Environ Biol Fish (2019) 102:365–381
https://doi.org/10.1007/s10641-019-00850-1

Movement and predation: a catch-and-release study on the acoustic tracking of bonefish in the Indian Ocean

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Received: 15 July 2018 / Accepted: 21 January 2019 / Published online: 30 January 2019

Abstract Tourism generated through bonefish (*Albula* spp.) fishing contributes to the economies of many isolated tropical islands and atolls. However, little research has been conducted on bonefish in the Indian Ocean. This study aimed to contribute to the understanding of bonefish ecology in the Indian Ocean by quantifying the spatial and temporal movements of *Albula glossodonta* at a near-pristine and predator-rich atoll in the Seychelles; however, to achieve this, an analysis to identify the occurrence of possible post-release predation bias was first necessary. An acoustic telemetry study was initiated at the remote St. Joseph Atoll, within an array of 88 automated data-logging acoustic receivers. Thirty bonefish were surgically implanted with Vemco V13 acoustic transmitters and tracked for one year. Only 10% of the tagged bonefish were detected for longer than two weeks. A comparison of the final 100 h of movement data from fish detected for less than two weeks to the movement data of the fish detected for longer periods revealed distinct differences in area use and significant differences in the average daily distance moved, speed of movement and frequency of detections. This suggested that mortality in the form of post-release predation was at least 43% of tagged fish. The three surviving bonefish were tracked for 210 to 367 days. These individuals remained in the atoll and showed high use of the marginal habitats between the shallow sand flats and the lagoon. A generalised linear mixed model identified that water temperature, diel cycle and tide were significant predictors of bonefish presence in the lagoon. The high post-release mortality highlights that catch-and-release is likely not as benign as previously believed and management and policy should be adjusted accordingly.

Keywords Acoustic telemetry · Bonefish · Catch-and-release · Indian Ocean · Predation bias

Introduction

Bonefish (Genus *Albula*) occur worldwide in tropical and subtropical areas and support valuable recreational fisheries (Levesque 2011; Fedler 2013). Their agility, strength and speed have given them a reputation as a highly prized sport fish (Murchie et al. 2009). Anglers targeting bonefish generally practice catch-and-release angling (Danylchuk et al. 2007a), a practice that is commonly regarded as an economically profitable and ecologically sustainable form of ecotourism (Humston et al. 2005). However, this industry is

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threatened by reported declines in bonefish stocks in several areas (Ram-Bidesi 2011; Frezza and Clem 2015; Santos et al. 2017).

Possible reasons suggested for the decline in bonefish stocks include pollution, habitat destruction and uncontrolled tourism (specifically recreational angling) (Debrot and Posada 2005; Murchie et al. 2015; Brownscombe et al. 2018). Bonefish are dependent on coastal sand flats and are therefore vulnerable to pollution and urban development in coastal areas (Szekeres et al. 2014). While the fisheries for these species are usually catch-and-release only, catch-and-release does not always ensure the survival of a fish post release (Brownscombe et al. 2017b). Bonefish are particularly susceptible to post-release predation, especially in areas with high densities of sharks (Humston et al. 2005; Danylchuk et al. 2007b). Post-release survival of bonefish depends on factors such as the capture environment (e.g. temperature), capture method (e.g. fishing gear and fight time) and handling practices (such as air exposure time) (Bartholomew and Bohnsack 2005; Cooke et al. 2013). Poor handling practices have been found to increase the likelihood of post-release predation; however, even with best handling practices, mortality estimates in bonefish studies range from 15% to 100% (Colton and Alevizon 1983b; Humston et al. 2005; Friedlander et al. 2008). Therefore, the vulnerability of bonefish to catch-and-release fishing requires further exploration, which in turn calls for an improved understanding of the species' ecology, in particular movement behaviour.

Movement studies are known to aid in the identification of suitable management methods for effective conservation of species (Dresser and Knieb 2007; Cowley et al. 2008; Revuelta et al. 2015). Acoustic telemetry has become a popular tool to study fish movement behaviour, as it provides accurate long-term positional data and is relatively simple to use in offshore and coastal environments (Biesinger et al. 2013). Using acoustic telemetry to track movement behaviour continuously, it is also possible to assess long-term post-release survival or mortality rates (Byrne et al. 2017). However, as study animals are equipped with surgically implanted transmitters, acoustic telemetry studies are susceptible to predation bias, which occurs when a tagged animal is preyed upon and the acoustic transmitter is ingested by the predator, resulting in the transmitter representing the movements of the predator as opposed to those of the original study animal (Gibson et al. 2015). Although a predation event cannot be proven unless directly observed (Brownscombe et al. 2013), sometimes when such a predation event occurs soon after release, a conspicuous change in movement may provide some evidence of post-release predation.

To reduce the impacts of recreational catch-and-release angling on bonefish, further information is required to facilitate their improved management. Little information is currently available on bonefish species in the Indian Ocean, despite the species supporting recreational angling in several countries (for example the Seychelles, Mauritius and Reunion) (Wallace 2015). Therefore, this study aimed to contribute to the knowledge on bonefish ecology in this region.

The St. Joseph Atoll, is a near-pristine, remote and uninhabited atoll in the Western Indian Ocean that supports a high density of bonefish *Albula glossodonta* that are subjected to comparatively low angling pressure. The atoll is home to a high density of sharks, mostly sicklefin lemon sharks *Negaprion acutidens* and blacktip reef sharks *Carcharhinus melanopterus* (von Brandis 2012; Filmalter et al. 2013). Given that bonefish are vulnerable to shark predation (Brownscombe et al. 2013; Murchie et al. 2013) and the high density of sharks in the atoll, a post-release predation event on acoustically tagged bonefish was probable during this study. The aim of this study was to analyse bonefish movements; however, to achieve this, an analysis to identify the occurrence of possible post-release predation bias was first necessary.

Methods

Study area

The St. Joseph Atoll is a remote, privately-owned atoll located on the Amirantes Bank, Seychelles (Fig. 1). Most ecological processes are in some way governed by the tides. At low tide, a large portion of the atoll is exposed, severely limiting

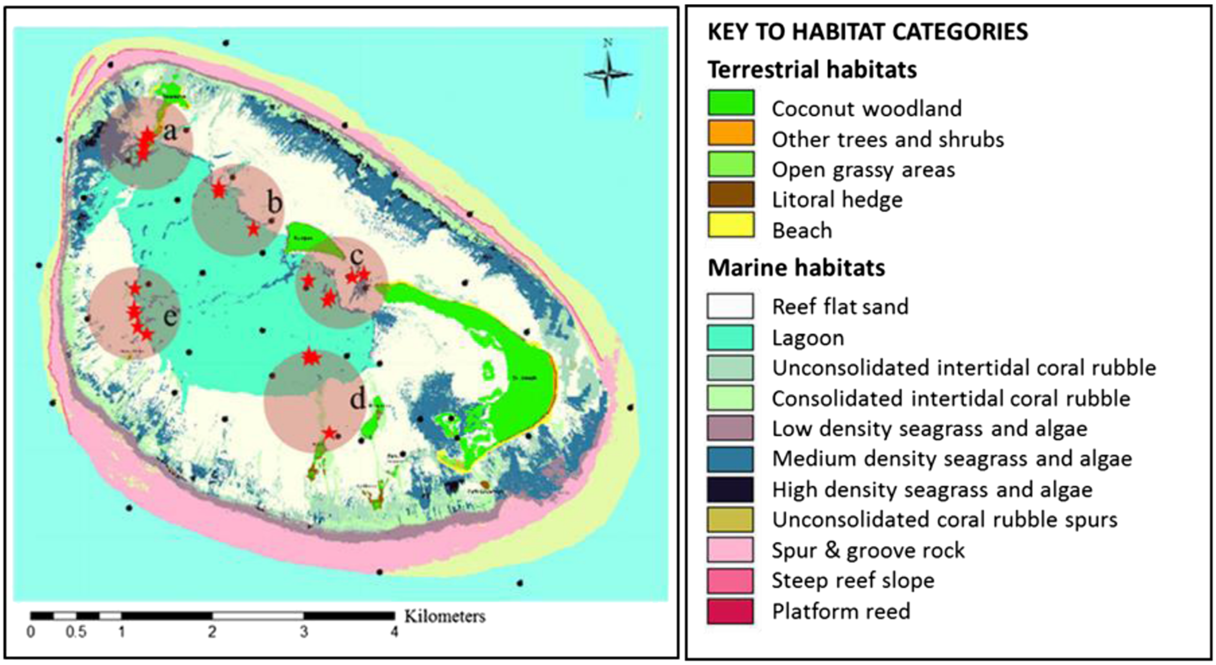

Fig. 1 Study site of acoustically tagged bonefish (*Albula glossodonta*) in the St. Joseph Atoll, Seychelles. Black dots represent the locations of the 41 acoustic receivers stationed in and around the St. Joseph Atoll (the remainder are dispersed along the Amirantes Bank). (b) Shaded red circles display the five tagging areas, with each letter referring to a separate tagging location. Stars show the release locations of the 30 acoustically tagged bonefish ($n = 6$ per location). Base maps adapted from Spencer et al. (2009)

the amount of tidal flats habitat available for aquatic animals (von Brandis 2012). The lagoon has a maximum depth of about 6.5 m, and the maximum tidal range is approximately 2 m (Stoddart et al. 1979). As there is no dominant channel into the atoll, water spills in and out over the encircling reef flat as the tides rise and fall (Filmalter 2011).

Acoustic telemetry study

The St. Joseph Atoll and surrounding area was equipped with an array of 88 omnidirectional single channel acoustic receivers (model VR2W, Vemco Ltd., Halifax, Canada). Within the atoll, receivers were deployed both on the shallow water reef flat and within the lagoon ranging in depth from 0.2 m to 6 m; depending on the location and tidal phase. The atoll has a variety of different marine habitat types including reef flats, seagrass beds, coral rubble and lagoon environments (Fig. 1). Care was taken during the placement of the acoustic receivers to ensure that the different habitats were adequately represented. However, certain areas of the sand flats could not host a receiver due to complete exposure at low tide, thus limiting acoustic coverage in this habitat.

Thirty bonefish were captured using hook and line from 4 to 9 May 2015 and surgically equipped with V13-1 L transmitters (Vemco Ltd.; random nominal delay 80 to 160 s, 69 kHz, 153 dB, estimated battery life 1118 days, 6 g in water, 13 mm diameter, 36 mm length). Six specimens were tagged at five selected locations around the atoll (Fig. 1). Fish were landed using a soft mesh, knotless dip net. Once the hook was removed, fish were transferred to an isolated keep-pen filled with fresh sea water. Here, a wet cloth was placed over the head and eyes and the fork length (FL) was measured to the nearest millimetre. Acoustic transmitters were surgically implanted following the methods of Humston et al. (2005). After surgery, an anti-bacterial gel was applied to the wound to minimise infection. For the release procedure, the surrounding waters were assessed for the presence of predators and once deemed 'safe' the fish was released from the keep-pen. If the area was deemed 'unsafe', meaning there was an abundance of predators, the fish was moved while contained in the keep-pen to an area nearby. Once the fish was released, visual observations were made for about three minutes to assess if the tagged fish had been predated. From the time that the fish was hooked until released, the procedure took an average time of 00:10:42. Air exposure was kept to a minimum during the entire process.

Data analysis

Passive acoustic tracking data were downloaded from the acoustic receivers in November 2015 (six-month receiver download) and again in May 2016 (twelve-month receiver download). The data obtained from the six-month download were analysed to investigate post-release predation bias. The data obtained from the 12-month download were analysed to assess the movement behaviour of bonefish that were not subjected to predation bias.

Assessment of predation bias

Detection data revealed that the number of tracking days varied considerably among individuals, ranging from zero to 204 days (Appendix Table 4). Further analysis revealed that of the 30 fish tagged, six (20%) were never detected and four (13%) were detected almost exclusively on a single receiver, hence yielded no movement data. An additional four fish were detected less than 75 times in total over their respective tracking periods and yielded limited movement data. Therefore, these 14 individuals were excluded from the analyses and the evaluation of predation bias was conducted on the remaining 16 individuals (Appendix Table 4). Before analysis, the detection data were filtered to remove all false detections. The first 48 h of data after release were excluded to avoid potential effects of capture and surgery (Kreiberg 2000). Single detections more than 30 min apart were considered false detections (Clements et al. 2005) and thus deleted. Where two detections of the same transmitter were made on the same receiver or an adjacent receiver within 30 min, the detections were retained.

To test for predation bias, the data were examined for abnormal behaviour. Abnormal behaviour in this study is defined as behaviour significantly different to observed bonefish movement patterns (see later). If a tagged bonefish was predated, then abnormal behaviour may be evident in the detection data for that transmitter, during the period of gastric tracking (while the transmitter is retained in the gastric tract of the predator). Literature suggests an average gastric retention time of acoustic transmitters ingested by sharks of three to six days (McKibben and Nelson 1986; Economakis and Lobel 1998). Therefore, by comparing the movement behaviour from the last 100 h (~ four days) of those fish that appeared to have suffered predation bias to that of fishes considered to be surviving bonefish (i.e. long-term retention of transmitters), we could quantify the level of possible predation bias.

Based on the tracking duration of the 16 individuals, two distinct groups were identified. Category 1 included 13 fish (fish 4, 5, 6, 9, 13, 15, 17, 20, 23, 26, 28, 29 and 30) with less than two weeks of tracking data and Category 2 included three fish (fish 14, 19 and 27), which were tracked for the entire six months. The latter three fish were assumed to be surviving individuals displaying bonefish behaviour. To test for differences in movement behaviour, the final 100 h (or part thereof) from Category 1 fish were compared to the full datasets of the Category 2 fish. The final 100 h from Category 2 fish were excluded to discount possible predation bias for these individuals. The aspects of movement that were compared included: spatial distribution, average distance moved per day, average speed and frequency of detection.

Spatial distribution: Area use by the tagged fish was plotted in ArcView 10.2 (Environmental Systems Research Institute Inc., Redlands, California). Movements were approximated using lines to connect the receivers visited (with reference to the sequence of movement). Depending on the region of the atoll in which the majority of the detections took place (namely the lagoon or the sand flats), the movements were classified as (a) predominantly detected on the sand flats (> 80%), (b) predominantly detected in the lagoon (> 80%) or (c) detections approximately evenly distributed between the lagoon and the sand flats (50% ± 10%).

Average daily distance: The cumulative distance (km) between consecutive receivers on which each fish was detected was calculated for each day, and then averaged across the total number of days that the fish was detected within the array, to provide an index of average daily distance travelled ($km.day^{-1}$).

Average movement speed: Where multiple receivers were visited within a 30-min time frame, fish speed ($m.s^{-1}$) was estimated by dividing the distance (m) between the two receivers by the time (s) between detections on the two receivers.

Frequency of detections: A residency index (RI) was calculated for each tagged fish, by dividing the total number of days that the transmitter was detected at any receiver within the array by the total number of monitored days until final detection (Abecasis and Erzini 2008). Residency index was expressed as a proportion from 0 (lowest, completely absent) to 1 (highest, detected every day).

Clustering of three of the above movement metrics (average daily distance, average speed and RI) was used to distinguish between individuals that were subject to predation bias and those that were not. Clustering was analysed in Primer-E (Ltd.; 7.0.10) using non-metric multidimensional scaling (nMDS) (Shepard 1962; Kruskal 1964). Similarities between metrics were identified through MDS ordination and hierarchical cluster analysis (Bray-Curtis similarity coefficient). The stress value indicated the goodness-of-fit of the model fitted to the observed data. Stress values less than 0.1 were considered good, 0.1 to 0.2 as potentially useful, and greater than 0.2 as arbitrary (after Clarke and Warwick 2001).

Mann-Whitney U tests were used to test for statistical differences between fish in Category 1 and Category 2 (Wilcoxon 1945; Mann and Whitney 1947), for the three metrics average daily distance travelled, average speed and RI. Tests for normality and homogeneity of variance (normal distribution of residuals) (Shapiro and Wilk 1965; $p < 0.05$), standard error skewness ($-1.96 < x < 1.96$) (Doane and Seward 2011) and a visual inspection of probability plots and histograms showed that the data were not normally distributed. Analyses were conducted in Statistica™ (DellTM StatisticaTM, StatSoft. Inc., USA). Alpha was set at 0.05.

Bonefish movement behaviour

Analysis of bonefish movement behaviour was based on the three surviving fish (fish 14, 19 and 27) using data collected from the one-year receiver download. Area use was assessed using a minimum convex polygon (MCP) that was calculated for each fish, based on the positions of all receivers visited during their respective monitoring periods. Individual MCPs were calculated in ArcView 10.2 (Environmental Systems Research Institute Inc., Redlands, California). Habitat use was analysed by dividing the atoll into two habitats namely the lagoon environment and the sand flats. According to the location of daily detections, an abacus plot was constructed in R 3.2.1 (R Core Team 2015), with colour coded bands representing the spatial use of the atoll (lagoon, sand flats or both) on a daily scale over the tracking period.

To assess the effects of environmental variables on the presence of bonefish in the lagoon, a generalised linear mixed model (GLMM) with a binomial distribution and a log-link function was fitted to the presence-absence data. The GLMM method was chosen due to its ability to incorporate random effects (such as individual fish) and compute binomial and non-normal data or data that are subjected to autocorrelation (Bolker et al. 2009; Zuur et al. 2009). Presence or absence of detections in the lagoon was used as the response variable, water temperature (°C) on the sand flats (measured on receiver 15), tidal height (m) and diel period [day (06:00 to 17:59) or night (18:00 to 05:59)] were included as fixed effects and individual fish ID was included as a random effect. As the response variable was of the form presence (1) or absence (0), the binomial distribution was used when computing the data (Zuur et al. 2009). Models were computed in R 3.2.1 (R Core Team

2015), using the lmer function from the package lme4 (Bates et al. 2015).

Results

Assessment of predation bias

Spatial distribution

A visual assessment of space use plots in the St. Joseph Atoll revealed that plots could be separated into three groups; transmitters with (a) majority of the detections recorded on the sand flats (average ± standard deviation; SD, 89% ± 5% of detections on the sand flats and 11% ± 5% of detections in the lagoon), (b) majority of the detections recorded in the lagoon (average = 94% ± 7% of detections in the lagoon and, 6% ± 7% of detections on the sand flats) and (c) approximately even spread of detections recorded on the sand flats and in the lagoon (average = 51% ± 8% of detections on the sand flats and 48% ± 9% of detections in the lagoon) (Fig. 2). Fish that fell into Category 1 (detections for less than two weeks) were found within all three groups. Fish that fell into Category 2 (detected for more than two weeks; fish 14, 19 and 27) were all placed into group c, as the distribution of detections was approximately even (average = 45% ± 3% of detections on the sand flats and 55% ± 3% of detections in the lagoon) (Table 1). Almost all fish, except fish 5, 14, 19 and 27, were detected on one or more of the most centrally located receivers in the lagoon.

Movement characteristics

Of the 16 individuals monitored, average daily distance travelled ($km.day^{-1}$) ranged from 1.1 (±1.4) to 14.7 (±7.3), average speed ($m.s^{-1}$) ranged from 0.6 (±0.5) to 3.8 (±4.7) and Residency Index (RI) ranged from 0.3 to 1.0 (Table 1). Multidimensional scaling of a Bray-Curtis similarity matrix, based on average daily distance moved, average speed and RI, revealed a clear clustering of tagged fish (Fig. 3). The cluster analysis separated individuals into five groups with the greatest separation found between Category 1 and Category 2 fish, indicating that fish 14, 19 and 27 showed significantly different behaviour to the other individuals.

Comparisons of Category 1 and Category 2 movement metrics revealed significant differences in daily distance ($km.day^{-1}$), speed ($m.s^{-1}$) and RI between the two groups (Mann-Whitney U tests, $Z = 2.56$, $p = 0.011$; $Z = 2.42$, $p = 0.015$ and $Z = -2.56$, $p = 0.011$ respectively). Category 2 fish (average = 1.15 $km.day^{-1}$, ± 0.095) moved less than Category 1 fish (average = 7.39 $km.day^{-1}$, ± 3.51) and at a lower average speed (Category 1: average = 2.25 $m.s^{-1}$, ± 0.86; Category 2: average = 1.02 $m.s^{-1}$ ± 0.46). Category 1 fish had significantly higher RI, being present daily (average = 1 ± 0), than Category 2 fish (average = 0.39 ± 0.11) (Fig. 4).

Bonefish movement behaviour

Fish placed into Category 2 (fish 14, 19 and 27) were deemed to be eligible for further analyses to assess bonefish behaviour. These fish were still active within the receiver array after the six-month download and some still at the time of the one-year download (Table 2). Detection data from these three fish was further analysed for spatial and temporal patterns.

Area use

Average area usage of the three bonefish, based on individual MCPs, was 5.4 km^2 (± 1.9 km^2; 25% of the atoll) (Table 2). The MCPs showed that bonefish remained primarily within the atoll boundaries. The margin of the lagoon and the sand flats along the northern side of the atoll were utilised most frequently by the fish, which also represents the area of overlap in home ranges of the three fish. The tagged bonefish were detected for an average (± standard deviation; SD) of 45% (± 10%) of the total number of days of their respective monitoring periods. Absence periods ranged from 1 to 26 consecutive days during their respective monitoring periods. The mean percentage of days (± SD) (of the 45% of the days detected) that a fish spent at each habitat type was 18% (± 2%) on the flats, 9% (± 3%) in the lagoon and 18% (± 12%) in both habitats (Fig. 5).

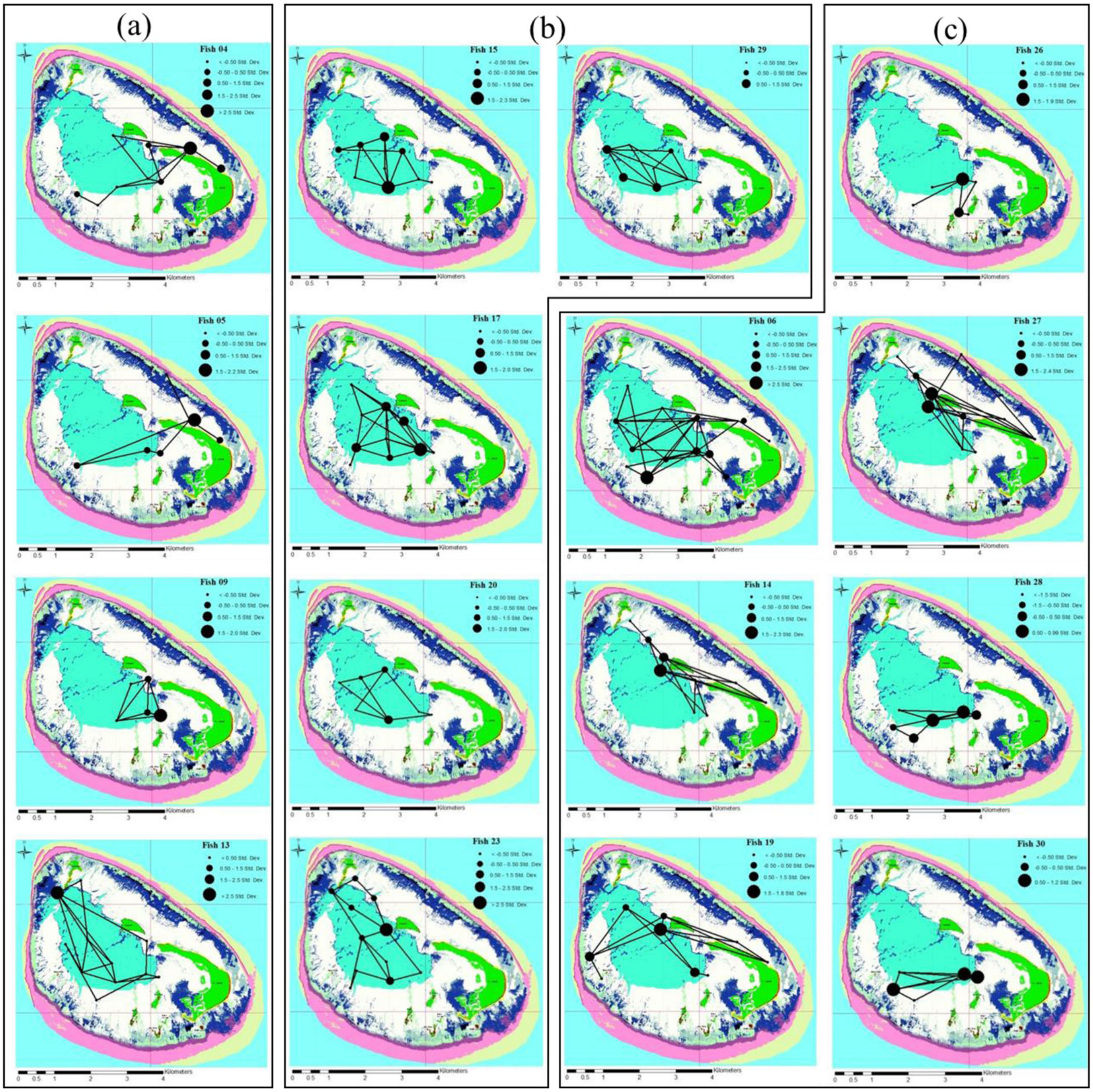

Fig. 2 Visual representation of the receivers that each fish was detected on with lines giving reference to the connecting sequence. Circles scaled to the frequency of detections for each fish at each receiver. Groups display the spatial distributions of the frequency of detections: (**a**) a greater proportion of detections on the sand flats, (**b**) a greater proportion of detections in the lagoon and (**c**) proportion of detections approximately evenly distributed between the lagoon and the sand flats. Base maps adapted from Spencer et al. (2009)

Effect of environmental variables on presence of bonefish in the lagoon

The probability of fish being present in the lagoon was tested using a GLMM. The model selection process was run for all factors (independent and combined), and the best fit model was identified as that with the lowest Akaike Information Criterion (AIC). The 'Wald' chi-square statistic and p value were then used to test the level of significance of the fixed effects (Alpha was set to 0.05). The model indicated that the probability of fish being present in

Table 1 Filtered data from the six-month download for the 16 fish eligible for further analysis

Fish ID	Category	Space use	Tracking duration	Ave. daily distance	Ave. speed	RI
4	1	a	5	0.6 ± 4.4	1.7 ± 1.7	1.0
5	1	a	6	0.9 ± 3.4	1.5 ± 0.8	1.0
6	1	c	5	14.7 ± 7.3	1.5 ± 1.1	1.0
9	1	a	5	6.4 ± 1.1	3.2 ± 2.6	1.0
13	1	a	5	8.9 ± 3.8	2.4 ± 2.9	1.0
14	2	c	191	1.1 ± 1.4	0.6 ± 0.5	0.5
15	1	b	4	6.4 ± 3.2	1.6 ± 1.2	1.0
17	1	b	5	14.1 ± 5.6	3.1 ± 2.6	1.0
19	2	c	193	1.3 ± 1.6	1.5 ± 1.3	0.3
20	1	b	4	4.0 ± 0.9	3.8 ± 4.7	1.0
23	1	b	3	7.3 ± 2.8	1.2 ± 0.7	1.0
26	1	c	5	4.5 ± 2.3	1.5 ± 1.9	1.0
27	2	c	190	1.1 ± 1.4	1.0 ± 0.9	0.4
28	1	c	5	6.1 ± 1.4	1.8 ± 2.1	1.0
29	1	b	4	7.7 ± 4.4	3.2 ± 2.9	1.0
30	1	c	3	7.5 ± 4.6	2.9 ± 2.3	1.0

Average daily distance represented in ($km.day^{-1}$) ± Standard deviation (SD) and average speed represented in ($m.s^{-1}$) ± SD

the lagoon (as opposed to the sand flats) increased significantly with increased water temperature on the sand flats ($W = 368.24$, $p < 0.001$) and decreased tidal height ($W = 5.530$, $p = 0.019$), but was significantly reduced at night ($W = 22.87$, $p < 0.001$) (Table 3). This indicates that fish were most likely to be present in the lagoon during the day when the temperature on the sand flats was high and the tide was low.

Discussion

Understanding movement patterns is essential to understanding a species' ecology and for effective conservation and management. However, for many species such information is lacking. Bonefish support thriving recreational fisheries; however, despite most of these fisheries being catch-and-release, there have been declines reported in bonefish stocks in many areas (Kamikawa et al. 2015; Rehage et al. 2019). Therefore, to contribute information for the improved management of bonefish stocks, an acoustic telemetry study was conducted at the St. Joseph Atoll, Seychelles, to address the lack of knowledge on bonefish in the Indian Ocean. A preliminary data assessment returned two distinct behaviours and a high proportion of post-release mortality of the tagged bonefish, suggesting possible predation bias, a phenomenon that

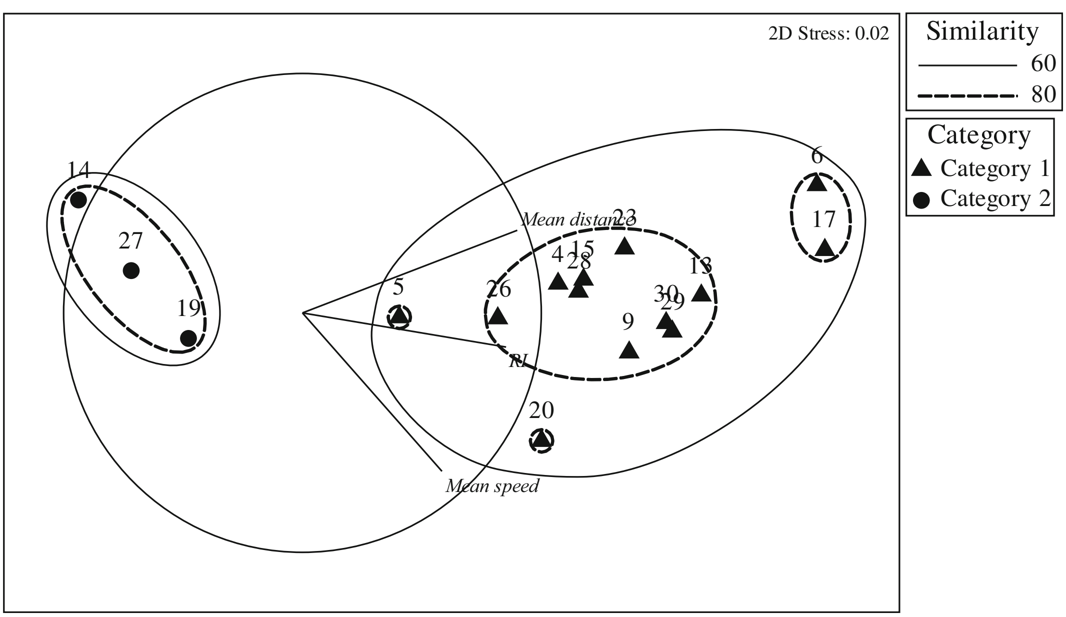

Fig. 3 Ordination by non-metric multidimensional scaling with a Bray-Curtis similarity matrix based on three factors; average daily distance ($km.day^{-1}$), average speed ($m.s^{-1}$) and residency index (RI) on the ordinal distribution of 16 fish tagged with acoustic transmitters and tracked in the St. Joseph Atoll

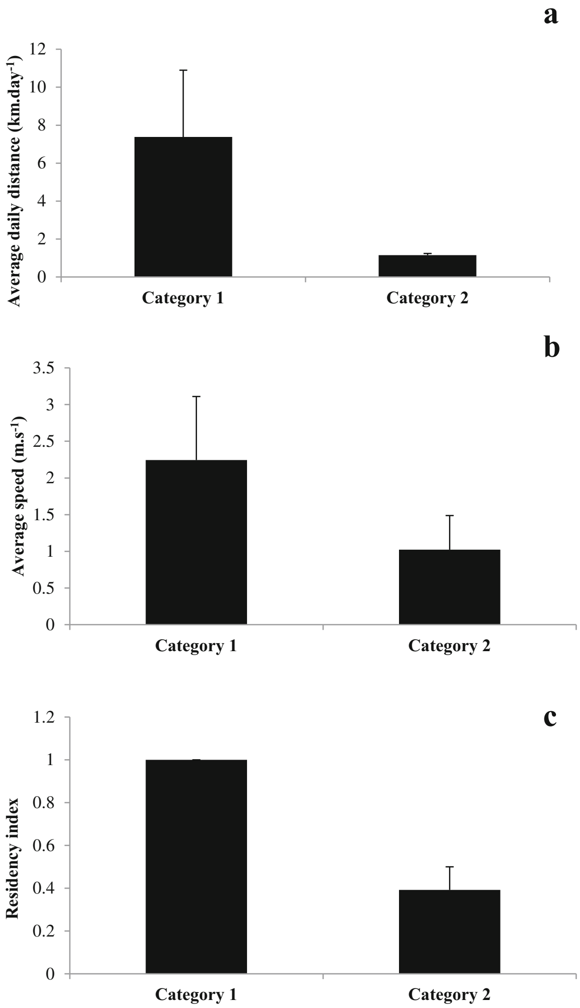

Fig. 4 Comparisons of movement metrics (average ± standard deviation; SD) (**a**) average daily distance (km.day^{-1}), (**b**) average speed (m.s^{-1}) and (**c**) residency index, between Category 1 fish (less than two weeks of tracking data) and Category 2 fish (more than two weeks of tracking data) for fish tagged in the St. Joseph Atoll, Seychelles

has been previously reported for bonefish in the literature (Colton and Alevizon 1983b; Humston et al. 2005; Danylchuk et al. 2007a, b; Friedlander et al. 2008; Murchie et al. 2013). The results provided by this study confirmed the need to investigate the possibility of predation bias using acoustic telemetry, particularly in predator-rich environments.

The first indication of predation bias within this study was observed in the variable spatial use observed. Space use and general movement behaviour of marine vertebrates play an important role as movements to certain areas serve a purpose and relate to alternative ecological processes (Jonsen et al. 2007). For instance, the use of the sand flats by bonefish has been associated with feeding and predator avoidance, and their use of the lagoon as a temperature refuge. This results in bonefish predominantly using the sand flats and the margin of the lagoon (Humston et al. 2005; Boucek et al. 2019). Similar patterns were observed in the bonefish tracked for more than two weeks (Category 2), and possibly in some of the individuals represented in group c (proportion of detections approximately evenly distributed between the lagoon and the sand flats). However, the movement observed from the other individuals, all of which fell within the short-term study group (Category 1) did not display such behaviour and rather displayed wider spatial use of the atoll, particularly the lagoon environment and more rapid movements. Similar movements were observed for sicklefin lemon and black tip reef sharks in the atoll (Filmalter et al. 2013; Lea et al. 2016), suggesting that several tagged bonefish were predated and that some acoustic telemetry data likely represented the movements of sicklefin lemon or blacktip reef sharks rather than bonefish.

In addition to the variable area use, differences in average daily distance moved, average speed and residency index were observed among

Table 2 Summary of the tracking data after the one-year download of the three surviving bonefish in the St. Joseph Atoll, Seychelles

Fish ID	Receiver detections	Total receivers visited	Total monitoring days	Days detected	Residency Index	MCP (km^2)
14	2773	9	188	91	0.5	3.4
19	1710	12	363	125	0.3	6.0
27	4827	12	303	162	0.5	7.0
Average	3103.3	11.0	284.7	126.0	0.5	5.4
SD	1584.5	1.7	88.9	35.5	0.1	1.9

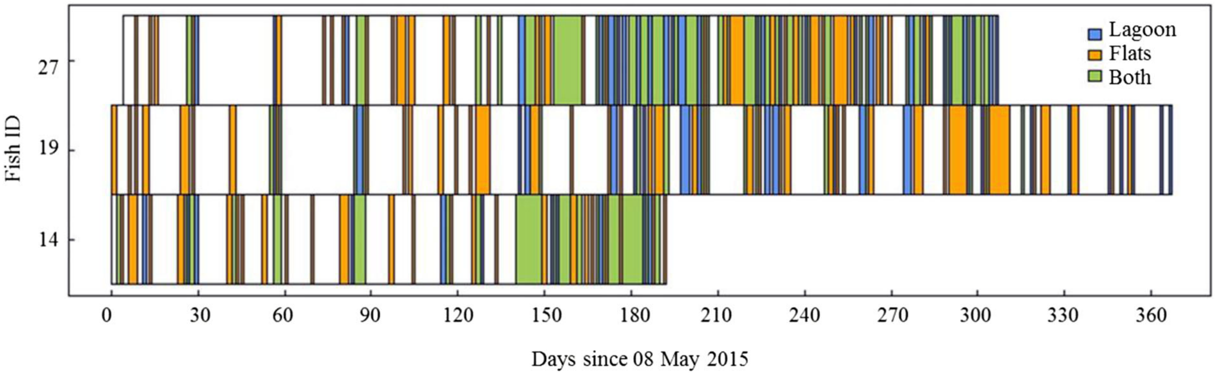

Fig. 5 Daily habitat use of bonefish (fish 14, 19 and 27) over the tracking period. Habitats include lagoon (blue), sand flats (orange) and daily detections on both the lagoon and sand flats receivers (green). White spaces represent periods of absence

individual fish. Based on these factors, the nMDS plot separated fish into two categories. The separation of the individuals within the nMDS was further evidence of predation bias in this study. The nMDS revealed a high level of variability among fish within the cluster of Category 1. This variability was likely due to different predator species (i.e. blacktip reef sharks and sicklefin lemon sharks) having preyed upon the tagged bonefish or due to the variable 'gut-retention' time of the transmitters ingested by the predators.

When assessing the individual factors used in the nMDS, a significant difference was found between Category 1 and 2 individuals. In general, a lower average daily distance and a lower average speed were noted for the three surviving fish (fish 14, 19 and 27). The speed and distance that an animal moves can reveal information pertaining to their feeding behaviour. For instance, sharks generally travel large distances at high speeds and hunt prey to meet their energy demands (Wetherbee et al. 1990; Pethybridge et al. 2014). In contrast, bonefish generally move shorter distances at slower speeds as they feed on small benthic organisms such as crustaceans and molluscs (Colton and Alevizon 1983a). The different area use of the atoll in combination with differences in behavioural tendencies (speed and distance) while traversing the atoll, suggests that different species, with different needs and ecological roles were being tracked during this acoustic telemetry study, thus further suggested predation bias.

The residency index values showed two distinct patterns: daily detections (average = 1 ± 0) for individuals tracked for short periods (Category 1) and detections within the array on fewer than half the tracking days (average = 0.39 ± 0.11) for individuals tracked for more than two weeks (Category 2). The results from the visual representation of fish movement, average daily distance and average speed reinforce the results of the RI calculations. Greater daily distances and higher average speeds within the atoll, with particular use of the lagoon (which had a greater receiver coverage), would have increased the probability of being detected,

Table 3 Summary statistics for a generalised linear mixed model, showing the effect of water temperature (°C) on the sand flats, tidal height and diel period on the presence of bonefish in the lagoon

	Estimate	SE	Wald Chisq	Df	z value	Pr (>Chisq)	
Intercept	−23.5492	3.4134			−6.899		
Temperature	0.9323	0.0486	368.2414	1	19.19	<0.0001	*
Tide	−0.5899	0.0251	5.5303	1	−2.352	0.01869	*
Diel (night)	−1.7615	0.2250	22.8674	1	−4.782	<0.0001	*

Shown are Wald chi-square statistics (Wald Chisq), standard error (SE), z values and degrees of freedom (df). Stars denote significance at the 0.05 level which explains the daily detections recorded for Category 1 individuals. In contrast, the long-term detected fish (Category 2) showed lower average daily distance, average speed and less frequent use of the lagoon environment and were, therefore, less active within the array, explaining the lower frequency of detections and thus lower RI. The literature on juvenile sharks reports a high RI and almost daily detections (Filmalter et al. 2013; Lea et al. 2016), while the literature on bonefish reports variable RI values (Murchie et al. 2013). This provides further support that the behaviour observed during this study for Category 1 fish is incongruent with known bonefish behaviour.

When calculating the distance moved per day detected and average speed, results are subject to bias. Shark speed is on average less than 1 $m.s^{-1}$ (Gruber et al. 1988; Papastamatiou 2008; Chin et al. 2013), with a burst speed of 5.57 $m.s^{-1}$ reported for *Negaprion brevirostris* (Sundström et al. 2001), while bonefish speed ranges from 0.18 to 6.4 $m.s^{-1}$ (Larkin 2011; Brownscombe et al. 2014). Speeds reported in this study may be under or overestimated due to the assumptions that (1) the fish movement was in a straight line and (2) the fish moved from the position of one receiver to the position of the next, therefore not accounting for alternative movement pathways or detection range (Gruber et al. 1988; Hedger et al. 2010). While these results may not represent the actual speeds and distances moved, the stark contrast between the tracks considered to represent bonefish and those considered to represent sharks, suggest that these estimates were sufficiently accurate in the context of this study.

This study provides strong evidence that Category 1 individuals were subjected to predation bias. That is, acoustically tagged bonefish were predated and the observed movements are due to the gastric ingestion of the transmitter by predators (most likely blacktip reef sharks or sicklefin lemon sharks). This evidence of predation bias occurred for 13 of the 16 fish (81%) analysed, indicating a high level of post-release predation. The 14 fish that could not be analysed due to insufficient detections on multiple receivers may have departed the study area or suffered mortality from sources other than predation. Therefore, total post-release predation rates for this study may have been lower (43%). However, it is possible that these 14 fish not analysed also fell prey to sharks soon after release. Thus, post-release predation may be as high as 90% (27 of 30 tagged fish).

To reduce mortality of tagged bonefish post release, guidelines for best handling practices have been documented in several studies. The most widely accepted methods for improving survival rate are to reduce air exposure and handling time and to ensure that bonefish are in a state of equilibrium before release (Cooke and Philipp 2004; Humston et al. 2005; Lennox et al. 2017). Nevertheless, despite following best handling guidelines, high post-release mortality in areas with medium to high predator abundance has been observed in this study and several others (Danylchuk et al. 2007b; Murchie et al. 2013). Conversely, bonefish studies in confined pools or areas with low predator abundance, report multiple recapture events of the same individuals, suggesting that mortality events are negligible, even when best handling and release practices are not followed (Crabtree et al. 1998; Danylchuk et al. 2007a). High predator abundance may, therefore, be one of the greatest reasons for high mortality rates in catch-and-release fisheries (Cooke and Philipp 2004). The results of this study indicate that mortality due to predation is an important factor. Consideration of post-release predation when implementing management strategies for catch-and-release fisheries, as well as acoustic telemetry or other tagging studies, is therefore essential.

Based on the classification of tagged individuals (Category 1 or 2) and several movement metrics, only three tagged bonefish appeared to have survived. Unfortunately, the low sample size limited the power of the bonefish movement analysis in this study. Movement data from these three fish revealed that bonefish showed fidelity to the atoll environment. The total area of the St. Joseph Atoll is 21.8 $km^{2.}$ Average area usage of the three surviving bonefish, based on individual MCPs, was 5.42 km^2 (± 1.85 km^2; 25% of the atoll), with fish 14, 19 and 27 using from 15% to 32% of the atoll. These results show that bonefish primarily remained within the atoll with preference to the sand flats and the margin of the lagoon. This finding is supported by studies elsewhere, for example, Humston et al. (2005) and Kamikawa et al. (2015) found that individuals or groups of bonefish frequently use an area of about 1.5 km^2. In mark-recapture studies by Larkin (2011) and Boucek et al. (2019), bonefish were generally recaptured at the tagging location or within 5 km of their tagging site. The high use of the sand flats was also consistent with the literature, which commonly reported bonefish (particularly *A. glossodonta* and *A. vulpes*) on the sand flats and other shallow water habitats (Donovan et al. 2015; Kamikawa et al. 2015). Prevalence for the sand flats may be due to their dietary preference of crabs, molluscs, shrimps, polychaetes, etc. which are commonly found in this habitat (Friedlander et al. 2008; Donovan et al. 2015) and predator avoidance as the sand flats are often too shallow for large-bodied fish and sharks (Humston et al. 2005). However, the lagoon environment is essential as a temperature refuge as bonefish are sensitive to extreme temperatures (Brownscombe et al. 2017a). According to Murchie et al. (2011a), the critical thermal maximum of *A. vulpes* was 36.4 ± 0.5 °C and 37.9 ± 0.5 °C for fish acclimated to 27.3 ± 1.3 °C and 30.2 ± 1.4 °C, respectively. Temperatures recorded on the shallow water sand flats at the St. Joseph Atoll sometimes exceed these values. The use of a limited area offers the benefit of familiarity which can optimise feeding, movement efficiency and predator avoidance (Hansler and Wisby 1958; Jadot et al. 2006). However, contrary to this study, some studies have also reported movements away from the study area for long periods (up to 339 days) or across great distances (> 100 km), possibly related to spawning behaviour (Larkin et al. 2008; Murchie et al. 2013; Boucek et al. 2019).

Factors affecting bonefish area use includes tidal phase, photoperiod and temperature (Colton and Alevizon 1983b; Brownscombe et al. 2014; Nowell et al. 2015). The GLMM analysis in the current study confirmed these expectations and indicated that bonefish movement was affected by all three of these factors. The predictability of bonefish movement makes them more vulnerable to fishing pressure, but also easier to manage (Grigg 1994; Meyer et al. 2000). An increase in water temperature, coinciding with a decrease in tidal height during daylight hours positively influenced bonefish presence in the lagoon. Solar heating occurs during the day, and to a greater extent at low tide, resulting in bonefish being more likely to move into the lagoon during the low tidal phase during the day. This reflects the findings of previous bonefish movement studies (Humston et al. 2005; Murchie et al. 2013; Brownscombe et al. 2017a). Since global sea surface temperatures are predicted to rise (Klein et al. 1999), this may have implications for bonefish populations worldwide. An increase in water temperature may force bonefish to use the lagoon environment more regularly, which may increase their vulnerability to predators and decrease their ability to feed.

Diel patterns in detections can be caused by an increase or decrease in the level of movement. For example, species such as the cow bream (*Sarpa salpa*) were shown to be less mobile during the day (Jadot et al. 2002). Furthermore, a change in activity is often periodical and location-specific, as has been identified in multiple species (Jadot et al. 2006; Oliveira et al. 2017). In this study, a decrease in night time detections, particularly in the lagoon environment was found. This decrease may be due to a reduction in night time activity, use of alternative habitats, or a combination of these. Literature on diel variation in bonefish movement is not consistent. Humston et al. (2005) and Brownscombe et al. (2014) reported that diel phases were a predictor of bonefish behaviour (e.g., resting, swimming, bursting, coasting and foraging). They found an increase in swimming activity during daylight hours (particularly dawn) and foraging on the sand flats at night. However, Murchie et al. (2011b) found no diel change in acceleration values or activity patterns for bonefish. Furthermore, bonefish may make more extensive use of the sand flats at night as they do not require the use of the lagoon as a temperature refuge. As predators are known to influence the habitat selection of fish (Brown et al. 1999), the use of the sand flats at night by bonefish may also reduce their encounter rate with predators, and thus their chance of predation, especially during low tide.

Conclusion and implications for management

Currently, despite their economic importance to many small island countries, bonefish in the

Indo-Pacific have no formal management plan, regulations nor conservation practices in place (Wallace 2015). The current study has provided information both on the potential impacts of catch-and-release fishing (i.e. post-release mortality), and on bonefish movement, which is new to this ocean region. This study has shown that catch-and-release of bonefish in a predator-rich ecosystem can result in high mortality (even with the implementation of best handling practices, and handling by trained researchers). A comparison of the movement patterns of long-term surviving fish (fish detected for more than two weeks) against short-term survivors revealed differences in area use, daily distance moved, speed of movement and residency index. The behaviour of the short-term surviving 'bonefish' matched existing information on shark movement behaviour and served as evidence for predation of tagged bonefish. The results of this study demonstrated the high susceptibility of bonefish to post-release mortality in predator-rich areas such as the St. Joseph Atoll. The high mortality rate (ranging from 43% to 90%) found in the current study has important management implications as it suggests that catch-and-release bonefish fisheries in predator-rich areas may not be as benign as expected. Accordingly, it is recommended that sustainable management interventions are developed. Further studies which make use of predator tags may be advisable to further understand this interaction.

The results for the movement study have demonstrated that bonefish are resident to the atoll, and highlight the importance of the sand flats and the lagoon habitat to this species. Bonefish movement is influenced by certain temporal cycles (e.g., tidal) and therefore, follow a degree of predictability. Management plans that may be developed for bonefish should therefore take this information into account. For instance, in the context of catch-and-release fisheries, the influences of tide, temperature and time of day on bonefish area use may have implications for post-release mortality of this species. The increased use of the lagoon area during low tides and during daylight hours when temperatures are at their peak, and the greater use of the lagoon habitat by predatory sharks suggest that the probability of post-release mortality as a result of predation may be greater during low tides and midday, when bonefish are more likely to enter the lagoon. This suggests that catch-and-release fisheries could reduce the risk of post-release predation though temporal restrictions on angling that take this information into account. Restricting angling to morning and evening periods, and higher tides, could thus have the effect of reducing post-release predation and mortality in these fisheries.

Unregulated fishing pressure on bonefish could potentially severely impact isolated bonefish populations. While the results may differ from one region to another, and be dependent on several factors such as fishing pressure, human habitation, development, predator density and level of protection, this study contributes valuable information that can be used towards the development of management plans for bonefish. Further research into bonefish predation and further studies of bonefish movement with a larger sample size, would enable an improved understanding of their movement and the timing of post-release predation events and would thus provide a better understanding of the processes involved in their movement and predator interactions. With an inevitable increase in the demand for exclusive ecotourism fishing, conservation efforts are essential to sustain the unique opportunities on offer in the Seychelles, and other island states where catch-and-release fishing is of economic value.

Acknowledgements This work was made possible thanks to the funding provided by Save Our Seas Foundation (SOSF) and the resources of D'Arros Research Centre (DRC), South African Institute for Aquatic Biodiversity (SAIAB) and Rhodes University. The authors also thank those who assisted in the field, in particular Kerryn Bullock, Christopher Boyes and Chantel Elston. James Lea and the Danah Divers are thanked for the management of the acoustic array and the downloading of the data and Dr. Amber Childs for assistance with data analysis.

Compliance with ethical standards

Conflict of interest The authors acknowledge that there were no conflicts of interest in this study.

Human studies This article does not contain studies involving human participants.

Ethical approval Ethical approval for this study was obtained by the relevant authorities.

Appendix

Table 4 Raw (non-filtered) metadata of acoustically tagged bonefish ($n = 30$), at St. Joseph Atoll (Seychelles) in May 2015

Fish ID		Date and time tagged	Fork length (mm)	Tagging location	No. of receivers visited	No. of receiver detections	No. of monitoring days	No. of days detected
1	*	5-5-2015 9:27	550	c	0	0	0	0
2	*	5-5-2015 15:48	470	d	0	0	0	0
3	*	6-5-2015 9:20	500	e	1	21	2	2
4		4-5-2015 17:26	465	c	10	102	5	5
5		4-5-2015 18:10	494	c	9	417	12	12
6		5-5-2015 8:47	525	c	21	375	12	10
7	*	5-5-2015 9:51	472	c	1	1	1	1
8	*	5-5-2015 14:56	499	d	0	0	0	0
9		5-5-2015 15:19	499	d	6	396	5	5
10	**	6-5-2015 9:15	519	e	6	64	2	2
11	**	6-5-2015 9:49	487	e	2	7	1	1
12	*	6-5-2015 10:07	452	e	0	0	0	0
13		8-5-2015 9:04	518	a	14	4860	124	124
14		6-5-2015 14:31	515	b	17	2969	204	115
15		6-5-2015 14:45	450	b	9	109	4	4
16	**	6-5-2015 15:05	470	b	7	58	3	3
17		8-5-2015 9:20	553	a	11	388	7	7
18	*	8-5-2015 9:38	525	a	1	35	2	2
19		6-5-2015 10:22	506	e	11	697	202	77
20		6-5-2015 10:57	551	e	11	83	4	4
21	*	6-5-2015 13:05	528	b	8	6387	105	100
22	**	6-5-2015 13:22	502	b	4	34	5	4
23		8-5-2015 5:58	495	a	12	185	39	4
24	*	8-5-2015 10:19	518	a	1	2402	25	24
25	*	5-5-2015 12:10	477	a	1	64,848	198	198
26		8-5-2015 16:28	532	d	6	268	42	9
27		9-5-2015 15:45	528	b	15	2358	196	106
28		8-5-2015 15:57	478	d	4	568	26	20
29		8-5-2015 16:11	462	d	10	109	4	4
30		5-5-2015 9:10	467	c	6	127	3	3

Asterisk symbols refer to fish removed from analyses, where * = fish not detected or detected exclusively or almost exclusively on one receiver, and ** = fish with fewer than 75 detections. Tagging location refers to the sites given in Fig. 1

Fish 21 was considered as part of the group 'detected almost exclusively on one receiver' as 98% of the detections were detected on one receiver

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