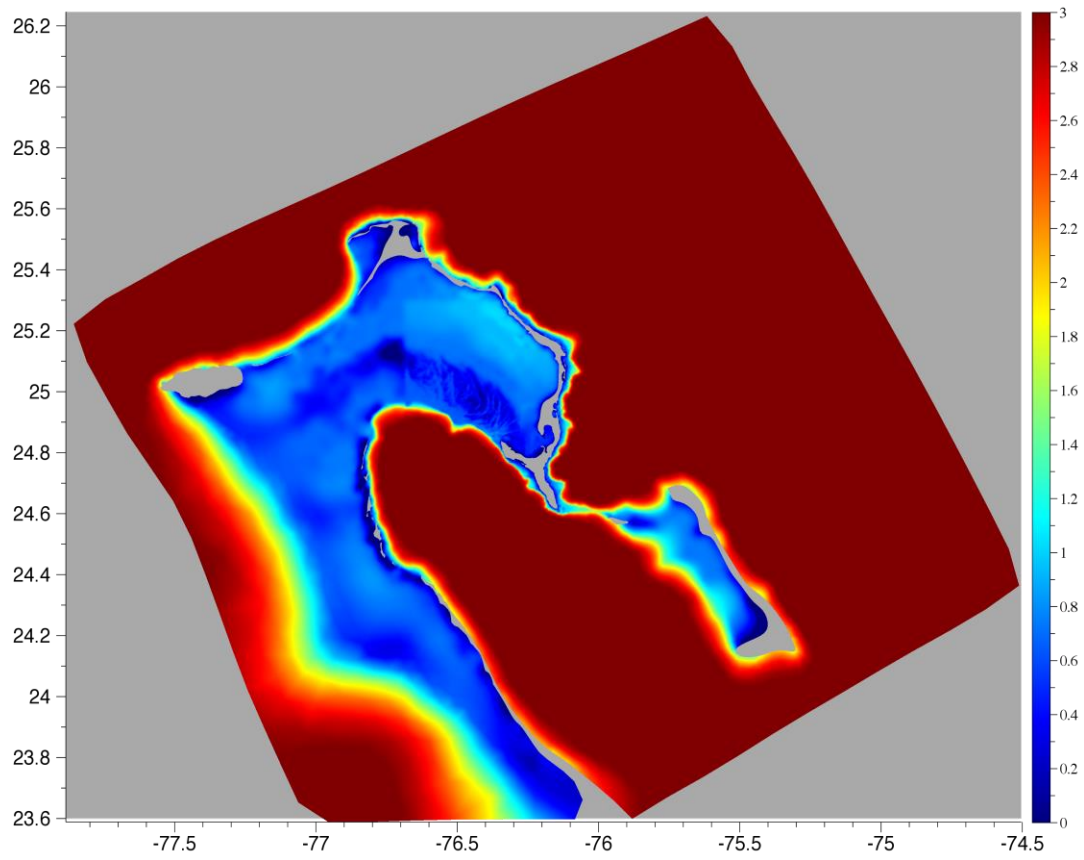
Figure 2C-1. Tidal model domain and bathymetry $\log_{10}(h)$ [m]
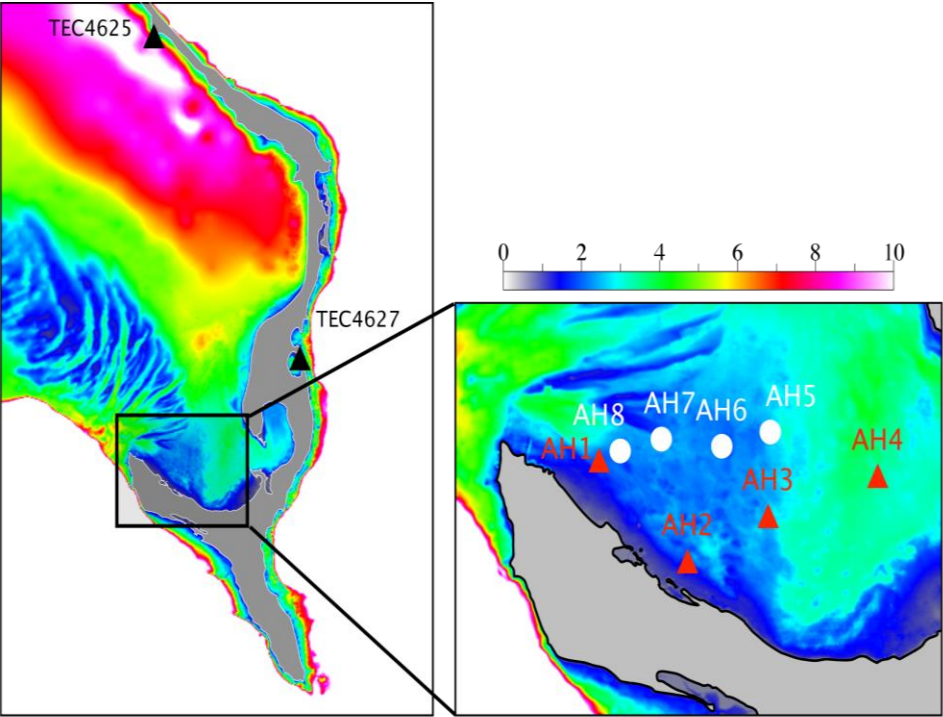
Figure 2C-2. Locations of tidal elevation stations on southern Eleuthera (upper) and locations of bottom pressure and near-bottom velocity measurements AH1-AH8 (lower).
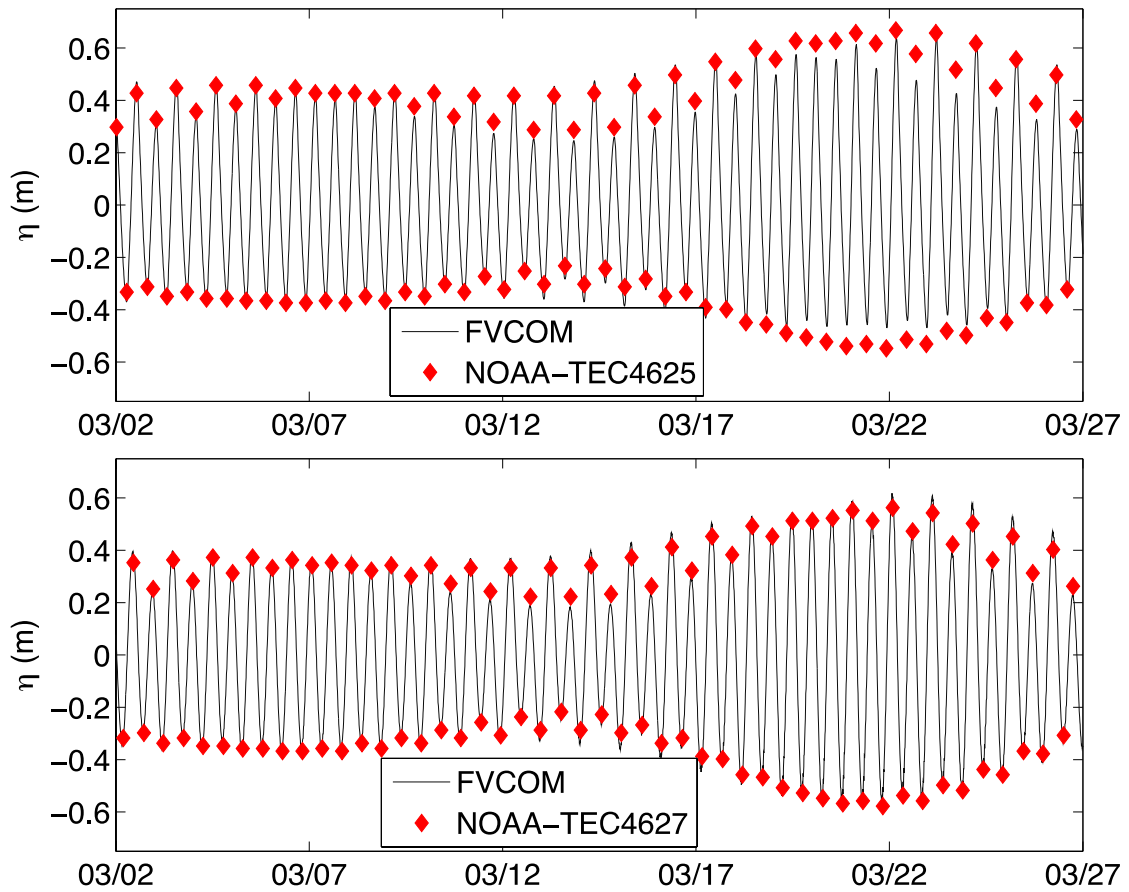
Figure 2C-3. Comparison of the model-computed tidal elevation (black lines) and observed high and low tide (diamonds) elevations for western Eleuthera (upper panel) and eastern Eleuthera (lower panel) for the month of March, 2015
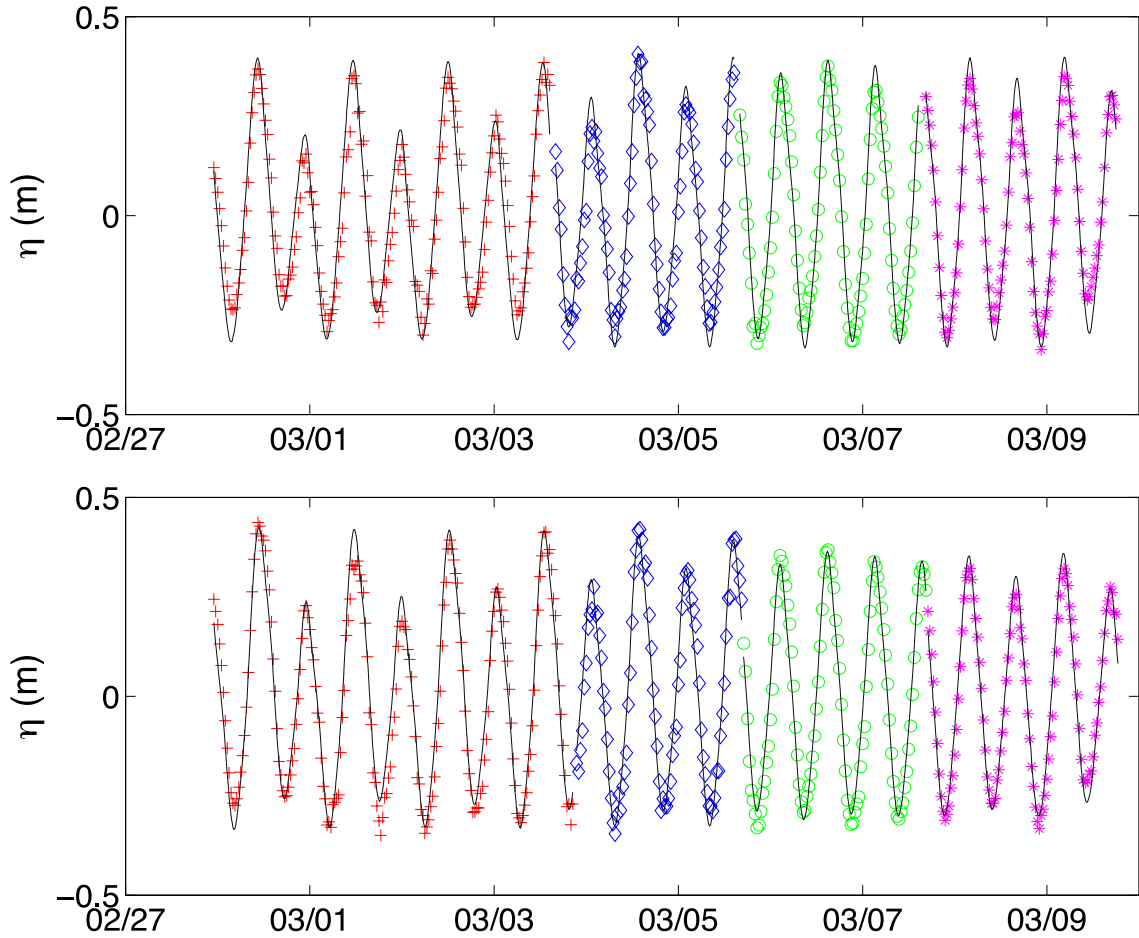
Figure 2C-4. Comparison of the model-computed tidal elevation (black lines) and observed data from mobile pressure gauges during spring 2015. Upper panel: Instrument 6165 at sites AH1 (red plus), AH2 (blue diamonds), AH3 (green circles), and AH4 (magenta asterisks). Lower Panel: Instrument 3761 at sites AH5 (red plus), site AH6 (blue diamonds), site AH7 (green circles), and site AH8 (magenta asterisks). Refer to Fig. 2C-2 for instrument locations.
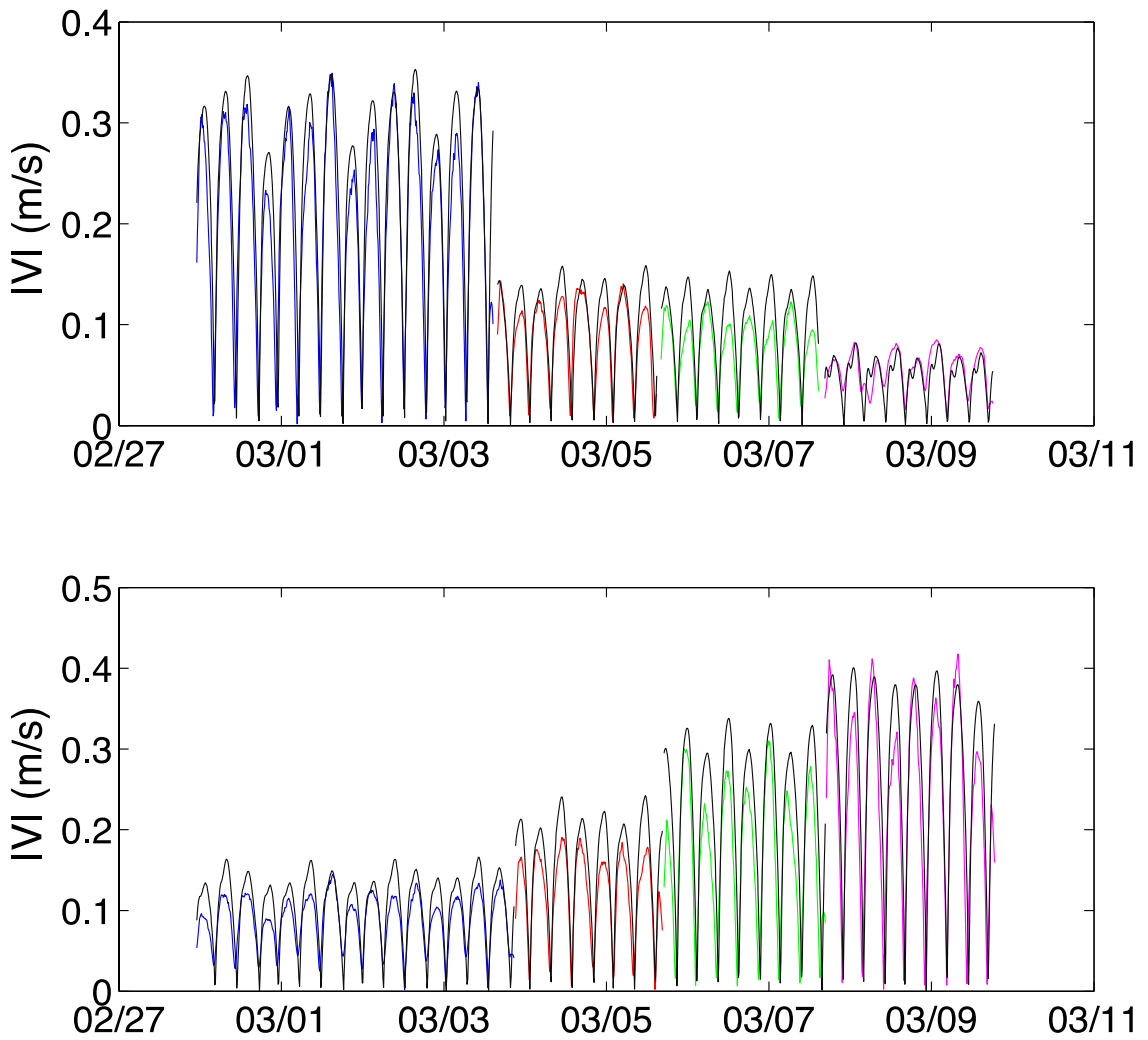
Figure 2C-5. Comparison of the model-computed velocity magnitude at 0.5 m above bottom (black lines) and observed data from tilt current meters during spring 2015. Upper panel: Instrument 14 at sites AH1 (red), AH2 (blue), AH3 (green), and AH4 (magenta). Lower Panel: Instrument 15 at sites AH5 (red), site AH6 (blue), site AH7 (green), and site AH8 (magenta). Refer to Fig. 2C-2 for instrument locations.
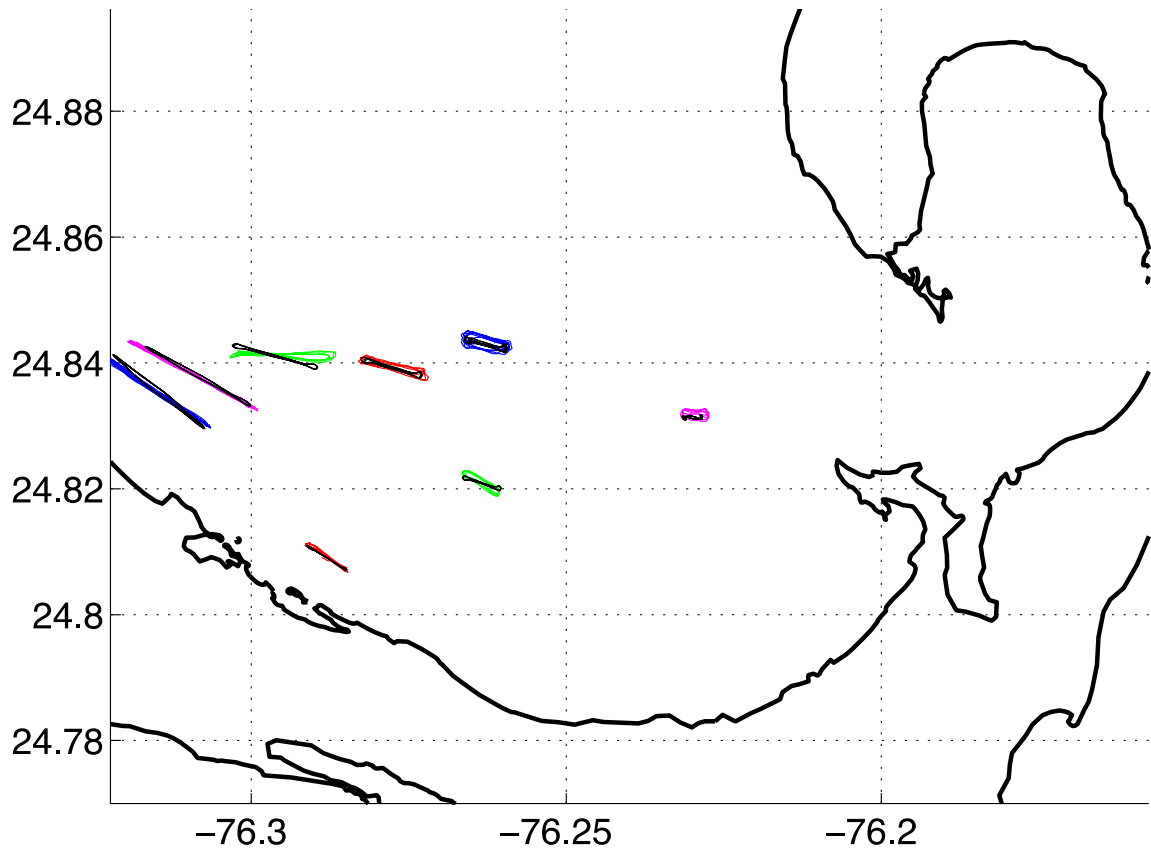
Figure 2C-6. Comparison of the model-computed velocity at 0.5 m above bottom (black lines) and observed data from tilt current meters during spring 2015 at sites AH1-AH8 (refer to Fig. 2C-2 for instrument locations).
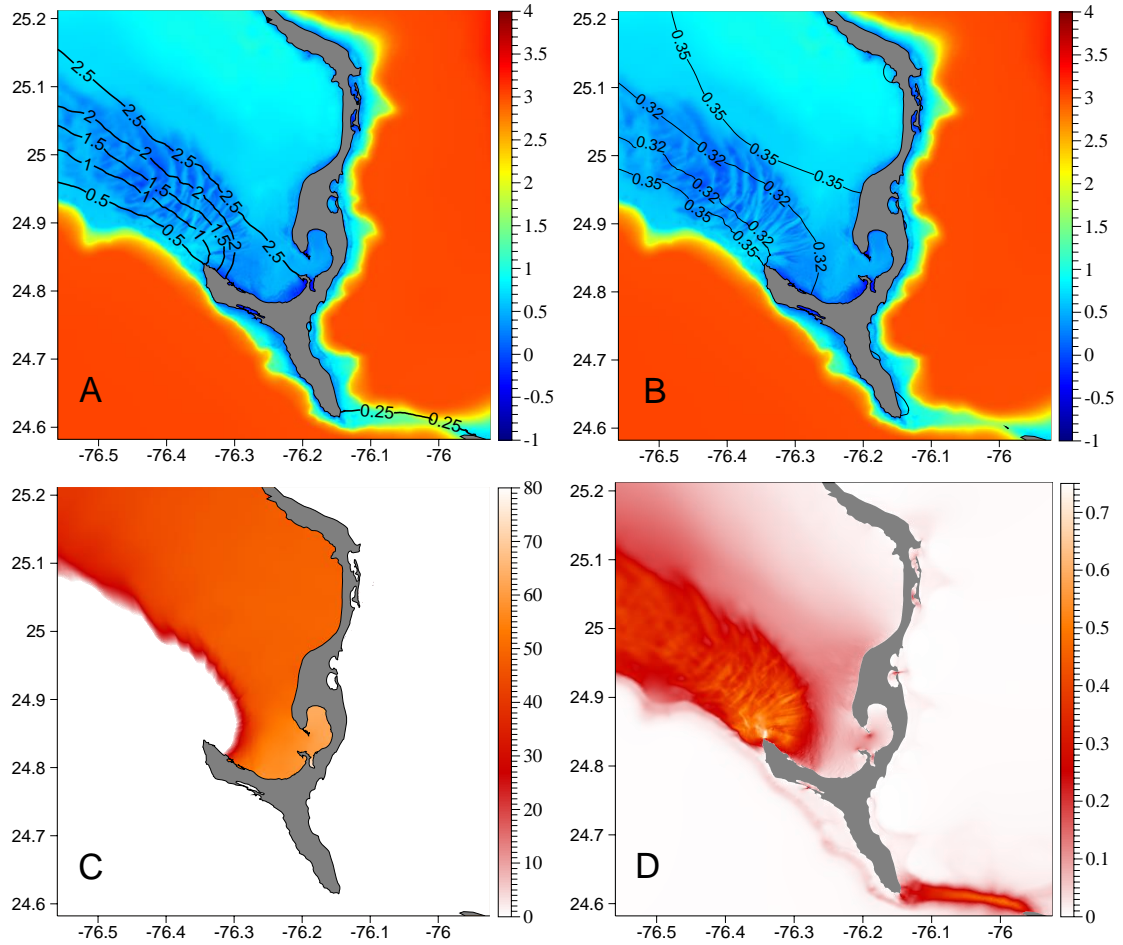
Figure 2C-7. Tidal characteristics for southern Eleuthera. A: Contours of model-computed M_2 phase [hours Greenwich] with bathymetry $\log_{10}(h)$ [m]; B: Contours of model-computed M_2 amplitude [m] with bathymetry $\log_{10}(h)$ [m] (*note:* amplitude in the deep water is approximately 0.036 m); C: Relative phase $2M_2-M_4$ [°G]; D: Mean annual depth-averaged velocity magnitude (ms^{-1})

2.12 Appendix 2D: Pilot Study

Cooccurrence of *A. vulpes* and *Eucinostomus* spp. in seine samples

Exploratory seine hauls (n=249) were conducted between May and October of 2011 at a subset of the stations included in the present study (n=12) employing methods analogous to those described in the main text. *Albula vulpes* juveniles were present in 29 seine hauls at 5 stations, with a mean abundance of 4.4 (median = 2) individuals per haul, producing a total of 128 individuals. *Eucinostomus* spp. occurred in a 164 seine hauls at 12 stations, with a mean abundance of 62.9 (median = 18) individuals per haul, totaling 9058 individuals. All but a single *A. vulpes* juvenile (>99 % of individuals) were captured among shoals of similarly-sized eucinostomids. In contrast, just 17% of *Eucinostomus* spp. occurrences were tied to the presence of *A. vulpes*. When the two taxa co-occurred, *A. vulpes* represented on average 10.5 % (median = 4.4 %) of their combined total abundance.

Cooccurrence of *A. vulpes* and *Eucinostomus* spp. in remote video surveys

Over three days in February 2014, three GoPro™ Hero 3 Black digital video cameras were moored in shallow littoral zone habitats where *A. vulpes* occurred with regularity in seine samples (stations 17 & 18). Concurrently-deployed recording units were separated by a minimum distance of 100 m. The resulting nine distinct time series totaled more than 17 hours of recording time, with each camera sampling approximately 4 m^2 of seabed. *Albula vulpes* juveniles were detected by 8 of the 9 recording units, for a total onscreen presence of 82 minutes (8 % of total recording time). *Eucinostomus* spp. were detected by all 9 units, for a total onscreen presence of 717 minutes (69 % of total recording time). Of the 82 minutes that *A. vulpes* were present on camera, 100 % of this

time coincided with the presence of similarly-sized eucinostomids. Meanwhile, the same period corresponded to just 11 % of the total onscreen time for *Eucinostomus* spp. Time-averaged counts of the two taxa during periods of overlap indicated a mean ratio of 0.10 (median = 0.08) *A. vulpes* per *Eucinostomus* spp. Qualitatively, surveys revealed that *A. vulpes* were embedded in eucinostomid shoals, actively foraging among them and often displaying coordinated movements (i.e., traveling in similar directions at similar speeds).

2.13 Appendix 2E: Additional Tables

Table 2E-1. Mean (±1 SD) of biotic predictors and relative abundance of *A. vulpes* for each sampling station.

	Samples	Mean depth	Vegetation cover	*Eucinostomus* spp.	*A. vulpes*	Total *A. vulpes*
	(*n*)	(m)	(%)	(#)	(#)	(Sum #)
Station 1	40	0.4±0.1	18.6±38.1	35.5±46.9	0.3±1	13
Station 2	78	0.5±0.2	33±44.6	35.4±68.7	0.5±1.6	43
Station 3	18	0.5±0.2	30.2±41.2	8.7±13.1	0±0	0
Station 4	44	0.5±0.2	22.7±39.3	4.9±8.7	0±0	0
Station 5	47	0.5±0.1	23.5±39.9	17.5±26.1	0±0	0
Station 6	57	0.4±0.1	15.1±33.1	16.5±21.1	0.3±1.7	21
Station 7	48	0.5±0.2	38.9±45.3	2±5.5	0±0	0
Station 8	40	0.6±0.1	2.3±8.3	2±6	0±0	0
Station 9	33	0.3±0.1	31.6±44.2	7.8±15.3	0±0	0
Station 10	28	0.5±0.2	25±44	5.6±13.5	0±0	0
Station 11	32	0.2±0.1	30.1±43.6	18±29.5	0±0	0
Station 12	49	0.2±0.1	7±14.5	28.4±42.9	0±0.1	1
Station 13	33	0.4±0.2	25.1±24.3	0.1±0.5	0±0	0
Station 14	26	0.2±0.1	35.6±42.3	58.1±70.9	0±0	0
Station 15	30	0.2±0.1	24.6±35.5	70.9±113.4	0±0	0
Station 16	28	0.3±0.1	18.8±20.5	18.7±56.2	0±0	0
Station 17	37	0.3±0.1	14.2±22.3	231±289.5	1.5±2.5	58
Station 18	29	0.4±0.2	18.4±25.8	327.5±311.2	1.3±2.4	39
Station 19	28	0.4±0.1	17.5±27.2	67.6±111.9	1±4.3	30
Station 20	27	0.7±0.1	2±8.7	0.2±1.1	0±0	0
Station 21	33	0.4±0.2	0±0	3.9±6.6	0±0	0

Table 2E-2. Mean (±1 SD) hydrodynamic model estimates of wave and tide-driven flow velocities for each sampling station. Refer to Table 1 for definitions of variables.

	Samples	U_{mean}	U_{max}	U_{inst24}	U_{anom24}	U_{tide}
	(*n*)	(cm s^{-1})	(cm s^{-1})	(cm s^{-1})	(cm s^{-1})	(cm s^{-1})
Station 1	40	19.1±7.6	26.6±5.4	19.7±8.4	0.5±4.8	0.4±0.2
Station 2	78	5.3±0.8	16.3±2.2	5.1±2.4	-0.2±2.3	1.3±0.5
Station 3	18	14.8±4.6	21.3±4.2	14.8±6.5	0±3.2	3.8±0.6
Station 4	44	20.2±5.5	31.6±3.4	20.6±6.9	0.3±8.3	0.3±0.1
Station 5	47	9.2±7	19.1±5.9	10±7.2	0.8±3.9	5.9±4
Station 6	57	2.7±0.4	22.2±2.3	2.4±0.9	-0.2±0.7	0.1±0
Station 7	48	22.9±6.9	39.7±7.2	26.3±12.3	3.4±10.7	0.2±0
Station 8	40	24.2±6.8	38.2±8.7	25.9±10.5	1.6±9.8	0.2±0
Station 9	33	2.5±0.4	15.9±3.3	1.3±1	-1.2±1	14.4±3.8
Station 10	28	9.4±0.4	25.7±0.5	10±7.3	0.5±7.3	18.7±3
Station 11	32	4.2±1.9	14.6±4.3	2.6±2.1	-1.6±2.7	10.4±3.2
Station 12	49	4.2±1.4	17.8±2.8	2±2	-2.2±2.1	8.1±2.6
Station 13	33	9.1±0.6	25.7±0.8	3.9±4.9	-5.2±4.5	4.5±0.4
Station 14	26	5.4±1.2	23.8±2.4	4.8±4.4	-0.5±4.5	3.7±0.6
Station 15	30	5.1±0.7	27±1.4	3.5±5.1	-1.5±4.8	2.4±0.4
Station 16	28	5.4±0.6	25.9±0.4	2.6±2.9	-2.7±2.9	4.2±0.5
Station 17	37	4.7±1.2	21.9±2.1	4±5.3	-0.7±5.1	0.6±0.1
Station 18	29	7.6±1.1	23.4±0.9	5.2±5.7	-2.4±5.3	0.8±0.1
Station 19	28	4.7±0.8	17.6±2.3	1.6±1.3	-3±1.3	1.3±0.6
Station 20	27	9.1±0.5	43.2±0.3	7.7±6.9	-1.4±6.8	5.3±0.1
Station 21	33	6.8±0.4	32.9±2.9	8.3±9.1	1.5±9.2	0.4±0

Table 2E-3. Spearman's rank-order correlation coefficients (ρ) for hydrodynamic model outputs and environmental predictor variables. Significant correlations are indicated in bold.

	U_{max}	U_{inst24}	U_{anom24}	U_{tide}	Mean Depth	Vegetation cover	*Eucinostomus* spp.
U_{mean}	**0.72**	**0.67**	-0.02	**-0.26**	**0.35**	-0.04	**-0.22**
U_{max}		**0.45**	**-0.07**	**-0.39**	**0.26**	**-0.1**	**-0.28**
U_{inst24}			**0.62**	**-0.36**	**0.31**	**-0.08**	**-0.2**
U_{anom24}				**-0.13**	0.07	-0.04	-0.06
U_{tide}					**-0.24**	**0.09**	-0.03
Mean Depth						0.05	**-0.35**
Vegetation cover							-0.05

CHAPTER 3

HYDRODYNAMIC AND ISOTOPIC NICHE DIFFERENTIATION BETWEEN JUVENILES OF TWO SYMPATRIC CRYPTIC BONEFISHES, *ALBULA VULPES* AND *ALBULA GOREENSIS*

3.1 Abstract

We employed numerical wave models, GIS, and stable isotope analyses of otolith material to identify interspecific differences in habitat and resource use among juveniles of two sympatric and morphologically indistinct bonefishes, *A. goreensis* and *A. vulpes* in littoral zones of The Bahamas. Both species occurred in similar water temperatures; however, *A. goreensis* juveniles occupied habitats characterized by greater wave-driven flow velocities and closer proximity to coral reefs than *A. vulpes*. Likewise, *A. goreensis* was present across a broader range of flow environments and sampling stations than *A. vulpes*, which was typically confined to sheltered, low-flow habitats. The results of stable isotope analyses were consistent with the species' relationships with environmental parameters, providing support for differential habitat and/or resource utilization. Otolith $\delta^{18}O$ did not differ significantly between species, suggesting they experience comparable thermal regimes. However, $\delta^{13}C$ varied substantially, with the otoliths of *A. goreensis* depleted in ^{13}C relative to *A. vulpes* by approximately 1‰, potentially signifying a greater reliance on pelagic carbon sources by the former, in agreement with observed distinctions in habitat use. In linear models, otolith $\delta^{13}C$ was negatively correlated with

ambient flow velocity and positively related to distance from coral reef habitats, and these relationships did not vary across species. After accounting for the effects of these variables, species-specific differences in otolith $\delta^{13}C$ remained, indicating that other unknown factors contributed to the observed disparities. Collectively, our findings suggest that niche partitioning between *A. goreensis* and *A. vulpes* is likely mediated by their differential abilities to compete across various flow environments, likely as a result of divergent behavioral and/or physiological adaptation.

3.2 Introduction

Bonefishes, *Albula* spp., are distributed throughout the world's tropical oceans, supporting valuable recreational fisheries across much of their ranges (Adams et al. 2014). Once thought to comprise just two species, the genus has undergone substantial phylogenetic revision in recent decades, and is now believed to include twelve distinct species, many of which share largely overlapping extents (Wallace 2014). This taxonomic uncertainty, however, remains due in large part to the unusually high degree of conservatism in morphological traits across members of the genus, among which observable distinguishing features are typically subtle or nonexistent (Pfeiler 1996; Colborn et al. 2001; Wallace 2014). Such cryptic species complexes can pose obvious difficulties for management efforts, potentially leading to false conclusions regarding conservation status or species-specific fundamental ecological requirements (Arlettaz 1999; Sattler et al. 2007). Accordingly, the relatively recent discoveries of several regional sympatric cryptic species complexes within the genus *Albula* (Pfeiler 1996; Colborn et al. 2001; Bowen et al. 2007; Wallace and Tringali 2010) has complicated

efforts to conserve bonefishes, which are experiencing declines throughout much of their range (Adams et al. 2014).

One of the more problematic *Albula* cryptic species complexes occurs in the tropical Northwest Atlantic Ocean, where some of the most developed and lucrative recreational fisheries exist (Fedler 2010, 2013) and where stocks have undergone one of the most notable declines (Frezza and Clem 2015; Santos et al. 2017). In this region, molecular genetic analyses have documented the co-existence of at least three sympatric species with no distinguishing morphological characters (Colborn et al. 2001; Crabtree et al. 2003; Wallace and Tringali 2010; Wallace and Tringali 2016), with recreational fisheries supported almost entirely by a single species, *Albula vulpes* (Adams et al. 2007; Wallace and Tringali 2016). Despite clear genetic divergence among the species, there is little empirical evidence of ecological niche differentiation between them (Colborn et al. 2001; Wallace and Tringali 2010; Wallace 2014). Of the three species, *Albula* sp. *cf. vulpes* (Wallace and Tringali 2010) has the lowest incidence in fishery catches, may be the most ecologically distinct, and appears limited primarily to more turbid, estuarine waters (Wallace 2014). However, the differences in environmental preferences and habitat utilization between *Albula goreensis* (Wallace and Tringali 2016) and *A. vulpes* are more obscure.

Mature *A. goreensis* are infrequently encountered on the shallow tidal flats where bonefish (primarily *A. vulpes*) are typically targeted by anglers, and limited anecdotal evidence suggests that mature *A. goreensis* and *A. vulpes* may occupy distinct positions along a depth-related gradient (Bruger 1974; Colborn et al. 2001; Crabtree et al. 2003). This pattern is similar to that described for *A. virgata* and *A. glossodonta* in the Hawaiian

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Islands (Donovan et al. 2015), although there are no known distinguishing morphological characteristics for the Atlantic species. Nonetheless, the separation is not well-defined and may vary geographically (Colborn et al. 2001), leading to some degree of overlap in habitat utilization between adults of the two species, which have been found to co-occur in back-reef habitats (E. Wallace, pers. comm.). This apparent niche overlap is more pronounced in early life stages, where the cooccurrence of *A. goreensis* and *A. vulpes* is frequently observed in coastal habitats (Colborn et al. 2001; Crabtree et al. 2003; Adams et al. 2007; Snodgrass et al. 2008; Haak, unpubl. data).

For a species that occupies distinct habitats throughout ontogeny, determining the basic habitat requirements for each life stage is an essential step in the process of developing a comprehensive fishery management plan (Minello 1999; Levin and Stunz 2005). In the case of *Albula* spp., efforts to identify these requirements have been hindered by the aforementioned taxonomic dilemmas, and uncertainty exists regarding the habitats occupied by early life stages of bonefishes prior to their recruitment into the recreational flats fishery. Early efforts to identify juvenile habitats of bonefishes (initially assumed to be *A. vulpes*) in Florida suggested that they occupied sparsely vegetated, moderately-exposed windward beaches, yet subsequent genetic analyses determined that the vast majority of these individuals were in fact *A. goreensis* (Crabtree et al. 2003; Adams et al. 2007; Snodgrass et al. 2008). More recent efforts in The Bahamas have revealed that juvenile *A. vulpes* also occupy sparsely vegetated littoral zone habitats but are limited to largely enclosed, sheltered embayments exposed to minimal wave energy (Haak et al. 2019). Based on these observations, it appears that while juveniles of both species share preferences for similar depths and benthic

microhabitats, they may exploit shorelines subject to distinct levels of wave exposure and varying degrees of connectivity with pelagic or coral reef habitats. Interspecific variation in the ability of fishes to negotiate wave driven flow is an important determinant of habitat use and assemblage structure in coastal marine habitats, even for closely related species (Bellwood and Wainwright 2001; Fulton et al. 2001). Accordingly, the preference for habitats subject to differential wave-driven flow regimes may constitute a fundamental niche difference between *A. vulpes* and *A. goreensis*, providing a much-needed ecologically-based descriptor from which species may be inferred.

Differences in resource use or ambient environmental parameters are often reflected in the isotopic composition of animal tissues, permitting retrospective inference about patterns of movement or habitat utilization (Hobson 1999; Rubenstein and Hobson 2004; McMahon et al. 2013). Ratios of stable carbon and oxygen isotopes in fish otoliths can provide information on broad scale geographic location, ambient temperature, resource utilization, and even physiology (Campana 1999). Consequently, isotopic ratios in otoliths are frequently employed as a tool for differentiating between fish stocks (Edmonds and Fletcher 1997; Gao et al. 2004; Correia et al. 2011) or elucidating patterns of migration or habitat utilization at a range of spatial scales (Hidalgo et al. 2008; McMahon et al. 2011a; Currey et al. 2014). Assuming that *A. vulpes* and *A. goreensis* juveniles do in fact exploit discrete habitats, it is probable that this will be reflected in the isotopic signatures recorded in otolith material, providing additional support for niche differentiation, and possibly permitting additional inference about the nature of interspecific differences in resource use.

In this study we compared environmental conditions, namely: (1) wave-driven water velocity; (2) proximity to coral reef habitats; (3) benthic vegetation coverage, and (4) ambient water temperature associated with the occurrence of *A. goreensis* and *A. vulpes* juveniles, with the goal of elucidating consistent distinctions in habitat use between the species. Additionally, we contrasted species-specific ratios of carbon and oxygen isotopes in otolith material from a subset of these individuals to further examine differences in habitat and resource utilization integrated over broader temporal scales. We expected the species to occupy distinct wave-driven flow regimes; expressly, that *A. goreensis* would be associated with more open, exposed habitats characterized by greater wave-driven water velocities (and concurrently reef proximities) than its counterpart, *A. vulpes*. Likewise, we expected that interspecific differences in otolith isotopic composition would be correlated with gradients in wave-driven flow and/or connectivity with reef habitats, reflecting disparities in flow-related habitat use between the species.

3.3 Methods

3.3.1 Fish sampling

Juvenile bonefishes were collected from six stations located along a roughly 40 km stretch of the windward (Atlantic-facing) shoreline of Eleuthera Island, situated on the eastern margin of the Bahamas Archipelago (Figure 3.1), between January 2012 and April 2013. This coastline was directly exposed to prevailing easterly trade winds, with a largely uninterrupted fetch and little physical sheltering except for the adjacent fringing reef. With the exception of two largely enclosed sounds, littoral zones were characterized by relatively high-energy sandy beaches subject to long-period oceanic swells and locally generated wind-waves. Specimens were captured using a 15.2 m × 1.2

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m, 3.2 mm mesh bagless beach seine, with each sample encompassing approximately 210 m^2 of seabed. During each haul, the composition of the seabed was monitored, and the proportion of moderately-to-densely vegetated bottom, defined following Harborne et al. (2008), was estimated and recorded. Seine hauls ranged in depth from 0 to 1.1 m. To permit subsequent estimation of wave-driven water velocities at the location of each sampling event, geographic coordinates for the approximate centroid of each seine haul were recorded using a handheld GPS receiver, and sea surface temperature was recorded in the vicinity of each seine haul using a digital handheld thermometer. Captured juvenile bonefish were immediately sacrificed and preserved on ice for transport, and then frozen at −20 °C. At a later date, specimens were thawed and measured to the nearest 1 mm fork length (FL). Fin clips were obtained from each fish, air-dried, and stored in acid-free filter paper for subsequent molecular genetic analysis at the University of Minnesota Genomics Center, following the methods outlined in Seyoum et al. (2008) and Wallace and Tringali (2010). For selected individuals, otoliths (sagittae) were extracted, rinsed in freshwater, air-dried, and stored in plastic vials until they could be prepared for stable isotope analysis (SIA).

Given that leptocephalus larvae of both species exploit similar pelagic environments prior to settling in coastal waters, their overlap during migration and settlement into neritic habitats is probable. As such, to limit the effects of habitat-mismatch; (i.e., to ensure that fishes were sampled from actively-selected settlement habitats rather than those they were incidentally "passing through"), we limited our analysis to fully-metamorphosed individuals >30 mm in fork length (FL). Likewise, to minimize the potential of including fish from subsequent ontogenetic stages that may

utilize distinct habitats, individuals larger than 150 mm FL were also excluded from consideration.

3.3.2 Environmental variables

Wave-associated hydrodynamic stress at the location of juvenile bonefish collections was quantified in terms of estimated maximum bottom orbital velocity (the peak near-bed wave-induced water velocity parallel to the seabed in the direction of dominant flow). Wave bottom orbital velocity provides a physically relevant measure of flow and has been employed extensively to represent the wave-related stresses experienced by demersal fishes (Fulton and Bellwood 2005; Gabel et al. 2011; Anton et al. 2014). Velocities were estimated using "response surface" or "surrogate" models (Box and Draper 1987) discretely relating local (wind) or remote (swell) forcing with hydrodynamic conditions experienced at each location of interest, based on a set of high-fidelity simulated wave fields produced using the numerical wave model SWAN (Booij et al. 1999). In SWAN, simulated surface gravity waves corresponding to forcing conditions are propagated through the model domain, where they are dynamically affected by bathymetry and coastal morphology based on physical principles and empirically-derived relationships, allowing the estimation of hydrodynamic parameters as waves travel to the shore. This approach permitted the high spatial resolution, large model domain, and physical accuracy necessary to resolve shallow-water wave processes in complex coastal habitats while keeping computational demands feasible. Wind and swell-driven bottom orbital velocities at seine haul locations were estimated independently, by interrogating the appropriate response surface model with the mean forcing (wind or swell) conditions corresponding to the time period of interest. For local

(wind) forcing, these inputs comprised wind speed and direction recorded at NOAA

station SPGF1 at Settlement Point on Grand Bahama Island, located 300 km NW of the

study area. Remote (swell) forcing, inputs included swell direction, significant wave

height, and dominant period recorded at NOAA NDBC 41047 located 500 km NE of

Eleuthera. The greater of wind and swell-driven orbital velocities was then taken to

reflect the most adverse conditions. Further information on the development and

validation of these models can be found in Haak et al. (2019).

To examine the effects of both spatial and temporal variability in flow, we related

the abundance of bonefishes to bottom orbital velocities at capture locations measured on

two discrete temporal scales. To reflect incident wave stress on fine timescales,

corresponding roughly to the moment of each sampling event, we estimated the mean

wind or swell conditions corresponding to the 24-h period preceding each seine haul

(U_{24}). This was deemed an appropriate temporal window, given not only the hourly to

daily timescales at which wave conditions develop and subside in coastal habitats, but

also the observations of others which suggest that temporal variability in the abundance

of fishes is more closely correlated with sea state measured over the preceding hours to

days than with instantaneous conditions (Lasiak 1984; Friedlander and Parrish 1998). To

approximate spatial gradients in wave-driven flow integrated over broader temporal

scales, likely to be more representative of the average conditions encountered at a

location on a diel basis, long-term mean near-bed velocity (U_{mean}) at each capture

location was determined by interrogating the surrogate models with hourly histories of

forcing parameters recorded at their respective NOAA stations for a 4-year timespan

encompassing the study period, (January 1, 2010 to January 1, 2014), and then

calculating the mean of the resulting distribution. Spatial variation in U_{mean} across the study area is depicted in Figure 3.2.

The minimum swimming distance from each seine haul location to the nearest coral reef habitat (heretofore referred to as Reef distance) was estimated to the nearest 100 m using a cost-distance function, with reef locations based on the 30 m spatial resolution United Nations Environment Programme-World Conservation Monitoring Centre global distribution of warm-water coral reefs database (UNEP-WCMC 2010). The estimated percent coverage of benthic vegetation characterizing the area sampled by each seine haul was obtained as described above under Fish Sampling.

3.3.3 Stable isotopes

Stable carbon isotope ratios ($\delta^{13}C$) incorporated in animal structures are commonly used to determine the sources of organic carbon in food webs, based on the contrasting isotopic fractionations exhibited by different primary producers (Peterson and Fry 1987; Fry and Sherr 1989; Post 2002). Because the dominant primary producers at the base of marine food webs tend to vary among discrete habitats or microhabitats, $\delta^{13}C$ can function as a naturally-occurring intrinsic marker, linking fishes to distinct habitats through dietary intake and trophic transfer (Hobson 1999; Kieckbusch et al. 2004; Nagelkerken and van der Velde 2004; Lugendo et al. 2006). Although dissolved inorganic carbon (DIC) from ambient seawater generally comprises the dominant proportion of carbon in otolith aragonite, the remaining fraction is composed of metabolically-derived carbon (Solomon et al. 2006). Accordingly, bulk otolith $\delta^{13}C$ ($\delta^{13}C_{oto}$) can be reflective of dietary intake (Radtke et al. 1996) and thus may provide

information about habitat use akin to that of muscle $\delta^{13}C$ (Jamieson et al. 2004; McMahon et al. 2011b).

However, the large DIC fraction of carbon in otolith aragonite results in a "dilution" effect, partially obscuring the dietary signal and making it difficult to draw conclusions about habitat or resource use from bulk otolith $\delta^{13}C$ values (McMahon et al. 2011b). In the case of the species considered here, isotopic data from an expanded collection of juvenile bonefishes taken from the study area demonstrates that $\delta^{13}C_{oto}$ correlates closely with muscle $\delta^{13}C$ within individuals (see Online Resource 1). Furthermore, in relatively stable oceanic environments such as the study area, the isotopic composition of DIC in seawater tends to vary little at the small scales encompassed by the present study (Hu and Burdige 2007). Therefore, it is reasonable to assume that variation in $\delta^{13}C_{oto}$ among the fishes examined here is largely attributable to dietary intake (Elsdon et al. 2010; Nelson et al. 2011), permitting insights into differential habitat or resource use via the sources of carbon at the base of food webs they occupy. Likewise, the relative proportions of DIC (exogenous) and metabolically-derived (endogenous) carbon incorporated into otolith material is a function of metabolic rate, with a greater fraction of metabolic carbon included during periods of increased metabolism (Jamieson et al. 2004; Dufour et al. 2007; Tohse and Mugiya 2008). Because carbon in ambient DIC is isotopically heavy compared to metabolically-derived carbon, bulk otolith $\delta^{13}C$ is inversely related to metabolic rate (Kalish 1991; Schwarcz et al. 1998; Høie et al. 2003). Accordingly, variation in $\delta^{13}C_{oto}$ may also be indicative of inter- or-intra-specific discrepancies in metabolism, potentially providing insights into physiological differences among *A. goreensis* and *A. vulpes*.

Oxygen stable isotope ratios ($\delta^{18}O$) in otolith material also provide valuable information about the environment experienced by fishes, reflecting the isotopic composition of ambient seawater and environmental temperature at the time of deposition (Thorrold et al. 1997; Høie et al. 2004). While temperature histories can be approximated from $\delta^{18}O$, this cannot be accomplished without knowledge of the relationship between temperature and isotopic fractionation, which must be experimentally determined, can be non-linear, and may vary substantially even among related species (Stormsuke et al. 2007; Godiksen et al. 2010). Nonetheless, assuming interspecific differences in temperature-dependent fractionation do not exist between *A. vulpes* and *A. goreensis*, otolith $\delta^{18}O$ may indicate relative differences in the thermal regime of habitats occupied by the two species.

The subset of individuals selected for SIA were constrained to similar size classes, both within and across species, to limit the potential for any size-related or ontogenetic effects. Otoliths from selected individuals were scrubbed, sonicated, rinsed in deionized ultrapure water, dried under a laminar flow hood, and stored in 1.5 ml plastic vials until analysis. Bulk SIA of otolith $\delta^{13}C$ and $\delta^{18}O$ was conducted at the University of Waterloo, following the methods described by Guiguer et al. (2003) and Storm-suke et al. (2007). Carbon and Oxygen isotope ratios are expressed in delta notation (δ) with concentrations measured in permil (‰), relative to Vienna Pee Dee Belemnite.

3.3.4 Statistical analyses

When observed data conformed to parametric assumptions, interspecific comparisons of fish size (FL), environmental variables at the time and place of capture, and otolith isotopic composition were conducted using Welch's unequal variances *t*-test

for independent samples. If parametric distributional assumptions were not satisfied, as was the case for many environmental parameters, the non-parametric Mann-Whitney U test was instead employed for comparisons. To examine the relationship between otolith $\delta^{13}C$ and environmental factors, we employed a linear mixed model (LMM), approximating $\delta^{13}C_{oto}$ as a function of the continuous fixed variables U_{mean} and Reef distance, as well as of the fixed factor variables Station and Species. To evaluate the potential for interspecific differences in the relationship between $\delta^{13}C_{oto}$ and U_{mean}, an interaction term was included between U_{mean} and Species. Furthermore, to account for any potential interdependency in response among fishes co-occurring in the same seine haul (i.e., cluster sampling bias; Nelson 2014), seine haul was modeled as a random intercept. Model selection was performed using backward elimination of fixed effects via likelihood ratio tests. Statistical analyses were performed using RStudio (Version 1.0.143) and the lme4, car, and MASS packages. Unless otherwise noted, values displayed in the text are presented as mean $\pm$ SD, and fish sizes are given as fork length (FL).

3.4 Results

3.4.1 Fish collection and environmental variables

A total of 106 juvenile bonefishes were collected across 37 distinct seine hauls. Molecular genetic analyses classified six individuals as potential hybrids, and these were excluded from subsequent analyses. Of the remaining 100 specimens, 77 individuals from 26 seine hauls at three different stations (1, 2, and 4, as depicted in Figure 3.1) were identified as *A. vulpes*, and 23 specimens, representing 13 distinct hauls at five different stations (1, 2, 3, 5, and 6) were classified as *A. goreensis*. The species co-occurred in

three seine haul samples; twice at station 1, and once at station 2, comprising 23 and 13%

of *A. vulpes* and *A. goreensis* specimens, respectively. While the lengths of *A. vulpes* (60

± 34 mm) were more variable than those of *A. goreensis* (53 ± 9 mm), size did not differ

substantively between species (Mann-Whitney U test, $U = 1088.5$, $Z = 1.66$, $p = 0.097$).

Water temperatures associated with the occurrence of *A. vulpes* (27.5 ± 2.4 °C) were

marginally lower than those corresponding to *A. goreensis* collections (28.9 ± 2.5 °C)

(Table 3.1), however this difference was not statistically significant (Welch's *t*-test, $t =$

1.589, df $= 22.81$, $p = 0.1257$). Likewise, there was no significant difference in the

coverage of benthic vegetation associated with the presence of each species (Mann-

Whitney U test, $U = 147.5$, $Z = -0.99$, $p = 0.319$), with both occurring primarily in

unvegetated or sparsely-vegetated habitats (Table 3.1).

Wave-driven flow regime at capture locations varied markedly and consistently

between species (Table 3.2). Twenty-four-hour mean bottom orbital velocities, U_{24},

preceding the occurrence of *A. goreensis* (22.1 ± 11.5 cm s^{-1}) were on average more than

three times those of corresponding *A. vulpes* collections (6.8 ± 6.5 cm s^{-1}), constituting a

significant interspecific disparity (Mann-Whitney U test, $U = 293.5$, $Z = 3.69$, $p =$

0.0002). A similar degree of asymmetry was apparent in the long-term mean bottom

velocities experienced at capture locations, U_{mean} (Mann-Whitney U test, $U = 301$, $Z =$

3.92, $p = <0.0001$), with *A. goreensis* taken from sites characterized by markedly greater

mean velocities (21.6 ± 8.4 cm s^{-1}) than those associated with the presence of *A. vulpes*

(7.5 ± 6.3 cm s^{-1}) (Figure 3.3a). While typically occupying comparatively higher-flow

habitats than *A. vulpes*, *A. goreensis* was also present in a notably broader range of water

velocities, which spanned from near 0 up to a maximum of 46.7 cm s^{-1}, nearly twice that

of *A. vulpes* (0–24.2 cm s^{-1}). Distance from coral reef habitats (Figure. 3.3b) also differed significantly between species (Mann-Whitney *U* test, $U = 57$, $Z = -3.37$, $p = 0.0007$), with *A. goreensis* (400 ± 600 m) regularly occurring in closer proximity than *A. vulpes* (1900 ± 900 m).

3.4.2 Stable isotopes

To control for any size-related or ontogenetic effects on isotope ratios, a reduced set of individuals ranging in length from 39 to 88 mm was selected for comparison of otolith isotopic composition (Table 3.3). This subset comprised twenty-three *A. vulpes* juveniles collected in 12 distinct seine hauls, and eighteen *A. goreensis* juveniles representing 12 discrete hauls. Within this group, the mean size of *A. vulpes* (55 ± 13 mm) corresponded closely to that of *A. goreensis* (54 ± 9 mm), with no significant difference in size between the two species (Welch's *t* test, $t = -0.403$, df $= 39.398$, $p = 0.688$). Examination of the data revealed no observable correlation between otolith δ^{13}C or δ^{18}O and fish length over the range of sizes considered, therefore no correction was applied to account for size effects on isotopic composition.

Mean δ^{13}C$_{oto}$ values recorded for *A. vulpes* (-1.15 ± 0.53 ‰) were enriched in ^{13}C by approximately 1‰ compared to those of *A. goreensis* (-2.04 ± 0.51‰) (Figure 3.4). This difference was highly significant (Welch's *t* test, $t = -5.428$, df $= 37.232$, $p < 0.0001$), signaling that the species exploited isotopically distinct environments and/or resources, or experienced contrasting metabolic demands. Although intraspecific variability in δ^{13}C$_{oto}$ was similar between the species, *A. goreensis* displayed a slightly broader range of values overall, evidencing the utilization of a greater variety of habitats or resources. Otolith δ ^{18}O spanned a similar range of values for *A. vulpes* and *A.*

goreensis and did not vary substantively between species (Welch's *t* test, $t = 0.783$, df $=$ 34.274, $p = 0.438$), suggesting they inhabited comparable thermal environments.

In linear models relating $\delta^{13}C_{oto}$ to environmental variables (Tables 3.4 and 3.5), the fixed effect of sampling station did not contribute to explaining observed patterns in otolith $\delta^{13}C$. The high collinearity between U_{mean} and Reef distance (r $= 0.77$) and consequent variance inflation precluded the simultaneous inclusion of both continuous fixed predictors; however, in discrete reduced models, $\delta^{13}C_{oto}$ was negatively correlated with U_{mean} ($F = 3.027$, df $= 38$, $p = 0.089$) (Figure 3.5a), and significantly positively correlated with distance from coral reef habitats ($F = 8.017$, df $= 38$, $p = 0.0073$) (Figure 3.5b). The absence of an interaction between either U_{mean} or Reef distance with Species indicated that these relationships did not differ substantively between *A. goreensis* and *A. vulpes*. Nonetheless, after accounting for these effects, there was still a significant effect of Species in the presence of both U_{mean} ($F = 6.9992$, df $= 38$, $p = 0.01179$) and Reef distance ($F = 8.2412$, df $= 38$, $p = 0.0066$), indicating that interspecific differences in $\delta^{13}C_{oto}$ could not be explained entirely by variation in ambient flow velocities or coral reef proximity, and therefore that interspecific discrepancies in other, unmeasured factors likely contributed to observed differences in otolith $\delta^{13}C$.

3.5 Discussion

Albula goreensis juveniles were present in habitats subject to substantially greater bottom orbital velocities than those of *A. vulpes*, supporting the notion that the two species occupy distinct positions along a gradient in the strength of wave-driven flow. Flow intensity was closely correlated with proximity to coral reef habitats, which likewise differed greatly between locations where the species occurred, further

underpinning interspecific divergence in habitat use. The broader range of locations and water velocities inhabited by *A. goreensis* suggests that this species may display a greater degree of adaptability to variation in incident flow. Contrasts (or the lack thereof) in otolith isotopic composition between the species were consistent with variation in the environmental conditions in which they occurred. The absence of interspecific differences in otolith $\delta^{18}O$ is congruent with the comparable ambient water temperatures that *A. goreensis* and *A. vulpes* were collected in, suggesting that both species share similar temperature-dependent fractionation relationships and that water temperature is not among the factors that differentiate their respective niches. Moreover, the clear disparity in $\delta^{13}C_{oto}$ between *A. goreensis* and *A. vulpes* juveniles suggests distinctions in habitat and/or resource utilization linked to gradients in flow velocity and/or reef proximity.

The differential resource use revealed here implies the existence of niche partitioning and habitat segregation between *A. goreensis* and *A. vulpes* with respect to the intensity of wave-driven water movement. Differences in flow-related habitat use among fishes are most commonly attributed to interspecific discrepancies in locomotor performance, typically associated with phylogenetic variation in morphological characteristics, such as body form or fin shape, that influence the ability of fishes to negotiate fast, unsteady or turbulent flows (Bellwood and Wainwright 2001; Fulton et al. 2001; Fulton and Bellwood 2005). However, the adaptive distinctions that accompany niche partitioning are not necessarily reflected in outward anatomical form. Behavioral differences, commonly paired with divergent physiological adaptations, can also have implications for resource use, constituting important niche determinants among

morphologically and functionally-similar organisms (Schmitt and Coyer 1982; Hartney 1989; Clarke et al. 2009). The conspicuous absence of any defining morphological characters between the species studied here seems to suggest that the disparate flow environments exploited by *A. goreensis* and *A. vulpes* may thus be related to differences in behavior and/or internal physiology.

Examples of niche partitioning or habitat segregation with respect to ambient flow can be found among several other sympatric, closely related fishes (Hyndes et al. 1997; Clarke et al. 2005; Davis and Wing 2012). For example, distinctions in feeding behavior and metabolic rate between congeneric blennies (*Acanthemblemaria* spp.) have been linked with fine-scale habitat partitioning along a vertical gradient in wave-driven water velocity (Clarke et al. 2009; Finelli et al. 2009). Such seemingly small differences in foraging microhabitat use can also give rise to segregation at much broader spatial scales (Hixon 1980; Holbrook and Schmitt 1989; Hyndes et al. 1997). For example, Hyndes et al. (1997) determined that trophic niche differentiation and landscape-scale habitat partitioning among juveniles of several sympatric, morphologically-similar members of the genus *Sillago* was attributable to relatively fine-scale differences in the use of foraging microhabitats, with *S. baseensis*, a species associated with exposed high-energy environments, exploiting invertebrate epifauna from detached macrophytes (drift algae), while its counterparts in more sheltered low-energy habitats foraged primarily on invertebrate prey from benthic sediments. Accordingly, if broad-scale environmental gradients in flow intensity are correlated with similar shifts in the abundance of distinct microhabitats or prey taxa upon which *A. goreensis* and *A. vulpes* differentially rely, one

might expect to observe interspecific contrasts in habitat utilization (spatial segregation) analogous to those observed here.

Wave energy is among the most fundamental factors structuring littoral zones (Brind'Amour et al. 2005), shaping the distributions of benthic sediments and primary producers (Keddy 1982; Fonseca et al. 1983), as well as the structure of invertebrate communities which inhabit them (Fenwick 1976; Snelgrove and Butman 1994; Boström et al. 2006). It is thus logical that gradients in wave-driven flow should be associated with shifts in the structure of plant and animal communities, and consequently the isotopic composition of the fishes which forage within them (Davis and Wing 2012). The higher energy habitats typically occupied by *A. goreensis* exhibited closer proximity and greater connectivity to pelagic and coral-reef environments, which are characterized by isotopically-lighter carbon sources such as phytoplankton (De la Morinière et al. 2003; Crawley et al. 2009; McMahon et al. 2016). In contrast, the more sheltered and enclosed flats habitats utilized by *A. vulpes* likely received greater inputs from isotopically heavier, neritic sources of carbon such as seagrasses (Fry et al. 1982; De la Morinière et al. 2003; Nagelkerken and van der Velde 2004), potentially contributing to the observed interspecific disparity.

Furthermore, variation in the strength of ambient flow can influence carbon uptake for primary producers, leading to ^{13}C depletion of plant tissues in high-flow environments (Trudeau and Rasmussen 2003; Cornelisen et al. 2007; McPherson et al. 2015), which in turn can be reflected in the isotopic composition of organisms at higher trophic levels (Finlay et al. 1999; Rasmussen and Trudeau 2010). Accordingly, the higher water velocities in habitats where *A. goreensis* occurred should be correlated with

[13]C depletion in algae or seagrasses relative to their analogs in the low-energy habitats occupied by *A. vulpes*, in agreement with observed trends. Whether a result of broad-scale changes in community structure and shifts in the dominance of distinct primary producers along a wave-energy gradient, or of flow-related intraspecific variation in δ^{13}C within similar communities of primary producers, the comparatively low δ^{13}C values observed in the otoliths of *A. goreensis* are consistent with the utilization of more open, pelagically-connected habitats exposed to greater wave energy.

Alternatively, the observed differences in δ^{13}C may be related to distinctions in resource exploitation occurring at much finer scales. In habitats akin to those surveyed in the present study, the isotopic composition of both producers and consumers can vary markedly over very small distances (Higgs et al. 2016; Tue et al. 2017). As such, species-specific discrepancies in prey selection and foraging microhabitat utilization (e.g., consumption of pelagic vs. epibenthic vs. infaunal invertebrate prey), may give rise to contrasts in the isotopic makeup of *A. goreensis* and *A. vulpes* even despite their functional similarity and broad-scale overlap in habitat use. In this event, variation in isotopic signatures between the species may reflect greater inputs from pelagic carbon sources in the diet of *A. goreensis*, possibly indicating increased utilization of prey from the water column or from detached macrophytes (Robertson and Lenanton 1984; Crawley et al. 2006), which can be the primary source of organic carbon for consumers in surf-zone habitats (Crawley et al. 2009).

Interspecific differences in metabolism may also have contributed to observed interspecific contrasts in otolith δ^{13}C. Assuming the species display equivalent δ^{13}C fractionation and have analogous dietary inputs, the isotopically-lighter otolith δ^{13}C

values of *A. goreensis* may be interpreted to suggest that this species maintains a higher

metabolic rate (Kalish 1991; Høie et al. 2003), consistent with the greater energetic

demands required by the comparatively high-flow or turbulent habitats it occupies

(Enders et al. 2003; Roche et al. 2014). Similar discrepancies in species-specific

metabolism or activity level have been linked with differential microhabitat and resource

use among other sympatric congeners and may represent adaptations that help to balance

habitat-specific energetic costs and resource availability (Hartney 1989; Clarke et al.

2005, 2009).

The more widely ranging $\delta^{13}C_{oto}$ values observed for *A. goreensis* suggest that this

species exploits a greater assortment of resources or microhabitats, in accordance with its

broader distribution among sampling stations and the notably more heterogenous

hydrodynamic regimes it occurred in. The seemingly more generalist nature of *A.

goreensis* may reflect interspecific distinctions in sensory capability, which often

accompany differences in resource use between closely related fishes (Lombarte et al.

2000; Cummings and J 2001; Schwalbe and Webb 2014), perhaps indicating that this

species exploits alternative or more diverse sensory mechanisms than its counterpart,

facilitating the detection of prey in a wider variety of habitats or sensory environments

(Deary et al. 2016).

Collectively, our observations suggest that *A. goreensis* and *A. vulpes* exhibit

divergent behavioral and/or physiological adaptations, likely linked to foraging and

microhabitat use, that influence their relative abilities to compete over a range of flow

conditions leading to differential distributions with respect to incident wave energy

(Pekcan-Hekim et al. 2016). The much more constrained range of flow environments

inhabited by *A. vulpes*, and consequently its more limited spatial distribution, indicate

that this species may be more of a habitat specialist compared to *A. goreensis*, a

supposition that appears compatible with the dietary habits of the two species (Griffin et

al. this issue). As such, *A. vulpes* may out-compete *A. goreensis* in hydrodynamically

stable low-flow habitats, possibly explaining the relative absence of *A. goreensis* from the

more sheltered stations (2 & 4) where *A. vulpes* predominated. Concurrently, however,

the greater specialization of *A. vulpes* may come at the cost of reduced adaptability,

limiting the species' capacity to compete in more variable flow environments (Poff and

Allan 1995) such as those occupied by *A. goreensis*, for which greater plasticity in

foraging mode or microhabitat utilization may permit the exploitation of more diverse

flow and resource regimes.

     While this work focuses on the role of wave-driven flow in shaping differential

habitat use, it is possible that unmeasured environmental factors that covaried with wave

exposure also contributed to producing the observed distributional patterns. Although

salinity and turbidity are important drivers of habitat use in estuarine waters (Blaber and

Blaber 1980; Cyrus and Blaber 1992; Akin et al. 2005), background levels of these

parameters vary comparatively little across the habitats surveyed here due to negligible

freshwater inputs and the generally oligotrophic nature of the study area (Buchan 2000).

Nonetheless, wave forcing can precipitate sediment resuspension in shallow coastal zones

(Arfi et al. 1993; Lawson et al. 2007), and the greater susceptibility of more exposed sites

to fluctuations in flow-related turbidity may have influenced habitat use. Likewise,

benthic microhabitat features that are affected by wave exposure may have acted, perhaps

more directly than wave-driven flow itself, to shape species distributions (Santin and

Willis 2007). We did not detect interspecific differences with respect to benthic vegetation cover; nevertheless, the composition of benthic flora communities may have varied at scales finer than were assessed here. Similarly, whilst there were no obvious differences in substrate composition across sampling stations (all of which were dominated by fine sand), subtle differences in the characteristics of benthic sediments may also have existed.

Our study did not explicitly evaluate variation in the presence or relative density of allochthonous algae or detached macrophytes across seine haul locations; yet the more exposed windward habitats where *A. goreensis* occurred certainly received greater inputs of drifting sargassum spp. than the more sheltered habitats used by *A. vulpes*. Given the interspecific differences elucidated here, and the observations of others with regard to the importance of drift algae as a source of invertebrate prey and organic carbon in surf-zone habitats similar to those occupied by *A. goreensis* (Robertson and Lenanton 1984; Crawley et al. 2006; Crawley et al. 2009), future studies should consider including this as an environmental predictor.

While divergence in habitat and resource utilization was clearly discernable between the species, the underlying mechanisms giving rise to these differences were less transparent. Although disparities in the resource use of *A. goreensis* and *A. vulpes* were correlated with gradients in ambient flow and connectivity to coral reef habitats, it is unclear whether these contrasts arose due to distinctions in fine-scale microhabitat utilization and/ or prey selection, or as a result of exploiting similar microhabitats or prey taxa but from distinct locations within broader-scale isotopic gradients (i.e., isoscapes). More detailed dietary analyses, optimally from the same region and with greater

taxonomic resolution, may help resolve these questions by identifying the habitat associations of prey taxa (e.g., benthic or pelagic). Likewise, more comprehensive stable isotope studies, employing muscle tissue and including the analysis of δ^{34}S may help reveal the relative importance of benthic vs. pelagic food webs between species, and emerging methods, such as compound-specific SIA of amino acids (McMahon et al. 2016) may provide even greater ability to distinguish between carbon sources. Measurements of species-specific metabolic rates, exercise capacity, and swimming performance may help to identify whether differential physiological adaptation plays a role in generating the observed contrasts, as may comparative anatomical studies of the species' sensory systems.

This work was the first to quantitively examine interspecific distinctions in the habitat and resource utilization patterns of sympatric bonefishes of any ontogenetic stage in the Atlantic region. In doing so, we revealed fundamental differences in the basic ecological requirements of *A. vulpes* and *A. goreensis* during a critical and poorly understood life stage. From the perspective of conservation this information should prove particularly valuable, offering guidance for habitat preservation efforts, while also providing a practical, field-applicable method for discriminating between species based on observable associations with the physical environment.

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3.7 Tables

Table 3.1 Summary information on juvenile bonefishes (*A. vulpes* and *A. goreensis*) captured in seine hauls and corresponding environmental variables recorded at the time of collection, including ambient water temperature (Temp) and the coverage of moderate-to-densely vegetated seabed (Veg cover) within the sweep area. Lengths are reported as fork length.

Species	n indivs	n hauls	Length $\pm$ SD (mm)	Length min/max (mm)	Temp $\pm$ SD (°C)	Temp min/max (°C)	Veg cover $\pm$ SD (%)	Veg cover min/max (%)
A. goreensis	23	13	53 $\pm$ 9	39/77	28.9 $\pm$ 2.5	24/32.1	0 $\pm$ 1.4	0/5
A. vulpes	77	26	60 $\pm$ 34	30/149	27.5 $\pm$ 2.4	21/32	9 $\pm$ 25	0/100

Table 3.2 Summary information on environmental parameters corresponding to locations where juvenile bonefishes (*A. vulpes* and *A. goreensis*) were captured in seine hauls, as estimated by numerical wave models and GIS. Flow-related metrics (U_{mean} and U_{24}) reflect estimated wave-bottom orbital velocities at capture locations averaged over a 4-year timeframe encompassing the study period (U_{mean}) and the 24-hour period preceding a given seine haul (U_{24}). Reef distance reflects the minimum swimming distance to coral reef habitats from a capture location, estimated using on a cost distance function.

Species	n hauls	$U_{mean} \pm$ SD (cm s^{-1})	U_{mean} min/max (cm s^{-1})	$U_{24} \pm$ SD (cm s^{-1})	U_{24} min/max (cm s^{-1})	Reef distance $\pm$ SD (m)	Reef distance min/max (m)
A. goreensis	13	21.7 $\pm$ 8.4	6.2/33.8	22.1 $\pm$ 11.5	1.4/46.7	400 $\pm$ 600	100/2300
A. vulpes	26	7.5 $\pm$ 6.3	1.9/25.1	6.8 $\pm$ 6.5	0.0/24.2	1900 $\pm$ 900	100/2500

Table 3.3 Summary of sizes and bulk-otolith stable isotope ratios ($\delta^{13}C$ and $\delta^{18}O$) for a subset of juvenile bonefishes (*A. goreensis* and *A. vulpes*) collected from six stations along the Atlantic coast of Eleuthera, The Bahamas. Lengths are reported as fork length (FL).

Species	*n indivs*	*n hauls*	Length ± SD (mm)	Length min/max (mm)	$\delta^{13}C$ ± SD (‰)	$\delta^{13}C$ min/max (‰)	$\delta^{18}O$ ± SD (‰)	$\delta^{18}O$ min/max (‰)
A. goreensis	18	12	54 ± 9	39/77	-2.04 ± 0.51	-3.10/-1.08	-0.29 ± 0.57	-1.33/0.77
A. vulpes	23	12	55 ± 13	40/88	-1.14 ± 0.53	-2.03/-0.15	-0.38 ± 0.54	-1.52/0.65

Table 3.4 Summary of reduced linear model results for fixed predictors U_{mean} + Species

Parameter	Estimate	SE	*t*-value	*p*-value
Intercept	-1.601	0.277	-5.779	<0.001
U_{mean}	-1.803	1.036	-1.740	0.090
Species	0.605	0.228	2.646	0.011

Table 3.5 Summary of reduced linear model results for fixed predictors Reef distance + Species

Parameter	Estimate	SE	*t*-value	*p*-value
Intercept	-3.295	0.470	-7.075	<0.001
$\log_{10}$(Reef distance)	0.526	0.186	2.832	0.007
Species	0.552	0.192	2.871	0.006

3.8 Figures
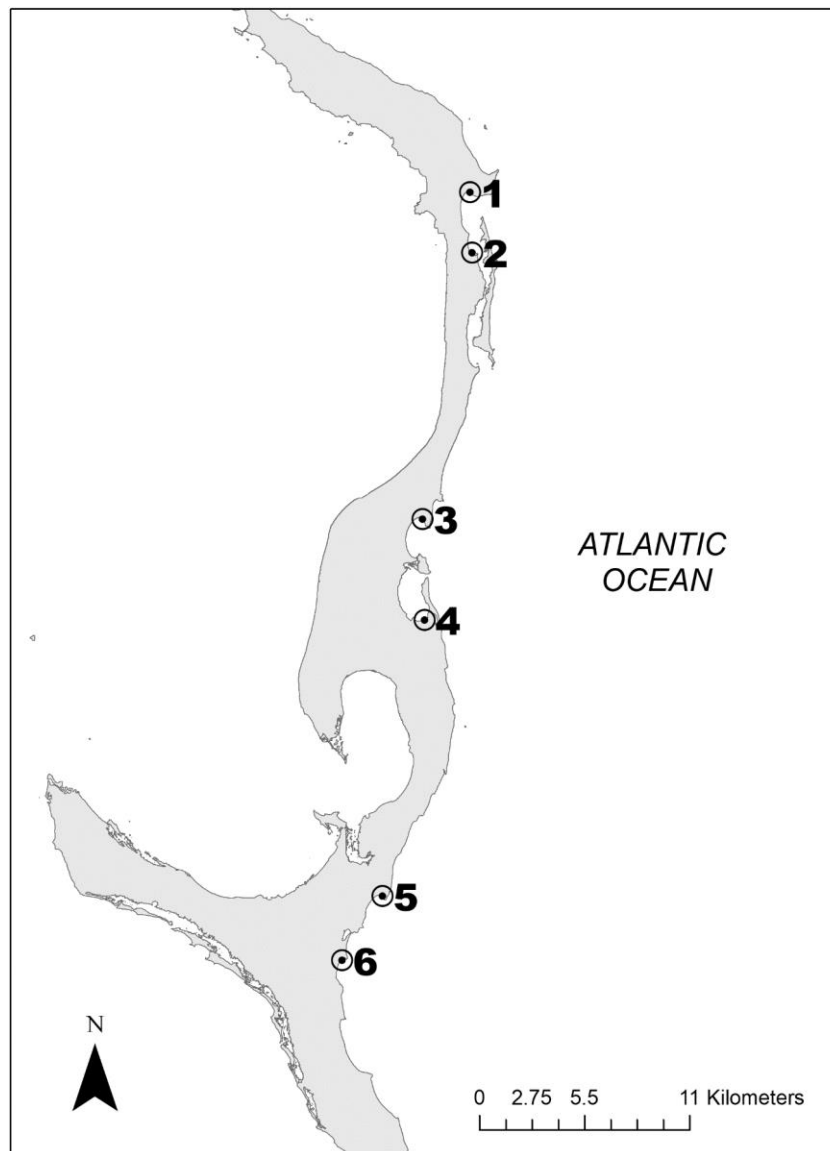
Figure 3.1 Map of the study area on the east coast of Eleuthera, The Bahamas, depicting locations of sampling stations numbered 1-6.
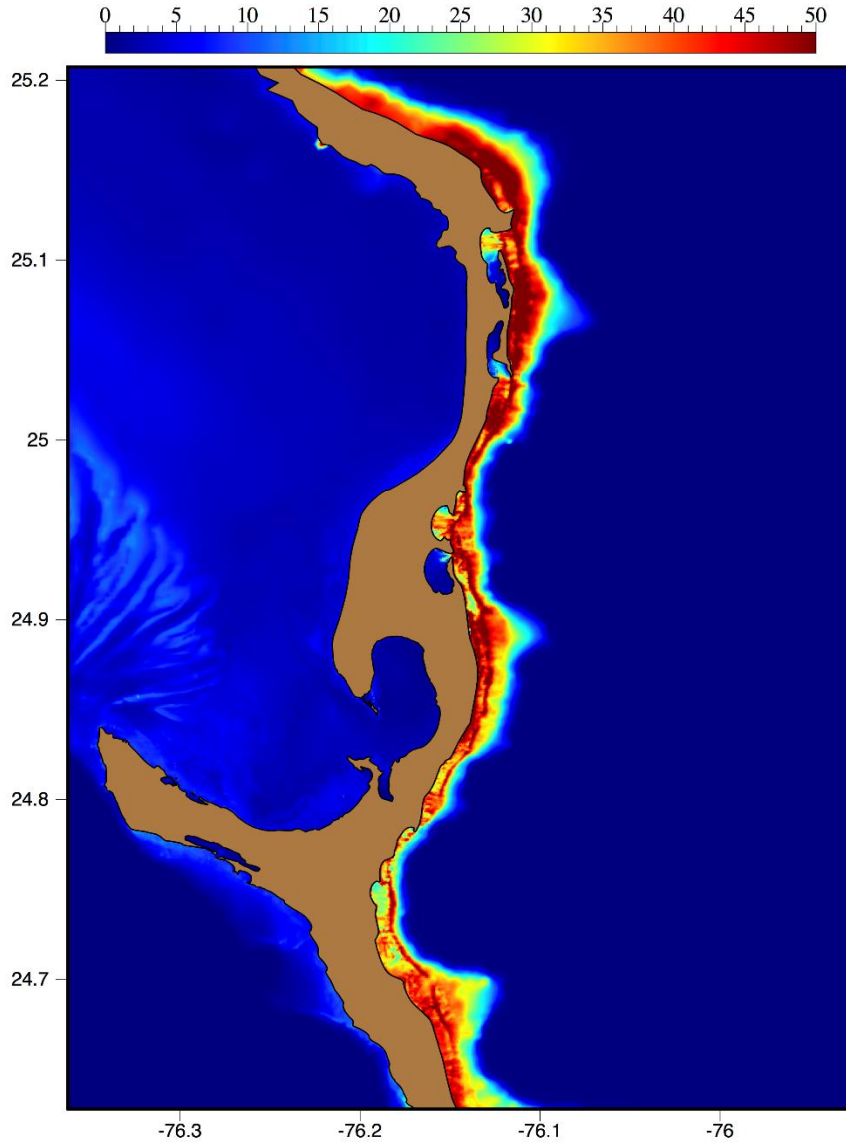
Figure 3.2 Map illustrating the distribution of long-term mean wave-induced bottom orbital velocity, U_{mean}, across the study area as estimated by the numerical wave model SWAN. To highlight variability at sampling stations, the maximum value depicted by the color gradient ramp has been truncated to 50 cm s^{-1}.

A

B
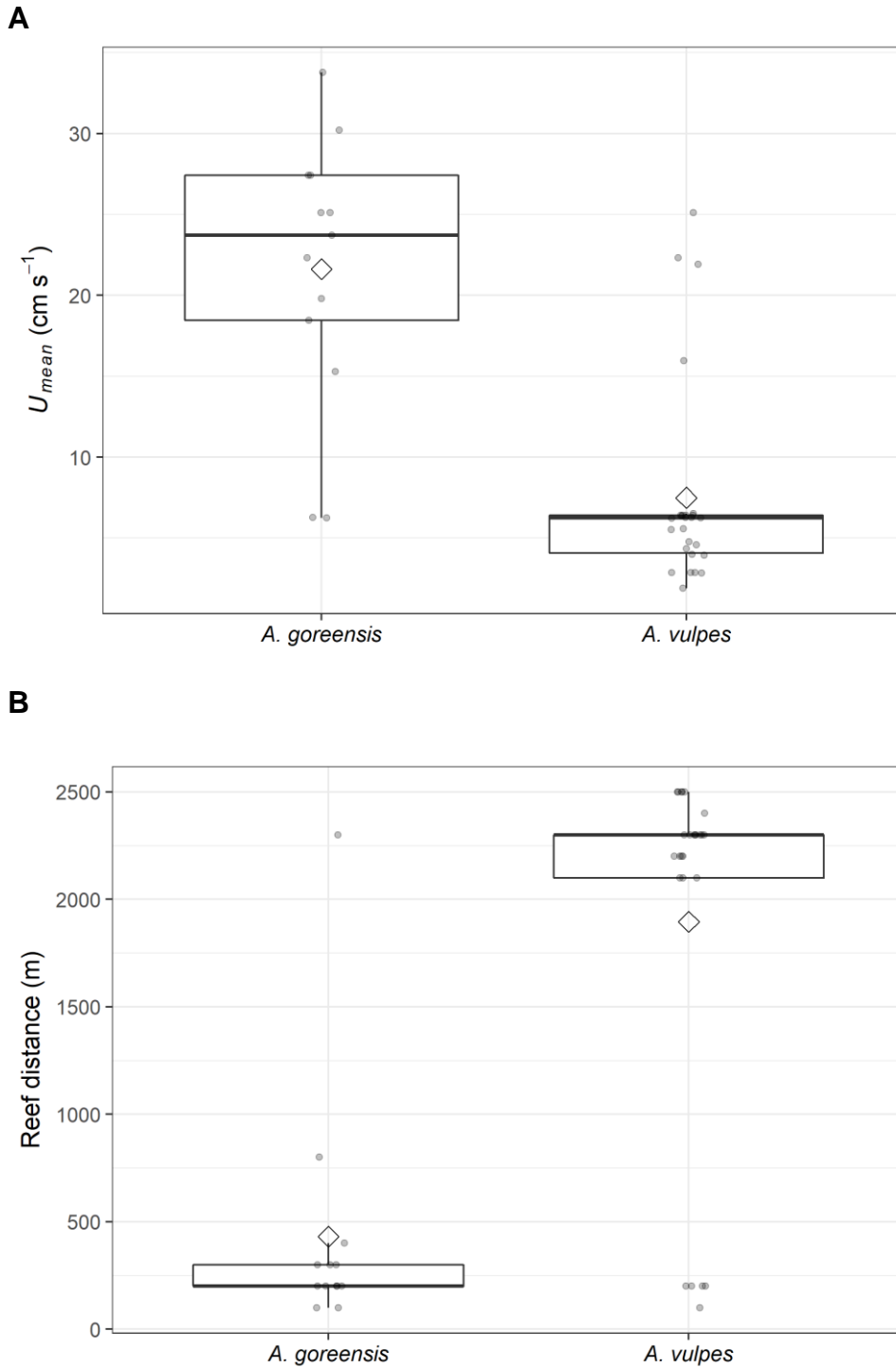
Figure 3.3 Boxplots depicting the distribution of: **A** long-term (4-year) mean wave bottom orbital velocities (U_{mean} [cm s^{-1}]), and **B** swimming distance to coral reef habitats (to the nearest 100 m), at the locations of seine hauls capturing *A. goreensis* (n=13) and *A. vulpes* (n= 26) juveniles. Solid grey dots represent individual observations, and diamonds denote the mean.
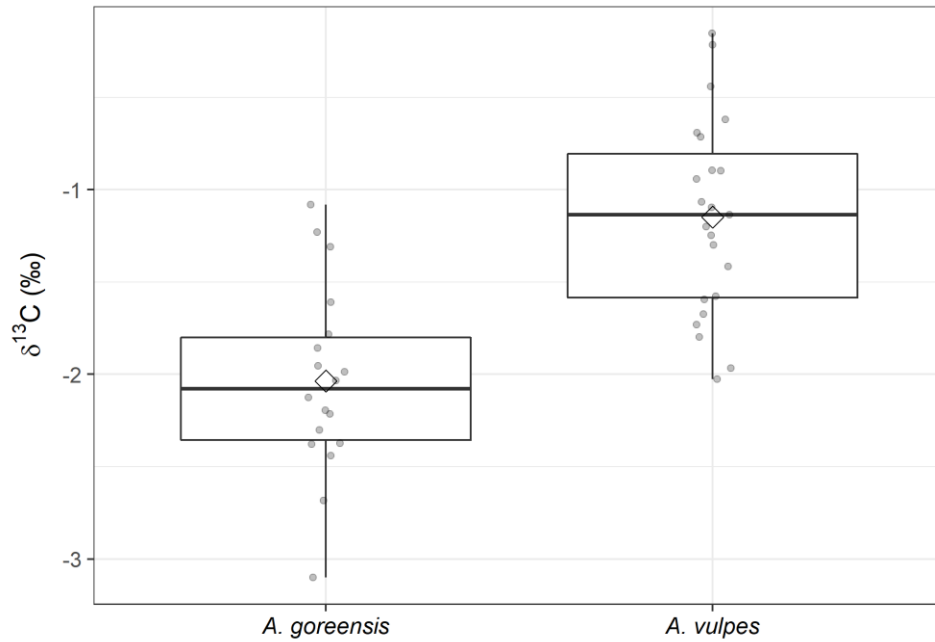
Figure 3.4 Boxplots depicting the distribution of $\delta^{13}C$ values (‰) of bulk otolith material from *A. goreensis* (n=18) and *A. vulpes* (n=23) juveniles. Solid grey dots represent individual observations, and diamonds denote the mean.
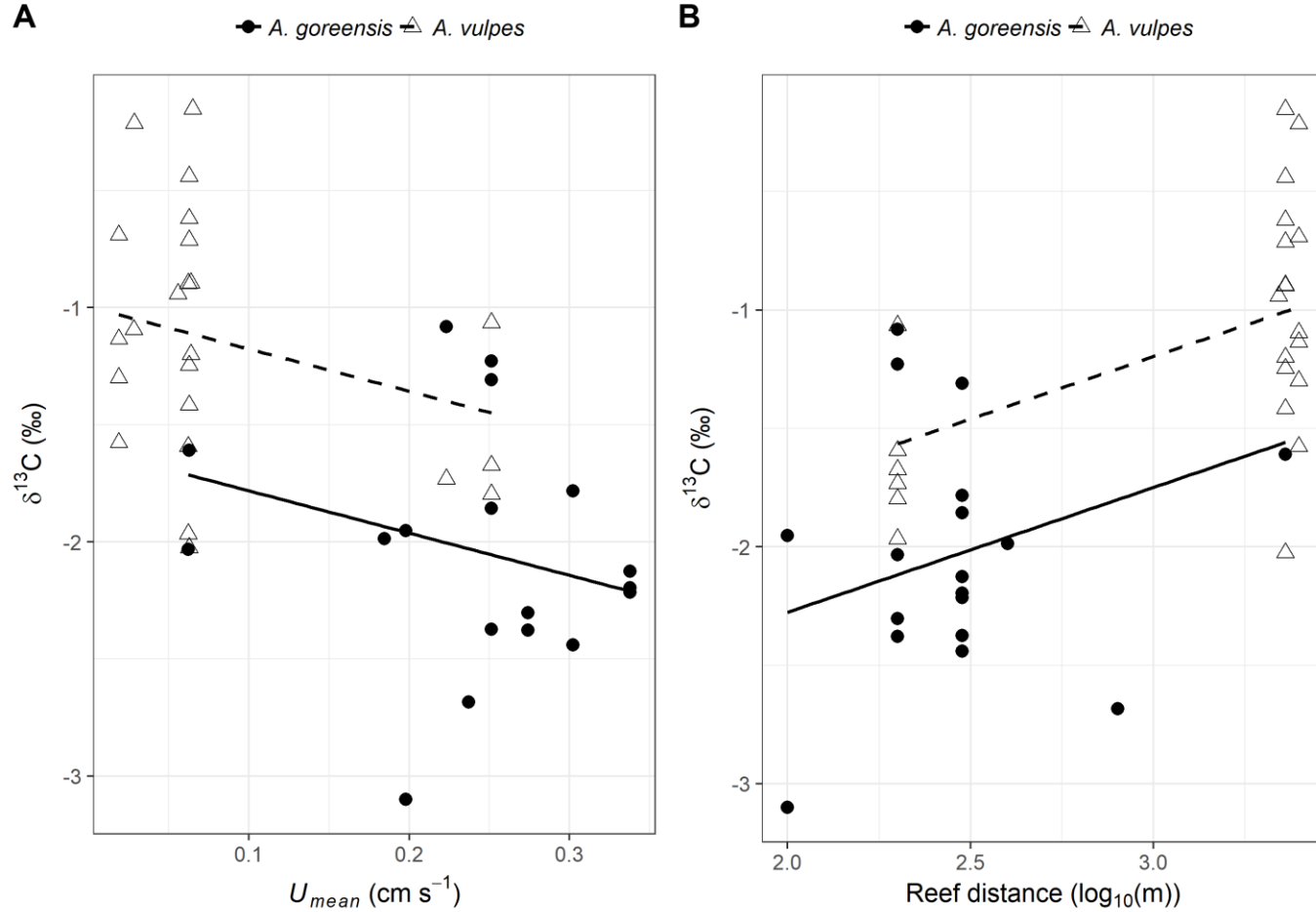
Figure 3.5 Scatterplots depicting observed values and the predictions of linear regression models relating bulk otolith $\delta^{13}C$ for *A. vulpes* and *A. goreensis* juveniles to: **A** long-term mean wave bottom orbital velocity (U_{mean} [cm s^{-1}]) at capture locations, and **B** swimming distance to coral reef habitats (to the nearest 100 m) from capture locations.

3.9 Appendix 3A: δ^{13}C in Otoliths and Muscle
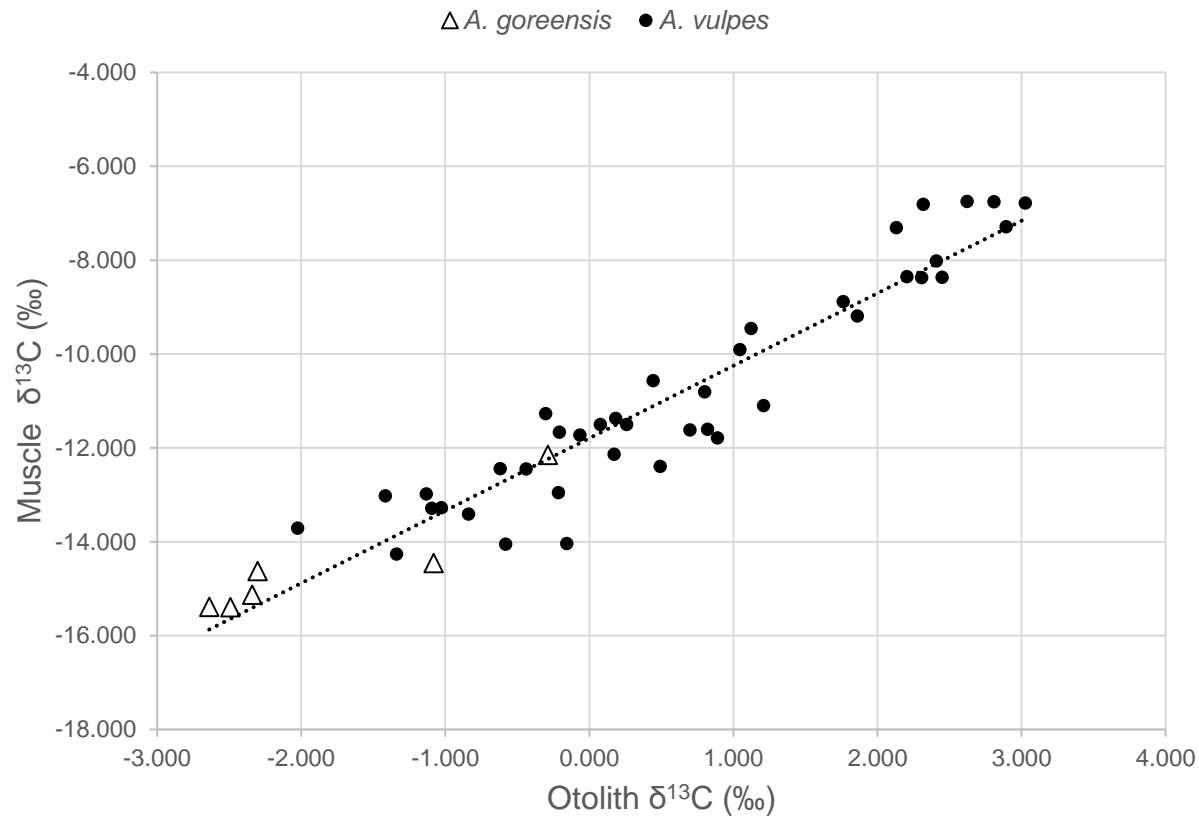
Figure 3A-1 Plot depicting the relationship between bulk otolith δ^{13}C and white muscle δ^{13}C for juvenile bonefishes (n = 46) collected from the littoral zones of Eleuthera, Bahamas. Otolith δ^{13}C was closely related to muscle δ^{13}C via the equation $y = 1.5447x - 11.794$, $r^2 = 0.91$.

CHAPTER 4

SOCIAL INFORMATION AND POSITIVE INTERSPECIFIC ASSOCIATIONS

SHAPE JUVENILE FISH ASSEMBLAGES

Haak, C. R., Hui, F. K. C., Cowles, G. W., and Danylchuk, A. J. (In Review). Social information and positive interspecific associations shape juvenile fish assemblages. Ecology.

4.1 Abstract

Social information use can play a fundamental role in structuring animal assemblages, giving rise to mixed-species groups whose members may obtain increased fitness through antipredator and foraging benefits. Heterospecific groups are well documented among fishes yet are notably more prevalent among juveniles than more advanced life stages. The relative predominance of positive interspecies associations during this developmental period may reflect correspondingly elevated rates of interspecific information transfer, as body-size uniformity inherent in early ontogeny yields greater overlap in predator and prey guild membership, thereby enhancing the relevance of social or public information across disparate taxa and consequently increasing the potential benefits obtained by joining others.

To evaluate patterns of heterospecific association and the role of information in shaping juvenile fish assemblages, we employed a joint species distribution model (JSDM), identifying non-random relationships among juvenile fishes collected in 785 seine haul samples from 21 stations in the shallow littoral zones of a subtropical island, while controlling for species-environment relationships. After accounting for environmental factors, which explained 39% of observed covariation in abundance

among 11 taxa, we detected high rates of positive association (84% of significant correlations) occurring predominantly between mutual guild members (benthivores), consistent with assemblage patterns predicted to evolve under widespread interspecific information use. These positive associations occurred primarily between species pairs characterized by neutral (i.e., non-interacting) or negative (i.e., predator-prey) relationships in later life stages, supporting the notion that heightened niche overlap linked to ontogenetically-imposed body size uniformity acted to increase the pertinence of information across species. Taxa had varying degrees of influence on assemblage structure, however *Eucinostomus* spp., a gregarious generalist with unusually high information-production potential, exerted an effect several times that of all other species combined, further evidencing the likely role of information in producing observed assemblages. Collectively, these results suggest that facilitative interactions mediated through information exchange are among the principal factors organizing juvenile fish assemblages at local scales, highlighting the importance of ontogeny and corresponding body size limitations in regulating the relevance of information across taxa, and offering a parsimonious explanation for the comparative preponderance of heterospecific association observed among juvenile fishes.

4.2 Introduction

Understanding the factors that drive species distributions and structure animal assemblages is essential to preserving natural communities and to predicting the ways ecosystems will respond to environmental change. While abiotic factors are typically thought to determine organismal distributions at broad geographic scales, biotic interactions can be influential in shaping communities at local scales, and thus there is

growing recognition of the need to consider their effects when modeling species distributions (Boulangeat et al. 2012, Kissling et al. 2012, Wisz et al. 2013). Although negative interactions such as competition or predation are typically the focus of such efforts, positive or facilitative interactions can be equally consequential (Bertness and Callaway 1994, Bruno et al. 2003).

Mixed-species grouping, or heterospecific association, represents one form of interaction that is frequently facilitative in nature, and can have broad implications for species distributions and community structure (Powell 1985, Mönkkönen et al. 1996, Goodale et al. 2017). Members of mixed-species groups are thought to obtain many of the foraging and antipredator advantages associated with monospecific group membership (Pavlov and Kasumyan 2000, Krause and Ruxton 2002, Ward and Webster 2016), while also benefitting from reduced intraspecific competition and larger group sizes than might be afforded by conspecifics alone (Morse 1977, Terborgh 1990, Goodale et al. 2017). Although the fitness benefits of group participation may be attributed in part to risk dilution and other intrinsic properties of being among high densities of individuals (Hamilton 1971, Foster and Treherne 1981, Landeau and Terborgh 1986), there is increasing acknowledgement that these mechanisms do not adequately account for the patterns of heterospecific association observed in nature (Wolters and Zuberbühler 2003, Schmidt et al. 2010); for example, the disproportionately large effect exerted by certain taxa, often referred to as "nuclear" or "sentinel" species, on the formation and cohesion of mixed-species groups (Moynihan 1962, Goodale and Kotagama 2005b, Srinivasan et al. 2010). Rather, mounting evidence indicates that access to social information is among the primary drivers of grouping behavior, and furthermore that the potential benefits to be

gained by joining mixed-species groups may in fact exceed those of monospecific groups (Mönkkönen et al. 1999, Seppänen et al. 2007, Gil et al. 2017). It therefore is not likely by coincidence that the attributes common to many nuclear or sentinel species, such as intraspecific gregariousness or unique sensory capabilities (Hutto 1994, Goodale and Kotagama 2005b, Srinivasan et al. 2010), correspond closely with the characteristics thought to maximize a species' information-production potential (Goodale et al. 2010), suggesting that the attractiveness of nuclear individuals is related to their value as informants (Goodale and Kotagama 2008, Hetrick and Sieving 2012).

Social information arising via intentional or more commonly inadvertent means can impact decision making and consequently the outcome of many fundamental ecological processes (Dall et al. 2005, Blanchet et al. 2010). Observing the density or behavior of foraging heterospecifics can reduce uncertainty about the distribution of resources (Valone and Templeton 2002), while eavesdropping on the visual, aural, or chemical alarm cues produced by others can aid in the detection of predators (Magrath et al. 2015), ultimately increasing individual fitness (McNamara and Dall 2010). However, information use is not without costs, and the application of unreliable or incompatible information can lead to maladaptive decisions (Giraldeau et al. 2002, Magrath et al. 2009, Rieucau and Giraldeau 2011). The relevance, and prospective profitability of information varies between individuals and is largely a function of their ecological similarity (Seppänen et al. 2007). Accordingly, the most valuable and thus attractive informants should be those sharing mutual resources and/or predators; i.e., species occupying similar niches. Consequently, the transfer of information across taxa should bring about predictable patterns of assemblage at local scales, distinguished by

unexpectedly high frequencies of co-occurrence among ecologically, phenotypically, or functionally-similar species characterized by high niche overlap (Seppänen et al. 2007, Sridhar et al. 2012, Hua et al. 2016), effectively the inverse structure expected in communities governed by competition (Dayan and Simberloff 2005).

Of the basic phenotypic characteristics that define an individual's ecological niche, body size may be the most fundamental, with sweeping ramifications for physiology, mobility, resource utilization, and predation risk (Peters 1986, Cohen et al. 1993, Hildrew et al. 2007). Heterogeneity in body size is frequently characterized as a means of niche-differentiation, promoting coexistence by reducing overlap through size-dependent controls on resource utilization (Hutchinson 1959, Wilson 1975, Basset 1995). Conversely, homogeneity in body size can heighten congruency in resource use and in the threat posed by predators, diminishing the ecological distance between species (Woodward and Hildrew 2002, Leyequién et al. 2007). Accordingly, the increased niche overlap among like-sized individuals should act to enhance the relevance of social information among phylogenetically disparate taxa, and in turn the fitness benefits to be gained by heterospecific association (Sridhar et al. 2012, Hua et al. 2016).

For most animals, body size is inextricably linked with developmental stage, and in few taxa is this relationship more striking than it is among fishes, for whom ontogenetic changes in body size commonly span several orders of magnitude. Thus, in the strongly size or stage-structured trophic webs characteristic of aquatic environments, ontogeny can have profound implications for species interactions (Polis 1984, Woodward and Hildrew 2002), at times playing an even greater role than phylogeny in defining a fish's ecological niche (Kohda et al. 2008, Soler et al. 2016). Interspecific information

transfer occurs among fishes in the context of both foraging (Coolen et al. 2003, Karplus et al. 2007) and predator avoidance (Mathis and Smith 1993, Mirza 2003), and is likely to be a key factor motivating the heterospecific associations among coral reef inhabitants (Gil and Hein 2017). Therefore, by extension, ontogenetic stage and related changes in body size should have substantial ramifications for the relevance of social information among fishes, and subsequently for patterns of heterospecific association.

While heterospecific association in fishes occurs throughout ontogeny, it is notably more prevalent among juveniles (Lukoschek and McCormick 2000, Overholtzer and Motta 2000, Moland et al. 2005), whose small body sizes are intrinsically more uniform and relatively invariable when contrasted with those of more advanced developmental stages, for whom sizes vary widely across species and are often plastic (Gust et al. 2002). We propose that the relative preponderance of mixed-species grouping behavior among juvenile fishes can be explained by correspondingly high rates of interspecific information exchange during this life stage, as the body size homogeneity inherent among less-developed fishes correlates with ecological niche convergence, increasing the relevance of social information among distinct taxa and expanding the pool of heterospecifics from which pertinent knowledge may be obtained.

To empirically evaluate the influence of heterospecific association and information use among juveniles, we examined the structure of fish communities in tropical inshore habitats, where a diverse array of fishes exploit shallow littoral zones during early ontogeny (Parrish 1989, Nagelkerken et al. 2000). Spanning a range of trophic guilds, from piscivorous apex predators to benthic invertivores and pelagic planktivores, these fishes vary greatly in size and in habitat use as adults, yet exhibit a

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high degree of overlap in space, time, and body size as juveniles (Serafy et al. 2003, Mateo and Tobias 2004, Newman et al. 2007). Consequently, while interactions among adults of these taxa are typically negative (e.g., predator-prey) or non-existent, there is considerable potential for positive interactions and information exchange among juveniles, which in turn should elicit patterns of heterospecific association similar to those predicted by Seppänen et al. (2007).

Species' co-occurrence or correlations in abundance are frequently utilized to identify species associations or patterns of community assemblage (Gotelli and McCabe 2002, Ulrich and Gotelli 2010), however inferring the nature of such relationships is a complex task, because associations may arise through several distinct mechanisms that can be difficult to disentangle (Kissling et al. 2012, Morueta-Holme et al. 2016). While positive correlations in abundance may signify facilitative interactions, they may also occur in the absence of interaction, as animals with coinciding traits occupy the habitats to which they are best adapted (Keddy 1992, Webb et al. 2002), and hence the inference of species interactions from raw correlations can be misleading. Recently emerged joint species distribution models or JSDMs (Pollock et al. 2014) provide a means of discriminating between different drivers of correlation, controlling for environmental filtering and thereby permitting more accurate and "conservative" inference of species interactions (Golding et al. 2015, Ovaskainen et al. 2017)

We therefore employed a JSDM to identify patterns of heterospecific association reflecting biotic interactions among juvenile fishes, assessing whether the observed assemblage structure was consistent with that predicted to arise under ecologically extended social information use. Following Seppänen et al. (2007), we expected that

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comparatively high rates of interspecific information transfer among juvenile fishes would be evidenced by correspondingly elevated incidences of positive non-random correlations in abundance, with these relationships being stronger or more frequent among mutual guild or functional group members. Likewise, if ontogenetic constraints on body size acted to enhance the relevance of information among juveniles relative to later life stages, we anticipated that positive associations would be evident between taxa that were unlikely to share positive relationships in later life. Finally, we postulated that if access to information was among the key factors stimulating heterospecific association, then species exerting an exceptionally large influence on assemblage structure (i.e., acting in a nuclear role) would display traits consistent with high information-production potential following Goodale et al. (2010).

4.3 Methods

4.3.1 Data collection

4.3.1.1 Community abundance data

Data on the composition of juvenile fish assemblages were collected at 21 distinct stations situated within the shallow littoral zones of Eleuthera Island in The Bahamas Archipelago (Figure 4.1). Spanning approximately 40 km along the windward and leeward coasts, sampling stations represented a diverse mosaic of habitat types including beaches, sandflats, seagrass beds, and mangrove creek systems, capturing a broad range of variation in physical and biological conditions. Stations were sampled repeatedly between January 2012 and April 2013, using a 15.2 m x 1.2 m, 3.2 mm mesh bagless beach seine hauled roughly parallel to shore for 20 meters, constituting a total sweep area of approximately 210 m^2 per sample. Upon the completion of each haul, the proportion

of swept area comprising moderate-to-dense benthic vegetation, as defined by Harborne et al. (2008), was estimated and recorded, as were the minimum and maximum depths encountered and the proximity to the mangrove fringe (up to 100 m). Ambient water temperature was measured with a handheld thermometer, and the location of each seine haul was recorded using a portable GPS unit. Following each sampling event, captured specimens were identified to the lowest possible taxon (genus or species) and enumerated before being released. Larger individuals (exceeding 150 mm TL) were recorded and immediately released on site. For smaller specimens (<150 mm TL), a representative subsample of up to 30 individuals of each taxon was retained from a subset of seine hauls and sacrificed to permit more precise identification & measurement. Additional details on sampling methodology and the study area can be found in Haak et al. (2019).

4.3.1.2 Environmental covariates

To accommodate the diversity of fishes collected, and the likelihood that species with varying ecologies and functional roles may be influenced by distinct environmental factors, we considered an extensive array of independent predictors quantifying variation in biotic and abiotic habitat characteristics over a range of scales. Physical covariates included basic parameters such as water temperature and depth, as well as several measures of flow-related environmental stress arising due to incident waves and tidal currents, obtained from hydrodynamic models as outlined in Haak et al. (2019). Biological predictors reflected both microhabitat characteristics and the arrangement of the broader seascape, comprising the coverage of benthic vegetation within the sampled area and its proximity to adjacent mangrove and coral reef habitats. Temporal fluctuations in species' abundance were accounted for via the inclusion of a seasonal

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covariate. The complete suite of explanatory environmental variables is defined in Table 4.1, and additional information detailing their measurement or estimation, as well as the rationale for their inclusion, is provided in Appendix 4A.

4.3.2 Statistical analysis

The present study employs a JSDM in the form of a latent variable model (LVM) which approximates correlation among species via their associations with underlying "latent" gradients, treated as random variables (Hui et al. 2015, Warton et al. 2015). By estimating the relationships with environmental predictors for multiple species concurrently, while explicitly modeling correlations in observed species abundance, JSDMs permit the partitioning of observed correlation into that which can be explained by species' responses to known environmental covariates ("environmental correlation"), and that which remains unexplained ("residual correlation"), which may reflect biotic interactions. While species' relationships with latent variables, quantified through their respective parameter coefficients, might ideally be presumed to reflect the outcome of species interactions, they may also reflect responses to additional, missing or unknown environmental covariates (Kissling et al. 2012, Warton et al. 2015, Ovaskainen et al. 2016). To further limit the potential influence of unmeasured environmental variability on the estimation of residual correlations, it was assumed that unobserved gradients displaying correlation within sampling stations were environmental in nature, and a random intercept at the level of station was included for each species to account for this, precluding its influence on latent variables and consequently residual correlations.

Inferring direct, pairwise species interactions from correlations is further complicated by the fact that observed correlations may reflect the results of indirect

interactions, potentially masking the true nature of species relationships (Harris 2016).

For example, two non-interacting species sharing a negative relationship to a third

species may in fact appear to exhibit a positive relationship with one another. To

overcome this challenge, several authors have proposed the use of partial correlations to

detect direct pairwise interactions while controlling for the effects of the remaining

species pool (Harris 2016, Morueta-Holme et al. 2016, Ovaskainen et al. 2016). We

therefore employed partial correlations, obtained through inversion of the residual

correlation matrix, in addition to raw residual correlations, to assess species relationships.

We fitted the JSDM discussed above using the R package boral (Hui 2016), which

employs Monte Carlo Markov Chain methods executed in JAGS (Plummer 2003) to

estimate model parameters. To maximize model parsimony given the presence of 11

taxa, species correlations were approximated through 2 latent variables; (testing with

additional latent variables found little difference from the results obtained here). Due to

the overdispersed nature of count data for many species, a negative binomial error

distribution was employed. All covariates were centered and standardized prior to model

fitting. We specified uninformative normal and uniform (when appropriate e.g., for

dispersion, or variance of the random intercept for station) priors for the hyperparameters

of the model. Three MCMC chains were run for 300,000 iterations each, with a burn-in

period of 10,000 iterations and a thinning factor of 30. Model convergence was assessed

using the Gelman-Rubin statistic (Gelman and Rubin 1992, Brooks and Gelman 1998),

the Geweke diagnostic (Geweke 1992), and visual examination of trace plots. Dunn-

Smythe residuals were inspected for evidence of violation of model assumptions

following Hui (2016). After fitting, terms were considered significant when their

corresponding 95% credible intervals (HPD intervals) did not encompass zero. Analysis was limited to include only fully-metamorphosed, post-larval juveniles less than 150mm FL, and rare taxa occurring in less than 1% of hauls were omitted from consideration. Finally, the power of environmental predictors (including random station effects) to explain covariation in observed species abundances was assessed by comparing the trace of the residual covariance matrix of the full model (including environmental predictors and random station effects) to that of a model containing only the 2 latent variables, following Warton et al. (2015) and Hui (2016).

To visualize relationships between taxa (as quantified by residual and partial correlations), and to evaluate each taxon's overall influence on assemblage structure, a network approach was utilized. Because correlations do not inherently reflect the often-unbalanced nature of interspecific relationships, the residual and partial correlations between each pair of taxa were weighted by an asymmetrical association index (Araújo et al. 2011, Sridhar et al. 2013). The index is based on the simple premise that the relative influence of one taxon (A) on another taxon (B) is equivalent to the proportion of occurrences of taxon B that coincided with taxon A, and vice versa. The resulting compositional effects of each species (or node) upon the other were then applied as edge weights in a directed network. The overall influence of each species on assemblage structure, depicted by node size, was approximated following Sridhar et al. (2013) as the normalized sum of the absolute value of the weights of each node's outgoing edges, or normalized weighted out-degree ($nwD_{out,}$)(Wasserman and Faust 1994). Due to the wide range of values, this metric was square-root transformed for the purposes of plotting. Network graphs were generated using the R package qgraph (Epskamp et al. 2012).

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4.4 Results

4.4.1 Community sampling

A total of 785 seine haul samples were conducted across the 21 stations between January 2012 and April 2013. A summary of the environmental parameters recorded or estimated across seine hauls is presented in Appendix 4A: Table 4A-1. Juvenile fishes collected in samples tended to represent two distinctive functional groups: (1) bottom-associated, largely benthivorous fishes; and, (2) pelagically-oriented planktivores, with the mean size of individuals varying little across taxa (Table 4.2). The most common taxa, in terms of frequency of occurrence, were *Eucinostomus* spp. (mojarras; 61%), *Atherinomorus stipes* (hardhead silversides, 41%), and *Sphyraena barracuda* (great barracuda, 21%). As might be expected, these also tended to be among the most abundant overall, with atherinids comprising the greatest number of all individuals (54%), followed by eucinostomids (42%) and the rarer but highly gregarious *Harengula* spp. (herrings, 2%). Raw patterns of co-occurrence, which disregard the effects environmental filtering, suggested strong relationships in the presence/absence and abundance of several taxa (Appendix 4B: Table 4B-1).

4.4.2 Joint Species Distribution Model

All environmental covariates were significant predictors for at least two taxa, and all fishes displayed a significant relationship with one or more environmental predictors (Appendix 4B: Table 4B-2). Among these variables, benthic vegetation coverage exerted a significant effect on the greatest number of taxa (n=7), although as might be expected it had little influence on more pelagically-oriented fishes such as atherinids and clupeids. Basic physical parameters, such as water depth and temperature, were significantly

related to the abundance of assorted demersal and pelagic fishes, as were hydrodynamic variables reflecting variation in wave and tidally-driven water velocities. Swimming distance to coral reef habitats was a significant predictor for several fishes with reef-associated adult life stages, and proximity to mangroves was likewise linked to the abundance of species known to exploit fringing mangrove habitats. Seasonal shifts in abundance were also detected for some fishes.

Significant positive and negative environmental correlations were detected among several community members (Table 4.3A), indicating that similarities and disparities in species-specific responses to explanatory variables (i.e., environmental filtering) acted in part to produce observed raw correlations in abundance. Collectively, environmental covariates, including random station effects, accounted for approximately 39% of the covariation in abundance among species. Environmental correlations tended to segregate along the lines of functional differences, with positive correlations occurring largely among fishes characterized by similar patterns of water-column utilization or foraging modes. For example, environmental preferences of the two most abundant and frequently occurring taxa, *Eucinostomus* spp. (a demersal benthivore) and *A. stipes*, (a pelagic planktivore) were negatively correlated with one another but were positively correlated with members of their respective functional groups (*Albula vulpes* or bonefish, and *Harengula* spp., respectively). *Eucinostomus* spp. showed the greatest number of positive environmental correlations, which may be attributed to its habitat-generalist nature. Several negative environmental correlations were observed for *Trachinotus falcatus* (permit), likely related to its unusual positive relationship with wave-driven water velocities.

Strong residual correlations were present between taxa after accounting for environmental preferences (Table 4.3B). Of the 19 significant relationships identified, 16 (84%) were positive, occurring primarily among fishes within a single functional group, the demersal benthivores. The strongest residual correlation was present between *Eucinostomus* spp. and *A. vulpes*, which is not surprising given that all but a single *A. vulpes* specimen co-occurred among mojarras. These two taxa also displayed the greatest number of significant residual correlations with other fishes (n=8 for both), followed by *S. barracuda* and *Bothus* spp., or lefteye flounders (n=4 for both). The high number of significant residual correlations observed for *A. vulpes* is unexpected considering the species' relative rarity and its infrequent co-occurrence with taxa other than eucinostomids; it therefore seems likely that these relationships arose as an indirect result of *A. vulpes'* near-obligate association with *Eucinostomus* spp. *T. falcatus* was the only species to display negative residual correlations, which it shared with three taxa.

Partial correlations revealed a considerably reduced set of significant interspecific associations (Table 4.4), with only four significant relationships remaining, all but one of which involved *Eucinostomus* spp. Foremost among these in terms of magnitude was a pronounced positive correlation between *A. vulpes* and *Eucinostomus* spp. Likewise, *Bothus spp*. and *S. barracuda* both displayed comparably strong positive correlations with eucinostomids. Following expectation, save for a somewhat weaker positive correlation between *A. vulpes* and *S. barracuda*, the relationships of these two species with other taxa were no longer significant after controlling for their close correspondence with eucinostomids. Despite the significant residual correlations and high rates of co-occurrence between several other fishes and *Eucinostomus* spp., (such as *Haemulon* spp.

or grunts, and *Albula goreensis*), partial correlations for these taxa were not significantly different from zero.

The influence of taxa in pairwise relationships were often heavily skewed or one-sided for both residual and partial correlations (Table 4.5 A and B, respectively). For example, in the case of the strongest estimated residual correlation, the effect of *Eucinostomus* spp. on *A. vulpes* was roughly 10 times, or an order of magnitude greater than, the corresponding influence of *A. vulpes* of eucinostomids. This pattern was consistent across all taxa that shared significant residual correlations with *Eucinostomus* spp., with eucinostomids exerting a comparatively much larger effect than their counterparts in any given species pair. Asymmetric relationships were also apparent in the case of other taxa such as *S. Barracuda,* but to a considerably lesser degree. Therefore, despite several fishes sharing similar numbers of significant residual correlations of often comparable strength, the overall estimated influence of distinct taxa on community structure ($nwD_{out,}$ Table 4.5 A and B) varied greatly, spanning several orders of magnitude. *Eucinostomus* spp. exerted a disproportionately large overall effect in the residual correlation network (Figure 4.2A), roughly four-times that of the next-most influential species, *S. barracuda*, and substantially greater than (roughly twice) that of all other significantly-correlated species combined. Analogous patterns emerged in the case of partial correlations (Figure 4.2B), with Eucinostomus spp. exhibiting by far the largest net effect on assemblage structure, on the order of four-times that of *S. barracuda* and approximately 2.5-times that of the other three taxa combined.

4.5 Discussion

This study is, to the authors' best knowledge, the first to examine the social structure and associational patterns of juvenile fish in wild communities while accounting explicitly for the effects of environmental variability on species distributions, accomplishing this through the application of an innovative and rigorous statistical approach. In so doing, this work advances our understanding of the factors that act to shape fish assemblages during a critical and often poorly-understood life stage, revealing the central yet under-recognized importance of facilitative or positive interactions among juvenile fishes. Simultaneously, this research presents an empirical examination of heretofore mainly theoretical predictions regarding the influence of social information on the organization of mixed-species fish shoals, suggesting that ontogenetically-mediated body-size uniformity may supersede phylogenetic disparities in determining the relevance of information in early life.

The patterns of species association elucidated by our analysis are consistent with those predicted to emerge in the presence of heterospecific information use by Seppänen et al. (2007), paralleling observations in mixed-species bird flocks (Sridhar et al. 2012). Even after accounting for environmental preferences, residual and partial correlations revealed a marked bias towards non-random positive associations, likely signifying facilitative interactions among similarly-sized juvenile fishes. Moreover, in further agreement with the predictions of Seppänen et al. (2007), positive interspecies associations were largely limited to ecologically similar taxa, occurring almost exclusively among species of the same functional group (benthivores). Furthermore, most of these associations occurred between fishes whose adult life stages were

characterized by sharply contrasting body sizes, trophic positions, and patterns of habitat use, and therefore by neutral, heavily asymmetric, or predator-prey relationships. Finally, there were marked differences in the number and strength of positive associations among taxa, with assemblage structure affected inordinately by a single taxon (*Eucinostomus* spp.) that, as discussed in detail below, demonstrates an uncharacteristically high potential for information production (Goodale et al. 2010). Collectively, these findings provide strong support for the hypothesis that interspecific information transfer, and its consequent effects on fitness, are a key factor selecting for the relatively high rates of heterospecific grouping observed among juvenile fishes; and furthermore, that the prevalence of information transfer across species likely arose due to increased niche overlap associated with body size congruency in early ontogenetic stages.

One might intuit given the random sampling strategy employed here that individuals collected in seine hauls may at times represent fractions of, or multiple and distinct, fish shoals (Blakeslee et al. 2009), and therefore that a proportion of observed joint occurrences were coincidental, resulting from species sharing habitats but not necessarily interacting or associating. In such a case, the regular co-occurrence and subsequently high correlations of several species with *Eucinostomus* spp. might be interpreted simply to reflect this taxon's relatively ubiquitous nature. However, our model explicitly accounts for this possibility by controlling for correlation due to such chance co-occurrences, considering not only species' relative abundances but also their overlap in habitat utilization. Thus, for species pairs such as *A. vulpes* and *Eucinostomus* spp. with similar habitat requirements evidenced by high environmental correlations (Table 4.2A), the threshold for detecting a non-random positive relationship was

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effectively adjusted upwards to compensate for the species' high probability of co-occurrence.

Likewise, the allocation of station-level random effects to estimated environmental correlations ensured that co-occurrence driven by inter-station variation in unmeasured factors did not bias the latent variables used to approximate species interactions. Although it is conceivable that unmeasured environmental variation at finer scales (i.e., independent of station) could theoretically have influenced latent variables, this seems improbable given the strength and consistency of observed relationships and the fact that such variables (e.g., local variation in benthic floral and faunal communities) would likely have been correlated with several of the measured environmental covariates (Brind'Amour et al. 2005, Boström et al. 2006). Thus, the techniques employed here likely represent the most conservative method possible for inferring species interactions from community abundance data.

While our approach to identifying heterospecific associations required no implicit assumptions about shoal membership or the spatiotemporal scales of species interactions, the exchange of social information to which we accredit these relationships is nevertheless contingent upon associated taxa occurring within close proximity in time and space (Seppänen et al. 2007); i.e., in a mixed-species shoal. Considering the extensive suite of environmental factors that were controlled for and the relatively small area sampled by seine hauls, there seems little doubt that the relationships inferred from significant partial correlations (and to a lesser degree residual correlations) are indeed reflective of species interactions occurring at local scales (Golding et al. 2015, Ovaskainen et al. 2017). This presumption is validated by observations obtained from

remote underwater video surveys, which not only produced incontrovertible evidence of

A. vulpes and *S. barracuda* juveniles consistently commingled within *Eucinostomus* spp.

shoals, but also revealed patterns of organization paralleling those inferred from the

JSDM (refer to Appendix 4C and Video Appendix 1 for details,).

Nonetheless, one might assert that mixed-species shoal participation simply

represents an adaptation to permit larger group sizes when the availability of conspecifics

is limited or unpredictable (Ogden and Ehrlich 1977), and thus that the observed patterns

of association are equally attributable to the numerical or statistical benefits of group

membership. In this event it seems logical that fishes most strongly influenced by or

closely associated with heterospecifics (i.e., *A. vulpes, S. barracuda,* and *Bothus spp.*)

should be among the rarer or less frequently encountered taxa; yet conversely, these were

all among the more commonly-occurring or abundant fishes. In fact, more advanced

developmental stages of *A. vulpes* and *S. barracuda* (which should theoretically be less

abundant) occur frequently in large schools (De Sylva 1963, Murchie et al. 2013),

implying that their consistently small conspecific group sizes were not a result of scarcity

(Table 4.2). Furthermore, the conspicuity arising from the invariably low abundance of

these taxa among *Eucinostomus* spp. shoals should carry high costs of phenotypic oddity,

greatly limiting or offsetting the dilution of risk gained by joining heterospecifics (i.e.,

eucinostomids), and instead favoring conspecifics as shoal partners if statistical benefits

were the main drivers of association (Wolf 1985, Landeau and Terborgh 1986).

Moreover, if such numerical advantages were indeed of primary adaptive importance,

then one would expect rare or associate taxa to exploit shoals of other commonly

available, numerically abundant and gregarious fishes, such as *A. stipes* or *Harengula* spp., yet no such relationships were detected.

Finally, the absence of agonistic interactions or "following and scavenging" behaviors (Lukoschek and McCormick 2000) noted among associating heterospecifics in remote video surveys suggests that direct feeding-related benefits (i.e., pilfering or prey flushing) are also unlikely to be among the major adaptive advantages of group participation (Appendix 4C). In light of the above considerations and given the close correspondence between the patterns of association we identified and those both theorized and empirically documented to arise in groups structured by social information (Seppänen et al. 2007, Sridhar et al. 2012, Gil et al. 2017), we reasonably conclude that interspecific information transfer provides the most plausible explanation for the organization of observed assemblages.

4.5.1 Ontogenetic constraints on body size and the relevance of information

The size of a fish has direct implications for swimming performance, metabolic requirements, prey handling, and gape limitation, determining the prey an individual is able to and should optimally capture or ingest (i.e., predator guild membership), and the predators to which it is vulnerable (i.e., prey guild membership) (Mittelbach 1981, Christensen 1996, Scharf et al. 2000); consequently, body size is closely correlated with the positions occupied by fishes in aquatic food webs (Jennings et al. 2001, Romanuk et al. 2011). Of the ways that ontogenically-imposed body size limitation can mediate ecological similarity and thereby enhance the relevance of information between heterospecifics, the most universally applicable to the fishes studied here may be through its convergent effect on prey guild membership, arising due to the size-dependent nature

of predation risk (Anderson 1988, Sogard 1997). It is worth noting that others have linked the elevated risk of predation associated with small body size to increased propensity for heterospecific group participation (Buskirk 1976, Thiollay and Jullien 1998, Sridhar et al. 2009), and while this may contribute to explaining the adaptive significance of grouping among juveniles, the principal mechanism we propose here is fundamentally different. We suggest that it is not necessarily the absolute level of vulnerability, but instead the relative homogeneity in vulnerability experienced across distinct species as juveniles (compared to later life stages) that acts primarily to amplify the benefits of heterospecific group participation during this life stage, by increasing the relevance of risk-related information across diverse species.

The fishes studied here exhibit adult body sizes ranging roughly an order of magnitude, and therefore are likely to occupy largely distinct prey guilds as mature individuals. Accordingly, the threat presented by a given predator will often be asymmetrical across adult heterospecifics; for example, the risk posed by a 500 mm FL young-of-year lemon shark (*Negaprion brevirostris*) is logically much greater for a typical *Eucinostomus* spp. adult (with a size on the order of 125 mm FL) than for an *A. vulpes* adult (with a size of roughly 500 mm FL). Given this discrepancy in vulnerability, behavioral cues conveying the threat perceived by adults of one taxa may be largely incompatible or irrelevant for adults of the other, leading to over-or-underestimation of risk and considerable costs to fitness or survival (Werner et al. 1983, Lima and Dill 1990), thereby limiting the utility of predator-related information across taxa. In contrast, the notably smaller body size differential between co-occurring juveniles of these two fishes means that same predator likely constitutes a much more symmetrical threat,

making risk-related information more equally pertinent and mutually beneficial across species. Following this reasoning, most if not all of the fishes examined here exhibit much greater equivalency in prey guild membership (i.e., share a more overlapping array of predators) as juveniles than as adults, and consequently stood to accrue greater benefits from "eavesdropping" on heterospecific cues signaling predation risk (Mathis and Smith 1993, Mirza 2003, Anderson et al. 2016), possibly leading to the high rates of association we observed.

The consequences of developmentally-imposed uniformity in body size can also change the basic nature of interspecific relationships, such that taxa typically regarded as predator and prey may in fact occupy similar trophic positions or prey guilds as juveniles (Werner and Gilliam 1984, Olson et al. 1995). Ontogenetic changes in body size can thus have direct repercussions for information use, determining whether heterospecific alarm cues elicit a defensive (i.e., antipredator) or aggressive (i.e., foraging) response (Brown et al. 2001, Harvey and Brown 2004, Elvidge et al. 2010), and such a phenomenon may be exemplified here in the relationship between *S. barracuda* and *Eucinostomus* spp. Though they comprise a reasonable fraction of the prey consumed by later-stage juvenile or subadult *S. barracuda*, gerrids are largely absent from the diet of early juveniles in the size class considered here (De Sylva 1963, Hammerschlag et al. 2010), as predators rarely consume prey with body sizes greater than 50% of their own (Popova 1978, Scharf et al. 2000), and the deep-bodied morphology of eucinostomids presents a further obstacle to ingestion by larger but more elongate predators (Hambright 1991). Hence, it appears that juvenile *S. barracuda* may undergo a pronounced ontogenetic shift in their response to the alarm cues of taxa such as *Eucinostomus* spp., exploiting the antipredator

benefits of heterospecific group association as early juveniles, yet possibly utilizing the same cues to identify feeding opportunities later in life, in a pattern not unlike that described for other piscivores (Sazima 2002).

In much the same manner that it produces congruency in prey guild membership, body-size uniformity in early ontogeny can also bring about convergence in predator guild membership, increasing the relevance of heterospecifically-produced information on foraging opportunities and contributing to the high rates of association we observed. Social information on the location or quality of resources is obviously of greater utility among individuals that exploit related resources in a similar manner or location; correspondingly the positive associations we detected occurred primarily among members of the same foraging guild or functional group, mirroring patterns observed in mixed-species bird-flocks (Sridhar et al. 2012, Hua et al. 2016). Nonetheless, even among mutual guild members, the applicability of information on the distribution of prey is also likely to be mediated by body size, particularly among small or juvenile fishes for whom strict size-related limitations on resource use yield narrowed trophic niches (Scharf et al. 2000, Woodward and Hildrew 2002). Thus, the body size homogeneity intrinsic among juveniles should correlate with increased trophic niche overlap, as individuals of distinct taxa are subject to similar prey size constraints.

For example, despite foraging in analogous habitats and consuming benthic invertebrates almost exclusively, adults of *A. vulpes* and *Eucinostomus* spp. occupy different trophic positions, exploiting distinct taxa and/or prey size spectra as dictated by the wide disparity in their adult body sizes and corresponding contrasts in the species' physical abilities and metabolic demands (Werner 1974, Mittelbach 1981). Conversely,

co-occurring juveniles of these two taxa utilize much more analogous prey fields (Layman and Silliman 2002), as size-related controls on prey utilization bring about elevated niche overlap (Woodward and Hildrew 2002). Likewise, although *Bothus* spp. are primarily piscivorous as adults, juveniles of the size class examined here are predominantly invertivorous (Randall 1967, van der Geest and Langevoord 1995). In fact, of the taxa exhibiting significant positive residual correlations, all but a single species (*S. barracuda*) can be classified principally as benthic invertivores during the developmental period considered here (Randall 1967, Layman and Silliman 2002). Accordingly, similitude in predator guild membership is much greater among juveniles of these fishes than amidst later life stages, making heterospecifically-derived information on the distribution of prey or patch quality (Buckley 1997, Valone and Templeton 2002) a more profitable commodity for juveniles and favoring group participation in early life.

The foraging advantages to be gained by the piscivorous *S. barracuda* are less immediately evident; while not typically characterized as a benthivore, early juveniles prey on small benthic fishes such as gobiids and cyprinodonts (De Sylva 1963, Schmidt 1989), and thus may obtain feeding benefits akin to those documented for juveniles of other shallow-water piscivores that participate in mixed-species groups, exploiting benthic prey that are attracted to (or flushed by) substrate disturbance caused by foraging *Eucinostomus* spp. (Sazima 2002).

4.5.2 Role of information-producing species

The contrasting ecological characteristics of different taxa affect the quality and quantity of information they produce, and those that most frequently and reliably convey information to the widest audience should be the most universally attractive informants,

consequently exerting the greatest influence on community structure (Goodale et al. 2010). As such, the exceptionally strong organizational effect of *Eucinostomus* spp. on the observed fish assemblages is not unexpected when one considers that this taxon exhibits several key characteristics thought to confer high information-production potential, and which likewise coincide with traits that distinguish nuclear species across diverse types of taxa and ecosystems.

The most universal of these traits, intraspecific gregariousness, has been linked to nuclearity in both mixed-species bird flocks (Hutto 1994, Goodale and Beauchamp 2010, Srinivasan et al. 2010) and fish shoals (Sazima et al. 2006). Eucinostomids are highly social, commonly occurring in large conspecific or congeneric shoals, and are often among the more abundant constituents of shallow lagoonal systems (Serafy et al. 2003, Newman et al. 2007), as evidenced in the present study. This large conspecific group size has positive implications for several stages of information production, increasing the probability of initial detection, but also the accuracy, reliability, and ultimately the accessibility of information that is transmitted (Goodale et al. 2010). Hence, the sociality of *Eucinostomus* spp. likely acts to enhance both the quality and volume of information they produce, accounting in part for their central role in shaping the observed species assemblages.

Attractive, information-producing or nuclear species are also distinguished by foraging modes or sensory adaptations that provide unique information detection abilities, often permitting them to maintain an unusually high degree of vigilance relative to other group members (Goodale and Kotagama 2005b, 2008, Srinivasan et al. 2010). *Eucinostomus* spp. possess unusual sensory physiology in the form of a direct physical

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connection between the inner ear, swim bladder, and ventrally-oriented anal fin spines, resulting in remarkably high otic sensitivity (Green 1971, Parmentier et al. 2011). This specialization is believed to play a role in the detection of benthic prey concealed within the substrate, imparting eucinostomids with a singular ability to locate resources that would otherwise remain undiscovered by visually-oriented foragers. Accordingly, foraging *Eucinostomus* spp. shoals are likely to serve as a source of invaluable public information on the distribution of prey for other benthic invertivores, particularly those that rely primarily on vision and, due to obvious perceptual constraints, are often inefficient at locating cryptic or buried prey.

This auditory adaptation may also explain the distinctive foraging behavior displayed by eucinostomids, which is characterized by extended periods of relatively motionless hovering and small positional corrections (presumably "listening"), interrupted by momentary and rapid pitching rotations to consume substrate (Sazima 2002, Parmentier et al. 2011). Because of this largely passive and intermittent or "saltatory" search strategy (O'Brien et al. 1989), eucinostomids can remain in a heads-up position while locating prey, permitting them to visually scan for predators and simultaneously forage exploiting two distinct sensory systems. This stands in contrast to the vigilance-keeping abilities of more active visual foragers, and particularly other benthivores, who typically scan the substrate for prey in a head-down orientation, leading to decreased awareness and increased predation vulnerability (Krause and Godin 1996, Overholtzer and Motta 2000). Accordingly, *Eucinostomus* spp. should be capable of maintaining an exceptionally high level of vigilance compared to other benthivores, further contributing to their attractiveness as shoaling partners for more active and

vulnerable foragers seeking to reduce their risk of predation by exploiting the vigilance of others (Buskirk 1976, Thiollay and Jullien 1998, Sridhar et al. 2009). Together, these qualities connote an unusually high capacity for information detection and production, further explaining the attractiveness of *Eucinostomus* spp., especially among benthic invertivores.

Goodale et al. (2010) predicted that the most widely attractive and thus most influential information providers will be generalist species, because the information they produce is likely to be both relevant to and available to a more diverse heterospecific audience. *Eucinostomus* spp. are habitat and trophic generalists, inhabiting an expansive array of tropical inshore habitats and exploiting a variety of benthic infaunal prey (Kerschner et al. 1985), a trait which is further evidenced by their relatively wide distribution in the present study. This generalist nature may explain the diverse range of species they appeared to influence, which included not only other demersal benthivores, but benthic flatfishes and even piscivores. Given their capacity to produce broadly relevant information about both predators and prey, and disproportionately large influence on the observed distributions of taxa spanning multiple guilds, *Eucinostomus* spp. might be considered "keystone" or "community" informants, upon which the growth and survival of some species may depend (Schmidt et al. 2010, Hetrick and Sieving 2012, Magrath et al. 2015).

4.5.3 Broader relevance

Historically, the consideration of biotic interactions as forces structuring fish communities has been mostly limited to the effects of resource competition and predation, (Robertson and Gaines 1986, Hixon and Beets 1993, Hixon and Jones 2005),

yet our findings reveal little evidence of such negative interactions among the juvenile

fishes studied here. Instead, our results imply that positive heterospecific associations

that facilitate access to social information produced largely by a single taxon are among

the primary factors organizing these assemblages at local scales, providing empirical

support for recent theoretical works on the role of interspecific information transfer in

shaping animal groups (Seppänen et al. 2007, Gil et al. 2017), and highlighting the

extensive influence that such "informant" species can exert on community assemblage

(Hetrick and Sieving 2012, Magrath et al. 2015). Simultaneously, these findings expose

the likely importance of ontogenetic stage, and correspondingly body size, in mediating

the relevance and subsequent exploitation of information among heterospecifics in size-

structured communities, offering a parsimonious explanation for the disproportionately

high incidence of heterospecific association between juveniles when compared to more

advanced ontogenetic stages. These observations are likely transferable beyond the taxa

and habitats studied here, potentially explaining the high rates of positive interspecific

association within juvenile fish assemblages in other systems such as tidal marsh

communities (Bretsch and Allen 2006, Blakeslee et al. 2009), or the attractiveness of

other so-called nuclear species such as goatfishes (*Mullidae)* which share many key traits

with eucinostomids.

Of the positive associations among juvenile fishes described in the literature, a

sizeable fraction take the form of mimetic relationships, many of which have been

characterized as cases of "social mimicry" (Dafni and Diamant 1984, Randall and

McCosker 1993, Moland et al. 2005), a phenomenon closely paralleled in the present

study by the association between *A. vulpes* and *Eucinostomus* spp. As juveniles, *A.*

vulpes display pigmentation almost identical to that of the eucinostomids with which they near-obligately associate; yet this resemblance rapidly fades as *A. vulpes* mature, outgrow, and cease to occur among eucinostomid shoals, in a pattern strikingly similar to that described for *Centropomus* spp. juveniles, whom also mimic eucinostomids (Sazima 2002). Collectively, these patterns suggest that access to heterospecific information may be among the adaptive benefits driving superficial character convergence between associate taxa such as *A. vulpes* or *Centropomus* spp. (i.e., putative mimics) and their informants (i.e., models, such as *Eucinostomus* spp.).

Yet information use is rarely considered among the evolutionary drivers of mimetic resemblance between juvenile fishes, the adaptive significance of which is typically credited to numerical advantages such as risk dilution or direct feeding-related benefits of joining others. It is somewhat ironic then that social mimicry, as originally defined by Moynihan (1968), referred to the co-evolution of superficial phenotypic traits (i.e., visual signals or vocal calls) among mixed-species bird flock participants that served, hypothetically, to promote group cohesion by facilitating interspecific communication. It is now generally recognized that information exchange is among the major factors structuring many heterospecific bird flocks, and that signal convergence may extend beyond flock members to broader communication networks spanning entire communities (Tobias et al. 2014). Our findings may be interpreted as support for the hypothesis of Moynihan (1968) from aquatic environments, suggesting that the adaptive benefits of social information use may have evolutionary ramifications that extend beyond behavior to the physical characteristics of fishes.

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4.7 Tables

Table 4.1 Summary of the environmental predictor variables corresponding to each seine haul sample that were included as covariates in the joint species distribution model (JSDM). Additional details on the selection and measurement of predictors are available in Appendix 4A.

Environmental Predictors	
U_{max}	Long-term (4 yr) near-maximal (99th quantile) wave bottom orbital velocity, estimated by hydrodynamic models described in Haak et al. (2019)
U_{anom24}	Wave bottom orbital velocity anomaly, or the instantaneous departure from long-term (4 yr) mean conditions in the 24 hours prior to sampling, estimated by hydrodynamic models described in Haak et al. (2019)
U_{tide}	Maximum tidal flow velocity associated with the M_2 (principal diurnal) tidal constituent at a height of 5 cm above the seabed, estimated by hydrodynamic models described in Haak et al. (2019)
Water depth	Mean water depth (in cm) sampled by each seine haul, approximated by averaging the minimum and maximum depths encountered at the time of sampling.
Mangrove proximity	Minimum distance to adjacent fringing mangrove habitats (up to a maximum of 100 m), estimated at the time of sampling.
Coral reef proximity	Minimum swimming distance from the geographic centroid of each seine haul to the nearest coral reef habitat as depicted by the United Nations Environment Program coral reef database (UNEP-WCMC 2010), estimated using a geographic information system (GIS).
Water temperature	Ambient seawater temperature in the vicinity of each seine haul, measured with a handheld thermometer (to the nearest 0.1 °C) at the time of sampling.
Benthic vegetation cover	Proportion of swept area comprising moderate to dense benthic vegetation (primarily seagrass) cover as defined by Harborne et al. (2008), visually assessed at the time of sampling following Mumby et al. (1997).
Season	Time of year that a seine haul was conducted, following the common wet season (May-Oct) and dry season (Nov-Apr) convention.

Table 4.2 Summary statistics describing the mean catch-per-unit-effort (CPUE), conspecific group size, frequency of occurrence, total numerical abundance, and mean size of juvenile fishes collected by seine sampling efforts. Lengths are reported as fork length (FL), with the exception of *Bothus* spp. and *H. bivitattus*, for which total lengths (TL) are presented.

	CPUE ± SD	Individuals per occurrence ± SD	Total occurrences (% of total)	Total individuals (% of total)	Length ± SD (mm)
A. vulpes	0.3±1.4	3.6±3.8	57 (7.26)	205 (0.26)	58±25
A. goreensis	0±0.3	1.7±1	15 (1.91)	26 (0.03)	51±10
Eucinostomus spp.	42.2±121.6	68.8±149.3	482 (61.4)	33147 (42.34)	50±19
S. barracuda	0.5±1.6	2.5±2.6	167 (21.27)	423 (0.54)	62±23
A. stipes	53.9±189.9	131.4±279.1	322 (41.02)	42326 (54.07)	33±10
Bothus spp.	0.2±1.1	2.6±3.1	61 (7.77)	156 (0.2)	43±20
H. bivitattus	0.1±0.4	1.7±1.5	31 (3.95)	54 (0.07)	35±4
Harengula spp.	1.9±20.8	43.6±90.3	35 (4.46)	1527 (1.95)	37±7
Caranx spp.	0.1±0.9	2.7±3.1	40 (5.1)	106 (0.14)	79±14
Haemulon spp.	0.2±2.1	5.3±9.6	29 (3.69)	153 (0.2)	45±11
T. falcatus	0.2±2.6	8.8±15.1	18 (2.29)	158 (0.2)	56±28

Table 4.3 Environmental correlations (**A**) and residual correlations (**B**) estimated by the joint species distribution model (JSDM). Environmental correlations reflect the pairwise correspondence in species' response to environmental covariates, while residual correlations represent the correlation in species' abundance after accounting for the effects of environmental covariates. Significant values are bolded.

A.

	A. vulpes	A. goreensis	Eucinostomus spp.	S. barracuda	A. stipes	Bothus spp.	H. bivitattus	Harengula spp.	Caranx spp.	Haemulon spp.
A. goreensis	0.006									
Eucinostomus spp.	**0.694**	-0.045								
S. barracuda	**0.590**	-0.106	**0.732**							
A. stipes	-0.052	0.166	**-0.292**	-0.067						
Bothus spp.	**0.317**	-0.067	**0.523**	**0.278**	-0.077					
H. bivitattus	-0.292	-0.053	-0.211	-0.143	0.157	0.164				
Harengula spp.	0.181	0.237	-0.155	-0.095	**0.452**	-0.149	0.098			
Caranx spp.	0.208	0.244	0.119	0.223	0.238	-0.139	0.119	**0.307**		
Haemulon spp.	0.288	-0.251	**0.374**	**0.311**	-0.224	0.039	0.098	0.015	0.195	
T. falcatus	-0.158	**0.356**	**-0.396**	**-0.409**	0.303	**-0.317**	0.078	**0.572**	0.152	-0.190

B.

	A. vulpes	A. goreensis	Eucinostomus spp.	S. barracuda	A. stipes	Bothus spp.	H. bivitattus	Harengula spp.	Caranx spp.	Haemulon spp.
A. goreensis	**0.854**									
Eucinostomus spp.	**0.991**	**0.844**								
S. barracuda	**0.837**	0.599	**0.854**							
A. stipes	-0.110	-0.399	-0.075	0.441						
Bothus spp.	**0.907**	0.840	**0.911**	0.669	-0.352					
H. bivitattus	**0.768**	0.801	**0.756**	0.378	-0.629	**0.857**				
Harengula spp.	-0.029	-0.348	0.009	0.406	0.881	-0.200	-0.466			
Caranx spp.	**0.800**	0.633	**0.826**	**0.855**	0.186	0.699	0.558	0.216		
Haemulon spp.	**0.832**	0.628	**0.848**	**0.881**	0.263	0.745	0.586	0.437	0.755	
T. falcatus	**-0.905**	-0.795	**-0.912**	-0.714	0.281	**-0.876**	-0.825	0.046	-0.785	-0.778

Table 4.4 Partial correlations obtained by inversion of the residual correlation matrix (Table 4.3B, above) reflect conditional species relationships by controlling for the remainder of the species pool and are therefore considered the to reflect direct pairwise interactions. Significant correlations are bolded.

	A. vulpes	*A. goreensis*	*Eucinostomus spp.*	*S. barracuda*	*A. stipes*	*Bothus spp.*	*H. bivitattus*	*Harengula spp.*	*Caranx spp.*	*Haemulon spp.*
A. goreensis	0.692									
Eucinostomus spp.	**0.978**	0.663								
S. barracuda	**0.716**	0.234	**0.754**							
A. stipes	-0.033	-0.484	0.019	0.673						
Bothus spp.	0.774	0.671	**0.779**	0.348	-0.412					
H. bivitattus	0.555	0.658	0.523	-0.098	-0.749	0.744				
Harengula spp.	-0.051	-0.518	0.013	0.625	0.951	-0.324	-0.664			
Caranx spp.	0.589	0.281	0.642	0.801	0.414	0.359	0.156	0.370		
Haemulon spp.	0.646	0.255	0.675	0.826	0.491	0.453	0.213	0.617	0.570	
T. falcatus	-0.755	-0.568	-0.768	-0.416	0.303	-0.707	-0.675	0.092	-0.567	-0.528

Table 4.5 Asymmetrically-weighted residual (**A**) and partial (**B**) correlations (the effect of column on row) and the respective normalized weighted out-degree (nwD$_{out}$) for each taxon, used to construct the compositional networks depicted in Figure 4.2. Non-significant correlations (i.e., with 95% HPD intervals encompassing 0) have been assigned values of 0.

A.

	A. vulpes	*A. goreensis*	*Eucinostomus spp.*	*S. barracuda*	*A. stipes*	*Bothus spp.*	*H. bivitattus*	*Harengula spp.*	*Caranx spp.*	*Haemulon spp.*	*T. falcatus*
A. vulpes	0	0.045	0.974	0.44	0	0.095	0.013	0	0.098	0.058	0
A. goreensis	0.171	0	0.732	0	0	0	0	0	0	0	0
Eucinostomus spp.	0.115	0.023	0	0.245	0	0.102	0.041	0	0.053	0.047	-0.002
S. barracuda	0.15	0	0.706	0	0	0	0	0	0.061	0.063	0
A. stipes	0	0	0	0	0	0	0	0	0	0	0
Bothus spp.	0.089	0	0.806	0	0	0	0.042	0	0	0	0
H. bivitattus	0.025	0	0.634	0	0	0.083	0	0	0	0	0
Harengula spp.	0	0	0	0	0	0	0	0	0	0	0
Caranx spp.	0.14	0	0.64	0.256	0	0	0	0	0	0	0
Haemulon spp.	0.115	0	0.789	0.364	0	0	0	0	0	0	0
T. falcatus	0	0	-0.051	0	0	0	0	0	0	0	0
nwD$_{out}$	0.151	0.013	1	0.245	0	0.053	0.018	0	0.04	0.032	0

B.

	A. vulpes	*A. goreensis*	*Eucinostomus spp.*	*S. barracuda*	*A. stipes*	*Bothus spp.*	*H. bivitattus*	*Harengula spp.*	*Caranx spp.*	*Haemulon spp.*	*T. falcatus*
A. vulpes	0	0	0.961	0.377	0	0	0	0	0	0	0
A. goreensis	0	0	0	0	0	0	0	0	0	0	0
Eucinostomus spp.	0.114	0	0	0.216	0	0.087	0	0	0	0	0
S. barracuda	0.129	0	0.623	0	0	0	0	0	0	0	0
A. stipes	0	0	0	0	0	0	0	0	0	0	0
Bothus spp.	0	0	0.689	0	0	0	0	0	0	0	0
H. bivitattus	0	0	0	0	0	0	0	0	0	0	0
Harengula spp.	0	0	0	0	0	0	0	0	0	0	0
Caranx spp.	0	0	0	0	0	0	0	0	0	0	0
Haemulon spp.	0	0	0	0	0	0	0	0	0	0	0
T. falcatus	0	0	0	0	0	0	0	0	0	0	0
nwD$_{out}$	0.107	0	1	0.261	0	0.038	0	0	0	0	0

4.8 Figures
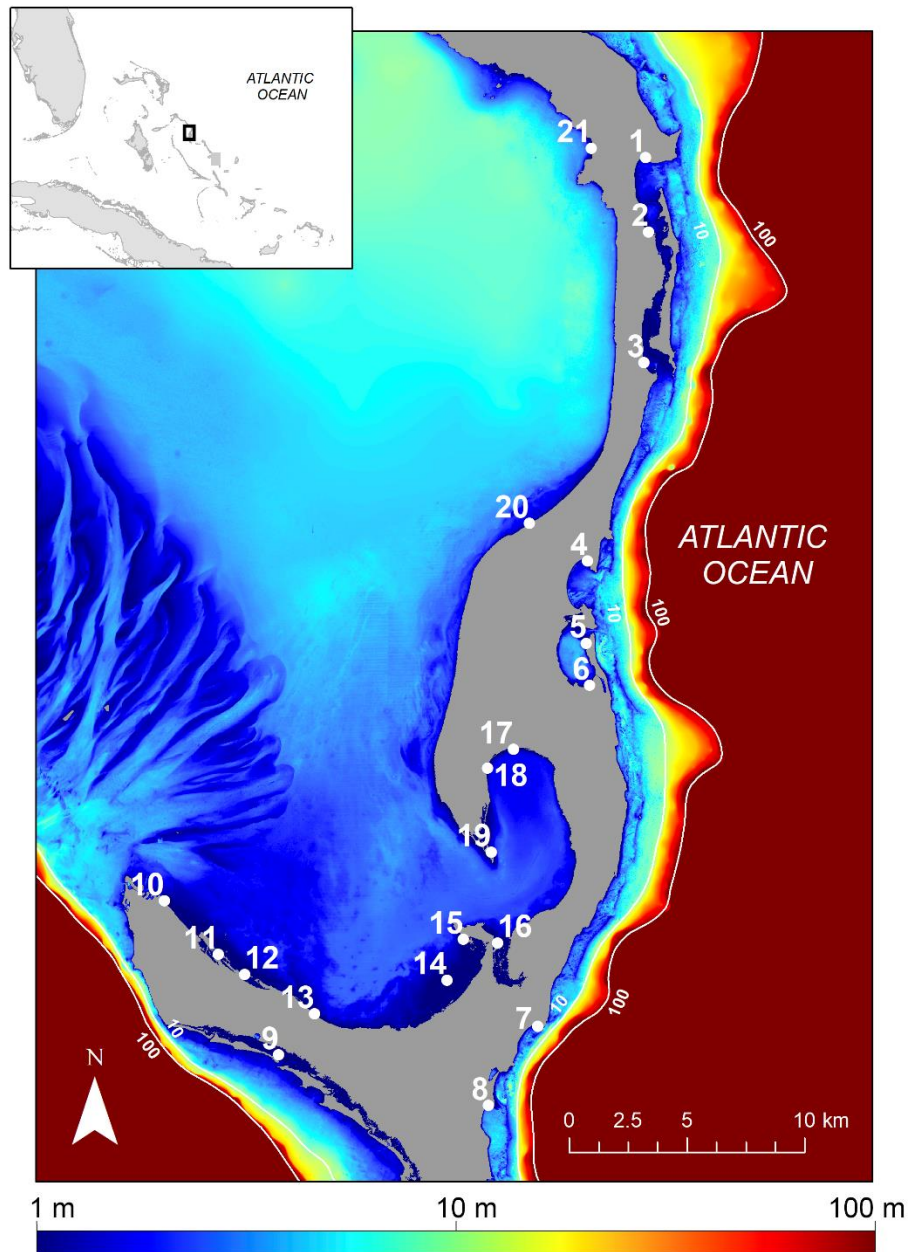
Figure 4.1 Map of the study area, depicting the locations of 21 stations where community abundance data was obtained by beach seine sampling. Grey shading signifies land, and the color gradient ramp represents $\log_{10}$ transformed bathymetry, measured in m, with minimum and maximum depths truncated to 1 and 100 m, respectively. The 10 m and 100 m isoclines are included for reference.

A.
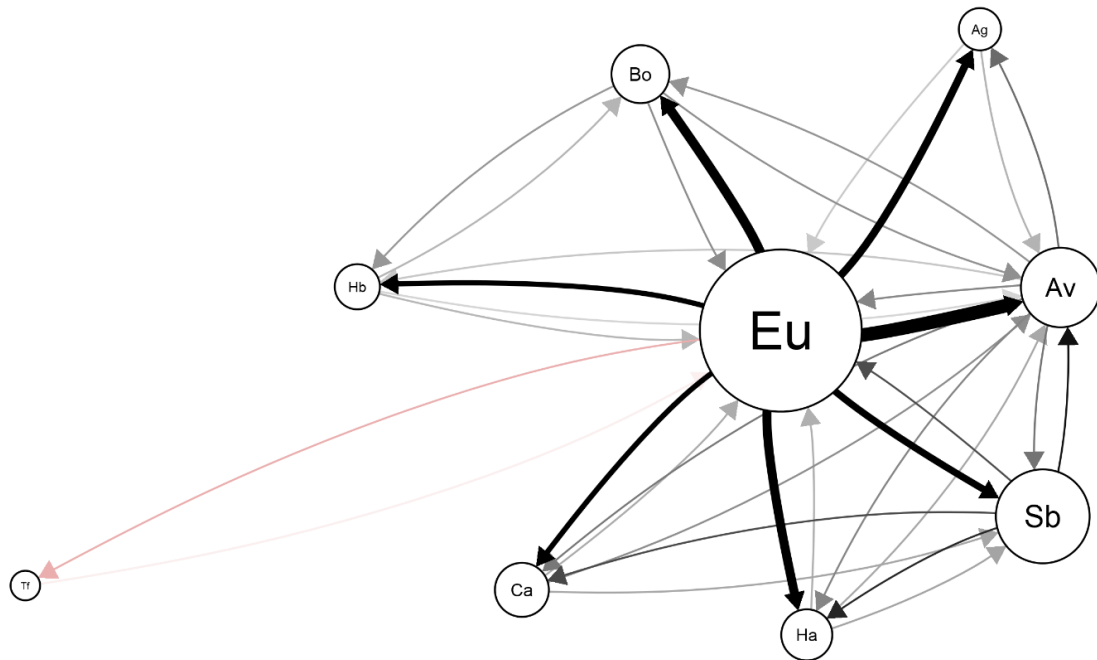
B.
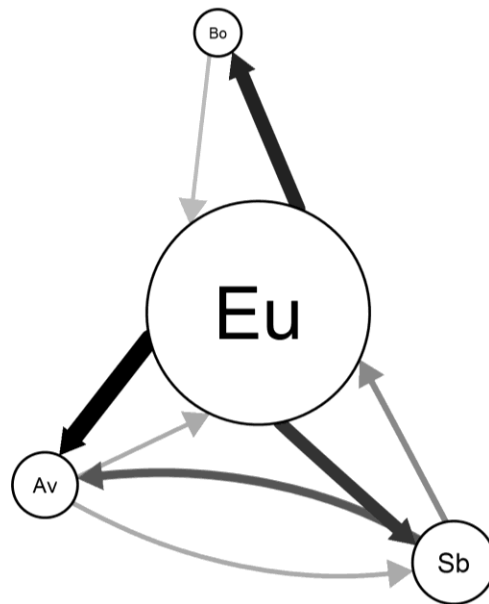
Figure 4.2 Compositional networks depicting asymmetrically-weighted residual correlations (**A**) and partial correlations (**B**) estimated by the JSDM. Nodes represent taxa, and directional edges (i.e., arrows) connecting nodes signify positive (black) or negative (red) pairwise associations. Edge widths and opacities are scaled to reflect asymmetric association strengths, and nodes are scaled by their respective normalized weighted out-degree (nwD_{out}), approximating their overall influence on assemblage structure. Taxa with no significant residual or partial correlations have been omitted. Taxa are abbreviated as follows: Av = *A. vulpes*, Ag = *A. goreensis*, Bo=*Bothus* spp., Ca= *Caranx* spp., Eu = *Eucinostomus* spp., Ha= *Haemulon* spp., Hb = *H. bivittatus*, Sb = *S. barracuda*, Tf = *T. falcatus*.

4.9 Video Legend S1

Video S1. Footage depicting *A. vulpes* and *S. barracuda* juveniles participating in mixed-species shoals with similarly-sized *Eucinostomus* spp., captured by remote underwater video surveys (RUVS) carried out as described in Appendix 4C. Distinct clips are designated by alphanumeric characters visible in the upper right-hand corner of the image and correspond to the accompanying timecodes and descriptions below.

A. (00:00:00 – 00:09:23) Several *S. barracuda* juveniles (1 individual background frame left, 3 individuals midground frame right) hover among a large group of *Eucinostomus* spp.

B. (00:10:00 – 00:19:23) A single *S. barracuda* juvenile (foreground, center frame) swims/drifts slowly towards frame left among a small group of *Eucinostomus* spp.

C. (00:20:00 – 00:24:23) An *S. barracuda* juvenile steady-swims across frame (from right to left) with a group of *Eucinostomus* spp.

D. (00:25:00 – 00:34:23) An *A. vulpes* juvenile among several *Eucinostomus* spp. enters from frame right and forages near the substrate in center frame (foreground).

E. (00:35:00 – 00:44:23) An *A. vulpes* juvenile among a large group of *Eucinostomus* spp. moves across frame from right to left.

F. (00:45:00 – 00:54:23) An *A. vulpes* juvenile and several *Eucinostomus* spp. jointly foraging as they move from frame right to frame left.

G. (00:55:00 – 00:59:23) Several concurrently foraging *A. vulpes* and *Eucinostomus* spp. (frame right, midground to background) display a synchronous flight response, abruptly burst-swimming in a uniform direction and with similar speeds, presumably reacting to a perceived threat beyond the camera's field of view. The inset located on the left half of the frame displays a 200% magnification of the area of interest.

4.10 Appendix 4A: Environmental Covariates

Selection and estimation of environmental covariates

Environmental covariates were chosen to comprise a broad suite of physical and biological predictors ranging from landscape to microhabitat scales. Gradients in hydrodynamic stress associated with wave or tide-driven water movement can influence fish distributions at a variety of spatiotemporal scales (Friedlander and Parrish 1998, Fulton and Bellwood 2005, Eggertsen et al. 2016). consequently, estimated wave and tide-driven flow velocities were obtained for sampling sites using high-resolution physical hydrodynamic models of the study area, as described in Haak et al. (2019). Hydrodynamic stress associated with waves was incorporated through two distinct covariates; spatial variability in wave-driven flow integrated over long timescales (i.e., years) was approximated as the 99th quantile bottom orbital velocity (the near-bed wave-induced water velocity parallel to the seafloor in the direction of dominant flow) predicted to occur at the location of each sampling event over a four-year time period encompassing the study, from Jan 1, 2010 to Jan 1, 2014, termed U_{max}. Spatio-temporal variability in wave-driven flow on finer timescales (i.e., days), likely to influence the outcome of discrete sampling events, was captured via a second covariate, temporal wave anomaly, or U_{anom24}, defined as the estimated deviation from long-term (4-year) mean bottom velocity at a sampling location in the 24 hours preceding each seine haul. Finally, spatial gradients in tidally-driven flow were expressed as the maximum predicted current velocity associated with the M_2 (principal lunar semidiurnal) tidal component estimated at a height of 5 cm above the substrate, termed U_{tide}, reflecting the typical velocities encountered on a diel (12.42 hour) basis. As the majority of fishes surveyed in the

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present work are bottom-associated, these metrics reflect flow conditions near the seabed, however in the shallow depths sampled they are nonetheless closely correlated with surface conditions.

Seasonal trends in the abundance of species, often related to reproductive periodicity or the timing of ontogenetic shifts, can lead to temporal variability in the composition of juvenile fish assemblages (Rooker and Dennis 1991, Mateo and Tobias 2004, Newman et al. 2007). Accordingly, season was included as a covariate, following the commonly used wet (May-Oct) and dry (Nov-Apr) season convention. Likewise, in shallow littoral zones such as those surveyed in the present study, pronounced spatiotemporal gradients in water temperature can exist, influencing patterns of habitat use and species distributions at multiple scales (Kupschus 2001, Harrison and Whitfield 2006, Murchie et al. 2011). Therefore, water temperature recorded at the approximate time and location of each sampling event was considered as an additional covariate.

Among the most commonly noted predictors of habitat association for demersal fishes, the presence or density of benthic vegetation, typically in the form of seagrasses, has been linked to the occurrence or abundance of a variety of juvenile fishes (Nagelkerken et al. 2000, Mateo and Tobias 2004, Nero and Sealey 2006). Thus, the proportional coverage of moderate-to-densely vegetated bottom within the sweep area of each seine haul, defined following Harborne et al. (2008) as seagrass (primarily *Thalassia testudinum,* often interspersed with macroalgae) standing crop densities of category 3 or greater on the visual scale presented by Mumby et al. (1997), was integrated as a predictor.

Shallow waters can serve as predation refugia for juvenile fishes by excluding larger piscivores (Ruiz et al. 1993, Paterson and Whitfield 2000), producing marked differences in relative predation risk over depth gradients of just tens of centimeters in habitats analogous to those surveyed in the present study (Rypel et al. 2007). As such, the estimated mean water depth encompassed by each seine haul was incorporated as a predictor by averaging the minimum and maximum water depths encountered. Likewise, several species of juvenile fishes exploit the physical structure provided by fringing mangroves as refugia (Laegdsgaard and Johnson 2001), and gradients in community composition and predation risk have been related to mangrove proximity (Jelbart et al. 2006, Newman et al. 2007, Hammerschlag and Serafy 2010). Hence, the distance to mangrove fringe, up to a maximum of 100 m, was considered as a predictor variable.

Connectivity with coral reef habitats can influence the structure of fish assemblages through a variety of mechanisms, with implications for the supply of recruits of reef-associated species as well as for the abundance of larger piscivorous predators (Shulman 1985, Kingsford and Choat 1989, Unsworth et al. 2008). Consequently, gradients in coral reef proximity have been linked to the distributions of juvenile fishes inhabiting shallow-water environments (Nagelkerken et al. 2000, Cocheret de la Morinière et al. 2002, Pollux et al. 2007). Therefore, the shortest swimming distance to coral reef habitat was estimated for each seine haul via a cost-distance function using Esri (Environmental Systems Research Institute, Redlands, CA) ArcGIS™, based on reef locations obtained from the 30 m spatial resolution United Nations Environment Programme-World Conservation Monitoring Centre global distribution of warm-water coral reefs database (UNEP-WCMC 2010).

Background levels of salinity and turbidity vary nominally across the habitats surveyed in the present study, which are all well-connected with relatively oligotrophic oceanic waters and receive nominal inputs from freshwater runoff and associated terrigenous sediments (Buchan 2000).   Accordingly, we did not quantify nor consider in variation in these factors.

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Tables

Table 4A-1. Summary statistics for continuous environmental covariates across all seine haul samples.

	Min	Max	Mean ± SD
U_{max} (cm s^{-1})	6.7	59.7	24.93±8.86
U_{anom24} (cm s^{-1})	-16.6	30.6	-0.5±5.87
U_{tide} (cm s^{-1})	0.1	28.9	3.7±5
Water Depth (cm)	8	107	46±23
Mangrove proximity (m)	0	100	57±44
Benthic vegetation cover (%)	0	100	25±39
Coral reef proximity (m)	100	11900	4053±3705
Water Temperature (°C)	21.0	36.0	28.6±3

4.11 Appendix 4B: Additional Tables

Table 4B-1. Raw co-occurrence matrix, displaying the proportion of all occurrences, and proportion of all individuals (in parentheses) of the taxon listed at the head of each row that occurred among the taxon listed at the head of each column.

	A. vulpes	A. goreensis	Eucinostomus spp.	S. barracuda	A. stipes	Bothus spp.	H. bivitattus	Harengula spp.	Caranx spp.	Haemulon spp.	T. falcatus
A. vulpes	1 (1)	0.053 (0.088)	0.982 (0.995)	0.526 (0.59)	0.404 (0.4)	0.105 (0.098)	0.018 (0.005)	0.07 (0.093)	0.123 (0.078)	0.07 (0.078)	0 (0)
A. goreensis	0.2 (0.115)	1 (1)	0.867 (0.846)	0.2 (0.154)	0.467 (0.5)	0.067 (0.077)	0.067 (0.077)	0 (0)	0.2 (0.269)	0 (0)	0.067 (0.115)
Eucinostomus spp.	0.116 (0.441)	0.027 (0.025)	1 (1)	0.286 (0.539)	0.402 (0.389)	0.112 (0.061)	0.054 (0.018)	0.039 (0.05)	0.064 (0.086)	0.056 (0.086)	0.002 (0)
S. barracuda	0.18 (0.215)	0.018 (0.012)	0.826 (0.872)	1 (1)	0.461 (0.499)	0.096 (0.08)	0.036 (0.026)	0.048 (0.033)	0.072 (0.121)	0.072 (0.071)	0.006 (0.002)
A. stipes	0.071 (0.021)	0.022 (0.009)	0.602 (0.543)	0.239 (0.285)	1 (1)	0.062 (0.054)	0.031 (0.011)	0.059 (0.071)	0.062 (0.059)	0.04 (0.012)	0.019 (0.016)
Bothus spp.	0.098 (0.128)	0.016 (0.006)	0.885 (0.897)	0.262 (0.276)	0.328 (0.237)	1 (1)	0.049 (0.032)	0.016 (0.026)	0 (0)	0.016 (0.006)	0 (0)
H. bivitattus	0.032 (0.019)	0.032 (0.019)	0.839 (0.87)	0.194 (0.241)	0.323 (0.315)	0.097 (0.074)	1 (1)	0.032 (0.019)	0.129 (0.093)	0.065 (0.074)	0 (0)
Harengula spp.	0.114 (0.063)	0 (0)	0.543 (0.599)	0.229 (0.409)	0.543 (0.783)	0.029 (0.001)	0.029 (0.012)	1 (1)	0.143 (0.065)	0.086 (0.06)	0.029 (0.033)
Caranx spp.	0.175 (0.123)	0.075 (0.057)	0.775 (0.802)	0.3 (0.321)	0.5 (0.377)	0 (0)	0.1 (0.047)	0.125 (0.057)	1 (1)	0.025 (0.009)	0 (0)
Haemulon spp.	0.138 (0.092)	0 (0)	0.931 (0.935)	0.414 (0.595)	0.448 (0.366)	0.034 (0.007)	0.069 (0.02)	0.103 (0.039)	0.034 (0.007)	1 (1)	0 (0)
T. falcatus	0 (0)	0.056 (0.025)	0.056 (0.013)	0.056 (0.057)	0.333 (0.468)	0 (0)	0 (0)	0.056 (0.038)	0 (0)	0 (0)	1 (1)

Table 4B-2. Coefficients (mean ± SD) relating species-specific abundance with environmental covariates, as estimated by the joint species distribution model. Significant relationships are bolded.

	U_{max}	U_{anom24}	U_{tide}	Water depth	Mangrove proximity	Benthic vegetation cover	Coral reef proximity	Water temperature	Season
A. vulpes	**-2.05 ±0.62**	**-1.46 ±0.42**	**-2.92 ±1.15**	-0.36 ±0.3	-0.38 ±0.34	**-0.98 ±0.29**	0.52 ±0.7	0.36 ±0.29	**1.57 ±0.56**
A. goreensis	1.08 ±0.66	0.13 ±0.5	-0.51 ±0.8	-0.15 ±0.59	-0.46 ±0.98	-1.36 ±0.87	-1.26 ±1.08	**1.2 ±0.61**	1.97 ±1.11
Eucinostomus spp.	**-0.54 ±0.19**	**-0.3 ±0.11**	**-0.48 ±0.22**	**-0.67 ±0.11**	**-0.49 ±0.15**	**-0.24 ±0.09**	0.18 ±0.33	**0.37 ±0.12**	**0.95 ±0.24**
S. barracuda	-0.33 ±0.22	-0.26 ±0.14	**-0.57 ±0.24**	-0.25 ±0.14	**-0.53 ±0.17**	**0.29 ±0.1**	-0.22 ±0.3	0.21 ±0.15	0.14 ±0.29
A. stipes	-0.04 ±0.21	-0.14 ±0.13	-0.22 ±0.2	**0.41 ±0.18**	-0.08 ±0.22	-0.09 ±0.14	**-0.65 ±0.26**	**-0.51 ±0.24**	-0.29 ±0.43
Bothus spp.	**-1.52 ±0.33**	-0.03 ±0.32	0.14 ±0.23	**-0.98 ±0.27**	-0.15 ±0.28	**-0.85 ±0.26**	**-0.89 ±0.34**	0.09 ±0.27	0.21 ±0.58
H. bivitattus	-0.17 ±0.45	-0.1 ±0.36	0.51 ±0.44	-0.87 ±0.45	0.39 ±0.48	**0.71 ±0.31**	**-1.15 ±0.59**	-0.68 ±0.47	-0.54 ±0.91
Harengula spp.	-0.19 ±0.81	0.04 ±0.61	**-2.92 ±1.34**	-0.63 ±0.78	1.95 ±1	-0.8 ±0.73	-0.67 ±1.13	**-2.08 ±0.86**	-2.2 ±1.57
Caranx spp.	-0.39 ±0.53	-0.48 ±0.28	**-1.73 ±0.88**	-0.47 ±0.35	-1.13 ±0.61	**0.7 ±0.29**	**-2 ±0.98**	-0.01 ±0.4	0.62 ±0.79
Haemulon spp.	-0.54 ±0.76	0.34 ±0.55	-0.47 ±0.79	-0.9 ±0.59	0.32 ±0.68	**1.38 ±0.41**	0.72 ±0.84	-0.46 ±0.58	-0.01 ±1.04
T. falcatus	**2.18 ±0.75**	0.07 ±0.43	-1.01 ±1.38	-0.72 ±0.8	1.88 ±1.42	-1.36 ±0.89	0.13 ±1.34	**-2.04 ±0.92**	-2.49 ±1.72

4.12 Appendix 4C: Remote Underwater Video Surveys

Data collection

To directly determine whether juvenile fishes co-occurring in seine hauls participated in mixed-species shoals, and to evaluate associational patterns and behaviors over the finer spatial scales at which information transfer is likely to occur, seining data was supplemented with remote underwater video surveys (RUVS). RUVS were carried out employing GoPro™ Hero 3 digital video cameras with a horizontal field of view of 114 °, recording at spatial and temporal resolutions of 1920 x 1080 pixels and 24 frames per second (fps), respectively. Preliminary range testing revealed that fish of sizes akin to those collected in seine hauls (~50 mm) could be correctly identified at distances approaching 2 m from the camera lens, resulting in an effective sampled area of approximately 4 m^2 of seabed (Figure 4C-1).

Surveys were conducted over three days in February of 2014 at two stations (17 and 18, as depicted in Figure 4.1 in main text) where seine sampling produced consistently high densities of the taxa exhibiting the strongest residual and partial correlations (*Eucinostomus spp., Albula vulpes, and S. Barracuda*). On each day, three recording units were deployed concurrently at distinct locations within shallow (10-30 cm water depth) sparsely-vegetated littoral zone habitats. Each unit was separated by a horizontal distance of at least 100 m. Cameras were moored to the substrate, aimed level to the horizon, and left to record for a minimum of 1 h before they were recovered, and video files archived for subsequent analysis.

Data analysis

Video files obtained from each camera deployment were reviewed independently in Adobe (Adobe Systems, San Jose, CA) After Effects™ image processing software, where qualitative and quantitative observations were undertaken. Substrate disturbance arising from the physical deployment of each camera produced high levels of turbidity that limited visibility in the initial periods of surveys, and thus the first 6.5 ± 4.3 min of each recording were excluded from analysis. Likewise, the final 3 min prior to camera retrieval were also omitted to account for potential disturbance caused by the approaching researcher.

For each taxon observed, a single time-series was generated reflecting its presence or absence in each frame of video for the duration of the recording; a taxon was considered present when one or more individuals were visible within the camera's field of view. To estimate the relative abundance of different fishes when they were detected in a recording, we used the MaxN index (Ellis and DeMartini 1995), defined as the maximum number of individuals of a taxon that are simultaneously visible in a single frame of video, thereby eliminating the potential for double-counting. Individuals of any taxon that were of a notably distinct size class or ontogenetic stage, distinguishable by marked differences in physical appearance and behavior, were logged separately from juveniles.

For each of the nine camera deployments, we produced a set of n (where n is the number of different taxa observed) parallel, longitudinal binary time series of equal length, with each series describing the presence/absence of a given taxon in each frame of video. The resulting nine sets of parallel time series were then converted to integer-range

sequences and analyzed in R with the IRanges package (Lawrence et al. 2013),

facilitating the calculation of summary statistics. Rare taxa, defined as those present for

less than 1% of total recording time (summed across all surveys) and occurring on fewer

than two distinct surveys, were excluded from further analyses. Using IRanges, the

duration of joint presence for each species pair occurring in each time series was obtained

by calculating their temporal intersection, or the number of video frames in which both

taxa were simultaneously visible in a given recording. This was then expressed as a

taxon-specific rate, dividing the observed duration of joint presence by the total duration

of time that a given taxon was present in a recording. The mean rate of joint presence of

each taxon with each other community member, averaged across all surveys in which

they jointly occurred, was assumed to be representative of the strength of species

associations.

Results & Discussion

Recording times varied from 69 to 147 min, with a mean duration of 115 ± 25

min, for a total observation time of 17.3 h summed across all 9 camera deployments. The

species composition of fish assemblages detected by RUVS (Table 4C-1) was similar to

that observed by seine sampling at the corresponding stations. *Eucinostomus* spp. was

the most ubiquitous taxon, detected by all 9 cameras, followed by *A. vulpes* and *S.*

barracuda, which occurred in 8 and 7 distinct surveys, respectively. *Atherinomorus*

stipes and *Haemulon* spp. were less common, captured by 3 and 2 cameras, while *Bothus*

spp. was completely undetected by RUVS, possibly a result of this taxon's cryptic

appearance and behavior.

Qualitative observation of recordings revealed that *A. vulpes*, *S. Barracuda,* and *Haemulon* spp. juveniles of the size classes collected by seine sampling co-occurred among much larger groups of similarly-sized *Eucinostomus* spp., typically as solitary individuals or in small conspecific groups (Video S1). Co-occurring heterospecifics of these taxa maintained equivalent vertical positions in the water column and typically occurred within several centimeters of each other, displaying physical proximities and behavioral responses (or a lack thereof) that were not discernably different from those between conspecifics. There was no obvious evidence of agonistic interactions among either conspecific or heterospecific juveniles of *A. vulpes*, *S. barracuda*, and *Eucinostomus spp*., and we identified no predator-prey interactions between juveniles of these taxa. In contrast, large groups of *A. stipes,* and several solitary predators including larger subadult *S. barracuda* and needlefishes (*Belonidae*), occupied markedly distinct vertical positions near the air-water interface, and approaching predators were actively avoided by other taxa. *Albula vulpes* and *Eucinostomus* spp. often foraged concurrently; on these occasions we documented no clear examples of conspecific or heterospecific individuals competing directly for a particular prey item, nor did we discern any instances of individuals exploiting specific prey items that had been located or flushed by others (i.e., "following and scavenging" behaviors, sensu Ormond (1980) and Lukoschek and McCormick (2000)). Rather, individuals of these taxa appeared to search independently for prey. No obvious foraging-related behaviors were visible among *S. barracuda* juveniles that occurred with eucinostomids.

The level of apparent organization and degree of coordinated movement among co-occurring conspecific and heterospecific group participants was variable and was

related to the types of general behaviors being exhibited. During periods of social foraging, shoals were loosely organized, with individuals oriented in and/or moving in seemingly random directions with respect to one another as they sought out and intermittently consumed benthic prey from the substrate (Video S1). Over longer timescales, however, members of these foraging groups tended to progress in a uniform direction relative to the camera. More closely-coordinated movements were frequent among non-foraging heterospecifics; both *A. vulpes* and *S. barracuda* were commonly seen steady-swimming alongside *Eucinostomus* spp. with uniform trajectories and speeds (Video S1). Likewise, several instances of coordinated flight response, with heterospecific group members burst-swimming synchronously in the same direction, were observed among *A. vulpes*, *S. barracuda*, and *Eucinostomus* spp. in the presence of predators.

Although the small number of independent observations (n=9) limited the potential for statistical inference using significance tests, quantitative analyses nonetheless elucidated some noteworthy patterns. Association strengths, as inferred from frequencies of joint presence (i.e., temporal overlap between taxa), varied markedly among fishes detected in RUVS (Table 4C-2). Across the 8 surveys in which they occurred for a total of 81.7 min, comprising 37 distinct individuals, *A. vulpes* juveniles displayed a 100% rate of joint presence with *Eucinostomus* spp. Likewise, of the 41.3 min that *S. barracuda* were present, corresponding to 17 individuals captured on 7 distinct recordings, more than 97% of this time (86 ± 38% on average) and all but a single individual coincided with the presence of Eucinostomids. Although much rarer, occurring on just 2 surveys for a total of 7.5 min, *Haemulon* spp. also exhibited a 100%

joint presence rate with *Eucinostomus* spp. For *A. stipes,* joint presence with

eucinostomids was less common and more variable, with a mean rate of $(46 \pm 40\%)$,

summing over 3 distinct surveys to 70% of the species total 26.5 min duration. Rates of

joint presence among the remaining taxa were comparatively low, rarely exceeding a

mean of 25%, and were markedly less consistent across surveys.

Estimates of mean conspecific group size and the relative abundance of co-

occurring taxa in RUVS, as estimated by MaxN, also correlated well with those obtained

by seining data (Table 4C-1). For the most gregarious taxa, *A. stipes* and *Eucinostomus*

spp., mean group sizes observed in RUVS were similarly interrelated but lower overall

than those estimated from seining data; this can be ascribed to the tendency of MaxN to

produce conservative estimates of group size (Campbell et al. 2015), particularly when

the physical size of shoals is large relative to area sampled by a camera. RUVS-derived

estimates of mean conspecific group size for the less ubiquitous associate taxa, *A. vulpes*,

S. barracuda, and *Haemulon* spp., were strikingly similar to those obtained in seining

data, falling consistently within ±1 individual.

Altogether, RUVS demonstrated clearly that juveniles of *A. vulpes* and *S.*

barracuda (the taxa correlated most closely with *Eucinostomus* spp. in JSDM results) did

in fact routinely, and in some cases exclusively, participate in shoals with *Eucinostomus*

spp. (Pitcher 1983), interacting at the fine spatial and temporal scales necessary for the

transfer of social or public information (Seppänen et al. 2007). The lack of any

perceptible competitive or agonistic interactions between these taxa over repeated,

independent surveys lends support to the notion that the relationships among these fishes

are for the most part commensal or facilitative in nature. Moreover, the notable absence

of "following and scavenging" behaviors suggests that such direct feeding-related advantages were not among the primary benefits obtained by group members. Instead, it seems probable that any interspecific exploitation of social information on resources more likely pertained to patch quality or the density of prey in a generalized area, as opposed to the location of individual prey items (Valone 1989). Furthermore, the lack of any distinguishable feeding-related behaviors by *S. barracuda* may indicate that foraging benefits are not among the primary drivers of association for this taxon.

The high rates of joint presence (i.e., temporal overlap) displayed by most fishes with *Eucinostomus* spp. can be attributed in part to eucinostomids' overall preponderance in RUVS. However, the unvarying 100% rate of joint presence between *A. vulpes* and *Eucinostomus* spp. consistently exceeded, by a substantial margin, the corresponding frequencies at which eucinostomids were present, suggesting it was not a result of chance. Likewise, the presence of *S. barracuda* was similarly, but somewhat less invariably, dependent upon the presence of *Eucinostomus* spp. These relationships stand in contrast to that of *A. stipes*, whose rate of joint presence with *Eucinostomus* spp. was comparatively low and markedly more variable. As such, the obligate or near-obligate frequencies that *A. vulpes* and *S. barracuda* were present among eucinostomids may be interpreted as evidence of organizational patterns comparable to those inferred from seining data by the JSDM, with strong positive yet largely asymmetrical relationships between these taxa and *Eucinostomus* spp., for whom reciprocal rates of joint presence were nominal.

Finally, the close correspondence in species composition, relative frequency of occurrence, and conspecific group size as estimated independently by RUVS and beach

seine sampling lends additional validity to the patterns of assemblage structure revealed

by seining data, indicating that despite its larger area, seine sampling provided an

accurate representation of shoal organization at finer spatial scales.

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Tables

Table 4C-1. Summary statistics describing the presence and relative abundance of juvenile fishes detected in remote underwater video surveys (n=9). MaxN was defined following Ellis and DeMartini (1995) as the maximum number of individuals of a taxon visible in a single frame of video, and provides an estimate of conspecific group size.

Species	# of surveys present	Duration present ± SD (min)	Total duration present (min)	Rate of presence ± SD	MaxN ± SD	Total MaxN (summed across surveys)
Eucinostomus spp.	9	79.7 ± 28.7	717.1	0.69 ± 0.18	44 ± 11	392
A. vulpes	8	10.2 ± 10.2	81.7	0.08 ± 0.08	5 ± 4	37
S. barracuda	7	5.9 ± 11.7	41.3	0.04 ± 0.08	2 ± 2	17
Haemulon spp.	2	3.8 ± 4	7.5	0.01 ± 0.01	4 ± 1	7
A. stipes	3	8.8 ± 8.4	26.5	0.02 ± 0.05	66 ± 20	199

Table 4C-2. Matrix depicting mean (±SD) taxon-specific rates of joint presence for co-occurring fishes observed in remote underwater video surveys. These reflect the relative rates at which the taxon listed at the head of each row was simultaneously detected within a camera's field of view with the taxon listed at the head of each column. High rates of joint presence are taken to be indicative of strong positive interspecific associations. The sample size, or the number of distinct surveys in which a given pair of taxa co-occurred, is displayed in parentheses below the estimated rate.

	Eucinostomus spp.	*A. vulpes*	*S. barracuda*	*Haemulon spp.*	*A. stipes*
Eucinostomus spp.	N/A	0.14 ± 0.16 (*n=8*)	0.05 ± 0.11 (*n=7*)	0.01 ± 0.03 (*n=2*)	0.02 ± 0.05 (*n=3*)
A. vulpes	1 ± 0 (*n=8*)	N/A	0.03 ± 0.05 (*n=7*)	0.01 ± 0.02 (*n=2*)	0 ± 0 (*n=3*)
S. barracuda	0.86 ± 0.38 (*n=7*)	0.24 ± 0.42 (*n=7*)	N/A	0 ± 0.01 (*n=2*)	0.15 ± 0.27 (*n=3*)
Haemulon spp.	1 ± 0 (*n=2*)	0.14 ± 0.04 (*n=2*)	0.35 ± 0.5 (*n=2*)	N/A	0.01 ± 0.02 (*n=2*)
A. stipes	0.46 ± 0.4 (*n=3*)	0 ± 0 (*n=3*)	0.33 ± 0.31 (*n=3*)	0.01 ± 0.01 (*n=2*)	N/A

Figures

Figure 4C-1. Diagram depicting the effective sampling area of GoPro™ Hero 3 cameras utilized for remote video surveys, approximated to be 4 m² based on an estimated horizontal field of view of 114° and maximum resolving distance of roughly 2 m from camera lens.

Area ≈ 4 m²

114°

2 m
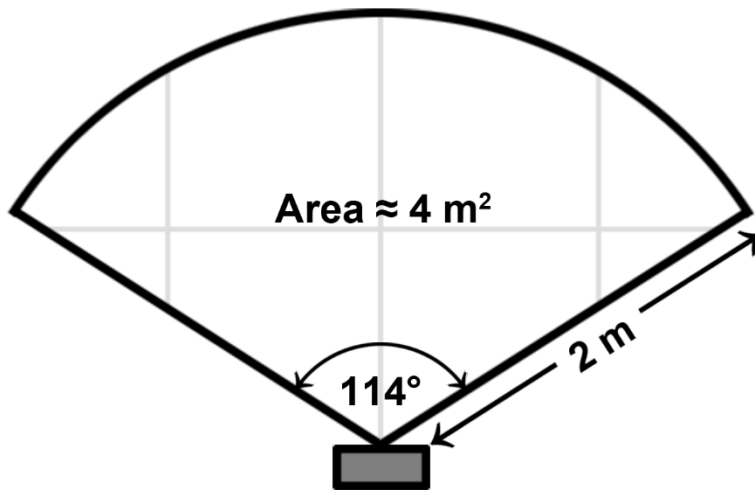
CHAPTER 5

ANTIPREDATOR VIGILANCE EXPLOITATION UNDERLIES THE STRONG POSITIVE INTERSPECIFIC RELATIONSHIP BETWEEN A NUCLEAR FISH *EUCINOSTOMUS* SPP. AND ITS CLOSE ASSOCIATE *ALBULA VULPES*

Haak, C. R., Power, M., and Danylchuk, A. J. (In Prep). Antipredator vigilance exploitation underlies the strong positive interspecific relationship between a nuclear fish *Eucinostomus* spp. and its close associate *Albula vulpes*. Behavioral Ecology.

5.1 Abstract

A growing body of work indicates that diminished predation risk is among the principal drivers of positive heterospecific association (interspecific sociality), with non-vigilant animals taking advantage of antipredator information produced by more vigilant ones, ultimately increasing their own fitness. However, access to risk-related social information is rarely considered by studies evaluating the adaptive advantages obtained by fishes in mixed-species groups, which tend to focus disproportionately on direct, food-related benefits. To assess the putative roles of antipredator social information and direct resource-related benefits in structuring mixed-species groups of fishes, we examined trophic niche overlap and relative vigilance levels as inferred from the foraging behaviors and activity levels of *Eucinostomus* spp. and its near-obligate associate, *A. vulpes.* Niche overlap, as determined by stable isotope analysis, was universally low, supporting previous work which suggested little evidence of agonistic interactions. Pronounced interspecific differences in $\delta^{34}S$ indicated that niche partitioning was mediated principally by differential inputs of benthic infauna sourcing sulfur from detrital sedimentary food webs, consistent with documented discrepancies in the functional morphology and

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sensory physiology of the two taxa. Quantitative behavioral analyses revealed clear

contrasts in foraging strategies, with the more active continuously-swimming search

strategy of *A. vulpes* implying markedly greater predation vulnerability than the passive,

intermittent search exhibited by *Eucinostomus* spp. Collectively, our findings suggest

that *A. vulpes* strong attraction to eucinostomids is unlikely to be related to direct food-

related benefits, but rather is driven by vigilance exploitation, which permits *A. vulpes* to

forage more aggressively while mitigating the risk of predation mortality.

5.2 Introduction

Animals that form groups obtain a variety of benefits that can ultimately increase

fitness and survival (Pavlov and Kasumyan 2000, Krause and Ruxton 2002, Ward and

Webster 2016). Several of these advantages arise directly through inherent physical or

statistical consequences of group participation; for example, access to prey that has been

flushed or uncovered by the actions of others (Aronson and Sanderson 1987, Strand

1988, Satischandra et al. 2007), reduced energetic costs of locomotion through the

exploitation of vortices produced by others (Weihs 1973, Weimerskirch et al. 2001,

Marras et al. 2015), or the decreased probability of attack (i.e., dilution of risk) when

among increased numbers of individuals (Hamilton 1971, Foster and Treherne 1981,

Beauchamp and Ruxton 2008). However, mounting evidence suggests that many

adaptive benefits of grouping behavior emerge less directly through social interactions, as

animals exploit behavioral, visual, aural, or chemical cues and signals produced by others

to inform their own decisions concerning shared resources or predators (Goodale et al.

2010, Schmidt et al. 2010, Gil et al. 2017)

Although sociality can be advantageous, the benefits of being in a group need to be weighed against potential costs (Rieucau and Giraldeau 2011). For instance, the close spatio-temporal proximity to ecologically-similar individuals that is required to obtain relevant information can also be conducive to increased resource competition (Seppänen et al. 2007). Due to this potential tradeoff, several works have suggested that the advantages gained through heterospecific group participation may in fact exceed those of monospecific group membership, based on the logical assumption that overlap in resource use, and thus competition, should be lower among heterospecifics than among conspecifics. (Morse 1977, Seppänen et al. 2007, Gil et al. 2017). The greater diversity of heterospecific groups has additional ramifications for the tradeoffs associated with group participation and the organization of mixed-species assemblages. Differences in the ability of various taxa to detect and communicate (advertently or inadvertently) information about predators or prey means that information transfer between heterospecifics can be heavily asymmetrical (Goodale and Kotagama 2005a, Magrath et al. 2009, Goodale et al. 2010). Correspondingly, the benefits accrued, and the costs incurred, as a result of group membership can likewise vary markedly across participants in both nature and degree, with species acting in fundamentally different roles (Hutto 1994, Hino 2000, Goodale and Kotagama 2005a, Srinivasan et al. 2010, Sridhar et al. 2013)

Species possessing traits that confer an exceptional ability to detect and reliably convey information on predators or resources should make particularly profitable partners and may be actively sought out by heterospecifics, and, in turn, have broad implications for group structure and community organization (Goodale et al. 2010, Sridhar et al.

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2013). Examples of such "nuclear" or "sentinel" species, sometimes referred to as "keystone informants" are common in avian mixed-species flocks, where they are often typified by unique foraging behaviors or sensory adaptations that correspond with an uncharacteristically high level of antipredator vigilance (Munn 1984, Goodale and Kotagama 2008, Sridhar et al. 2009). Conversely, species whose ecological traits correlate with heightened vulnerability to predation may stand to profit disproportionately from risk-related social or public information, and thus may experience greater selective pressures to take advantage of the collective vigilance of groups (Buskirk 1976, Thiollay and Jullien 1998, Beauchamp 2002). The resulting dynamic gives rise to predictable systems of organization, wherein more vulnerable taxa preferentially associate with more vigilant ones, in a pattern of "vigilance exploitation" that has been well-documented in mixed-species bird flocks (Sullivan 1984, Ragusa-Netto 2002, Sridhar et al. 2009), leading several recent works to conclude that access to risk-related information is the principal adaptive benefit driving heterospecific association in avian communities (Sridhar and Shanker 2014, Hua et al. 2016, Martínez and Robinson 2016).

Heterospecific groups are common among marine fishes (see Lukoschek and McCormick (2000) for review), and often involve putative "nuclear" or "leader" species that are joined by "associates" or "followers" whom are thought to derive benefits, principally in the form of enhanced foraging success, as a result of this relationship (Aronson and Sanderson 1987, Sikkel and Hardison 1992, Baird 1993). However, most works examining these "heterospecific foraging associations" have focused almost exclusively on the role of direct mechanisms, specifically the uncovering or flushing of prey due to physical disturbance caused by nuclear individuals ("following and

scavenging" *sensu* Ormond (1980)), in producing these benefits (Strand 1988, Sazima et al. 2007, Krajewski 2009), with little consideration given to the role of antipredator vigilance (but see Overholtzer and Motta (2000)). Yet recent work demonstrates that sociality and its implications for the perceived risk and individual behavior of coral reef fish can also bring about enhanced foraging success through less direct means (Brandl and Bellwood 2015, Gil and Hein 2017).

Several juvenile fishes that inhabit subtropical littoral zones display exceptionally strong positive, and heavily asymmetric (one-sided) associations with like-sized *Eucinostomus* spp. (mojarras), giving rise to heterospecific shoals whose organization is influenced disproportionately by this seemingly "nuclear" taxon (Chapter 4). Although many of their "associate" species share a mutual foraging guild with eucinostomids, qualitative observations of jointly-foraging individuals revealed very little in the way of competitive or agonistic interactions, and scant evidence of following, scavenging, or area-copying behaviors that would indicate the exploitation of flushed prey items, suggesting that direct food-related benefits play a negligible role in explaining these relationships (Chapter 4). Rather, the apparent attractiveness of *Eucinostomus* spp. has been attributed to this taxon's singularly high propensity for information detection and production, stemming from its gregariousness, distinctive sensory physiology, and foraging ecology that is conducive to maintaining an uncharacteristically high level of antipredator vigilance (Chapter 4).

Of the species that associate with *Eucinostomus* spp., *Albula vulpes* (bonefish) juveniles exhibit by far the strongest relationship, co-occurring among eucinostomids with near-obligate consistency (Haak et al. 2019, Chapter 4). Moreover, qualitative

observations of *A. vulpes* foraging in the presence of *Eucinostomus* spp. identified striking contrasts in the species' respective foraging modes concomitant with broad ecological differences (Huey and Pianka 1981), particularly with respect to antipredator awareness and susceptibility to predation, with the behaviors displayed by *A. vulpes* connoting a comparatively high degree of vulnerability that is likewise associated with a propensity for group participation (Chapter 4). When considered in light of the strong asymmetry in vulnerability implied by their behavioral discrepancies, the habitual association of *A. vulpes* with *Eucinostomus* spp. appears consistent with patterns of vigilance exploitation and the use of risk-related social information commonly described in heterospecific bird flocks.

A closer investigation of the mechanisms underlying the relationship between these fishes presents an opportunity to evaluate fundamental assumptions and hypotheses regarding the adaptive benefits and associated tradeoffs that promote heterospecific association and ultimately structure mixed-species groups of fishes. To examine the potential for competition between *A. vulpes* and *Eucinostomus* spp. while assessing the hypothesis that redundancy in resource use between closely-associating heterospecifics should be minimal, we apply stable isotope analyses, approximating niche space in three dimensions to obtain a holistic assessment of trophic overlap. In addition, we employ video-based analyses of jointly-foraging individuals of these taxa to quantify interspecific differences in foraging behavior and evaluate the hypothesis (based on past qualitative observation) that *A. vulpes* and *Eucinostomus* spp. are characterized by divergent foraging strategies associated with differential levels of antipredator awareness and/or predation vulnerability. Furthermore, we integrate the results of behavioral and isotopic

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analyses to elucidate the likely factors that mediate resource partitioning between the species. In keeping with the lack of agonistic interactions described elsewhere, we expected that *A. vulpes* and *Eucinostomus* spp. would demonstrate limited isotopic/trophic niche overlap, partitioning resources in a manner that can be explained by fundamental differences in their sensory physiology and functional morphology. Likewise, consistent with the hypothesis of vigilance exploitation by *A. vulpes*, we predicted that that the two taxa would display quantifiably distinct foraging strategies commensurate with disparate levels of antipredator awareness and predation vulnerability, with *Eucinostomus* spp. characterized by behaviors that implied (based on existing theory) a markedly greater capacity for vigilance-keeping.

5.3 Methods

5.3.1 Niche overlap from Stable Isotopes

Stable isotope analysis of animal tissues (SIA) can be a powerful tool for evaluating resource utilization and the trophic dynamics of fishes (Peterson and Fry 1987, Post 2002, Layman et al. 2012), providing an assessment of the basal carbon sources assimilated by an animal and its relative trophic position integrated over timescales on the order of weeks to months (Hesslein et al. 1993, Herzka 2005, Vander Zanden et al. 2015). As such, the "isotopic niche" of an individual may be considered largely reflective of its dietary niche (Bearhop et al. 2004, Newsome et al. 2007, Jackson et al. 2012), permitting interspecific comparisons of resource utilization. Accordingly, stable isotope ratios in carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) have been employed extensively to examine resource partitioning and niche overlap among sympatric fishes (Bootsma et al. 1996, Woodland and Secor 2011, Mumby et al. 2017). However, similarities in $\delta^{13}C$

and/or $\delta^{15}N$ among distinct producers can obscure differences in resource use, potentially leading to erroneous assessments of niche overlap. In such cases, sulfur stable isotope ratios ($\delta^{34}S$) can facilitate discrimination between trophic resources that might otherwise be indistinguishable using the traditional dual-element ($\delta^{13}C$ and $\delta^{15}N$) approach (Peterson et al. 1985, Connolly et al. 2004). Because it reflects the relative importance of sedimentary detrital versus pelagic food webs, $\delta^{34}S$ has proven to be particularly valuable for evaluating resource use in benthivorous fishes such as those studied here (Thomas and Cahoon 1993, Croisetière et al. 2009, De Brabandere et al. 2009). Accordingly, we employed a trivariate approach to quantify niche overlap based on $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ recorded in the muscle tissue of *A. vulpes* and *Eucinostomus* spp.

5.3.1.1 Sampling and laboratory protocols

Co-occurring juvenile *A. vulpes* (n=46) and *Eucinostomus* spp. (n=30) were collected in 19 distinct seine hauls conducted in two sheltered embayments located on the banks-facing (west) and Atlantic (east) coasts of Eleuthera island (labeled A & B, respectively, in Figure 5.1) in The Bahamas between February 2012 and November 2015, using methods described in Haak et al. (2019). Full specimens were frozen and stored at -20° C for laboratory processing at a later date. Subsequent processing involved the thawing of individuals, weighing, measurement to the nearest 1 mm fork length (FL), and the extraction of muscle tissue from the dorsal region. Tissue samples were then dried, homogenized and prepared for SIA as described in Murchie et al. (2018). Analyses of $\delta^{13}C$ and $\delta^{15}N$ were carried out as outlined in Murchie et al. (2018) on a Delta Plus Continuous Flow Stable Isotope Ratio Mass Spectrometer (Thermo Finnigan, Bremen, Germany) coupled to a Carlo Erba elemental analyzer (CHNS-O EA1108, Carlo Erba,

Milan, Italy). Analyses of δ^{34}S were completed on an Isochrom Continuous Flow Stable

Isotope Ratio Mass Spectrometer (GV Instruments, Micromass, Manchester, UK)

coupled to a Costech Elemental Analyzer (CNSO 4010, Costech Analytical Technologies

Inc., Valencia, USA). Internal laboratory standards were calibrated against the

International Atomic Energy Agency standards CH6 for δ^{13}C, N1 and N2 for δ^{15}N, and

SO-5, S1 and S2 for δ^{34}S and were run as controls to ensure the continued accuracy of all

measurements (± 0.2 ‰ for δ^{13}C, ± 0.3 ‰ for δ^{15}N, and ± 0.5 ‰ for δ^{34}S in organic

material). Stable isotope ratios are presented using delta notation (δ), expressed as permil

deviation (‰) relative to the standards of Vienna Peedee Belemnite (VPDB),

atmospheric nitrogen, and Vienna-Canyon Diablo Troilite (VCDT) for δ^{13}C, δ^{15}N, and

δ^{34}S, respectively.

5.3.1.2 Statistical analyses

Isotopic contrasts and estimates of niche overlap were conducted independently

for fishes from each embayment. This was deemed appropriate because previous works

identified substantial differences in the isotopic composition of *A. vulpes* inhabiting the

two embayments where specimens were obtained (Murchie et al. 2018), and because of

the nearly 100 km minimum swimming distance separating the sites, making inter-

embayment connectivity extremely unlikely for the small juveniles studied here.

To estimate isotopic niche overlap between taxa considering the full suite of

isotopes simultaneously, we used the techniques developed in the R package

nicheROVER (Swanson et al. 2015). NicheROVER integrates uncertainty through a

Bayesian framework to obtain a posterior distribution and subsequently approximate the

niche region encompassing a specified proportion of the population of each taxon in

isotopic space, corresponding in the present case to 3-dimensional ellipsoids within which any given individual has a 40% (core niche, sensu Jackson et al. (2012)) or 95% (total niche) probability of occurring. The overlap between each taxon's respective niche is then estimated using a probabilistic approach, by obtaining the likelihood that a randomly selected individual of one species will fall within the respective niche region (i.e., 40% or 95% ellipsoid) of the other species, and vice-versa. As such, nicheROVER provides asymmetric or directional (i.e., species-specific) estimates of niche overlap that include error via credible intervals and are likewise robust to variation in sample size. For these analyses, we used the default (uninformative) prior, and 10,000 samples drawn from the posterior distribution.

For distinct elemental comparisons between taxa, we used linear-mixed models (LMMs) describing observed isotope ratios as a function of Species. To control for the potential influence of fish size on isotopic composition, we considered Length (FL) as an explanatory covariate in all models, likewise including a Species:Length interaction to allow the effect of length to vary across species. Furthermore, to account for the possibility of interdependence among individuals collected together in the same seine haul (i.e., cluster sampling bias, Nelson (2014)), we included a random intercept term at the level of seine haul. Models were reduced via backward stepwise selection, conducted by comparing nested models using likelihood ratio tests with single-term deletions of fixed effects, and p-values for coefficients were obtained based on Satterthwaite-approximated degrees of freedom using the R package lmerTest (Kuznetsova et al. 2017).

5.3.2 Foraging Behavior

The physical activities, sensory demands, and habitats associated with the search for, capture, and ingestion of prey are often largely incompatible with those that facilitate the detection or avoidance of predators, leading to a well-documented tradeoff between energy gain (i.e., foraging) and predation risk (Milinski 1986, Lima and Dill 1990, Houston et al. 1993). Nonetheless, some foraging strategies and their associated behaviors are fundamentally more (or less) conducive to balancing the conflicting requirements of maintaining antipredator vigilance and feeding (O'Brien et al. 1990, McAdam and Kramer 1998, Kramer and McLaughlin 2001), consequently influencing an animal's potential value as an informant (Sridhar et al. 2009, Goodale et al. 2010) or, conversely, its propensity to exploit the vigilance of others (Buskirk 1976, Thiollay and Jullien 1998).

Foremost among the behavioral traits that can influence the vulnerability of foraging animals is activity level, as the increased conspicuity associated with heightened rates of movement can stimulate detection by predators (Woodward 1983, Skelly 1994, Martel and Dill 1995). Moreover, the larger areas searched by animals that vigorously seek out food may serve to elevate not only prey encounter rates but those with predators as well (Norberg 1977, Huey and Pianka 1981). Heightened activity in the form of increased feeding or strike rates can also have negative implications for predator detection efficiency and thus the risk of predation mortality (Milinski 1984, Godin and Smith 1988). In contrast, animals that display lower activity levels or that spend more time at rest are less likely to draw attention from predators, and typically experience diminished rates of attack (Woodward 1983, Skelly 1994, Martel and Dill 1995).

Furthermore, pauses in locomotion can yield perceptual advantages by aiding in the recognition of sensory stimuli (Kramer and McLaughlin 2001). Consequently, foragers that move in an intermittent or "saltatory" manner are thought to maintain relatively high levels of antipredator awareness, experiencing diminished risk while feeding (McAdam and Kramer 1998, Kramer and McLaughlin 2001, Trouilloud et al. 2004). Accordingly, to elucidate species-specific differences in the foraging strategies of *A. vulpes* and *Eucinostomus* spp. that implied differential levels of vigilance and predation vulnerability, we quantified behavioral traits that reflected these aspects of activity.

5.3.2.1 Behavioral observations

Behavioral data were obtained by reviewing high-definition imagery captured by remote underwater video surveys (RUVS), carried out as described in Haak et al. (2019). Video was captured using GoPro™ Hero 3 (San Mateo, California) digital video cameras with a spatial resolution of 1920 x 1080 pixels recording at a rate of 24 frames per second (fps) and sampling an effective area of approximately 4 m^2 of seabed. On each of three days in February 2014, three recording units were deployed concurrently in shallow (< 0.3 m), sparsely-vegetated littoral zone habitats within embayment B (Figure 5.1), separated by a horizontal distance of at least 100 m. Cameras were oriented level to the horizon and left in place to record for a minimum of 1 h before they were recovered. Video recordings obtained from the respective surveys were then screened and analyzed using Adobe (Adobe Systems, San Jose, CA) After Effects™ image processing software.

Behavioral analyses were limited to recordings where at least one individual of both *A. vulpes* and *Eucinostomus* spp. was observed to engage in a feeding event. Because the invertebrate prey consumed by these fishes are typically small, cryptic, and

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unlikely to be resolved by video recordings, feeding events were identified based on "strikes" on benthic substrates (i.e., sand or vegetation), evidenced in both taxa by conspicuous and clearly-discernable behaviors which are described in detail below. Due to the relative rarity of *A. vulpes* compared to *Eucinostomus* spp. in recordings, instances of *A. vulpes* feeding were identified first, followed by examples of feeding by eucinostomids that occurred in close temporal proximity (i.e., typically seconds, at most a few minutes) of feeding *A. vulpes*.

Foraging individuals were then screened against a set of criteria designed to confine our analyses to fishes whose dominant direction of movement and position relative to the camera minimized the inaccuracies or ambiguities that arise due to the limitations and biases inherent when inferring three-dimensional (3-D) motion from two-dimensional (2-D) imagery such as monoscopic (single-camera) video footage. For example, due to obvious shortcomings in the utility of 2-D (i.e., x, y) imagery to accurately assess movement in the z-axis (i.e., directly towards or away from the lens, parallel to the camera's direction of view), we limited consideration to individuals whose movement occurred primarily along the x and y axes, where it could be reliably measured. Likewise, to minimize the effects of camera-subject distance and perspective on apparent velocity as measured at the image plane (i.e., in x, y pixel space), we limited evaluation to individuals who spent the majority of their recorded duration within a relatively narrow range of distances from camera (i.e., z-depths), omitting those in very close proximity to (< ~ 0.25 m), or distant from (> ~ 1 m) the lens. Finally, subjects that were obscured from view by other fish or benthic vegetation for extended periods (> 5 seconds) were omitted.

Of the individuals meeting the above constraints, the foraging behaviors of all *A. vulpes* and a randomly-selected subset of *Eucinostomus* spp. were evaluated using motion analysis. In After Effects, a path depicting the motion of each individual was generated by placing a series of "keyframes" at its sequential positions in 2-D (x, y) pixel coordinate space, using the fish's eyeball as a reference point, for the duration it was visible within the camera's field of view (FOV). Keyframes were spaced adaptively, at intervals not exceeding 12 frames (0.5 s) and as small as a single frame, to ensure that rapid or complex movements were well-resolved. When individuals were briefly occluded (for < 5 seconds) when passing behind objects such as other fish or benthic vegetation, their position at intermediate keyframes was linearly interpolated. From the resulting motion paths or time-series of 2-D coordinates, the distance (in pixels) traveled by an individual between every two consecutive keyframes was approximated and then divided by the length of the corresponding time interval, producing a time series of velocity magnitudes (measured in pixels s^{-1}). Finally, a second time series was generated for each individual, recording to the nearest frame (0.04167 s) the moment of each discernable strike or prey capture attempt on benthic substrates.

From the resulting data, we generated three metrics reflecting distinct and complementary aspects of foraging activity. The faster or more frequent movements characteristic of an active search for prey equate with a larger area searched per unit time (Eklöv 1992); consequently, a more active forager should transit a predefined area more rapidly (on average) than a comparatively passive one. Following this assumption, we calculated the total amount of time an individual was present within the camera's FOV, (i.e., the temporal duration of its corresponding motion path, in seconds), termed "Transit

time", which served as a proxy for overall activity level. Furthermore, to evaluate differences in the activity and movement patterns exhibited by a fish while it was present within the camera's FOV, we estimated the proportion (percentage) of Transit time that each individual was at rest (i.e. not detectably moving with respect to the environment), termed "Time at Rest". We considered an individual to be at rest when its mean velocity magnitude during a given time interval (i.e., between two consecutive keyframes) did not exceed 1 pixel frame^{-1} (i.e., a distance corresponding to roughly 0.0125 % of the camera's horizontal FOV per 1 s). Finally, we determined the strike rate for each individual by dividing their total observed number of strikes by their total transit time.

5.3.2.2 Statistical analyses

Behavioral characteristics were compared between species using regression models. In the case of the continuous responses Transit time and Strike rate, we used linear regression models describing Log-transformed dependent variables as a function of Species, via the R package lme4 (Bates et al. 2015). When dependent variables took the form of proportional data with values between 0 and 1 (e.g., Time at rest), beta regression models with a variable (species-specific) dispersion component were employed, using the R package betareg (Cribari-Neto and Zeileis 2010). Additionally, to elucidate basic differences in the way that the two species integrated locomotion in the act of foraging, we modeled the relationship between Strike rate and Time at rest across the two species. For all models, we considered Survey as a supplemental fixed covariate to account for any differences in environmental conditions that may have introduced dependency in the behaviors displayed by individuals at the level of each recording. Furthermore, to allow for species-specific differences in reaction to environmental variation, a Species:Survey

interaction term was included. Reduced models were selected using backward elimination via likelihood ratio tests with single-term deletions.

5.4 Results

5.4.1 Isotopic niche overlap

Overall, SIA indicated low to moderate levels of isotopic niche overlap, occurring primarily in the outer margins of the species respective niche volumes (Figure 5.2). In embayment A, the mean directional total (i.e., 95%) niche overlap of *A. vulpes* on *Eucinostomus* spp. (i.e., the probability that a randomly-selected *A. vulpes* fell within the 95% niche region of *Eucinostomus* spp.) was 40.42% (95% credible interval (CI) = 20.45 – 63.75), nearly equivalent to the estimated overlap of *Eucinostomus* spp. on *A. vulpes* (37.83%, 95% CI = 18.70 – 60.12). Total niche volumes were typically smaller, and overlaps less symmetrical, in embayment B, where the probability of overlap for *A. vulpes* on *Eucinostomus* spp. (22.04%, 95% CI = 7.48 – 43.80) was less than half the probability of overlap in the opposite direction (56.14 (95% CI= 23.90 – 84.87). Corresponding probabilities of core (40%) niche overlap were universally low across both sites. In embayment A, the mean core overlap of *A. vulpes* on *Eucinostomus* spp. was just 5.59% (95% CI = 0.61 – 15.72), similar to that of eucinostomids on *A. vulpes* (9.62%, 95% CI = 2.83 – 19.88). Core overlaps in embayment B were even smaller, with the mean of 4.60% (95% CI = 0.94 – 11.61) for *A. vulpes* on *Eucinostomus* spp. comparable to the reciprocal overlap of *Eucinostomus* spp. on *A. vulpes* (3.70 (95% CI= 0.05 – 16.6).

Resource use (as inferred from isotopic composition) varied between embayments, however some species-specific differences were consistent across both sites

(Tables 5.1 and 5.2). Most notably, muscle tissue from *Eucinostomus* spp. was significantly more depleted in ^{34}S (by approximately 4‰) than that of *A. vulpes* in both embayments ($F_{1,39} = 29.504$, $p < 0.00001$ for embayment A, $F_{1,30} = 11.054$, $p = 0.00232$ for embayment B), likely evidencing a greater contribution of isotopically-lighter sulfides produced by bacterial reduction in benthic sediments (Peterson et al. 1986, Fry and Chumchal 2011). Conversely, although only statistically significant in embayment A ($F_{1,9} = 75.141$, $p < 0.0001$), the muscle of *Eucinostomus* spp. was enriched in ^{13}C by roughly 1‰ in both embayments compared to that of *A. vulpes*, likely evidencing greater inputs of carbon from isotopically-heavy benthic primary producers. No significant interspecific differences were detected for δ^{15}N in either embayment, suggesting that both taxa occupied similar trophic levels.

5.4.2 Behavioral analyses

Examples of joint foraging behavior were discernable in 6 of the 9 recordings, comprising all 3 survey dates. However, strong near-bed orbital water movement associated with high levels of wave-induced turbulence during one of these days introduced frequent and large involuntary excursions to the position of individuals, precluding reliable inferences about activity level based on motion paths. As such, recordings from this day were omitted from consideration and quantitative analyses were based on *A. vulpes* and *Eucinostomus* spp. present in recordings obtained from three distinct cameras during the two remaining survey days. Of these, a total of 20 *A. vulpes* and 33 *Eucinostomus* spp. occurrences met the criteria established above and were employed in detailed motion analyses (Table 5.3).

From a qualitative perspective, the locomotor patterns displayed by foraging *Eucinostomus* spp. and *A. vulpes* were clearly different, suggesting fundamentally disparate strategies for the location and capture of prey (refer to Video Appendix 1 for examples). Eucinostomids moved in a stop-and-go manner, remaining stationary in an upright posture for long periods that were punctuated by occasional, isolated strikes at the substrate or short repositioning movements. Prey capture in eucinostomids was characterized by a sudden and swift forward pitch rotation that oriented the head towards the substrate, followed immediately by a single rapid protrusion of the mouthparts into the benthic sediments and a subsequent return to an upright position, where sediment was frequently expelled from the mouth and/or gills in a pattern consistent with that described by others (Zahorcsak et al. 2000, Sazima 2002, Parmentier et al. 2011). In contrast, foraging *A. vulpes* swam continuously in a seemingly random search pattern, slowing or pausing only when they appeared to sense the presence of a potential prey item. The presumable detection of prey by *A. vulpes* elicited a transition to a notably more head-down posture, with the fishes' snout nearly contacting the sediment, suggesting a narrowed focus on benthic substrates that was sustained until the prey was located and captured, often via several consecutive, closely-spaced strikes.

The results of reduced regression models supported the qualitative observations, with clear evidence of interspecific contrasts across all activity metrics (Tables 5.4 and 5.5), highlighting marked distinctions in the foraging behavior of the two species. The fixed covariate Survey did not contribute appreciably to explaining variation in any of the response variables, nor did its interaction with Species, indicating that observed patterns of behavior were insensitive to variation in environmental conditions across distinct

camera deployments. The mean (±SD) Transit time, or time required to traverse the

camera's FOV, for *Eucinostomus* spp. (64.61 ± 39.68 s) was more than three times that of

A. vulpes (21.91 ± 12.04 s), constituting a highly significant difference ($F_{1,51}$ = 37.447, R^2

= 0.412, P < 0.00001), and suggesting that *A. vulpes* searched a larger area per unit time

than *Eucinostomus* spp. Interspecific differences in Time at rest were of a similar

magnitude, with the mean for *Eucinostomus* spp. (69.58 ± 9.58%) representing roughly

three times that of *A. vulpes* (20.77 ± 12.74%), another highly significant difference (χ^2 =

50.779, *df*=1, pseudo-R^2 = 0.7097, P < 0.00001). Strike rates likewise differed greatly

between species ($F_{1,51}$ = 122.85, R^2 = 0.7009, P < 0.00001), with *A. vulpes* engaging in a

prey capture attempt once every 3 seconds on average (0.3002 ± 0.1640 strikes s^{-1}), more

than six times as often as *Eucinostomus* spp. (0.04944 ± 0.02479 strikes s^{-1}), which struck

approximately once every 20 s.

Strike rate was a strong predictor of Time at rest for both *A. vulpes* and

Eucinostomus spp. (χ^2 = 70.636, *df*=2, pseudo-R^2 = 0.8032, P < 0.00001), but the

direction of this relationship differed between taxa (Table 5.6, χ^2 = 42.286, *df*=1, P <

0.00001). In the case of *Eucinostomus* spp., these variables were inversely correlated,

with increased strike rates linked to reductions in Time at rest, a correspondence one

might intuitively expect (Figure 5.3). However, the correlation was reversed in the case

of *A. vulpes,* among whom higher strike rates were associated with increased Time at

rest; in other words, *A. vulpes* engaging in more frequent prey capture attempts spent a

greater proportion of time at near-zero velocities. The underlying cause of this

unexpected relationship became evident upon inspection of typical velocity profiles for

the two taxa (Figure 5.4). For *Eucinostomus* spp., which spent the majority of their time

at rest, strike behavior involved a marked increase in rates of movement; however, relative to the continuous steady swimming that characterized *A. vulpes'* search for prey, their behavior during prey capture amounted to a notable decline in movement rate. Thus, while the moments surrounding a strike typically represented the periods of most vigorous activity for *Eucinostomus* spp., they constituted the lowest activity levels for *A. vulpes*, explaining this somewhat paradoxical relationship.

5.5 Discussion

Our results revealed clear differences in resource use and evidence of niche partitioning between *A. vulpes* and *Eucinostomus* spp., accompanied by correspondingly strong discrepancies in foraging behavior and activity level between to the two taxa. In both cases, observed differences were well-explained by documented differences in the two taxa's functional morphology and sensory physiology, as discussed below. Strong disparities in foraging behavior and associated activity levels connoted differential degrees of antipredator awareness and predation vulnerability between the taxa, consistent with the hypothesis that *A. vulpes'* close association with *Eucinostomus* spp. is driven in large part by vigilance exploitation, through which *A. vulpes* obtains risk-related information and consequent fitness benefits (Sridhar and Shanker 2014, Hua et al. 2016, Martínez and Robinson 2016).

5.5.1 Stable isotopes

The generally low and overwhelmingly peripheral overlap in resource use revealed by SIA implies that the likelihood of direct resource competition between *A. vulpes* and *Eucinostomus* spp. is correspondingly low. This finding agrees with

qualitative behavioral observations documenting little evidence of agonistic interactions between the two taxa (Chapter 4) and is furthermore consistent with the generally-accepted hypothesis that the competitive costs associated with joining heterospecifics should be small relative to those of joining conspecifics (Seppänen et al. 2007). Despite a limited degree of asymmetry in embayment B, isotopic niche overlap and inferred potential of resource competition were generally similar for both taxa when considered at the level of interacting individuals. However, when one takes into account the inordinately small numerical representation of *A. vulpes* compared to *Eucinostomus* spp. in heterospecific shoals (~1%, as described by Haak et al. 2018), the competitive pressure imposed by *A. vulpes* on eucinostomids at the population level should be largely inconsequential relative to the that of interspecific competition. In light of this, it seems that *A. vulpes* should face greater competition; yet the near-obligate consistency with which juveniles occur among eucinostomids implies the active selection of *Eucinostomus* spp. as partners, and consequently that any putative costs are outweighed by the benefits obtained from this association.

Interspecific contrasts in isotopic composition shed light on the likely mechanisms through which niche partitioning between *A. vulpes* and *Eucinostomus* spp. arise. Because both taxa display a high degree of overlap in habitat utilization, occurring and even foraging jointly, species-specific disparities in isotopic composition are almost certainly indicative of fine-scale differences in microhabitat use or prey preference, reflected by consistent and substantive differences in δ^{34}S, and to a lesser degree δ^{13}C. The relative enrichment in ^{13}C found in tissues of *Eucinostomus* spp. may be interpreted to reflect a greater reliance upon prey that assimilate isotopically-heavier carbon from

seagrass habitats (Fry et al. 1982, Cocheret de la Morinière et al. 2003, Nagelkerken and van der Velde 2004), a hypothesis compatible with documented differences in microhabitat use between the two taxa, which suggest that *A. vulpes* avoid more densely-vegetated seagrass beds while eucinostomids utilize them more readily (Chapter 4).

The larger role of sedimentary detrital food webs in the diet of *Eucinostomus* spp. implied by interspecific contrasts in δ^{34}S may be taken to indicate a greater reliance upon infaunal prey which occupy deeper strata within benthic sediments, a finding that aligns well with interspecific differences in the function and morphology of mouthparts. The terminally-located tubular and highly-protrusible mouth of *Eucinostomus* spp. permits this taxon to dig or "excavate" deep into substrates, extracting considerable volumes of benthic sediment which it subsequently sifts through and expels from the mouth and gills, facilitating the capture of more deeply buried organisms (Cyrus and Blaber 1982, Sazima 1986). In contrast, the subterminal inferior mouth of *A. vulpes* is an adaptation consistent with the more selective capture of epifaunal prey or infauna near the surface of substrates. The exploitation of prey that occupy distinct vertical positions on, or within, benthic sediments is also consistent with differences in the sensory physiology employed by the two taxa for prey detection. While *A. vulpes* is thought to be a largely visual predator (Hannan et al. 2015, Taylor et al. 2015, Grace and Taylor 2017), *Eucinostomus* spp. is believed to locate prey acoustically, through the use of a unique physiological adaptation that produces exceptional hearing sensitivity, allowing this taxon to identify the position of buried organisms such as polychaete worms that are completely obscured by sediments (Green 1971, Parmentier et al. 2011).

5.5.2 Behavioral analyses

Large interspecific disparities in Transit time, Time at rest, and Strike rate evidence fundamentally different foraging strategies in *A. vulpes* and *Eucinostomus* spp., corresponding well with qualitative behavioral descriptions and consistent with the differential resource use implied by SIA, particularly with respect to the exploitation of exposed (i.e., epifaunal) versus buried (i.e., infaunal) prey. Following foraging theory, the optimal rate of movement while searching for prey reflects a tradeoff between prey encounter rate and prey detection probability. While a faster search speed increases the rate of encounter, it has the inverse effect on detection probability, as less time is devoted to inspecting a given area (Gendron and Staddon 1983, 1984). Because the "base" probability of detection for hidden or cryptic prey is comparatively low relative to that of conspicuous prey, the optimal search speed or rate of movement should decline as prey become increasingly hidden or cryptic, permitting increased inspection time (Gendron and Staddon 1983, 1984, O'Brien et al. 1990). In light of this, the extended Transit times and large proportion of time spent at rest (presumably listening for prey) documented for *Eucinostomus* spp. are in close keeping with the hypothesis that this taxon exploits relatively hidden or hard-to-find prey items, such as those concealed within sediments. Likewise, the comparatively high search speeds displayed by *A. vulpes* are consistent with the exploitation of more conspicuous or exposed epifaunal prey.

The contrasting relationships observed between Strike rate and Time at rest for *A. vulpes* and *Eucinostomus* spp. elucidate another clear divergence in foraging strategies; specifically, the manner in which the two taxa integrate locomotion in the act of prey capture. (Higham 2007, Rice and Hale 2010). The notable deceleration prior to

consuming prey and the correspondingly limited speeds displayed by *A. vulpes* during

capture are consistent with behaviors described for suction feeders (a group to which *A. vulpes* belongs), for whom high ram speeds can diminish the strength and effectiveness of

suction (Higham et al. 2005, 2006). The discrepancy in prey capture tactics is likewise in

keeping with morphological differences between the taxa; the comparatively small gape

of *A. vulpes* is thought to demand more adaptive and precise mouth positioning with

respect to prey, made possible by prolonged approach times associated with a lower

closing speed (Higham et al. 2007). Conversely, the greater strike speeds exhibited by

Eucinostomus spp. are consistent with a larger gape which requires less exacting

precision, as is demonstrated by this taxon's habit of ingesting considerable volumes of

sediment (Cyrus and Blaber 1982, Sazima 1986).

5.5.3 Implications of behavior for species-specific vigilance

Collectively, the pronounced differences in behavior found here between *A. vulpes* and *Eucinostomus* spp. imply a contrast in the species' respective abilities to

maintain vigilance and in their vulnerability to predation while foraging. The nearly

continuous locomotion and much more active search mode of *A. vulpes* serves to attract

predator attention and to increase rates of encounter with them, leading to heightened

predation risk (Wright and O'Brien 1982, Howick and O'Brien 1983). On the contrary,

the extended pauses that comprised nearly 70% of eucinostomids' time are thought to

enhance sensory perception and processing, facilitating the detection of predators and

prey while simultaneously reducing predator encounter rates and visual conspicuity

(McAdam and Kramer 1998, Kramer and McLaughlin 2001, Trouilloud et al. 2004). The

comparatively high strike rate displayed by *A. vulpes* likewise correlates with heightened

predation susceptibility among foraging fish (Milinski 1984, Godin and Smith 1988), and the effect of feeding rate on vigilance may be exceptionally relevant to the benthivorous fishes studied here, for whom the act of feeding necessitates a head-down posture that in itself is linked with reduced antipredator awareness and elevated risk of mortality (Krause and Godin 1996, Foam et al. 2005). As such, the tendency of *A. vulpes* to make multiple strikes in close succession implies a prolonged period of focus on benthic substrates suggesting further divergence in predation vulnerability when juxtaposed with the single, rapid strike that is characteristic of *Eucinostomus* spp.

The contrasting locomotor integration patterns displayed by *A. vulpes* and *Eucinostomus* spp. have additional consequences for relative vigilance levels as inferred here from Time at rest, which had unexpected and fundamentally different implications for the vulnerability of each taxon. While pauses in the movement of foragers are typically presumed to correlate with periods of relatively high antipredator awareness (Kramer and McLaughlin 2001, Trouilloud et al. 2004), the assumption did not hold in the case of *A. vulpes,* for whom Time at rest (near-zero-velocities) instead corresponded to prey capture behavior, typified by a sustained head-down posture and a seemingly myopic focus on benthic substrates, connoting a high degree of vulnerability. Conversely, Time at rest among *Eucinostomus* spp. conformed to this presupposition, characterized by hovering well above the substrate in an upright posture conducive to visual scanning and high antipredator awareness. As such, while Time at rest was intended to express the prevalence of vigilance-related behaviors (as in the case of *Eucinostomus* spp.), the variable likely captured the inverse for *A. vulpes*, instead reflecting periods of this species' greatest vulnerability.

Aforementioned differences in the sensory physiology employed by *A. vulpes* and

Eucinostomus spp. for the detection of prey may serve to further amplify the asymmetry

in inferred relative vigilance levels between these taxa. A central concept underlying the

theorized tradeoff between foraging and predation risk is the notion of limited attention

(Dukas and Kamil 2000, Dukas 2002); specifically, it is assumed that the performance of

a task (i.e., predator detection) is degraded by the simultaneous performance of a second

task (i.e., prey detection). However, when concurrent tasks involve distinct sensory

modalities, (i.e., one task is visual and one is auditory), the presumed performance deficit

is largely abated (Duncan et al. 1997, Martens et al. 2010). Accordingly, the sensory

adaptations which permit *Eucinostomus* spp. to detect prey acoustically may endow this

taxon with a unique ability to search for prey while simultaneously scanning visually for

predators in an upright position, all without suffering the attention deficits that are

traditionally associated with multitasking and providing *Eucinostomus* spp. with a

singular capacity for antipredator vigilance.

5.5.4 Vigilance exploitation, derived benefits, and community assemblage

The obvious disparity in relative vigilance level implied by interspecific

differences in foraging strategy reveals that *A. vulpes* and *Eucinostomus* spp. occupy

opposing ends on a spectrum reflecting the species' potential as producers of antipredator

information versus the degree to which they may profit from risk-related information

produced by others, suggesting they play fundamentally distinct roles in heterospecific

groups (Sridhar et al. 2009, Goodale et al. 2010, Srinivasan et al. 2010). The high level

of vigilance implied by the foraging ecology and sensory physiology of *Eucinostomus*

spp. connotes a high capacity for the detection and production of antipredator information

that corresponds closely with characteristics of sentinel or "informant" species, and is further amplified by the gregariousness of this taxon (Goodale and Kotagama 2005b, 2008, Magrath et al. 2009, Goodale et al. 2010). In contrast, the comparatively high level of vulnerability associated with the foraging ecology of *A. vulpes* has been linked with a greater tendency for group association and suggests that this species may depend inordinately on the vigilance of others (Buskirk 1976, Thiollay and Jullien 1998, Beauchamp 2002). In light of these observations and the limited importance of direct food-related benefits inferred from SIA (and from previous qualitative behavioral observations), we propose that *A. vulpes'* close association with *Eucinostomus* spp. is best explained by vigilance exploitation, with *A. vulpes* utilizing risk-related social information produced by eucinostomids in a pattern commonly described for members of mixed-species bird flocks.

While discrepancies in vigilance and information-production potential imply that information transfer between these taxa is largely unidirectional and asymmetrical, with *A. vulpes* likely deriving the majority of benefits, the absence of discernable competition and low overlap in resource use evinced by SIA suggests that *Eucinostomus* spp. incurs little in the way of competitive costs as a result of the association, supporting the conclusion of Chapter 4 that the relationship is at least commensal in nature. This supposition is likewise consistent with findings of others in both fish (Lukoschek and McCormick 2000, Sazima et al. 2006) and bird (Satischandra et al. 2007, Goodale and Kotagama 2008) communities, which suggest that nuclear individuals typically experience little in the way of negative effects. Rather, it is possible that *Eucinostomus* spp. may in fact benefit from the presence of *A. vulpes*; not only through the dilution of

risk and heightened collective vigilance afforded by increased group size (Pulliam 1973, Powell 1974) but also from the "accumulated information" collected by the more diverse sensory abilities of divergent taxa (Morse 1977, Goodale and Kotagama 2005a) Moreover, shared predators may selectively attack more conspicuous (by their oddity) or more vulnerable heterospecific group members (Fitzgibbon 1990) such as *A. vulpes*, effectively diminishing risk for eucinostomids.

Access to information regarding shared predators appears to be the principal factor promoting *A. vulpes*' close relationship with *Eucinostomus* spp., a finding that contributes to explaining the broad attractiveness of eucinostomids, which extends to juveniles of diverse taxa occupying disparate trophic guilds (e.g., piscivores such as *S. barracuda*) for whom food-related information would be largely irrelevant (Chapter 4). Unlike information that pertains to food, the relevance of social information regarding predators does not require that fishes overlap in trophic resource use, and thus the exploitation of risk-related information may be inherently less costly and more likely to evolve among heterospecifics, particularly in aquatic communities where ontogenetic constraints on body size are often more important than phylogeny in determining which predators pose a threat to a given individual (Werner and Gilliam 1984, Woodward and Hildrew 2002). Even among species that do compete directly for resources, the reduced spatial proximities required for the sharing of risk-related information, when considered relative to those necessary to exploit social cues on the location of food items, may serve to further mitigate the costs of competition incurred through antipredator information sharing (Sridhar & Shanker 2014).

The absence of evidence for direct, resource-related benefits does not mean that enhanced feeding success is not among the primary means by which *A. vulpes* profit from their association with *Eucinostomus* spp., as foraging benefits can also arise through indirect social mechanisms that are independent of resource use. Individuals in groups perceive reduced levels of risk and adjust their behaviors accordingly (Pulliam et al. 1982, Popp 1988, Roberts 1996), often feeding more readily or allocating increased time to foraging (Caraco 1979, Beauchamp 1998). Social mechanisms such as behavioral coupling can likewise stimulate foraging among fishes (Baird et al. 1991, Ryer and Olla 1991), and this appears to extend to heterospecific groups (Overholtzer and Motta 2000, Brandl and Bellwood 2015, Gil and Hein 2017), suggesting that *A. vulpes* (and to a lesser degree *Eucinostomus* spp.) may obtain similar food-related advantages, reducing time devoted to vigilance and/or foraging more aggressively. Moreover, heterospecific group participation can expand the breadth of species' foraging niches, permitting them to exploit riskier habitats or forage in circumstances where they otherwise would not (Wolters and Zuberbühler 2003, Tubelis et al. 2006, Darrah and Smith 2013). In a similar manner, heterospecifics that overlap in their foraging habitats, as do *Eucinostomus* spp. and *A. vulpes,* may benefit from enhanced foraging success in each other's presence despite exploiting disparate resource pools.

Alternatively, it is possible that *A. vulpes* do benefit, at least opportunistically, from social information on resources produced by *Eucinostomus* spp. Although it did not imply strong competition, isotopic niche overlap was substantially greater than zero, and the lack of differences in δ^{15}N indicates that the species share a similar trophic position. Therefore, heterospecifically-produced information signaling the location or density of

prey may nonetheless be of relevance across species. Such information use may simply occur on broader scales than are discernable by our video surveys; for instance, *A. vulpes* may exploit public information, in the form of eucinostomid densities or behaviors (i.e., aggregations of feeding eucinostomids) as indicators of overall patch quality or productivity (Buckley 1997, Valone and Templeton 2002, Valone 2007), identifying general areas in which to forage but searching independently for distinct prey items within them.

Are the relatively non-vigilant behaviors exhibited by *A. vulpes* representative of this species in general, or do they also reflect social context and the diminished risk perceived by *A. vulpes* when associating with *Eucinostomus* spp.? Unfortunately, efforts to disentangle these factors are complicated by the fact that *A. vulpes* occur almost singularly in the presence of eucinostomids, preventing the establishment of a "baseline" vigilance level (i.e., when among conspecifics only). As such, a controlled experimental setting may present the only reasonable way to approach this question. Nonetheless, the more rapid growth and much greater maximum size achieved by *A. vulpes*, and the correspondingly greater metabolic demands of this species, are typically associated with less risk-averse behavior (Abrahams and Sutterlin 1999, Huntingford et al. 2010).

Seppanen et al. (2007) suggested that the tradeoff between access to relevant social information and the associated cost of competition is mediated by ecological distance. In the context of *A. vulpes* and *Eucinostomus* spp., this distance may be attributed primarily to interspecific distinctions in the sensory modalities used to locate prey (i.e., visual vs. acoustic), and their differential implications for the detection of benthic invertebrate prey in different microhabitats (i.e., depths of burial in sediment)

(Siemers & Schnitzler 2000, Lombarte et al. 2000; Schwalbe & Webb 2014). Thus, while these fishes occupy a mutual foraging guild, feed in analogous habitats, and overlap in the use of certain prey taxa (Layman and Silliman 2002), their differing limitations on prey detection may produce complimentary inefficiencies and under-exploitation of resources that moderates competition and facilitates coexistence (Powell 1989).

Collectively, our work supports the notion that, through the their unusually high capacity for antipredator vigilance and information production, *Eucinostomus* spp. act as "community" or "keystone" informant. The hypothesis, along with suppositions regarding the sensory modalities employed by eucinostomids for the detection of predators and prey (and their consequent implications for vigilance) could certainly be tested in an experimental setting. More broadly, the results of this study parallel observations in bird communities, suggesting that vigilance exploitation and antipredator information sharing may play an important role in structuring mixed species assemblages of fishes, particularly among juveniles occupying open or relatively unstructured habitats where the lack of predation refugia may increase the selective pressures for grouping.

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5.7 Tables

Table 5.1 Summary of fork lengths (FL) and stable isotope ratios (δ^{13}C, δ^{15}N, δ^{34}S) recorded in white muscle tissue of juvenile *A. vulpes* and *Eucinostomus* spp. collected from two distinct embayments on the west (A) and east-facing (B) coasts of Eleuthera, The Bahamas.

Species	Embayment	*n*	FL (mm) mean ± SD	δ^{13}C (‰) mean ± SD	δ^{15}N (‰) mean ± SD	δ^{34}S (‰) mean ± SD
A. vulpes	A	26	72 ± 24	-8.66 ± 1.75	8.4 ± 0.57	12.88 ± 1.65
	B	20	74 ± 40	-12.06 ± 0.8	7.06 ± 0.4	8.55 ± 2.96
Eucinostomus spp.	A	15	60 ± 15	-7.63 ± 1.33	8.48 ± 0.53	8.11 ± 3.94
	B	15	59 ± 13	-10.71 ± 0.48	7.42 ± 0.52	4.63 ± 1.63

Table 5.2 Summary of reduced linear mixed models relating stable isotope ratios (δ^{13}C, δ^{15}N, δ^{34}S) recorded in white muscle tissue of juvenile *A. vulpes* and *Eucinostomus* spp. from embayments on the west (A) and east-facing (B) coasts of Eleuthera, The Bahamas, to the fixed predictors Species and Fork length (FL). No significant interactions were detected between Species and FL.

Response variable ~ Predictor variable	Coefficient	SE	df	z value	p value
δ^{13}C (embayment A) ~					
Intercept	-8.447	0.477	9.656	-17.708	<0.00001
Species	0.815	1.391	5.982	0.586	0.579
δ^{13}C (embayment B) ~					
Intercept	-13.284	0.225	4.456	-59.047	<0.00001
Species	1.504	0.173	8.951	8.668	<0.0001
FL	0.017	0.003	5.945	6.422	<0.001
δ^{15}N (embayment A) ~					
Intercept	7.475	0.268	27.616	27.877	<0.00001
FL	0.014	0.004	35.975	3.877	<0.001
δ^{15}N (embayment B) ~					
Intercept	6.124	0.318	6.075	19.275	<0.00001
FL	0.012	0.003	8.587	3.384	<0.01
δ^{34}S (embayment A) ~					
Intercept	12.875	0.531	39	24.251	<0.00001
Species	-4.768	0.878	39	-5.432	<0.00001
δ^{34}S (embayment B) ~					
Intercept	8.032	0.961	7.007	8.357	<0.0001
Species	-3.023	0.909	30.47	-3.325	<0.01

Table 5.3 Summary of the distribution of *A. vulpes* (n=20) and *Eucinostomus* spp. (n=33) used for behavioral analyses across three distinct remote underwater video surveys (referred to here as A, B & C).

Survey ID	*A. vulpes* (*n*)	*Eucinostomus* spp. (*n*)
A	7	9
B	9	13
C	4	11
Total	20	33

Table 5.4 Summary statistics describing the behaviors and relative activity levels of jointly-foraging *A. vulpes* and *Eucinostomus* spp., as ascertained from quantitative motion analysis of remote underwater video surveys. Transit time measures the duration (in s) required for an individual to traverse the camera's horizontal field of view, reflecting overall activity level (more active individuals should do so more rapidly on average). Time at rest is the proportion of an individual's total Transit time spent at near-zero velocities (defined as a speed of 1 pixel frame^{-1}, or a distance corresponding to roughly 0.0125 % of the camera's horizontal field of view per 1 s). Strike rate represents the frequency of prey capture attempts, or strikes, at benthic substrates, displayed by an individual.

Species	Transit time (s)		Time at rest (%)		Strike rate (strikes s^{-1})	
	(mean ± SD)	(min – max)	(mean ± SD)	(min – max)	(mean ± SD)	(min – max)
A. vulpes	21.9 ± 12	7.3 – 49	20.77 ± 12.75	0.01 – 0.46	0.3 ± 0.16	0.07 – 0.72
Eucinostomus spp.	64.6 ± 39.7	15.4 – 171.8	69.59 ± 9.58	0.48 – 0.84	0.05 ± 0.02	0.02 – 0.13

Table 5.5 Summaries of reduced linear and beta regression models describing the behavioral response variables Transit time, Time at rest, and Strike rate as a function of the fixed predictor Species. Dispersion parameter estimates are included for beta regressions.

Response variable ~ Predictor variable	Coefficient	SE	z value	p value
Transit time ~				
Intercept	1.275	0.059	21.639	<0.0001
Species	0.457	0.075	6.119	<0.0001
Time at rest ~				
Intercept	-1.36	0.187	-7.26	<0.0001
Species	2.186	0.202	10.823	<0.0001
Intercept (Dispersion model)	2.039	0.309	6.589	<0.0001
Species (Dispersion model)	1.144	0.393	2.913	0.004
Strike rate ~				
Intercept	-0.595	0.054	-10.94	<0.0001
Species	-0.764	0.069	-11.08	<0.0001

Table 5.6 Summary of the reduced beta regression model describing Time at rest as a function of the fixed predictor Strike rate and the interaction between Strike rate and Species. Dispersion parameter estimates are included.

Response variable ~ Predictor variable	Coefficient	SE	z value	p value
Time at rest ~				
Intercept	-0.204	0.259	-0.788	0.431
Strike rate	2.133	0.476	4.477	<0.0001
Strike rate : Species	-2.899	0.335	-8.661	<0.0001
Intercept (Dispersion model)	2.691	0.314	8.557	<0.0001
Species (Dispersion model)	0.724	0.397	1.823	0.068

5.8 Figures
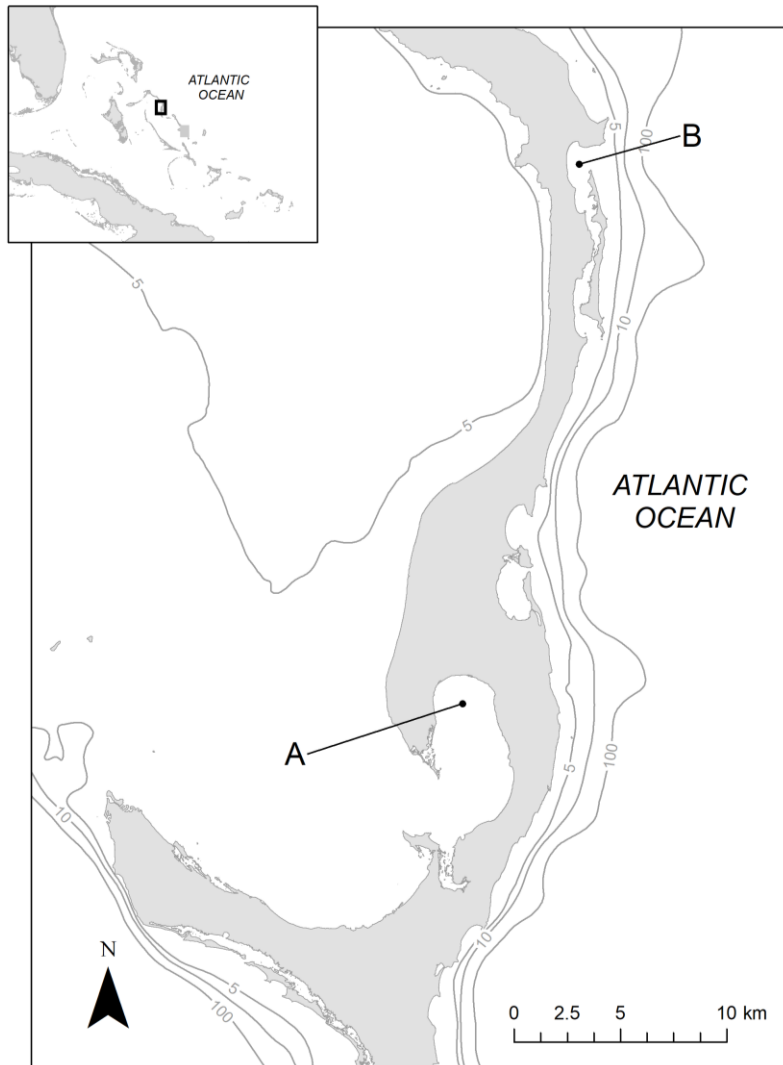
Figure 5.1 Map of the study area on the island of Eleuthera, The Bahamas, depicting the locations of west (A) and east-facing (B) embayments where *Albula vulpes* juveniles were collected for stable isotope analyses. Remote underwater video surveys for behavioral analyses were conducted only in the west-facing embayment (A).
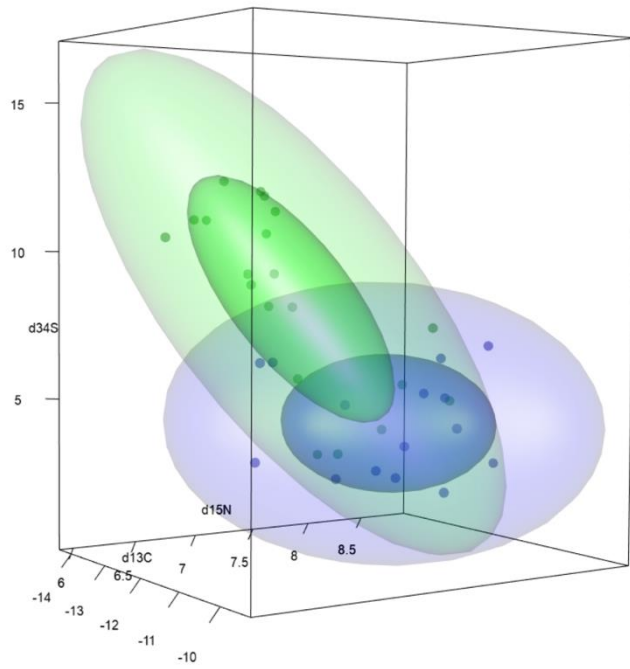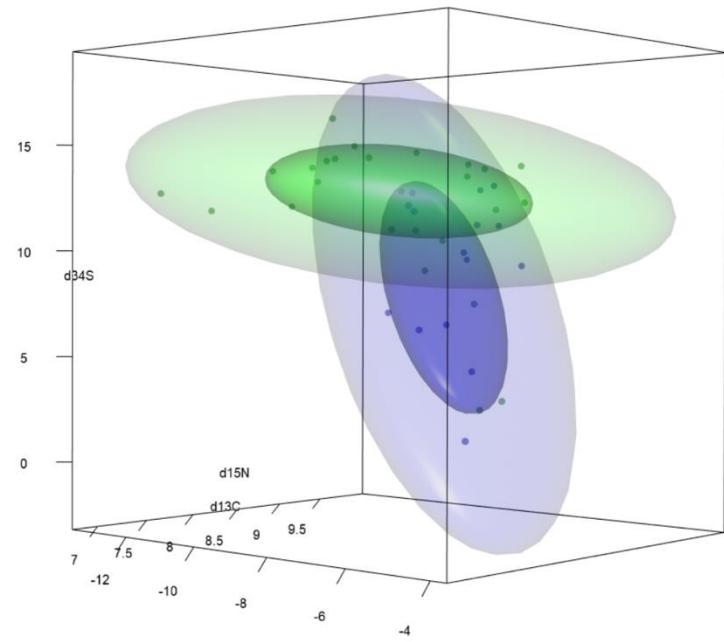
A　　　　　　　　　　　　　　　　　　　　　　**B**

Figure 5.2 Plots depicting the 3-dimensional core (40%) and total (95%) isotopic niche (δ^{13}C, δ^{15}N, δ^{34}S) volumes of *A. vulpes* (in green) and *Eucinostomus* spp. (in blue) collected from west-facing (A) and east-facing (B) embayments of Eleuthera island in The Bahamas. Points represent individual observations, while the smaller and larger ellipsoids represent the estimated core and total niches volumes, respectively.
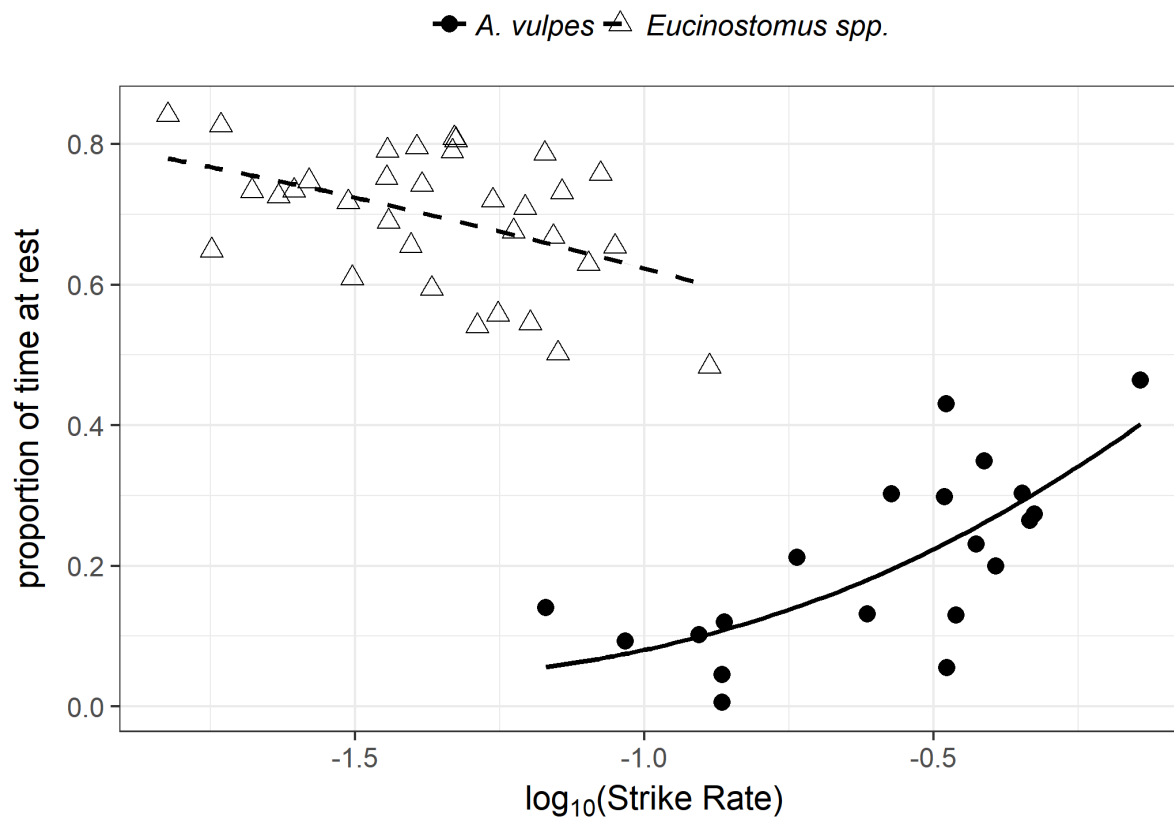
Figure 5.3 Scatterplot depicting the relationship between Strike rate (the mean number of distinct strikes on benthic substrates by a given individual per unit time [s]) and Time at Rest (the proportion of time spent at near-zero velocities by a given individual) for jointly-foraging juvenile *A. vulpes* (solid dots) and *Eucinostomus* spp. (outlined triangles) as assessed from remote underwater video surveys conducted in an embayment (labeled "A" in Figure 5.1) on Eleuthera, the Bahamas.
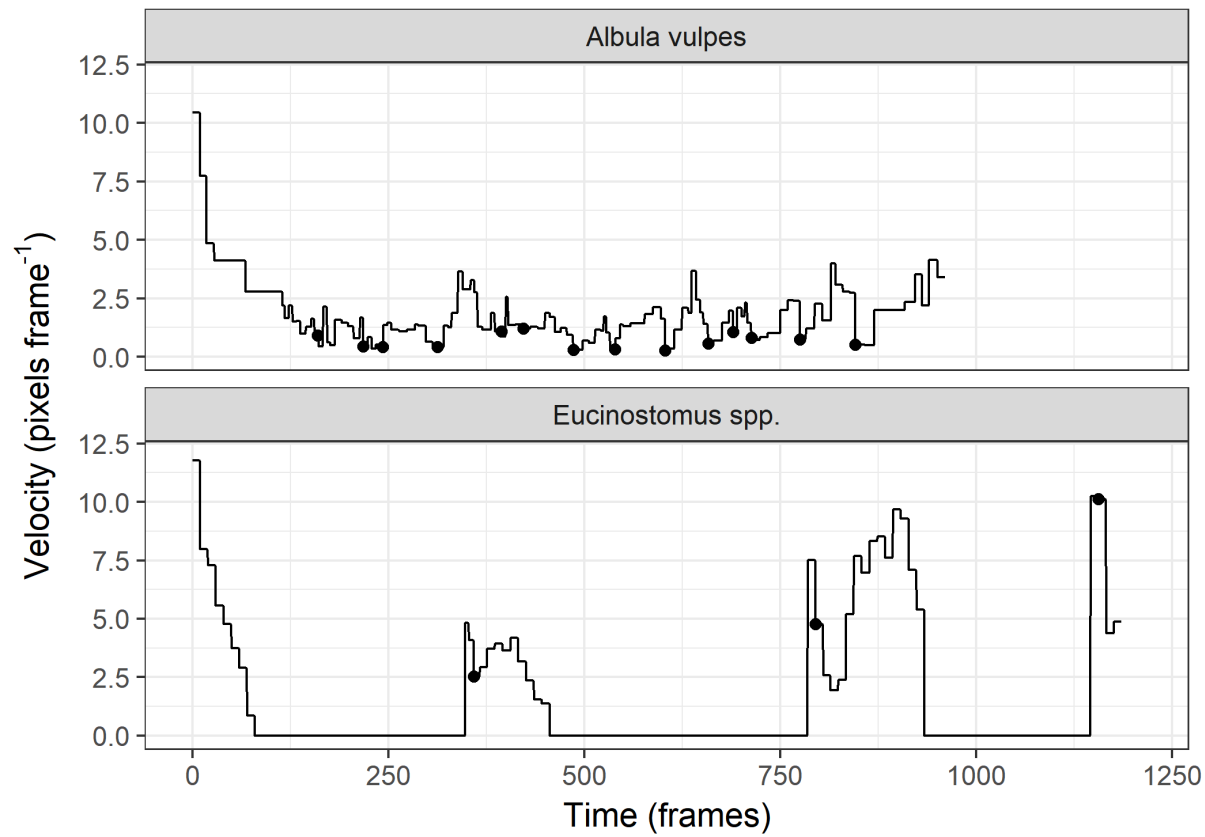
Figure 5.4 Time-series plots representing typical velocity profiles (in pixel/s) for jointly foraging *A. vulpes* (A) and *Eucinostomus* spp. (B) as estimated by motion analysis of remote underwater video surveys.

CHAPTER 6

SYNTHESIS

In this dissertation, I sought to highlight basic differences in the dominant physical and biological factors that control the distribution of juvenile demersal fishes using shallow littoral zone habitats typified by disparate levels of structural complexity. While myriad publications have assessed species-environment relationships among juvenile fishes in tropical back-reef systems akin to those we studied, none (to the best of my knowledge) have identified hydrodynamic variables as important environmental predictors. Yet, Chapter 2 demonstrated that among *A. vulpes* juveniles, which exhibited a strong negative relationship with benthic vegetation, spatio-temporal variation in the strength of incident flow was likely the most influential factor governing distributions. Similarly, Chapter 3 showed that species-specific differences in response to wave-driven flow intensity can explain differential patterns of habitat use and niche partitioning among morphologically indistinct congeners, when benthic habitat preferences offer negligible explanatory power. Perhaps the strongest support for the hypothesis that habitat-complexity mediates the impacts of flow can be found in the multi-species analysis of Chapter 4, where wave-driven flow intensity exerted consistently strong and significant effects on a diverse group of demersal fishes using unvegetated or sparsely-vegetated habitats (*A. vulpes*, *Bothus* spp., *Eucinostomus* spp., and *T. falcatus*), yet had weak or nonexistent effects on species exploiting dense benthic vegetation (*S. barracuda*, *H. bivitattus*, *Caranx* spp., and *Haemulon* spp.).

Chapters 4 and 5 together suggest that positive interspecific associations (mutualisms or commensalisms), driven principally by access to risk-related social information, had a profound effect on the structure of the juvenile fish assemblages I studied. However, the importance of these interactions also appeared to be linked to benthic habitat complexity; with the exception of *S. barracuda* (which showed a weak but significant positive relationship with benthic vegetation density), taxa exhibiting the most robust positive relationships (*A. vulpes*, *Eucinostomus* spp., and *Bothus* spp.) were all associated with unvegetated habitats. Conversely, fishes exploiting dense vegetation tended to show the weakest interspecific relationships (*Haemulon* spp., *H. bivitattus*, and *Caranx* spp.).

Assuming they are not simply a result of oversight, the apparent incongruities between my findings and those of previous works in similar systems are best explained by the almost singular focus of past studies on the role of seagrass and mangrove habitats as nurseries for coral-reef species, and consequently by fundamental differences in the nature of the predominant habitats and species surveyed. The physical structure provided by submerged aquatic vegetation such as seagrasses acts to strongly attenuate near-bed water velocities (Fonseca and Cahalan 1992, Peterson et al. 2004, Bradley and Houser 2009), markedly reducing flow-related stresses and their associated energetic costs for animals below the canopy. As such, densely-vegetated microhabitats may function not just as refuges from predation but also as a form of flow refugia (Johansen et al. 2007), permitting sedentary or site-attached species such as most reef fishes (Chapman and Kramer 2000, Green et al. 2015) to occupy relatively high-flow environments when contrasted with species utilizing unvegetated habitats of equivalent exposure to wave or tide-driven currents.

The apparent relationship between benthic habitat use and the prominence of positive interactions may likewise be accounted for by habitat-specific differences in structural complexity, and their ramifications for the nature of predator-avoidance behavior (Terborgh 1990). In topographically complex environments, fine-scale structural microhabitats are an important factor moderating predation risk for many small juvenile fishes, who exploit them as refuge from piscivores (Buchheim and Hixon 1992). However, the finite or limited availability of refugia means that this resource can rapidly become saturated when the density of competitors is high, making predation risk strongly and positively density-dependent (Beukers and Jones 1998, Holbrook and Schmitt 2002, Hixon and Jones 2005).

The relative absence of topographic complexity in unvegetated habitats offers little in the way of fine-scale structural refugia, likely necessitating that juvenile fishes adopt alternative strategies for predator evasion. In open habitats, evidence from terrestrial communities suggests that sociality, and its concomitant benefits for the detection and avoidance of predators may present the most effective strategy for mitigating risk (Terborgh 1990, Thiollay and Jullien 1998). Accordingly, in habitats of limited complexity, the risk of predation mortality may in fact be inversely density-dependent, as potential competitors serve to reduce predation risk through both intrinsic and information-related mechanisms. This explanation is consistent with the results of experimental studies demonstrating that fish display increased flight initiation distances (Nunes et al. 2015), elevated sensitivity to heterospecific alarm cues (Pollock and Chivers 2003), and a greater propensity for antipredator shoaling (Orpwood et al. 2008) in habitats lacking structural refugia, and by field observations documenting an inverse

relationship between rates of social foraging and habitat complexity among coral reef fishes (Auster and Lindholm 2008).

6.1 Flow-related stress as a driver of distributions

6.1.1 Flow-morphology paradigm

While Chapters 2, 3 and 4 cement the importance of flow as an environmental filter, the species-specific responses to hydrodynamic variables estimated by the JSDM in Chapter 4 may shed light on various traits through which flow acts to determine differential patterns of habitat use. A large body of work in lotic freshwater and coral-reef systems suggests that the varying abilities of different fishes to persist in distinct flow environments are governed principally by locomotor performance (Fulton et al. 2001, Fulton et al. 2005). Following the morphology-performance-fitness paradigm (Arnold 1983), swimming performance is in turn a predictable function of morphology, determined largely by the balance of various traits that tradeoff stability and maneuverability (i.e., unsteady swimming performance) for efficient, long-distance cruising efficiency (i.e., steady swimming performance) (Blake 2004, Langerhans and Reznick 2010) .

The species-flow relationships elucidated in Chapter 4 can be seen as generally supporting this hypothesis. For example, of the fishes I studied, *A. vulpes* exhibits morphological adaptions most characteristic of a steady-swimming phenotype (a streamlined fusiform body and high-aspect ratio caudal fin), and likewise displays the most pronounced negative response to the intensity of wave-driven (i.e., unsteady) flow. At the opposite end of the morphological continuum, the unique body form of *T. falcatus* reflects adaptations that are consistent with the directional stability and maneuverability

required for negotiating turbulent or unsteady flows (a laterally-compressed body with a forward-shifted center-of-mass, and mid-laterally inserted, highly-tapered pectoral fins), and accordingly this species showed a strong and singular positive relationship with wave-driven flow intensity. Occupying an intermediate location on the spectrum, *Eucinostomus* spp. possess what might be described as a hybrid swimming phenotype (a somewhat laterally compressed body form with elongated pectoral fins), and appropriately displayed a moderated, but negative, relationship with flow intensity.

Nonetheless, several fishes presented clear exceptions to the predictions of the hypothesis, indicating that morphological constraints on swimming performance did not act in isolation to determine a fish's hydrodynamic niche. For example, despite their quintessential steady-swimming morphology, *A. vulpes* showed a strong negative relationship with tide-driven flow (Chapters 2 & 4), demonstrating the importance of water column utilization and benthic boundary layer effects (Meyers and Belk 2014). Likewise, pelagic planktivores such as *A. stipes* and *Harengula* spp., whose morphology does not imply high unsteady swimming performance, were largely unaffected by wave-driven flow (Chapter 4), likely explained by the more Eulerian perspective that is concomitant with feeding on items suspended in the near-field water column, and likewise by the potential for turbulent flow to increase foraging success among planktivores (Anderson and Sabado 1995, Finelli et al. 2009). Certainly, the most glaring of these inconsistencies occurred in the case of *A. goreensis*, whom despite exhibiting an archetypal steady-swimming morphology identical to that of *A. vulpes* utilized significantly higher-flow habitats (Chapter 3) and displayed an anomalous positive relationship with wave-driven flow intensity more akin to that of *T. falcatus* (Chapter 4),

underscoring the putative importance of behavior and/or physiology. Collectively, these apparent contradictions serve to highlight the complex nature of fish-flow relationships, and the myriad biological and ecological factors that interact to determine a species' hydrodynamic niche.

6.1.2 Flow as a component of energy landscapes

The energy landscape model (Wilson et al. 2012) proposes that the energetic costs of locomotion vary across space and time in a predictable manner, and that animal movements and patterns of habitat use can be explained as efforts to maximize access to resources while minimizing the locomotory costs of traversing the physical landscape (i.e., the value of a resource patch is not just a function of its productivity but is offset by the energetic expenditures required to exploit it). While the costs of locomotion vary across species, mediated by intrinsic factors including morphological and physiological constraints on swimming performance (Ohlberger et al. 2005), they are nonetheless governed directly and in large part by the characteristics of incident flow (Facey and Grossman 1990, Enders et al. 2003, 2005, Roche et al. 2014). As perhaps the most influential extrinsic physical factor governing the energetic expenditures for fishes in shallow coastal environments, variation in wave or tide-driven water movement also exhibits a pronounced spatial component (Chapter 2), making it integral to defining the energy landscape they inhabit. As such, the energy landscape paradigm may provide a valuable framework for conceptualizing the ways in which flow variability impacts the movements and habitat use of fishes.

Energy landscapes associated with coastal marine environments are complex and often highly dynamic (Shepard et al. 2013), reflecting energetic costs associated with

several distinct forcing agents (tides, local or remotely generated waves) that can vary inversely and are characterized by differing magnitudes and timescales of variability, ultimately diverging markedly in their predictability (Denny 1988). In such dynamic landscapes, strategies for the efficient use of space should be fundamentally different from those in static environments, since animals must weigh the magnitude of potential energetic costs against their predictability. The important role of uncertainty in driving habitat use may be exemplified in Chapter 2 by the remarkably greater explanatory power of long-term near-maximal velocity compared to long-term mean, indicating that relatively rare, extreme, and unpredictable events, essentially constituting "outliers", acted most strongly to exclude *A. vulpes* from higher-flow habitats, even during periods of relative calm. This can be interpreted to suggest that the avoidance of exposed habitats by *A. vulpes* (and several other taxa in Chapter 4) may be better explained by temporal volatility than by typical flow intensity.

These observations parallel conclusions drawn by studies examining finer-scale habitat use by fishes in lotic environments, which suggest that fish tend to avoid areas where flow velocity varies widely or in unpredictable ways (Liao 2007), and that the consistency of turbulent flow is more influential than its intensity in determining the use of space (Goettel et al. 2015). Flow predictability on finer spatio-temporal scales may likewise have consequences in marine habitats, potentially influencing the way fish are affected by different wave spectra. Due to the dispersive nature of surface gravity waves, incident swell that was generated remotely is inherently more uniform in its periodicity and direction; while waves generated by local wind forcing are more random, comprising a broader spectrum of wavelengths and directions. As such, one might expect that the

relative predictability of remote swell, with longer periods and more regularly-spaced lulls, should present a lesser obstacle to foraging success or habitat use than short-period wind waves, despite driving greater near-bed velocities. Some support for this hypothesis may be found in the results of Gabel et al. (2011), who observed greater prey capture rates among dace (*Leuciscus leuciscus*) foraging in pulsed, intermittent waves (akin to swell) compared to those exposed to continuous (i.e., wind-wave) treatments.

6.1.3 Energy landscapes and the landscape of fear

Energetic costs are not the only factor that juvenile fishes must consider when navigating the physical landscape and selecting which habitats to occupy or forage in; in order to survive and reproduce, animals must also avoid predation. Accordingly, (Gallagher et al. 2017) integrate the energy landscape model with the "landscape of fear" (Laundré et al. 2001), suggesting quite logically that animal movement patterns and behaviors should reflect spatial variation in both the costs of locomotion and the risk of predation. Shallow littoral zone habitats have long been considered predation refugia for small juvenile fishes, as they are generally presumed to exclude larger piscivores (Blaber and Blaber 1980, Ruiz et al. 1993, Paterson and Whitfield 2000). This hypothesis is particularly well-supported in the habitats I studied, where depth gradients on the order of tens of centimeters corresponded with steep increases in relative predation risk (Rypel et al. 2007), likely contributing to the inverse relationships with water depth displayed by *Eucinostomus* spp. and *Bothus* spp. in Chapter 4.

However, wave-induced orbital velocities are also inversely related to water depth, and turbulent eddies associated with breaking waves can produce particularly high velocities along shorelines (Denny 2006, Webb et al. 2010), such that for a given set of

forcing conditions, the shallow intertidal margins that function as predation refugia are subject to notably more intense wave-induced water movement. As such, following Gallagher et al. (2017), the energy landscape and the landscape of fear place contradicting constraints on the use of space, suggesting that fishes seeking to occupy these habitats as refugia may face a tradeoff between diminished predation risk and elevated energetic costs. This hypothetical balancing act should be of particular consequence for taxa such as *Eucinostomus* spp., *Bothus* spp., or *A. vulpes*, which exhibited strong negative relationships with wave-driven water velocities. In fact, the outcome of this tradeoff may be reflected in the negative responses of *A. vulpes* and *Eucinostomus* spp. to short-term fluctuations in wave-driven flow, which suggests that these fish opted to leave shallower habitats during periods of increased hydrodynamic stress, either via short cross-shore movements to deeper water (Friedlander and Parrish 1998), or via more extended long-shore migrations to locations with greater physical sheltering (Layman 2000).

6.1.4 Flow metrics, and future considerations

Although it represents a vast improvement over categorical classifications or exposure indices, the use of water velocity as a metric for quantifying hydrodynamic stress still fails to consider several fundamental aspects of water movement that can determine the locomotor impacts and associated energetic costs that flow imposes upon fishes (Kerr et al. 2016). For example, velocity magnitude does not reflect the oscillatory nature of wave driven flow, nor does it consider the effects of turbulent eddies that accompany wave-breaking in shallow habitats, both of which can impose perturbations that require stabilizing corrections and incur additional expenditures (Enders et al. 2003,

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Roche et al. 2014). Moreover, the physical forces imposed by incident flow are mediated by intrinsic characteristics of the fish itself, such as size, mass, and morphology (Webb et al. 2010); accordingly, wave orbitals or eddies have the greatest impacts when their length scale is similar to that of the fish itself (Pavlov et al. 2000, Nikora et al. 2003, Webb et al. 2010). More comprehensive frameworks for approximating flow-related stress, which take into account the above factors, have been proposed (Lacey et al. 2012, Cotel and Webb 2015), yet the application of such metrics outside of a laboratory setting is currently a daunting task. Nonetheless, future efforts to quantify fish-flow relationships could benefit from implementing more nuanced metrics and/or assessing factors beyond velocity magnitude, such as oscillatory periodicity, orbital diameters, and relative length scales.

6.2 Social interactions and assemblage structure

6.2.1 Role of body size and ontogeny

Body size differential (or the size ratio between two individuals) is commonly used as a proxy from which to infer the types and strengths of pairwise interactions that are likely to occur in size-structured trophic webs (Emmerson and Raffaelli 2004, Gravel et al. 2013). Recent work suggests this extends to social information use in avian and terrestrial mammal communities, where body size differential is inversely related to the likelihood that one species responds to the alarm cues of another (Hua et al. 2016, Meise et al. 2018), and experimental evidence suggests that changes in relative body size modify the use of risk-related social information between fishes (Brown et al. 2001, Harvey and Brown 2004, Elvidge et al. 2010). In most of these animals, body size is inextricably linked to ontogeny, yet the relationship between ontogeny, social

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information use, and associated positive interspecific interactions has received surprisingly little consideration. In the case of birds or terrestrial mammals, this may be explained in large part by basic aspects of these animals' ecologies (i.e., limited mobility) or life histories (i.e., extended parental care) which are not conducive to interspecific social interactions in early ontogeny.

Yet the remarkable variation in body size, relative lack of parental care, and comparatively high mobility among young marine fishes is conducive to high rates of encounter (social, trophic, or otherwise) between individuals of heterogenous sizes, stages, and species, with major repercussions for demography and community structure. As such, the importance of ontogenically-induced changes in body-size ratio between species has been long-acknowledged with respect to its implications for "intra-guild predation" (Polis and Holt 1992, Woodward and Hildrew 2002); wherein predators and their prey can become competitors, or vice versa. The present work suggests that similar consideration should be given to the impact of developmental stage on social information use, and the positive relationships or "intra-guild mutualisms" (Crowley and Cox 2011) that can arise between competitors (or even predators and their prey), further highlighting the need to integrate ontogeny and demography (not just phylogeny) in models of community dynamics (De Roos et al. 2003, Rudolf and Rasmussen 2013).

6.2.2 Support for the stress gradient hypothesis

Central to the scientific dialog regarding positive interactions, the stress gradient hypothesis (SGH) proposes that positive interactions between potentially competing species should grow progressively more prevalent under increasing levels of environmental stress (Bertness and Callaway 1994). Most evidence in support of the

SGH comes from communities of sessile organisms (Callaway 2007), where facilitative relationships serve to ameliorate abiotic environmental stressors, however, in its original context the SGH also considered the role of facilitation in mitigating biotic environmental stresses such as consumer pressure. When viewed in this light, the predominance of positive interspecific associations in Chapter 4, presumably indicative of facilitative interactions among juvenile fishes is compatible with the predictions of the SGH. Predation mortality in fishes is inversely related to body size, producing a steep ontogenetic gradient in predation risk, with early life stages constituting by far the greatest consumer pressure faced by an individual over its lifetime (Houde 1997, Goatley and Bellwood 2016). While little quantitative data exists with which to compare rates of positive interactions among the study species in later life stages, it is obvious given the their fundamentally distinct ecologies and adult body sizes that neutral, competitive, or predator-prey interactions should predominate. Therefore, following the SGH, the emergence of positive interspecific interactions and heterospecific group formation amongst juvenile fishes might be explained as an adaptive response to the extreme biological stress induced by elevated predation pressure in early ontogeny, as fishes exploit social information on predators (as well as intrinsic or direct antipredator benefits of grouping) in a form of "associational defense". In light of this, the patterns documented in the present study may be interpreted as a rare example of empirical support for the SGH from a community of motile taxa.

It has been proposed that positive interspecific interactions can serve to expand the realized niche of a species, allowing organisms to persist in environmental conditions that might otherwise be untenable (He and Bertness 2014, Crotty and Bertness 2015).

Although niche expansion in the context of the SGH is typically considered with respect to the abiotic physical tolerances of an organism, it may nonetheless apply to other niche dimensions. Heterospecific bird flock participants frequently benefit from spatio-temporal expansion of their foraging niche, as diminished levels of perceived risk permit the devotion of increased time to feeding and likewise broaden the range of habitats and scenarios in which they are inclined to forage (Darrah and Smith 2013, Ridley et al. 2014). While it is not possible to say with certainty whether *A. vulpes* extended their physical use of space, it seems likely that the aggressive foraging behavior and correspondingly low level of antipredator awareness displayed by the species in the presence of eucinostomids reflects such a form of niche expansion. In this way (returning briefly to the landscape context), the positive relationship between *A. vulpes* and *Eucinostomus* spp. may be thought of as directly moderating the landscape of fear as ascertained by *A. vulpes,* effectively permitting a more optimal or efficient use of the energy landscape by relaxing the constraints exerted by the threat of predation mortality.

6.2.3 Nuclear species as informants

While numerical antipredator benefits of grouping such as risk dilution, the selfish herd effect, and predator confusion may certainly be among the factors that promoted high rates of positive interspecific association among juveniles in Chapter 4, these intrinsic benefits do little to explain the disproportionately strong positive and asymmetrical relationship with *Eucinostomus* spp. shared by several species whose diverse phenotypes should theoretically have imposed strong costs of oddity. Considering the high capacity for antipredator vigilance implied by the behavior of *Eucinostomus* spp. in Chapter 5, and likewise the unusually high potential for information

detection and production imparted by this taxon's gregarious nature and unique sensory physiology, the apparent attractiveness of eucinostomids and their central role in structuring assemblages is best explained by their value as "community informants", in a role not dissimilar to that of parids in bird communities (Contreras and Sieving 2011, Hetrick and Sieving 2012).

If access to antipredator information gained by interspecific association acts to increase the fitness of individual, then one might expect selection to favor adaptations that facilitate signal recognition, sociality and/or group cohesion among associates. Indeed, similar mechanisms are thought to have given rise to phenotypic convergence in alarm calls, and even vocal mimicry, in avian communities (Tobias et al. 2014, Dalziell et al. 2015). While convergence in outward physical appearance has received lesser attention in bird communities (but see Moynihan (1968)), visual phenotype matching is a strong determinant of social organization in fish shoals, as similarity in shape, coloration, and patterning have strong positive implications for group cohesion among fishes (McRobert and Bradner 1998, Saverino and Gerlai 2008) By extension, it is logical that species such as *A. vulpes* which rely heavily upon social information produced by heterospecifics should evolve physical traits similar to those of their informants, serving not only to enhance sociality but also to mitigate the potential costs of phenotypic oddity, ultimately suggesting that information use may be an important evolutionary driver of mimicry in fishes.

6.3 Implications for community dynamics

Ultimately, a key motivation for identifying the abiotic and biotic factors that structure communities is the ability to predict how they will respond to change, whether

in the form of environmental stress associated with climate change, habitat loss or degradation, or species extirpations. From the abiotic perspective, the near-universally negative relationships with flow and the central role of extreme events demonstrated in Chapters 2 and 4 suggests that increases in fetch due to sea level rise, coupled with more frequent and more intense storm events should generally give rise to increased energetic costs for fishes. These costs may furthermore be inflated by physiological limitations on swimming performance related to increases in dissolved carbon dioxide concentrations, elevated water temperatures, and corresponding declines in dissolved oxygen levels (Allan et al. 2013).

My results suggest that different guilds or functional groups may be differentially affected, with the most pronounced negative implications for demersal benthivores that exploit shallow habitats and the least noticeable effects on pelagic planktivores. Interestingly, species associating with benthic vegetation, which typically demonstrated the weakest relationships with flow, may end up enduring some of the greatest stresses, as continuing declines in seagrass coverage reduce the availability of vegetative flow refugia, possibly leaving these fishes ill-equipped for coping with hydrodynamic stress in more open habitats. The decreasing abundance of relatively rare low-flow habitats such as those occupied by *A. vulpes* may lead to increased competition and negative density-dependent effects on this species, permitting the encroachment of its congener *A. goreensis*. In contrast, fishes that are uniquely adapted to capitalize on high-flow habitats, such as *T. falcatus*, may thrive. On a more positive note, the apparently high plasticity and seemingly rapid adaptive response of morphological and physiological

traits that affect swimming performance may enable fishes to accommodate an increasingly challenging flow environment (Binning et al. 2015, Istead et al. 2015).

Environmental change may likewise have implications for information use and the nature of species interactions. Considering the aforementioned influence of physical structure on the nature of predator avoidance and the primary mechanisms governing community assemblage, it seems possible that the continuing decline of corals, seagrasses, and other important "ecosystem engineers" that provide structural refugia for juvenile fishes could in fact lead to an increased prevalence of positive interspecific interactions, as species are forced to turn increasingly towards social mechanisms as a means of mitigating predation risk. At the same time, increases in turbidity and pollutants associated with anthropogenic activities can adversely influence fishes' propensity for social interactions and the value of adaptive benefits derived from them (Kimbell and Morrell 2015).

Broadly speaking, the amelioration of stress (abiotic or biotic) and relaxed competition that typify positive interspecific interactions are thought to promote increased diversity and to exert a stabilizing effect on communities, facilitating recovery from disturbance (Hacker and Gaines 1997, Stachowicz 2001). Moreover, the comparatively high functional redundancy permitted by intraguild mutualisms should promote resilience to the loss of a given species. Nonetheless, subtle and previously unacknowledged fine-scale differences in the functional roles of fishes are increasingly recognized (Brandl and Bellwood 2014, Adam et al. 2015) and may also serve to ameliorate competition among the species studied here, as Chapter 5 suggests may be the

case between *A. vulpes* and *Eucinostomus* spp., where millimeter-scale differences in the depths occupied by prey within benthic sediments may help to mediate coexistence.

On the other hand, while the extirpation of a competitor will likely mean increased resource availability and/or niche expansion for other species, the loss of benefits provided by a mutualist may not be so easily offset (Gross 2008). This effect can be particularly acute with the collapse of a "foundation species", whose disproportionate importance can have cascading, potentially community-wide negative effects (Jones et al. 1997). In the context of the present work, the far-reaching influence of *Eucinostomus* spp. as a "keystone informant" suggests that the stability of the juvenile fish community we studied may be closely linked to that of eucinostomid populations. This notion is particularly interesting in light of observations in the Florida Keys, where a nearly three-fold decline in the abundance of eucinostomids (Thayer et al. 1999) has been coincident with steep declines in *A. vulpes* populations (Frezza and Clem 2015, Santos et al. 2017).

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