



# The spawning migrations of an exploited *Albulid* in the tropical Pacific: implications for conservation and community-based management

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Received: 26 May 2019 / Accepted: 14 June 2020  
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**Abstract** Teleost fish that form predictable spawning aggregations and undertake reproductive migrations can be particularly vulnerable to overexploitation. To support community-based management of an artisanal fishery that targets bonefish (*Albula glossodonta*) spawning aggregations, we used a combination of acoustic telemetry, biological sampling, and remote imagery to reveal the spatiotemporal spawning migrations of bonefish on Anaa Atoll in the Tuamotu Archipelago, French Polynesia. The spawning migrations of bonefish tracked with acoustic telemetry were restricted to the northern section of the atoll, with 99.6% of all detections at offshore spawning habitats occurring on fixed acoustic

receivers adjacent to the atoll's artisanal fish trap complex. Male bonefish undertook spawning migrations more frequently than females and these spawning migrations were common during the Austral winter and fall. The movements of bonefish spawning aggregations coincided with the lunar cycle, as a network analysis revealed an increase in network size and the diversity of habitat use within our acoustic array throughout the duration of the waning moon. Our results highlighted the need for the management of the artisanal trap fishery to prevent the overharvest of bonefish during their peak spawning periods. In response to the spatiotemporal management recommendations derived from this

**Electronic supplementary material** The online version of this article (<https://doi.org/10.1007/s10641-020-00996-3>) contains supplementary material, which is available to authorized users.

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research, the local government established an Educational Managed Marine Area that includes the atoll's bonefish spawning migratory corridor adjacent to Tukuhora village and a *Rahui* (i.e., seasonal closure) to improve the sustainability of the fishery.

**Keywords** Bonefish · *Albula glossodonta* · Lunar migrations · Acoustic telemetry · Traditional management · Artisanal fisheries

## Introduction

Many marine species have broad home ranges and must aggregate in close spatiotemporal proximity to successfully spawn (Secor 2015). To this end, the formation of large spawning aggregations concentrates conspecifics, from a wide geographic area, to maximize the probability of fertilization, enhance genetic diversity, and minimize risk of predation to adults and gametes (Sala et al. 2003; Danylchuk et al. 2011; Domeier 2012; Sadovy de Mitcheson and Erisman 2012). This spawning strategy is particularly evident among tropical species where the diverse trophic structure of coral reefs has led to convergent evolution in reproductive behavior, in which normally shallow water species leave their littoral habitats to spawn in the pelagic environment (Johannes 1978; Domeier and Colin 1997). Broadcast spawning in the pelagic environment reduces predation on larvae and aides in their dispersal to new locations, creating meta populations whose connectivity helps strengthen a species' resilience to local ecological changes and anthropogenic stressors (Hughes et al. 2005; Cowen and Sponaugle 2009). The success of broadcast spawning is hypothesized to be influenced by localized currents and the synchronized movement of spawning aggregations. Moreover, spawning is often linked to environmental conditions that favor fertilization, transport and or retention of larvae, which leads to seasonal and/or lunar periodicity of spawning, making the occurrence of their aggregations spatially and temporally predictable (Johannes 1978; Claydon 2004).

High quality reproductive habitats where conditions for large-scale aggregation and larval transport are favorable generally occur in areas that are discrete from productive feeding habitats (Jørgensen et al. 2008; McBride et al. 2015). Therefore, many marine animals migrate between foraging and reproductive habitats to facilitate spawning (Secor 2015). However, this

behavior can be perilous to commercially exploited teleosts, particularly during predictable reproductive events when conspecifics that would normally be dispersed across a seascape become spatially and temporally concentrated, making them highly vulnerable to overexploitation (Beets and Friendlander 1998; Sala et al. 2003; Sadovy and Domeier 2005; Russell et al. 2012; Erisman et al. 2017). Harvesting fish from spawning aggregations can directly change the abundance, sex ratio, and body sizes of a population, thereby restricting reproductive output (Sadovy and Domeier 2005; Sadovy de Mitcheson et al. 2013; Secor 2015). These fisheries can also impose artificial selection against traits and behaviors that would normally increase an individual's fitness if left unfished, such as multiple spawning events or time on the spawning site (Heino and Godø 2002; Law 2007; Secor 2015). Ultimately, depensation may prohibit exploited populations from recovering from overexploitation (Rowe and Hutchings 2003; Gascoigne and Lipcius 2004; Sadovy and Domeier 2005). Maintaining spawning aggregations and managing their respective fisheries is extremely difficult without a clear understanding of which segments of a population are moving, when these movements occur, and the locations to which they are directed (Russell et al. 2012; Gruss et al. 2014). Therefore, research into the spatial and temporal characteristics of spawning migrations is a priority in developing conservation strategies for marine fisheries (Sadovy de Mitcheson and Erisman 2012).

Bonefish (*Albula spp.*) are a classic example of neritic fishes that undertake migrations to the pelagic environment for reproduction in tropical seas (Danylchuk et al. 2011; Adams et al. 2018). These migrations have historically been targeted by artisanal fisheries in the Pacific Islands and traditional ecological knowledge from this region suggests that bonefish synchronize their spawning migrations with the lunar cycle and displace from their lagoon habitats to discrete offshore locations and spawn in association with the full moon (Johannes and Yeeting 2000; Friedlander et al. 2007; Allen 2014). The lunar periodicity of *Albulid* spawning has also been documented in the Atlantic where offshore aggregations of *A. vulpes* have been observed during the full moon (Danylchuk et al. 2011, 2018; Adams et al. 2018). An understanding of these phenomena and their lunar predictability could help manage anthropogenic impacts to these reproductive events. However, in many locations the specifics of

*Albulid* migratory movements remain an enigma and it is an area of active research for *A. vulpes* in the Atlantic (Humston et al. 2005; Larkin et al. 2007; Danylchuk et al. 2011; Adams et al. 2018).

The remote atolls of French Polynesia support some of the world's last viable artisanal fisheries where *A. glossodonta* aggregations are targeted by rock traps during their spawning migrations (Caillart and Morize 1990; Allen 2014; Torrente 2015; Filous et al. 2019a, 2019b). Analogous fisheries in Oceania have been overexploited (Beets 2000; Johannes and Yeeting 2000; Friedlander et al. 2007; Adams et al. 2013) and consequently local governments have been forced to regulate the harvest of this species in the absence of scientific data (Cook Islands Government 2010; Ram-Bidesi 2011). On Anaa Atoll in the Tuamotu Archipelago, *A. glossodonta* is heavily exploited and although the community possesses traditional knowledge regarding the lunar movements of bonefish there are many unanswered questions concerning the dynamics of these events, such as the directionality of the spawning migrations between the lagoon and ocean as bonefish circulate in the trap complex and the underlining reproductive significance of these movements (Filous et al. 2019a, 2019b, 2019c).

Acoustic telemetry can provide a record of a fishes movements throughout its environment and has been used to characterize the timing and habitats utilized by fish during their spawning migrations to improve fisheries management (Crossin et al. 2017), including bonefish spawning aggregations in the Atlantic and in this setting, it has the potential to reveal the spatiotemporal patterns of bonefish reproductive migrations on Anaa Atoll (Danylchuk et al. 2011, 2018; Adams et al. 2018). This information would represent an essential component of the knowledge base in the Pacific Ocean where *A. glossodonta* is a vulnerable species (Adams et al. 2012), and fisheries management could benefit from an in-depth understanding of these movements, which can supplement local ecological knowledge and support traditional management initiatives (Crossin et al. 2017; Lennox et al. 2018). To this aim, we used a combination of acoustic telemetry, biological sampling, and remote imagery to quantify the spawning migrations of *A. glossodonta* on Anaa Atoll. Our specific objectives were to document the spatiotemporal movement patterns of bonefish, assess the importance of the different corridors between the inner lagoon of Anaa Atoll to the outer reef, determine whether spawning migrations were

linked to seasonal and/or lunar cycles, and determine if there were any sex related differences in spawning behavior. This research was intended to inform community-based management by providing a comprehensive understanding of the spatiotemporal dynamics of these reproductive events and their interaction with anthropogenic activities.

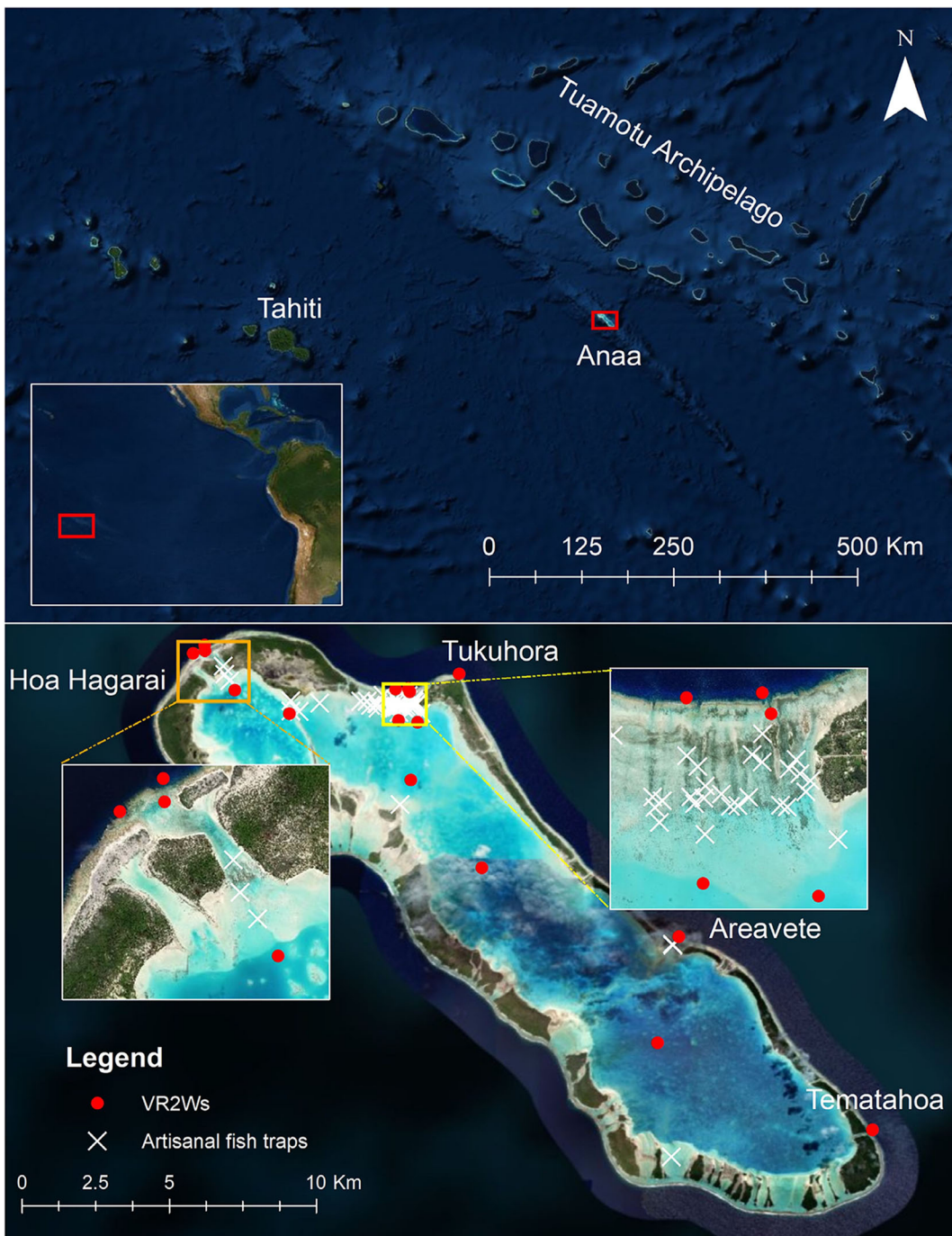
## Methods

### Study site

Anaa is a small atoll (38 km<sup>2</sup>) 350 km east of Tahiti in the Tuamotu Archipelago of French Polynesia (Fig. 1). The atoll has one village, Tukahora, with approximately 500 residents. The land mass of Anaa is bordered by a coral reef that drops off into the open ocean (to depths of >1000 m) and surrounds a shallow lagoon with 11 small islands known as “*motu*” and fringing sand flats. Unlike most atolls in the Tuamotus, Anaa is closed (i.e., the reef crest forms a barrier around the atoll) and therefore lacks a deep oceanic pass between its interior lagoon and outer reef. The predominant southwesterly ocean swells periodically inundate the lagoon and water exits the atoll from a series of small cuts in the reef crest along its eastern perimeter (Andréfouët et al. 2001). Traditional ecological knowledge suggests that a series of small openings in the reef crest adjacent to Tukahora village and Hoa Hagarai serve as the primary movement corridors into and out of the lagoon (Fig. 1). Marine life must negotiate these narrow back reef channels between *motu* to transition between habitats, which are often shallow (10–20 cm) during low water events (i.e. when there is little prevailing swell). The corridors to these passages form the basis of a permanent fishing installation comprised of artisanal rock weir-style traps (Fig. 1). These artisanal traps capture at least 62 different species of fishes and are highly efficient at capturing bonefish during their spawning migrations, which numerically account for up to 49% of the yield taken with this gear type (Filous et al. 2019a).

### Passive tracking

The long-term spawning migrations of bonefish were studied with fixed station acoustic telemetry. We partnered with local fishers to design the acoustic receiver array based on their traditional ecological



**Fig. 1** The location of Anaa Atoll, the eastern most atoll in the Tuamotu Archipelago of French Polynesia, and Anaa with the locations of artisanal fish traps and the two important migratory corridors for bonefish, the Hoa northwest of Tukahora village

(yellow extent indicator) and Hoa Hagarai (orange extent indicator). White X's indicate the locations of artisanal fish traps and red dots represent locations of VR2W acoustic receivers, the names of villages and important landmarks are labeled in white

knowledge of bonefish foraging and migratory corridors. Sixteen Vemco acoustic receivers (VR2W, 308 mm long × 73 mm diameter, Amirix Inc., Bedford,

NS, Canada), were strategically placed in the lagoon, back reef adjacent to oceanic passes, along the outer reef where spawning aggregations were believed to occur

and every other significant outlet to the outer reef along the perimeter of the atoll (Fig. 1). Range testing was conducted with a VR-100 receiver and directional hydrophone (Amirix Inc., Bedford, NS, Canada) following the methods of Filous et al. (2017). Forty-three bonefish (21F:22M) were captured in artisanal fish traps during their spawning migrations and tagged with Vemco V-13 coded transmitters (13 mm diameter, 45 mm long, transmission rate 75–125 s, battery life of 561 days). For tagging, individual fish were placed in an aerated salt-water bath and transmitters were surgically implanted into the body cavity of each fish through a 2-cm incision in the abdominal wall and closed with an interrupted nylon suture (PDS 3/0, FS-1 reverse cutting needle, Ethicon, New Brunswick, NJ). During the surgical procedure, the sex of all tagged fish was identified by the presence of oocytes or sperm in the abdominal cavity. After surgery, all fish were measured (fork length, FL, to the nearest cm) and tagged with a 10-cm individually numbered plastic dart tag (10 cm PDL, Hallprint, Australia) to externally identify fish that were recaptured. After tagging, marked fish were placed into a holding pen for up to 4 h to allow for recovery and once recuperated, they were released together in the lagoon adjacent to the trap complex.

#### Active tracking

Migrating bonefish captured in the atoll's artisanal fish traps were tagged with Vemco V9-2XH continuous transmitters (9 mm diameter, 29 mm long, transmission rate 2000 ms, battery life of 37 days). Upon capture, the fish were placed in an aerated saltwater bath and the transmitter was inserted into the stomach of the fish with a smooth plastic tube and plunger that was gently pushed into the fish's esophagus (Cooke and Philipp 2004; Danylchuk et al. 2007, 2011). Tagged fish were allowed to recover and were subsequently released following the same manner described above. After release, these fish were tracked with a VR-100 receiver and directional hydrophone. To complement the data acquired from active and passive tracking, Ad hoc visual surveys were conducted during tracking events with a DJI Mavic Air unmanned aerial vehicle (DJI, Shenzhen, China) and in-situ snorkel surveys following the methods of Danylchuk et al. (2018). Behavioral observations of bonefish aggregations were recorded on GoPro Hero 3 (Go-pro, San Mateo, CA) and DJI Mavic Air video cameras and qualitatively assessed for the

spawning behavior described in Danylchuk et al. (2018), including shoal structure, “ventral nudging” and “porpoising”. Furthermore, to determine the reproductive status of bonefish in the monitored aggregations, we sub-sampled the gonads of bonefish that were captured in association with transmitter equipped fish and determined their reproductive state with histology and gonadosomatic index measurements following the methods described in Filous et al. (2019c).

#### Statistical analyses

All statistical analyses were conducted using R and values are reported as means and one standard deviation, unless otherwise stated.

#### Passive tracking

To reduce the possibility of false detections, we filtered the passive tracking data to remove detections from individuals that did not occur in our array at least twice over the course of a 24-h period. After filtering, to identify initial patterns of bonefish behavior and movement throughout the acoustic array, we pooled the 16 acoustic receivers by habitat type and hypothesized migratory pathways. These include non-migratory lagoon habitats characterized by silt and coral substrate in the center of the lagoon where bonefish schools are commonly observed feeding, inter-lagoon pre-spawning aggregation sites characterized by a sand bottom adjacent to hypothesized migratory corridors in the fish trap complex, back reef pre-spawning aggregation sites characterized by shallow (~1 m) hard bottom inside of the reef crest on the seaward side of the trap complex, outer reef spawning sites in the north characterized by coral reef hard bottom along a steep drop off to the pelagic environment, and outer reef sites adjacent to passes in the south of the atoll. Diel scatter plots with day and night shading were generated of detections at the five habitats for each transmitter-implanted fish and analyzed to investigate seasonal periodicity, frequency and extent of bonefish movement through the array (Filous et al. 2017).

#### Lunar network analysis

To evaluate spatiotemporal distribution of bonefish movement across the lunar cycle, we conducted a network analysis (Jacoby and Freeman 2016). We first

classified the detections of each fish based on the eight phases of the lunar cycle during which it was detected at a given receiver (full, waning gibbous, last quarter, waning crescent, new, waxing crescent, first quarter, or waxing gibbous). The lunar phases at the time of detection were determined using the `lunar.phase` function in the `lunar` package. These data were then filtered for the eight lunar phases and network analyses were fit to each lunar phase with receiver locations as nodes and fish movement in-between nodes as weighted edges. Network fitting was implemented with the `graph_from_data_frame` function in the `igraph` package. Networks for each of the eight moon phases were then summarized by the number of nodes, mean distance, edge density, and the mean and standard deviation of node closeness and betweenness (i.e., the number of paths through a receiver) for a given moon phase (Csardi 2015; Jacoby and Freeman 2016).

#### Seasonal, lunar and diel patterns in bonefish spawning migrations

To investigate seasonality of bonefish spawning migrations, we pooled detections across receivers in oceanic spawning (backreef and outer reef) and inter-lagoon non-spawning habitats and calculated a monthly index of spawning activity by taking the total number of bonefish detected in the spawning habitats during a given month and dividing by the total number of bonefish detected in lagoon non-spawning habitats in that month (Danylchuk et al. 2011). The monthly spawning index was then plotted on polar coordinates with `ggplot2` (Wickham 2016) and tested for uniformity with a Rayleigh test of uniformity by converting month to degree (multiplying numeric month values by 30) and using the `r.test` function in the `CircStats` package. We then determined the maximum likelihood estimates for the mean and concentration of the degree (i.e., month) assuming a Wrapped Cauchy distribution with the `mle.wrappedcauchy` function in the `Circular` package.

Patterns in diel movement of bonefish spawning aggregations between back reef refuges on the reef crest and the outer reef were investigated by pooling detections across the receivers in these two habitat types. The timing of sunrise and sunset was determined for each detection date with the `getSunlightTimes` function in the `suncalc` package and detections were classified as occurring during night or day if they fell between sunrise and sunset or beyond. The number of detections in these

two habitats were plotted for each hour of the diel cycle and a mixed-effects logistic regression was used to test for a difference in the number of night and day detections using the `glmmPQL` function in the `MASS` package.

The presence of bonefish in these two habitats in relation to lunar illumination was investigated by determining the lunar illumination on the night each fish was detected, with the `lunar.illumination` function, in the `lunar` package. Then, for each fish's detections in back reef refuges and outer reef we calculated the mean lunar illumination during which it was detected and plotted the density distribution of individual means in these habitats. We then tested for circular uniformity in the relationship between lunar illumination and the presence of bonefish in the two spawning habitats, using the Rayleigh test and determined the maximum likelihood estimates for the mean degree (i.e., illumination) and concentration assuming a Wrapped Cauchy distribution as described above. Finally, to estimate the frequency of male and female spawning activity we calculated the total number of days each transmitter equipped fish was detected in spawning habitats and tested the difference in the number of days male and female bonefish were detected in these locations with a negative binomial generalized linear model.

#### Active tracking

Data were filtered to ensure that at the time of detection tracked fish were in proximity to the GPS locations recoded by the VR-100 by excluding any detections less than 70 db in signal strength. The movements of bonefish pre-spawning aggregations were then illustrated in relation to the atoll's fish traps by plotting their GPS waypoints in GIS, overlaid on satellite imagery of Anaa Atoll. To evaluate the space used by pre-spawning aggregations, the area of the minimum convex polygon (MCP) encompassing all their geographic coordinates was calculated with the `mcp` function in the `adehabitatHR` package (Calenge 2006). To evaluate the site fidelity exhibited by pre-spawning aggregations, we then calculated the Index of Refuge (IOR) between tracks of equivalent monitoring time.

$$IOR = [OV (A1 + A2)] / (A1 + A2) \quad (1)$$

Where IOR is the index of refuge,  $[OV (A1 + A2)]$  is the area of overlap between two tracks, and  $(A1 + A2)$

total area of both tracks. A value of 0 indicates no overlap in space use, and a 1 indicates 100% overlap of space use (Papastamatiou et al. 2009)

## Results

### Range testing

The maximum instantaneous detection ranges of receivers in the acoustic array ranged from 65 to 576 m and were variable among habitat type. Receivers located within the lagoon had an average detection range of  $421 \pm 92$  m, receivers located in refuges on the back-reef had an average detection range of  $81 \pm 3$  m and receivers located on the outer reef slope had an average detection range of  $108 \pm 40$  m.

### Spawning migrations

Between May 18th, 2017 and July 9th, 2018, a total of 101,020 detections were recorded from 32 of the 43 bonefish tagged with coded transmitters, spanning from 1 to 415 days ( $223 \pm 147$  d). Of the 11 undetected bonefish, eight were confirmed to have been immediately recaptured and harvested in the artisanal fishery on the date of release (i.e., they swam directly into a fish trap after release from which they were collected), while the remaining three mortalities could be attributed to under reporting in the artisanal fishery or post-release predation by black tip reef sharks (Lennox et al. 2017). Additionally, three bonefish with detection spans of 3 days or less were assumed to be predated after release (Friedlander et al. 2007) and removed from the study, bringing to total number of monitored bonefish to 29 (Table 1). Eight additional bonefish were tagged and tracked with continuous transmitters throughout the course of this study, but only one (a 57 cm FL female) rejoined the spawning aggregation immediately after tagging and was included in our description of the movement of bonefish spawning aggregations on June 12th, 2017.

Bonefish equipped with coded transmitters were detected on 15 of the 16 receivers deployed in the array, with the receiver located on the outer reef at Tematahoa, being the only VR2W to remain unvisited by any of the tagged bonefish (Fig. 1). Bonefish movements on the outer reef were limited to the areas immediately adjacent to the heavily fished passageways in the north of the

atoll, with 99.6% of all detections in oceanic habitats occurring at stations situated outside of Tukahora village and Hoa Hagarai, as opposed to the 0.4% of detections made by the station outside the passage at Areavete and no detections outside the passage at Tematahoa outer reef (Fig. 1). These offshore migrations were common during the austral winter and fall, with bonefish being consistently detected in spawning habitats from March to September, and the peak in activity at these locations occurring between April ( $120^\circ$ ) and May ( $180^\circ$ ),  $\mu = 146.7^\circ$ ,  $\rho = 0.34$ . Although some bonefish were detected in spawning habitats during the spring and summer, the proportion of bonefish engaged in spawning activity throughout the year was non-uniform ( $\bar{r} = 0.34$ ,  $P < .05$ ), suggesting that this species exhibits a seasonal but protracted spawning season, which we inferred to coincide with the cooler months of the year (Fig. 2).

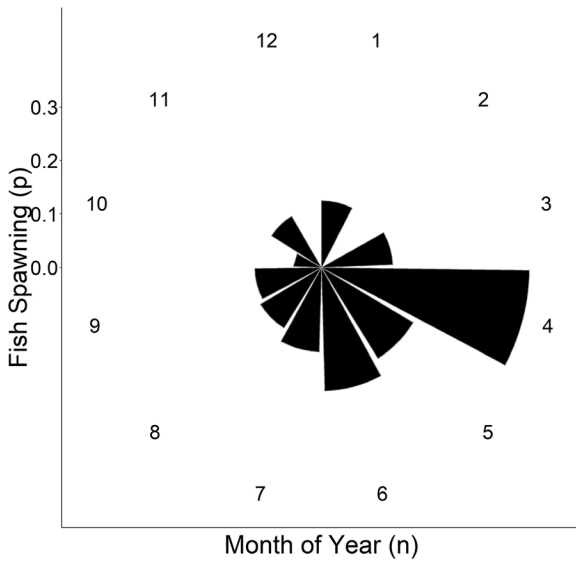
A network analysis indicated that bonefish spawning migrations coincide with the phases of the waning moon (Fig. 3). During the full moon, bonefish movements were restricted to lagoon receivers. During that period, the network was smallest, being comprised of seven out of the 16 possible nodes and nodes exhibited the highest centrality (Table 2). Following the full moon, the size and diversity of habitat use within the network increased dramatically, which is illustrated by the increasing number of nodes, edges spanning the entire atoll, occupancy of reef crest and outer reef oceanic habitats, increasing receiver betweenness, and decreasing centrality throughout the duration of the waning moon (Table 2, Fig. 3). Typically, these migrations began during the waning gibbus moon at approximately 92–85% lunar illumination as bonefish formed a large pre-spawning aggregation immediately adjacent to Tukahora village. The increasing node weight of the receivers located on the lagoon side of the trap complex illustrates the movements of bonefish aggregations into this migratory corridor (Fig. 3).

We actively tracked the fine scale movements of these pre-spawning aggregations on two separate occasions June 12th, 2017 and May 2nd, 2018 (Fig. 4). In both cases, tracking events occurred 3 days after the full moon on 90% and 92% lunar illumination and the aggregations were estimated to contain several thousand individuals that were observed periodically “porpoising” at night fall, as they presumably filled their swim bladders with air in preparation for spawning (Danylchuk et al. 2011, 2018). This pre-spawning

**Table 1** Tagging and detection summary data for 43 bonefish tagged with V13 coded acoustic tags at Anaa Atoll (all fish marked with an asterisk (\*) were excluded from the analysis due to being immediately recaptured in the artisanal fishery or low detection spans)

Fish ID	Date tagged	Sex	FL	Date first detected	Date last detected	Total detections	Total days	Total receivers	Detection span
ALGL1*	5/13/2017	M	48	–	–	0	0	0	–
ALGL2*	5/13/2017	F	58	6/11/2017	6/14/2017	435	4	3	3
ALGL3	5/13/2017	M	51	12/30/2017	6/3/2018	2045	18	9	155
ALGL4	5/16/2017	F	59	6/6/2017	5/3/2018	19,400	189	6	331
ALGL5*	5/16/2017	F	59	–	–	0	0	0	–
ALGL6*	5/16/2017	M	44	–	–	0	0	0	–
ALGL7*	5/16/2017	M	51	–	–	0	0	0	–
ALGL8	5/16/2017	F	53	6/8/2017	6/30/2018	1253	39	8	387
ALGL9*	5/17/2017	F	54	5/18/2017	5/19/2017	114	2	1	1
ALGL10*	5/17/2017	F	61	–	–	0	0	0	–
ALGL11	5/17/2017	F	56	5/27/2017	3/1/2018	9408	199	6	278
ALGL12*	5/17/2017	M	47	–	–	0	0	0	–
ALGL13*	5/17/2017	F	50	–	–	0	0	0	–
ALGL14	5/17/2017	F	60	5/18/2017	5/1/2018	20,951	244	3	348
ALGL15*	5/17/2017	F	60	–	–	0	0	0	–
ALGL16	5/17/2017	M	46	6/8/2017	6/28/2018	1966	80	5	385
ALGL17	5/17/2017	M	47	5/30/2017	4/5/2018	681	53	6	310
ALGL18*	5/17/2017	F	55	–	–	0	0	0	–
ALGL19*	5/17/2017	M	46	–	–	0	0	0	–
ALGL20	5/17/2017	M	46	5/18/2017	12/7/2017	286	40	4	203
ALGL21*	5/17/2017	F	51	–	–	0	0	0	–
ALGL22	5/19/2017	F	58	5/20/2017	3/8/2018	926	20	5	292
ALGL23	5/19/2017	M	52	6/4/2017	2/21/2018	4071	102	8	262
ALGL24	5/19/2017	F	52	10/25/2017	6/10/2018	51	26	3	228
ALGL25	5/19/2017	M	47	6/7/2017	7/5/2018	3553	79	6	393
ALGL26	5/19/2017	M	52	5/19/2017	6/4/2018	3034	88	7	381
ALGL27	5/19/2017	M	48	5/19/2017	7/8/2018	2253	75	6	415
ALGL28	5/19/2017	M	47	12/23/2017	1/5/2018	17	4	3	13
ALGL29	6/13/2017	F	65	6/13/2017	4/5/2018	544	4	7	296
ALGL30	7/1/2017	F	60	7/1/2017	4/4/2018	125	3	4	277
ALGL31	7/1/2017	F	59	7/1/2017	7/15/2017	659	14	6	14
ALGL32	7/1/2017	F	56	7/1/2017	7/3/2018	1852	69	7	367
ALGL33	7/1/2017	M	46	7/14/2017	7/7/2018	3368	86	7	358
ALGL34	7/1/2017	M	51	7/1/2017	7/5/2018	11,066	189	14	369
ALGL35*	7/3/2017	F	67	7/3/2017	7/4/2017	4	2	2	1
ALGL36	7/3/2017	F	69	7/16/2017	10/5/2017	948	25	2	81
ALGL37	7/13/2017	M	49	7/13/2017	7/7/2018	1643	51	7	359
ALGL38	7/13/2017	M	51	7/14/2017	7/9/2018	3179	95	8	360
ALGL39	7/13/2017	F	68	7/13/2017	11/13/2017	2608	50	8	123
ALGL40	8/24/2017	M	50	8/25/2017	10/21/2017	102	7	2	57
ALGL41	11/7/2017	M	47	12/15/2017	1/6/2018	81	6	4	22
ALGL42	4/12/2018	M	52	4/12/2018	6/18/2018	4149	45	9	67
ALGL43	6/19/2018	M	50	6/20/2018	7/9/2018	248	9	6	19





**Fig. 2** The proportion of tagged bonefish that undertook migrations to oceanic spawning habitats across the month of the year

staging site was used by all of the bonefish that were subsequently detected on outer reef receivers during these two spawning migrations, suggesting that this location is the primary gathering site prior to dispersing throughout the atoll’s two principal spawning movement corridors at Tukahora village and Hoa Hagarai (Fig. 1). During both pre-spawning events, the locations of the aggregation exhibited spatial overlap, with an IOR of 0.21 for the minimum convex polygons of the two tracks (Fig. 4) and on both occasions catches numbering up to 1000 fish were recorded in the artisanal trap fishery throughout the following day as bonefish began to traverse the trap complex (Fig. 1) to access oceanic spawning habitats 4 days after the full moon (Online Resource 1). Histology samples taken from

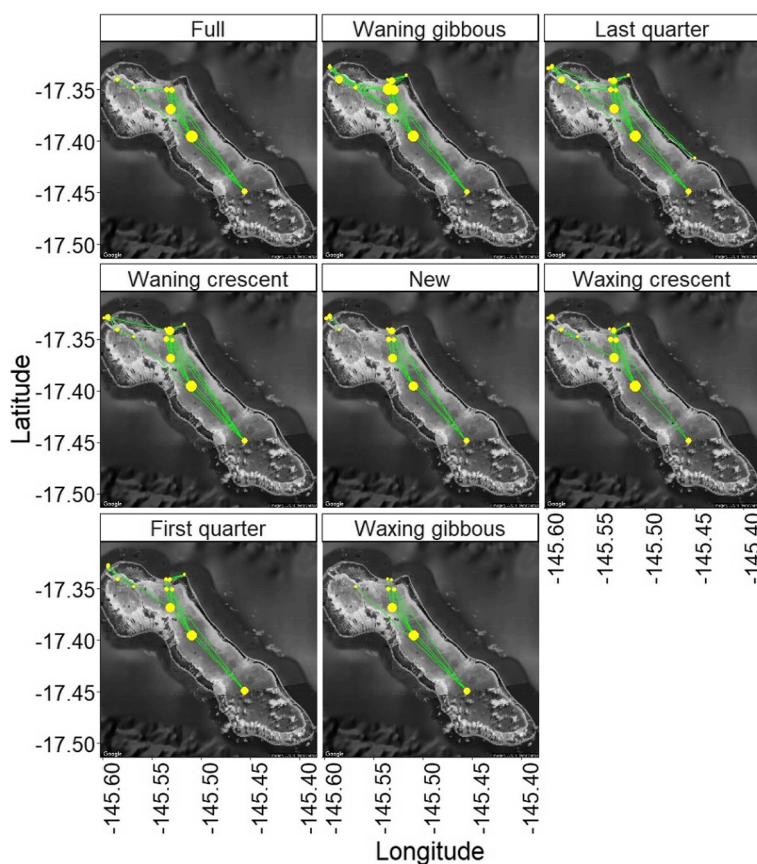
bonefish harvested in the fishery on the mornings following these tracking events indicated that the primary cohort of oocytes in females had developed into vitellogenic stage 3 (Fig. 5a). These out-migrating fish are locally referred to as “*kiokio hopaki*” and distinguished by a light grey coloration, stout body mass, and ripe eggs characteristic of bonefish on the spawning migration.

On the fourth day after the full moon, bonefish aggregations move from the lagoon pre-spawning aggregation site described above through the shallow back reef adjacent to Tukahora village or through the Peti-lagoon to Hoa Hagarai to access the pre-spawning aggregation sites on the backreef (Online Resource 1). These aggregations generally moved in waves every two hours and often circled back and forth between the lagoon and backreef where they are vulnerable to harvest in the artisanal fish traps. After traversing the trap complex, the pre-spawning aggregation staged in a backreef refuge just inside of the passes to the open ocean while waiting for nightfall to exit the atoll and ostensibly spawn in the pelagic environment (Fig. 6). We observed three species of reef shark: *Triaenodon obesus*, *Carcharhinus melanopterus*, and *C. amblyrhynchos*, actively pursuing bonefish spawning aggregations inside of the backreef refuge (Online Resource 1). In some cases, on the fourth day after the full moon, bonefish aggregating in this passageway returned to the lagoon pre-spawning aggregation site and came back to this backreef pre-spawning aggregation site the following day to spawn 5 days after the full moon. These gravid fish staging on the backreef are characterized by oocytes in the advanced stages of maturation, including

**Table 2** Summary of network characteristics for the eight lunar phases

Phase	Node count	Mean distance	Edge density	Mean (sd) betweenness	Mean (sd) closeness
Full	7	1.69	0.69	7.43 (7.16)	0.03 (0.02)
Waning gibbous	13	2.02	0.40	17.40 (16.62)	0.02 (0.01)
Last quarter	15	2.51	0.32	32.73 (29.40)	0.01 (0.00)
Waning crescent	14	2.91	0.30	30.86 (29.76)	0.02 (0.00)
New	12	1.78	0.29	5.39 (4.90)	0.01 (0.00)
Waxing crescent	14	2.05	0.26	9.32 (10.14)	0.01 (0.00)
First quarter	13	2.00	0.26	8.62 (12.87)	0.01 (0.00)
Waxing gibbous	8	1.75	0.41	6.69 (4.68)	0.03 (0.00)

**Fig. 3** A unipartite plot of bonefish detections in the acoustic array across the eight phases of the lunar cycle, overlaid on georeferenced satellite imagery. Yellow dots represent receivers scaled to their corresponding node weights, and green lines indicate edges which represent movements between nodes (note the differing scale of the nodes across the lunar cycle)

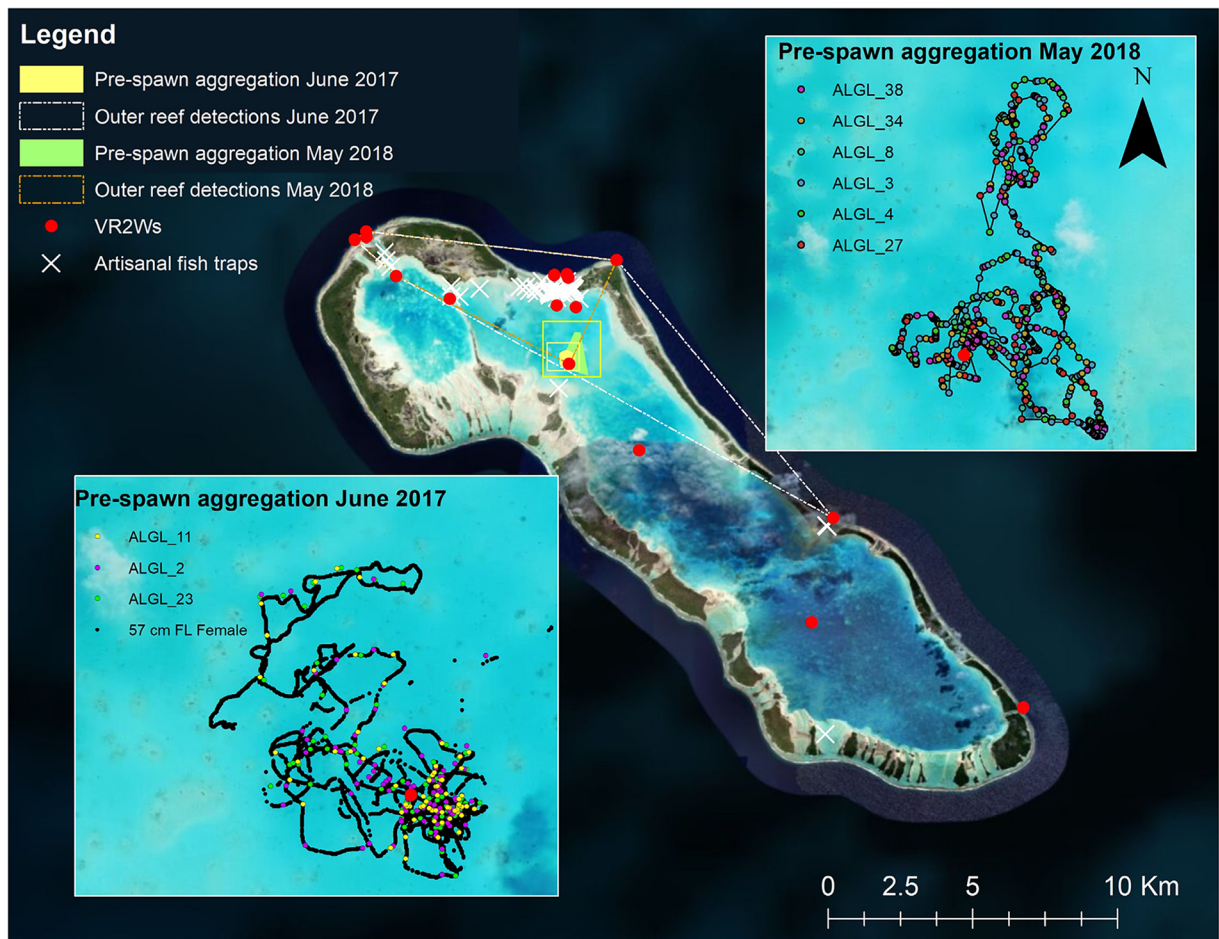


geminal vesical migration, geminal vesical break down (Fig. 5b), dilated cloacae and can be distinguished by a darker coloration on the dorsal side of the body as their chromatophores adapt to camouflage in the oceanic environment.

During these circulating movements in and around the trap complex, bonefish were often observed “ventral nudging” and “porpoising” (Danylchuk et al. 2018) suggesting that the back and forth movements between the backreef and lagoon are a pre-spawning courtship behavior. The movements of bonefish from shallow refuges in the backreef, to the open ocean follow the diel cycle, as bonefish were detected moving offshore during nocturnal hours, with 99% of the overall detections offshore occurring at night and 90% of the detections on the backreef occurring during daylight hours (Fig. 7). The mixed-effects logistic regression indicated that the observed differences in the presence of bonefish in these two habitats between night and day are significant ( $P < 0.005$ ). Peaks in bonefish activity on the reef crest and outer reef occurred 3–5 days after the full moon and at approximately 85–70% lunar illumination

( $\mu = 0.73$ ,  $\rho = 0.99$ ; Fig. 8). The mean lunar illumination of bonefish detections in the spawning habitats was non-uniform, suggesting that the observed patterns are cyclical ( $\bar{r} = 0.56$ ,  $P < 0.005$ ). After spawning, bonefish begin their return migration from the backreef refuges back through the trap complex into the lagoon habitats during the last quarter moon phase. These returning fish are referred to as “*kiokio tua*” by local fishers when they are captured in their traps; these post-reproductive fish are distinguished by a dark coloration, skinny body type, and females with spent ovaries, characterized by post ovulatory follicles (Fig. 5c).

An analysis of the diel scatter plots suggests that males engage in spawning migrations and presumably spawn more frequently than females throughout the course of the reproductive season. For example, an illustration (Fig. 9) depicts the movements of ALGL11, a 56 cm FL female bonefish; this fish left its lagoon habitat in the big lagoon (turquoise dots) immediately prior to the waning gibbous moon in June 2017 to aggregate before the trap complex adjacent to Tukahora village (green dots, this fish was present in the spawning



**Fig. 4** The movements of a 57 cm female bonefish on June 12th, 2017, while associating with a large bonefish pre-spawning aggregation the day before migrating through the trap complex. The aggregation was estimated to be 2000 in number and the passive tagged fish ALGL\_23, ALGL\_2 and ALGL\_11 were present in the aggregation. The movements of ALGL\_38, ALGL\_34,

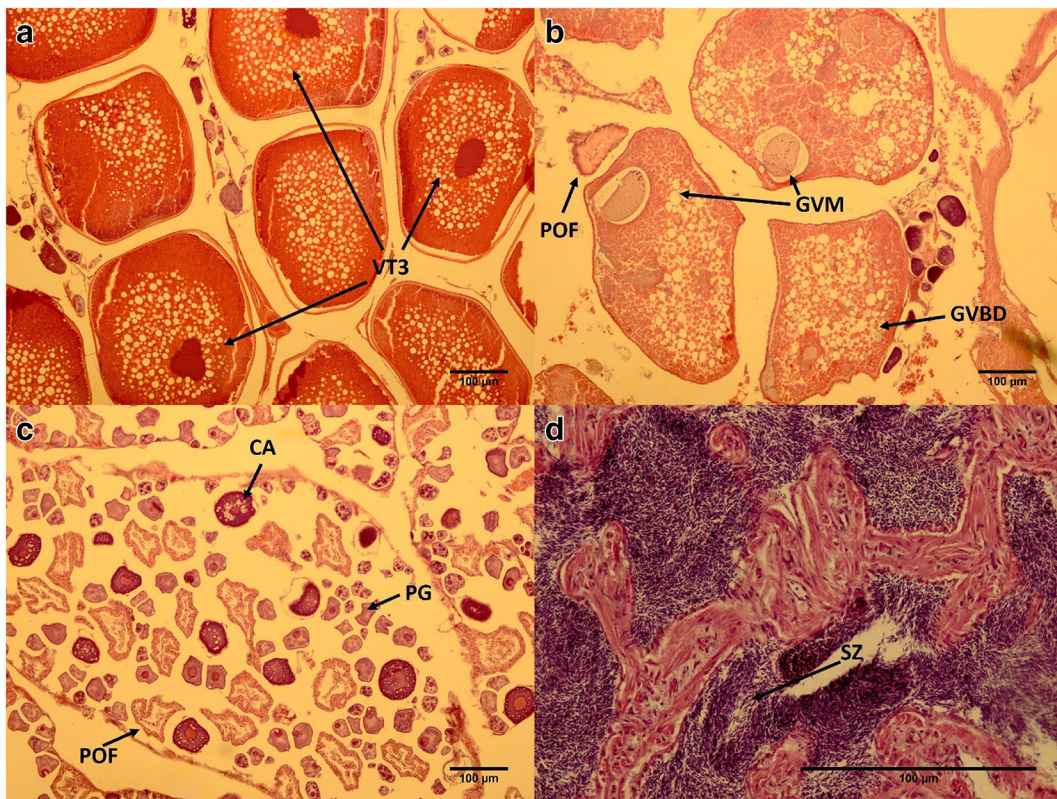
ALGL\_8, ALGL\_3, ALGL\_4, and ALGL\_27 in the pre-spawning aggregation tracked the following year on May 2nd, 2018. In both cases respectively all fish were subsequently detected on outer reef receivers enclosed in the white and orange dashed polygons during the days following the tracking event

aggregation depicted in Fig. 4), after being detected in the pass on the back reef adjacent to Tukahora village (red dots), it was redetected the same night outside the passage at Areavete (navy-blue dot), a minimum movement of 12 km along the outer reef where it presumably re-entered the lagoon and remained for the duration of the year. In contrast, ALGL26 a 52 cm FL male, made multiple repeated migrations to back and outer reef spawning habitats (red and black dots) during each waning gibbous moon for the duration of the 2017 season. This pattern was consistent between male and female bonefish and the number of days present on the spawning habitats were drastically different, even with outliers removed (i.e., ALGL 34 a male who spent

147 days in the spawning habitats and was recaptured twice over the duration of the study). The negative binomial generalized linear model indicates that the difference in the number of days on the spawning habitats between male and females is statistically significant ( $P < 0.005$ ), with males spending  $11 \pm 1.6$  se days and females spending  $3 \pm 1.5$  se days on the spawning habitats.

### Discussion

Our results provide a unique understanding of the spatiotemporal dynamics of the spawning migrations of an



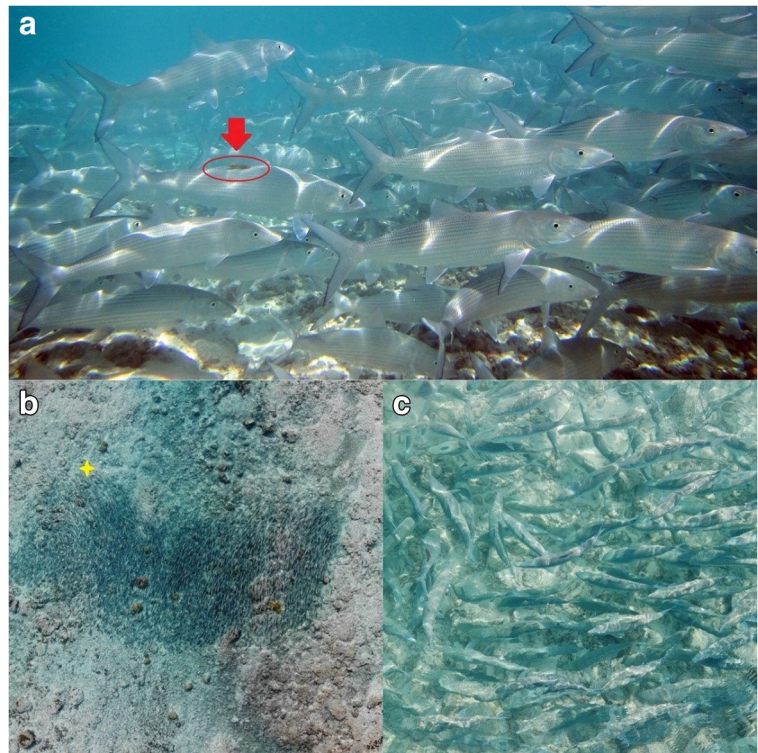
**Fig. 5** Histology samples stained with Hematoxylin and Eosin, that were taken from bonefish in various stages of their spawning migration. Panel A is a mature spawning capable 59 cm FL female harvested in the artisanal fish traps during the initial pulse of a spawning migration on June 13th, 2017 (see Fig. 4), that coincides with the start of the actively spawning subphase (VTG3 = tertiary vitellogenic oocyte, 10x magnification), panel B is a mature spawning capable 61 cm FL female undergoing oocyte maturation and hydration that was netted from a spawning aggregation in the backreef refuge while in association with ALGL 26, a 52 cm FL male on August 14th, 2017 (see Fig. 9). Their aggregation depicted in Fig. 6a was staging in the passage on the seaward side

of the trap complex several hours before spawning (GVM = germinal vesicle migration, GVBD = germinal vesicle breakdown, POF = postovulatory follicles, 10x magnification), and panel C is a mature 58 cm FL female that is regressing (i.e., spent) and was harvested in the artisanal fish traps while in association with ALGL 34, a 51 cm FL male on September 25th, 2017, while returning from spawning (PG = primary growth oocyte, CA = cortical alveolar oocyte, 10x magnification). Finally, panel D is a 50 cm FL mature male harvested in the artisanal fish traps during a spawning event (see Fig. 4) on June 13th, 2017 (SZ = spermatozoa, 40x magnification)

economically important and vulnerable *Albulid* and their interaction with an artisanal fishery. The movement patterns of bonefish described in this study represent those of a spawning aggregation, defined by Domeier (2012) as high densities of reproductively mature individuals predictably aggregating in space and time with movement to locations and habitats that are distinct from their normal home range, and the readiness of individuals associated with the aggregation to spawn (Domeier 2012; Adams et al. 2018). Although we did not physically observe the act of spawning, all the female bonefish we subsampled during tracking events exhibited oocyte development that was consistent with their movement to and from oceanic habitats where

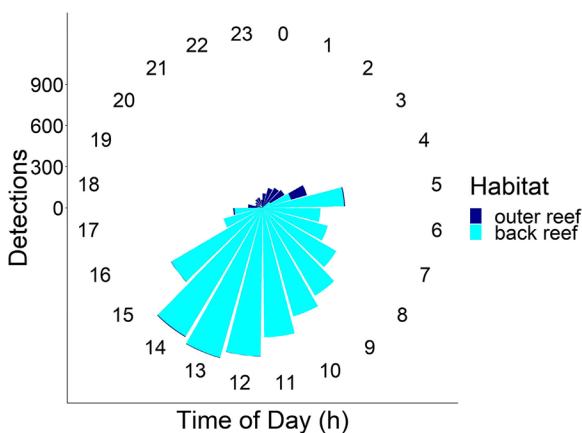
spawning is believed to have occurred (i.e. gravid late vitellogenic stage fish moving towards the ocean and spent fish returning from the ocean to the lagoon). Furthermore, bonefish that were subsampled in association with acoustic tagged fish which were staging in back reef habitats before night fall, were undergoing germinal vesicle breakdown immediately prior to being detected on the outer reef. Germinal vesicle breakdown is the final stage of oocyte development prior to hydration, which had never been documented in *Albulids* and this finding suggests that spawning was imminent and likely occurs in the oceanic environment (Crabtree and Harnden 1997; Brown-Peterson et al. 2011; Luck et al. 2018; Filous et al. 2019c).

**Fig. 6** Underwater (a) and aerial (b, c) images of bonefish spawning aggregations that have traversed the trap complex and are waiting for night fall in their backreef refuge, to exit the atoll and spawn in the pelagic environment (the yellow star indicates the location of a VR2W acoustic receiver, depicted in the map in Fig. 1 and represented by red dot detections in Fig. 9, note the tagged fish indicated by the red arrow in panel A)



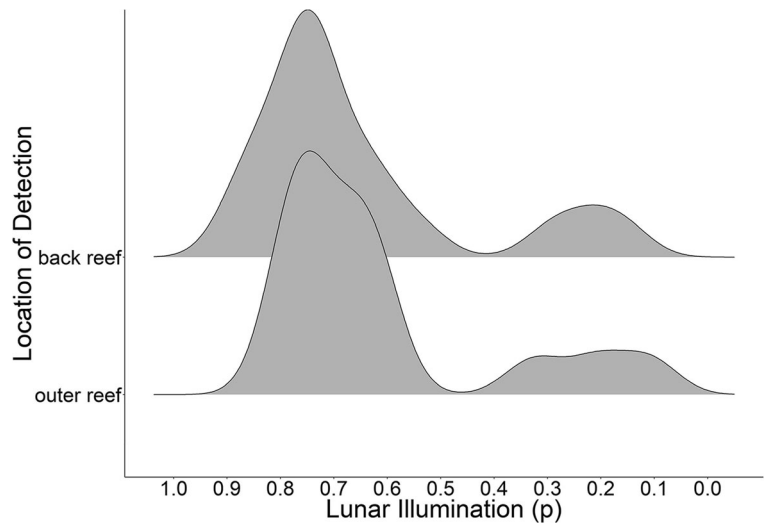
The bonefish movements we observed toward oceanic spawning habitats during the austral fall and winter paralleled the increased gonadosomatic index of male and female bonefish that was documented through large-scale sampling of bonefish harvested in the artisanal fishery by Filous et al. (2019c), and previous authors also reported protracted spawning seasons for

*Albulids* that coincide with the cooler months in their respective hemisphere (Crabtree and Harnden 1997; Danylchuk et al. 2011; Donovan et al. 2015, 2016). The frequency of tagged fish movement to oceanic spawning habitats across this time period suggest that female reproductive effort is staggered throughout the spawning season while males participate in multiple spawning events, accompanying newly developed females during each successive migration. This reproductive strategy may lead to unbalanced sex ratios in the population as males, which spawn numerous times throughout the course of the season, move through the trap complex more frequently and are likely exposed to higher levels of fishing mortality. Surveys of bonefish harvested in the artisanal fishery indicate that the monthly median sex ratio of trap catches declined from 61% to 16% female bonefish over the course of the spawning season (Filous et al. 2019b). These sexually dimorphic spawning behaviors, coupled with intense fisheries harvest during spawning events, could be responsible for the drastic differences in the age and size distribution of male and female bonefish that have been observed in this population, with males being younger on average and obtaining smaller maximum sizes than females (Filous et al. 2019b, 2019c).



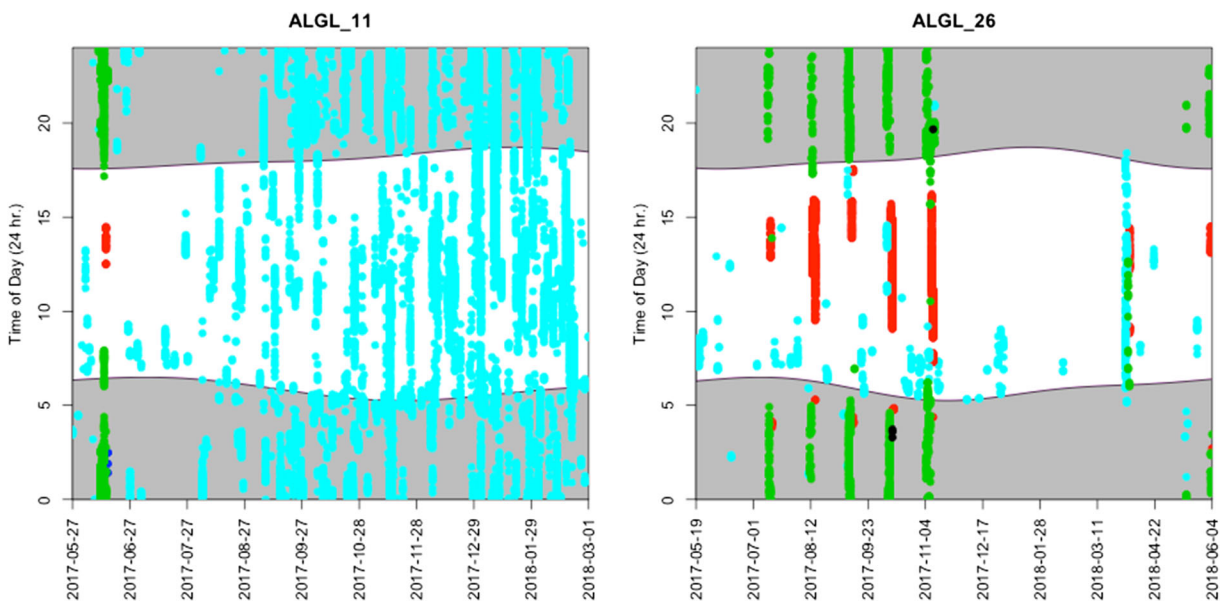
**Fig. 7** The temporal movements of bonefish spawning aggregations between shallow refuges in the backreef and open ocean (note, the y-axis is the total number of bonefish detections recorded in each habitat at a given hour of the day, based on their corresponding colors in the stacked bars)

**Fig. 8** The density distribution of bonefish detections in the shallow refuges in the backreef on the seaward side of the trap complex and the open ocean, relative to the lunar illumination (note, the y-axis represents the density distribution of the total number of bonefish detections recorded in each of the two spawning habitats at a given lunar illumination)



The effect of the lunar cycle on reproductive behavior is pervasive throughout a diverse assemblage of fishes (Johannes 1978, 1981; Taylor 1984; Takemura et al. 2004a, 2004b; Zhdanova and Reebbs 2005). Our lunar observations of these bonefish spawning migrations were strikingly similar to the traditional ecological knowledge of the species movements at Tarawa Atoll

(Johannes and Yeeting 2000). In both destinations, bonefish pre-spawning aggregations amass in close proximity to a discrete location where they migrate from the lagoon to the ocean during a specific night of the lunar month and the only discrepancy in our results is the lunar timing in the start of monthly spawning events, which in Tarawa is believed to occur during the waxing



**Fig. 9** Examples of diel scatter plots for two bonefish (ALGL\_11 a 56 cm FL female and ALGL\_26 a 52 cm FL male). Turquoise dots represent receivers located in the big lagoon, green dots represent receivers in the big lagoon that are located immediately adjacent to the trap complex where lagoon pre-spawning aggregations form prior to migrating towards the ocean, red dots indicate the receivers at the back reef refuge between the lagoon and the open ocean adjacent to Tukahora village, black dots indicate

receivers on the outer reef in the norther section of the atoll, and navy-blue dots indicate the location of outer reef receivers adjacent to passes in the southern portion of the atoll. Both the red, black and navy-blue dots are spawning habits located on the seaward side of the trap complex. Day and night shading are overlaid on the scatter plots based on the timing of sunrise and sunset over the duration of the monitoring period (note differing scales on the x-axis)

gibbous and full moon phase (Johannes and Yeeting 2000). Although smaller reproductive movements occur during the waxing moon phase at Anaa, our results suggest that the most significant reproductive events coincide with the waning gibbous moon. However, in addition to Tarawa, recent research from the Atlantic suggests that *A. vulpes* spawns during the full moon and it is possible that heterogeneity in lunar spawning stimulus could exist between species and destinations. This variability highlights the importance of site specific research when designing conservation strategies for *Albulids* (Danylchuk et al. 2011, 2018; Adams et al. 2018).

Nearly all of the spawning migrations to the outer reef were recorded by receivers outside of the atoll's northern passes at Tukahora village and Hoa Hagarai, demonstrating that these two passageways are the principle migratory corridors for the atoll's bonefish population. Spawning site selection of tropical fishes has often been linked to locations that favor the displacement of gametes and newly fertilized embryos away from the predation pressure of coral reef environments such as outer reef promontories, points, and channels that generate currents, which transfer micro-nekton to the pelagic environment (Johannes 1978; Claydon 2004; Domeier 2012). These two passageways meet this criterion as they are the only significant outlets of the lagoon and water flows seaward during all stages of the tide, thus favoring short distance dispersal of gametes release into this current from the immediate reef crest. However, exclusively long-distance displacement of developing larva could inhibit population growth on this isolated atoll (Sponaugle et al. 2002; Domeier 2004) and there is evidence to suggest neritic broadcast spawning fishes select locations with oceanic gyres to increase the likelihood of self-recruitment (Johannes 1978; Basterretxea et al. 2013). The geomorphology of the atoll, its orientation, and the prevailing wind and swell direction from the southwest, suggest that in theory a stable eddy pair, could exist on the down current (northeast) side of Anaa, where bonefish spawning aggregations are found, thus facilitating self-recruitment in this isolated ecosystem (Johannes 1981). This behavior has been observed among *A. vulpes* (Danylchuk et al. 2011) and we hypothesize that the combination of both outflowing currents to disperse larva short distances away from the immediate reef and an oceanic gyre to retain a

proportion of larva within settling range of the atoll at the time of metamorphosis makes these two passageways at Tukahora village and Hoa Hagarai important spawning habitat. However, regardless of the potential environmental drivers of this phenomenon, the absence of bonefish spawning aggregations in the passages located in the southeast of the atoll highlights the need for management of the artisanal trap fishery.

#### Management implications

Over the twentieth century, the loss of traditional management, anthropogenic development and introduction of new fishing technologies has led to the over exploitation of *A. glossodonta* in locations where it co-occurs with human inhabitants throughout the Indo-Pacific (Beets 2000; Friedlander et al. 2007, 2015; Bunce et al. 2008; Adams et al. 2013; Allen 2014; Wallace 2015). Consequently, the findings of this research provide an important perspective on the spawning behavior of this species and shed light on how these fisheries can be managed to moderate the effect of harvesting this species during this vulnerable stage of its life history.

Collectively, this work demonstrated that a significant proportion of the bonefish spawning stock moves through two migratory passageways where it is subjected to intense fishing pressure. Over 90% of the atoll's artisanal trapping effort is exerted in this region, suggesting that all the available migratory corridors are heavily fished throughout the duration of the spawning season. History suggests that the practice of harvesting bonefish prior to spawning is unsustainable (Johannes and Yeeting 2000; Adams et al. 2013; Friedlander et al. 2015). For example, before western colonization, fishing spawning aggregations during their initial staging and out migration was prohibited in Tarawa, effectively allowing gravid females to reproduce before they were harvested (Johannes and Yeeting 2000). However, with the demise of this traditional management practice, the harvest of gravid females in the ensuing years has been partially attributed to the collapse of this fishery (Beets 2000; Johannes and Yeeting 2000; Ram-Bidesi 2011).

Congruently, the declining bonefish population on Anaa Atoll is likely a consequence of overexploiting their spawning aggregations and management is essential to ensure the fishery continues to provide sustainable yields into the future (Filous et al. 2019a, 2019b, 2019c, 2019d). The community of Aitutaki Atoll faced similar

challenges to the management of their bonefish spawning aggregations. In response to a decline in their bonefish population and the economic opportunities presented by fly-fishing tourism, the government enacted the Marine Resources (Aitutaki and Manuae Bonefish Fishery) Regulations of 2010, which prohibited fishing in bonefish spawning aggregation sites 3 days before and 3 days after the new moon, prohibited gillnetting in spawning aggregation sites and prohibited the commercial sale and or export of bonefish (Cook Islands Government 2010). However, the reality of life in Anaa and other less developed remote islands of the Pacific, is that bonefish are a food resource that contributes to the local economy and the harvest of this species is an important part of the community's cultural identity.

Consequently, we emphasize the need to strike a balance between harvest and conservation of these spawning aggregations. Given the protracted spawning season and spatiotemporal predictability of migratory events demonstrated above, a reduction in the overall number of traps and or temporary fishing closures in these migratory corridors, for 3 months of the spawning season, would be a management action to ensure the escapement of bonefish to spawn, while minimizing the regulatory cost to artisanal fishers (Heppell et al. 2012; Gruss et al. 2014; Erisman et al. 2017). To this aim, the most practical solution for the trap fishery would be to deactivate the “cod ends” of the stone traps for 3 months. However, if more liberal regulations are needed to permit the subsistence harvest of other species during these months, our results suggest that the traps could be deactivated during the waning moon phase. These nights of the moon are known on the traditional Tahitian fishing calendar as *Ra'au Mua* (92% lunar illumination), *Ra'au Roto* (86% lunar illumination), *Ra'au Muri* (70% lunar illumination), *Ore'ore Mua* (61% lunar illumination), *Ore'ore Roto* (50% lunar illumination), and *Ore'ore Muri* (42% lunar illumination). A resurgence of community-based management and the institution of a *Rahui* during these time periods would reduce fishing mortality and allow moderated harvest of this resource (Johannes 2002; Hamilton et al. 2011; Bambridge 2016; Friedlander 2018).

In addition to the threat of overfishing, this research highlights the importance of the connectivity between inter-lagoon and oceanic habitats to bonefish and the essential role these migratory corridors play in the life history of this species (Danylchuk et al. 2011; Adams

et al. 2018). Habitat modifications such a channel dredging, marina creation, and causeway construction are frequently proposed to facilitate the development of islands and other tropical marine systems (Maragos 1993; Hinrichsen 1999). Habitat modifications that directly alter the nature of spawning sites or restrict access to them, can affect the viability of bonefish populations on local and regional scales (Adams et al. 2018). One often-overlooked factor in the collapse of the bonefish population at Tarawa Atoll was the construction of a series of causeways that connected a road between the atoll's landmasses from the 1960s to 1980s. Analogous to the effect of dam construction on diadromous fish (Limburg and Waldman 2009; Mattocks et al. 2017), these causeways obstructed migratory corridors that historically permitted passage of bonefish spawning aggregations between lagoon and offshore habitats and resulted in the loss of the atoll's most prolific spawning aggregations (Beets 2000; Johannes and Yeeting 2000). This history is important to Anaa Atoll, as previous local governments have proposed dredging the primary passageway in the back reef pictured in Fig. 6, where bonefish spawning aggregations seek refuge during daylight hours, to facilitate the passage of boats and develop a marina adjacent to Tukahora village. Our results suggest that the physical characteristics of this passageway and its currents are critical for bonefish reproduction and the modification of this essential habitat could irreparably damage the ability of the atoll's bonefish population to regenerate and ultimately lead to the loss of this keystone fisheries resource.

There has been a renaissance of community-based management in Oceania and raising awareness for fisheries conservation is an essential prerequisite for the success of these endeavors (Johannes 2002; Friedlander 2018). Most communities will be unable to conduct acoustic tracking studies; however, information on the status of fish stocks and how to manage them can also be obtained from less expensive studies such as the combination of traditional ecological knowledge, conventional tagging and data limited stock assessments (Filous et al. 2019a, 2019b, 2019c, 2019d). Ultimately, sharing the results of fisheries research is invaluable for engaging communities in resource management and we recommend that scientists work with local school systems to incorporate the results of their research into fisheries conservation lessons and educate the next generations in communities like Anaa Atoll.



In response to the information and educational outreach provided by this research, the community of Anaa Atoll established an Educational Managed Marine Area that overlaps with the bonefish migratory corridor adjacent to Tukuhora village and instituted a temporal *Rahui* for the duration of the peak months of the spawning season (i.e., March, April and May) to preserve this fishery resource for future generations (<https://www.radio1.pf/anaa-a-son-aire-marine-educative/>). This management action has been perpetuated annually since 2019 and we therefore emphasize that the future of this resource is positive and investment into scientific research, education, and motivated local conservation leaders can make a significant contribution to fisheries management in a region of the world oceans that is largely overlooked by contemporary conservation efforts.

**Acknowledgements** We would like to acknowledge and thank the fishers of Anaa Atoll, who welcomed the presence of A.F. in their community. Specifically, we would like to acknowledge the help of Ruben Matai, Ganaanui Raveino, Gregory Raveino, and Teangi Willams who assisted in the maintenance of the acoustic array. Additionally, we thank Toma Teaku, Jean Dexter, Hotea Tevaitau, and Clayton Teaku for their assistance in recovering recaptured bonefish in the artisanal fish traps. We also gratefully acknowledge the assistance of Raymonde Raveino, Louise Raveino and the entire Raveino family, who cared for A.F. both on Anaa Atoll and Tahiti. These individuals provided in depth local knowledge and logistical support that was instrumental to the success of this research. We would like to thank the children at the school of Anaa Atoll and their director Jean Pierre Beaury who were indispensable in communicating the results of this work to the larger community and supporting fisheries conservation. We thank Hinano Bagnis and Mathew Mchugh for providing logistic support to this research and taking care of A.F. while he was in French Polynesia. We would also like to acknowledge the assistance of the CRIOBE (Centre de Recherches Insulaires et Observatoire de l'Environnement) and Dr. Serge Planes in obtaining research permits to work in French Polynesia. Furthermore, we would like to acknowledge the generous donation from an anonymous donor to The Island Initiative that funded this work, Indifly and Fly Odyssey who also provided extensive support for this project. A. Danylchuk is supported by the National Institute of Food & Agriculture, U.S. Department of Agriculture, the Massachusetts Agricultural Experiment Station, and Department of Environmental Conservation and is also a Bonefish & Tarpon Trust Research Fellow.

#### Compliance with ethical standards

All international, national, and institutional guidelines for the care and use of animals were followed and fish handling methods were reviewed and approved by the University of Massachusetts Amherst Institutional Animal Care and Use Committee, IACUC protocol number 2016–0049.

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