MOVEMENTS OF BONEFISH (*ALBULA* SPP.) IN THE BAHAMAS: MULTIPLE MIGRATION ROUTES AND ASSOCIATED ENVIRONMENTAL CUES

By

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A THESIS

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ABSTRACT

MOVEMENTS OF BONEFISH (*ALBULA* SPP.) IN THE BAHAMAS: MULTIPLE MIGRATION ROUTES AND ASSOCIATED ENVIRONMENTAL CUES

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Migration, whether for the purpose of predator avoidance, foraging, or reproduction, results in the movement of individuals from one habitat to another spatially distinct habitat. Many tropical marine fishes migrate from foraging grounds to form spawning aggregations that are spatially and temporally distinct, highlighting a critical time and area for fish reproduction. In The Bahamas, bonefish (Albula vulpes) form spawning aggregations, migrating from nearshore flats and mangrove creeks to deep water shelf edges to spawn. Bonefish support a catch-andrelease recreational fishery valued at approximately \$141 million USD annually in The Bahamas. To manage and protect this economically-important fishery, the purpose of this thesis was to identify and describe migration patterns of bonefish on the Bahamian island of Eleuthera. Six spawning aggregation sites on four Bahamian islands have been identified, but recent findings indicate that islands may support multiple migration routes and aggregation sites. From 2015 to 2017, 78 bonefish were tagged in 11 main foraging grounds across five regions on Eleuthera and tracked using broad-scale acoustic telemetry arrays. This study identified four new migration routes and aggregation sites on Eleuthera. Migration routes on Eleuthera were shorter than those documented on other Bahamian islands and bonefish made repeated migrations throughout the study period. Bonefish migrated between October and June; migration activity was correlated with the first half of the lunar cycle, high tidal range, colder temperatures, and calm weather. The areas identified in this study should be protected from development and fishing pressures to ensure future reproductive success of bonefish in The Bahamas.

Copyright by GEORGIANA MARCHANT BURRUSS 2018 This thesis is dedicated to my family, from Massachusetts to Eleuthera.

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vi

TABLE OF CONTENTS

LIST OF TABLES	ix
LIST OF FIGURES	X
THESIS INTRODUCTION	1
LITERATURE CITED	6
CHAPTER 1	9
EVIDENCE OF MULTIPLE BONEFISH (ALBULA SPP.) MIGRATION ROUTES ON	
ELEUTHERA ISLAND: IMPLICATIONS FOR CONSERVATION	9
ABSTRACT	9
INTRODUCTION	10
METHODS	13
Study location	13
Fish collection	13
Tag deployment	14
Acoustic telemetry arrays	18
Visual observations	21
Data analysis	21
RESULTS	22
South West Region	26
North West Region	29
North East Region	32
East Region	35
South East Region	38
Regional comparison of migration patterns	41
DISCUSSION	44
Management implications	49
APPENDIX.	52
LITERATURE CITED	56
CHAPTER 2	60
CHARACTERIZING THE TIMING OF BONEFISH (ALBULA VULPES) SPAWNING	
MIGRATIONS ACROSS A BAHAMIAN ISLAND	60
ABSTRACT	60
INTRODUCTION	61
METHODS	65
Study location	65
Fish collection and tag deployment	65
Acoustic telemetry arrays	65
Environmental variables	66
Data analysis	66

RESULTS	67
Lunar day	72
Tidal range	75
Air temperature	75
Wind speed	75
Precipitation	75
DISCUSSION	
LITERATURE CITED	85

LIST OF TABLES

Table 1.1: Summary of tagging, biological, and monitoring data for 78 bonefish tagged onEleuthera from 2015 - 2017. Asterisk indicates a hybrid A. vulpes x A. goreensis
Table 1.2: Number of migratory trips made by individuals in each year of the study across all five regions. There were no significant differences in the number of migrations made by an individual based on sex or tagging region. U represents fish for which sex could not be determined
Table 1.3: Mean number of days spent at suspected spawning areas in each region of Eleuthera. The North West region was significantly different from the South East ($p = 0.0003$) and the South West regions ($p = 0.0086$)
Table S1.1: Description of 2015-2016 acoustic receiver array designed to identify the direction fish migrated from foraging grounds to deep water; category refers to migration routes (M), suspected spawning locations (S), and foraging grounds (FG)
Table S1.2: Description of 2016-2017 acoustic receiver array designed to determine migration routes to deep water; category refers to migration routes (M), suspected spawning locations (S), and foraging grounds (FG)

LIST OF FIGURES

Figure 1.7: *North East Region*: Total detections of bonefish on the receiver array in 2015-2016 (A) and on receiver array in 2016-2017 (B). Fish were tagged in foraging grounds. Receivers

Figure 1.10: 2016-2017 detection log for bonefish #46867 tagged in Half Sound in the East region in 2016. Receivers R41 through R43 were placed inside Half Sound in the protected bay. Receivers R34 through R36 were placed outside Half Sound in deeper water. The fish made two movements to deep water outside Half Sound, on December 4, 2016 and February 5, 2017; both of these movements occurred at night, indicating that the fish was aggregating inside Half Sound during the daytime and making nighttime movements over the deep reef environment at night..37

Figure 1.13: Distances of migrations of fish across four tagging regions: East (r	n = 3), North East
(n = 12), North West $(n = 23)$, and South East $(n = 5)$. Significant differences b	etween regions
are denoted with differing letters.	

Figure 2.1: Daily detection data for fish in migration and aggregation areas represented as percent of fish tagged for 2015-2016 (A, n = 30 fish tagged and detected on array) and 2016-

THESIS INTRODUCTION

Animals migrate for a variety of reasons: to forage, to reduce predation risk, and to reproduce. High-trophic level predators like squid, sharks, and skates migrate to the eastern Patagonian Shelf to feed on the seasonally productive plankton blooms (Arkhipkin et al., 2012). Zooplankton make diel vertical migrations in lakes and oceans to avoid predation (Bollens et al., 1991; Iwasa, 1982). Nassau grouper (*Epinephelus striatus*) in the Caribbean migrate hundreds of kilometers to form spawning aggregations, joining thousands of conspecifics to broadcast spawn, releasing gametes *en masse* (Bolden, 2000). The cost of any type of migration, in terms of energetic demand and predation risk, must be outweighed by the benefit of using a spatially distinct area. Specifically, fish that form spawning aggregations migrate at specific times to spawn with conspecifics, releasing gametes at specific sites to increase their reproductive output more than if they were to spawn elsewhere (de Mitcheson & Colin, 2012; Domeier & Colin, 1997). The migratory routes and spawning sites for species that form spawning aggregations are critical for reproduction (Domeier & Colin, 1997).

Spawning aggregations cause an increased biomass of a species in one distinct area for a short period of time (de Mitcheson & Colin, 2012). In some systems, spawning sites serve as cues to predators due to the sudden increase of fish biomass in a distinct area, resulting in an evolutionary tradeoff between reproduction and survival. Spawning aggregations of various species of coral reef fishes in Johnston Atoll in the North Pacific Ocean has been shown to temporarily increase the abundance of a predatory species, the Bluefin trevally (*Caranx melampygus*), in the area (Sancho et al., 2000). Additionally, the regular occurrence of spawning aggregations of grouper and snapper species has been shown to support large populations of gray reef sharks (*Carcharhinus amblyrhynchos*) in French Polynesia (Mourier et al., 2016). While

adult spawners are often the target of predators, planktivores like whale sharks (*Rhincodon typus*) form feeding aggregations at spawning sites to feed on released gametes (Hoffmayer et al., 2007). As a result, migrations and aggregations of individuals in particular sites can be considered ecologically important for more than just the species undertaking a migration.

Migration routes and spawning aggregation locations are often spatially specific; fish use the same areas repeatedly within a single spawning season and on an annual basis. Many tropical spawning aggregation locations are on outer reef areas where the water depth rapidly increases (Colin, 2012). Spawning aggregation sites are typically located on these shelf-edge sites or promontories, which are projections of the reef structure (Bolden, 2000; Colin, 2012). As most of these species have pelagic larval life stages, spawning occurs at sites close to pelagic habitats to decrease larval mortality (Colin, 2012; Domeier & Colin, 1997). Migration routes are also spatially specific; when migrating to reach these deep water sites, many species avoid open ocean areas where the water is several hundred meters deep, instead fish have been tracked swimming along contiguous reef areas and some species appear to use shelf edges as guides during migration (Colin, 1992; Colin, 2012; Starr et al., 2007). Multiple individuals throughout spawning seasons and on an annual basis use the same migration routes from foraging grounds to aggregation sites (Colin, 2010; Colin, 2012; Johannes, 1978). Additionally, nearly all known spawning aggregation locations are used by multiple species for forming spawning aggregations (Colin, 2010; Colin, 2012; Starr et al., 2007). Thus, migration routes and spawning aggregation locations are critical locations for reproduction of many fish species.

Migrations for the purpose of reproduction draw hundreds to thousands of individuals from varying distances, depending on the species. As these migrations and spawning aggregations are spatio-temporally distinct, cues must exist for when individuals should begin to

migrate. Examples of migration cues include time of day (bonefish, *Albula vulpes*, spawn after sunset; Danylchuk et al., 2011), tide (humphead wrasse, *Cheilinus undulatus*, spawn 2-2.5 hours after high tide; Colin, 2010), moon phase (Nassau grouper, *Epinephelus striatus*, spawn during full moons; Bolden, 2000), and season (cubera snapper, *Lutjanus cyanopterus*, spawn seasonally from March to October; Heyman et al., 2005). Some species appear to use several environmental variables as cues to migrate; for example, Nassau grouper spawn during full moons in the winter months (Bolden, 2000). Water temperature is likely a driving force behind species migrating to form spawning aggregations seasonally (Colin, 2012). In the face of climate change, understanding what environmental variables species use as cues to migrate is important when considering how early or late migrations might affect reproductive output, larval survival, and settlement success of larvae.

Identification of migration routes and spawning sites and understanding temporal dynamics of migration serves as the first steps towards effective protection and management of fish species (Russell et al., 2012). Spawning aggregations predictably increase fish biomass in one specific area, making them attractive sites for fishers (Domeier & Colin, 1997; Russell et al., 2012). Fishers view the aggregations as plentiful; unfortunately this illusion of plenty can result in the overexploitation and collapse of spawning aggregations as documented by the disappearance of Nassau grouper spawning aggregations throughout the Caribbean (Aguilar-Perera, 2006). Many of these sites host spawning aggregations of multiple species so identifying and protecting these areas during peak spawning periods is important. Understanding the spatio-temporal dynamics of fish spawning allows for better management and conservation of ecologically and economically important species (Russell et al., 2012).

In The Bahamas, bonefish (A. vulpes) form spawning aggregations, migrating from shallow foraging grounds to deep water areas to release gametes (Danylchuk et al., 2011; Murchie et al., 2015). Bonefish support an economically-important catch-and-release recreational fishery valued in The Bahamas at \$141 million USD annually (Fedler, 2010). The bonefishing industry attracts anglers from around the world to the productive shallow waters of mangrove creeks and tidal flats of The Bahamas. This valuable industry represents an important sector of tourism for many of the Bahamian islands (Fedler, 2010). While in these mangrove creeks and flats, bonefish feed primarily on benthic invertebrates and exhibit high site- and school-fidelity (Murchie et al., 2013). Recent acoustic telemetry studies discovered that bonefish migrate away from shallow foraging grounds along the shoreline to deep water areas where shelf edges come close to shorelines and form prespawning aggregations in protected bays (Danylchuk et al., 2011; Murchie et al., 2015). Bonefish aggregations remain at these sites for several days, moving over deep reef environments after sunset, likely releasing gametes near the shelf edge (Danylchuk et al., 2011). Six bonefish migration and spawning aggregation locations have been identified on Andros, Abaco, Grand Bahama, and Eleuthera (A. Shultz, personal communication; Danylchuk et al., 2011; Murchie et al., 2015); furthermore, recently three spawning aggregation sites were identified on Grand Bahama (Murchie et al., 2015), introducing the possibility of multiple migration routes and aggregation sites on each Bahamian island.

Identification of bonefish migration and spawning aggregation sites is critical for ensuring the future health of this economically important fishery. Bonefish spawning sites are often in areas where shelf edges occur closest to shore, possibly to decrease larval predation in reef habitats. These sites are also ideal locations for development such as marinas and ports as deep water areas necessary larger vessels is closest to shore at these locations. To protect this

important species, spawning sites should be protected from development, especially since the ability of fish to adapt to spawning in new sites is unknown (Russell et al., 2012). While bonefish have been documented utilizing man-made canals as migration routes (Murchie et al., 2015), the proportion of fish that successfully migrate to spawning sites compared to the pre-development spawning population is unknown. Identification of migration routes and spawning sites is critical to understanding how future development may impact these populations.

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CHAPTER 1: EVIDENCE OF MULTIPLE BONEFISH (*ALBULA* SPP.) MIGRATION ROUTES ON ELEUTHERA ISLAND: IMPLICATIONS FOR CONSERVATION

ABSTRACT

Bonefish (Albula vulpes) use nearshore flats and mangrove creeks for feeding, followed by periodic migrations to deeper water to form spawning aggregations. A total of six spawning aggregation sites on four islands of The Bahamas have been identified. A full understanding of bonefish migration routes and spawning aggregations is necessary to manage and protect a \$141 million USD per year fishery. The purpose of this study was to identify and describe migration patterns of bonefish across the Bahamian island of Eleuthera to better inform local and national conservation efforts. From 2015 to 2017, 78 bonefish were tagged in 11 main foraging grounds across five regions on Eleuthera and tracked using broad-scale acoustic telemetry arrays. Telemetry data indicated these populations do not mix at deep water suspected aggregation areas, using five separate migration routes aggregation sites. Several bonefish made repeated migrations (up to 6 trips per year) from foraging grounds to aggregations sites during each spawning period that the arrays were deployed. In this study, bonefish migrated at an average of 55.25 cm/s, which was similar to or exceeding those of other fish species migrating to spawn. Migration distances on Eleuthera ranged from 0.83 to 22.63 km, which were shorter than those documented on other Bahamian islands possibility due to the proximity of foraging grounds to deep water, exposure to wave action, and predation risk outside of foraging grounds. To conserve this recreational fishery, managers should consider incorporating bonefish migration routes and spawning aggregations into management plans, specifically the design of marine reserves.

INTRODUCTION

Migration, movement away from a home range that is not associated with daily behaviors, is performed for a variety of reasons: to forage, to reduce predation risk, and to reproduce (Hobson & Norris, 2008). Depending on the length of the migration, species will need to store enough energy to complete the migration or they must stop to forage to replenish energy reserves (Sapir et al., 2011). The energetic cost of migration, as well as the risk of predation in different habitats, must be outweighed by the benefit of utilizing two spatially distinct ecosystems for foraging, predator avoidance, and/or reproduction. Migrations for the purpose of reproduction are common among fishes; many saltwater species migrate between distinct habitats to form spawning aggregations, gathering with hundreds to thousands of conspecifics to release gametes en masse. Often tropical marine fishes form spawning aggregations at outer reef areas with shelf edges close to open ocean (several hundred meters deep; Colin, 2012). Several species have also been noted migrating along specific paths, appearing to avoid crossing open ocean areas (Colin, 2012). The distances between foraging grounds and spawning sites can vary widely; some coral reef fishes such as bluehead wrasse (Thalassoma bifasciatum) form spawning aggregations on large reefs, migrating short distances within a reef (Warner, 1995), while pelagic fish species such as black marlin (Istiompax indica) migrate 1,000-2,000 kilometers to spawn at the Great Barrier Reef (Domeier & Speare, 2012). During migration, fish are typically not foraging and swim at fast speeds (de Mitcheson & Colin, 2012). Many migrating species use the same route and spawning location year after year; the path along which Atlantic cod (Gadus *morhua*) migrate tens of kilometers is so spatially precise that is referred to as a 'highway' (Rose, 1993). Specific migration routes and spawning sites are of critical importance to sustain the species that use them.

Fidelity to migration routes and spawning sites may increase exposure of marine fish species to both natural and anthropogenic threats; as a result, protection of these areas is a key component of many conservation and management strategies. Predictable increases in fish biomass at specific sites can act as cues for species preving on both adults and eggs; for example, whale sharks form feeding aggregations in the Gulf of Mexico to feed on gametes from spawning aggregations (Hoffmayer et al., 2007; Mourier et al., 2016; Sancho et al., 2000). Similarly, fishers can track the regular occurrence of spawning aggregations, leading to overfishing and stock depletions, such as with Nassau grouper (Epinephelus striatus; Aguilar-Perera, 2006). Coastal development resulting in habitat degradation at spawning sites and along migration routes threatens species that form site-specific spawning aggregations (Murchie et al., 2015). Specificity of site selection for migration routes and spawning sites varies among species and their ability to adapt to development remains unknown (de Mitcheson & Colin, 2012). As a result, identification and subsequent protection in the form of marine reserves of important reproductive habitat, especially migration routes and spawning sites, is critical to successful management and conservation of fish species (Russell et al., 2012).

In The Bahamas, bonefish (*Albula vulpes*) migrate to form spawning aggregations (Danylchuk et al., 2011; Murchie et al., 2015). Bonefish are a popular sportfish, supporting a catch-and-release recreational fishery estimated to generate \$141 million USD annually for the Bahamian economy (Fedler, 2010). Bonefish forage as adults in shallow tidal areas (0.25 - 2meters deep) referred to as flats and mangrove creeks. In foraging grounds, bonefish act as mesopredators; prey species include benthic invertebrates such as small crabs and shrimp. Predator species include great barracuda (*Sphyraena barracuda*), juvenile lemon sharks (*Negaprion brevirostris*), and occasionally osprey (*Pandion haliaetus*).

Acoustic telemetry studies on bonefish have determined that these fish use nearshore flats and mangrove creeks for feeding (Murchie et al., 2013) followed by migrations to deep water to form spawning aggregations (Danylchuk et al., 2011). Bonefish migrate along coastlines away from foraging grounds to areas where deep water (>20 m depth) is close to shore, forming prespawning aggregations in protected bays (3-5 m depth; Danylchuk et al., 2011). Bonefish schools move after sunset from prespawning locations towards the deep water where it is expected that they release gametes (Danylchuk et al., 2011; Murchie et al., 2015). Fish remain in the spawning sites for several days, making repeated nightly movements to deep water, before returning to foraging grounds (Danylchuk et al., 2011). Migration routes to six spawning sites have been identified in The Bahamas, on Eleuthera, Abaco, Andros, and Grand Bahama (Danylchuk et al., 2011; Murchie et al., 2015; A. Shultz, personal communication), with migration distances varying from 7 km on Eleuthera (Danylchuk et al., 2011) to 100 km on Grand Bahama (Murchie et al., 2015). Multiple migration routes and three spawning aggregation sites have been identified on Grand Bahama (Murchie et al., 2015) but current knowledge of these critical locations on Eleuthera is limited to one site in South Eleuthera.

Acoustic telemetry has been successfully used to identify migrations and aggregation sites of bonefish and other aggregating species (Danylchuk et al., 2011; Murchie et al. 2015; Starr et al., 2007). The overall aim of this study is to determine where bonefish migrate on Eleuthera and to use this information to identify sites for protection from degradation and fishing pressure. The objectives of this study were as follows: (1) locate migrations and spawning locations of bonefish around Eleuthera, (2) simultaneously track island-wide bonefish populations on Eleuthera, and (3) characterize movements between foraging grounds and spawning aggregations. The results of this research can act as a guide for using an island-wide

telemetry array to identify multiple migration routes and spawning locations for nearshore fish species.

METHODS

Study location

This study was conducted on the island of Eleuthera, The Bahamas (24.9314° N, 76.1900° W). Eleuthera measures 180 kilometers long and has an average width of 2 kilometers, separating the deeper east side of the island from the shallower Great Bahama banks on the west side of the island (BNT, 2018; Figure 1.1). The waters surrounding Eleuthera contain a mosaic of seagrass beds (0-2 m), sand bars (0-3 m), mangrove creeks (0-2 m), coral reefs (3-10 m) and rocky bottoms (>20 m). Mangrove creeks and tidal flats on Eleuthera are small systems, often enclosed in bays and coastlines, separated by deeper sand or calcium carbonate (hard bottom) habitats (Figure 1.1). This study was conducted from 2015 to 2017 during late fall to early summer, the time of year when spawning activity is likely or near its peak (Danylchuk et al., 2011; Murchie et al. 2015).

Fish collection

Across the island, fish were tagged from 11 locations; these locations were chosen because they are the main foraging areas for bonefish on Eleuthera. Bonefish were captured by using a seine net (100 m x 1.2 m net, 0.95 cm mesh) through either the block or spot seine technique as described by Murchie et al. (2009). In systems with narrow channels or mouths of mangrove creeks, the seine net was deployed at high tide across the mouth of a mangrove creek. As the water flowed out the creek, bonefish were corralled with the net as they exited the creek system. In wider systems without a channel or mouth, schools of fish were sighted from the shore or a boat. A net was deployed further down the shoreline from the fish and a boat was used

to push fish along the shoreline into the deployed net. After capture, bonefish were transferred to a flow-through holding pen (1/4 inch mesh, 0.6 m x 0.9 m x 1.5 m), which held fish before and after surgery.

Tag deployment

Between December 5, 2015 and February 9, 2016, 39 fish were implanted with a tag; between October 26, 2016 and December 20, 2016, 39 more fish were implanted with tags (Table 1.1). Tag implantation procedures follow those of previous telemetry studies conducted on bonefish (Danylchuk et al., 2011; Murchie et al., 2015). Fish with a minimum fork length of approximately 410 mm were selected for tag implantation so that the tag weight was less than 2% of the fish's body weight (Winter, 1983). All fish were implanted with V13 coded tags (69 kHz, 13 mm diameter, 36 mm long, 6.0 g in water, 45s minimum delay to 135s maximum delay, 513 day battery life; Vemco Inc., Halifax, NS, Canada). To induce stage three surgical anesthesia (total loss of equilibrium and no response to touch stimuli), an individual fish was placed in an anesthetic bath (30 ppm eugenol in seawater, 0.5 ml in 16L seawater) for 3-5 minutes. The fish was then placed supine on a foam-lined trough for the surgical procedure. To ensure the fish remained in stage three anesthesia during surgery, recirculating seawater containing a maintenance dose of eugenol (10ppm, 0.5ml in 52L of seawater) was supplied continuously to the fish's gills using a hose and a small bilge pump. All surgical tools and tags were disinfected with iodine prior to contact with the fish. A 2-3 cm incision was made posterior to the pectoral fins along the ventral midline. The tag was activated and inserted into the coelomic cavity through the incision and two to three simple, interrupted sutures (Ethicon 3-0 PDS II, Johnson & Johnson, New Jersey, USA) were used to close the incision. The fish was also tagged externally using a plastic-tipped dart tag (PDS model, 88 mm long, Hallprint, South Australia, Australia)

for identification in the event of recapture, fork length was measured, and a small fin clip was taken for genetic analysis (n = 77 *A. vulpes*, n = 1 *A. vulpes* x *A. goreensis*). The surgical procedure took an average of 7.10 +/- 2.95 minutes and then the fish was transferred into the holding pen for a recovery period of at least one hour (Danylchuk et al., 2011; Murchie et al., 2009; Murchie et al., 2015). When possible, tagged fish were released with conspecifics to minimize the risk of post-release predation.

Region	Location	Date	Tag ID	FL (mm)	Sex	# of detections in 2015/2016	# of detections in 2016/2017
East	Half Sound	2015-12-09	20878	460	U	177	0
		2015-12-09	20879	495	F	73	0
		2015-12-09	20881	475	F	89	0
		2015-12-09	20885	500	U	5	0
		2015-12-09	20886	440	F	255	0
		2015-12-09	20887	475	U	37	37
		2016-11-12	46860	530	U		731
		2016-11-12	46866	510	U		129
		2016-11-12	46878	460	М		956
		2016-11-13	46867	460	U		7695
		2016-11-13	46872	470	F		14691
		2016-11-13	46879	490	F		129
	Savannah Sound	2016-01-18	39463	430	U	3877	0
		2016-01-18	39478	420	U	8	61
		2016-01-19	39468	450	F	0	13
		2016-02-09	39480	425	U	0	32
		2016-11-10	46861	440	М		52
		2016-11-10	46865	530	U		9
		2016-11-11	46868	520	F		0
		2016-12-08	46863	480	U		31
		2016-12-08	46876	440	М		117
		2016-12-08	46895	440	U		0
North East	Bottom Harbour	2015-12-15	39457	470	F	9	0
		2015-12-15	39482	435	U	0	7172
		2016-01-25	39453	492	F	20	0
		2016-01-25	39472	473	М	12	5172
		2016-01-25	39473*	410	М	371	44087
	Dump Flat	2015-12-15	39477	476	U	14	388
	-	2016-12-05	46882	525	F		0
		2016-12-05	46885	470	М		0
		2016-12-05	46886	500	F		0
		2016-12-05	46887	500	U		107
		2016-12-05	46888	460	U		51
		2016-12-05	46894	470	F		136
North West	Current	2016-01-28	39459	455	F	4096	0
		2016-01-28	39464	452	М	7791	16
		2016-01-28	39465	435	М	0	876
		2016-01-28	39469	500	F	55	0

Table 1.1: Summary of tagging, biological, and monitoring data for 78 bonefish tagged on Eleuthera from 2015 - 2017. Asterisk indicates a hybrid *A. vulpes* x *A. goreensis*.

Table 1.1 (cont'd)

Region	Location	Date	Tag ID	FL (mm)	Sex	# of detections in year 1	# of detections in year 2
		2016-01-28	39474	470	U	5440	0
		2016-01-28	39479	495	F	4844	0
		2016-12-07	41123	445	F		0
		2016-12-07	41124	449	F		167
		2016-12-07	46870	450	U		1857
		2016-12-07	46874	450	U		753
		2016-12-07	46875	500	F		1878
		2016-12-07	46884	440	U		32
South East	Deep Creek	2016-01-20	39471	430	U	75	0
	Hartford Creek	2016-11-01	46862	460	F		0
	John Millers	2016-02-06	39454	480	М	3	0
		2016-02-06	39460	495	F	3	198
		2016-02-06	39470	485	F	0	338
		2016-02-06	39475	457	М	5	1476
		2016-11-29	46880	500	F		68
		2016-11-29	46881	500	F		307
		2016-11-29	46883	470	F		0
		2016-11-29	46889	450	М		1209
	Plum Creek	2015-12-10	20880	475	F	22	0
		2015-12-10	20882	515	U	6	0
		2015-12-10	20883	515	F	122	0
		2015-12-10	20884	495	U	110	0
		2016-10-26	39455	560	U		152
		2016-10-26	41122	495	М		0
	Wemyss Bight	2016-01-21	39458	516	F	31	0
		2016-01-21	39466	523	U	0	7580
		2016-01-21	39476	502	U	0	2110
		2016-01-21	39481	551	F	0	96
		2016-10-27	46864	455	F		2416
		2016-10-27	46869	476	F		28
South West	Kemps Creek	2016-01-08	39456	430	U	3727	0
		2016-01-08	39461	450	F	87	0
		2016-01-08	39462	510	U	448	0
		2016-01-08	39467	550	F	3195	0
		2016-12-20	41121	525	F		0
		2016-12-20	46871	535	F		2
		2016-12-20	46873	505	F		3248
		2016-12-20	46890	440	U		0
		2016-12-20	46891	420	U		47

Table 1.1 (cont'd)

Region	Location	Date	Tag ID	FL (mm)	Sex	# of detections in year 1	# of detections in year 2
South West	Kemps Creek	2016-12-20	46892	420	М		308

Acoustic telemetry arrays

Bonefish movements were recorded on large scale, passive acoustic telemetry monitoring arrays. Acoustic receivers (69 kHz, model VR2W (2015-2016, n = 61; 2016-2017, n = 43), model VR2Tx (n = 1), Vemco Inc., Halifax, NS, Canada) were secured to stations with stainless steel hose clamps (70-95 mm) and zip ties (61 cm); stations consisted of a 0.61 m piece of steel rebar cemented into one side of a cinderblock. Receivers were placed at depths ranging from 1.22 to 24.3 m. Receiver detection was influenced by water depth, wave action, and boat noise. The detection distance ranged from 200 m at the shallowest depths (range tests performed August 2016 and November 2018, 1.5 - 3 m) up to 400 m at the deeper stations (Danylchuk et al., 2011; Murchie et al., 2013). Receivers were stationed away from marinas and in protected areas in order to maximize the detection distance. Receivers were placed approximately 250 m from shore as bonefish have been documented to migrate close to shorelines (Danylchuk et al., 2011; Murchie et al., 2015). Receiver stations were removed permanently during the summer months to avoid potential equipment loss due to hurricanes and bonefish spawning activity is likely minimal during this period (Crabtree et al., 1997; Danylchuk et al., 2011).

From November 23, 2015 to July 4, 2016, a total of 62 receivers were deployed in an array to determine directionality of fish moving out of shallow foraging grounds towards deep water (> 30 m); habitat type and depth were recorded at each location (Figure 1.1, Table S1.1). Receivers were deployed at choke points (areas where wave action, reef, or deep water would likely restrict fish movement close to shore), a strategy that has been employed to locate

potential spawning aggregation sites (Danylchuk et al., 2011; Murchie et al., 2015). Receivers were placed at the mouths of mangrove creeks and/or adjacent to feeding areas to document migrations away from foraging grounds. This receiver array deployment period will be referred to as 2015-2016. These migrations from foraging grounds were used to inform the design of the receiver array the following year, October 18, 2016 to July 29, 2017. This second study period focused on determining finer scale migration routes to potential spawning aggregations in deep water areas in the five regions. Depth and habitat type were recorded at each of the 44 receiver locations (Figure 1.1, Table S1.2). This receiver array deployment period will be referred to as 2016-2017.



Figure 1.1: 2015-2016 acoustic receiver array designed to identify the direction fish migrated from foraging grounds to deep water (A) and the 2016-2017 receiver array (B). Tagging locations were shallow mangrove creeks (i.e., foraging grounds) and receivers were placed in deeper water along potential migration routes. Receiver locations are denoted by yellow circles and tagging locations are denoted with purple triangles.

Visual observations

Snorkel surveys were conducted at the known prespawning aggregation location in South Eleuthera repeatedly between 2015-2017 to confirm the presence of a spawning aggregation of bonefish. Indirect signs of spawning were used to confirm spawning related activity. These indirect signs included spawning-related behaviors of ventral nudging/nuzzling of larger fish by smaller fish, porpoising (fish jumping out of the water and gulping air at sunset), absence of feeding, and fish with swollen abdomens indicating presence of hydrated eggs (Danylchuk et al., 2011; Murchie et al., 2015).

Data analysis

To determine how far fish were moving, the distance between each receiver was calculated using the cost-distance tool (Spatial-Analysis Toolbox, ArcMap 10.5), calculating the shortest path between receivers through the water only instead of Euclidean distance (cell size = 10 m). Detection logs were downloaded into VUE (Vemco Inc., Halifax, NS, Canada) and then exported into Excel and RStudio 3.0 for analyses. Receiver stations were assigned numbers (1-64; Table S1.1) in the first year of the study and, in the subsequent year, receiver stations were named alphanumerically (R1-R43, St28; Table S1.2). As there is little connectivity between mangrove creeks and tidal flats on Eleuthera, the tagging locations on the island were classified into five regions based on proximity of foraging grounds to each other (South West, South East, East, North East, and North West) and analyzed detection data for fish within each region. Migrations were classified as rapid movement (encompassing less than 48 hours) away from foraging areas to deep water followed by rapid movement back to foraging areas several days later (Danylchuk et al., 2011; Murchie et al., 2015). These movements (cm/s) were calculated by the time between the last detection at one receiver to the first detection at a different receiver

divided by the distance between those receivers. This speed calculation is a conservation estimate assuming that fish are traveling the shortest distance between receivers. Days at suspected spawning areas were classified as the days between forward and return migrations, and as such, were only calculated for individuals with migratory movements with both forward and return detections. To determine significance of migration distance, speed, and number of days spent at an aggregation location, a Kruskal-Wallis rank sum test was conducted. If there was significance, a post hoc test to determine what variables were significant was used (Dunn test; Dinno, 2017).

RESULTS

In 2015-2016, 30 out of 38 *A. vulpes* were detected with 34,636 total detections (Table 1.1). In 2016-2017, 15 fish from the previous year and 29 of the 39 newly tagged *A. vulpes* were detected on the array designed to identify migrations to potential spawning sites, with a total of 44 bonefish and 63,519 detections (Table 1.1). From 2015 to 2017, 108 migratory movements by 46 individual fish were recorded (Table 1.2). In 2015-2016, 21 bonefish (13 females, 3 males, 5 unknown sex; 450-550 mm fork length range) were tracked making migrations. In 2016-2017, 31 bonefish (12 females, 6 males, 13 unknown sex; 435-560 mm fork length range) were tracked making migrations. Bonefish were detected migrating in five distinct routes in the South West, North West, North East, East, and South East regions (Figure 1.2). These migrations towards deep water were repeated by individual fish multiple times as well as by multiple fish in each region, thus confirming that these routes were repeatedly used across both years of the study.

Year	Region	Tag ID	Migrations	Size	Sex
2015-2016	North West	39459	1	455	F
		39469	1	500	F
		39479	2	495	F
	North East	39453	1	492	F
		39472	1	473	М
		39457	1	470	F
		39477	1	476	U
	East	20879	1	495	F
		20881	2	475	F
		20885	1	500	U
		20887	1	475	U
	South East	39454	1	480	М
		39460	1	495	F
		39475	1	457	М
		20880	1	475	F
		20883	2	515	F
		20884	3	495	U
		39458	1	516	F
	South West	39461	1	450	F
		39462	1	510	U
		39467	4	550	F
2016-2017	North West	39465	1	435	М
		41123	5	445	F
		46870	4	450	U
		46874	4	450	U
		46875	6	500	F
	North East	39472	3	473	М
		39482	2	435	U
		39477	3	476	U
		46887	1	500	U
		46888	1	460	U
		46894	2	470	F
	East	20879	2	495	F
		20887	3	475	U
		46860	3	530	U
		46866	1	510	U
		46867	2	460	U
		46872	1	470	F

Table 1.2: Number of migratory trips made by individuals in each year of the study across all five regions. There were no significant differences in the number of migrations made by an individual based on sex or tagging region. U represents fish for which sex could not be determined.

Table 1.2 (cont'd)

Year	Region	ID	Migrations	Size	Sex
2016-2017	East	46879	2	490	F
		46861	1	440	М
		46876	1	440	М
	South East	39460	1	495	F
		39470	2	485	F
		39475	4	457	М
		46881	1	500	F
		46889	1	450	М
		39455	2	560	U
		39466	6	523	U
		39476	6	502	U
		39481	1	551	F
		46864	5	455	F
	South West	46873	2	505	F


Figure 1.2: Total detections of bonefish on the 2015-2016 receiver array designed to determine directionality of fish moving out of foraging grounds (A) and on 2016-2017 array to determine migration routes to deep water (B). Number of detections are denoted by the size of the red circle; detections were divided into five quantiles. Receivers with no detections are represented with yellow circles.

South West Region

Three fish were detected in both 2015-2016 and 2016-2017 from December to March migrating 7 km from Kemps Creek to receiver 1/St28, a prespawning aggregation (Figures 1.3, 1.4). Fish were detected during the daytime at the prespawning aggregation site, from 0700-1800 hrs (Figure 1.4). Two fish made the migration more than once (range 1-4 trips). Fish spent an average of 2.57 +/- 2.07 days at the confirmed spawning aggregation location (Table 1.3). In addition, bonefish in aggregations in No Name Harbour were observed to have swollen abdomens, indicating the presence of hydrated eggs; porpoising was also observed when aggregations were present at this location.



Figure 1.3: *South West Region*: Total detections of bonefish on the receiver array in 2015-2016 (A) and on receiver array in 2016-2017 (B). Fish were tagged in foraging grounds. Receivers were placed in deeper water and habitat types not associated with foraging. Number of detections are denoted by the size of the red circle; detections were divided into five quantiles. Receivers with no detections are represented by yellow circles.



Figure 1.4: 2015-2016 detection log for bonefish #39467 tagged in Kemps Creek in the South West region in 2016. Receivers Bull3, 59, Bull1, Bull7, and Bull6 were located along the previously identified migration route from the foraging ground at Kemps Creek to the prespawning aggregation location at receiver 1. Receivers 8 and 9 were placed in deeper water near the shelf edge to document nighttime movements of the aggregation. The fish was detected in the prespawning aggregation site for 1 day on March 29, for 2 days from April 12-13, for 1 day on May 11, and for 3 days between May 19 and May 21, 2016.

Mean Days at Site	SD
4.78	3.50
2.35	1.71
2.57	2.07
	Mean Days at Site 4.78 2.35 2.57

Table 1.3: Mean number of days spent at suspected spawning areas in each region of Eleuthera. The North West region was significantly different from the South East (p = 0.0003) and the South West regions (p = 0.0086).

North West Region

In 2015-2016, three bonefish were detected moving from the tagging location near receiver 54 through a cut between Current Island and Eleuthera (receiver 50) past receiver 49 to a bay east of Spanish Wells at receiver 45 (Figure 1.5). In 2016-2017, five bonefish were detected from January through June moving from R11 through a cut between Current Island and Eleuthera (R12) past R12 along the shoreline (R13, R16, R17, R18), into a bay east of Spanish Wells (R19) and towards deep water (R20, R21) (Figure 1.6). Bonefish were detected at R19, R20, and R21 during the nighttime, between 1800-0500 hrs. Five fish in this region made the migration more than once (range 1-6 trips). The mean migratory distance was 15.03 km (+/-4.17) with a minimum constant speed of 63.73 cm/s (+/- 34.72). Fish spent an average of 4.78 +/- 3.50 days at deep water sites (Table 1.3). The substrate along the coastline of North Eleuthera between receiver 54/R11 and receiver 45/R19 is predominately sandy, ranging at depths between 0.9 and 3 m. Receivers R21 and R22 were placed on coral and rocky substrate at 10 m deep.



Figure 1.5: *North West Region*: Total detections of bonefish on the receiver array in 2015-2016 (A) and on receiver array in 2016-2017 (B). Fish were tagged in foraging grounds. Receivers were placed in deeper water and habitat types not associated with foraging. Number of detections are denoted by the size of the red circle; detections were divided into five quantiles. Receivers with no detections are represented with yellow circles.



Figure 1.6: 2016-2017 detection log for bonefish #41123 tagged in Current Settlement in the North West zone in 2016. Receiver R11 through R18 were placed along the shoreline between the foraging ground and the suspected aggregation area (R18/R19) and receiver R20 was placed in deep water. The fish moved rapidly from its foraging ground area along the migration route to receivers R18/19/20 five times during this study period. The fish stayed at the suspected aggregation area for 4 days from January 2-6, for 4 days from February 24-28, for 2 days from April 5-7, for 4 days from May 2-6, for 6 days from May 31-June 5, 2017.

North East Region

One bonefish was detected in 2015-2016 moving between the tagging location at Dump Flat to receiver 39, 4.88 kilometers away and three fish tagged in Bottom Harbour were detected at receiver 39 (Figure 1.7). In 2016-2017, four fish tagged at Dump Flat were detected from November to June moving from receivers R23, R24, R25, R26, to R27 at Whale Point and to the deep water environment of R28 and R29 (Figure 1.8). Two bonefish tagged in Bottom Harbour were also detected moving between receivers R25, R26, R27 towards R28 and R29 (Figure 1.7). Bonefish were detected at the deep water receivers R28 and R29 during the nighttime, from 1900 to 0500 hrs. Three fish made the migration more than once (range 1-3 trips). The mean migratory distance was 1.51 km (+/- 0.52) with a minimum constant speed of 59.36 cm/s (+/- 31.53). Fish ID 39473, an A. vulpes x A. goreensis hybrid, was tagged in Bottom Harbour in the North East region. In 2015-2016, the hybrid fish was detected repeatedly at receiver 39 between February 17, 2015 to June 25, 2016, three of these detection periods corresponded with at least one other fish tagged in the North East region. In 2016-2017, the hybrid was detected making the same migratory movement as other fish tagged in the region, moving at night from receivers R23 and R24 to receivers R28 or R29, in a deeper water environment (Figure 1.7). The hybrid made this migratory movement eight times between November 11, 2016 and June 4, 2017; four of these migrations corresponded with at least one other A. vulpes tagged in the North East region. Receivers along the inside of Bottom Harbour were placed at depths between 1.2 and 4.9 m. The substrate of Bottom Harbour is almost exclusively seagrass beds. Receivers R28 and R29 were placed at depths of 6.9 and 10.9 m, respectively in sand patches between patch reefs.



Figure 1.7: *North East Region*: Total detections of bonefish on the receiver array in 2015-2016 (A) and on receiver array in 2016-2017 (B). Fish were tagged in foraging grounds. Receivers were placed in deeper water and habitat types not associated with foraging. Number of detections are denoted by the size of the red circle; detections were divided into five quantiles. Receivers with no detections are represented by yellow circles.



Figure 1.8: 2016-2017 detection log for bonefish #39477 tagged in Dump Flat in the North East region in 2016. Receivers R23 through R27 were placed along the shoreline in Bottom Harbour. Receiver R28 was placed in deep water outside of the protected bay of Bottom Harbour. The fish made two movements to deep water, the first occurring from January 3-8 and the second occurring from March 1 to March 3.

East Region

In the East region, three bonefish were detected in 2015-2016 outside of Half Sound at receiver 27 at night, indicating that fish were staying inside of Half Sound during the day and moving out towards deep water at night (Figure 1.9). Thus, in 2016-2017, receivers were placed along the inside eastern shoreline of Half Sound, at depths between 2.7 and 3.4 m in seagrass beds (Figure 1.9). Three fish were detected from November to June moving from R43 to R42, then moving outside of Half Sound at R35 at night, between 1850-0250 hrs (Figure 1.10). Six fish made the migration more than once (range 1-3 trips). The mean migratory distance was 2.03 km (+/- 0.87) with a minimum constant speed away from foraging ground of 48.11 cm/s (+/- 13.96).

Detections from fish tagged in Savannah Sound indicated that fish only move out of the south end, but detection data was limited for this area (Figure 1.9).



Figure 1.9: *East Region*: Total detections of bonefish on the receiver array in 2015-2016 (A) and on receiver array in 2016-2017 (B). Fish were tagged in foraging grounds. Receivers were placed in deeper water and habitat types not associated with foraging. Number of detections are denoted by the size of the red circle; detections were divided into five quantiles. Receivers with no detections are represented by yellow circles.



Figure 1.10: 2016-2017 detection log for bonefish #46867 tagged in Half Sound in the East region in 2016. Receivers R41 through R43 were placed inside Half Sound in the protected bay. Receivers R34 through R36 were placed outside Half Sound in deeper water. The fish made two movements to deep water outside Half Sound, on December 4, 2016 and February 5, 2017; both of these movements occurred at night, indicating that the fish was aggregating inside Half Sound during the daytime and making nighttime movements over the deep reef environment at night.

South East Region

Seven fish tagged in Plum, Wemyss, and John Millers creeks were detected in 2015-2016 moving along the shoreline (R15 and R16) towards R17, an area closest to deep water (Figures 1.11, 1.12). In 2016-2017, ten fish were detected from October to June moving from Plum, Wemyss, and John Millers creeks to an area south of John Millers creek (Figure 1.11). Fish were detected at receivers near deep water (R7, R8, and R9) during the nighttime, between 1830-0600 hrs. Eight fish made the migration more than once (range 1-6 trips). The mean migratory distance was 10.19 km (+/- 0.10) with a minimum constant speed away from foraging ground of 10.64 cm/s (+/- 3.53). Fish spent an average of 2.35 +/- 1.71 days at deep water sites (Table 1.3).



Figure 1.11: *South East Region*: Total detections of bonefish on the receiver array in 2015-2016 (A) and on receiver array in 2016-2017 (B). Fish were tagged in foraging grounds. Receivers were placed in deeper water and habitat types not associated with foraging. Number of detections are denoted by the size of the red circle; detections were divided into five quantiles. Receivers with no detections are represented by yellow circles.



Figure 1.12: 2015-2016 detection log for bonefish #20884 tagged in Plum Creek in the South East region in 2015. Receivers 15 and 16 were placed outside of foraging grounds in shallow nearshore areas between the foraging ground at Plum Creek and the suspected aggregation area. Receiver 17 was placed at the suspected aggregation area in a bay where the shelf edge comes in closest to shore. The fish made rapid movements from its foraging ground to the suspected aggregation area on January 24 and March 1, 2016 and was detected near the suspected aggregation site on January 26, March 1, and March 24, 2016.

Regional comparison of migration patterns

Minimum migratory distances and minimum constant speeds from 2015 to 2017 were grouped by tagging region in Figures 1.13 and 1.14; due to limited number of receivers placed in the migration route in the South West region, detections in this region were excluded from distance and speed analyses. Migration distances ranged from 1.51 km to 15.72 km (Figure 1.13). Bonefish in the North West migrated farther than fish in the North East and East (North West 15.72 km, North East 1.51 km, East 2.03 km, p = 0.000 and p = 0.0124 respectively, Figure 1.13). Bonefish in the South East migrated a longer distance than fish in the North East (South East 10.18 km, p = 0.0138, Figure 1.13). Bonefish in the South East migrated slower than fish in the North East and North West (South East 10.63 cm/s, North East 59.35 cm/s, North West 63.73 cm/s, p = 0.0039, p = 0.0008, respectively, Figure 1.14), and the other regions did not differ significantly from one another (Figure 1.14). The mean number of days spent at an aggregation area was determined for three of the five regions; the East and North East regions were excluded due to limited detections at deep water receivers (Table 1.3). Fish in the North West spent longer at aggregation areas than those in the South East and the South West (North West 4.78 days, South East 2.35 days, South West 2.57 days, p = 0.0003, p = 0.0086 respectively; Table 1.3).



Figure 1.13: Distances of migrations of fish across four tagging regions: East (n = 3), North East (n = 12), North West (n = 23), and South East (n = 5). Significant differences between regions are denoted with differing letters.



Figure 1.14: Migration speed across four tagging regions. Significant differences between regions are denoted with differing letters.

DISCUSSION

This study documented four new migration routes and aggregation areas on Eleuthera, meaning Eleuthera has five total migration routes; this study corroborated the concept of multiple migration routes on one island (Murchie et al., 2015). During this study, 43 fish exhibited migratory movements similar to spawning migrations documented in previous studies (Danylchuk et al., 2011; Murchie et al., 2015) and similar to migrations by fish in the South West region to the known spawning aggregation site at No Name Harbour. Migrations between foraging grounds and deep water areas in the North West, North East, East, and South East regions were documented in this study. Fish were tracked making these migratory movements repeatedly, with some fish repeating the migrations up to six times per year. Fish moved rapidly along migration routes between foraging grounds and deep water sites, suggesting that these fish were not foraging along this route. Rapid movement between foraging grounds and deep water sites, detections in shallow water during the day and movements towards deep water at night, and multiple migrations over the primary spawning period all indicate that these movements were spawning related.

This study was designed to simultaneously track bonefish from 11 foraging grounds, which were separated by deeper water (>5 m). By designing the array to determine directionality of fish migrating away from foraging grounds in 2015-2016, we were able to minimize the number of receivers used in each area while still informing the placement of receivers for the receiver array in 2016-2017. Using detection data from 2015-2016, clustered receivers in 2016-2017 allowed for the identification of migratory routes and suspected aggregation areas in four of the five regions, with the fifth region already having a documented migration route and spawning aggregation site (Danylchuk et al., 2011). Migrations in South West region remained consistent

with Danylchuk et al. (2011), confirming that bonefish use the same migration routes and spawning aggregation sites on a year-to-year basis. Since we tagged fish in the major foraging grounds of Eleuthera, it is likely that we have identified most of the migration routes and aggregation areas on this island. Using an island-wide telemetry approach, this study successfully identified the most migration routes and aggregation areas for bonefish on one island to date.

Migratory distances on Eleuthera are shorter than other documented bonefish migrations, leading to possible differences in energetic demands of migration. Mean migration distances in the five regions of Eleuthera ranged from 1.42 km to 15.71 km, which are shorter distances compared to those documented on Grand Bahama by Murchie et al. (2015), in which fish migrated up to 100 km. Migrations on Eleuthera are likely shorter due to the disparate nature of foraging grounds along Eleuthera's shoreline and close proximity to deep water and shelf edges (>20 m deep) required for bonefish spawning (Danylchuk et al., 2011; Murchie et al., 2015). Comparatively, on many islands in The Bahamas, such as Andros, Abaco, and Grand Bahama, deep water is often located on the opposite side of islands relative to the primary bonefish foraging grounds, thus, fish have to travel greater distances to reach deep water spawning habitats (Murchie et al., 2015). Shorter migration distances could allow for different energetic demands, population dynamics, and migration patterns on Eleuthera than on these other islands as the cost of migration is likely lower. Energetic costs of migration by pink (Oncorhynchus gorbuscha) and sockeye (Oncorhynchus nerka) salmon were shown to differ based on habitat characteristics of natal streams (Standen et al., 2002). Additionally, sockeye salmon in the Fraser River that have shorter, low elevation migrations exhibited lower densities of somatic energy and fewer eggs when compared to salmon with longer, high elevation migrations (Crossin et al.,

2004). Thus, habitat differences along migration routes and migration distance could affect energetic cost of migration for bonefish, resulting in different energetic demands of bonefish within islands and across different islands in The Bahamas. The lower potential cost of migration on Eleuthera could explain the repeated migrations made by 25 fish throughout this study. Future studies could focus on determining energetic cost of migration for bonefish across islands as it could influence the number of spawning migrations made by individuals.

The average minimum migratory speed of fish was 58.63 cm/s, with 15 migrations with speeds over 70 cm/s, though this is likely a conservative estimate given that speeds were calculated as if fish moved directly from one receiver to the next; it is likely fish traveled a greater distance between receivers. Average swimming speeds of bonefish in a wetland mesocosm ranged between approximately 10 - 28 cm/s (Brownscombe et al., 2014). These speeds associated with foraging and non-migratory bonefish behaviors are much slower than those documented in this study, associated with migrations away from foraging grounds. Comparatively, the critical swimming speed for bonefish in a swim tunnel was 96 cm/s at 28 °C (Nowell et al., 2015). Thus, bonefish in this study were moving at speeds approaching their critical swimming speed. Bonefish migratory speeds documented in this study are similar to those of other species in reproductive migrations; sockeye salmon on spawning runs upriver swam at speeds between 30 and 60 cm/s in the Fraser River (Hinch & Rand, 1998) and mutton snapper (Lutianus analis) swam to spawning areas in Dry Tortugas, Florida at approximately 63 cm/s (Hanson et al., 2008). When compared to other studies documenting bonefish swimming speeds, the conservative estimates of bonefish swimming speeds documented in this study indicate rapid movement, comparable to reproductive migratory behavior in other fish species.

In this study, no bonefish tagged in one region were detected in another region. Though it is possible that bonefish without transmitters traveled between regions, due to the distance between foraging grounds and the presence of deep water habitat for spawning within each region, it is unlikely that fish regularly mix between regions. Additionally, foraging grounds on Eleuthera typically host smaller schools of bonefish than on islands with large, connected foraging grounds (i.e. the Marls on Abaco, the north side of Grand Bahama, and the west side of Andros; A. Shultz, personal communication). The lack of fish moving between regions on Eleuthera indicates that deep water (>10 m) may act as a physical barrier, restricting movement for bonefish due to a lack of shallow water habitat connectivity. Additionally, bonefish may experience a greater risk of predation in deep water due to greater abundance of predators; predation risk in The Bahamas has been shown to increase with increasing water depth (Rypel et al., 2007). Similarly, the exposed coastlines of Eleuthera experience more turbulent water, which could act as a barrier to movement. Turbulent waters restrict movement of juvenile brown trout (Cotel et al., 2006). While this study documents a lack of connectivity between regions on Eleuthera as adults, pelagic larvae likely disperse in the currents of deep ocean basins, either to be entrained by circulating currents or rapidly dispersed by fast-moving currents (Hamner & Largier, 2012), which may result in genetic connectivity around Eleuthera and the Bahamian archipelago.

It is possible that the lack of adult bonefish movement between regions is due to the natural barrier of deep water that fish would encounter when attempting to move between regions. In South Eleuthera, the offshore dropoff (>30 m deep) in the Exuma Sound comes in to the coastline between the foraging grounds in the South East and the spawning site in the South West region. Bonefish tagged in the foraging grounds in the South East moved further southeast,

migrating along this shallower route, possibly to avoid the deep-water area. Most documented barriers to fish passage are man-made (i.e. dams, roadways, culverts, etc.), but natural barriers to migration exist as well (Powers & Orsborn, 1984). Nassau grouper have been tracked migrating longer distances around deep water ocean basins rather than moving across open water (>30 m deep; Bolden, 2000; Starr et al., 2007). This study adds to those documenting natural, physical barriers to fish migration; natural barriers on other islands could be used to predict where bonefish migration routes occur throughout the Bahamian archipelago.

This study documented four new migration routes to four distinct sites on Eleuthera, meaning there are five total migration routes for bonefish on one island in The Bahamas. Additionally, fish in the South West region were observed making the same migrations as those documented by Danylchuk et al. (2011), indicating that migration routes and spawning sites remain consistent year to year. These results highlight the importance of habitat connectivity and the nearshore environment on Eleuthera. Bonefish on Eleuthera are migrating shorter distances to potential aggregation sites, but making multiple migrations during the spawning season. The shorter migration distances and, thus, potential lower cost of migration on Eleuthera could lead to increased reproductive output of fish on this island. Future efforts could compare costs of migration across Caribbean Islands and determine how cost of migration influences reproductive output and population dynamics. The findings of this study, along with those of Murchie et al. (2015), suggest that there are multiple bonefish spawning aggregations on every island that hosts populations of bonefish. Future studies could use the habitat characteristics of these five migration routes on Eleuthera, such as depth, bottom type, and proximity to deep water, to predict migration routes on other Caribbean islands using a geographic information system (GIS) and hyperspectral imaging. GIS models have been used to predict barriers to migration in

chinook salmon (*Oncorhynchus tsawytscha*) based on habitat characteristics of an area compared to known characteristics of migration routes (Meixler et al., 2009) and to predict migrations of black bears (*Ursus americanus*) by combining habitat data and expert-opinion (Clevenger et al., 2002). Acoustic telemetry studies remain expensive and time-intensive to achieve results, thus using GIS predictive mapping could be a cost- and time-efficient method for documenting migration routes and spawning aggregation locations of bonefish throughout their range.

Management implications

Migration routes and suspected aggregation areas on Eleuthera are located in nearshore areas; on Grand Bahama, bonefish migration routes are located in areas of coastal development (Murchie et al., 2015). Habitat degradation or intense angling of spawning aggregations could impact reproductive success of aggregations, especially as predators such as coastal sharks are known to consume fish released after capture events (Cooke & Philipp, 2004; Raby et al., 2014). Recently, The Bahamas has initiated a study to identify coastal areas in need of protection through the creation of marine reserves or protected areas. Bonefish were identified as one of several species of economic and ecological importance that should be protected. Unfortunately, on most Bahamian islands, there is a lack of basic information regarding the location of spawning aggregation sites and migration corridors needed for bonefish reproduction, which could be targets for protection.

The areas identified in this study should be protected to support healthy bonefish populations throughout the region. Marine Protected Areas (MPAs) in The Bahamas have been established around critical sites as a result of similar studies identifying spawning aggregations of bonefish as well as grouper and snapper on other Bahamian Islands. In 2008, The Bahamas committed to the Caribbean Challenge Initiative of protecting 20% of their marine area by 2020.

Currently, 18 MPAs protect only 10% of the marine area and there have been no MPAs designated for Eleuthera. This study has the potential to aid in the implementation of Eleuthera's first MPA, protecting critical sites for fisheries. The Bahamas MPA Network centers on protecting representative habitats, including spawning aggregation sites and other such critical habitats, as well as connectivity between habitats (BREEF, 2015). As this study identified critical migratory habitat for bonefish related to reproduction, these areas are ideal candidates for the establishment of protected areas. Additionally, as bonefish on Eleuthera were documented making multiple migrations in this study, the reproductive output on this island could be greater than other islands; as such, the areas identified in this study should be studied to determine reproductive output.

Bonefish support an economically important catch-and-release fishery, supplying jobs to many on the Family Islands and increasing tourism to more remote areas in The Bahamas (Fedler, 2010). Bonefish are culturally, economically, and ecologically important to The Bahamas, especially the Family Islands, like Eleuthera; thus, conservation and management of bonefish is essential for the continued success of this recreational fishery. Effective conservation and management plans must identify critical habitats, including reproductive habitats. Identification of bonefish migration routes and spawning sites throughout the Bahamian archipelago remains important for effective conservation of the fishery. Our study's finding of five migration routes and suspected aggregation sites on one island suggests that each island has the potential to host multiple migration routes and spawning sites. Current knowledge surrounding bonefish reproductive sites throughout their range is limited; future research should aim to identify critical sites so that these sites can be protected.

All research was conducted in accordance with the Institutional Animal Care and Use Committee at Michigan State University (03/17-032-00) and under research permits MAMR/FIS/17 and MAMR/FIS34^A issued by The Bahamas Department of Marine Resources to the Cape Eleuthera Institute. APPENDIX

APPENDIX

Region	Name	Category	Depth (m)	Bottom Type
South West	1	S	0.91	Edge of channel, sandy
	2	S	16.15	Sandy, rocky, reef
	3	S	13.41	Sandy bottom
	4	S	13.41	Patch corals
	5	S	13.72	Big coral heads
	6	S	23.68	Big coral heads
	7	S	20.91	Big coral heads
	8	S	2.74	Sandy hard bottom
	9	S	4.57	Sandy hard bottom
	10	S	5.49	Sand on top of rock
	11	S	20.42	Sandy
	12	S	17.07	Sandy
	13	М	5.94	Sand, coral heads
	58	FG	1.59	Macroalgae & sand
	59	М	4.39	Macroalgae & sand
South East	14	М	2.74	Sandy, algae
	15	М	4.30	Rocky sand, algae
	16	М	2.13	Sandy/rocky
	17	S	2.87	Hard bottom, soft coral nearby
	18	М	5.88	Sand, hard bottom
	19	М	2.39	Sandy
	20	М	0.61	Sandy
	21	М	2.44	Sand, sparse seagrass
	22	М	2.13	Sand, coral rubble
	64	S	1.22	Sandy
East	23	М	8.53	Sandy, shoal grass
	24	М	8.53	Sandy, shoal grass
	25	FG	2.44	Sandy
	26	М	7.01	Sand, some rocks
	27	М	5.49	Sandy bottom
	28	М	0.91	Sandy, turtle grass
	29	M	5.49	Sandy, manatee grass
	30	FG	3.96	Sandy, turtle grass
	31	M	3.96	Sandy, shoal grass
	32	M	2.44	Sandy
	33	M	5.49	Turtle grass
	34	M	8.53	Sandy
	35	M	8.53	Sandy
	36	M	6.10	Sandy
	37	M	5.49	Sandy
	38	M	5.39	Sandy
	61	М	2.44	Sandy, turtle grass

Table S1.1: Description of 2015-2016 acoustic receiver array designed to identify the direction fish migrated from foraging grounds to deep water; category refers to migration routes (M), suspected spawning locations (S), and foraging grounds (FG).

Table S1.1 (cont'd)

Region	Name	Category	Depth (m)	Bottom Type
East	62	М	2.39	Sandy
	63	Μ	0.89	Sandy
North East	39	Μ	6.10	Thick turtle grass
	40	М	6.10	Sand, near reef
	41	М	5.49	Sandy
	42	Μ	2.44	Sand, manatee grass, algae
	43	М	3.96	Sand, algae
	44	Μ	1.83	Sand, turtle grass
North West	45	М	3.05	Sandy
	46	М	0.91	Sand, seagrass
	47	Μ	3.05	Sandy
	49	М	1.22	Hard bottom, algae
	50	М	3.35	Hard bottom, algae
	51	М	3.05	Sand, seagrass
	52	М	5.49	Sand, turtle grass
	53	М	2.13	Sand, turtle grass
	54	FG	3.05	Sand
	55	FG	1.83	Sandy
West	56	М	3.29	Seagrass & sand
	57	Μ	3.29	Seagrass & sand

Region	Name	Category	Depth (m)	Bottom Type
South East	R1	М	2.44	Sandy
	R2	М	2.13	Sandy
	R3	S	1.22	Sand, hard bottom, seafans
	R4	S	3.35	Sandy, corals
	R5	S	1.52	Sandy, seafan, hard bottom
	R6	S	2.74	silty, sand, hard bottoms
	R7	S	21.95	Sandy w/ rock/reef nearby
	R8	S	17.68	Sandy, coral bommies
	R9	S	17.68	Sandy, coral bommies
North West	R10	FG	1.99	Sand
	R11	М	2.69	Sand
	R12	М	0.91	Seagrass
	R13	М	1.83	Sand, seagrass
	R14	М	1.83	Seagrass
	R15	М	1.83	Seagrass, sand
	R16	М	1.22	Sand
	R17	М	0.91	Sandy seagrass
	R18	М	0.91	Seagrass, sand patch
	R19	S	2.44	Sand
	R20	S	3.96	Sand
	R21	S	10.06	Sand, nearby reef
	R22	S	10.06	Flat reef, on rock
	R23	FG	1.89	Seagrass
	R24	FG	1.19	Seagrass
	R25	М	1.19	Seagrass
	R26	М	2.99	Seagrass
	R27	М	4.89	Seagrass
	R28	S	6.89	Sand w/ nearby reef
	R29	S	10.89	Sand w/ nearby reef
East	R30	S	17.68	Sand, rubble
	R31	S	13.11	Sandy, coral bommies
	R32	М	3.66	Sandy
	R33	М	1.83	Sandy
	R34	М	2.13	Seagrass
	R35	М	2.44	Sandy
	R36	S	6.71	Sandy
	R37	S	8.23	Rocky
	R38	М	4.27	Sandy
	R39	S	9.14	Rocky, dead coral
	R40	S	8.84	Low rock grooves w/ sand
	R41	М	1.52	Silty
	R42	FG	2.74	Sand, seagrass
	R43	FG	3.35	Sand, seagrass
South West	St28	S	0.91	Hard bottom, sand/algae

Table S1.2: Description of 2016-2017 acoustic receiver array designed to determine migration routes to deep water; category refers to migration routes (M), suspected spawning locations (S), and foraging grounds (FG).

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CHAPTER 2: CHARACTERIZING THE TIMING OF BONEFISH (*ALBULA VULPES*) SPAWNING MIGRATIONS ACROSS A BAHAMIAN ISLAND

ABSTRACT

Spawning aggregations are spatio-temporally specific; these predictable gatherings draw fish from large catchment areas to specific sites to spawn at certain times of year. Fish that migrate to form spawning aggregations use a variety cues to trigger migration; these cues can be biotic or abiotic. Understanding the triggers of migration and integrating this information into conservation and management plans is critical to ensuring reproductive successes of species, especially if fish are responding to cues that could be impacted by climate change. In The Bahamas, bonefish (*Albula vulpes*) migrate to form spawning aggregations from October to June. Previous studies have suggested that bonefish migrate in response to moon phase, specifically at the new moon and full moon, which are the peaks in the lunar cycle, yet the environmental cues for their migration remain largely unstudied. This study aimed to characterize the timing of bonefish migrations on the Bahamian island of Eleuthera. Bonefish migrate in synchrony across regions of Eleuthera, suggesting that there is an environmental trigger for their migration. Bonefish migrations correlated with the first half of the lunar cycle, high tidal ranges, colder air temperatures, and calmer weather. These findings indicated that there is no single environmental cue for migration in bonefish; as such, a concerted effort to study the environmental cues of migration should be conducted. As bonefish migration correlated with environmental cues like temperature and weather patterns, it is possible that climate change's effects on these environmental variables could impact bonefish reproduction.
INTRODUCTION

Fish migrations, specifically those for the purpose of spawning, result in large schools of fish gathered in specific areas, which attract predators and fishers to exploit these large and predictable aggregations (Domeier & Colin, 1997). The predictable nature of fish spawning aggregations has led to the overexploitation of marine fishes, resulting in the disappearance of spawning aggregations in some sites (Aguilar-Perera, 2006; Sadovy & Domeier, 2005; Sala et al., 2001). Spawning migrations, drawing individuals from large catchment areas to specific spawning sites, can be triggered by both biotic cues, such as an older individual leading younger fish to spawning sites, and abiotic cues, like lunar phase or temperature (de Mitcheson & Colin, 2012; Domeier & Colin, 1997; Johannes, 1978; Leggett, 1977). Understanding when a species will migrate to spawn is a critical aspect of understanding population dynamics and the ecology of species.

Marine fishes often optimize spawning when they use the same environmental triggers for migration across the entire catchment area. Synchrony of spawning adults can increase reproductive output by saturating egg predators (Johannes, 1978), and ensuring larval settlement at particular times of year (Christy, 1978). Synchrony of migration may also benefit adults by reducing the risk of predation (by schooling to avoid predation) at spawning sites or in migration routes (Robertson et al., 1990). To achieve synchrony, the cues for migration must be consistent and observable across the catchment area; as such, fish respond to various environmental triggers, the best studied of which include moon phase and temperature (de Mitcheson & Colin, 2012; Johannes, 1978). For example, while the cubera snapper (*Lutjanus cyanopterus*) spawns across many months, from March to October, spawning activity and spawning aggregations size peaks at the full moon (Heyman et al., 2005). Many tropical marine species use moon phase as a

cue to migrate, as moonlight is easy to perceive through clear, tropical waters (Colin et al., 1987), but which moon phase triggers spawning depends on the species. For example, coral trout (Plectropomus leopardus) spawn during the new moon (Samoilys, 1997) and Nassau grouper (*Epinephelus striatus*) form spawning aggregations during the full moons in the winter (Colin, 1992). Lunar periodicity may correlate with spawning because the tidal influences may increase larval survival as most species that form spawning aggregations have pelagic larval stages (de Mitcheson & Colin, 2012; Johannes, 1978). Strong tidal phases associated with peaks in the lunar cycle, the new moon and the full moon, would likely move more larvae away from complex reefs than weak tides (e.g., quarter moon) by pulling larvae into pelagic environments with fewer egg predators (Shapiro et al., 1988). Tide phase drives spawning migrations of striped mullet (Mugil cephalus) and white mullet (M. curema) in the Gulf of Mexico (Ibáñez & Benítez, 2004). Temperature has also been found as the trigger for migration and spawning in many fish species (de Mitcheson & Colin, 2012; Johannes, 1978; Leggett, 1977), especially for fishes found in temperate zones where temperature regimes vary significantly across seasons (Dahl et al., 2004; Humston et al., 2000). Migration patterns can also be related to weather patterns, photoperiod (Johannes, 1978), sunlight, geomagnetic fields, and olfaction (Leggett, 1977). The different environmental variables that can serve as cues for migration must remain constant over large areas to attract individuals from the entire catchment area to spawning sites.

Understanding the temporal patterns of fish migration and spawning and the associated environmental triggers is important when considering how climate change will impact fish species. Climate change is expected to affect fish in various ways, from food availability to habitat connectivity and dispersal patterns (Lett et al., 2010; Petitgas et al., 2013); similarly, climate change can impact the timing of migration. For fish species that migrate and spawn in

relation to colder water temperatures, increasing water temperature associated with climate change could result in less fish migrating and, thus, less reproductive output in the future (Walther et al., 2002). For example, increased temperatures due to climate change resulting in early migrations of flounder (*Platichthys flesus*; Sims et al., 2004). Changes in reproductive timing could result in altered dispersal of pelagic larvae because this life stage depends on seasonal currents, ultimately affecting structure and dynamics of future populations (Lett et al., 2010). As a result, determining how fish migration is related to environmental variables is critical to predicting how climate change will influence a species.

Bonefish (*Albula vulpes*) are one of many tropical fish species that migrate to form spawning aggregations in The Bahamas (Danylchuk et al., 2011; Murchie et al., 2015). Bonefish support a recreational, catch-and-release fishery valued at \$141 million USD annually in The Bahamas (Felder, 2010). Previous acoustic telemetry studies found that adult bonefish forage in shallow tidal areas and mangrove creeks (Murchie et al., 2013) and make migrations to deep water to form spawning aggregations between October and May (Danylchuk et al., 2011; Murchie et al., 2015). Larval recruitment studies indicate that peaks in spawning occur from October to January with another peak in June (Mojica et al., 1995). Similarly, gonadosomatic indices showed that spawning occurred between November and June, indicating a prolonged spawning season (Crabtree et al., 1997; Murchie et al., 2010). While spawning occurs across a large time scale, it is likely that fish use environmental cues to form large spawning aggregations during certain times across the spawning season.

Bonefish have been documented to have an extended spawning season, studies have suggested that there are peaks in activity, possibly seasonally driven (Crabtree et al., 1997; Murchie et al., 2010). Telemetry data indicated that bonefish migrate in response to lunar phase,

specifically that bonefish spawn during the new and full moons (Danylchuk et al., 2011; Murchie et al., 2015). Johannes (1978) also noted that another species of bonefish in Palau spawn between lunar days 27-4, peaking near the new moon. Additionally, as bonefish have pelagic leptocephalus larvae (Jordan, 1905; Gill, 1907), it was suspected that they would spawn in relation to tidal range to increase the ability of their larvae to reach pelagic environments post-spawn. Other fish species spawn in relation to the strongest tidal pull to reduce egg predation from complex reefs (Shapiro et al., 1988). Spawning patterns in bonefish could also be driven by temperature and weather patterns as they are in other tropical fishes (Johannes, 1978). Many tropical marine species migrate and spawn during winter months, possibly using cooler water temperatures as a cue to migrate. Additionally, as bonefish are often observed avoiding areas with high wave action, it was suspected that during stormy or rough weather they would avoid migration routes, which are often located in exposed areas. The potential environmental cues for migration in bonefish have not been investigated across multiple locations and years.

The overall aim of this study was to characterize the timing of bonefish spawning migrations across an island. The objectives of this study were (1) to determine if bonefish migrate in synchrony across an entire island, Eleuthera, and (2) to determine what environmental variables (e.g. moon phase, tidal range, temperature, wind speed, or precipitation) correlate with bonefish migration on Eleuthera. Understanding fish migration patterns and triggers will help inform management and conservation of this economically important species.

METHODS

Study location

This study was conducted on the island of Eleuthera, The Bahamas (24.9314° N, 76.1900° W). Eleuthera measures 180 kilometers long and has an average width of 2 kilometers, separating deeper east side of the island from the shallower Great Bahama banks on the west side of the island (BNT, 2018). The waters surrounding Eleuthera contain a mosaic of seagrass beds (0-2 m), sand bars (0-3 m), mangrove creeks (0-2 m), coral reefs (3-10 m) and rocky bottoms (>20 m). Mangrove creeks and tidal flats on Eleuthera are small systems, often enclosed in bays and coastlines, separated by sand or calcium carbonate (hard bottom) habitats. This study was conducted over two years during the expected spawning peak (Danylchuk et al., 2011; Murchie et al., 2015): the periods of November 23, 2015 to July 4, 2016 will be referred to as 2015-2016 and October 18, 2016 to July 29, 2017 will be referred to as 2016-2017.

Fish collection and tag deployment

Bonefish were collected and tagged in 11 main foraging areas on Eleuthera. Fish were captured in seine nets (100 m x 1.2 m net, 0.95 cm mesh) as described by Murchie et al. 2009 and as outlined in Chapter 1. In 2015-2016, 39 fish were implanted with V13 coded tags (69 kHz, 13 mm diameter, 36 mm long, 6.0 g in water, 45s minimum delay to 135s maximum delay, 513 day battery life; Vemco Inc., Halifax, NS, Canada) between December 5, 2015 and February 9, 2016. In 2016-2017, 39 fish were implanted with V13 tags between October 26, 2016 and December 20, 2016. The surgical procedure for tag implantation is described in Chapter 1.

Acoustic telemetry arrays

Fish were tracked at the island level using a passive acoustic telemetry array made up of acoustic receivers (69 kHz, model VR2W (2015-2016, n = 61; 2016-2017, n=43), model VR2Tx

(n = 1), Vemco Inc., Halifax, NS, Canada) deployed around the island of Eleuthera. Receivers in 2015-2016 of the study were deployed to determine directionality of fish moving away from foraging grounds. Receivers in 2016-2017 were deployed in suspected migration routes and aggregation areas to identify important reproductive habitats for bonefish. Array design, deployment, and detection range are described in Chapter 1.

Environmental variables

Environmental variables were collected throughout the length of the study using passive environmental monitoring devices. Lunar day was determined based on the 30-day lunar cycle with day 1 representing the new moon and day 15 representing the full moon. Tidal range was calculated from the tide data published by the National Oceanic and Atmospheric Administration (Eleuthera Island, station TEC4627, NOAA Tides and Currents). Tidal range (cm) was calculated as the height of the peak high tide at night subtracted from the height of the next low tide for each day of the study period. Weather data (air temperature, wind speed, and precipitation) was collected by Weather Underground from the Nassau International Airport station from 2015 to 2017 because this was the closest weather station to Eleuthera. Air temperature (Celsius) was used as a proxy for water temperature because receiver depth and therefore relative water temperature varied across the island. Wind speed (km/hr) and precipitation (mm) were used to understand how bonefish movements are impacted by varying degrees of severe weather.

Data analysis

Detection logs were downloaded into VUE (Vemco Inc., Halifax, NS, Canada) and then exported into Excel and RStudio 3.0 for analyses. For each day of the study, the number of individual fish detected in a migration routes and aggregation areas was determined. Initial

detections of fish in migration and aggregation areas were determined. Additionally, the number of regions on Eleuthera (see Chapter 1) in which fish were detected in migration routes and aggregation areas was determined. Migrations away from foraging grounds towards spawning habitat were included and migrations back to foraging grounds were excluded from analyses to ensure analyses were addressing what environmental variables were associated with fish initially moving into migration routes and aggregation areas. Individual environmental variables (e.g. lunar day, air temperature, etc.) were correlated with spawning-related migrations and presence at aggregation sites. The number of fish detected was then compared to lunar day using circular statistics because of the cyclical nature of the moon phases across months (Oriana 4.0 software; Kovach, 2011). The mean lunar day was determined if the data passed Rayleigh's test. Rao's spacing test was applied to determine if the detection data was uniformly distributed across the lunar cycle. First, the day on which fish were initially detected in migration routes and aggregation areas was compared to tidal range, air temperature, wind speed, and precipitation using a linear model and tested for significance using an ANOVA. Because the placement of receivers was in 2016-2017 was concentrated around suspected aggregation sites, a second comparison was conducted to determine if any environmental variables correlated with the number of fish detected in migration and aggregation areas. Comparisons of number of fish detected in migration routes and aggregation areas to season, tidal range, air temperature, wind speed, and precipitation were conducted in RStudio using a linear model and tested for significance using an ANOVA.

RESULTS

In 2015-2016, 30 of 39 tagged bonefish were detected on the receiver array; of those 30 fish, 21 were detected making 29 migrations throughout the study period; 0 - 3 individual fish

were detected daily in migration routes and aggregation areas (median = 0 for 2015-2016 study period). In 2016-2017, 44 fish were detected on the receiver array (15 fish tagged in 2015-2016 and 29 of 39 fish tagged in 2016-2017); of those 44 fish, 31 were detected making 79 migrations throughout the study period, a range of 0 – 10 individual fish were detected daily in migration routes and aggregation areas (median = 1). The greatest number of fish were detected in these areas occurred between January and May in 2015-2016 and between December and March in 2016-2017 (Figure 2.1). In 2015-2016, there were only six days over the course of the study in which fish were detected in migration and aggregation areas in more than one region across the island of Eleuthera (Figure 2.2 A). In 2016-2017, there were 14 days in which fish were detected in migration areas in at least two regions on Eleuthera (Figure 2.2 B). When comparing detections across all five regions, fish were detected migrating in at least two regions every month in 2016-2017, with the most fish migration occurring between December and March (Figure 2.3).



Figure 2.1: Daily detection data for fish in migration and aggregation areas represented as percent of fish tagged for 2015-2016 (A, n = 30 fish tagged and detected on array) and 2016-2017 (B, n = 44 fish tagged and detected on array). Gray area represents period during which arrays were deployed.



Figure 2.2: Number of regions (0-5) in which bonefish were detected in migration and aggregation areas for each day of the detection period in 2015-2016 (A) and 2016-2017 (B). Gray area represents period during which arrays were deployed.



Figure 2.3: Daily detections of fish in migration and aggregation areas in 2016-2017 by region, North West (A), North East (B), East (C), South East (D), and South West (E). Gray area represents time periods when fish were detected in at least two regions in migration and aggregation areas.

Lunar day

The mean lunar day for the initial detection of fish in migration routes and aggregation areas was day 8.15 (Rayleigh's test, p < 0.0001, Figure 2.4). The pattern of initial detection data was not uniformly distributed across each day of the lunar cycle (Rao's spacing test, p < 0.01, Figure 2.4). There were two distinct peaks in the lunar cycle, with the most fish initially detected migrating on days 6 and 15 (two days before the first quarter moon and the full moon, respectively, Figure 2.4). The mean lunar day for fish detected in migration routes moving towards aggregation areas was day 8.81 (Rayleigh's test, p < 0.0001, Figure 2.5). The pattern of this detection data was not uniformly distributed across each day of the lunar cycle (Rao's spacing test, p < 0.01, Figure 2.5). Most fish were detected migrating towards aggregation areas during the first half of the lunar cycle, the period from new moon to full moon (Figure 2.5).



Figure 2.4: Total count of fish detected initially in migration routes or aggregation areas across the lunar cycle from 2015 to 2017 (n = 123 initial detections). Lunar day (1-30) appears around the outside of the plot; peaks in the lunar cycle are represented by the symbols (black circle = new moon on day 1, half circle = first quarter moon on day 8, open circle = full moon on day 15, and half circle = third quarter moon on day 23). Each of the bars represents the total number of fish detected in migration routes and aggregation areas throughout the study period. Increasing number of individual fish detected is represented by darker blue colors.



Figure 2.5: Total number of fish detected on each day of the lunar cycle from 2015 to 2017 (n = 52 fish, n = 108 migrations). Lunar day (1-30) appears around the outside of the plot; peaks in the lunar cycle are represented by the symbols (black circle = new moon on day 1, half circle = first quarter moon on day 8, open circle = full moon on day 15, and half circle = third quarter moon on day 23). Each of the bars represents the total number of fish detected in migration routes and aggregation areas throughout the study period. Increasing number of individual fish detected is represented by darker blue colors.

Tidal range

The mean tidal range for 2015-2017 was 78.00 ± 16.83 cm. Tidal range did not correlate significantly with the initial movement of bonefish into migration and aggregation areas (ANOVA, p = 0.2446, Figure 2.6 A). Tidal range also did not correlate significantly with the number of fish detected in migration routes and aggregation areas (ANOVA, p = 0.1329, Figure 2.7 A).

Air temperature

The mean air temperature for 2015-2017 was 25.05 ± 2.86 degrees C. Lower air temperature correlated significantly with the initial movement of bonefish into migration and aggregation areas (ANOVA, p = 0.0502, Figure 2.6 B). Additionally, lower air temperature correlated with more fish detected in migration routes and aggregation areas (ANOVA, p < 0.0001, Figure 2.7 B).

Wind speed

The mean wind speed for 2015-2017 was 9.90 ± 5.93 kilometers per hour. Lower wind speed correlated with more initial detections of bonefish in migration routes and aggregation areas (ANOVA, p = 0.0075, Figure 2.6 C). Lower wind speed also correlated with more fish detected in migration routes and aggregation areas (ANOVA, p = 0.0341, Figure 2.7 C).

Precipitation

The mean precipitation for 2015-2017 was 2.04 +/- 7.12 mm. Precipitation did not correlate significantly with the initial movement of bonefish into migration and aggregation areas (ANOVA, p = 0.2217, Figure 2.6 D). Lower precipitation correlated with more fish detected in migration routes and aggregation areas (ANOVA, p = 0.0128, Figure 2.7 D)



Figure 2.6: Count of initial detections of fish in migration routes and aggregation areas compared to tidal range (A), air temperature (B), wind speed (C), and precipitation (D) for 2015-2017. Lines represent linear models.



Figure 2.7: Number of fish detected in migration routes and aggregation areas compared to tidal range (A), air temperature (B), wind speed (C), and precipitation (D) for 2015-2017. Lines represent linear models.

DISCUSSION

The synchrony of bonefish movements into migration routes and aggregation areas across multiple regions of Eleuthera indicated that bonefish use environmental cues to trigger migration. This study suggests several environmental cues such as lunar phase, air temperature, and weather correlate individually with bonefish migrations. Variation in annual patterns of bonefish migration are likely related to the two different arrays used in this study as the receiver array in 2016-2017 had more receivers in migration and aggregation areas than the array in 2015-2016. Additionally, in 2015-2016, lack of synchrony of migration between regions is likely due to the limited number of migration detected as there were only 39 fish tagged. In 2016-2017, 39 more fish were tagged and the increased array deployment period allowed for more detections of fish migrations, allowing for more statistical power in the analyses. Over the two years of this study, bonefish were detected in migration and aggregation areas across from October to June, though peaks in detections occurred from December to March. This result supports the findings of previous studies that the spawning season for bonefish is protracted, with increased activity in the colder months, but spawning occurs between October and June (Crabtree et al., 1997; Danylchuk et al., 2011; Mojica et al., 1995; Murchie et al., 2015). Fish were detected in migration and aggregation areas across all five regions of Eleuthera in January and February and activity in multiple regions simultaneously occurred from December to March. This synchrony of migrations across Eleuthera suggests that fish must be responding to environmental cues that are apparent at an island scale.

One of the main suspected migration triggers for bonefish is the lunar cycle, specifically the full and new moons. There were two peaks associated with two days before the first quarter moon and the full moon when compared to the initial day of detection in migration routes and

aggregation areas. Migrations towards aggregated areas occurred evenly across the first half of the lunar cycle. Thus, we hypothesize that bonefish migrate in response to the increasing light at night during the waxing phases, from the new moon (day 0) to the full moon (day 15). Bonefish could also use this cue to take advantage of strong tides after the new moon to increase larval dispersal and survival. Comparatively, other marine fishes that aggregate to spawn tend to have distinct peaks in spawning-related activity in the days before and after either the new moon or the full moon (Colin, 1992; Heyman et al., 2005; Samoilys, 1997). Lunar cycle cues are assumed to be related to either adult synchrony, to increase reproductive output, satiate predators on adults, or increase larval survival with strong tidal pull to sweep larvae away from egg predators on the reef complex (Johannes, 1978; Shapiro et al., 1988). This study indicates that bonefish on Eleuthera use the increasing light from the waxing phase (days 0-15) of the moon at night to trigger migration across catchment areas to spawning sites.

It has been hypothesized that fish that spawn in response to the lunar cycle are doing so due to tidal influences (Johannes, 1978). As bonefish spawn in deep water environments, typically over reef complexes, where egg predators are prevalent, spawning-related activity would correlate with the tidal range, or how strong the tidal pull is during a time period. It was hypothesized that spawning related activity would increase for bonefish as the tidal range increased, which correlates with the largest difference in the water level of tidal phases. There was no correlation between tidal range and bonefish migration in this study. Fish could be responding to tidal influences on a finer scale, specifically by cueing into the presence of currents at spawning sites or the timing of tidal changes (Sancho et al., 2000). Bonefish aggregations spawn at night near deep-water shelf edges, so it is possible that tidal flows and currents could influence when and where bonefish spawn at night. Future studies could use flow

meters to track currents at bonefish spawning sites while tracking aggregation movements at a finer scale in order to understand how water flow influences where and when bonefish release gametes.

As bonefish spawning has been suggested to peak in the winter months (Crabtree et al., 1997; Danylchuk et al., 2011; Mojica et al., 1995; Murchie et al., 2015), it was suspected that the number of fish in migration routes and aggregation areas would decrease in response to increasing temperature. Bonefish migration correlated with lower air temperatures. However, to avoid equipment loss during hurricane season, receivers were deployed in the colder months, so temperature preference could be biased by the time period during which the array was in place. Additionally, temperature patterns in the tropics are less clearly pronounced than in temperate regions and less likely to be used as a cue for spawning migrations of tropical species (Leggett, 1977). Air temperature likely does not influence water temperature at receivers placed in deeper water as readily as shallower receivers, thus, in the future, temperature loggers could be placed alongside acoustic receivers at spawning sites to better estimate in-situ temperature that fish would be experiencing.

While bonefish are known to have an extended spawning season, it was suspected that they would prefer to migrate during calm weather to avoid adverse weather conditions. Specifically, bonefish are known to avoid areas with increased wave action (A. Shultz, personal communication) and as most of the migration routes and aggregation areas are in exposed areas of Eleuthera, it was suspected that fewer bonefish would be detected in these sites as wind and precipitation increased. Wind and precipitation had negative relationships with the number of fish detected in migration and aggregation areas. Nearshore waters are strongly affected by high wind speeds, so it is expected that bonefish would avoid swimming through rough waters.

However, this could be biased because detection ranges of acoustic receivers are influenced by wind and wave conditions (Heupel et al., 2006), resulting in fewer fish detections during periods of increased wind and wave action. Avoidance of rough weather conditions in migration and aggregation areas by bonefish could also be related to turbidity, which would increase with increasing wind and precipitation. Similarly, juvenile coho salmon (*Oncorhynchus kisutch*) avoid areas of increased turbidity (Bisson & Bilby, 1982). Bonefish could be avoiding areas of potential increased predation like deep water environments during conditions that would cause decreased water visibility. While the findings of this study indicate that bonefish did not migrate during rough weather conditions, observations at known spawning sites should be conducted across various conditions to understand how weather conditions could impact spawning activity and behavior at aggregation sites.

In this study, bonefish were detected in migration routes and aggregation areas throughout most of the study period, with increasing activity during the first half of the lunar cycle and lower temperatures, wind speeds, and precipitations. Receivers in this study were placed with the intention of identifying critical bonefish habitat; to better understand the triggers to migration, receivers should be placed inside foraging grounds, along migration routes, and at aggregation areas to determine when bonefish initiate migration and arrive at spawning sites. As analyses were done for individual environmental variables, it is possible that bonefish are relying on a combination of these and other possible cues. Future studies could track bonefish migrations across multiple years to understand how this pattern changes annually and then generate a model with multiple environmental variables to predict spawning (Paragamian & Kruse, 2001). Furthermore, while bonefish on Eleuthera may respond to these environmental variables, these patterns may not hold true for other Bahamian islands. In order to more effectively study the

environmental triggers of migration in bonefish, several populations of bonefish need to be tracked simultaneously across the Bahamian archipelago to determine how these patterns vary across different spatial scales. This would also allow for better estimation of larval dispersal since currents change over the year.

When attempting to understand how fish from various sites throughout the catchment area migrate at once to a spawning site, it is often assumed that a single or several environmental triggers that remain consistent across the catchment area are used as triggers to migrate (Johannes, 1978). However, as the migration and spawning season for bonefish is extended, it is possible that there is a behavioral component to migration. Specifically, one or several fish may act as a leader to whole schools of fish in foraging grounds, leaving the foraging ground and triggering other fish to follow. This has been documented in French grunts (Haemulon *flavolineatum*); juveniles follow older fish along migration paths, learning migration paths from resident adults (Helfman et al., 1982; Helfman & Shultz, 1984). Similar social learning of migration patterns was documented in transplanted bluehead wrasse (*Thalassoma bifasciatum*) over a period of 12 years (Warner, 1988). Bonefish could learn migration routes and timing socially from older individuals in foraging grounds. Transplant experiments of juveniles and newly recruited adults could be used to determine the extent to which migration is socially learned in bonefish. Fish migrations could also be a result of both behavioral and environmental cues, resulting in migration (Hubbard et al., 2004). Future studies could integrate biotic and abiotic cues, such as the ones identified in this study, to model bonefish migration.

The findings in this study suggest that the triggers for spawning migrations and aggregations for bonefish are complex. Migration activity on Eleuthera is driven by the lunar cycle, and temperature, with wind, rain, and biotic factors likely playing a lesser role.

Understanding temporal patterns of spawning is important when the impacts of climate change are taken into consideration. Environmental triggers for migration like storm activity and water temperature will likely be impacted by climate change (Walther et al., 2002). As temperature and storm activity increases, bonefish spawning may decrease or larval recruitment may decrease, resulting in decreased stocks in the future, threatening the health of this economically important recreational fishery. Future work should focus on further clarifying the temporal patterns of spawning and migration to understand how this species will be impacted by climate change and to develop potential mitigation techniques. Many previous acoustic telemetry studies have used movement data to study possible environmental cues of migration; however, these studies were intended to primarily identify spatial distribution of species, not the environmental factors associated with movement (Bijoux et al., 2013; Danylchuk et al., 2011; Murchie et al., 2015; Semmens et al., 2010; Zeller, 1998). It is evident that concerted efforts need to be made to study biotic and abiotic cues of migration at various temporal and spatial scales. By determining what behavioral and/or environmental cue(s) can predict when bonefish will migrate to reproductive areas, population dynamics and the potential impacts of climate change on bonefish can be investigated. Managers can conduct surveys of spawning adults to better estimate abundance of adult fish and reproductive output. Further investigations into bonefish reproductive ecology will improve current management of this species as knowledge is still limited and incomplete throughout their range. This study was an important step towards identifying that bonefish use environmental cues to trigger migration; we strongly encourage that future studies take place as environmental and behavioral cues could change due to climate change, impacting bonefish migration and reproduction.

All research was conducted in accordance with the Institutional Animal Care and Use Committee at Michigan State University (03/17-032-00) and under research permits MAMR/FIS/17 and MAMR/FIS34^A issued by The Bahamas Department of Marine Resources to the Cape Eleuthera Institute. LITERATURE CITED

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