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Movement patterns of bonefish (*Albula vulpes*) in tidal creeks and coastal waters of Eleuthera, The Bahamas

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ABSTRACT

Bonefish (*Albula* spp.) are a group of fishes that inhabit tropical and subtropical marine waters worldwide. Large gaps in our understanding of the ecology of these fishes exist despite their economic importance as a sport fish and their potential role in the ecological functioning of coastal systems. Using a passive acoustic telemetry array, we monitored the movement patterns of *A. vulpes* along the north coast of Cape Eleuthera, The Bahamas. During the course of the study, we successfully detected 15 individuals for periods exceeding six months that permitted us to observe several previously unknown movement patterns for bonefish. Data indicate that bonefish exhibit periods of site fidelity where they repeatedly visit the same tidal creeks, interspersed with transient periods (up to 339 days) in which they utilize large areas of shallow coastal habitats or disappear from the study area entirely. Relative activity space, as measured by minimum linear dispersal, median distance traveled, and mean number of receivers visited daily, did not vary with fish size. Individuals associated in schools tended to display nearly synchronous movements. School-fidelity in bonefish may be influenced by school size, the duration in which an individual has been in the school, and the frequency with which schools mix. Bonefish responded to tidal influences and tended to move out of tidal creeks on outgoing tides and into creeks or shallow habitats during incoming tides. There was also evidence of increased use of tidal creeks during daytime when controlling for tidal phase. Seasonal movements toward the seaward portion of the array likely correspond with spawning. In general, the movement patterns of bonefish we observed demonstrate the importance of this species in the connectivity between nearshore (e.g., mangrove tidal creeks) and offshore habitats. Moreover, because residency patterns in a given area vary greatly among individuals and over time, this work points to the need to examine population mixing and spatial ecology over larger temporal and spatial scales.

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1. Introduction

With over 60% of the world's population living in a coastal band 50 km wide, and half of these residents in developing countries

(Barnabé and Barnabé-Quet, 2000), degradation of coastal environments is widespread. Mangrove forests, which once covered more than 200 000 km² of coastline in tropical and subtropical latitudes (Duke et al., 2007), have been heavily exploited by humans for aquaculture, timber, industry, tourism and other coastal developments (Alongi, 2002; Blaber, 2007). Destruction of mangroves results not only in the direct loss of ecosystem services provided by such habitats, but also indirect losses of services provided by the habitats connected to mangroves (Boaden and Seed, 1985; Kathiresan and Bingham, 2001). Over the decades, public and political recognition of this major transformation in the coastal zone

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has been scant (Valiela et al., 2001). It was not until after the 2004 Indian Ocean tsunami that the importance of mangroves for coastal protection received attention, as the greatest loss of human life occurred in areas where there was no vegetation to absorb wave energy (Williams, 2005). With the increased perception of the value of these natural resources (Williams, 2005) and the current momentum for ecosystem-based management plans (Hofmann and Gaines, 2008), there is a critical need for life history data on the organisms occupying nearshore coastal areas.

Shallow flats (<4 m) in tropical and subtropical coastal marine environments represent a transition zone between the land and sea. This ecotone consists of a number of habitat types including mangrove forests, seagrass beds, algal and sand plains, as well as patch reefs. Because of the regular submersion and exposure of mangrove habitats associated with semidiurnal tides in most tropical and subtropical areas, few fish can use these immediate nearshore areas exclusively, but rather move in and out of these areas, using alternative habitats such as seagrass beds when mangroves are unavailable at low tide (Sheaves, 2005). As such, the habitat mosaic comprising flats systems are inherently interconnected not only through physicochemical processes associated with tidal cycles, but also through the biota that move among them (Moberg and Folke, 1999; Semeniuk, 2005; Mumby, 2006).

Because the movement of organisms promotes energy flow across habitat boundaries (Depczynski et al., 2007; Gaines et al., 2007), knowledge of the spatial distribution of animals is fundamental to the basic understanding of ecological functioning within an ecosystem (Abecasis et al., 2009). To understand or predict the distribution of organisms among various available habitats, it is necessary to track individuals moving about freely in their natural environment (Claireaux et al., 1995). Empirical studies of the unrestrained movement of animals are facilitated through the use of biotelemetry, where spatial ecology and environmental relations under natural conditions can be investigated (Lucas and Baras, 2000; Cooke et al., 2004; Childs et al., 2008).

Bonefish (*Albula* spp.) are a group of fishes that inhabit tropical and subtropical marine waters worldwide (Pfeiler et al., 2000) that not only demonstrate the interconnectedness of the habitats found in tropical tidal flats and tidal creeks, but also the connectivity of the flats with other marine ecosystems. Throughout much of their distribution, it is thought that bonefish move onto shallow flats to feed on invertebrates and small fish during high tide, and then move into deeper water presumably to digest and defecate at low tide (Colton and Alevizon, 1983a, 1983b; Humston et al., 2005), serving as nutrient transporters. Because bonefish are a schooling species and can be found in groups of hundreds to thousands (see Johannes and Yeeting, 2000; Danylchuk et al., 2011) they can account for a significant portion of the fish biomass in tidal flat areas, influencing the distribution of benthic prey (see Engstrom, 1984). Bonefish also carry the distinction of being a popular sport fish and thus play an important role in many local economies (Pfeiler et al., 2000; Ault, 2008; Danylchuk et al., 2008). To date, there have been three published studies using biotelemetry to study the spatial ecology of *A. vulpes* with the intent of examining individual movements – two studies in Florida (Humston et al., 2005; Larkin et al., 2008) and one in The Bahamas (Colton and Alevizon, 1983b). There was an additional study on a congeneric species (*A. glossodonta*) in an area of the central Pacific approximately 1600 km south of Hawaii (Friedlander et al., 2008). Unfortunately, because these studies were hampered by low sample sizes of fish studied ($n \leq 3$) or by limited recording periods (i.e., days to months) they were unable to conduct rigorous analyses of the data to characterize temporal trends across seasons or years.

The objective of this study was to document the spatial ecology of bonefish (*A. vulpes*) on tidal flats and in tidal creek areas near Cape Eleuthera, Eleuthera, The Bahamas. Using acoustic telemetry,

we investigated patterns of habitat use, relative activity space of individuals, schooling behavior, and the influence of tidal cycles. Collectively this work will serve to fill a critical knowledge gap in bonefish ecology, and will be useful for developing single-species (i.e., bonefish) and ecosystem-based management plans.

2. Materials and methods

2.1. Study site

This study was conducted along a 23 km section of the north coast of Cape Eleuthera, Eleuthera, The Bahamas (N 24° 50' 05" and W 76° 20' 32") (Fig. 1). A number of tidal flats and four distinct tidal creeks (Page Creek, Kemps Creek, Broad Creek, and Starved Creek) are located along this stretch of coastline. The creeks contain a mosaic of habitats including mangroves, seagrasses, sand, algal plains, and patch reefs, with sharp calcium carbonate outcroppings throughout (Danylchuk et al., 2007a). Semi-diurnal tides occurred with a maximum daily range of 0.8 m.

2.2. Fish capture, transmitter implantation, and passive monitoring

Preliminary genetic analyses on bonefish from the study area indicated that all specimens were *A. vulpes* (Danylchuk et al., 2007a). Between November 1, 2005 and March 16, 2007, 47 bonefish (495 ± 45 mm total length; mean \pm SD) were implanted with acoustic transmitters (model V13 coded tags, 13 mm diameter, 36 mm long, 6 g, 700 day battery life, 40–120 s random on/off time: Vemco Inc., Shad Bay, NS). Specific details of fish capture and surgery can be found in Murchie et al. (2011). Fish were measured (total length; mm), and when possible, the sex was determined via internal examination. The entire procedure generally took less than five minutes. Bonefish were held for up to one hour in the flow-through net pens to recover following anesthetization. Tagged fish were released simultaneously with a group of untagged bonefish from the same school to reduce the likelihood of short-term post-release mortality via predation (see Murchie et al., 2012).

To track the movements of tagged bonefish, a series of 27 hydrophone receivers (VR2 and VR2W models, Vemco Inc., Shad Bay, NS) were placed strategically throughout the study area (Fig. 1) as described in detail in Danylchuk et al. (2011). Range tests were performed upon the initial deployment of the receivers, revealing that receivers deployed in water greater than 1 m deep had a coverage radius of 250 m, whereas receivers in shallow water had a coverage radius as small as 30 m. Wind and wave conditions as well as tidal cycles influence the detection range of individual receivers (Heupel et al., 2006). Although the range of coverage for receivers in shallow water was considerably less, they did provide the necessary coverage to monitor choke points (i.e., creek mouths) and as such we did not correct for receiver detection range in our data analysis. Even when the tides were at slack low, all of the receivers were covered by at least 20 cm of water and could still receive signals from tagged fish. Receivers were deployed between November 2005 and May 2008 (Table A.1) and were visited approximately every two months to download data and to clean the hydrophone of accumulated plant material. Data used in this study were collected from November 1, 2005 to February 18, 2008.

2.3. Defining 'site' and other spatial extents

For the purpose of this study, a 'site' is defined as the individual hydrophone receiver location. To elucidate trends in movement patterns at larger spatial scales, strategic groupings of receiver locations were selected within the study site. Receiver locations were grouped into seven areas along the shoreline that were associated

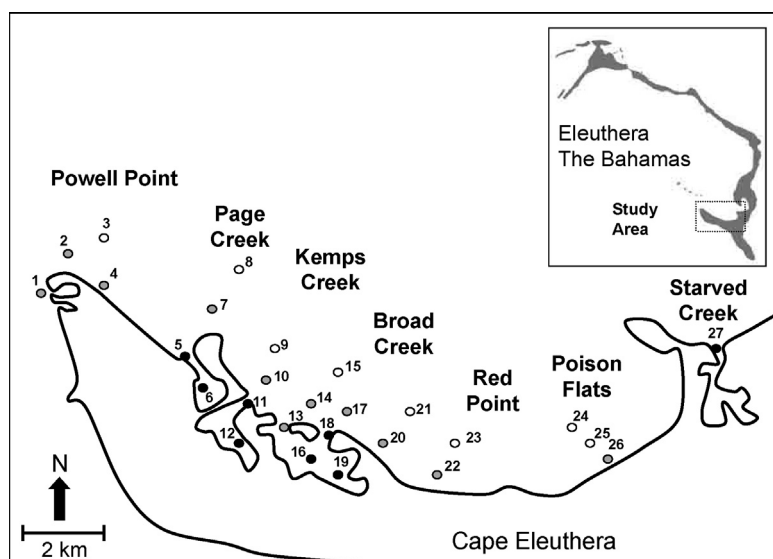


Fig. 1. Study area along the north coast of Cape Eleuthera, Eleuthera, The Bahamas, showing the locations of the 27 hydrophone receivers (numbered circles), and the various tidal creeks and tidal flats areas. 'Within-creek' receivers were designated as black circles, 'nearshore' receivers as gray circles, and 'offshore' receivers as white circles (see materials and methods for a definition of each habitat zone). The inset map displays the entire island of Eleuthera with the study area highlighted. Note that receiver detection ranges were as little as 30 m at 'within-creek' receivers, whereas all other receivers typically had a radius coverage of 250 m or more.

with one of the tidal creeks, points, or large open flats (Powell Point, Page Creek, Kemps Creek, Broad Creek, Red Point, Poison Flats and Starved Creek) (Fig. 1 and Table A.1). Receiver locations were also grouped into three habitat zones (within-creek, nearshore, and offshore). Within-creek receivers were located in creek mouths or the backwaters of creeks and were characterized typically by mangrove forests, sand and algal plains, along with seagrass habitats. Water depth at within-creek receivers ranged from 0.3 m in the backwaters to 1.25 m in the creek mouths. Near-shore receivers were located 200 m or less from shore but were outside of the creeks and typically included sand and algal plains, some seagrass habitats and patch reefs. Water depth at near-shore receiver sites ranged from 1.5 to 2.0 m. Offshore receivers were located more than 200 m from shore, were typically included sand and algal plains, and patch reefs, and were in water depths of 2.0–2.5 m (Table A.1).

2.4. Data analysis

For each receiver, the total number of detection records was tallied from the date of deployment to the last date downloaded (February 18, 2008). To account for the fact that not all receivers were deployed for an equal length of time, the total number of detections was divided by the number of days the receiver was deployed (as per Murchie et al., 2010). The total number of detections per days deployed was compared for receivers in each of the three habitat zones (within-creek, nearshore, and offshore) using a repeated measures analysis of variance (ANOVA) where individual fish were nested within the habitat zone, and a random effects model was applied. Detection records were further sorted by transmitter identity, date, and time so that individual habitat preferences and movement patterns could be elucidated. The relative activity space of bonefish was examined by comparing the sites most frequented to the location of tagging, as well as by calculating the median distance traveled and minimum linear dispersal by each individual. The median distance traveled was determined by calculating the distance between the receiver with the highest percentage of detections and all other receivers visited, and then taking the median of those distances (see Murchie et al., 2010). The minimum linear dispersal is defined as the straight line distance between the two most distant receivers which detected the

individual (see Chapman et al., 2005). Distance measurements were made using MapSource version 6.13.7 (Garmin). In addition, the minimum, maximum, and mean number of receivers that individual bonefish visited daily was calculated for the study period. The relationship between bonefish size and minimum linear dispersal, and the mean number of receivers visited daily was examined using linear regression analysis. The relationship between bonefish size and median distance traveled was examined using Spearman's Rho non-parametric correlation as this data was not normally distributed. To determine if there were repeatable patterns in movements on a daily to seasonal basis, detections of individual fish at the various receivers were plotted over time. Investigations into seasonal movement patterns specifically looked to discern any noticeable trends in behavior during the proposed spawning season for bonefish in the Western Atlantic (i.e., winter and early-spring) (Crabtree et al., 1997; Posada et al., 2008; Danylchuk et al., 2011). Comparisons of plots over time allowed an assessment of the propensity for fish to be detected with each other as well as the duration of their synchronous movements, which is relevant to schooling behavior. A repeated measures ANOVA was used to determine whether tidal phase influenced the presence of bonefish in the backwater portions of tidal creeks, and also to determine whether photoperiod influenced the use of the backwater portions of the creeks. Photoperiod was divided into day (06:00–17:59) and night (18:00–5:59) and divisions were based on sunrise and sunset timing data from a weather station located on Cape Eleuthera. Detailed data analysis was conducted only on data from fish detected beyond one week post-release. All statistical analyses on collected and derived data were completed using JMP 7.0.2 (SAS Institute, Cary, NC). Maximal type-1 error rates were set at $\alpha = 0.05$.

3. Results

3.1. Tracking characteristics

Out of the 47 bonefish captured and tagged from either Broad Creek or Kemps Creek, seven were male, eight were female, and thirty-two were of unknown sex (Table 1 and Table A.2). Two of the bonefish (#101 and #4073) were not detected after release, and 13 other bonefish were not detected beyond one week after release

Table 1
Summary of the tagging, biological, and monitoring data for the bonefish used in this study, collected from Cape Eleuthera, The Bahamas. Note that while 47 bonefish were originally collected and tagged, this table only includes the 32 bonefish which were at large > 7 days post-release.

Date tagged	Location tagged	Transmitter ID	Total length (mm)	Sex	Date last detected	Total # of days at large	Total # of days detected	% of days detected while at large	Total # of detections		
18-Feb-06	Kemps Creek	4075	550	Unknown	18-Feb-08	731	260	36	20,489		
19-Feb-06	Broad Creek	4076	400	Unknown	19-Feb-07	366	1	<1	1		
		4077	400	Unknown	04-Sep-06	198	9	5	1245		
		4079	490	Unknown	30-Jan-08	711	611	86	63,533		
27-Aug-06	Kemps Creek	108	440	Unknown	10-Jan-07	137	132	96	8910		
		109	440	Unknown	30-Oct-06	65	60	92	1522		
		4080	495	Unknown	30-Jan-08	522	30	6	1700		
		4082	530	Unknown	06-Jan-08	498	82	17	2804		
		4086	450	Unknown	27-Oct-06	62	10	16	407		
		4087	420	Unknown	20-Feb-07	178	5	3	62		
28-Aug-06	Broad Creek	102	550	Unknown	22-Feb-07	179	107	60	1008		
		106	500	Unknown	19-Sep-06	23	8	35	222		
		107	450	Unknown	04-Feb-07	161	43	27	1099		
20-Feb-07	Kemps Creek	928	515	Female	10-Apr-07	50	50	100	5596		
		933	515	Male	13-May-07	83	64	77	3499		
		936	480	Male	05-Apr-07	45	44	98	4837		
		2376	465	Male	25-Mar-07	34	6	18	1077		
		2378	570	Male	01-Mar-07	10	7	70	1702		
		2379	530	Female	30-Dec-07	314	142	45	5200		
		2381	520	Female	13-Feb-08	359	353	98	52,480		
		2382	475	Female	16-Feb-08	362	272	75	16,035		
		2383	515	Male	30-Nov-07	284	259	91	41,683		
		2385	520	Female	01-May-07	71	68	96	7354		
		16-Mar-07	Broad Creek	926	475	Unknown	06-May-07	52	38	73	1074
				927	555	Unknown	29-Mar-07	14	13	93	268
				929	560	Female	09-May-07	55	3	6	150
931	515			Unknown	05-Apr-07	21	5	24	149		
932	540			Female	29-Sep-07	198	189	96	11,069		
934	460			Male	18-Feb-08	340	278	82	14,748		
937	460			Unknown	16-Feb-08	338	237	70	10,010		
2375	560			Female	18-Feb-08	340	252	74	22,947		
2377	455	Unknown	14-Feb-08	336	255	76	21,362				

(Table A.2). In contrast, 15 bonefish were at large for periods of six months or more (Table 1). The maximum number of days over which an individual was detected within the hydrophone array was 611 days for bonefish #4079, resulting in a total of 63 533 detections (Table 1). In general, 27 bonefish were detected more than 75% of the days they were at large (Table 1). Herein, we restrict statistical analysis to those fish that were detected beyond one week post-release ($n = 32$), with a total of 324 242 detections to base inferences on (Table 1).

3.2. Habitat use and site fidelity

The north coast of Cape Eleuthera was a very active site for bonefish movements. The nearshore channel east of Powell Point had the highest number of detections per days deployed (Fig. 2a). Receivers located outside of the mouth and within the mouth of Kemps Creek, had the 2nd and 3rd highest number of detections per days deployed, respectively (Fig. 2a). The entire 23 km study area was utilized by the tagged bonefish as all receivers detected the presence of three or more tagged individuals during the course of the study (Fig. 2b). There was no significant difference ($F = 2.94$, $p > 0.05$; repeated measures ANOVA) in the number of detections of bonefish per days the receivers were deployed within the three habitat zones (i.e., within-creek (0.43 ± 0.21), nearshore (0.91 ± 0.19), and offshore (0.27 ± 0.21); mean \pm SE) although there was a general trend of fewer detections offshore.

Although no individual utilized the entire study area, five bonefish (#108, #928, #2377, #2382, and #2383) were detected at ≥ 20 receivers (Table 2 and Table A.3). The mean number of receivers used by bonefish during the study period was 13 (range 1–24). The total number of tidal creeks that bonefish utilized varied from zero to three. A consistent trend noted was that when bonefish were

detected in more than one creek, they always used creeks adjacent to each other (Table 2). Broad Creek was used by 25 bonefish, Kemps Creek by 23 bonefish, and Page Creek and Starved Creek by seven and three individuals, respectively (Table 2). A relatively high degree of site fidelity (with most of the detections located at a receiver within 1500 m of the tagging location) was displayed by 50% of detected bonefish in this study (Table 2). The range in median distance traveled was 118–10 691 m (Table 2). The Spearman's Rho revealed no significant relationship between the median distance traveled and the total length of the individual ($r_{s[31]} = -0.1498$, $p = 0.421$). Minimum linear dispersal ranged from 235 to 15 498 m (Table 3), and was not significantly related to bonefish body size ($r^2 = 0.007$, $p > 0.05$). Measures of daily activity level and site fidelity were also examined by calculating the minimum, maximum, and mean number of receivers that individual bonefish were detected at on a daily basis. The minimum number of receivers ranged from one to four; the maximum ranged from one to fourteen; and the overall mean number of receivers visited daily by bonefish was three (± 0.9 ; SD) (Table 2). There was no significant relationship between the mean number of receivers visited daily and bonefish body size ($r^2 = 0.068$, $p > 0.05$).

3.3. School fidelity

Because fish were captured in a school leaving either Broad Creek or Kemps Creek on an outgoing tide and then released as a group (including untagged conspecifics from the same school), it was possible to investigate the cohesion of the school through time. Within hours of being released from Kemps Creek on February 20, 2007, tagged individuals disassociated into two sub-schools with 60% of the tagged fish heading east toward Poison Flats or Starved Creek (#s 928, 2376, 2378, 2381, 2382, 2385), and the remaining

Table 2

Indicators of the relative activity of bonefish tagged along the north coast of Cape Eleuthera, The Bahamas. Bonefish detected less than seven days post-release are not included. Note that n/a means not applicable, P represents Page Creek, K represents Kemps Creek, B represents Broad Creek, and S represents Starved Creek. Median distance traveled was determined by calculating the distance between the receiver with the highest percentage of detections and all other receivers visited, and then taking the median of those distances, whereas minimum linear dispersal is the straight line distance between the two most distant receivers which detected the individual bonefish. †denotes male bonefish while ‡ denotes female bonefish.

Transmitter ID	Receiver with highest proportion of detections	Creeks used	Median distance traveled (m)	Minimum linear dispersal (m)	Total # of receivers visited	Minimum # of receivers visited daily	Maximum # of receivers visited daily	Mean (\pm SD) # of receivers visited daily
4075	R10	K	118	235	2	1	2	1.1 \pm 0.3
4076	R07	n/a	n/a	n/a	1	1	1	1.0
4077	R13	P, K, B	1185	4802	10	4	9	6.3 \pm 1.5
4079	R07	P, K, B	2271	7170	18	1	7	2.4 \pm 1.4
108	R11	P, K, B	1605	8691	21	2	14	6.2 \pm 2.6
109	R13	P, K, B	1343	7828	13	1	8	4.8 \pm 1.7
4080	R21	P, K, B	1233	4802	11	1	10	2.2 \pm 2.8
4082	R08	n/a	1184	2324	5	1	4	1.1 \pm 0.4
4086	R13	K, B	1185	4627	8	1	8	4.9 \pm 2.6
4087	R10	n/a	1503	4627	6	1	3	2.0 \pm 1.0
102	R19	B	954	13,659	12	1	7	1.7 \pm 0.9
106	R13	P, K, B	1163	3618	9	1	8	4.8 \pm 2.6
107	R22	B	1575	2551	4	1	3	1.1 \pm 0.3
928‡	R27	K, B, S	10,691	15,498	20	1	14	3.8 \pm 3.6
933†	R26	K, B, S	7392	11,733	18	1	9	2.0 \pm 1.7
936†	R04	K	5749	13,316	16	1	9	2.4 \pm 1.7
2376†	R26	K	7569	10,002	16	2	13	5.2 \pm 4.0
2378†	R04	K	3729	4202	6	1	5	2.3 \pm 1.4
2379‡	R11	K, B, S	1789	12,625	19	1	11	1.5 \pm 1.5
2381‡	R04	P, K, B	4202	7543	19	1	10	3.8 \pm 1.7
2382‡	R11	K, B	1789	13,156	21	1	8	2.5 \pm 1.3
2383†	R26	K, B	7660	13,156	21	1	12	4.2 \pm 2.4
2385‡	R04	K, B	4202	5980	11	1	7	2.0 \pm 1.2
926	R26	B	7824	13,659	15	1	5	2.2 \pm 1.2
927	R26	B	7534	9036	13	1	6	2.7 \pm 1.9
929‡	R17	B	672	3480	8	1	8	4.3 \pm 3.5
931	R17	B	358	1343	5	1	4	2.0 \pm 1.4
932‡	R13	K, B	960	7224	13	1	7	2.7 \pm 1.3
934†	R26	K, B	7776	13,156	19	1	8	2.7 \pm 1.4
937	R10	K, B	1729	9036	14	1	7	2.2 \pm 1.0
2375‡	R13	K, B	1185	7543	18	1	9	3.9 \pm 1.6
2377	R10	K, B	2021	14,094	24	1	9	3.7 \pm 1.7

40% of the tagged fish (i.e., #s 933, 936, 2379, 2383) heading west toward Powell Point. Over the course of a few days, the bonefish that went east were detected only in the eastern portion of the array, and the individuals that went west were detected only in the western portion of the array. On the fourth day post-release, two bonefish (one from each sub-school) headed back toward the release site at Kemps Creek. Bonefish #936 was later detected joining individuals that were located in the eastern portion of the array at Poison Flats, and bonefish #2376 was last detected in transit as it headed west toward Powell Point. Although the duration of detection post-tagging was variable for individuals tagged on February 20, 2007, one individual from each sub-school (i.e., bonefish #2381 from the 'west' sub-school and #2383 from the 'east' sub-school) was at large for over 280 days while being detected for greater than 90% of those days within the array (Table 1). Bonefish #2381 and #2383 continued to remain in separate sub-schools utilizing different areas within the hydrophone array for a majority of the time they were detected, but occasionally their paths crossed near Powell Point, Kemps Creek, or Broad Creek (Fig. 3).

When bonefish remained with other individuals from the school in which they were captured, movements tended to be relatively synchronized over time (Fig. 4). For example, bonefish #108 and #109 (captured, tagged and released from Kemps Creek on August 27, 2006) displayed repeatable and synchronous patterns of movement throughout the array during the two months they were detected together (see Fig. 4 for a sub-sample of their movement data). Between August 28, 2006 and October 29, 2006 bonefish #108 and #109 moved together from a receiver offshore of Page

Creek to sites within and nearshore of Kemps Creek and Broad Creek, and then to receivers as far east as Red Point.

3.4. Inter- and intra-individual variability in movement patterns and seasonal trends

Repeatable patterns of movement were apparent in all tagged individuals, but the duration of these repeatable patterns varied, as did the amount of relative activity space that individuals occupied. Inter- and intra-individual variability was observed for all bonefish detected for extended periods of time. For example, bonefish #4079 was at large for 711 days, and was detected on 86% of those days (Table 1). Examination of its movement patterns throughout 2007

Table 3

Distribution of detections of bonefish in the backwater portions of tidal creeks during various tidal phases.

Tidal phase	Number of detections
2 h after low tide	223
3 h after low tide	1233
4 h after low tide	1945
5 h after low tide	1394
6 h after low tide	166
<1 h after high tide	1590
1 h after high tide	1753
2 h after high tide	1846
3 h after high tide	1247
4 h after high tide	78
5 h after high tide	17

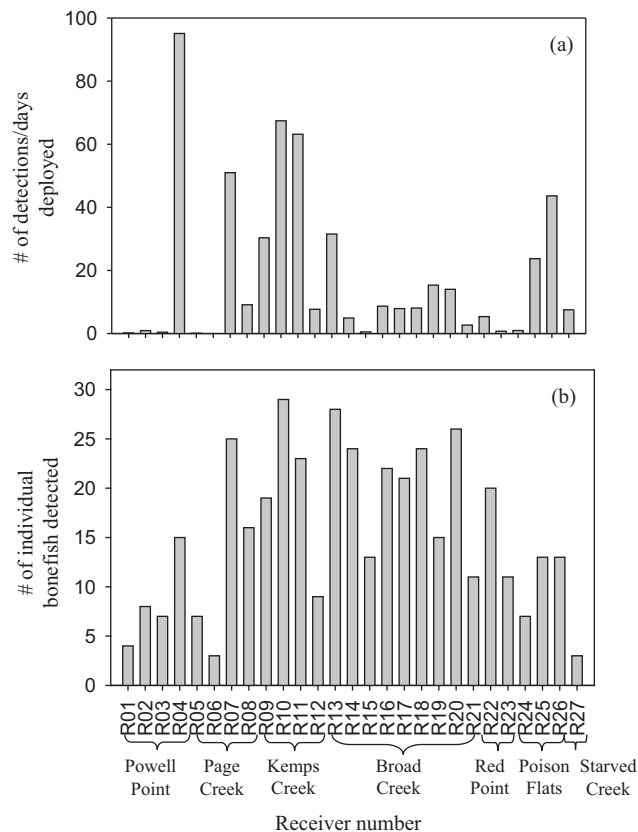


Fig. 2. The number of detections of bonefish per days deployed at each receiver (a), and the number of individual bonefish detected at each receiver (b). Receivers are numbered from west to east along the north coast of Cape Eleuthera, The Bahamas.

demonstrate that this fish used the within-creek habitat of Broad Creek (i.e., receivers 16, 18, 19) most heavily between mid-June to the end of August, whereas the rest of the year detections were rare or non-existent (Fig. 5). The increased use of within-creek habitat zones during peak water temperatures was not observed in other tagged bonefish. When examining the data for any winter or late-spring trends in movements that could correspond to spawning, a consistent observation is that bonefish are only detected at the most westerly receiver in the array (R01), between early November and late January.

3.5. Influence of tide and photoperiod

Although bonefish could be observed at any location during high tide, it was observed that bonefish were not detected in the backwater portions of tidal creeks during periods of low tide. Rather, fish were detected as early as 2 h after low tide and up to 5 h after

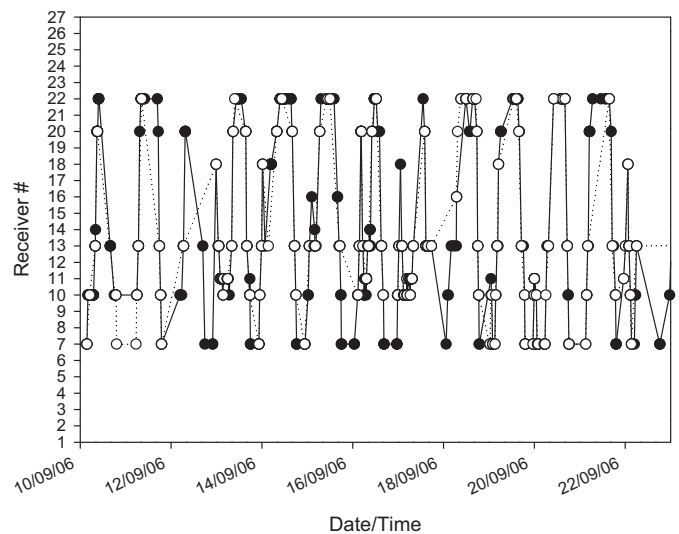


Fig. 4. Movement patterns of bonefish #108 (solid circle) and #109 (open circle) through the hydrophone array for a 2-week period in September, 2006. Receivers are numbered from west to east along the north coast of Cape Eleuthera, The Bahamas. Dates are given as dd/mm/yy.

high tide in the backwater portions of creeks. The number of detections increased as time after low tide increased, then began to fall as time after high tide increased (Table 3). There was a significant difference ($F=3.95, p < 0.0001$; repeated measures ANOVA) in the number of detections of bonefish among tidal categories, with the differences lying between the number of detections 4 h after low tide and the number of detections 4 and 5 h after high tide ($p > 0.05$). The number of detections of bonefish in the backwater portions of tidal creeks was also dependent on photoperiod. A significantly higher number of detections occurred during the day ($n = 10\ 040$) versus the night ($n = 1452$) ($F = 10.13, p = 0.003$; repeated measures ANOVA), despite semi-diurnal tidal phases.

4. Discussion

This study provides the longest continuous monitoring of bonefish movement patterns through the use of a passive acoustic telemetry array. The benefit of the extended monitoring period allowed seasonal trends and individual variation in movement patterns to be rigorously evaluated. For all 15 bonefish that were tracked over six months, a continuum of movement behaviors was observed with repeatable diel movements showing site fidelity, as well as forays to more distant receivers and disappearance from the array constituting transient behavior. Our results are contradictory to all three other studies on *A. vulpes* movements which suggest bonefish are either transient or site attached. The lack of observed mixed behaviors of bonefish in these studies, however, is

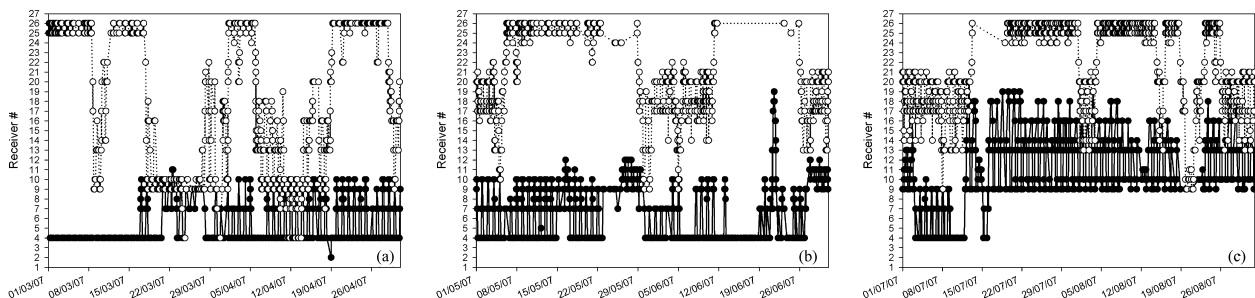


Fig. 3. Movement patterns of bonefish 2381 (solid circle) and 2383 (open circle) over their time at large within the study area. Panels a–c cover the months of March–April, May–June, and July–August, respectively. Dates are given as dd/mm/yy.

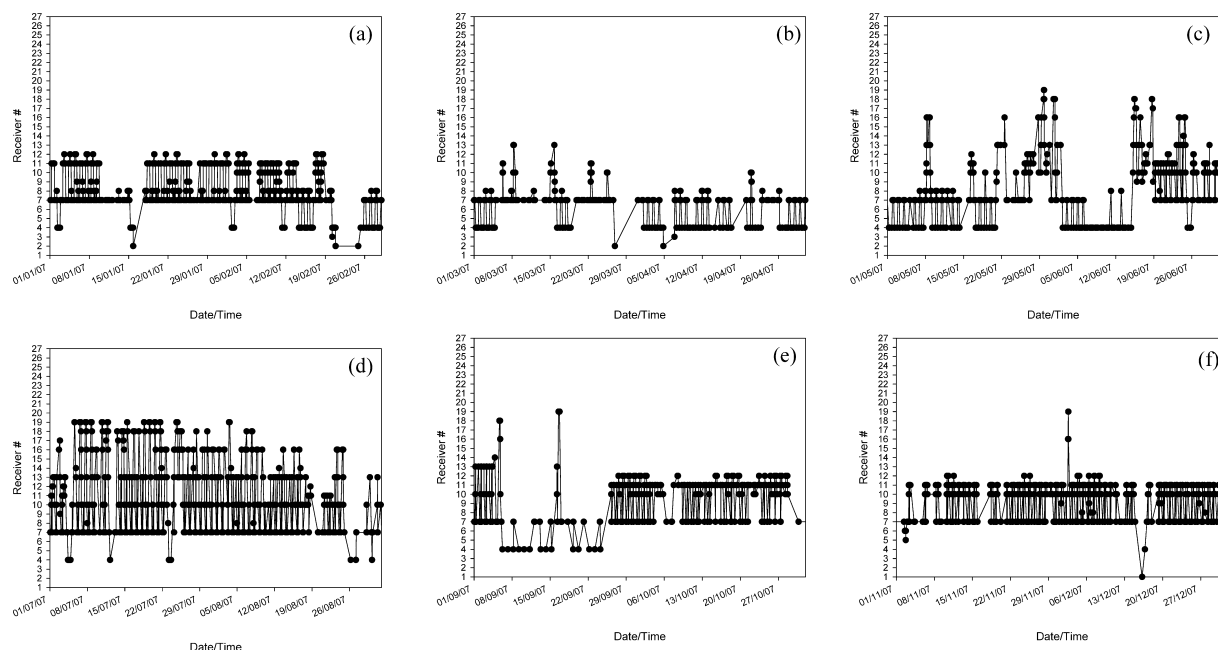


Fig. 5. Movement patterns of bonefish 4079 as it was detected through the hydrophone array during the entire year of 2007. Panels a–f cover the months of January–February, March–April, May–June, July–August, September–October, and November–December 2007, respectively. Dates are given as dd/mm/yy.

likely an artifact due to the duration of individual monitoring, the tracking methodology, and low sample size. For example, Colton and Alevizon (1983b) concluded that bonefish were highly transient in nature after having limited success with manually tracking 13 transmitter-implanted bonefish by boat or with recapturing any conventionally tagged bonefish in a mark-recapture program. Out of 13 fish, only three were located after 24 h, with two being monitored for a total of 16 and 30 h, respectively, and one fish being tracked for a total of 32 h over a period of 100 days. Humston et al. (2005) tagged 11 bonefish and monitored their movements via an automated hydrophone array. Only eight fish were detected post-release. Of the eight fish, two of the fish were suspected to be dead or to have shed their transmitters based on highly localized or no movements. Another four individuals left the study area after only one to four days, suggesting transient behavior. The remaining two fish were located within the array for a total of 40 and 61 days, respectively, suggesting site fidelity (Humston et al., 2005). Larkin et al. (2008), who also incorporated analyzed data from a nine year mark recapture program, found substantial variability between individual movement patterns with some fish moving >100 km (i.e., transient), versus others that moved ≤ 2 km from where they were tagged (i.e., strong site attachment). Unfortunately the authors provide limited information on individual movement patterns of acoustically tagged fish as they were picked up in the array, but the majority of fish (78%) were detected for less than 30 days, limiting the opportunity to examine movement patterns over a greater temporal scale.

Intra-specific variation in movement patterns has been documented for many marine animals (see Quinn and Brodeur, 1991), and shifts between site fidelity and transient behavior may occur for reasons related to the establishment of home ranges of sufficient size to meet life requirements (see Morrissey and Gruber, 1993; Carfagno and Weatherhead, 2008). The relatively short duration of effective monitoring in previous studies may also reflect high levels of post-release predation associated with a combination of capture and implantation-related stress. In this study, two bonefish were not detected after release, and 13 other bonefish were tracked only for a short duration (hours to a week). Although it

is not possible to know with certainty the fate of those animals, research has revealed that exercise and handling stress associated with catch-and-release fishing can induce post-release predation in bonefish by lemon sharks (*Negaprion brevirostris*) and barracuda (*Sphyraena barracuda*) (Cooke and Philipp, 2004; Danylchuk et al., 2007a, 2007b). Despite our attempts to provide extended recovery times, to optimize surgical procedures, and to minimize stress, it was still likely that some post-release predation occurred. We also noted thermal-specific trends in the post-release fate of individuals, with a lower percentage of the fish tagged at warmer temperatures being tracked for longer periods compared to fish tagged at cooler temperatures (Murchie et al., 2012). This observation lends further support to the conclusion that post-release predation and/or mortality, more than migration from the study site, accounts for the loss of animals (see Murchie et al., 2012).

In many animals, including fish, body size can influence home range (Kramer and Chapman, 1999). In this study, there was no relationship between the size of bonefish and the size of its relative activity space as determined by the median distance traveled, the minimum linear dispersal, or the mean number of receivers visited daily. We did, however, only use a relatively small size range of bonefish for tagging. Although the sizes of fish tagged are representative of those typically captured in south Eleuthera (see Murchie et al., 2009), we cannot exclude the possibility that smaller or larger fish may display different behaviors.

Schooling behavior is common among fishes (Klimley and Holloway, 1999) and the benefits of such behavior (e.g., predator avoidance, foraging) have been well documented (see Partridge, 1982; Krause, 1993). Indeed, even fitness can be enhanced by fish that associate with familiar rather than unfamiliar conspecifics as cooperative antipredator behaviors increase with school cohesion (Chivers et al., 1995; Ward and Hart, 2003). Bonefish can be observed in schools of hundreds to thousands of fish (anecdotally based on angling lore, our observations; Johannes and Yeeting, 2000; Danylchuk et al., 2011), but to date no one has investigated school fidelity in this group of fishes. Results from our study suggest that the structure of bonefish schools is dynamic. The duration in which individuals remain with one school before joining another

varies, but observations are limited by the duration with which the tagged fish remained within the hydrophone array. In our study, individuals captured in a school, tagged, and released simultaneously with un-tagged conspecifics from the same school, either stayed together with school-mates for periods of hours to days to months, or had movement patterns that were distinct from other fish with temporary interludes of overlap. One possible explanation for the varying degrees of school fidelity observed may be that when schools overlap frequently there are many opportunities for individuals to switch groups (Ward et al., 2002), and in large schools it is challenging for fish to stay together because they cannot possibly recognize 200 or more individuals (Griffiths and Magurran, 1997). The amount of time that individuals are together in a school, and thus have time to become familiar with each other, will also influence schooling preferences (Brown and Colgan, 1986; Griffiths and Magurran, 1997). Sharp (1978) found that tuna (*Thunnus* spp.) school-mates are often related and are of similar size, implying a common birth date and location. Relatedness of individual bonefish within schools could be conducted via genetic analysis of fin clips taken during implantation of acoustic transmitters in future studies.

The association of movement patterns of bonefish and tidal cycle were noted by both Colton and Alevizon (1983b) and Humston et al. (2005). Colton and Alevizon (1983b) observed bonefish accessing shallow waters of tidal flats during high tide, and moving to deeper water on an ebbing tide. Humston et al. (2005) found that bonefish staged in edge/interface locations next to shallow areas prior to high tide, and then disappeared from detection following peak high tides, likely into shallow interior areas of tidal flats where no receivers were located. Our data indicate similar movement patterns with the tides; specifically that bonefish are only detected in the backwater portions of tidal creeks when water depth is sufficient (i.e., between two hours after low tide and up to 5 h after high tide). During periods of high tide, however, bonefish are not found exclusively in tidal creeks or flats but can be found in waters that are accessible through the entire tidal cycle such as near R04 (3 m deep). The occasional transient behavior of bonefish may enable individuals to assess habitat suitability in other places, or perhaps allow resource recovery in preferred habitats (see Morrissey and Gruber, 1993). The disproportionate use of backwater portions of creeks observed between day and night despite tidal phase (i.e., increased use during daytime), however, may be a combination of foraging strategy and/or predator avoidance and deserves further study. In general, such bonefish movement patterns associated with the tidal cycle in other areas of their geographic distribution will be dependent on the particular site characteristics, such as local bathymetry and hydrology.

The use of deep (≥ 2 m) water channels by bonefish has been debated, with some evidence that these habitats are used as routes between foraging areas and/or areas of thermal refuge but are often avoided due to predation risk (see Humston et al., 2005). Receiver R04 received the overall greatest number of detections per days deployed during this study, suggesting that this deep water channels is of importance to bonefish along the north coast of Cape Eleuthera. Visual surveys via snorkeling have documented bonefish feeding in this deep water channel (Murchie, unpublished data). Use of this specific location for both feeding and migration are plausible and a more detailed examination of the habitat characteristics is warranted in future studies.

The only discernable pattern in seasonal trends that emerged from the data was the movement of bonefish to the most westerly-located receiver (R01) at the mouth of the Cape Eleuthera Marina between November and late January. The timing of these movements corresponds to the spawning period for bonefish in The Bahamas and has been discussed extensively in Danylchuk et al. (2011). Unfortunately this receiver was not deployed until mid May

2007, limiting the opportunity for a full year's worth of data to be examined within this data set; however, no detections were made on this receiver during months outside the proposed reproductive period. Seasonal avoidance of shallow flats in Florida during the warmest and coldest periods of the year was suggested by Ault et al. (2002), however, our results in The Bahamas indicate otherwise. The use of tidal flats and tidal creeks by bonefish occurred year round.

Bonefish are presumed to play an important role in the connectivity of habitats in coastal systems and such information is critical for effective ecosystem management on a seascape level (Verweij and Nagelkerken, 2007). This study documented a number of bonefish movements between tidal creeks, tidal flats, and along the open coastline of South Eleuthera, demonstrating their role in habitat connectivity as well as providing a mechanism for energy flow. Although we did not explicitly study trophic ecology or energy dynamics, given that bonefish movement and feeding activities may be performed by hundreds of individuals in a school and involves transiting a mosaic of habitats, their potential to transport nutrients is high. Indeed, even the regulation of sediment processes in these nearshore areas could be influenced by the benthic feeding habits of bonefish, as massive sediment plumes can often be seen in areas where bonefish are feeding (Colton and Alevizon, 1983a). The extensive use of nearshore habitats by bonefish is concerning because these areas are typically most vulnerable to habitat alteration and degradation (Blaber, 2007). Continued research into the basic ecology of bonefish (particularly population mixing and movement studies over larger spatial and temporal scales) will not only aid in the management of this fishery, but provide more information into coastal ecosystem dynamics.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.fishres.2013.03.019>.

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