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Behavioral observations of bonefish (*Albula vulpes*) during prespawning aggregations in the Bahamas: clues to identifying spawning sites that can drive broader conservation efforts

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Abstract Bonefish are typically thought of as ‘flats fish’ that reside in shallow, tropical and subtropical nearshore coastal waters. However, evidence from tagging and acoustic tracking studies indicate that bonefish migrate to staging areas, form large aggregations (>5000 individuals), and then move to deep-water drop-offs at dusk to spawn. Because the offshore spawning occurs under the cover of darkness, visual observations of the actual bonefish spawning events are not possible. Fortunately, behaviors during prespawning aggregations provide clues related to putative spawning bouts. For multiple locations in The Bahamas, we report on repeatable, predictable behaviors of

bonefish in large prespawning aggregations. Just prior to moving from shallow to deeper waters, bonefish are observed breaking the water surface (‘porpoising’) and then returning to the aggregation. Bubbles are then observed emerging from the swirling aggregation; potentially gas being released from the bonefish. Ventral nudging, when one fish rubs its snout on the ventral region of another, has also been observed, but not as consistently as porpoising. Based on the depth profile of acoustically tagged fish, we hypothesize that porpoising is related to ‘pneumatic assist’ for egg release during spawning bouts. Although these observations provide circumstantial evidence that these behaviors are related to spawning, they are consistent with the prespawning behaviors of other marine fish that broadcast spawn. More research is needed to actually document a spawning bout; however, these clues in addition to other traits may be enough to encourage conservation measures to protect this important life history event for bonefish.

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Introduction

Spawning is a critical life history event that ensures the maintenance of fish populations (Stearns 1978). For many marine fishes, particularly those that broadcast spawn, this event is facilitated through the formation of large aggregations (Sadovy de Mitcheson et al. 2008).

Aggregating behavior associated with spawning brings fish together that normally compete for other resources during the rest of their lives, and has evolved to occur at locations that increase the likelihood that successfully fertilized eggs will survive and disperse to areas where post-settlement larvae can be recruited to the population (Dahlgren et al. 2008).

Determining that a fish aggregation is associated with spawning can be defined by characteristics and behaviors that are not common to the fishes' everyday lives (Domeier and Colin 1997). Domeier (2012) provides specific criteria for validating that a fish aggregation is related to spawning, including the gathering of reproductively active conspecifics at densities and/or numbers higher than those found in the area during non-reproductive periods, as well as courtship behaviors not normally observed when not in aggregations. These traits have been used to document spawning aggregations for coral reef fishes, such as Nassau grouper (*Epinephelus striatus*, Bolden 2000; Whaylen et al. 2004) and red hind (*Epinephelus guttatus*, Sadovy et al. 1994; Beats and Friedlander 1998), and coastal species such as common snook (*Centropomus undecimalis*, Lowerre-Barbieri et al. 2003) and two species of bonefish (Johannes and Yeeting 2001, *Albula glossodonta*; Danylchuk et al. 2011, Adams et al. 2018, *Albula vulpes*).

Bonefish (*Albula* spp.) are a group of 12 species of benthivorous fish that are typically associated with shallow tropical and sub-tropical flats habitats (Alexander 1961; Ault 2008; Murchie et al. 2013). However, using passive and active tracking with acoustic telemetry, Danylchuk et al. (2011) was first to demonstrate that *A. vulpes* in Eleuthera, The Bahamas, seasonally moved away from their flats, aggregated at 'transitional' habitats near a deep-water drop-off, and then moved offshore. These aggregations coincided with the new and full moons between December and April, and movements offshore happened at dusk, independent of tidal cycle (Danylchuk et al. 2011). These movement patterns documented by Danylchuk et al. (2011) fit well with the criteria outlined by Domeier and Colin (1997), and were later used by Adams et al. (2018) and Boucek et al. (2018) to locate other potential bonefish spawning aggregation sites in The Bahamas.

Given that bonefish are prized by recreational anglers (Danylchuk et al. 2008) and support local and regional economies in developed (Florida Keys; Fedler 2013) and developing nations (e.g., Bahamas, Fedler 2010;

Belize, Fedler 2014), mapping the specific locations of spawning aggregation sites could be critical for the use of appropriate management tools to ensure their protection (Coleman et al. 1996; Domeier and Colin 1997; Roberts and Hawkins 1999; Musick et al. 2000; Sala et al. 2001; Adams et al. 2018). One caveat is that many government agencies likely do not have the financial and logistical capacity to undertake detailed tracking studies that initially allowed Danylchuk et al. (2011) and Adams et al. (2018) to locate bonefish prespawning aggregations. As such, identifying highly conspicuous behaviors that are solely related to bonefish prespawning aggregations and spawning activity could prove essential for identifying the location of spawning sites, especially across vast geographic areas.

During the study by Danylchuk et al. (2011) several behaviors were observed that were not previously documented for *A. vulpes* (or any other species of bonefish), including ventral nudging and porpoising. Ventral nudging, or one fish bumping into another, has been observed for Atlantic tarpon (*Megalops atlanticus*, Baldwin and Snodgrass 2008) and common snook (Lowerre-Barbieri et al. 2003), and suggested to be related to courtship. Porpoising or breaching, which is when individuals fully or partially jump out of the water, has also been observed for fishes and marine mammal, and often hypothesized to be related to a range of motivations, including predator avoidance (de Lima Filho et al. 2012), feeding (Martin et al. 2005; Curtis and Macesic 2011), overcoming physical barriers (Banks 1969), cooperative hunting (Klimley et al. 1996), removal of ectoparasites (Compagno 1984), and courtship and mating (Klimley et al. 1996). Even so, the only direct account of mating-related breaching for a teleost fish was observed for leopard grouper (*Mycteroperca rosacea*) with fish during a horizontal spawning rush ascending in the water column from 3 to 8 m and breaking the surface following the release of gametes (Erisman et al. 2007). Details of these reported behaviors, including their context, are different than the porpoising behaviors observed for *A. vulpes* by Danylchuk et al. (2011). Specifically, Danylchuk et al. (2011) also observed bubbles emerging from the aggregation synchronous to when porpoising was occurring, which happened for a 30–60 min period as the fish began moving offshore. Following these behaviors, tracking and telemetry data showed that these bonefish indeed moved towards a deep-water drop-off (>1000 m), and within days tagged fish were detected back in the shallow coastal flats

where bonefish are typically found (Danylchuk et al. 2011). Danylchuk et al. (2011) also observed these movement patterns and behaviors during multiple times within the putative spawning season as well as across years at the same location.

Given the unique context of observations made by Danylchuk et al. (2011), understanding the ubiquity of these putative pre-spawning behaviors could provide important clues that could be used as confirmation that specific bonefish aggregations are associated with spawning. For this study, local fishing guide knowledge to direct us towards other locations in The Bahamas where large aggregations were seasonally observed away from their typical shallow water flats (see Adams et al. 2018). We then used surface, underwater, and aerial observations to document whether ventral nudging and porpoising behaviors occurred at these locations, as well as manually tracked acoustic tagged bonefish to confirm their movement offshore at dusk. Confirming the ubiquity of these patterns and further quantifying the specific behaviors can only validate their potential as indicators of spawning areas, as well as shed light on the specific reproductive biology of bonefish.

Methods

Study sites

Field observations and tracking were conducted in The Bahamas between December 2013 and January 2016. Prior to the fieldwork, ad hoc interviews and information sharing were conducted with fishing guides, with the intent to identify as many potential bonefish pre-spawning aggregation sites as possible. Given that detailed observations and tracking of fish would occur from before dusk and into the night, final site selection was contingent upon the relative ease of logistics and safety. Site selection was also based on receiving multiple independent reports about large aggregations of bonefish during the late fall, winter, and early spring, in atypical habitats, especially locations adjacent to deep water (see Adams et al. 2018).

Two locations were selected, one on Abaco Island and another on Andros Islands. To protect the bonefish populations from potential overexploitation and disturbance, either via catch-and-release recreational angling or through subsistence harvest, we are purposely not

disclosing the exact locations of these bonefish aggregation sites. Instead, only general area names will be used to reference the sites moving forward. For Abaco, the Cross Harbour (CH) site was visited 12–17 November, 2013 (full moon), and 03–10 December 2014 (full moon). For Andros, the South Andros (SA) site was visited 20–26 January, 2016 (full moon).

Behavioral observations

At each location, we conducted ad hoc visual surveys from boats and using small, unmanned aerial vehicles (UAVs, custom built and DJI Phantom 3 Pro, DJI Innovations, Shenzhen, China) to first determine the presence of bonefish aggregations. If located, we slowly approached the aggregation by boat and then snorkelers were deployed to make in-water observations. In-water surveys consisted of snorkelers staying at least 30 m away from any aggregation and floating motionless to make initial observations. Depending on the disposition of the aggregation, the snorkelers either slowly approached at approximately 5 m intervals, or remained still, especially if the fish within the aggregation moved on their own towards snorkelers. Snorkelers remained in the water following the aggregations until the sun set or if conditions became unsafe.

Snorkelers used a combination of sport cameras (Hero 3+, Hero 4, Go Pro Inc., San Mateo, CA, USA) and a video camera in underwater housing (Canon VIXIA HFS11, Tokyo, Japan, with Equinox HD6 housing) to record the behaviors of the aggregation and individual bonefish. We opted not to make observations on SCUBA because of concerns related to disturbing the aggregation, either from bubbles or being perceived as a predator or threat. Depending on surface conditions, water clarity, light availability, and distance from the aggregation, snorkelers continuously recorded video, intermittently recorded video, took still images, or just made ad hoc visual observations of the aggregation. When conditions permitted, additional UAV surveys were also conducted.

On location, digital video and images were downloaded and reviewed daily, and then stored on multiple hard drives. Digital images were viewed by multiple individuals to confirm whether the behaviors documented by Danylchuk et al. (2011) were observed. Video footage was viewed at full speed and half speed to allow for viewing individual behaviors, especially when bonefish were in dense aggregations that were

constantly moving. Once confirmed, video footage were used to quantify the frequency at which the behaviors occurred. For particular behaviors, video footage was imported into ImageJ to better facilitate counting (manually) and to quantify the orientation of fish. For porpoising, we measured the approximate angle of ascent in relation to the water's surface, whether the fish fully or partially breached the surface, and the angle of descent back to the aggregation. For ascent and descent angles, given that the water's surface was dynamic, three separate measures were determined for each fish and then aggregated as a mean.

Manual tracking

Manual tracking was conducted using a mobile acoustic receiver with a directional hydrophone (VEMCO VR-100, Amirix Inc., Shad Bay, NS, Canada) and continuous transmitters with depth sensors (V9P 2H, 9 mm diameter, 21 mm in length, 1.6 g in air, 2000 ms transmission period, pressure sensor limit 50 m). Bonefish were caught via hook and line or via cast net from the aggregation, and transmitters were quickly inserted into the stomach following Danylchuk et al. (2011). Specifically, the continuous transmitter was fitted into the end of a smooth plastic tube that was gently inserted into the esophagus. Once in the stomach of the bonefish, a plunger inside the tube was used to release transmitter, with the entire procedure taking <30 s. Fork length (mm) and sex (release of gametes when males were gently palpated or females cannulated, see Adams et al. 2018) was determined for each fish. Following gastric implant, bonefish were held in a plastic tote (35 × 61 × 25 cm) for approx. 3 min in the event the tag would be regurgitated, and then the fish was released back into the aggregation. Once at large, we manually tracked tagged bonefish from a boat while drifting 30–50 m from the aggregation or slowly following the aggregation as it moved. Tracking was done continuously unless conditions became unsafe for boating or if we lost track of the tagged fish and had to broaden our movements to relocate them.

Data from manual tracking were downloaded from the VR100, and used to map the movement patterns and depth profiles of the tagged bonefish. Mapping of the movement patterns was done using Google Earth Pro, and individual variation in depth profiles analysed using univariate statistics in JMP Pro (version 13.0.0; SAS Institute Inc., Cary, NC, USA).

Results

Locating aggregations & aggregation behavior

Large aggregations of bonefish (approx. 2000–5000+ individuals) were located on both Abaco and Andros Islands at locations revealed by local guides, and around the full moon periods. On Abaco, the same location was visited in two consecutive years (November 12–17, 2013; December 3–10, 2014), and each time large bonefish aggregations were located. Only boat and snorkelling surveys were used on Abaco, as weather conditions and equipment issues prevented the use of a UAV for aerial surveys and imagery. The aggregations on Abaco were initially spotted in approximately 2 m of water over mixed hard bottom habitat adjacent to a point of land, and then observed moving into 8–10 m water with sand bottom and small coral heads. Conversely, on Andros (January 20–26, 2016), both topside boat and UAV surveys were used to find bonefish aggregations, while the UAV was used to scan adjacent habitats and larger areas of the shoreline for other schools of bonefish. The aggregation on Andros was found in a dredged channel, approximately 5 m deep. Aerial surveys were able to identify the bonefish aggregations, especially in locations where the benthos was relatively light (i.e., sand), water relatively shallow (>5 m), when cloud cover was minimal, and when the aggregation was not moving rapidly (Fig. 1).

In all cases, bonefish within the aggregations moved in a circular rotation around a central core, either in a clockwise or counter clockwise direction (See YouTube



Fig. 1 Oblique aerial image of a bonefish aggregation (UAV elevation, 25 m) in The Bahamas

video - <https://www.youtube.com/watch?v=RyYtheGXEr4>). The compactness and overall shape of the aggregations differed temporally, beginning more dispersed and oblong and then becoming more compact and resembling a 'baitball', similar to what is often seen for pelagic fishes such as sardines. The shape of the aggregations also changed when a shark, great barracuda, or even a sea turtle approached, with the aggregation either quickly spreading out and recondensing, or creating a halo of bonefish around the transient animal. The diversity and abundance of potential predators, such as sharks, great barracuda, and large snappers and groupers, differed daily when observing the aggregations, as well as among aggregation sites. The extremely large aggregation we observed on Abaco had large Cubera snappers (*Lutjanus cyanopterus*) occasionally rising from coral heads below as well as a solitary large barracuda drifting by, but sharks were only observed one of the 2 years. On Andros, we observed as many as three Caribbean reef sharks (*Carcharhinus perezii*) occasionally passing by or through the aggregation, and local fishers reported also seeing bull and hammerhead sharks in this location at other times. Of note is that the aggregations behaved differently when approached by a potential predator versus when a snorkeler slowly approached or if the aggregation moved towards a snorkeler on their own, thus allowing us to obtain rather detailed images and video of their behaviors, particularly when water clarity was good. Interestingly, even when we observed potential predators, we did not observe a predatory encounter on bonefish in any of the aggregations.

Bonefish behavior in aggregations

We observed porpoising behavior at both locations prior to sunset, just before or while the aggregations began moving offshore (See YouTube video - https://www.youtube.com/watch?v=3NXFXa_dnUw). The most vigorous porpoising was observed during the survey on Abaco in 2013, with bonefish emerging from an aggregation of well over 5000 fish (Fig. 2a). Porpoising at the Abaco location in the following season was not as prominent, likely masked by choppy surface conditions. During the time of our second survey on Abaco, the bonefish aggregation was also considerably smaller (approx. 2000 fish) and the number of potential predators, particularly sharks, was

higher. For the Andros location, porpoising behavior occurred over a more protracted timeframe, beginning sporadically around 15:00 h, but intensifying at approximately 17:30 h, just as the sun began to set.

In all cases, porpoising was episodic (i.e., not continuous) and displayed by bonefish emerging from the top of the aggregation (Fig. 2b). Although single fish were observed porpoising, it was more common that episodes of multiple bonefish (2–200 individuals) occurred lasting from 3 to 65 s. In most cases, the frequency of porpoising bouts increased as the sun approached the horizon and as the aggregation began to move offshore, with the total duration of observed sequential bouts occurring over approximately 20 min.

Bonefish that were observed porpoising ascended from the aggregation at a mean angle of $28 \pm 8^\circ$ SD (Fig. 2b) and broke the surface head first, either jumping partially or fully out of the water (Fig. 2c). In all cases, at least the portion of the fish anterior of the dorsal fin emerged from the water, exposing the mouth and operculum (Fig. 2d). Bonefish that partially emerged tended to land ventrally on the surface ('belly flopped') and then descend, while bonefish that fully emerged tended to land snout first; in both cases fish descended back towards the aggregation at a mean angle of $39 \pm 12^\circ$ SD. There was a significant difference between the angle of ascent and descent (t-test, $t = 6.26$, $df = 242$, $p < 0.001$). We attempted to determine whether the same individuals were porpoising sequentially, however this was not possible using the video footage because the aggregations were too dense to follow individual fish for more than 30 s.

In situ observations and video footage showed bubbles emerging from the bonefish aggregations (Fig. 3), but only during or shortly following bouts of porpoising. Reducing the speed of video playback showed that the bubbles were originating predominantly from the opercula. Because of the orientation of the bonefish and angle that the video was captured, it was difficult to determine whether bubbles were also emerging from the vent.

Detailed scan sampling of over 180 min of video files from both locations revealed only three individual accounts of ventral nudging. For the video footage with the greatest water clarity (Abaco in 2013), the bonefish aggregation was large and very dense, making it difficult to observe behaviors of bonefish that were not swimming along the perimeter of the mass of fish.

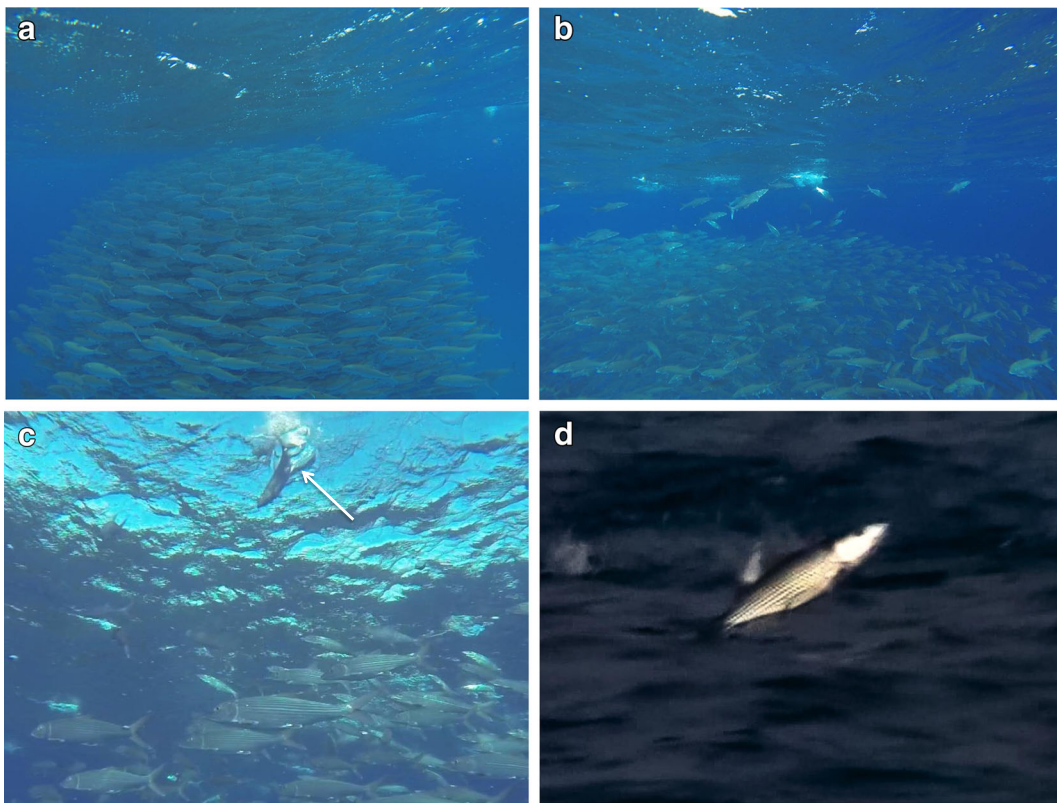


Fig. 2 **a** Aggregation of bonefish in approximately 10 m of water, as it moved parallel to shore, near where the island shelf meets a deep-water drop-off; **b** Bonefish rising from the aggregation, porpoising, and descending back to the aggregation; **c** a bonefish

re-entering the water after porpoising (as indicated by white arrow); and **d** a bonefish porpoising with the entire body above the surface of the water

Offshore movement patterns

For both Abaco and Andros locations, bonefish were gastrically tagged as soon as possible after we identified a large prespawning aggregation. On Abaco, two female (430 ± 28 mm FL) and three male (409 ± 31 mm FL) bonefish were gastrically tagged in 2013, and two female (450 ± 42 mm FL) and one male (390 mm FL) bonefish in 2014, while on Andros two female (448 ± 18 mm FL) and two male (433 ± 11 mm FL) were tagged in 2016.

On Abaco, in 2013 and 2014 the aggregations moved relatively slowly (approx. 2 km/h) parallel to shore along the 8–10 m contour, with the aggregation remaining between the surface and 5 m in depth during the mid-afternoon, and then turning slightly seaward at approximately 17:00 h toward where the reef shelf met a deep-water drop-off approximately 100 m further offshore. The onset of offshore occurred within 20–40 min after sunset. On Andros, at 17:44 h the aggregation

moved almost perpendicular to shore and towards the outer reef and drop-off of the Tongue of the Ocean. We were able to track three of the gastrically tagged



Fig. 3 Bubbles (as indicated by the white arrows) rising from a bonefish aggregation

bonefish for over 1.5 km as they moved from the pre-spawning aggregation site along a dredged channel to just before the barrier reef edge. These fish covered this distance in 44 min (approximately 2 km/h), however rough seas and darkness prevented us from staying close to the aggregation beyond the barrier reef.

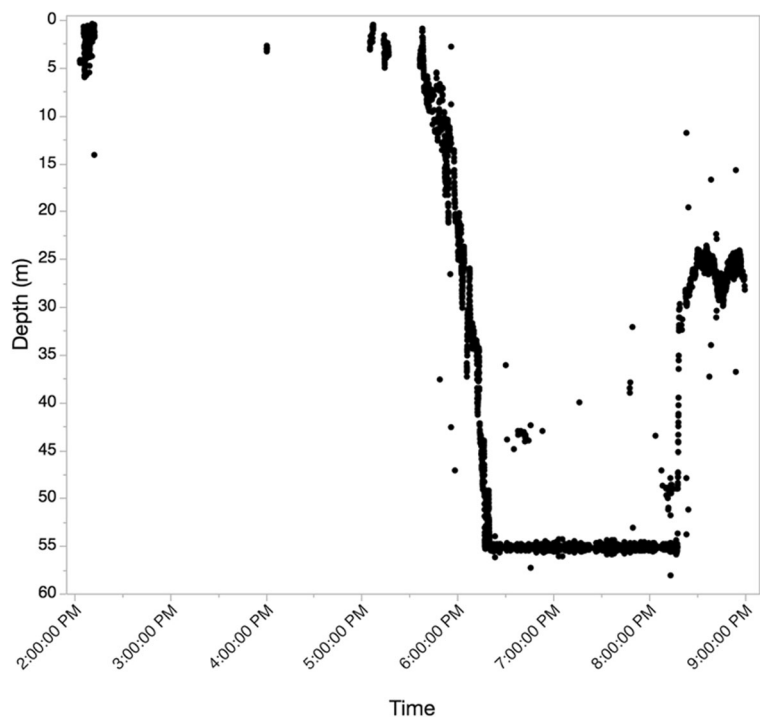
For Abaco in 2013, we were able to follow the aggregation for nearly 10 h as conditions were calm and our boat could remain close to the transmitters' signals. Approaching sundown, snorkelers periodically verified that we were following the aggregation, however they ceased doing so once it was dark; we did not want to use dive lights in the event it disrupted the aggregation. Simultaneously, we used the directional hydrophone to manually track a single bonefish that was in the aggregation (female, 450 mm FL), and followed it as it moved off the edge of the drop-off. Depth detections from this transmitter indicated that it descended from 5 m to greater than 50 m between 17:38 and 18:17 h (at a rate of 0.02 m/s; Fig. 4). We could not determine the final depth this bonefish had reached because the depth surpassed the 50 m depth limit of the sensor. Between 20:17 and 20:30 h the bonefish quickly ascended from >50 to 25 m, at a rate of 0.32 m/s, after which we followed the bonefish along

the edge of the drop off as it slowly moved back into shallower water at a relatively consistent depth. Water past the edge of the drop off exceeded 1000 m in depth. Unfortunately, tracking ceased when the battery in the manual hydrophone expired at 22:04 h. We returned to the aggregation site the following morning (06:57 h) and could not relocate any of the tagged bonefish. On Abaco in 2014, we manually tracked three individuals in an aggregation that moved towards the edge of the drop off near close to where the aggregation moved offshore in 2013, however a combination of strong winds, rough seas, and boat issues stopped us from following these fish beyond the drop-off into open water.

Discussion

While attempting to observe and track fish at dusk and into the night, on each occasion we observed sizable, dense bonefish aggregations moving away from the shore towards deep-water drop-offs during full moon periods in winter months. At each location, we also observed multiple individuals porpoising at dusk just prior to or during the transition offshore – a behavior not observed for bonefish when they are found on shallow

Fig. 4 Depth profile for a female bonefish (450 mm FL) as it moved in an aggregation from inshore to beyond the edge of a deep-water drop-off. Note that tag sensor limit was 50 m



flats (see Adams et al. 2018). These repeated observations are consistent with the criteria provided by Domeier (2012) regarding the identification of spawning aggregations, as well as with observations made by Danylchuk et al. (2011) for bonefish on a different island in The Bahamas. Even though actual spawning bouts were not observed, these repeatable patterns of aggregations and behaviors could be used to help characterize locations that are critical for the reproductive life history phase of bonefish, especially when combined with other information such as traditional ecological knowledge, larger scale tagging efforts, and biological sampling (e.g., oocyte histology) (Adams et al. 2018). As seen with other fish species that aggregate to spawn, identifying and protecting such locations should in most cases reduce the risk of overharvest and habitat loss, and thus be of considerable conservation value (Sala et al. 2001).

The most obvious and predictable behaviors were that they moved offshore at dusk (independent of the daily tidal cycle) and some individuals in the aggregations were porpoising. Danylchuk et al. (2011) postulated that porpoising behavior could be for gulping air to fill their swim bladders as a way to increase buoyancy prior to moving into deep water, where they potentially spawn near the surface of the water column. In their study, Danylchuk et al. (2011) tagged a small number of bonefish with coded tags equipped with depth sensors and detected an individual at 5.7 m on a fixed acoustic receiver moored in 26 m of water at the edge of the drop off of the Exuma Sound. This is similar to what we recorded on Abaco when manually tracking one individual in a large aggregation as it moved towards a deep-water drop off; however, once at the drop off this bonefish descended to a depth of over 50 m and then ascended rapidly, all within a 3 h period. Even though this was quantified for just one bonefish, the pattern resembles the ‘spawning rush’ behavior displayed by aggregating broadcast spawners, such as groupers (Peta et al. 2005) and snappers (Carter and Perrine 1994), when males chase females up into the water column where both release their gametes for fertilization (Johannes 1978). Perhaps, given that porpoising occurred as the aggregation moved offshore, and that bonefish are physostomus, any air trapped in the swim bladder and potentially the gastrointestinal track would be compressed with increasing water depth. In fact, a female bonefish (430 mm FL) captured from the aggregation on Andros that died (after an attempt to induce

ovulation via hormone injections) and subsequently dissected had a fully inflated swim bladder measured to be approximately 172 cc (19 cm long \times 3.5 cm in diameter). If this individual moved offshore and descended past 50 m, the swim bladder would compress to 5 cc, allowing for 167 cc of abdominal space for expansion of oocytes as they hydrate. If female bonefish are hydrating their eggs as they descend (see Adams et al. 2018), then the expansion of air could help force the eggs out of the gonoduct (i.e., ‘pneumatic assist’) during a rapid ascent, potentially when males are releasing their sperm. This hypothesis is also supported by observations from *A. glossodonta* in French Polynesia that are harvested when they migrate from inshore pre-spawning aggregations and also when returning to the flats, with the former having fully inflated swim bladders and the later deflated swim bladders (A. Filous, unpubl. data).

Other hypotheses for the evolution of porpoising behavior are that it is a form of male courtship display (Molloy et al. 2012), or that gulping air and the release of bubbles is an anti-predator behavior especially when the large aggregation moves into deeper water at night (Nøttestad 1998). Regardless of its purpose, the predictability of porpoising when large aggregations move offshore suggests that it is related to spawning, yet clearly more work is needed to understand this behavior. Increased sampling (capture and dissection) of bonefish immediately before and after they move offshore, descend to considerable depth, and then return to shallow water may provide additional insights into the purpose of porpoising, especially if sampling reveals that only females porpoise.

Group breeding and associated behaviors have adaptive benefits for adults, ranging from increased mate-encounter rates, increased reproductive output, and reduced predation rates on adults and resulting fertilized eggs (Molloy et al. 2012). Although aggregations can increase conspicuousness to predators, we did not directly observe potential bonefish predators (sharks, barracuda, large snapper or groupers) actually preying on any fish in an aggregation. Nevertheless, once the sun set, predator-prey dynamics at the aggregations could have changed with predators becoming more aggressive as the ability of bonefish to see decreased. In fact, during our work on Abaco in 2014, there was a distinctive fishy odour in the air after the sun set, which could have been related to bonefish being preyed upon. Fishy odours during aggregations could also result from the release of oils related to spawning activity or other biological activity.

Although it is challenging to directly evaluate the costs and benefits related to the evolution of spawning aggregations in fish (Molloy et al. 2012), the fact that spawning aggregations and associated behaviors can be conspicuous and occur at discrete times and locations may increase the potential to structure management strategies to protect this critical life stage. For *A. vulpes*, the predictable nature of aggregations and porpoising behavior could be used to locate seasonal spawning areas throughout The Bahamas, the Florida Keys, and the Caribbean. These traits could also be used to compare the reproductive ecology of *A. vulpes* to that of other species of bonefish that occur in the Indo-Pacific. Given their economic value as a sportfish, developing countries with limited funding and resources for detailed tagging and telemetry studies could rely on visual observations of aggregations as well as limited biological sampling to confirm the location of bonefish spawning aggregation sites, and afford these locations the appropriate protection.

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