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Aggregations and offshore movements as indicators of spawning activity of bonefish (*Albula vulpes*) in The Bahamas

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Abstract To identify the timing and location of spawning activity for bonefish (*Albula* spp.) in the Bahamian archipelago, we used an acoustic telemetry array spanning 44 km^2 of shallow tidal creeks, flats, and adjacent deeper coastal waters near Cape Eleuthera. In two successive years, we surgically implanted transmitters in male and female bonefish ($n = 60$) and examined their movement patterns within the array. Eight bonefish surgically implanted with transmitters as part of an earlier study were also tracked. In 2009, the telemetry information was complemented with snorkeling observations, underwater video, and manual tracking of the same acoustically tagged fish, as well as fish ($n = 3$) gastrically implanted with continuous transmitters. During a period of 4–7 days spanning the full and new moons, primarily between October and May, bonefish moved from their typical shallow flats and aggregated at sites in close proximity to the deep water drop-off of the Exuma Sound. Localized movements of the large schools of bonefish (often >1,000 fish) at these presumptive pre-spawning aggregation sites included brief trips (<8 h) just after sunset until just prior to sunrise to the abyssal wall at the edge of the Exuma Sound (i.e., >1,000 m depth). Tagged bonefish detected at these aggregation sites were subsequently detected back in the tidal creeks and coastal flats shortly after new and full moons and remained at these more typical shallow sites (i.e., <2 m depth). Although we did not directly observe spawning events, we did observe ventral nudging and porpoising behaviors, which are potentially associated with courtship. Timing of the observed movements and possible courtship behaviors was coincident with periods when gametes were well developed. Collectively, our study provides the first objective evidence suggesting that the aggregation and seasonal migration of bonefish to deep shelf environments during certain moon phases is for spawning.

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Introduction

Fish undertake migrations to find food (Choat 1982; Block et al. 2001), avoid predators (Gillian and Fraser 2001), avoid unfavorable environmental conditions (Winemiller and Jepsen 1998; Albanese et al. 2004), and to reach spawning sites (McCormick et al. 1998; Fox et al. 2000; Meyer et al. 2007). The spatial and temporal scale of these migration patterns can range from daily distances of several hundred meters (Domeier and Colin 1997) to annual migrations over thousands of kilometers (Jones et al. 1984). Such migration patterns in fishes can be highly predictable and have been correlated with a range of abiotic (Quinn et al. 1996; Sims et al. 2004) and biotic (Gross et al. 1988) environmental cues. From an evolutionary perspective, migratory behavior in fishes, as well as many other animals (Frank et al. 1998; Dingle and Drake 2007), is adaptive because the energetic and life history costs of relocating, even over vast distances, are outweighed by the benefits of residing in a more suitable location, even if only temporarily (Huntingford 1993; Claydon 2004).

Many species of marine fish migrate to predictable locations and specific times to form aggregations for the purpose of spawning (Domeier and Colin 1997; Claydon 2004). Transient spawning aggregations are the gathering of reproductively active conspecifics at densities and/or numbers higher than those found in the area of the aggregation during non-reproductive periods (Domeier and Colin 1997; Claydon 2004). A well-studied group of fishes that form transient, site-specific spawning aggregations are the Serranidae, such as the red hind (*Epinephelus guttatus*; Sadovy et al. 1994; Beats and Friedlander 1998) and Nassau grouper (*Epinephelus striatus*; Bolden 2000; Whaylen et al. 2004). Documenting the spatial and temporal dynamics of grouper, spawning aggregations has helped to characterize the biology and ecology of this important group of coral reef fishes (Whaylen et al. 2004), as well as highlighted the need to learn more about other marine fishes that aggregate to spawn (Sadovy and Domeier 2005).

Understanding the dynamics of spawning aggregations also has important implications for the conservation and management of fish stocks, since fish that aggregate at specific times and locations can be especially vulnerable to intense fishing pressure and overharvesting (Coleman et al. 1996; Domeier and Colin 1997; Roberts and Hawkins 1999; Musick et al. 2000; Sala et al. 2001). Even non-extractive recreational catch-and-release fisheries could have negative effects on fish as they move to or reside at aggregation sites, especially if the stresses associated with being captured and handled influence spawning success (Hutchings et al. 1999; Lowerre-Barbieri et al. 2003; Suski et al. 2007). Given the site-specific nature of many spawning aggregations, the modification and destruction of coastal habitats could also negatively affect movements to spawning sites, spawning behavior, and ultimately the sustainability of fish stocks (Turner et al. 1999; Musick et al. 2000; Roberts et al. 2002; Claydon 2004).

Bonefish (*Albula* spp.) inhabit shallow tropical and subtropical flats worldwide (Alexander 1961), and their wariness and speed make them one of the most prized groups of marine fishes among recreational anglers (Kaufmann 2000). Due to their popularity, bonefish are the focus of a tourism-based recreational angling industry that provides substantial revenue to coastal communities (Ault et al. 2008; Danylchuk et al. 2008). Because bonefish often reside in large schools and feed mostly on benthic invertebrates (Colton and Alevizon 1983a); this group of fishes may also play an integral role in the ecology of shallow marine flats (Ault et al. 2008). Despite their importance, there is limited information on the life history and ecology of bonefish, especially when compared to other recreationally angled marine species (e.g., striped bass, *Morone saxatilis*, Rulifson and Dadswell 1995; Atlantic tarpon, *Megalops atlanticus*, Ault et al. 2008).

One aspect of the life history of bonefish that has proven particularly difficult to study is their reproductive ecology (Ault et al. 2008). Although some published information on the life history of bonefish is now confounded by recent studies indicating that a greater number of species exist throughout their range than was previously thought (Bowen et al. 2008), general findings suggest that bonefish move from their typical flats habitat to form pre-spawning and spawning aggregations elsewhere (Johannes 1978; Johannes and Yeeting 2000). In Palau, local knowledge of fishers indicated that *Albula glossodonta* form large pre-spawning aggregations in coastal lagoons 1–3 day prior to the full moon and then the fish migrate to the outer reef edge to spawn in large numbers (Johannes 1978; Johannes and Yeeting 2000). Movement of these bonefish was noted to occur in the late afternoon and early evening (i.e., 1600–2200 h) concurrent with the high spring tides (Johannes and Yeeting 2000). In addition, bonefish caught from the pre-spawning aggregations had body cavities filled with gonads, whereas fishers reported bonefish being spent once fish returned to the lagoon (Johannes and Yeeting 2000). Knowledge of these “spawning runs” by local fishers, as well as the disruption of movement corridors from shoreline modifications, are thought to have resulted in the severe depletion of local bonefish stocks in Palau (Johannes and Yeeting 2000; Friedlander et al. 2008).

Other evidence regarding the timing and location of spawning activity in bonefish comes from measures for reproductive condition, larval dynamics, and general movement patterns. By measuring the gonadosomatic index across all moon phases for *Albula glossodonta* from Palmyra Atoll, Friedlander et al. (2008) showed that although males were ripe throughout the lunar cycle and throughout the year, females were most reproductively active around full moons. In the Western Atlantic, however, seasonal trends in the allocation of energy to gonad development and vitellogenisis suggest that spawning occurs in winter and early spring (Crabtree et al. 1997; Posada et al. 2008; Murchie et al. 2010). When studying the energetics of bonefish off Eleuthera in The Bahamas, Murchie et al. (2010) found that decreases in whole-body lipid content and energy density in the winter months coincided with greater allocation of energy to gonadal development, potentially reflecting seasonal reproductive activity. In addition, trends in the abundance, age, and recruitment of bonefish larvae in The Bahamas support the notion that bonefish spawn in the winter and spring (Mojica et al. 1995). As for where spawning occurs, the absence of fully hydrated oocytes for bonefish caught on the flats (Posada et al. 2008), as well as the offshore movements of fish in the winter months documented via acoustic telemetry (Larkin et al. 2008) offers some suggestion that bonefish in the Western Atlantic spawn in deep water drop-off of coral reef shelves, similar to what was observed for bonefish in Palau (Johannes and Yeeting 2000). The planktonic nature of larval bonefish as well as their patterns of onshore migrations from offshore waters also provides support that bonefish in the Western Atlantic are spawning near deep water (Dahlgren et al. 2008). Visual observations made by fishing guides and commercial fishers also support this notion (Danylchuk et al. 2008).

Although there is growing evidence that bonefish in the Western Atlantic move from their typical shallow water flats (Colton and Alevizon 1983b; Humston et al. 2005) to deep waters associated with outer coral reef edges to spawn, the migration patterns and formation of spawning aggregations for bonefish in this region have yet to be investigated systematically. The purpose of this study was to use a combination of fixed acoustic monitoring, manual acoustic tracking, and visual observations to determine whether or not bonefish move from their more typical shallow water flats to deeper offshore waters to participate in seasonal spawning activity.

Materials and methods

Study site

This study took place along the north shore of Cape Eleuthera, Eleuthera, The Bahamas (24°50′05″N, 76°20′32″W; Fig. 1). Cape Eleuthera is a 14-km long peninsula orientated on roughly an east to west axis from the island of Eleuthera and extends from the shallow waters (<3 m) of The Great Bahamas Bank to within 1–3 km of the abyssal waters of the Exuma Sound. The substrate along the north shore of Cape Eleuthera is a mosaic of habitat types ranging from sand flats, seagrass beds (*Thallassia testidunium* and *Syringodium filiforme*), algal and sponge plains, exposed calcium carbonate hard bottom, and small patch reefs, while the substrate between the western end of Cape Eleuthera and the Exuma Sound also includes larger patch reefs, coral reef buttresses, and contiguous coral reef along the edge of the almost vertical wall that descends into the deep sound. Eastward, 4–6 km from the end of Cape Eleuthera, are three small tidal creeks that are lined with red and black mangroves (*Rhizophora mengal, Avicennia germinans,* respectively) and that have small channels and basins that drain onto the shallow bank when the tide recedes. The tidal range along the north shore of Cape Eleuthera is approximately 1 m and the predominant tidal currents run along the east–west axis of the peninsula.

Since 2005, we have been studying the ecology of bonefish inhabiting the tidal creeks and flats along the north shore of Cape Eleuthera. Genetic analyses of bonefish ($n = 184$) from this area indicated that all specimens were *Albula vulpes* (Danylchuk et al. 2008; J Koppelman, Missouri Department of Conservation, unpubl data).

Fish collection and tag deployment

For implantation of acoustic tags, bonefish were collected from tidal creeks along the north shore of Cape Eleuthera. In 2007, bonefish were collected from Broad Creek and Kemp's Creek (approx. 1.5 km apart; Fig. 1). In 2008, however, because telemetry data indicated that bonefish frequently move between these two systems (Danylchuk et al. 2007; Murchie 2010), all bonefish were collected from Kemp's Creek. In both years, bonefish were collected in early December because previous studies (e.g., Murchie et al. 2010) indicated that the sexes should be in later stages of gonadal development, allowing the sexes to be discernable either through the release of gametes when the abdomen of fish was palpated or visually after the incision was made to insert a transmitter (see below). Because bonefish are not easy to sex using external traits, direct observation of gonads or gametes was critical to ensure that both sexes were tagged, especially since reproductive tactics could differ for males and females (Balon 1984).

To capture bonefish, a seine net (45.72 m × 1.22 m seine with a 1.22 m bag, 0.95 cm mesh) employed as a block net was stretched across narrow channels or the mouths of tidal creeks. Bonefish were then ushered into the block net as they exited the creek system when the tide ebbed, and the net was closed. Following capture, all bonefish were placed in several submerged portable pens open to the surface (1.3 m × 0.8 m × 1.25 m tall, 3.1 cm extruded plastic mesh). Fish were held for up to 4 h following

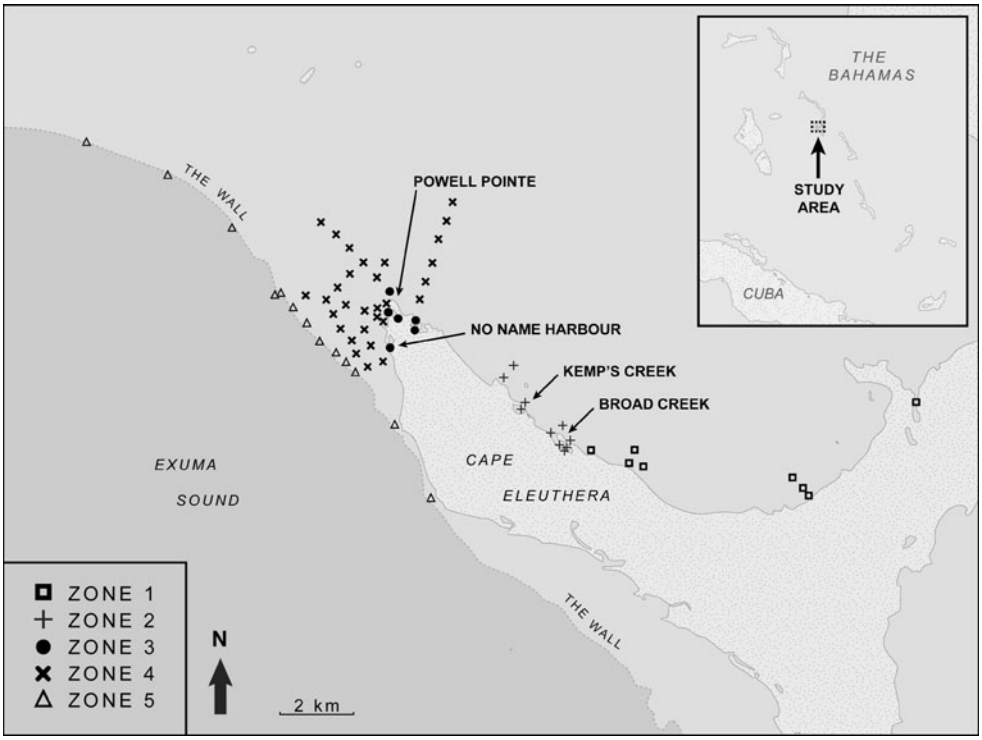


Fig. 1 Study area along the north coast of Cape Eleuthera, Eleuthera, The Bahamas, showing the locations of fixed hydrophone receivers in each of five zones. *Zone 1* (*open square*) shallow coastal flats, *Zone 2* (*cross*) tidal creeks (location where tagged fish were deployed), *Zone 3* (*closed circle*) Powell Pointe, Cape Eleuthera Marina, No Name Harbor, *Zone 4* (*bold* ×) >250 m offshore of Powell Pointe but not including the deep drop-off of the Exuma Sound, and *Zone 5* (*open triangle*) within 100 m of the deep drop-off of the Exuma Sound

capture. In each year, a total of 30 bonefish were surgically implanted with acoustic transmitters; in 2007, all fish were implanted with V13-coded tags (69 kHz, 13 mm diameter, 36 mm long, 6.0 g in air, min and max delay times 45–135 s, 700 day battery life, Vemco Inc., Halifax, NS.), while in 2008, 20 bonefish were implanted with V13-coded tags and 10 bonefish were implanted with V9AP tri-axial accelerometers (69 kHz, 9 mm diameter, 46 mm long, 6.3 g in air, 50 m depth range, min and max delay times 45–135 s, accelerometer parameters 5 samples/sec with a 25 s sample time, 160 day battery life, Vemco Inc., Halifax, NS). In both years, we attempted to implant transmitters in an equal number of males and females.

Prior to surgery, individual bonefish were removed from the holding pen, anesthetized with MS-222 (approx. 100 ppm) in a cooler (45 l), and then placed on a surgery table in a small skiff. While on the surgery table, the fish's gills were supplied with a maintenance dose of MS-222 (approx. 50 ppm) in fresh seawater using a recirculating pump. Transmitters and surgical tools were cleaned with Betadine, and the surgeon wore vinyl gloves. To implant transmitters, a small incision (2–3 cm) was made to the right side of the ventral midline, posterior to the pectoral fin girdle. Prior to inserting the transmitter, sex was visually confirmed by inspecting the gonads through the incision. Care was taken to insert the transmitter through the incision and slide it gently toward the pectoral fins. The incision was closed with 3 or 4 simple interrupted sutures (Ethicon 3-0 PDS II, monofilament absorbable suture material, Johnson and Johnson, New Jersey), and the total length of the fish (to nearest mm) was measured. The entire surgical procedure took less than 5 min per fish and was always conducted by the same trained surgeon under the guidance of the team veterinarian. Prior to release, bonefish were held for up to 1 h in flow through holding pens in situ. Following the recovery period, bonefish were released with both tagged and untagged conspecifics to encourage schooling behavior similar to when the group of bonefish was captured. All methods used in this study were in accordance with the policies of the Canadian Council on Animal Care as administered by the Carleton University Animal Care Committee (Protocol B07-03, B07-05, and B07-06).

Telemetry arrays, manual tracking, and visual surveys

Movement patterns of tagged bonefish were monitored through the use of a fixed acoustic receiver array (VR2 and VR2W receivers, Vemco Inc., Halifax, NS; Appendix 1). Individual receivers were secured to a short piece of rebar anchored into a concrete block. Receivers were positioned vertically in the water column when at depths greater than 1 m at low tide and were positioned either horizontally or 5°–10° above horizontal when the water depth at low tide was less than 1 m. Range tests determined that receivers located in water greater than 1 m had a radius coverage of 250–400 m, whereas receivers in shallow water (<1 m) had a radius coverage of 30 m. Even at slack low tides, all of the receivers were covered by at least 20 cm of water and could detect tagged fish. Receivers were visited regularly for downloading and cleaning, and all data were initially sorted and analyzed using VUE software (Vemco Inc., Halifax, NS). From December 2007 through June 2009, downloads occurred prior to the new and full moons to assess whether pre-spawning aggregations were occurring at the end of Cape Eleuthera. Data from the remote receivers were then used to focus manual tracking and visual observation efforts necessary to document the aggregations.

Prior to the deployment of tagged bonefish in December 2007, the telemetry array covered points along a 23 km stretch of the north coast of Cape Eleuthera. Receivers were strategically deployed at choke points (e.g., creek mouths) and as curtains extending in a line up to 1.5 km perpendicular to the shoreline (Fig. 1) as a means to cover large areas while also being able to adequately monitor the movements of bonefish in and among the tidal creeks. Data from the array for bonefish that had been tagged earlier (i.e., between November 2005 and November 2007) showed that individuals moved toward the end of Cape Eleuthera (and deeper water) in the winter and early spring (Murchie 2010), consistent with reports from the literature on their movements associated with spawning. Consequently, in late November 2007, the array was extended beyond the end of Cape Eleuthera so that it consisted of 53 remote receivers spanning 44 km^2 from the shallow flats of the bank to the edge of the deep drop-off of the Exuma Sound (Fig. 1; total area of coverage was calculated using a complex polygon connecting the outer most receivers in the array). Receivers at the end of Cape Eleuthera and toward the Exuma Sound were deployed as three curtains radiating out from the tip of the peninsula, at choke points including the distal ends and internal basin of a flow-through marina, and as concentric nets that could allow for the direction of movement away from the end of the peninsula to be determined. Some receivers were part of a separate study examining the movement patterns of coastal sharks (Brooks et al., unpublished data), and they were deployed as non-overlapping nodes spaced along a 16 km transect of the edge of the deep drop-off (Fig. 1). After preliminarily reviewing data in the summer of 2008, some receivers were repositioned offshore of the end of Cape Eleuthera in an attempt to increase the resolution at which we would be able to detect the movements of bonefish to the edge of the drop-off in the Exuma Sound (Appendix 1).

From December 2008 through June 2009, manual tracking was conducted at discrete points at the end of Cape Eleuthera and along the edge of the wall of the Exuma Sound using a portable receiver and hydrophone (VR100, Vemco Inc., Halifax, NS). Discrete points for manual tracking were established based on data collected by the remote receivers that indicated the general vicinity near the end of Cape Eleuthera that bonefish were frequenting. Manual tracking was conducted from a boat, and the manual hydrophone was lowered to a depth of 1–2 m below the surface of the water. Given the burst interval of the coded transmitters (min and max 45–135 s), presence/absence determinations were conducted for a minimum of 300 s (5 min) at each site. When detected, the codes of tagged bonefish were recorded and then visual surveys were conducted. To supplement the tracking of fish implanted with coded tags, we also used V9 continuous pinger transmitters (9 mm diameter, 21 mm long, 2.9 g in air, 1,000 ms pulse interval, 21 day battery life, Vemco Inc., Halifax, NS) gastrically implanted into two bonefish caught directly from a suspected pre-spawning aggregation. The transmitter was inserted into the stomach of the fish through a smooth plastic tube and plunger that was gently inserted into the esophagus. The entire procedure took less than 30 s and was conducted while the fish were entirely submerged. Continuous transmitters allowed for more precise manual tracking of movement patterns because of a limited delay between transmissions, and gastric implantation allowed fish to recover quickly from tag deployment (Danylchuk et al. 2007). Visual surveys were conducted using snorkel and SCUBA equipment. The estimated number of bonefish observed, their position in the water column, and their behaviors were recorded both manually on dive slates and using digital still and video imaging when lighting permitted.

Data analysis

We grouped remote receivers into five spatial zones based on the physical characteristics of the coastal region, including water depth and the proximity of small tidal creeks to the deep coral shelf offshore (Fig. 1). Zone 1 included the most easterly extent of the array and was comprised of a tidal creek (Starved Creek) as well as a wide, shallow flat (8 km^2). Zone 2 included two small tidal creeks (Broad Creek and Kemp's Creek) and a series of small bays and flats; all transmitter-implanted bonefish were collected from and redeployed in this zone. Zone 3 included the end of Powell Pointe, a flow-through marina constructed in the 1960s at the end of the peninsula, and a small defunct dredged marina known as No Name Harbor. Zone 4 included receivers that were greater than 200 m offshore of Powell Pointe, but did not include those receivers positioned within 30 m of the edge of the deep drop-off of the Exuma Sound ("the wall"). Receivers along the edge of the wall, including one receiver placed at 42 m down the edge of the wall, constituted Zone 5.

For each receiver, the total number of detections was tallied from the date of deployment to the last date downloaded (06 June 2009). To examine seasonal differences in movement patterns, we compared the proportion of detections for individual fish for each month (December 2007 through June 2009) among study zones. We also compared the number of fish using each zone in each month to the total number of tagged fish detected by all receivers in the array as an indicator of zone use across seasons. To determine usage patterns within zones, we calculated the number of detections for each receiver weighted by the number of days the receiver was deployed. The total number of detections per days deployed was then compared for receivers in each of the five zones using a repeated measures analysis of variance (ANOVA). Comparisons between sexes were also conducted. Plots of individual fish movements over time were examined to determine whether there were repeatable patterns in movements on a daily to seasonal basis. Data from manual tracking were mapped and used to determine fine-scale movement patterns. Behavioral observations made in the field or recorded on still, and video cameras were categorized and synchronized with movement data recorded via manual and remote acoustic telemetry.

Results

Bonefish surgically implanted with transmitters ranged in size from 447 to 605 mm total length (Table 1). Female bonefish implanted with transmitters in both years were significantly larger than males (2007, males 479 ± 22 mm, $n = 16$, females 512 ± 38 mm, $n = 14$, $t = -2.94$, *df* 28, $p = 0.007$; 2008, males 491 ± 20 mm, $n = 15$, females 520 ± 37 mm, $n = 15$, $t = -2.69$, *df* 28, $p = 0.012$), and there was no difference in the size of males ($t = -1.61$, *df* 29, $p = 0.12$) or females ($t = -0.620$, *df* 27, $p = 0.54$) between years. The transmitter-implanted bonefish still at large from an earlier study ranged in size from 475 mm to 560 mm ($n = 8$, one male, four females, and three of unknown sex; Table 2).

Between 02 December 2007 and 06 June 2009, there were a total of 1,139,456 detections for the 60 bonefish implanted with transmitters specifically for this study (Table 1), and an additional 278,965 detections for the eight additional transmitter-implanted bonefish from an earlier study. Following a review of the detection histories, paying particular attention to fish that showed continuous detections on a single receiver for multiple days when visual observations showed no fish in the area (implying tag expulsion or death), we omitted six individuals (8878, 8886, 8896, 8904, 54352, and 54353) from further analyses. With their omission, we subsequently used data from a total of 62 bonefish that produced 1,081,696 reliable detections (fish deployed in Dec 2007, $n = 26$, detections = 573,254; fish deployed in Dec 2008, $n = 28$, detections = 229,477; previously tagged fish, $n = 8$, detections = 278,965) to examine whether bonefish make offshore movements during the suspected spawning season. For bonefish surgically implanted with transmitters in 2007, the duration of detection ranged from 5 to 549 days (mean of 129 ± 74 days), whereas fish tagged in 2008 had duration of detections ranging from 2 to 178 days (mean of 125 ± 63 days; Table 2).

Movement patterns within zones

Bonefish were detected in Zones 1 and 2 in every month throughout the study (Fig. 2; Tables 1, 2). A total of 45 tagged bonefish (73%) used in Zone 1, and the proportion of individuals using this zone when compared to the total number of tagged bonefish being detected throughout all zones ranged across months from 15 to 81% (Tables 1, 2). The greatest number of detections in Zone 1 occurred for receiver PF1, which was situated 200 m from shore on a shallow coastal flat (Appendix 1). All tagged bonefish ($n = 62$) used Zone 2 during the course of the study, with more than 75% of the tagged bonefish in each month being detected in this zone (Tables 1, 2). The mean proportion of detections among individuals using Zone 2 exceeded 80% in December 2007, January 2008, June through November 2008, and June 2009 (Fig. 2). From February through May 2008, as well as from December 2008 through May 2009, the proportion of detections in Zone 2 declined and was accompanied by an increase in the mean proportion of detections in Zone 1 and Zone 3 (Fig. 2).

Although the mean proportion of detections in Zone 3 was greatest in February and March 2008, and December 2008 through June 2009 (Fig. 2), outside these periods the mean proportion of detections was less than 2% for any given month. When compared to the total number of individuals detected in all zones for each month, Zone 3 was used by more than 30% of tagged fish from December 2007 through March 2008, and October 2008 through May 2009 (Table 3). Of the 62 bonefish included in the analyses, a total of 44 different individuals (71%) used Zone 3 at some point during the study. The mean proportion of detections in Zone 4 never exceeded 2.5%, with no detections occurring in May through July 2008 and June 2009 (Fig. 2). When Zone 4 was used, the proportion of tagged individuals compared to the number of tagged individuals in all zones ranged from 7% in January, August, and September 2008, to 70% in March 2008 (Table 3). For Zone 5, bonefish were detected in March and April 2008, September 2008 through March 2009, and May 2009, and the mean proportion of detections in this zone did not exceed 0.22% (Fig. 2). For months where tagged bonefish were detected in Zone 5, the proportion of tagged individuals using this zone when compared to those at large throughout the array ranged from 6% (Feb 2009) to 50% (April 2008). Of the

Table 1 Summary of tagging, biological, and monitoring data for the 60 bonefish used in this study, collected from the north coast of Cape Eleuthera, The Bahamas

Date tagged	Location tagged	Transmitter ID	Total length (mm)	Sex	Date last detected	Total no. days at large	Total no. of detections	Total no. of receivers detected on
2-Dec-07	Kemps Creek	8877	475	M	6-Jul-08	217	27,647	15
		8878	468	F	16-Jun-08	197	115,036	13
		8879	495	M	15-Feb-08	75	8,126	13
		8881	509	F	23-Apr-09	508	39,407	30
		8886	455	M	3-Jun-09	549	13,989	13
		8888	520	M	11-May-08	161	10,524	25
		8890	484	F	6-Oct-08	309	16,371	20
		8891	474	F	16-Jun-08	197	25,768	30
		8892	460	M	14-Dec-07	12	2,826	12
		8894	525	F	3-Feb-08	63	8,501	18
		8895	480	M	20-Dec-07	18	1,745	8
		8896	490	F	22-Mar-08	111	1,775	11
		8897	560	F	1-Oct-08	304	13,694	18
		8898	505	F	30-Dec-08	394	19,702	24
		8900	471	F	25-Jan-09	420	9,370	17
		8902	490	M	3-Jun-09	549	32,298	29
		8905	452	M	20-Feb-08	80	17,805	19
3-Dec-07	Broad Creek	8880	509	F	13-Feb-08	72	10,649	16
		8882	458	M	4-Jun-09	549	47,927	29
		8883	485	M	2-Apr-08	121	15,823	27
		8884	605	F	15-Apr-09	499	60,366	30
		8885	497	M	17-May-09	531	16,214	13
		8887	447	M	11-May-09	525	34,039	31
		8889	470	M	8-Dec-07	5	1,109	17
		8893	499	F	26-Mar-09	479	7,638	13
		8899	514	M	4-Jun-09	549	28,485	33
		8901	524	F	7-May-09	521	40,997	29
		8903	475	M	31-Oct-08	333	17,304	23
		8904	548	F	30-May-09	544	61,836	15
		8906	495	M	20-Jul-08	230	481	13
8-Dec-08	Kemps Creek	54348	490	M	4-Jun-09	178	20,073	13
		54349	492	F	4-Jun-09	178	16,921	12
		54350	487	F	4-Jun-09	178	27,792	25
		54351	516	M	17-Mar-09	99	5,756	18
		54352	470	M	9-Dec-08	1	9	2
		54353	476	F	19-Jan-09	42	14,407	14
		54354	511	M	16-Apr-09	129	5,427	10
		54355	540	F	29-May-09	172	1,682	9
		54356	452	M	4-Jun-09	178	10,324	12
		54357	500	M	10-Apr-09	123	5,872	11
		54358	489	F	2-Feb-09	56	451	8
		54359	470	M	4-Jun-09	178	11,618	14
		54360	483	M	4-Jun-09	178	18,599	26
		54361	520	F	4-Jun-09	178	13,127	22
		54362	490	F	16-Dec-08	8	1,399	6

Table 1 continued

Date tagged	Location tagged	Transmitter ID	Total length (mm)	Sex	Date last detected	Total no. days at large	Total no. of detections	Total no. of receivers detected on
		54363	470	F	15-Mar-09	97	10,443	8
		54364	537	F	1-Jun-09	175	13,922	9
		54365	480	M	14-Apr-09	127	7,276	11
		54366	555	F	15-Apr-09	128	5,710	16
		54367	485	M	17-Feb-09	71	19,642	13
		A128/129	555	F	1-Jun-09	175	982	7
		A130/131	578	F	3-Apr-09	116	2,373	9
		A132/133	475	M	31-May-09	174	5,017	18
		A134/135	510	M	10-Dec-08	2	57	7
		A136/137	520	M	31-May-09	174	4,526	17
		A138/139	590	F	20-Mar-09	102	3,090	13
		A140/141	520	F	10-Dec-08	2	158	8
		A142/143	515	F	1-Jun-09	175	6,864	14
		A144/145	495	M	1-Jun-09	175	5,638	12
		A146/147	515	M	31-May-09	174	4,738	16

Last download of receivers 06 June 2009

Table 2 Summary of tagging, biological, and monitoring data for bonefish implanted with acoustic transmitters prior to 02 Dec 07 that were still at large in the study area off the north coast of Cape Eleuthera, The Bahamas

Date tagged	Location tagged	Transmitter ID	Total length (mm)	Sex	Date last detected	Total no. days at large	Total no. of detections
19-Feb-06	Kemps Creek	4079	490	Unknown	30-Jan-08	710	78,888
20-Feb-07	Kemps Creek	2379	530	F	30-Dec-07	313	5,195
		2381	520	F	20-Feb-08	365	51,992
		2382	475	F	01-Dec-08	650	25,126
16-Mar-07	Broad Creek	934	460	M	04-Jun-09	811	25,476
		937	460	Unknown	02-Jun-09	809	29,872
		2375	560	F	28-Mar-08	378	32,100
		2377	455	Unknown	25-Dec-08	650	30,316

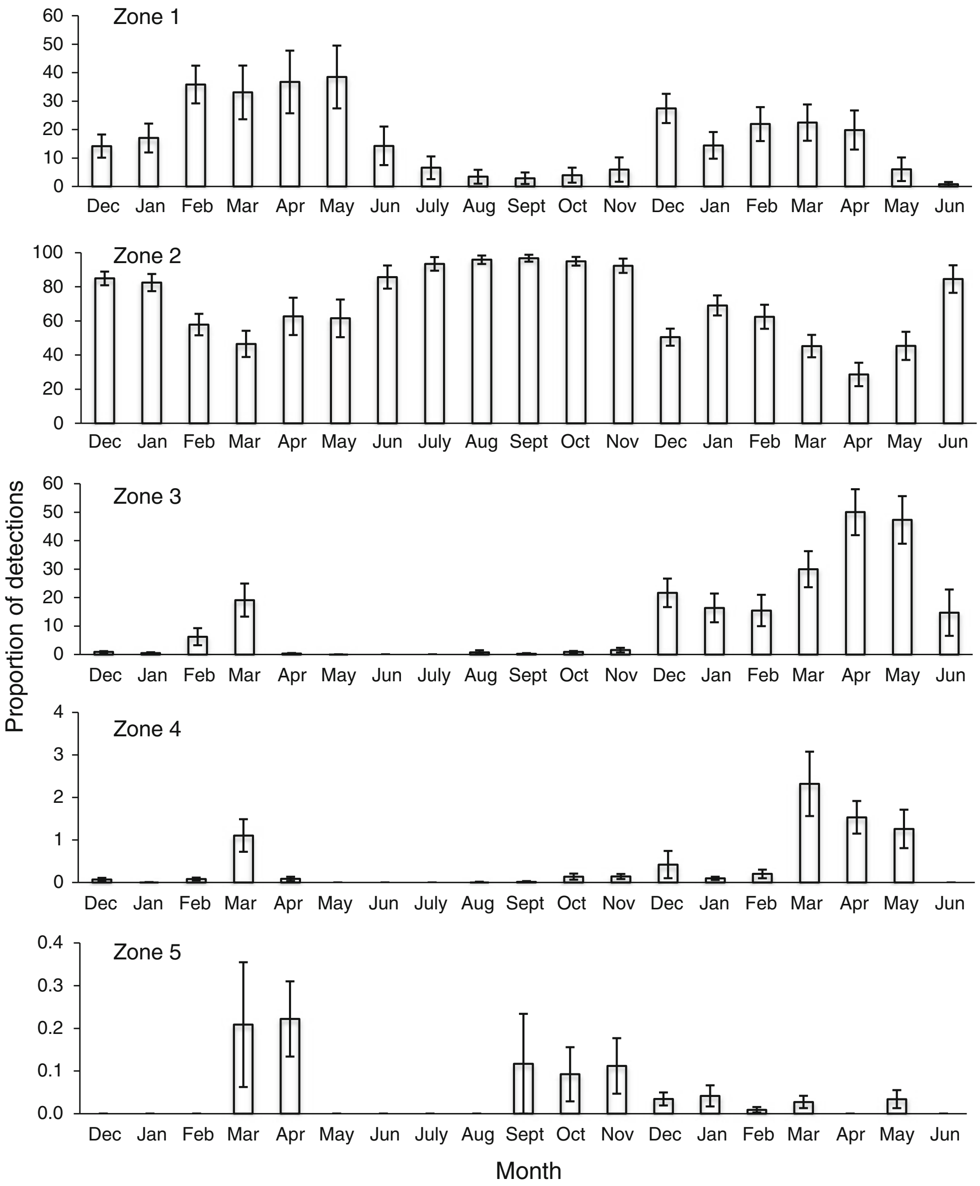
bonefish included in these analyses, a total of 20 different individuals (32%) were detected in Zone 5 at some point during the 19 months of the study. The greatest number of detections in Zone 5 was recorded by WZ9, WZ3, WZ2, WZ7, and WZ5 (Appendix 1), all of which were located in 9–26 m of water and within 100 m of the edge of the deep drop-off (>1,000 m) of the Exuma Sound.

The total length of both males and females that used Zone 3 was not significantly different than those tagged bonefish that remained in Zones 1 and 2 (Zone 3: males 484 ± 22 mm vs. Zone 1 and 2: males 489 ± 22 mm, $t = -0.57$, $p = 0.57$; Zone 3: females 528 ± 39 mm vs. Zone 1 and 2: females 505 ± 26 mm, $t = 1.69$, $p = 0.10$). There was also no difference in the size of male and female bonefish that were detected in Zones 4 and 5 (males 486 ± 22 mm, females 530 ± 40 mm) when compared to those that used Zone 3 (males, $t = 0.17$, $p = 0.87$, females, $t = 1.54$, $p = 0.14$). The number of males detected in each of Zones 3, 4, and 5 (23, 17, and 9, respectively) were not notably different than the number of females detected in each of these zones (19, 14, and 10, respectively).

Movement patterns among zones

Of the 45 bonefish detected in Zone 1 (tidal flats), 32 of these individuals (71%) were also detected in Zone 3 (end of Cape Eleuthera) at some point during the study. Of the 44 tagged bonefish detected in Zone 3, 34 of these individuals (77%) were detected in Zone 4 (transition area between Powell Pointe and the edge of the wall), while 21 of these

Fig. 2 Mean proportion of detections (±1 SD) for bonefish in relation to study zone for each month of the study



individuals (47%) were also detected in Zone 5. Only one fish (8906) was detected in the transition area between Powell Pointe and the edge of the wall (Zone 4) without being detected in Zone 3, while all bonefish detected in Zone 5 were also detected in Zones 2, 3, and 4 at some point during study. A total of 16 of the fish detected in Zone 5 were also detected in Zone 1. Of the 21 individuals detected at or near the drop-off (Zone 5), 13 (67%) used this zone on multiple occasions throughout the study period, with the greatest number of separate periods of detections being for fish 8887 ($n = 6$), 8891 ($n = 4$), and 8902 ($n = 4$). The number of males ($n = 10$) and females ($n = 10$) detected at or near the drop-off was similar, as was the movement patterns among zones between the sexes.

Plots of the dates and times of detections were used to infer when tagged bonefish moved among study zones (Figs. 3, 4 display detection patterns for four individuals). Traces of bonefish tracked for nearly the entire duration of the study (e.g., fish 8884, 8887, and 8899, Table 1) showed that although movements between the tidal flats and tidal creeks (Zones 1 and 2) occurred throughout the year, movements from these zones to the end of Cape Eleuthera and offshore (Zones 3–5) occurred primarily between late October and May (Fig. 3). Periods of detections in Zones 3–5 were preceded by detections in Zones 1 and 2 (e.g., fish 8884) or just Zone 2 (e.g., fish 8887, 8899, 54350; Fig. 4). In addition, periods of detection in Zones 3–5 ranged in duration from 1 to 6 days at which bonefish returned to Zones 1 and 2 (Fig. 3). During these periods of detection in Zones 3–5, as many as four separate detections were made in Zone 5 often on successive days (Figs. 3, 4).

Table 3 Total number of tagged bonefish detected by remote receivers for each month of the study, as well as the number of tagged bonefish detected in each of the five receiver zones. Number in parentheses is the percentage of detected individuals by zone compared to the total number detected among zones

Zone	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun
Total across zones	34	29	27	20	18	17	16	16	15	15	14	13	40	33	32	30	29	23	13
1	23 (68)	20 (69)	22 (81)	9 (45)	10 (56)	8 (47)	6 (38)	4 (25)	3 (20)	4 (27)	5 (36)	4 (31)	23 (58)	16 (48)	18 (56)	19 (63)	11 (38)	4 (17)	2 (15)
2	34 (100)	29 (100)	27 (100)	19 (95)	16 (89)	14 (82)	15 (94)	16 (100)	15 (100)	15 (100)	14 (100)	13 (100)	40 (100)	31 (94)	30 (94)	26 (87)	22 (76)	20 (87)	13 (100)
3	11 (32)	10 (34)	10 (37)	14 (70)	4 (22)	1 (6)	0 (0)	0 (0)	1 (7)	1 (7)	5 (36)	9 (69)	19 (48)	12 (36)	14 (44)	19 (63)	18 (62)	16 (70)	3 (23)
4	7 (21)	2 (7)	10 (37)	14 (70)	6 (33)	0 (0)	0 (0)	0 (0)	1 (7)	1 (7)	4 (29)	5 (38)	13 (33)	7 (21)	6 (19)	11 (37)	13 (45)	13 (57)	0 (0)
5	0 (0)	0 (0)	0 (0)	4 (20)	9 (50)	0 (0)	0 (0)	0 (0)	0 (0)	1 (7)	2 (14)	4 (31)	8 (20)	5 (15)	2 (6)	6 (20)	0 (0)	3 (13)	0 (0)

Note that the number of fish indicated in each zone may not add up to the total number among zones since some individual bonefish were detected in multiple zones for any given month

Movements to the deep drop-off (Zone 5)

The frequency of detections on receivers in Zone 5 was greatest approaching the third quarter and new moon (Fig. 5). All bonefish detected at or near the drop-off (Zone 5) were present between 1818 h and 0457 h, and 71% of these observations were between 2200 h and 0200 h. The greatest number of individuals detected offshore on a single receiver on a particular day was eight fish on 02 April 2008 between 0115 h and 0124 h (on receiver WZ9). All of these fish that were detected on 02 April 2008 moved back to tidal creeks and inshore coastal flats (Zones 1 and 2) within 12 h of last being detected at or near the drop-off (Zone 5), except for fish 8888 that was never detected again. A total of four fish were also detected in Zone 5 between 25 and 28 Jan 2009, followed by a return to Zones 1 and 2 (e.g., fish 8899, Fig. 4). Detections in Zone 5 between 25 and 28 Jan 2009 occurred on WZ7 and WZ9 located along the top of the Exuma Sound, as well as on WZ9D, which was located offshore of WZ9 in 45 m of water down the face of the drop-off (Appendix 1). Two of the three fish detected by WZ9D (934 and 8902) were not detected by WZ4 during this period. Although detections on WZ9D also occurred on 26 Oct 2008 (fish 2377) and 08 May 2009 (fish 54361), these fish were also detected on WZ9 within 5–10 min either before or after being detected by WZ9D.

Only two of the bonefish implanted with accelerometers (A128/129 and A138/139, both females) were detected at or near the drop-off (Zone 5). Fish A138/139 was detected by WZ9 on 19 March 2009 at 2100 h at a depth of 5.7 m. Given that the water depth at the WZ9 was 26 m, this fish was at least 20 m off of the substrate at the time of detection. Fish A128/129 was detected by WZ3 on 12 May 2009 at 0102 h at a depth of 8.5 m. Six accelerometer-implanted bonefish were detected in the area between Powell Pointe and the deep drop-off (Zone 4), at a mean depth of 4.2 ± 1.4 m ($n = 224$ detections). Water depth where these fish were detected ranges from 4 to 6 m, suggesting that these individuals were swimming relatively close (0.86 ± 0.4 m) to the substrate. Similarly, depth measurements detected for bonefish in Zone 3 (8 individuals, 7566 detections) showed that individuals were at a mean depth of 2.5 ± 1.4 m, at or near the bottom. All of the depth measurements (25651 detections) for bonefish ($n = 10$) in the tidal flats and creeks (Zones 1 and 2) also showed that fish were close to the substrate, however, much of this habitat is very shallow (i.e., <2 m). Because of the relative paucity of acceleration data collected, we do not present those data here.

Manual tracking and visual observations

Based on data collected from fixed receivers, manual tracking and visual observations were conducted primarily in No Name Harbor (NNH, small dredged marina at the end of Cape Eleuthera) as well as along the edge of the deep drop-off (Zone 5). A total of 189 individual manual tracking events occurred over 37 separate days. Detection data from the fixed receiver in NNH showed that individual fish were only at this site from dawn to dusk, and all fish left NNH simultaneously, usually in a single school (Fig. 6). This information was used to concentrate manual tracking and visual observations around dusk when bonefish were moving out of NNH and were subsequently detected on receivers in Zones 4 and 5. Visual observations estimated that between 500 and 2,000 bonefish were in NNH when

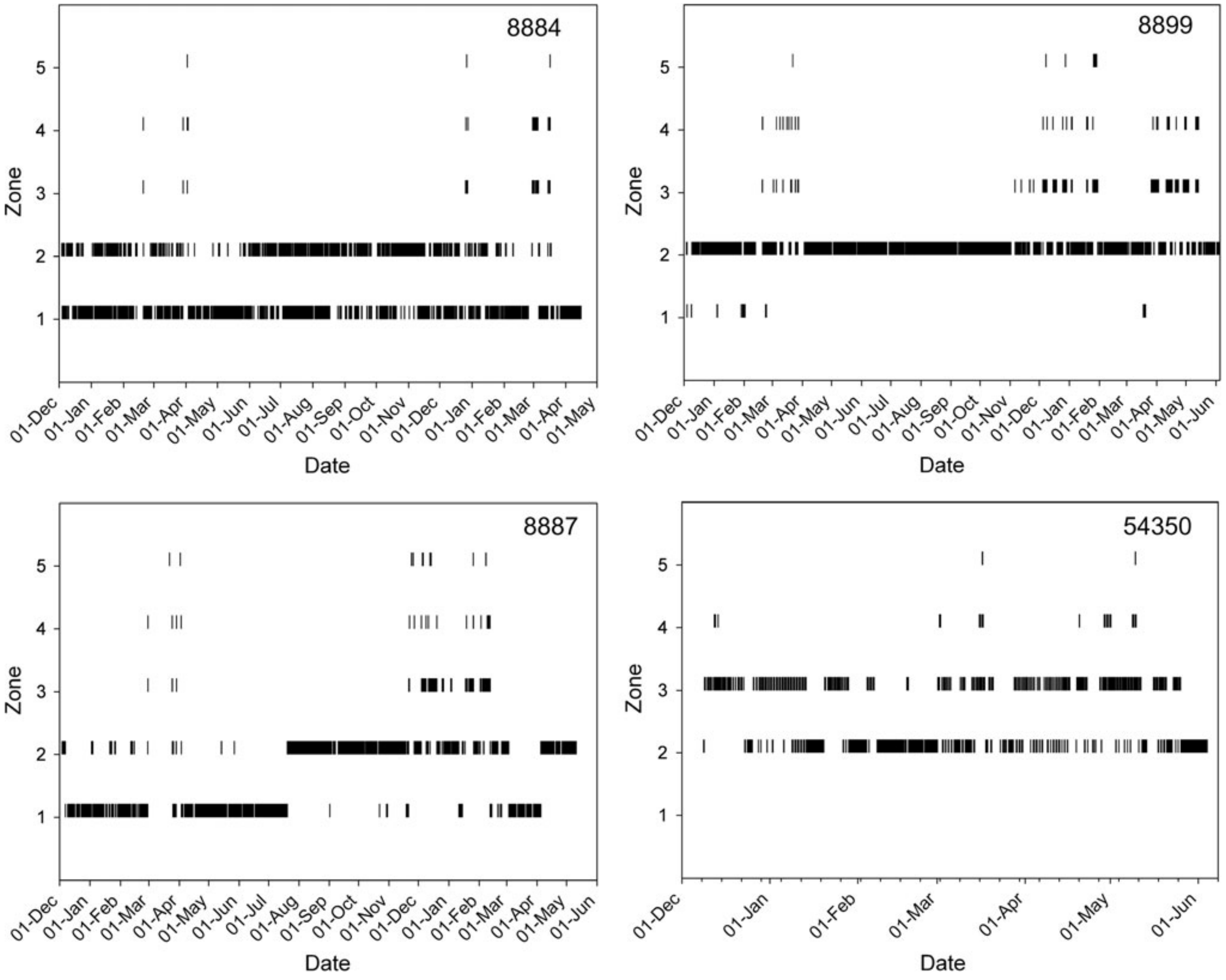


Fig. 3 Detection histories of four representative bonefish (8884, 8887, 8889, and 54350) in relation to study zone, from the time of deployment to the end of the study

tagged fish were detected in this location via manual tracking, and that all fish moved out of NNH at dusk (approx. 1800–1900 h) consistent with data from the receiver. On five occasions, bonefish were manually tracked to the drop-off of the Exuma Sound, however, attempts at visual observations using SCUBA were not successful.

We captured bonefish from NNH on 10 April 2009 (female, 560 mm TL) and 11 April 2009 (male, 520 mm TL) and gastrically implanted them with continuous transmitters. Both fish released nearly hydrated gametes when being handled. These fish were continuously tracked on five separate nights from before sunset to close to sunrise. Between 5 and 7, bonefish carrying coded tags were also detected in the same school during the overnight continuous tracking. Manual tracking of these individuals revealed that bonefish leaving NNH initially moved either directly offshore of the mouth of the bay or turned south and moved parallel to the shoreline (Fig. 7a, b). The shoreline south of NNH becomes closer to the deep drop-off of the Exuma Sound, with the shortest distance between the shoreline and the drop-off of approximately 350 m (near where receiver WZ2 was deployed). Given that the tracks are that of the vessel and do not take into consideration the range of detection of the manual receiver, there is an even greater likelihood that the fish tracked on these occasions were using the edge of the wall.

Visual observations and video recordings made during daylight hours in NNH showed that bonefish were aggregated in one large school swimming within the bottom half of the water column, but not associated continuously with the substrate. Bonefish in these aggregations were rarely observed feeding. Close to dusk, bonefish were observed physically interacting, displaying behaviors that involved one fish swimming behind another, and then rubbing its snout on the posterior end of the ventral region (i.e., ventral nudging). For up to 1 h prior to such bonefish aggregations moving offshore, individuals were also observed breeching the surface of the water or “porpoising” (See video footage

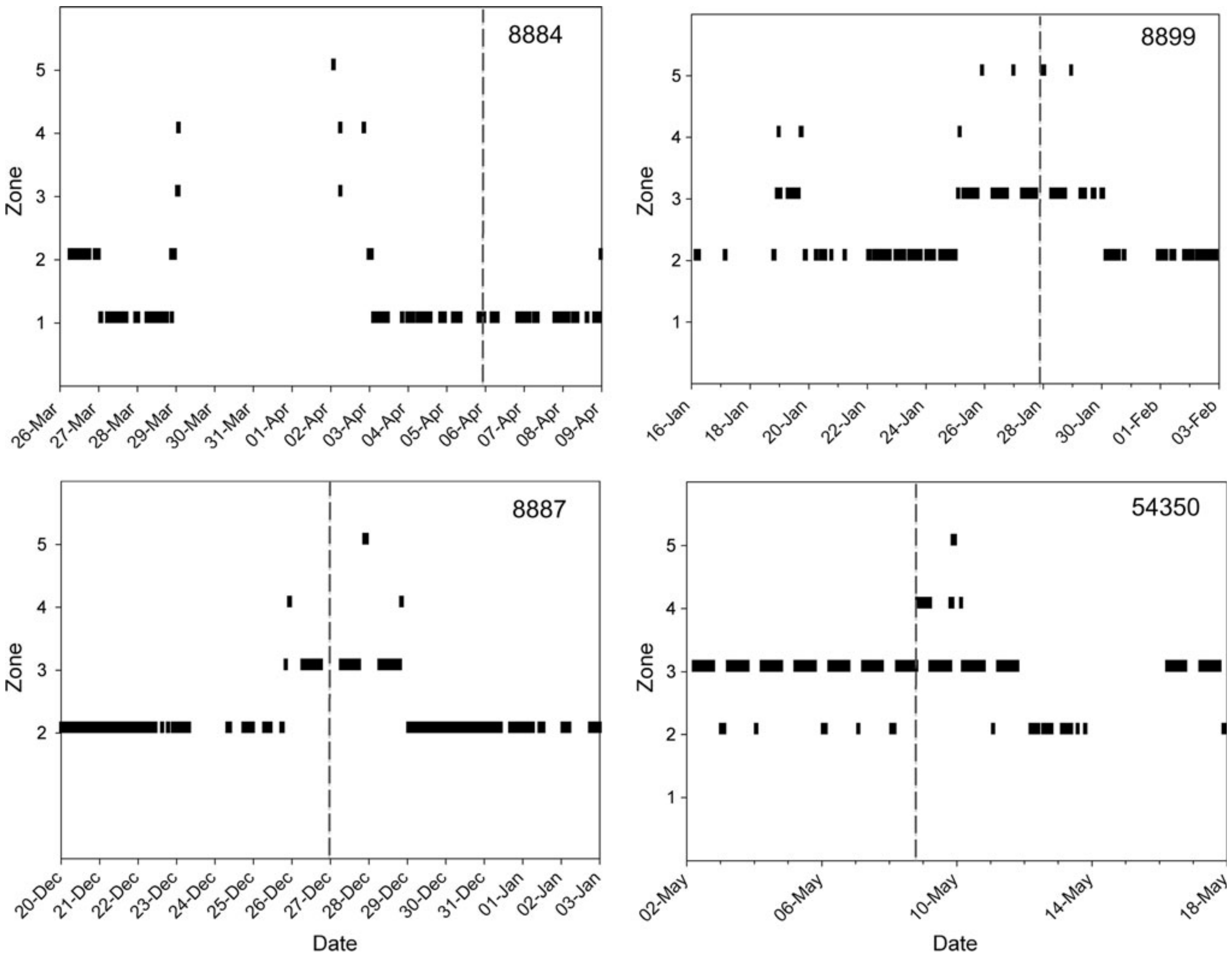


Fig. 4 Detection histories of four representative bonefish (8884, 8887, 8889, and 54350) for 7 days before and 7 days after being detected in Zone 5 for selected periods during the study. Note that the *vertical dashed line* represents a peak in the lunar cycle

posted on YouTube: http://www.youtube.com/user/FishForward#p/a/u/0/Id0vO1DUxgs). These individuals appeared to be gulping air as many bubbles were seen coming out from the fish's mouth and gill areas.

Discussion

Movement patterns

Previous studies that employed acoustic telemetry to examine the movement patterns of bonefish showed that individuals frequently used tidal creeks and coastal flats (Colton and Alevizon 1983a; Humston et al. 2005; Murchie 2010), often with a high degree of site fidelity. Bonefish in these studies predictably moved into shallow tidal creeks and coastal flats with the rising tide and then moved out of these habitats as the tide receded (Humston et al. 2005; Murchie 2010). Based on a diet study conducted in The Bahamas by Colton and Alevizon (1983b), the use of shallow tidal creeks and flats appears to be related to foraging. One exception to this pattern may occur during summer periods when bonefish may avoid shallow flats because water temperatures approach or exceed their physiological thermal maxima (Humston et al. 2005; Murchie et al. 2011). Collectively, movements of bonefish, including migrations, could be occurring when suitable areas for feeding and breeding are spatially separated, but when the costs of migration are outweighed by the benefits of being in more suitable areas (Dingle and Drake 2007).

Although the movement patterns of bonefish to the end of Cape Eleuthera between October and May could be related to foraging opportunities, no typical shallow tidal creeks and coastal flats exist in this area. Because bonefish are benthivores, their feeding ecology is tightly linked to the productivity of the benthos and availability of preferred prey. Diet studies in The Bahamas and Florida found that bonefish predominantly consumed benthic invertebrates, such as xanthid crabs and alpheid shrimp (Colton and Alevizon 1983b; Crabtree et al. 1998; Layman and Silliman 2002), and a greater abundance of these prey items are often associated with highly productive tidal mangrove creeks and sea grass beds especially when compared to other tropical coastal marine habitats (Kathiresan and Bingham 2001). Visual observations of the bonefish during the day suggested that individuals in aggregations were rarely feeding and spent most of their time in mid-water column. In addition, even though the dredged bays at the end of Cape Eleuthera were relatively deep (3 m) and always contained enough water for bonefish to remain throughout the tidal cycle, our telemetry data showed that bonefish not only remained throughout the entire daylight period, but also regularly left these bays every evening from dusk to dawn, regardless of the tide. This is considerably different than the movement patterns of bonefish inhabiting the inshore tidal creeks, which consistently moved with the tides regardless of the time of day (Murchie 2010).

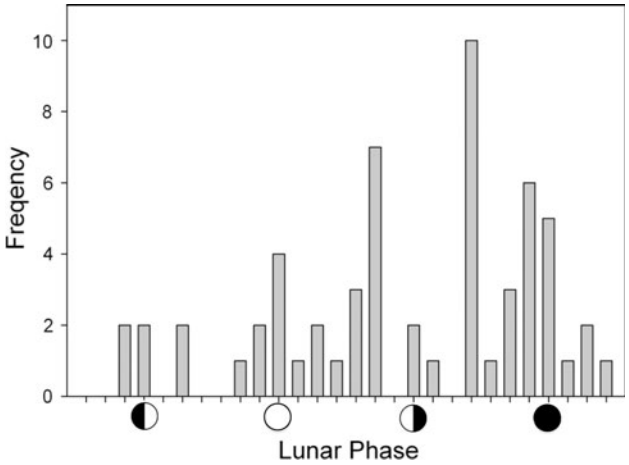
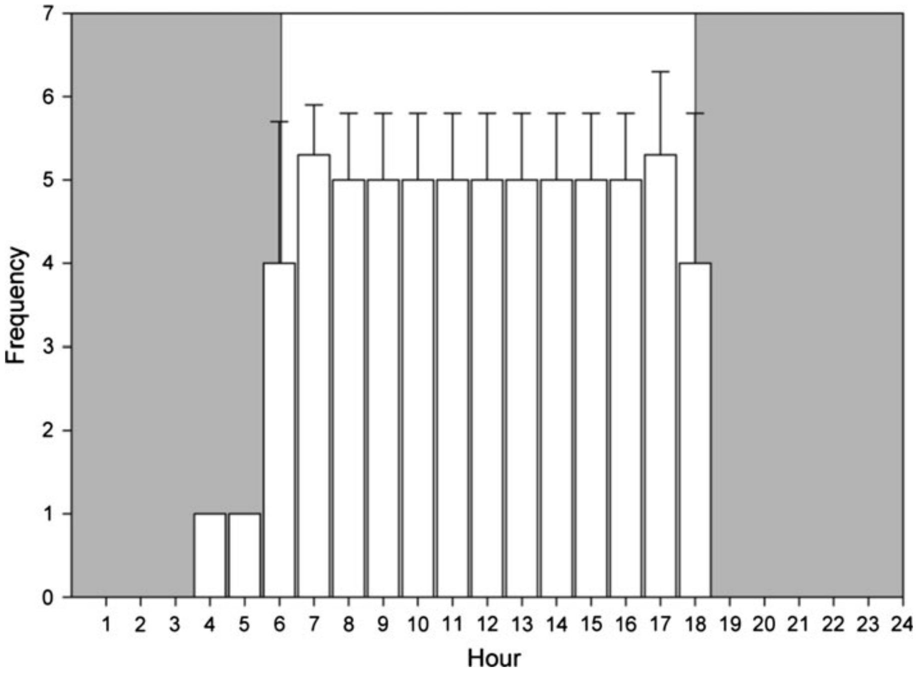


Fig. 5 Number of bonefish detected on receivers in Zone 5 in relation to lunar phase for all months combined (2007 and 2008). *Open circle* represents full moon and *closed circle* represents new moon

A more likely explanation for the movement of bonefish to the end of Cape Eleuthera between October and May is for spawning. The migration of bonefish from inshore flats and tidal creeks to deeper coastal habitats to form large aggregations, followed by their synchronous movements from these deeper coastal habitats to the drop-off of the Exuma Sound associated with peaks in the lunar cycle, is similar to reproductive patterns of many other fishes inhabiting coral reef environments (Domeier and Colin 1997). Many coral reef fishes, particularly those that are pelagic broadcast spawners, migrate to form temporary aggregations for the specific purpose of spawning, and the timing of the aggregations and spawning bouts are often specifically linked to peaks in the lunar cycle (Johannes 1978). Given that tides are relatively strong during new and full moons, one possible benefit of migrating to offshore locations to spawn is an increase in the dispersal of pelagic larvae, an outcome that could help increase the chances of offspring finding food resources (Doherty et al. 1985; Domeier and Colin 1997). Indeed, the unique lifecycle of the Albulidae involves a prolonged planktonic larval stage (the leptocephalus), which appears to be an adaptation to long-distance dispersal (Dahlgren et al. 2008). Many pelagic broadcast spawners are also known to ascend toward the surface as a potential mechanism to promote greater egg dispersal (Johannes 1978). Even though we only recorded one

Fig. 6 Mean number of tagged bonefish (±1 SD) detected by the receiver in No Name Harbor (NNH) in relation to hour of day between 22 Jan and 28 Jan 2009. Note that the receiver detected a maximum of eight transmitter-implanted bonefish during this period. *Shaded areas* represent night time, while the *open area* represents daylight hours



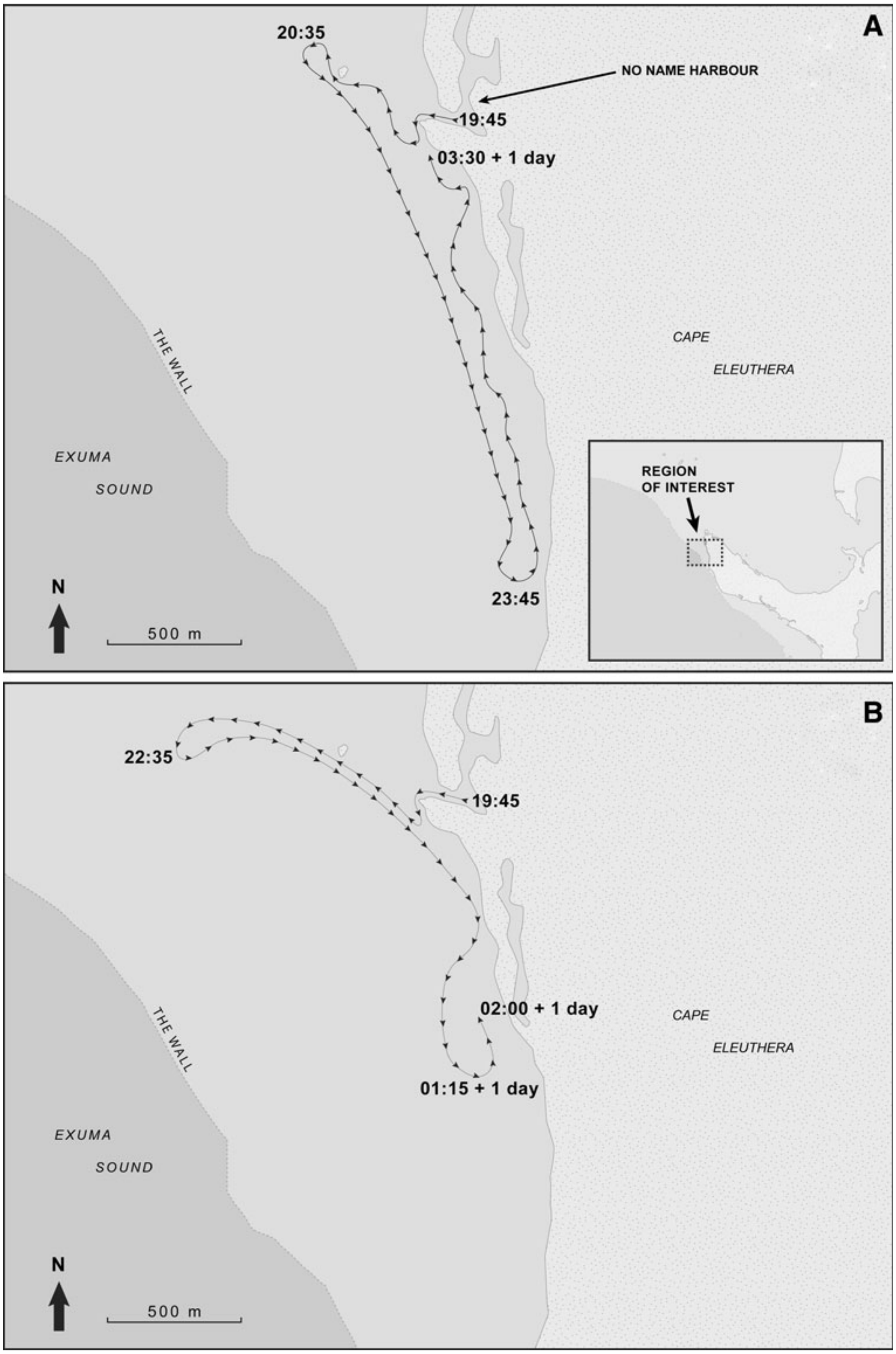


Fig. 7 Traces of bonefish from No Name Harbor on 10 April 2009 (**a**) and 11 April 2009 (**b**) that were gastrically implanted with continuous transmitters and manually tracked from before dusk until early morning the following day

depth measurement for an accelerometer-implanted bonefish along the edge of the wall of the Exuma Sound, this individual was detected well off the bottom, especially when compared to depth measurements recorded for bonefish in the other study zones. Interestingly, Colin (1995) found that oceanographic currents in the Exuma Sound are relatively self-contained, resulting in a gyre that potentially increases the likelihood of self-recruitment for fishes that have a pelagic larval stage. Indeed, bonefish in the Exuma Sound were shown to have a 41–71 day larval period (Mojica et al. 1995), potentially contributing to self-recruitment, a life history characteristic that increases the need to manage local fish stocks (Sponaugle et al. 2002). Other possible benefits of aggregating to reproduce include reduction in egg predation, increased genetic exchange, and higher fertilization rates (Domeier and Colin 1997; Bolden 2000; Sala et al. 2003). The fact that the movements of bonefish offshore occur between dusk and dawn may also help reduce mortality both on eggs and on spawning adults, especially in predator-rich environments such as tropical coral reefs (Johannes 1978).

Spawning-related behavior

Although the offshore movement of bonefish at night precluded our ability to specifically observe spawning behavior and the release of gametes, other evidence supports the supposition that the movement patterns we quantified are indicative of reproductive activity. When examining the seasonal variation in body composition and condition of bonefish inhabiting the tidal creeks and flats along the north coast of Cape Eleuthera, Murchie et al. (2010) found that the allocation of energy to gonads (measured as gonadosomatic index) was significantly greater in winter months for both sexes. In addition, whole-body lipid content and energy density for bonefish from this region were significantly lower in winter months, indicating that individuals during these periods were likely mobilizing energy stores for the purposes of allocating these resources to reproduction (Murchie et al. 2010). In fact, bonefish angled from aggregation sites at the end of Cape Eleuthera from January to May 2009 were found to be ripe, with those killed as part of another study showing relatively high gonadosomatic indices and advanced stages of gonad development (Danylchuk et al. unpublished data).

Behavioral observations made while bonefish resided in large aggregations at the end of Cape Eleuthera are also consistent with courtship prior to spawning activity recorded for other species of tropical marine fishes (Lowerre-Barbieri et al. 2003; Baldwin and Snodgrass 2008). Specifically, “ventral nudging” has been documented for common snook, *Centropomus undecimalis*, (Lowerre-Barbieri et al. 2003), and Atlantic tarpon (Baldwin and Snodgrass 2008), a behavior that involved males bumping and rubbing the ventral region of females. Ventral nudging among bonefish in the large aggregations was also observed in our study just prior to their offshore movement, but has not been described in other contexts. Another behavior that we observed that could be related to spawning is porpoising (or breaching), which was also performed by bonefish in the large aggregations only at times approaching dusk, when they were ready to move toward offshore habitat. Although the purpose for this porpoising has yet to be determined, we postulate that bonefish may be gulping air to fill their air bladders as a way to increase buoyancy prior to moving into deeper water, where they potentially spawn near the surface of the water column.

Although our study provides the most robust evidence to date as to when and where spawning activity occurs for bonefish, we believe that the ability to observe spawning behavior directly was hampered by the fact that it occurs at night. In addition, during our attempts to observe this behavior at night off the deep water drop-off of the Exuma Sound, approaching the tagged bonefish with lights caused them to move away from the boat. As a result, visually documenting spawning events for bonefish may prove particularly challenging. It may be necessary, therefore, to visualize spawning events for bonefish using advanced technology such as duel beam sonar. Even without formally observing the specific behaviors related to the act of spawning, our study has demonstrated how multiple tracking techniques can be useful for determining the location and timing of spawning aggregations for coastal marine fishes.

This new understanding of the movement patterns and life history of bonefish has significant implications for the management of bonefish stocks particularly as they face increasing modification and destruction of coastal habitats including coral reefs. Given that transitional habitats between shallow and deep water are often desirable locations for marinas and tourism developments, knowledge that bonefish are not just residents of shallow flats but use transitional habitats on their way to deep water spawning sites can be instrumental for the development of comprehensive management strategies to protect bonefish stocks. An important next step is to determine the regional distribution of pre-spawning aggregations sites as well as the relative contribution of individual spawning aggregations to the maintenance of bonefish stocks. Collectively greater information on the reproductive life history of bonefish will ensure that bonefish stocks continue to support local economies through recreational fisheries.

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Appendix

See Table 4.

Table 4 Summary of hydrophone receiver array on the north coast of Cape Eleuthera, The Bahamas

Zone	Easting (UTM)	Northing (UTM)	Receiver code	Water depth (m)	Date deployed	Final date at location	Duration of deployment (days)
1	18380193	2744888	SC	0.5	2-Dec-07	8-Nov-08	342
1	18376913	2742032	PF1	1	2-Dec-07	4-Jun-09	550
1	18376734	2742269	PF2	1.5	2-Dec-07	4-Jun-09	550
1	18376416	2742584	PF3	2	2-Dec-07	8-Nov-08	342
1	18371426	2743032	RP1	1	2-Dec-07	4-Jun-09	550
1	18371599	2743434	RP2	1.5	2-Dec-07	10-Jan-09	405
1	18370258	2743423	BC1	1.5	2-Dec-07	8-Nov-08	342
2	18370431	2374393	BC2	2.5	2-Dec-07	8-Nov-08	342
2	18369630	2743734	BC3	1.5	2-Dec-07	4-Jun-09	550
2	18369031	2743970	BC4	1.5	2-Dec-07	4-Jun-09	550
2	18369392	2744189	BC5	2	2-Dec-07	4-Jun-09	550
2	18369297	2743602	BC6	0.3	2-Dec-07	4-Jun-09	550
2	18369525	2743509	BC7	0.3	2-Dec-07	7-Nov-08	341
2	18369486	2743451	BC8	0.3	2-Dec-07	4-Jun-09	550
2	18368248	2744887	KC1	1.5	2-Dec-07	4-Jun-09	550
2	18368118	2744691	KC2	1	2-Dec-07	4-Jun-09	550
2	18367592	2745659	PC1	1.5	2-Dec-07	4-Jun-09	550
2	18367891	2746016	PC2	2.5	2-Dec-07	4-Jun-09	550
3	18364871	2747098	GC1	2.5	14-Apr-09	4-Jun-09	51
3	18364898	2747390	BCEM	3	2-Dec-07	4-Jun-09	550
3	18364357	2747448	CEM	3.5	14-Jan-08	4-Jun-09	507
3	18364062	2747636	MCEM	5.5	2-Dec-07	4-Jun-09	550
3	18364110	2746555	NNH	4.5	28-Nov-08	4-Jun-09	188
4	18363523	2746627	CN1	5	08-Nov-08	4-Jun-09	208
4	18362603	2747144	CN2	4	08-Nov-08	4-Jun-09	208
4	18362383	2747592	CN3	5	08-Nov-08	4-Jun-09	208
4	18362513	2748402	CN4	6	10-Jan-09	4-Jun-09	145
4	18362887	2748821	CN5	6	08-Nov-08	4-Jun-09	208
4	18363949	2749173	CN6	6.5	08-Nov-08	19-Feb-09	103
4	18363900	2746137	FH1	5.5	8-Feb-09	4-Jun-09	116
4	18363431	2745976	FH2	6	8-Feb-09	4-Jun-09	116
4	18363073	2746382	FH3	6.5	8-Feb-09	4-Jun-09	116
4	18363335	2747118	SWC1	4	24-Jun-08	4-Jun-09	345
4	18362947	2746784	SWC2	6	24-Jun-08	4-Jun-09	345
4	18365028	2748038	PPO	2.5	2-Dec-07	4-Jun-09	550
4	18365205	2748591	EC1	3.5	2-Dec-07	4-Jun-09	550
4	18365418	2749163	EC2	3.5	2-Dec-07	4-Jun-09	550
4	18365602	2749890	EC3	4	2-Dec-07	4-Jun-09	550
4	18365841	2750444	EC4	4	2-Dec-07	4-Jun-09	550
4	18366026	2751013	EC5	4	2-Dec-07	4-Jun-09	550
3	18364106	2748277	MC1	3	2-Dec-07	4-Jun-09	550
4	18363716	2748716	MC2	6	2-Dec-07	4-Jun-09	550
4	18363306	2749177	MC3	6	2-Dec-07	4-Jun-09	550
4	18362880	2749613	MC4	6.5	2-Dec-07	4-Jun-09	550
4	18362467	2750030	MC5	7	2-Dec-07	4-Jun-09	550
4	18362001	2750409	MC6	7	2-Dec-07	4-Jun-09	550

Table 4 continued

Zone	Easting (UTM)	Northing (UTM)	Receiver code	Water depth (m)	Date deployed	Final date at location	Duration of deployment (days)
4	18363344	2747693	WC1	6	2-Dec-07	4-Jun-09	550
4	18362763	2747876	WC2	6	2-Dec-07	4-Jun-09	550
4	18362168	2748033	WC3	8	2-Dec-07	4-Jun-09	550
4	18361534	2748166	WC4	22	2-Dec-07	4-Jun-09	550
4	18363967	2747878	MNNE	3	19-Feb-08	8-Feb-09	355
4	18363723	2747506	MNSW	3.5	19-Feb-08	8-Feb-09	355
4	18363719	2747777	MNNW	3.5	19-Feb-08	8-Feb-09	355
4	18363905	2747368	MNSE	3	19-Feb-08	8-Feb-09	355
5	18365367	2741959	WZ1	10	8-Jun-08	4-Jun-09	361
5	18364258	2744213	WZ2	8	2-Dec-07	4-Jun-09	550
5	18363062	2745818	WZ3	9	8-Feb-09	4-Jun-09	116
5	18362779	2746128	WZ4	20	19-Feb-09	4-Jun-09	105
5	18362464	2746422	WZ5	22	8-Jun-08	4-Jun-09	361
5	18361966	2746767	WZ6	22	19-Feb-09	4-Jun-09	105
5	18361577	2747322	WZ7	22	24-Jun-08	4-Jun-09	345
5	18361154	2747803	WZ8	24	19-Feb-09	4-Jun-09	105
5	18360783	2748241	WZ9	26	14-Jan-08	4-Jun-09	507
5	18360637	2748227	WZ9D	42	2-Jul-08	4-Jun-09	337
5	18359289	2750246	WZ10	27	8-Jun-08	4-Jun-09	361
5	18357327	2751850	WZ11	26	8-Jun-08	4-Jun-09	361
5	18354841	2752852	WZ12	26	8-Jun-08	4-Jun-09	361

Receivers were grouped by zone extending from the most easterly inshore part of the array to the most westerly segment of the array associated with the abyssal wall of the Exuma Sound. *Zone 1* Starved Creek, Poison Flat, Red Point; *Zone 2* Broad Creek, Kemps Creek, Page Creek; *Zone 3* Powell Point, including two dredged marinas at the end of Cape Eleuthera; *Zone 4* receivers >200 m offshore of Cape Eleuthera but not associated with the deep wall of the Exuma Sound; *Zone 5* receivers positions along the edge of the wall of the Exuma Sound (note some of these receivers were deployed as part of another study)

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