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Identifying pre-spawning aggregation sites for bonefish (*Albula vulpes*) in the Bahamas to inform habitat protection and species conservation

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Abstract Many species of tropical marine fish aggregate to spawn, and the dynamics of these aggregations make them especially susceptible to overfishing and habitat loss. Spawning aggregations tend to attract reproductive adults from a large geographic area, sites are traditionally used across generations, and larval dispersal can help supply regional fish stocks. Thus, anthropogenic impacts to spawning sites can have population-level consequences over local and regional scales. A critical component in the challenge to conservation of aggregation-spawning species is identification and subsequent protection of spawning sites. Here we summarize fieldwork conducted to create a protocol for identification of pre-spawning aggregation sites for bonefish, *Albula vulpes*, in The Bahamas. The mixed-methods, field-based protocol includes Traditional Ecological Knowledge, assessment of spawning readiness, tracking using acoustic telemetry, behavioral observations, and mark-recapture, that combined meet the requirements for identifying pre-spawning aggregation sites. Pre-spawning site identification, in conjunction with information on other life stages and habitats, is essential for successful spatial management strategies. Since bonefish and many other tropical fishes that form spawning aggregation are 'data poor' and occur in regions where enforcement of fishery regulations is lacking, spatial management is often the best conservation strategy. This protocol builds upon similar previous efforts to identify spawning sites for groupers and snappers, and will contribute to information needs for conservation is an essential component in the conservation of aggregation-forming species such as bonefish across broad spatial scales.

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Introduction

Many species of tropical marine fish aggregate to spawn, typically gathering in much larger groups than occur in non-spawning seasons and locations. Domeier (2012) defines a spawning aggregation as "a repeated concentration of conspecific marine animals, gathered for the purpose of spawning, that is predictable in time and space. The density/number of individuals participating in a spawning aggregation is at least four times that found outside the aggregation. The spawning aggregation results in a mass point source of offspring." In addition, for many species, these aggregations occur in locations and habitats that are spatially distinct from individuals' normal home ranges – locations that are often used annually as spawning sites over many years (reviewed in Sadovy de Mitcheson et al. 2008), and are reached via traditional spawning migration routes between home ranges and the spawning site.

Several metrics have been used to differentiate spawning aggregations from other non-reproductive groupings of fish. First, a species must be present in significantly higher abundance than is normally encountered at non-spawning locations and outside of the typical spawning season: Domeier (2012) defines the spawning aggregation threshold as four times the normal density observed in non-spawning locations and outside of the spawning season. Additionally, spawning aggregation sites typically have a high density of mature fish at a location and habitat that is distinct from individuals' normal home range outside of spawning season. For example, adult striped mullet (*Mugil cephalus*) typically reside in shallow (<3 m) estuarine and coastal habitats, but migrate in large aggregations to offshore waters exceeding 40 m depth to spawn during winter (Anderson 1958).

Direct visual observation of reproductive behaviors is often used to confirm spawning activity. The rapid ascent behavior of Nassau grouper, for example, is a well-documented spawning behavior that occurs only at spawning aggregations as part of the act of spawning (Whaylen et al. 2004). However, for many species, abiotic factors (e.g., water clarity, time of day, depth, weather) prevent visual observation of spawning behaviors. In these cases, other behavioral and physiological cues that are indicative of an immediate readiness to spawn can be used as proxies for identifying spawning sites (Danylchuk et al. 2011). These include pre-spawning behavior (e.g., courting, nudging, color change), physiological readiness to spawn (e.g., spawning-ready eggs, males exuding sperm), and the aforementioned formation of unusually large aggregations in which individuals behave differently than when they are in non-spawning locations.

Because individuals from a large geographic area can be highly concentrated at aggregating sites, these spawning aggregations and their associated populations are especially vulnerable to human impacts such as overfishing, and habitat degradation and loss. Loss of productivity due to harvest or habitat disturbance at a localized aggregating site may have population-level consequences. Harvest of fish from spawning aggregations has caused regional population declines for Nassau grouper (Sadovy and Domeier 2005) and other species (reviewed in Sadovy de Mitcheson et al. 2008). Loss or degradation of habitat at spawning locations can also negatively impact aggregating species. Coastal development has impacted Nassau grouper spawning sites in the Mexican Caribbean (Sadovy de Mitcheson et al. 2008). Similarly, construction of causeways that disrupted bonefish spawning migrations on Kiribati have contributed to the cessation of spawning at numerous sites (Johannes and Yeeting 2001) and changes in bonefish population demographics (Beets 2001).

Population declines from impacts on spawning aggregations may be preventable with a more thorough understanding of movement patterns associated with spawning aggregation formation, and identification of pre-spawning and spawning sites that result in conservation actions to protect the aggregation sites. Important spawning aggregation sites have been effectively protected in some locations (e.g., red hind in the United States Virgin Islands: Beets and Friedlander 1998; Nemeth 2005). Indeed, research has even been conducted to identify spawning sites proactively – prior to fisheries exploitation or habitat degradation – to inform conservation for commercially important species (Heyman et al. 2014).

Worldwide, bonefishes (*Albula* spp.) are economically and ecologically important constituents of tropical, shallow-water systems. In the Caribbean Sea and western North Atlantic Ocean, *Albula vulpes* supports economically important recreational fisheries. (For the remainder of this manuscript, "bonefish" refers exclusively to the species *A. vulpes*). For example, the estimated annual economic impact of the recreational fishery for bonefish in the Bahamas, exceeds $141 million USD (Fedler 2010). Bonefish, tarpon (*Megalops atlanticus*)

and permit (*Trachinotus falcatus*) comprise the recreational *flats fishery* that collectively generates an annual economic impact exceeding $465 million in the Florida Keys (Fedler 2013) and $50 million in Belize (Fedler 2014). The economic importance of bonefish has led to the creation of strict regulations to protect the fishery in some countries: bonefish are catch and release only in Florida, Belize, Puerto Rico, and the U.S. Virgin Islands. In other locations, the recreational catch and release fishery coexists with consumptive fisheries that are subject to varying levels of management. In the Bahamas, capture with nets and commercial sale are illegal, but harvest with hook and line for personal consumption is allowed. The recreational flats fishery in Cuba occurs within marine protected areas designated as recreational catch and release zones, outside of these zones there are no regulations on what appears to be an intensive net fishery with high harvest (Rennert et al. this issue; J. Angulo, Univ. Florida, pers. comm.). In addition to their fishery value, the abundance of bonefish in shallow coastal habitats, the dominance of benthic invertebrates in their diet (Colton and Alevizon 1983; Crabtree et al. 1998), and their role as prey for sharks and barracudas (Cooke and Philipp 2004; Danylchuk et al. 2007a) suggest that bonefish play an important ecological role in structuring tropical shallow-water food webs (Danylchuk et al. 2007b).

An International Union for the Conservation of Nature assessment classified bonefish as Near Threatened due to habitat loss and fragmentation (particularly mangroves and seagrasses), coastal development and urbanization, declines in water quality, and harvest by commercial, artisanal and recreational fisheries (Adams et al. 2013). In Cuba, for example, there is intense harvest of multiple bonefish PSAs, with estimates of up to 20 tons harvested annually (J. Angulo, Univ. Florida, pers. comm.); Rennert et al. (this issue) obtained bonefish samples for age-growth study from gillnet fishers who targeted spawning migrations. In the Yucatan Peninsula of Mexico, fishers have traditionally targeted purported bonefish spawning migrations (A. Perez, ECOSUR, pers.comm.). In locations with recreational fisheries and no commercial harvest, the chief concern is habitat loss and degradation, though illegal harvest and lack of enforcement are also threats: two of the PSA sites identified in The Bahamas, for example, have been proposed as sites for deepwater ports/marinas.

Recent and ongoing research provides a general understanding of bonefish ontogeny. Adults exhibit high home range fidelity to shallow flats habitats of sand, seagrass, mangroves, and hardbottom during non-spawning time periods (Murchie et al. 2013; Boucek et al. this issue). Adults undergo migrations to pre-spawning sites – shallow protected bays immediately adjacent to deep water –between October and April (Danylchuk et al. 2011). Bonefish aggregate at pre-spawning sites before moving offshore at dusk to spawn at night, with putative spawning occurring at depths >50 m at or near deep-water drop-offs (>1000 m total depth), before fish return to their shallow water flats habitats (Danylchuk et al. 2011). Planktonic larval duration ranges from 41 to 71 d (Mojica et al. 1995). Settlement and early juvenile habitats are sand or sandy mud bottoms in shallow, protected bays adjacent to deeper water channels that provide larval access and are near eventual adult habitats (C. Haak, University of Massachusetts Amherst, pers. comm.).

This manuscript outlines development of a mixed-methods protocol we developed to identify bonefish pre-spawning aggregation (PSA) sites, and to demonstrate connectivity between these PSA sites and home ranges. This protocol is now being used to identify pre-spawning sites to inform conservation efforts in The Bahamas. Indeed, the Bahamas National Trust has already used this information to identify and create new national parks to protect bonefish PSAs. Plans for applying this protocol throughout the bonefish's range in the Caribbean Sea and western North Atlantic Ocean are under development.

Methods

This protocol was designed to use multiple metrics to identify bonefish PSAs and demonstrate connections to non-spawning home ranges relatively quickly and with limited personnel and cost (Fig. 1). A critical component of the protocol is integration of local fishers who take part in the fishery. This protocol uses Traditional Ecological Knowledge (TEK), estimates of spawning readiness, tracking using acoustic telemetry, behavioral observations, and mark-recapture. The methods described here were developed during research on the islands of Grand Bahama Island, Abaco, and Andros in The Bahamas (Fig. 2).

Fig. 1 Flow chart showing the
progression of methods used to
identify pre-spawning aggrega-
tion (PSA) sites and estimate
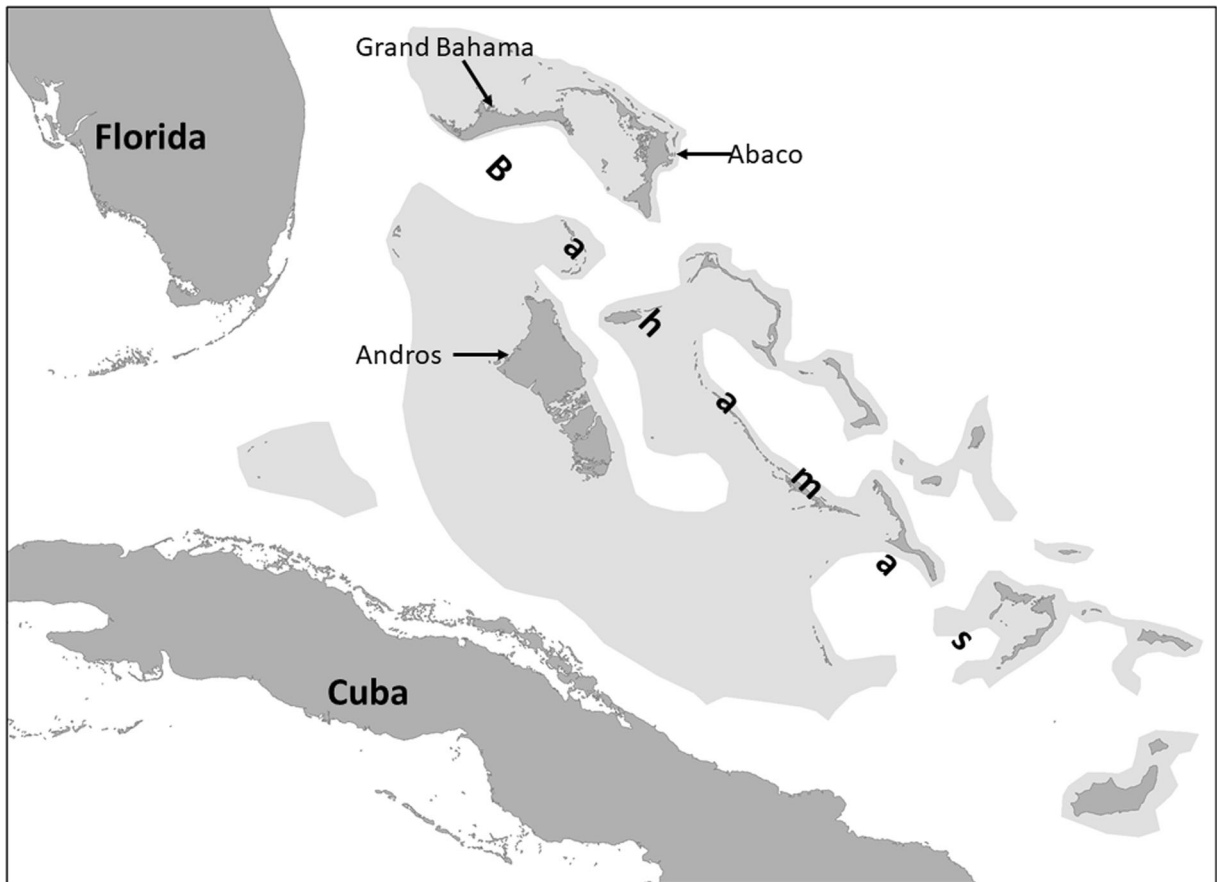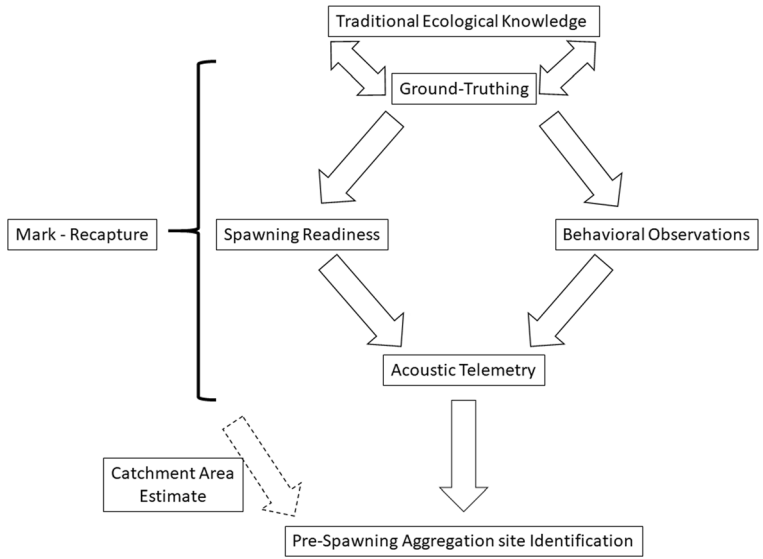catchment area. Spawning Readi-
ness is assessed via gonad
sampling

Fig. 2 Map showing the islands of The Bahamas where the pilot study to develop the protocol was conducted

Traditional ecological knowledge

We did not conduct formal interviews. Instead, we questioned guides during informal conversations at fishing lodges, while fishing with them on fishing skiffs, or in non-fishing social settings. This approach was essential to building trust with the guides, which greatly increased the amount and reliability of information that they shared. Importantly, this trust and involvement in the process generally made them supportive of PSA identification and protection. For example, numerous guides became advocates for national park designations for PSA sites during the public meeting process required for national park implementation. Other guides interacted with residents who harvested from PSAs to discourage harvest.

In conversations with professional fishing guides, we used the observations summarized in Danylchuk et al. (2011) to describe characteristics of bonefish PSA sites (habitat types, proximity to deep water, spatial separation from the normal flats fishing areas), seasonality (October through April), lunar phase, and bonefish behavior in PSAs (Danylchuk et al. this issue). With this broad description as background, we then used a non-structured interview to ask guides a series of questions relevant to narrowing our spatio-temporal search patterns for PSA sites:

–   Are there specific months between October and April when bonefish are in significantly reduced abundance on the flats? If yes, we then worked with them to remember approximate dates so we could estimate lunar phase. Guide estimate of relative abundance refers solely to his perception of the number of bonefish encountered on the flats while fishing, and was not associated with catch rate since catch rate varies due to many factors independent of fish abundance (e.g., angler skill, presence of predators, weather).
–   Between the months of October and April, have you observed schools of bonefish leaving the flats or migrating along pathways outside of the flats? Are these fish behaving differently than what you typically see on the flats (e.g., solely intent on travel)? If yes, we then worked with them to determine month(s) and date(s) so we could estimate lunar phase and locations to assist in our search for PSA sites.

–   Have you observed large schools of non-traveling bonefish in deeper water locations off the shallow flats? If yes, we again work with them to determine month and date so we could estimate lunar phase. We also asked them to show us, or provide specific directions to, the site.
–   Have you ever observed large schools of bonefish exhibiting porpoising behavior (gulping of air at the surface)? If yes, we again worked with them to determine approximate month and date, to identify the location, and to determine time of day the behavior was observed. Extensive observations (Danylchuk et al. 2011, this issue) show that PSA porpoising occurs exclusively in late afternoon and early evening in association with pre-spawning aggregations.
–   When possible, we showed them a video of bonefish behavior in a PSA (https://www.youtube.com/watch?v=5KMGm39zOqI).

Once a potential PSA site was identified, we visited the site in the afternoon during one or more full moons (typically during a period beginning 5 days prior and ending 5 days after full moon) during bonefish spawning season (October through April), usually with the guides who helped identify the site. Although acoustic telemetry data indicate that PSAs also form during other lunar phases, the full moon phase is the most common phase for PSA formation, so observations during full moon maximize the likelihood of observing a PSA considering time limitations. If bonefish were not observed at the site, we repeated the TEK process with the guides to generate additional potential PSA sites. Once a PSA was found, we conducted sampling to assess spawning readiness, made behavioral observations, acoustically tagged bonefish to characterize temporal patterns, and tagged bonefish with external tags.

Gonad sampling

Bonefish were caught from the PSA using hook and line and cast-nets (3 m diameter, 6 mm mesh). Bonefish were briefly retained in water-filled, aerated live wells on the fishing boats or quickly transferred by coolers to 0.9 m dia × 1 m deep Frabill floating net pens kept in shallow water along the shore. Bonefish were then individually removed from the holding container, fork length (FL) measured, turned ventral side up, their

abdomens gently squeezed, and their gonoduct examined for exuded sperm or eggs. No females released eggs, while many males released milt. For those that did not release gametes, we used cannulation to determine sex and egg stage (i.e., spawning readiness). A soft-tube catheter (Bard 100% latex-free infant feeding tube, 8Fr (2.27 mm diameter, 26 cm length), with the terminal end cut 3 mm short) was inserted into the gonoduct, and gametes removed using gentle suction from a 3-mL syringe barrel. Eggs were examined visually to provide a rough estimate of stage (Rhody et al. 2013) or photographed in the field using a small and easily portable DinoLite AM4815ZTL digital microscope with a DinoLite MSBL-CDW dark-field illumination base, with images saved to a laptop computer or tablet. Bonefish were then tagged (see below), and released into the PSA. Releasing the tagged fish directly into the PSA reduced post-release predation (predation was observed on occasions when bonefish were not released into the PSA).

Behavioral observation

Although there is considerable circumstantial evidence that bonefish spawning occurs at night, the actual spawning event has yet to be observed. As such, behavioral observations made by Danylchuk et al. (2011) were used as diagnostic clues to determine whether aggregations could indeed be related to putative bonefish spawning activity. Danylchuk et al. (2011) witnessed that prior to the full and new moons, large aggregations of bonefish were seen at 'transitional' habitats – areas slightly deeper than and spatially distinct from the flats bonefish normally inhabit and in close proximity to deep-water drop-offs where depth exceeds 1000 m. While in these areas, the aggregations remained in the mid- to upper-water column, not on the bottom where bonefish typically reside. Foraging behaviors were not observed in these aggregations.

Just prior to sunset, some bonefish in the aggregation were observed 'ventral nudging' which consisted of one fish swimming behind another and then bumping or rubbing its snout on the side or posterior end of the ventral region of the lead fish (Danylchuk et al. 2011). Similar pre-spawning behavior has been observed in Atlantic tarpon (Baldwin and Snodgrass 2008) and common snook (Peters et al. 1998). At the same time, individual fish were observed 'porpoising', consisting of either partially or fully jumping out of the water, and

then returning to the school. As the aggregation began to move offshore at dusk, streams of bubbles could be seen emerging from the bonefish themselves. Although the specific purpose of these behaviors and observations remains under investigation, such behaviors are only witnessed in bonefish that have formed pre-spawning aggregations right before they move offshore at dusk.

When on location at potential bonefish PSA sites, we used a combination of ad hoc surveys from a boat and with a small aerial drone (UAVs, custom built and DJI Phantom 3 Pro, DJI Innovations, Shenzhen, China) to locate and begin to observe bonefish aggregations. Once located, ad hoc snorkeling surveys were used to observe the behavior of bonefish. Small action 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) were used to digitally document individual and group behaviors until dusk, after which visual observations were not possible. For more details on bonefish behavior in PSAs see (Danylchuk et al. this issue).

Acoustic telemetry

To confirm that bonefish in the PSA were following the temporal patterns observed by Danylchuk et al. (2011) – synchronous movement offshore at dusk – we anchored an acoustic receiver (VR2W, Vemco, Nova Scotia) at the center of one PSA site on Andros. We then implanted 10 bonefish captured from the PSA with acoustic transmitters (Vemco, V9, 9 mm diameter, 21 mm long, 3.3 g in air, min and max delay times 45–135 s). For implantation, a 2 cm incision was made on the ventral surface, and the transmitter inserted into the peritoneal cavity. The incision was closed with sutures (Ethicon 3–0 PDS II, Johnson and Johnson, New Jersey). Bonefish recovered in an aerated cooler or floating mesh pens for approximately 30 min before being released into the PSA. The receiver remained anchored at the PSA site through the spawning season to monitor for ingress and egress of individual acoustically tagged fish to the PSA site.

Mark-recapture

In a concurrent project, Boucek et al. (this issue) tagged bonefish on the flats using dart tags to examine bonefish movements and to identify home ranges. In this study, we recaptured from PSAs bonefish that had been tagged

on the flats by Boucek et al. (this issue). We also used PDL dart tags (Hallprint, Australia) to tag all bonefish captured from the PSA that were examined for spawning readiness and all bonefish that were fitted with acoustic transmitters. Some of the bonefish that we tagged at PSAs were later recaptured on the flats by Boucek et al. (this issue). This mark-recapture linked PSA sites to home ranges, and provided estimates of catchment areas (Sadovy de Mitcheson et al. 2008; Boucek et al. this issue) for the PSAs.

Results

From 2012 through 2017 we worked with fishing guides to identify a total of five PSA sites on the islands of Abaco, Grand Bahama, and Andros. The multi-island, multi-year effort was an iterative process that allowed us to refine the protocol. The initial site identified was on Abaco, with positive identification of a PSA after three spawning seasons of work. This effort relied on TEK, assessment of spawning readiness, and behavioral observations to identify it as a PSA site, and mark-recapture to estimate the catchment area. The second and third sites identified were on Grand Bahama Island, and used TEK, mark-recapture, and assessment of spawning readiness to identify sites. In addition, a separate study used acoustic telemetry to document migratory pathways on Grand Bahama (Murchie et al. 2015). To identify the two PSA sites on Andros we used TEK, assessment of spawning readiness, behavioral observations, acoustic telemetry, and mark-recapture.

Traditional ecological knowledge

The level of fishing guide knowledge relevant to PSA site identification was mixed. Some guides noted time periods when bonefish relative abundance on the flats was low and had observed migrating schools of bonefish. In fact, some guides had figured out the pattern and actively fished the migrating schools with anglers. Migration pathways or migrating schools were reported for three of the PSA sites identified in this study. Four of the PSA sites identified in this study were known by some fishing guides. In two cases, guides fished the PSAs with anglers. Although the fishing of the PSAs was catch and release, given the high abundance of predators (primarily sharks) the likelihood of post-release survival

was low. Many guides had observed large schools of bonefish off the flats, at what were later identified as PSA sites, but had neither fished them nor knew that they were PSA sites. These guides passed the PSAs traveling to and from flats fishing grounds. No guides had observed the porpoising behavior. This is likely because this behavior occurs in the late afternoon or evening, after the fishing day is complete, and the guides were no longer on the water.

Although some guides did indeed provide observations relevant to the identification of PSAs, many other guides were not able to identify time periods during which bonefish abundance on the flats was notably lower than other times of year. Weather, tides, and angler ability confounded estimates for many guides because they were unable to separate bonefish abundance from catch rate: although angler ability is not a factor in bonefish abundance, it does affect the catch rate, and the number of bonefish caught is often most remembered by guides rather than overall fish abundance. Similarly, most guides had not observed schools of migrating bonefish either on the flats or on other habitats.

Often, when asked about porpoising behavior, guides described seeing bonefish feeding at the surface while in large groups on the flats on calm days during summer. This behavior, which the guides in the Bahamas call "bibbling", appears to be associated with feeding on shrimp. Colleagues in Cuba collected water samples and stomachs from bonefish from a school exhibiting this behavior (which they termed "cha-cha-cha"), and determined that the bonefish were feeding on shrimp (Callianassidae) swarms (Lazaro Vinola Valdes, Zapata Swamp National Park, Cuba, pers. com.). After discussion of bibbling behavior with the guides, we further described the time of year, site characteristics, and if possible showed them underwater video of a PSA taken at a PSA site on Abaco, The Bahamas (https://www.youtube.com/watch?v=5KMGm39zOqI). With this more detailed description, and knowing that bibbling on the flats was not spawning activity, some guides were able to identify potential PSA sites. In some locations, the large spawning migrations and PSAs were generally known in the community – the seasonally high fish abundance was a traditional food source. Using information gathered in these discussions, we then prioritized sites for examination based on the extent the sites met the physical characteristics described in Danylchuk et al. (2011).

Gonad sampling

In previous unpublished research, we examined egg biopsies and whole ovaries collected from a bonefish PSA to determine egg stages following a protocol developed by Rhody et al. (2013). Histological examination indicated that bonefish have group synchronous gonadal development, and are determinate-total spawners. To assess spawning readiness in this study, we examined 66 bonefish (33 males, 33 females) from PSAs. No females exuded eggs and a portion of males exuded sperm with gentle abdominal pressure. All of the 33 cannulated females contained oocytes that were deemed to be very close to spawning: easily extracted, slippery to the touch, fully yolked and ranging from 600 to 800 μm in diameter (Fig. 3). These oocytes had yet to undergo the final stages of maturation prior to ovulation and spawning (i.e. separation of oil droplets from yolk proteins, nuclear migration and breakdown of the nuclear membrane). Ongoing field and laboratory research has confirmed that egg hydration occurs in the hours between bonefish movement offshore at dusk and offshore spawning (W.J. Halstead and J. Shenker, unpubl. data).

Behavior

We observed behaviors documented by Danylchuk et al. (2011) being displayed by bonefish in PSAs on Abaco, Andros, and Grand Bahamas Island in The Bahamas. The most obvious and consistent behavior was porpoising that occurred as the aggregations moved offshore at dusk from the transitional habitat toward deep water. In many instances, more than one PSA was present at a site. At each location, aggregations were at or near the surface, and for approximately 30–45 min before sunset select individuals from the top and center of the aggregation were observed partially or fully jumping out of the water (see Danylchuk et al. this issue). Bouts ranged from several fish porpoising over the timespan of 3–5 s to several dozen bonefish breaking the surface for over a minute. Very rarely did we observe only one bonefish porpoising, and video analyses showed that individuals rarely broke the surface more than once in any given bout. During and after the bouts of porpoising, bubbles were observed ascending from the aggregation, even as the bonefish PSA maintained its position at the top of the water column. Unlike observations made by Danylchuk et al. (2011) on Eleuthera, ventral nudging was infrequently documented in the PSAs observed during this study.

Acoustic telemetry

Ten bonefish (five males, five females) were fitted with acoustic tags at a suspected PSA site on Andros,

Fig. 3 Photograph of fully yolked oocytes cannulated from a female bonefish captured from a PSA site near Andros, Bahamas. Photographed using a DinoLite AM4815ZTL digital microscope with a DinoLite MSBL-CDW dark-field illumination base, with image saved to a laptop computer

500 μm
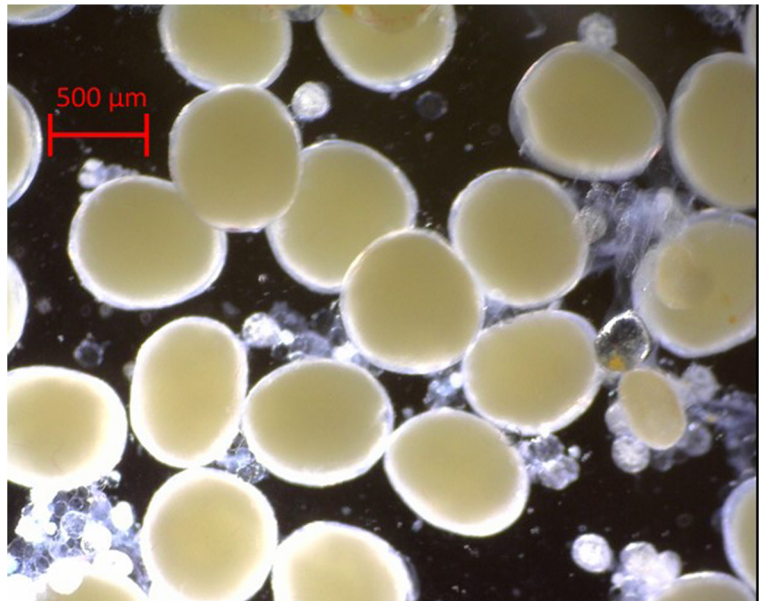
The Bahamas, during the full moon in January 2017 (Table 1). Two of the transmitters were never detected after fish release. The remaining eight transmitters were detected at the PSA site on the day of release. One fish was detected only on the day of release, never again detected. Of the remaining seven fish, three (ID 47564, 47,565, 47,451) remained at the site and exhibited synchronous departure from the PSA site at dusk, and return at dawn for multiple days (Fig. 4). This confirms the findings of Danylchuk et al. (2011), who documented that bonefish in the PSA begin to exhibit pre-spawning behavior in the late afternoon, and then the PSA rapidly moves offshore at dusk. Some individuals returned to the PSA site and repeated the offshore spawning run on subsequent nights. The remaining four fish were only detected briefly on the date of tagging, and then detected at later dates: fish ID 47566 returned for a single day on January 28, departing at dusk (Fig. 5a); fish ID 47567 returned May 1–5, and exhibited dusk-dawn patterns consistent with Danylchuk et al. (2011) (Fig. 5b); fish ID 45769 returned March 7–10, and exhibited dusk-dawn patterns consistent with Danylchuk et al. (2011) (Fig. 5c). The returning fish support findings of Danylchuk et al. (2011) that PSA sites are likely traditional.

Mark-recapture

Ten bonefish were either tagged on a flat and recaptured at a PSA site, or tagged in a PSA and recaptured on a flat (Boucek et al. this issue). The maximum distance traveled between a flat and PSA site ranged from 20 km to 80 km, and bonefish from different flats locations traveled to the same PSA site (Boucek et al. this issue). In contrast to these long-distance spawning migrations, non-spawning bonefish show high site fidelity, with the majority of bonefish recaptured within 5 km of the tagging location (Boucek et al. this issue).

PSA identification protocol

The execution of the PSA identification protocol should be an iterative process: as information is learned via TEK, site visits are made (often with fishing guides who provided the TEK) based on most likely locations, months, and lunar phases. If an initial site-date combination did not result in observing a likely PSA, we worked with the guides to revise our search. The first step in applying the protocol is to develop the relationships with fishing guides as part of the TEK conversation process. If mark-recapture is going to be used to estimate catchment area, this should also begin at the outset of work. This is because it takes considerable time and effort to mark sufficient bonefish to achieve recaptures. In our case, if Boucek et al. (this issue) had not been conducting a large-scale mark-recapture project, we may not have included this aspect of the protocol. Once a likely PSA site has been identified, assessment of spawning readiness, behavioral observations, and acoustic telemetry are applied.

Table 1 Bonefish captured from a pre-spawning aggregation on Andros and implanted with acoustic transmitters

Acoustic tag ID	Fork length (mm)	Sex	Detection dates	Lunar phase
47,563	370	M	Not Detected	
47,564	433	F	January 15 through January 20	Full moon January 12
47,565	497	F	January 15 through January 19	Full moon January 12
47,566	427	F	January 28	New moon January 27
47,567	430	M	May 1 through May 5	First quarter moon May 2
47,568	434	M	January 27	New moon January 27
47,569	498	F	March 7 through March 10	Full moon March 12
47,570	440	M	Not Detected	
47,571	Not Recorded	F	January 15 through January 19	Full moon January 12
47,572	379	M	January 15	Full moon January 12

Detection dates = the range of consecutive days the transmitter was detected by receivers at the pre-spawning aggregation site. Lunar phase = the moon stage during the days the bonefish was detected or closest to the dates of detection. All fish were tagged on January 15, 2017. All detection dates are in 2017
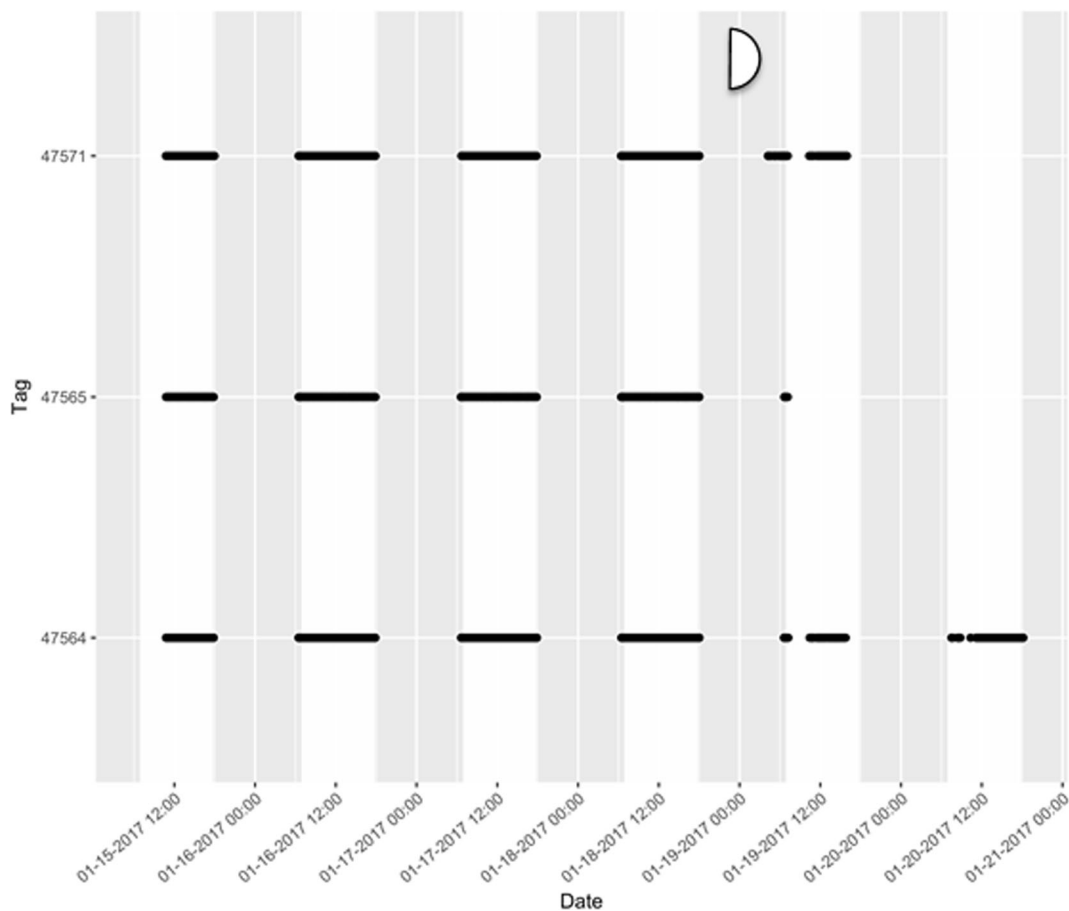
Fig. 4 Synchronous movements of acoustically tagged bonefish at the PSA site as detected by an acoustic receiver placed at the center of the PSA site near Andros Island, Bahamas. All transmitters were implanted in bonefish on January 15, 2017. Detections began upon their release into the PSA. Lack of detections beginning at dusk correspond to offshore movements to spawning area, and return from offshore to the PSA site at dawn, following the observations by Danylchuk et al. (2011). Full Moon January 12, Third Quarter Moon January 19. See Table 1 for sex and size of the bonefish shown in this figure. Fish ID 47564 = female, 433 mm; Fish ID 47565 = female,497 mm; Fish ID 47571 = female, length not recorded

Discussion

A top need for conservation of fish species that aggregate to spawn is identification of spawning sites so that these sites can be protected (see review by Erisman et al. 2017). Indeed, the realization that identification and protection of fish spawning aggregations is of vital conservation value was the impetus behind the Science and Conservation of Fish Aggregations (SCRFA.org). The challenge is to identify these sites in a timely and cost-effective manner. We have developed a protocol that relies upon multiple metrics to identify pre-spawning aggregation (PSA) sites for bonefish, an economically valuable species in the Caribbean Sea and western North Atlantic Ocean. Our methods build upon similar work on groupers, snappers, and other spawning aggregating species (reviewed in Sadovy de Mitcheson et al. 2008), and allow PSA site identification that does not require the time- and labor-intensive, and logistically challenging task of observing the act of spawning in offshore waters at night.

One of the great challenges to conservation of bonefish and other tropical fish species that aggregate to spawn is that most exist in data poor situations. There has never been a stock assessment of bonefish, for example, and only recently have data on age and growth (Crabtree et al. 1996; Rennert et al. this issue), and movements (e.g., Murchie et al. 2013;
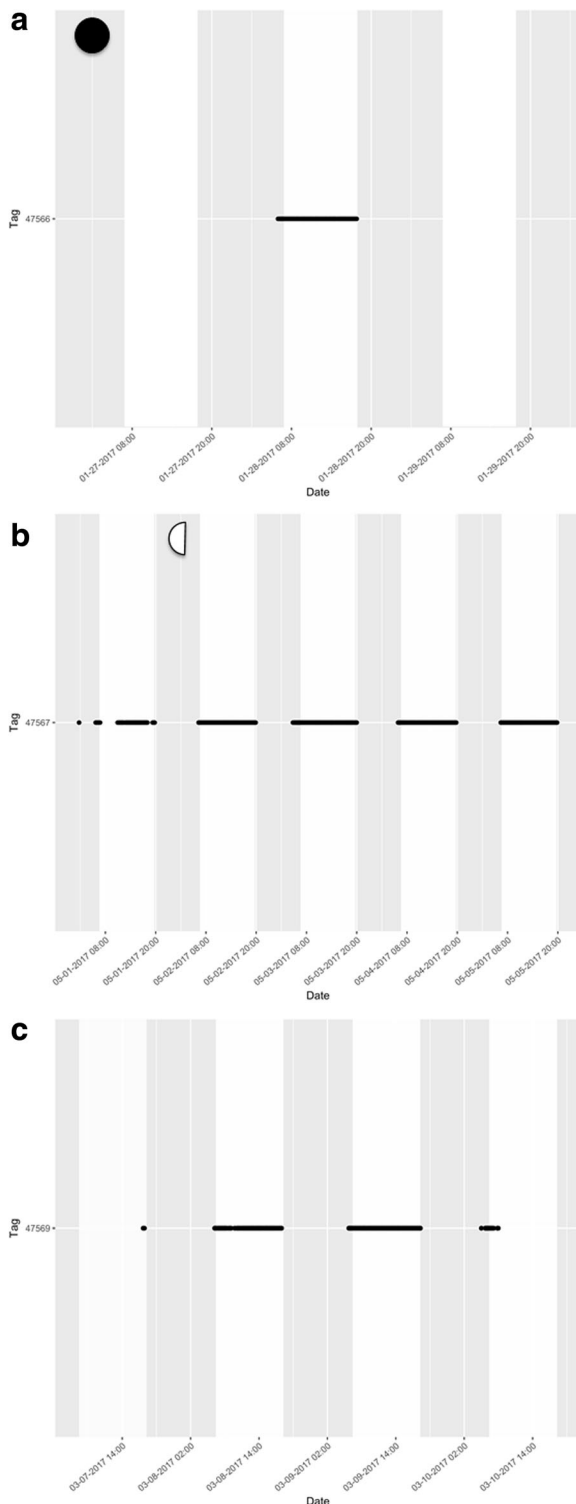
Fig. 5 Detections for bonefish caught from the PSA in Andros implanted with acoustic transmitters on January 15, 2017, that returned to the PSA site on later dates. Lunar phase is shown at the top of each chart. **a** Detections of bonefish ID 47566 (female, 427 mm) returning to the PSA site on a single day after the new moon in late January 2017. **b** Detections of bonefish ID 45767 (male, 470 mm) returning to the PSA site around the first quarter moon – May 2, 2017. Dusk and dawn movements as described in Danylchuk et al. 2011). **c** Detections of bonefish ID 47569 (female, 498 mm) returning to the PSA site before the full moon in March 2017. Dusk and dawn movements as described in Danylchuk et al. 2011)

Humston et al. 2005) been reported. Indeed, the first scientific documentation of a bonefish PSA was not published until 2011 (Danylchuk et al. 2011). Moreover, most research has occurred in a small portion of the species' geographic range (The Bahamas and Florida Keys). Although more data are available on commercially important species like groupers (Serranidae), fisheries management for these species still occurs in data poor circumstances (Sadovy de Mitcheson et al. 2008), resulting in many overfished populations and conservation challenges. It is unlikely the data poor status is going to improve substantially. It is therefore essential to develop fisheries and habitat management strategies that allow conservation with limited data (Johannes 1998).

The use of multiple, complementary metrics to identify PSA sites is essential. This approach has been used extensively for groupers and snappers, where TEK, site surveys, and gonad examination are frequently used to evaluate potential spawning aggregation sites (summarized in Sadovy de Mitcheson et al. 2008). Similar to studies that used TEK to identify spawning sites for groupers and other species (Colin et al. 2003; Aguilar-Perera and Aguilar-Dávila 1996), in this study TEK was a powerful tool for guiding identification of PSA sites. The fishing guides have extensive experience on the water both as guides and independent fishers. Many guides, for example, were commercial or subsistence fishers prior to becoming fishing guides, and many maintain that status during periods when they are not guiding recreational anglers. Moreover, TEK is often the only source of baseline data for data-poor fisheries, and is essential for monitoring trends in the fishery (e.g., Johannes et al. 2000; Robinson et al. 2004; Sáenz-Arroyo et al. 2005). In our study we found it best to forego a structured or semi-structured interview

process (e.g., Sadovy de Mitcheson et al. 2008), and instead developed a relationship with fishing guides, and included them in our field assessments of potential PSA sites and tagging. This built trust by the guides, and they in turn helped to spread that trust through the flats fishing guide community, similar to findings for other species (e.g., Gerhardinger et al. 2006). In fact, fishing guides involved in this research became leading advocates for protection of identified PSA sites on Grand Bahama Island and Abaco, and this pattern is holding true on Andros and other islands in the Bahamas.

Because the data are sensitive, as a rule we do not share locations of PSA sites outside of discussions with resource managers about protecting the sites. For this reason, we do not share PSA locations here. A PSA site may be known by a local community or some fishing guides, but generally not outside the immediate community. Given the apparently large geographic catchment area of PSA sites (Boucek et al. this issue) (catchment area = geographic extent of adults migrating to a PSA site and extent of larval dispersal from a PSA site – Sadovy de Mitcheson et al. 2008), impacts to a site would have wide-ranging effects on the fishery. This practice has become more common in scientific literature that incorporates sensitive information on species distributions and TEK (e.g., Robinson et al. 2004; Sadovy de Mitcheson et al. 2008).

Since bonefish move offshore to spawn at night toward water that reaches abyssal depths, direct observation of spawning has never occurred. Similar to Danylchuk et al. (2011), during this study we attempted numerous times to track bonefish offshore to obtain a measure of spawning behavior (e.g., via snorkel, tracking with continuous acoustic tags, sonar). However, the difficulties of following fast-moving fish offshore, in poor weather and high seas, and safety concerns caused us to terminate these efforts and to focus on metrics associated with PSAs. Even if one of these attempts to observe spawning had been successful, it would not be reliably repeatable. Although the reasons behind the unique behaviors displayed by bonefish in the PSAs are still unclear, the fact that these behaviors are only observed just prior to the large aggregations moving offshore near dusk is an indication that they are related to a reproductive event. These unique behaviors are useful in the preliminary identification of PSAs through the geographical range of bonefish, and behavioral observations do not require a large investment in time and resources.

The rapid assessment of spawning readiness via gonad sampling provides a valuable metric for identifying PSA sites. This is a common practice for groupers, snappers, and other species that are harvested from spawning aggregations. However, in those cases, ovaries can be extracted from fish that have been harvested. Since bonefish support a catch and release fishery, it was important to develop a method to non-destructively sample gonads. The small digital microscope and laptop or tablet, which can be used on a small boat or on shore, allowed us to conduct and record a rapid field assessment of spawning readiness based on egg appearance and size.

The use of acoustic telemetry to confirm synchronous movements that follow the results of Danylchuk et al. (2011), as shown in Fig. 4, is an especially powerful approach to confirming a PSA site. It requires a relatively small investment of a single acoustic receiver, a relatively small number of acoustic transmitters, and a day on site when a PSA is present. Site visits are required to assess behavior and spawning readiness, and implantation of transmitters occurs as part of this process. We recommend fitting at least 10 fish with transmitters to allow for mortality, and tagging equal numbers of males and females. It is essential to release tagged fish directly into the PSA: to do this we slowly motored a small boat over the PSA, and released bonefish back into the aggregation. An added benefit of the acoustic telemetry approach is that we are able to document sites as traditional based on returns of acoustically tagged fish to the site (as in Fig. 5).

The most difficult data to obtain are mark-recapture data to determine links between home ranges and PSA site, and thus an estimate of the catchment area of a PSA. This is because mark-recapture requires intensive effort over an extended period of time, and recapture rates for tagged fish tend to be low. In the concurrent mark-recapture study of bonefish in the Bahamas, recapture rate was 3% (Boucek et al. this issue), and in a similar study in Mexico and Belize, recapture rate was 7% (Perez et al. this issue). Thus, a large number of bonefish must be tagged to ensure adequate recaptures. Additionally, considerable outreach with the fishing and guide community must occur to ensure that recaptured fish are reported because under-reporting is common in mark-recapture studies (e.g., Ahrens et al. 2015). Finally, capture of tagged bonefish from a PSA that contains thousands of fish is

difficult, and frequently requires selective harvest of a tagged fish in an otherwise catch and release fishery. All of these activities require large investments of personnel time. However, such data are essential for estimating the geographic catchment area of a PSA site so that spatial protections are appropriately scaled, and managers know how large of an area would be impacted if a PSA site is lost (Sala et al. 2001). In this study, recaptures suggest a large geographic catchment for a single PSA sites (Boucek et al. this issue). Clearly, negative impacts to a bonefish PSA site will have far-reaching consequences for the fishery.

Bonefish and other species that aggregate at pre-spawning and spawning sites are particularly susceptible to population declines related to exploitation or habitat loss at these locations. Many species of groupers that aggregate to spawn are listed as threatened by IUCN (iucnredlist.org), for example, often due to harvest from spawning aggregations (Sadovy de Mitcheson et al. 2008). Although harvest of bonefish at PSA sites or during spawning migrations is not currently an issue in The Bahamas, this does occur in Cuba and Mexico. The effects of harvest of bonefish from PSAs in Tarawa Atoll were lower abundance, smaller size, and earlier sexual maturation (Beets 2001), and similar impacts are expected in the Caribbean. Although sample size makes conclusions difficult, the truncated size distribution of bonefish where PSA site harvest occurs in Cuba suggests these impacts may already be occurring (Rennert et al. this issue).

Habitat loss and degradation also threaten the functionality and long-term persistence of PSA sites. In some cases, PSAs have been identified in areas that are particularly vulnerable to development. For example, the proximity of deep water to a protected shoreline, an important characteristic for bonefish spawning, is appealing to those interested in developing deep-water ports or marinas. Indeed, a bonefish PSA site recently given national park protection in The Bahamas had been previously targeted for development as a marina. Similarly, deep-water areas near ocean currents have been targeted for sewage outfalls. It is unclear how habitat modification or degradation at critical PSA sites might affect aggregation formation, spawning success, or larval survival.

Because bonefish from a large geographical area make use of traditional localized PSA sites, it is critical that these locations be protected from development and pollution. Like groupers that aggregate to spawn, bonefish likely locate spawning sites via social learning (Colin 1996), whereby newly mature fish will follow older individuals to traditional spawning sites (traditional sites = used across generations). Under this scenario, habitat loss or degradation at a localized spawning site may result in population-level impacts. Individuals may continue to spawn at the traditional site, but alterations to the site may negatively affect fitness. If the PSA is able to shift to a non-traditional location following disturbance, important linkages between spawning site, larval transport pathways, juvenile habitats, and adult habitats may be severed.

Identification of bonefish PSA sites (this study) and catchment area (Boucek et al. this issue) have direct applications to conservation. Indeed, data from these studies has already been used to identify and create five new national parks by the Bahamas National Trust on Abaco and Grand Bahama Island. Ongoing collaboration between Bonefish & Tarpon Trust, Bahamas National Trust, and The Nature Conservancy is applying this protocol to identify PSA sites and other important habitats on other islands in the Bahamas to inform additional national park designations. Once new parks are created, the next step is to formulate management plans for each park, with the focus being habitat conservation. The Bahamanas National Trust operates under the BNT Act, which empowers BNT to create parks, rules, regulations through bylaws that are nationally gazette and become national law (BNT Act: http://laws.bahamas.gov. bs/cms/images/LEGISLATION/PRINCIPAL/1959 /1959-0021/TheBahamasNationalTrustAct_1.pdf; 2010 Amendment: http://laws.bahamas.gov. bs/cms/images/LEGISLATION/AMENDING/2010 /2010-0031/BahamasNationalTrustAmendmentAct2010. pdf). PSA sites are being identified in Belize (Perez et al. this issue), and information is being presented to management agencies for similar habitat protection designations to protect the PSA sites. Given that enforcement of fisheries regulations in the Bahamas, Belize, and many other locations where bonefish occur is lacking, and that habitat loss/degradation is the top threat to the fisheries, spatial management, whereby important habitats are protected, is arguably the best conservation approach. This is especially the case is situations where local buy-in and voluntary adherence to such regulations is a valid approach (Cooke et al. 2013).

Conclusion

The protocol outlined here provides a mixed-methods approach to identify bonefish PSA sites, and to estimate the adult portion of the geographic catchment area for the PSA. Given the lessons from overharvest of other species that aggregate to spawn, and the documented impacts of habitat degradation on a different species of bonefish in the Pacific, efforts to identify and protect bonefish PSAs should be increased immediately. Spatial protections, however, should not focus solely on the PSA sites, but should include the foraging areas, spawning migration pathways, and larval settlement locations within the catchment area.

As with groupers, snappers, and other tropical species that aggregate to spawn, the bonefish fishery is data poor. Lack of data, however, is no excuse for lack of management. In fact, such data poor situations provide an opportunity to combine TEK with field assessments to develop protocols as outlined here to use a spatial approach to manage bonefish and other species that are managed with high levels of data uncertainty (Johannes 1998).

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