



Novel deep-water spawning patterns of bonefish (*Albula vulpes*), a shallow water fish

Steven M. Lombardo¹ · Aaron J. Adams^{1,2} · Andy J. Danylchuk³ · Cameron A. Luck^{1,4} · Matthew J. Ajemian¹

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Abstract

Coastal marine fishes that form spawning aggregations most commonly exhibit a two-point movement pattern, with locations separated by migration: home range to spawning aggregation site and return to home range. However, the bonefish, *Albula vulpes*, partakes in a unique three-point spawning migration. Bonefish migrate up to 80 km from shallow water home flats to form nearshore pre-spawning aggregations (PSA) before moving offshore to spawn. Although these broad patterns have previously been documented, details of the offshore spawning-associated diving behavior have yet to be rigorously examined. Using active acoustic telemetry and sonar data in 2019 in Abaco, The Bahamas, we provide a complete account of bonefish offshore spawning movements and novel deep diving behavior to 137.9 m. Bonefish were continuously observed at depths ≥ 100 m for 2 h; a time period that included multiple depth changes and culminated in a spawning ascent to 67.3 m at 0.57 m s^{-1} . These new data on bonefish offshore movements and deep dives, coupled with CTD data, suggest that bonefish actively spawn at pycnoclines and thermoclines. Two previous tracking attempts (2013, 2018) at this location reflect spatiotemporal plasticity in spawning, a behavior counter to other aggregation forming fishes. This is the first detailed documentation of such deep spawning for a shallow water coastal fish species. The ecological motivation for diving to the deepest depths remains speculative. Future work must examine the dynamic relationship between bonefish diving behavior, spawning site selection, and oceanographic features.

Introduction

Spawning aggregations are a unique ephemeral reproductive strategy where fish come together en masse under certain environmental conditions to spawn. Spawning aggregations for coastal marine fishes may either be resident, where fish spawn within or near their home range, or transient, migrating beyond the bounds of a realized home range (Domeier

and Colin 1997). Unlike the somewhat plastic selection of foraging grounds, and to some extent nursery habitat (Petitgas et al. 2012), transient spawning aggregations are highly predictable in that they are temporally and spatially restrictive, occurring at the same locations and times with regularity (Johannes 1978; Ciannelli et al. 2015). Spawning aggregation formation is synchronous with seasonal and physical cycles, allowing fish to migrate and arrive at spatially and temporally distant spawning grounds under consistent conditions.

Many identified spawning aggregation sites for coastal fishes have been located at promontories and slope drop-offs (Sadovy de Mitcheson et al. 2008), positioned to take advantage of hydrodynamic retention features (Johannes 1978). Migrations from a home range to a spawning aggregation often repeatedly follow landmarks and bathymetric features (Colin 1992; Mazeroll and Montgomery 1998; Feeley et al. 2018). For coastal aggregating fishes, the migration distance can be tens to thousands of kilometers to reach an aggregation site (Bolden 2000; Feeley et al. 2018). Some grouper species have been documented using unconsolidated proximal staging areas surrounding the aggregation site, where

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✉ Steven M. Lombardo
slombardo2018@fau.edu

¹ Harbor Branch Oceanographic Institute, Florida Atlantic University, Fort Pierce, FL, USA

² Bonefish and Tarpon Trust, Miami, FL, USA

³ Department of Environmental Conservation, University of Massachusetts Amherst, Amherst, MA, USA

⁴ Present Address: North Carolina Division of Marine Fisheries, Morehead City, NC, USA

they exhibit no reproductive behaviors or coloration (Rhodes and Sadovy 2002a; Robinson et al. 2008). More closely associated to the spawning aggregation site, the courtship arena is where reproductive behaviors begin (Nemeth 2012). Delineation of the components of spawning habitat that surrounds an aggregation site can often be difficult (Feeley et al. 2018), as such the proximal areas have often been treated as a contiguous destination (Rhodes and Sadovy 2002b). Generally, migrations to and from spawning aggregation sites are uninterrupted (Nemeth 2012), following a home range—spawning aggregation—home range migration pattern (McCann et al. 2005). Bonefish (*Albula* spp.), which comprises 12 circumtropical shallow water species (Pickett et al. 2020), are a unique exception in that their migration is interrupted spatially and temporally by a distinct pre-spawning behavior (Danylchuk et al. 2019).

Albula vulpes (hereafter bonefish) are an economically and culturally important fish that supports recreational catch-and-release and artisanal fisheries throughout the Caribbean Sea and western North Atlantic Ocean (Adams et al. 2014). The estimated annual economic impact of the catch-and-release flats fishery, which includes bonefish, tarpon (*Megalops atlanticus*) and permit (*Trachinotus falcatus*), is US\$50 million in Belize (Fedler 2014), US\$169 million in The Bahamas (Fedler 2019), and US\$465 million in the Florida Keys (Fedler 2013). Bonefish show high site fidelity to their home range, foraging for invertebrates over a habitat mosaic of intertidal sand flats, seagrass beds, mangroves, and hardbottom (Boucek et al. 2019; Brown-scombe et al. 2017, 2019; Murchie et al. 2013). In The Bahamas, bonefish migrate from their shallow water home flats to nearshore deeper-water locations where they form pre-spawning aggregations (PSA). These activities occur over 4–7 days spanning the new and full moons of October through April (Danylchuk et al. 2011). The initial migration can cover distances of up to 80 km (Boucek et al. 2019) and culminates with an aggregation of 2000–5000 fish in 5–10 m of water (Danylchuk et al. 2011, 2019). At sunset bonefish begin “porpoising,” where they gulp air at the surface (see Danylchuk et al. 2019), and then proceed to move offshore following the edge of the continental shelf (Danylchuk et al. 2011, 2019). Similar pre-spawning behavior and potential offshore migrations by *A. vulpes* have been observed in other locations such as Belize (Perez et al. 2019), Cuba (Posada et al. 2008), and Mexico (Zeng et al. 2019). Additionally, this behavior has also been observed in the congener *A. glossodonta*, in Kiribati (Johannes and Yeeting 2000) and Tetiaroa and Anaa, French Polynesia (Filous et al. 2019a, 2020). Spawning behavior of any kind has yet to be documented for the remaining ten albulid species.

Data describing the offshore spawning movements of bonefish are limited, but of high importance due to the economic value and conservation needs of the species and genus

throughout their distributions (Adams et al. 2014; Fedler 2013, 2014, 2019; Filous et al. 2019b). Danylchuk et al. (2011) used both passive and active acoustic telemetry techniques to characterize the timing and location of offshore spawning movements in Cape Eleuthera, The Bahamas; the first study to do so. Logistical and technological limitations of both the passive and active acoustic equipment precluded any determination of spawning depth, but did reveal consistent offshore movement behaviors towards the shelf edge and waters exceeding 42 m, followed by a return to the shallow water flats habitat. Danylchuk et al. (2019) provided a more detailed description of pre-spawning behavior and offshore movements from active acoustic tracking efforts from 2013 and 2014 in Andros and Abaco, The Bahamas. The 2013 Abaco active tracking event yielded the first ever recording of diving movements during the offshore spawning migration. However, the description of fish vertical movement through the water column was restricted due to the depth rating (50 m) of the pressure sensor within the acoustic tags. In this study, we build upon the efforts and data of Danylchuk et al. (2019), presenting the spatiotemporal variability of spawning movements in Abaco. Most significantly, we document for the first time the complete deep diving and presumed spawning behavior of bonefish via several additional active tracks.

Materials and methods

Study site

The study took place along the southern shore of Abaco, The Bahamas. Previous work by the authors identified a bonefish PSA at Long Bay that occurs with regularity that allows for repeatable observation. Long Bay is a south-facing bay along a western-extending point, comprised of a mosaic of marl, seagrass (*Thalassia testudinum* and *Halodule wrightii*) and patch reef habitat. To the south of Long Bay the continental shelf narrows, and at 1.5 km offshore the benthos transitions to a steep vertical drop-off of more than 1000 m. The location of Long Bay provides 180-degree protection from NNW to SSE winds and access to the adjacent north bay with protection from S winds. Ocean surface currents typically flow SSE to NNW with quasi-permanent cyclonic-gyres forming on the west-side of Abaco and south of Grand Bahama (Chérubin 2014).

Fish collection and tag deployment

Offshore spawning migrations from the PSA site were actively tracked with acoustic telemetry in 2013 (see Danylchuk et al. 2019), 2018, and 2019. Active tracking methods were chosen rather than the deployment of a

passive acoustic telemetry array due to the logistical and technological constraints of working in offshore waters of > 1000 m, and experience gained by previous efforts detailed in Danylchuk et al. (2011, 2019). Methods for fish collection were maintained throughout the study, while tag selection and deployment methods changed across iterations of the study as more information about bonefish diving behavior was revealed.

Upon locating the PSA and visually confirming behaviors indicative of an imminent offshore migration (see Adams et al. 2019 for PSA identification method), fish were captured using hook-and-line and cast net (0.355 mm monofilament, 2.4 m radius \times 31.8 mm stretch mesh). Sex was determined by ventral palpation or cannulation to identify females. We tagged bonefish at a 1:1 sex ratio. Implantation of acoustic telemetry tags was conducted in a small plastic cooler (33 L) filled with ambient seawater with the fish held ventral side up. Two tagging methods were used, with results yielded from the 2013 tags and tagging method informing future tag choice and tagging method. In 2013, bonefish were gastrically tagged with Vemco continuous acoustic transmitters with pressure sensors (V9P-2H, 9 mm diameter, 21 mm in length, 1.6 g in air, 2000 ms transmission period). These tags had a pressure sensor depth limit of 50 m (see Danylchuk et al. 2019). In 2018 and 2019, Vemco continuous pressure and temperature tags (V9TP, 9 mm diameter, 31 mm long, 4.9 g in air, period 1000 ms) with a 250 m depth limit were surgically implanted (Innovasea Systems Inc., Massachusetts). Each tag emitted a unique frequency at an interval of 1000 ms with an assumed detection range of 300 m (Melnichuk and Christensen 2009). The maximum number of at large V9TP continuous acoustic tags was limited to 6 due to the number of available unique frequencies manufactured. A 2 cm incision was made on the fish's ventral side, just posterior of the pelvic fins, with the transmitter inserted into the peritoneal cavity. The incision site was closed with two interrupted sutures (Ethicon 3-0 PDS II; Johnson and Johnson, New Jersey). Bonefish were allowed to recover in an aerated cooler to ensure that stress levels were reduced and equilibrium was constantly maintained prior to release to maximize survival (Brown-scombe et al. 2013). Once recovered, bonefish were then placed back into the PSA to further reduce the likelihood of predation (see Adams et al. 2019).

The number of individuals tracked offshore from the PSA location were less than the number of tags deployed due to predation events, tag failures, and lost contact with tagged fish during tracking efforts. Initial offshore movements of the entire PSA school were visually confirmed, though the number of individuals successfully tracked through the initial dive ranged from one (2013 and 2019) to three (2018) individuals.

Data collection and analysis

Fish were actively tracked using a Vemco VH-110 directional hydrophone connected to a Vemco VR100 receiver and deck box (InnovaSea Systems Inc., Massachusetts). Based on challenges in previous tracking attempts, in 2019, we modified the directional hydrophone mount to create a vertically (i.e., pitch) modulated directional hydrophone, allowing the directional hydrophone transducer head to be articulated vertically from the standard horizontal position. Offshore school movements were also monitored using hull-mounted Compressed High-Intensity Radiated Pulse (CHIRP) and sidescan sonars (Axiom 600 W sonar and RV-212 transducers; Raymarine, United Kingdom). GPS position, water temperature (2018 and 2019 only), depth, and time were recorded every 3 s. In 2019, water property data were collected daily along transects from shore to the edge of the continental shelf using a CastAway CTD rated to 100 m (SonTek YSI, Xylem Inc., New York). Additional CTD casts were conducted during active tracking and at the culmination of the spawning event. Data visualization and estimations of rates of movement were constructed in R 3.4.1 (R Core Team, Vienna, Austria) and tracking maps were constructed using ArcMap 10.3.1 (ESRI, Redlands, CA).

Total migration path distance was estimated due to the periodically circuitous path taken by the boat while following the aggregation within the 300 m detection range. Therefore, horizontal movements were described as straight-line distances with coarse directional changes, and rates of movement were estimated over time periods of straight-line surface movement. Dive and ascent movement rates were calculated using simple linear regression, and the upper quartile (Q_3) of the instantaneous rates of movement reported as a measure of the maximum. The upper quartile was selected as a representation of maximum movement rates to filter the inherent noise in acoustic telemetry data, which increases with range (Melnichuk and Christensen 2009).

Results

Tagging

In 2013, Danylchuk et al. (2019) tagged two females (430 ± 28 mm FL) and three males (409 ± 42 mm FL) with Vemco V9P-2H tags. In 2018, three females (436 ± 46 mm), two males (421 ± 5 mm), and one unknown (405 mm) were tagged with Vemco V9TP tags. In 2019, two females (520 ± 5 mm) and two males (450 ± 0 mm) were tagged with Vemco V9TP tags. Not all tagged fish were successfully tracked, as some fish emigrated, were lost to predation, or experienced tag failure. The resulting

number of fish tracked across 2013, 2018, and 2019 were 1, 3, and 1, respectively. We include the Danylchuk et al. (2019) data here to enable description of the spatiotemporal variability in spawning-related movements.

On 16 November 2013 at 12:23 EST, one night before the full moon, all four tags were deployed. However, signals from three of the four tagged bonefish were lost shortly thereafter due to predation or emigration. On 18 November 2018, five nights before the full moon, from 13:22 EST to 13:32 EST three of the six total fish were tagged. The signal was lost for two fish at approximately 15:30 EST and 15:34 EST. The PSA did not make any offshore movements by 21:31 EST, and tracking efforts were terminated. The following morning no tags were detected near the PSA location. On 19 November 2018, four nights before the full moon, at approximately 17:11 EST the final three of six total fish were tagged. On 8 November 2019, four nights before the full moon, two of the four total fish were tagged. The PSA remained within Long Bay for the rest of the evening and two more days. One additional fish was tagged each day, of which the last of the four total tagged fish was lost to a predation event approximately 1 h post-release. The three fish that were at large from the 8th to 10th remained within close proximity to the PSA location, occasionally moving in an offshore direction each night, but stopping prior to leaving the reef, only to return back to the PSA location. Two of the three fish were lost shortly after the fish began moving offshore, leaving the

first fish tagged (Female, 525 mm) on 8 November 2019 to be tracked.

Lateral movement

PSA formation and movement offshore varied in relation to lunar and solar position. In 2013, the PSA formed one night before the full moon and the aggregation of bonefish proceeded to move offshore that night at 17:06 EST, 2 min before sunset. In 2018, the PSA formed five nights before the full moon and didn't move away from the PSA location until four nights before the full moon at 17:11 EST, at sunset. In 2019, the PSA formed four nights before the full moon and did not commit to moving offshore until one night before the full moon at 18:15 EST, 55 min after sunset.

Generally, fish followed the steep drop-off of the continental shelf as they migrated southward and up-current (Fig. 1), moving at depths of 0–5 m. Maximum horizontal movement rates were calculated as 1.21 m s^{-1} in both 2013 and 2019, and 0.62 m s^{-1} in 2018. On all tracks, porpoising behaviors sporadically occurred during offshore movement, lasting 5–10 min. Porpoising was noted four times throughout the 2019 spawning migration. The number of times porpoising occurred during offshore migration was not noted in 2013 and 2018. The distance traveled, location of, and timing of the initial dive varied considerably across all years (Figs. 1, 2). The single fish tracked in 2013 moved the shortest distance, traveling 0.9 km (± 0.3 km) at 143° SE

Fig. 1 Spawning migration pathways of bonefish tagged at a PSA location in South Abaco, The Bahamas. Across all 3 years, an initial descent from surface movements was observed (indicated by X). In 2013 and 2019, the final ascent was observed (indicated by O)

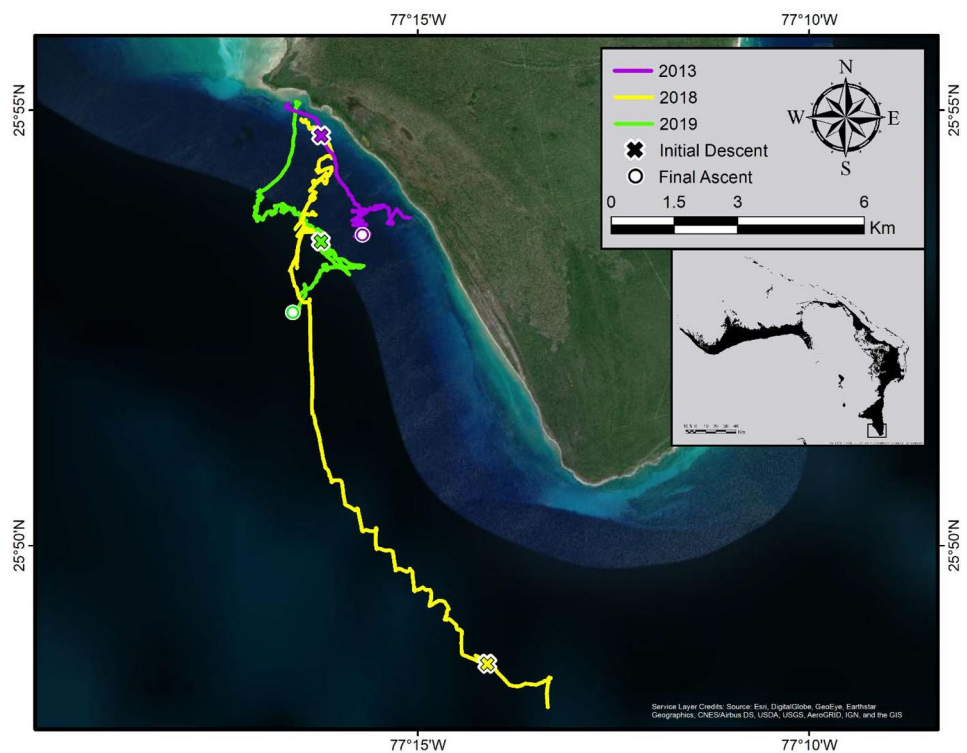
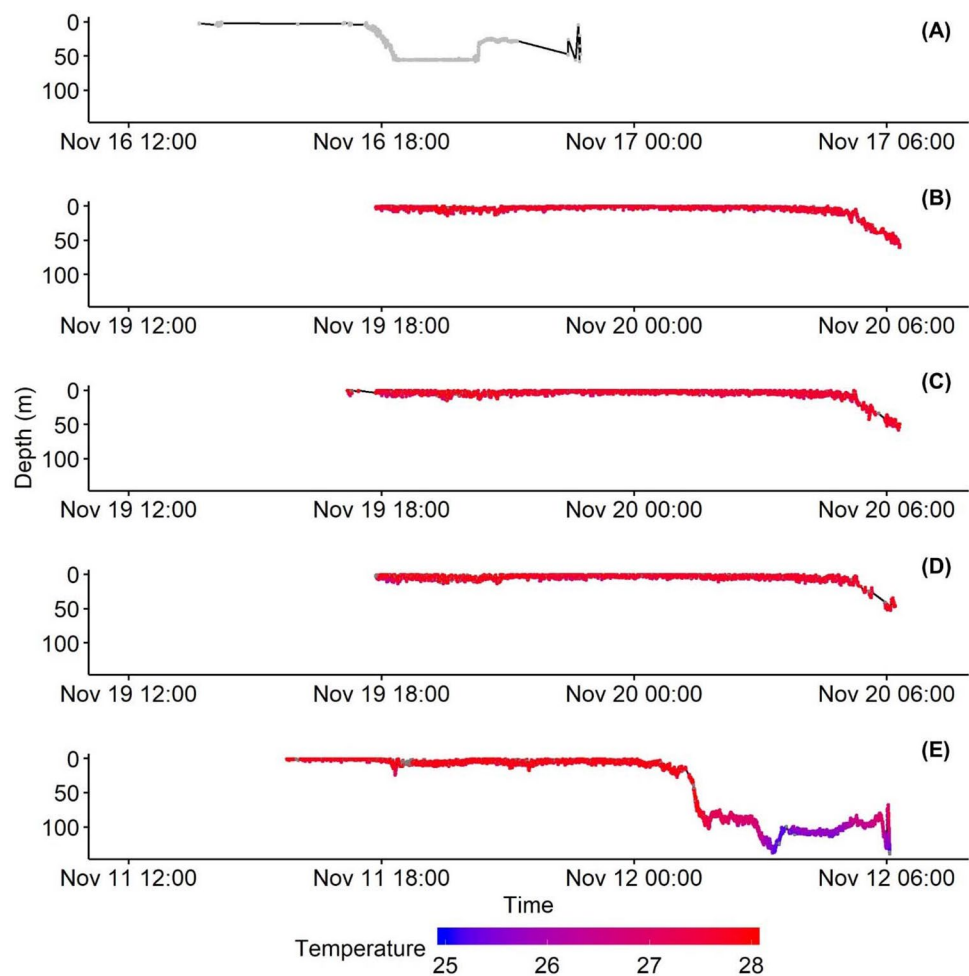


Fig. 2 Dive profiles for actively tracked bonefish in 2013 (a) (Danylchuk et al. 2019), 2018 (b–d), and 2019 (e). Acoustic telemetry tags were depth limited to 50 m in 2013, and tags did not have a temperature sensor. Active tracking in 2018 ended when the fish were lost descending below 58 m. Bonefish were tracked in 2019 up until the tag was ejected in a likely spawning event



from the PSA site to the initial descent site, arriving 38 min later at 17:38 EST. The fish continued their lateral movement at depth, moving another 2.6 km (± 0.3 km) over 159 min before ascending and moving toward shore. The track was ended at this time because previous studies using passive acoustic telemetry (Danylchuk et al. 2011) and local ecological knowledge had already described the return movement.

In 2018, the aggregation moved the furthest distance, with the three tagged bonefish migrating 17.3 km (± 0.3 km) from the PSA to the descent site beyond the southern tip of Abaco. The migration to the descent site took 327 min from when the fish began moving offshore, arriving at approximately 05:15 EST. The fish made an initial offshore movement with a heading of 199° SSW, followed by a prolonged migration 153° SSE. The fish continued to move SSE for 1.7 km (± 0.3 km) before the tag signals were lost in rough seas.

In 2019, the fish moved 5.1 km (± 0.3 km) from the PSA to the descent site, arriving 257 min later at 00:32 EST. Before the initial dive, the aggregation began moving 191° S before abruptly turning to 127° ESE. The fish continued an ESE heading while at depth before heading 236° SW further

beyond the drop-off, covering another 3.1 km (± 0.3 km) before completing a likely spawn.

Vertical movement

Depth profiles in 2013 (see Danylchuk et al. 2019) and 2018 provided limited information due to equipment limitations and rough seas. However, in 2019, a complete likely spawning cycle was observed (Fig. 3). The first dive to 25.3 m began on 12 November 2019 at 00:32 EST, 466 min after leaving the PSA site. After its initial descent, the bonefish underwent six descents and seven ascents (Table 1) with the collective aggregation of bonefish being observed along the way by sonar (inset Fig. 3). The second descent was the longest continuous dive with the greatest difference in depth, from 13.2 to 102.1 m over 33 min (0.04 m s^{-1} ; $Q_3 = 0.57 \text{ m s}^{-1}$). The dive is composed of two measurably distinct rates of descent, with the first portion from 13.2 to 69.1 m descending at 0.07 m s^{-1} and the second portion from 69.1 to 102.1 m descending at 0.02 m s^{-1} . During the dive, hydrostatic pressure increased +871.8 kPa to 1001.2 kPa. The deepest

Fig. 3 Dive profile of the female bonefish tracked during the 2019 spawning migration, colored to temperature transmitted by the acoustic telemetry tag. Sidescan and CHIRP sonar images of the aggregation are inset at times that the boat passed over the moving aggregation. Black arrow indicates tag ejection

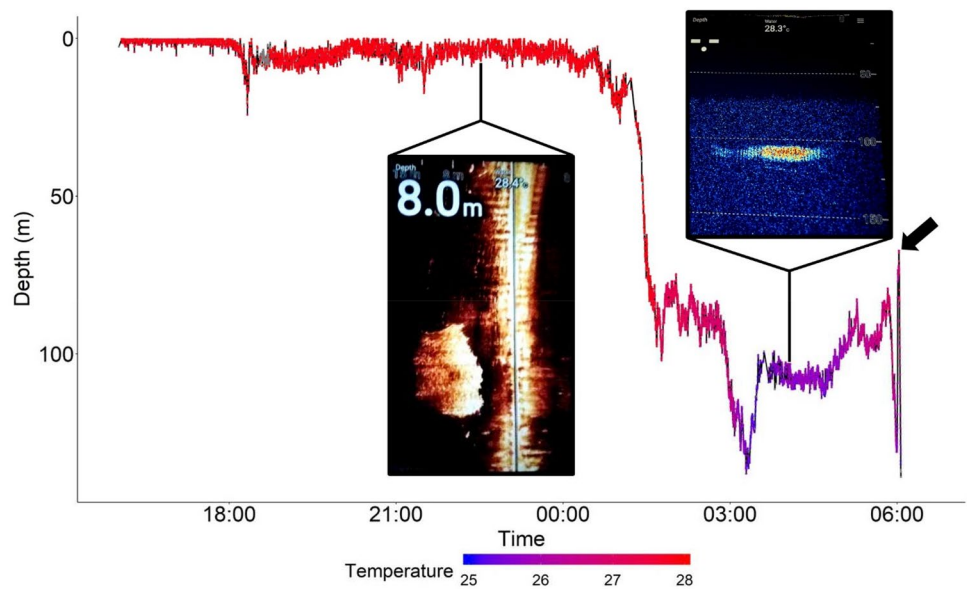


Table 1 Summary of 2019 bonefish offshore movements

Movement	Depth start (m)	Depth end (m)	Abs. depth change (m)	Time elapsed (min)	Overall rate (m s ⁻¹)	Q3 instantaneous rate (m s ⁻¹)
Descend	3.1	25.3	22.1	29	0.01	0.40
Ascend	25.3	11.6	13.7	4	0.03	0.57
Descend ¹	13.2	69.1	55.9	15	0.07	0.54
Descend ¹	69.1	102.1	33.0	18	0.02	0.57
Ascend	102.1	78.2	13.9	5	0.07	0.55
Descend	74.8	94.2	19.4	5	0.06	0.57
Ascend	92.4	78.1	13.3	3	0.04	0.40
Descend	78.1	97.6	19.5	10	0.02	0.60
Descend	85.6	137.9	51.1	30	0.02	0.57
Ascend ²	137.9	120.3	17.6	6	0.03	0.40
Ascend ²	124.8	104.4	20.4	4	0.08	0.56
Ascend	112.3	87.3	25	34	0.01	0.53
Ascend	98.6	82.7	15.9	12	0.02	0.40
Descend ³	82.7	114.5	31.8	4	0.12	0.45
Descend ³	106.6	131.0	24.4	2	0.14	0.55
Ascend	131.0	67.3	63.7	2	0.57	1.15

Movements are listed in chronological order, with incongruencies in subsequent start and end depths temporally separated by horizontal and vertical oscillatory movements. In instances where single movements are composed of distinct movement rates, movements are detailed by their components and denoted by the same superscript. Times are rounded to the nearest whole minute

dive started at 02:47 EST from 85.6 m and ended at a depth of 137.9 m (1352.3 kPa). The final descent began 4.5 km (± 0.6 km) from the PSA site, at 05:52 EST. Fish descended to 129.9 m in two movements interrupted by a 1 min ascent. Both movement rates exceeded 0.12 m s⁻¹ ($Q3 = 0.45$ m s⁻¹; $Q3 = 0.55$ m s⁻¹). Depth was maintained near 129.9 m for 1 min before the final measured ascent at approximately 06:00 EST. The final ascent plateaued

abruptly at 74.4 m, oscillating for 1 min until reaching a depth of 67.3 m, upon which the tag was ejected from the coelomic cavity and proceeded to fall at a constant rate. The ascent was completed in 2 min, with the fish moving at a rate of 0.57 m s⁻¹ ($Q3 = 1.15$ m s⁻¹, max = 2.55 m s⁻¹). During the final ascent, fish experienced a 613.9 kPa decrease in pressure over 2 min, and a 962.3 kPa decrease in pressure from the deepest dive. The entire track lasted

14 h and 16 min, from departing the PSA site to presumed spawning, with fish occupying depths > 100 m for approximately 2 h.

CTD profiles

CTD casts were taken each of the 3 days prior to the 2019 spawning run and during the spawning track. These revealed an offshore pycnocline and thermocline, formations that were not present in waters < 2.2 km from shore and inside the 200 m contour. Three days prior to the spawning run, at a location 3.1 km SE of the location where the spawning ascent occurred, the initial signal of a pycnocline was detected at 68.4 m (1024.0 kg m^{-3}) with a thermocline at 67.5 m ($27.7 \text{ }^\circ\text{C}$). The CTD cast at the location of the final spawning ascent displayed pycnocline and thermocline signals at 75.9 m with measurements of 1024.0 kg m^{-3} and $27.7 \text{ }^\circ\text{C}$, respectively (Fig. 4).

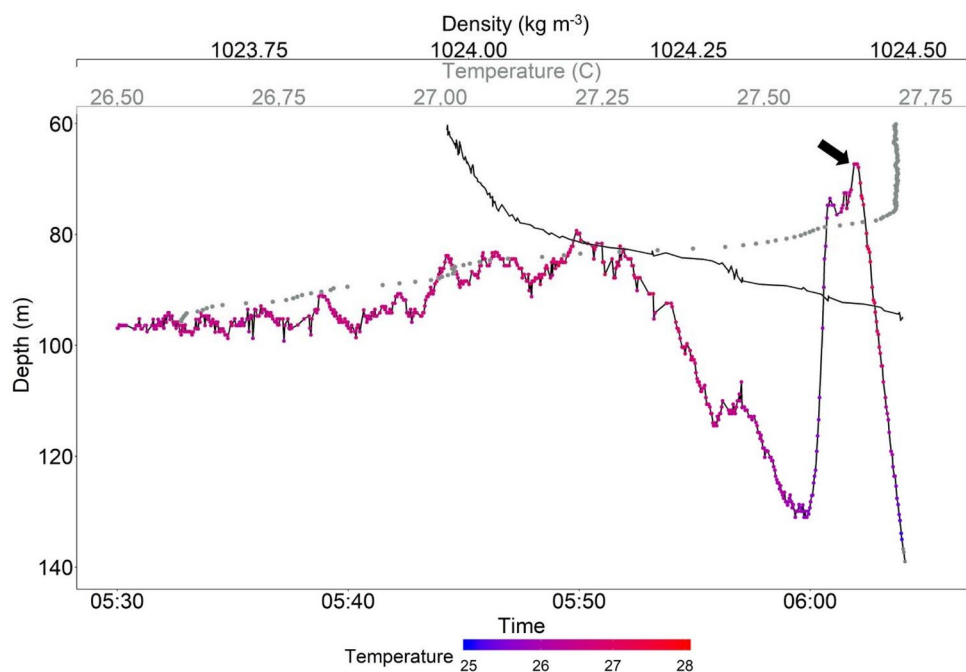
Discussion

Through 3 years of effort we were able to iteratively build upon knowledge of bonefish offshore movements and diving behavior associated with presumed spawning off South Abaco. PSAs in South Abaco formed 1–5 days prior to the full moon, with offshore movements beginning from 2 min before to 55 min after sunset. Active tracking revealed that bonefish show substantial spatial and temporal variation in spawning locations, counter to high site fidelity in forming PSAs (Johannes and Yeeting 2000; Danylchuk et al. 2019;

Filous et al. 2020). Offshore movements were directed toward the nearest southern point, as seen in Cape Eleuthera (Danylchuk et al. 2011). However, the departure angles and migration paths taken were different each of the 3 years with the location and time where the fish began to descend varying considerably. The maximum rate of horizontal movement also appears to reflect inversely on the travel distance to where bonefish begin to descend to depth. In 2019, the first detailed dive profile logged bonefish moving offshore and diving to depths > 137 m during their spawning migration, with spawning likely occurring at 67.3 m, following a rapid ascent. The spawning aggregation spent > 2 h below 100 m, as indicated by the acoustic telemetry tagged fish and corroborated by CHIRP sonar images. Tracking data and CTD data also suggest that bonefish spawn at depths associated with pycnocline and thermocline features. These data are the first detailed documentation of the novel deep diving movements of spawning bonefish, and the first documentation of such spawning depths for shallow water coastal species.

The spawning migration of bonefish beyond the continental shelf break and diving to such great depths, as documented in this study, are novel behaviors within the coastal marine teleost assemblage, and are certainly unique for bonefish, which spend a majority of their time in waters < 1 m deep (Danylchuk et al. 2011; Murchie et al. 2013; Boucek et al. 2019). Generally, coastal marine fish that form transient spawning aggregations migrate uninterrupted between their home range and spawning aggregation site (Nemeth 2012), which form with high spatial and temporal fidelity (Sadovy de Mitcheson et al. 2008). Bonefish

Fig. 4 Final 2 h of the 2019 dive profile, as portrayed in Fig. 3. Tag ejection at the pycnocline and thermocline can be seen from 06:02 EST. Colored line depicts ambient temperature of bonefish at depth, black line is CTD density, gray dots are CTD temperature, black arrow indicates tag ejection



reproductive behavior differs from other species that share adjacent habitats (coral reefs) in that they show high fidelity to a pre-spawning location and apparent variability in actual spawning location. Migration to reef promontories is a common strategy for many coastal marine fish species (Johannes 1978; Kobara and Heyman 2006). By moving further offshore and away from the reef, fish are able to take advantage of lower zooplanktivore densities, and retention features such as slow-moving coastal boundary layers (Nickols et al. 2012) and gyres (Johannes 1978; Lee et al. 1994; Lindeman et al. 2001; Paris and Cowen 2004). Bonefish may spawn in habitat independent of bathymetric features, such as promontories, and instead cue in on the formation of frontal systems.

The CTD cast taken immediately after the acoustic telemetry tag was ejected from the fish showed signals of the upper stratification of a pycnocline and thermocline at 75.9 m. This was 7 m below the depth that the tagged bonefish presumably spawned, but the clines are exactly at the depth where “mixing” movements, balling and swirling behaviors when spawning (Heyman et al. 2005), can be observed in the dive profile (Fig. 4). The respiratory and reproductive physiology of bonefish lends support for the expulsion of the acoustic telemetry tag (which measured 9 mm diameter, 31 mm long) from the peritoneal cavity during a spawning rush as the most parsimonious explanation. Bonefish are gymnovarian spawners; as such, their eggs are released from the ovary into the coelomic cavity before being expelled via the oviduct. It has been hypothesized that the porpoising pre-spawn behavior sequesters air into the swim bladder at the surface, and that the diving and spawning rush motion acts as a pneumatic assist to expel eggs (Danylchuk et al. 2019). However, the depth and temperature data acquired in this study suggest that the surface volume of the swim bladder is not enough. A 172 cc swim bladder (Danylchuk et al. 2019) would compress to 1.2 cc at 137.9 m and only expand to 2.4 cc at 67.3 m. In order to create sufficient gas expansion for a pneumatic assist to occur, gas must be sequestered at depth. We hypothesize that this is accomplished using swim bladder gas gland cells located throughout the epithelium of the swim bladder, a trait that may be conserved within the superorder Elopomorpha and identified in the also physostomous European eel, *Anguilla anguilla* (Prem and Pelster 2000; Smith and Croll 2011). Increases in swim bladder volume at depth are further supported by the target strength of the sonar backscatter from the aggregation at depths > 100 m (inset Fig. 3.), which would be decreased or absent in a physostomous fish with a compressed swim bladder following Boyle’s Law (Blaxter et al. 1979; Mukai and Iida 1996; Mukai and Foote 1997; Benoit-Bird et al. 2003).

It is possible that the tagged bonefish may have been consumed by a predator along the offshore migration or

that the tag ejection may have been caused by a predator consuming the tagged fish, as sharks were observed via sidescan sonar following the aggregation offshore at depths < 8 m (inset Fig. 3). However, the data and observations suggest no predation event occurred. The rate of movement preceding tag ejection was consistent with movement rates throughout the offshore migration, and sonar images of the spawning migration confirmed we were tracking the bonefish aggregation and not a predator (inset Fig. 3). Additionally, no excessive rates of movement that may be associated with predator avoidance were observed, and previous observations of sharks consuming tagged bonefish in shallow waters resulted in the shark leaving the aggregation (pers. obs.).

Oscillations above and below the pycnocline were evident throughout the 5 h that the fish spent at depth in 2019. These oscillations may have been an exploratory behavior, where bonefish were sampling water column conditions (i.e., pycnocline and thermocline) before identifying where to spawn. This oscillatory behavior has not been examined for any fish species in relation to oceanographic features, but water column position of larvae is often correlated with stratified oceanographic features (Moser and Smith 1993; Sabatés and Olivar 1996; Sánchez-Velasco et al. 2007). This correlation has been documented in multiple Elopomorphs, with anguilliform larvae having been found at 50–100 m depth (Tsukamoto 1992) and larvae of *Albula* sp. being found as deep as 200 m but in the highest abundance when associated with a stable stratified layer outside of a cyclonic eddy in the Gulf of California (Sánchez-Velasco et al. 2013). These studies support the hypothesis that other Elopomorphs actively search out similar conditions. Therefore, pelagic spawning habitat for some fish, such as bonefish, may be subject to inspection and selected for based on perception of physical characteristics of the water column. This behavior would explain why the tag was not spawned out of the female fish until the final upward rush, aided perhaps by the change in hydrostatic pressure (Domeier and Colin 1997; Graham and Castellanos 2005; Whaylen et al. 2004), which likely facilitated gamete release and acoustic tag expulsion into the water column; a fate not observable in 2013 due to the gastrically implanted tags. Additionally, it is possible that multiple spawning rushes occurred with different individuals spawning during each event, with the tagged fish not spawning or completing its spawn until the seventh ascent. Measurements of movement rates throughout the spawning run indicate that the final descent and ascent were unique, reaching rates of movement at least two and seven times greater than other measured movement rates, respectively. As such, it is likely that the tagged bonefish only spawned once over the observation period. However, it remains unknown whether bonefish release gametes multiple times throughout a spawning run.

There are many benefits to spawning within a frontal system boundary layer, such as a pycnocline or thermocline. Pycnocline boundary layers can act as a retention feature for planktonic organisms, which includes larval fish and prey that support early growth (Kiørboe et al. 1988; Bjorkstedt et al. 2002; McManus and Woodson 2012). Retention within the boundary layer provides organisms an environment independent of the larger masses of water, subjecting them to reduced turbulence and flow velocities (Doostmohammadi et al. 2012), and likely a more predictable and stable dispersal mechanism (Paris and Cowen 2004; Nickols et al. 2012). While we know these frontal systems play an important role in the transport of bonefish larvae (Zeng et al. 2019) during their 41–71 days pelagic larval duration (Mojica et al. 1995), dispersal pathways from the Providence Channel at depths > 0.5 m have not yet been quantified. These data could provide crucial information on which bonefish populations of The Bahamas are being supported by the spawning aggregations observed herein off South Abaco.

These studies in The Bahamas can provide the foundation for a conceptual model in studying bonefish spawning movements, which can then be applied to other populations of *A. vulpes* and potentially other albulid species. Further observations of bonefish diving behavior should be made throughout the Caribbean. Locations with gradually sloping coastal bathymetry, like the Florida Keys, and also nearshore drop-offs like South Abaco and Cape Eleuthera will provide additional perspective on bonefish spawning habitat selection. Observations of other elopomorph spawning events, beyond the presence of pelagic larvae, are needed to confirm that the diving behavior exhibited by bonefish are not unique to the species. We still do not understand the physiology and ecology of why bonefish dive to depths > 137 m. Adams et al. (2019) hypothesized that egg hydration is occurring as bonefish descend, while Danylchuk et al. (2019) hypothesized the behavior is related to pneumatic assist for releasing eggs, and here we propose a modified pneumatic assist hypothesis accounting for the deep diving depths and spawning movements. Additional work examining the significance of diving to the deepest depth, and the physiological mechanisms that allow bonefish to compensate for repeated, rapid and extreme pressure changes should be pursued.

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Author contributions SL, AA, AD, CL, and MA were all involved in field operations and data acquisition, with AA and AD conducting work in 2013, and SL, AA, CL, and MA conducting work in 2018 and 2019. AA performed surgery and tagging procedures. The text, analyses, table, and Figs were prepared by SL, and internally edited and reviewed by AA, AD, CL, and MA.

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Data availability The datasets presented in this article are not readily available due to their inclusion in ongoing research. You may reach out to the authors regarding data requests.

Code availability The R code written and executed within R Studio may be provided through a request to the authors. No novel data handling schemas or tools were created in the analysis process of this research.

Compliance with ethical standards

Conflict of interest The submitted work was not carried out in the presence of any personal, professional, or financial relationships.

Ethical approval The non-profit institution Bonefish and Tarpon Trust conducted the tagging, and does not have a formal animal care and safety requirement for research. All precautions were taken to ensure fish survival, and BTT uses commonly accepted and applied methods for fish care. All measures were taken to minimize animal pain and suffering during collection and tagging. Research methods and procedures were reviewed and approved by The Bahamas Ministry of Agriculture and Marine Resources under permit: MA&MR/FIS/17.

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