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Short-term space use of small-bodied fish in coastal flats ecosystems in The Bahamas: an acoustic telemetry study using the smallest commercially available transmitters

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Abstract Nearshore fish communities in marine flats ecosystems are recognised as being key for early life stages of socio-economically valued fish species, as well as small-bodied forage fishes, yet little is known about the spatial ecology of these fishes. Recent advances in acoustic telemetry have allowed for the tagging of small fish. Here, we used the smallest commercially available acoustic transmitter to tag and track several juvenile or small-bodied species of a flats fish assemblage in Rock Sound, Eleuthera, The Bahamas. Fish species tagged included juvenile bonefish (*Albula vulpes*; $n = 2$), juvenile great barracuda (*Sphyraena barracuda*; $n = 22$), juvenile redfin needlefish (*Strongylura notata*; $n = 21$), and yellowfin mojarra (*Gerres cinereus*; $n = 20$), and their movements were recorded by twenty hydrophone receivers deployed in nearshore flats habitats extending ~3 km along the shoreline. Yellowfin mojarra had the highest site fidelity and were detected most commonly during diurnal periods. Juvenile bonefish had the lowest site fidelity and travelled throughout the array area, primarily detected at night (albeit sample size was low). Juvenile barracuda and juvenile redfin needlefish were mobile but tended to spend the majority of their time near several receivers. Juvenile barracuda were least present during the morning but were detected during all other times of the day. Similarly, juvenile redfin needlefish had the lowest residency during the morning and were more resident during the other period. Some of the space use patterns observed appeared to be correlated with water temperature (e.g. for barracuda there were more detections at warmer water temperatures). This preliminary study reveals that it is possible to tag and track small flats fishes which opens the door for longer-term and more fine-scale (e.g. with 2-day positioning) studies to understand habitat associations and environmental drivers of behaviour although receiver detection range was somewhat limited in these shallow and dynamic habitats.

Keywords Marine · Coastal · Habitat · Telemetry · Spatial ecology

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Introduction

Coastal flats ecosystems (including estuaries, tidal creeks, and lagoons) in sub-tropical and tropical regions support diverse fish communities (Adams 2017). In particular, they serve as nursery grounds for the juvenile stages of large-bodied fishes, many of which are of socio-economic value (Beck et al. 2003;

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Dahlgren et al. 2006; Adams and Cooke 2015), and as refuges and life-long habitats for a number of small-bodied fishes (Beck et al. 2003). Flats ecosystems are characterised by a mosaic of shallow habitats including seagrass beds, algal plains, limestone rock, sand flats, and soft sediment beds (Boström et al. 2011; Adams and Cooke 2015; Murchie et al. 2015), often interspersed with or fringed by mangroves (Blaber 2007). Such nearshore habitats are incredibly productive yet are also under immense threat as a result of coastal development pressures (Hinrichsen 1999; Crain et al. 2009). Such threats have the potential to impact fish populations (Courrat et al. 2009) that support fisheries and generate diverse ecosystem services that benefit nature and people (Holmlund and Hammer 1999). To effectively protect, manage, and restore flats habitats that support nearshore fish communities, it is necessary to characterise critical habitats (Rosenberg et al. 2000; Levin and Stunz 2005) and understand how fish interact with each other and their environment (Gladstone 2009).

Studying the spatial ecology of small-bodied fishes in coastal systems is inherently challenging (Miller et al. 1984; Murchie et al. 2012). Fish can be highly mobile, juvenile fish are small and often sensitive to handling, and some species are cryptic. Moreover, nearshore environments are characterised by complex habitats (Robertson and Duke 1987) and are inherently dynamic as a result of tides, diel variation in water temperature, and fluxes in salinity (Murchie et al. 2015; Brownscombe et al. 2019; Haak et al. 2019). Collectively, these constraints make it difficult to track individual behaviour and habitat use using methods such as snorkelling or mark recapture (Miller and Dunn 1980; Miller et al. 1984) whereas other techniques, such as otolith microchemistry, provide data at too coarse of a scale spatial and temporal (Fodrie and Herzka 2008). Acoustic telemetry has become widely embraced for studying marine fishes given that it can be used to study the movement and behaviour of individual fish at diverse spatial scales (from fine-scale meter accuracy positioning, to across ocean basins; Hussey et al. 2015; Matley et al., 2022). However, most studies using acoustic telemetry have focused on adult fish and/or large-bodied species of socio-economic value (Matley et al., 2022). Acoustic tag size represents a major constraint given that a high tag burden in small fish can impair behaviour and lead to post-tagging mortality (Jepsen et al. 2005). As such, little is known about the behaviour and habitat use of juvenile life stages of many fish species or the adults of small-bodied species (Levin and Stunz 2005), including for fish that use nearshore tropical and subtropical flats systems.

Recent innovations in acoustic telemetry have led to the development of micro acoustic transmitters. Initially designed for tracking juvenile salmonids (McMichael et al. 2010), commercially available micro acoustic tags have recently been used to study space use of small-bodied coastal marine fish in the Mediterranean Sea (Aspillaga et al. 2021a, b). However, to our knowledge, there are no such studies that simultaneously track multiple juvenile or small-bodied species in a tropical or subtropical flats fish community. To that end, the objectives of this study were to (i) characterise the diel spatial ecology and residency of four species of fish in a nearshore subtropical flats system, (ii) identify the environmental drivers of space use and movement, and (iii) determine the extent to which there are common patterns among the four species. This study focused on juvenile bonefish (*Albula vulpes)*, great barracuda (*Sphyraena barracuda*), redfin needlefish (*Strongylura notata*), and yellowfin mojarra (*Gerres cinereus*).

Juvenile bonefish are a teleostean marine benthivore that inhabit nearshore environments in tropical and sub-tropical waters. Juvenile bonefish and mojarra are frequently observed shoaling together in nearshore flats environments (Haak et al. 2020; Szekeres et al. 2020), as they are both demersal fish, residing in shallow water (<2 m), and primarily prey on benthic invertebrates (Teixeira and Helmer 1998). Conversely, redfin needlefish and barracuda often occupy pelagic zones and are piscivorous (Sogard et al. 1989; Porter and Motta 2004). However, as juveniles, both species tend to be found in shallow, nearshore environments, and they are often caught together when sampling.

At the time of our study, we used the smallest commercially available acoustic tags which, because of their size, had a battery life of approximately 1 month. As such, we could only track these fishes for a relatively short duration. Because the receivers used for this study also inherently had a limited detection range, the spatial scope of our array was relatively small. Given these collective limitations—including a low sample size for bonefish—we consider this a preliminary study with the hope that it will serve as a foundation for a larger scale (both time and space) study of the spatial ecology of juvenile and small flats fishes in the future.

Methods

Study site

This study was conducted in Rock Sound, Eleuthera, The Bahamas (N 24° 88′ 30″, W 76° 18′ 91″; Fig. 1) during two time periods: February 28 to March 16, 2016, and April 13 to 30, 2016. The array was removed between March 16 and April 13, 2016. The reasoning for the two deployments was due to the low capture numbers of juvenile bonefish in February/March leading to project postponement with the intention to recommence activities in April with warmer water temperatures and fairer weather with the hopes that bonefish would be more abundant. The habitat in the vicinity of the telemetry array included red mangroves (*Rhizophora mangle*) in the intertidal zones, with the nearshore (within 200 m) substrate dominated by sand and hard limestone rock bottom, as well as sparse aquatic vegetation including turtle grass (*Thalassia testudinum*), green algae (*Batophora oerstedii*), shoal grass (*Halodule wrightii*), and red algae (*Laurencia sp.*). The range between low tide and high tide for the study area was 0.50 to 1.19 m.

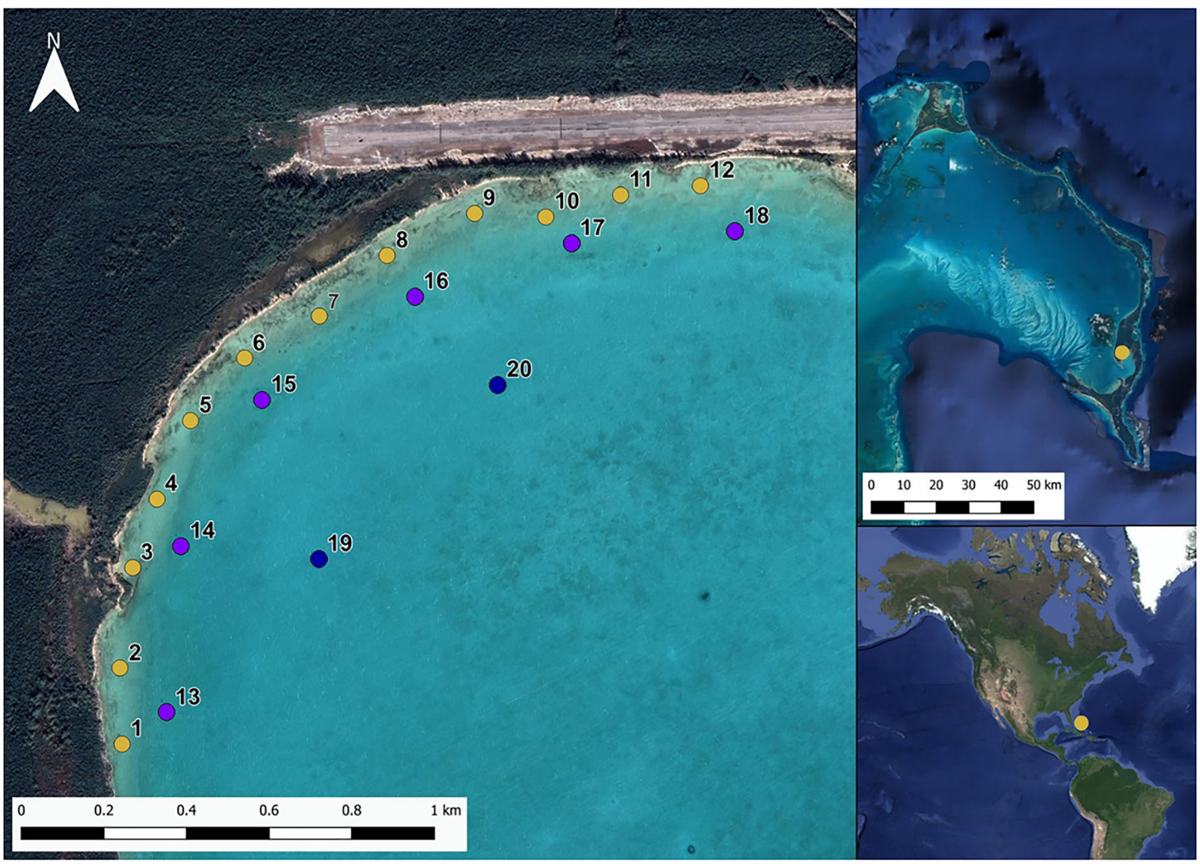

Fig. 1 The bottom right panel shows the location of The Bahamas in North America (yellow dot) whereas the top right panel shows the location of Rock Sound on Eleuthera (yellow dot). The larger panel to the left illustrates the acoustic telemetry array extent in Rock Sound, Eleuthera, The Bahamas. The yellow receiver points denote receivers that were horizontally deployed facing shore in shallow water (~0.5 m). Purple receivers were deployed in slightly deeper water vertically (~1.5 m), while the blue receivers were deployed vertically in deep water (~2 m)

Telemetry array

The acoustic telemetry array was deployed in February/March and again in April 2016. The entire telemetry array encompassed an area of ~ 3 km^2, in an area known as the Airport Flats. Twenty omnidirectional hydrophone acoustic telemetry receivers (WHS4250; Lotek Wireless, Newmarket, Ontario). Twelve receivers (1–12) were deployed nearshore, within 60 m of shore, and were 150–200 m apart in a water depth of 0.50–0.75 m (Fig. 1). All nearshore receivers were secured to cinder blocks with the hydrophone tip facing toward shore (i.e. horizontally); nearshore water depth was insufficient to allow for the hydrophone to be secured vertically. Another row of six receivers were deployed approximately 150 m offshore and staggered between the twelve nearshore receivers, between 350 and 400 m apart in 1.40–1.65 m of water. These hydrophones were secured to rebar that had been anchored into the substrate, with the hydrophone mounted vertically, allowing for more omnidirectional detection range. Lastly, two receivers were deployed in deeper water (2.05-m depth), 430 m from shore at the closest distance, and 550 m apart. These receivers were also secured to rebar secured into the substrate. All receivers had a plasticised iButton (iButtonLink; model DS1921G-F5; Whitewater, Wisconsin) secured to them and they were programmed to record water temperature (°C) every 10 min.

Range testing was conducted using a receiver 30 m from shore (~ 0.5-m water depth) with the hydrophone tip facing shore, as well as one 130 m from shore (~ 2-m water depth) with the hydrophone tip facing up. For the receiver range test, the tag was tested for 60 s (20 detections) every 5 m; this was first completed perpendicular to shore up to a distance of 50 m away from the shallow receiver in the NE and SW orientation. It was also tested from shore every 5 to 130 m offshore, where the deeper receiver was located. Both the nearshore receiver and the deep-water receiver were set to detect the test tag.

Fish capture and transmitter implantation

All fish were captured using a beach seine (15.2 m long × 1.2 m high, 3.2-mm mesh size) in shallow habitats (≤ 1 m) on the northwest shoreline of Rock Sound. Once captured, fish were held in flow-through net pens (1.2 m × 0.6 m × 0.6 m) after capture for several hours before being surgically implanted with a JSATS transmitter (L-AMT-1.416: 10.7 × 5.4 × 3.1 mm, 0.28-g dry weight, 5-s burst rate, expected maximum battery life 25 d; Lotek Wireless, Newmarket, Ontario) using 416.7-kHz transmitter frequency and transmitter power of 158 dB. Transmitters and surgical equipment were disinfected in a 10% Betadine solution prior to each surgery. Fish were anaesthetised with MS-222 before surgery and were administered a knock-down dose as well as a maintenance dose (~ 50% of knockdown concentration) during surgery (varied based on fish size, ranging from 45 to 72 mg/L). While the fish had the maintenance dose of fresh saltwater pumping over their gills, a small (< 10 mm) incision was made anterior to the pelvic girdle, and the transmitter was surgically implanted using forceps. The incision was closed using a single absorbable suture (4/0 monofilament PDSII; Ethicon, Somerville, New Jersey). Each surgery took ≤ 5 min and fish recovered from anaesthesia in ≤ 3 min. Fish were left to recover from surgery for up to 4 h in the flow-through net pens before being released at the location of capture. Fish weighed between 9 and 129 g with a maximum tag burden of 3%, thus swimming ability was not anticipated to be inhibited (Brown et al. 1999). Fish were released at the location of capture after ~ 1 h of recovery.

Data analyses

Data analysis was conducted using a combination of R Software version 4.1.2 and Tableau Public 2021.3. As the data required restructuring to a format viable for data analysis, two R packages were useful for this task—data.table and tidyverse (Dowle and Srinivasan 2021; Wickham et al. 2019). Because of relatively low sample sizes and short-duration tracking, we approached our analysis from a largely descriptive perspective. Data visualisation techniques (e.g. bar graphs and line plots) were used to visualise residency of the four species in the near-shore areas. Five-number statistics, the mean, and standard deviation of detection count were calculated to provide insight into variability in the detection count of each species. A linear mixed effects model analysis was also done with temperature as the fixed effect, and the unique identifier for each fish as a nested random effect. The bar graphs combined with line plots inform the total daily detection count and number of fish that were detected on the specified day. The stacked area plot informs the diel spatial residency of the four species. To evaluate temperature as an environmental correlate of space use and movement, a Spearman correlation test was performed between the mean diel temperature and the mean diel detection count. Specifically, to account for variations in the number of fish that were detected across the days and/or hours, the total number of detections for the specified hour was divided by the number of fish that were detected. The Spearman correlation was also used to evaluate correlation among species.

Results and discussion

Only two juvenile bonefish were captured and tagged during the study (114- and 117-mm fork length), both during the February/March deployment. Given the low sample size, juvenile bonefish were excluded from some of the analyses. Two juvenile barracuda (153- and 194-mm fork length) were also captured and tagged during the February/March deployment. More juvenile barracuda were collected and tagged during the April deployment ($n = 20$, 132–254-mm fork length), along with juvenile needlefish ($n = 21$, 185–361-mm fork length), and mojarra ($n = 20$, 73–90 mm fork length). With most fish in the study tagged and tracked during the April array deployment, much of our analyses focused on that time period.

The two bonefish were both successfully tracked for ~ 20 days (18 and 21 days; Fig. 2, Fig. 5). The average bonefish detection count was 3347 ± 2356, with one individual having considerably more detections than the other (Fig. 2, Table 1). Relatively few detections occurred in February and were spread rather evenly among receivers (Fig. 3). In March, over 50% of bonefish detections ($n = 3{,}622$) occurred on a single receiver on the same day (receiver 17; Figs. 3 and 5). This receiver was located at the east end of the array (Fig. 3), was in deeper water (1.5 m), and in an area of silty fine substrate and sparse *Thalassia* and *Laurencia*. Both of the bonefish were released

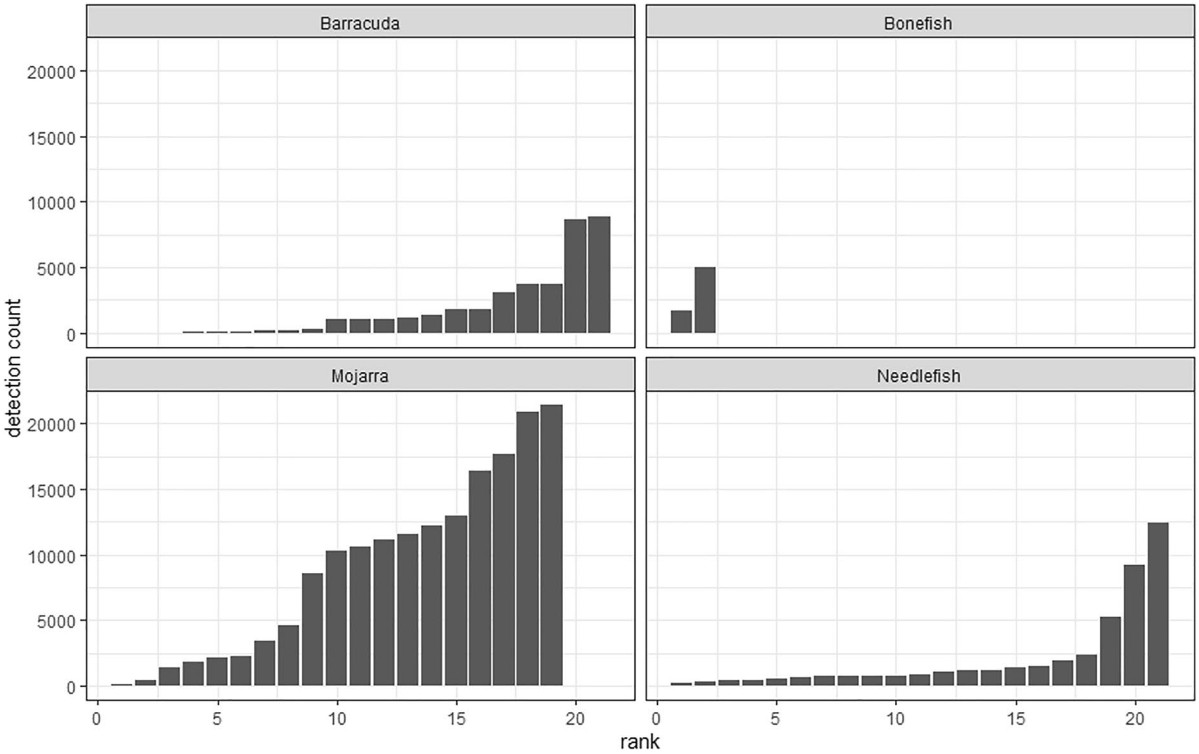

Fig. 2 Bar graph of detection count for each tagged fish. The rank is based on each species, with each fish having a rank. The minimum rank, 1, informs the fish with the lowest detection while the maximum rank informs the fish with the most detection

Table 1 Detection count and its summary statistics for the different species

Species	Mean	Standard deviation	Minimum	25th percentile	50th percentile	75th percentile	Maximum
Barracuda	1813	2595	11	109	1025	1836	8908
Bonefish	3347	2356	1681	2514	3347	4180	5014
Mojarra	8932	6946	134	2205	10,258	12,583	21,452
Needlefish	2093	3133	175	679	856	1525	12,409

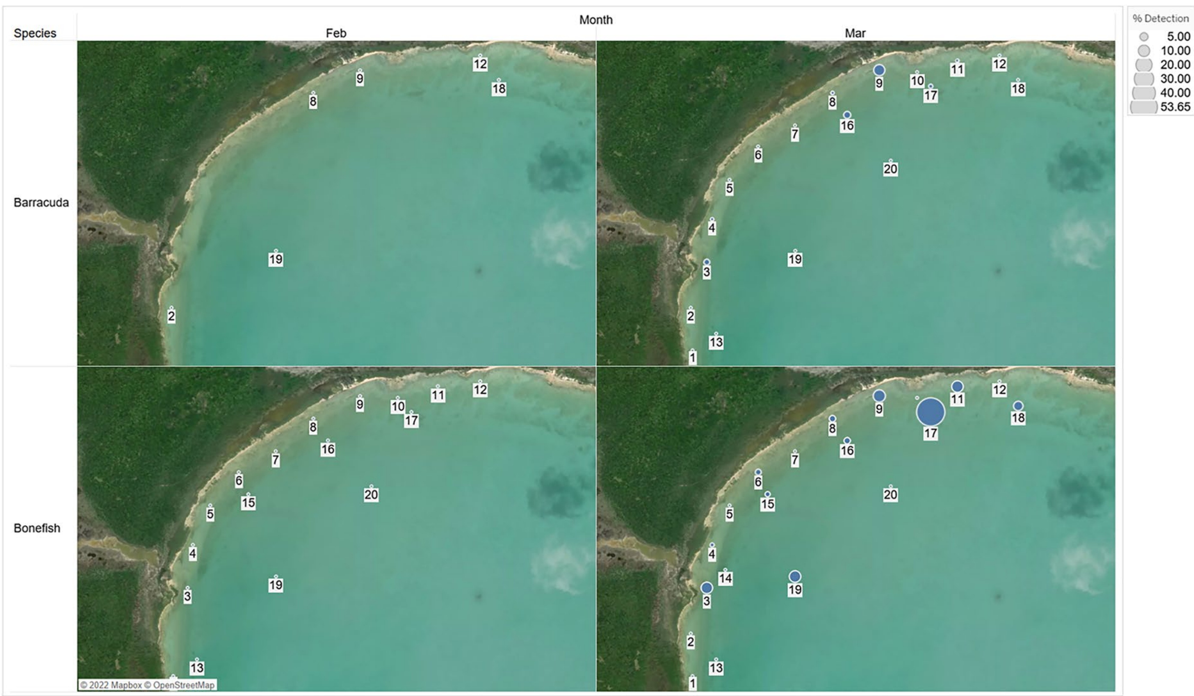

Fig. 3 Percent detection at each receiver for both bonefish and barracuda during the February and March deployment period

approximately 1.1 km from this receiver. Four other receivers had greater than 500 detections from the tagged bonefish (receivers 3, 9, 11, 19; Fig. 3). Receiver 3 was a nearshore receiver in 0.5 m of water, with a substrate of soft sand, *Batophora, Halodule,* and *Laurencia*; this was the closest receiver to the bonefish release location (200 m). Receivers 9 and 11 were both nearshore receivers and near receiver 17 (which was deeper water; Fig. 3). Receiver 9 was in 0.6 m of water with dense *Laurencia* in adjacent deeper water, and soft sand, *Thalassia, and Halodule* in the immediate proximity. Receiver 11 was in 0.6 m of water, and a substrate of soft sand and *Thalassia*. Receiver 19 was one of two offshore receivers (Fig. 3) in 2.1 m of water, with an uneven silty bottom and dense *Thalassia*, and located 400 m from the bonefish release location.

To inform our interpretation of juvenile bonefish space use and to better understand the relatively low number of acoustic detections, wind intensity and direction were qualitatively investigated using both field notes and data from station SPGF1 in Grand Bahama (approximately 300 km northwest of the study area; data recorded every 10 min) accessed from the National Oceanic and Atmospheric Administration (NOAA) National Buoy Data Center (NBDC). Interestingly, the day of highest detections was on March 6, 2016, when a shift from predominantly southeast winds to a strong north wind was recorded (SPGF1 detected max wind speeds of 37 km/hr), before the wind shifted to a prevailing east wind and maintained strong max wind speeds until the study was terminated on March 16, 2016 (avg wind speed SPGF1 March 6–16 = 24 ± 1.2 km/h SE; 41.6-km max wind speed on March 9). Although there was not a large enough sample size or fine-scale wind data to conduct a rigorous analysis, those observations support the findings of Haak (2019) wherein the distribution of juvenile bonefish is partially driven by wave and wind action.

Although very descriptive, there have been no other studies on fine-scale space use of juvenile bonefish, making the results for the two fish we tracked novel natural history data. Overall, very little is known about the juvenile life stage of bonefish aside from limited information about diet (e.g. Haak et al. 2019; Griffin et al. 2019). Our efforts focused in an area of Eleuthera where juvenile bonefish had previously been captured by seine net (Haak et al. 2019; Griffin et al. 2019; Szekeres et al. 2020), but our capture success was much lower. Indeed, this project was initially intended to focus primarily on juvenile bonefish to determine their spatial habitat use. Pausing the study and resuming in April was a (failed) attempt to achieve higher catches with warmer temperatures and fairer weather. With no catches of taggable juvenile bonefish (with over 150 seine pulls) in April, the project scope was shifted to include other nearshore fish species. Future studies on the space use of juvenile bonefish should likely consider greater seining effort across a range of seasons to potentially account for temporal variation in abundance.

Juvenile barracuda in our study were tracked for an average of 11 days (range 2–17 days; Figs. 3 and 4). Both of the juvenile barracuda tagged in February/March and 19 of the 20 tagged in April were successfully tracked—only one barracuda was not detected by the receiver array (Fig. 2). Two individuals made up a disproportionate amount of detections when compared with the other tagged barracuda (Fig. 2, Table 1). Unsurprisingly, relatively few detections occurred in February, given that only two fish were tagged (Fig. 3). In February/March, most detections occurred on a single receiver (receiver 9; Fig. 3) which was deployed in 0.6 m of water in an area with soft sand substrate, *Thalassia* and *Halodule*, and

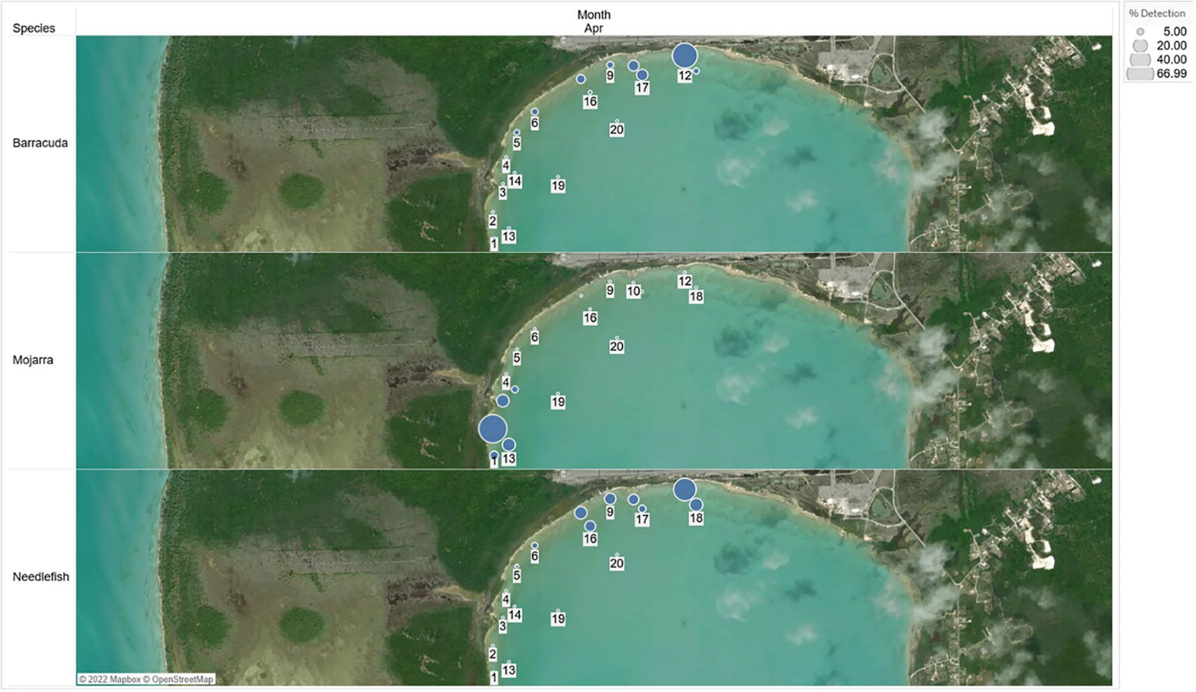

Fig. 4 Percent detection at each receiver for barracuda, mojarra, and needlefish during the April deployment period

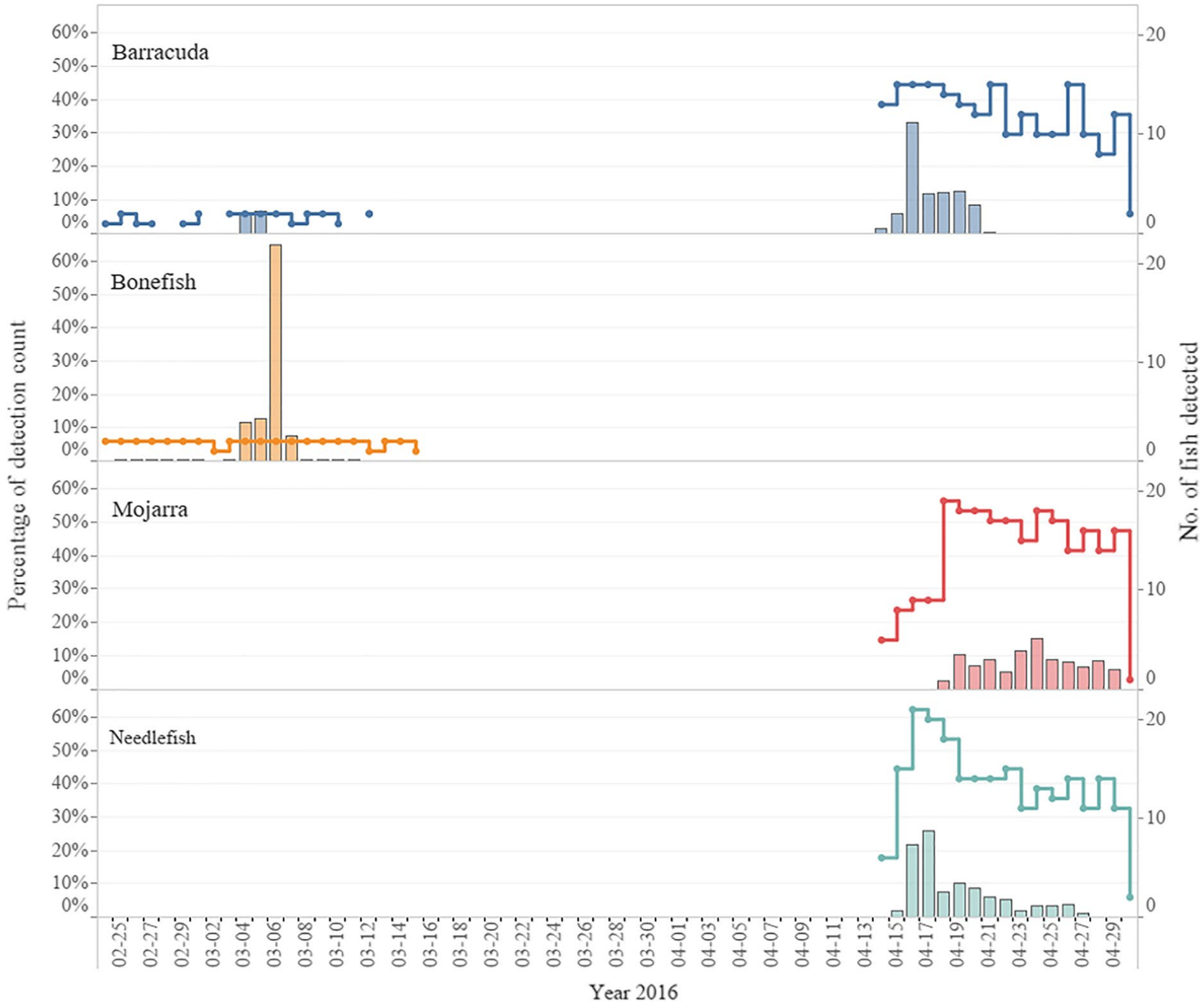

Fig. 5 Bar plots paired with line plots informing daily detection data of the different fish species; with the bar plots informing the detection percentage of the respective species, and the line plot informing the number of fish that were detected

considerable *Thalassia* coverage in nearby deeper water. Receiver 9 was within 800 m of the barracuda release location. In April, detections occurred on several receivers but were dominated by 20,479 (54%) detections on receiver 12 (Fig. 4), located between 30 and 800 m from the barracuda release location. Receiver 12 was deployed in 0.6 m of water, in an area with sand on a limestone substrate and sparse *Thalassia*. Two other receivers (10, 17) had greater than 300 detections (Figs. 4 and 5). Receivers 10 and 17 were in proximity to one another, with receiver 10 being nearshore (0.8-m depth) and receiver 17 approximately 80 m deeper (1.5-m depth). Habitat adjacent to receiver 10 had soft sand on hard limestone substrate, and *Thalassia* and *Laurencia* nearby. The deeper receiver (17) had a silty substrate and sparsely distributed *Thalassia* and *Laurencia*. Tagged barracuda in April were detected more frequently in the days following release, and decreasingly throughout the April study period (Fig. 5). Although great barracuda have previously been studied with acoustic telemetry (see O'Toole et al. 2011), those efforts focused on adults that were substantially larger than the juveniles studied here and that tended to occupy much deeper water (O'Toole et al. 2010). Netting studies have revealed that juvenile barracuda tend to occupy complex nearshore habitats (e.g. de Sylva 1963; Murchie et al. 2015; Hansen 2015) which

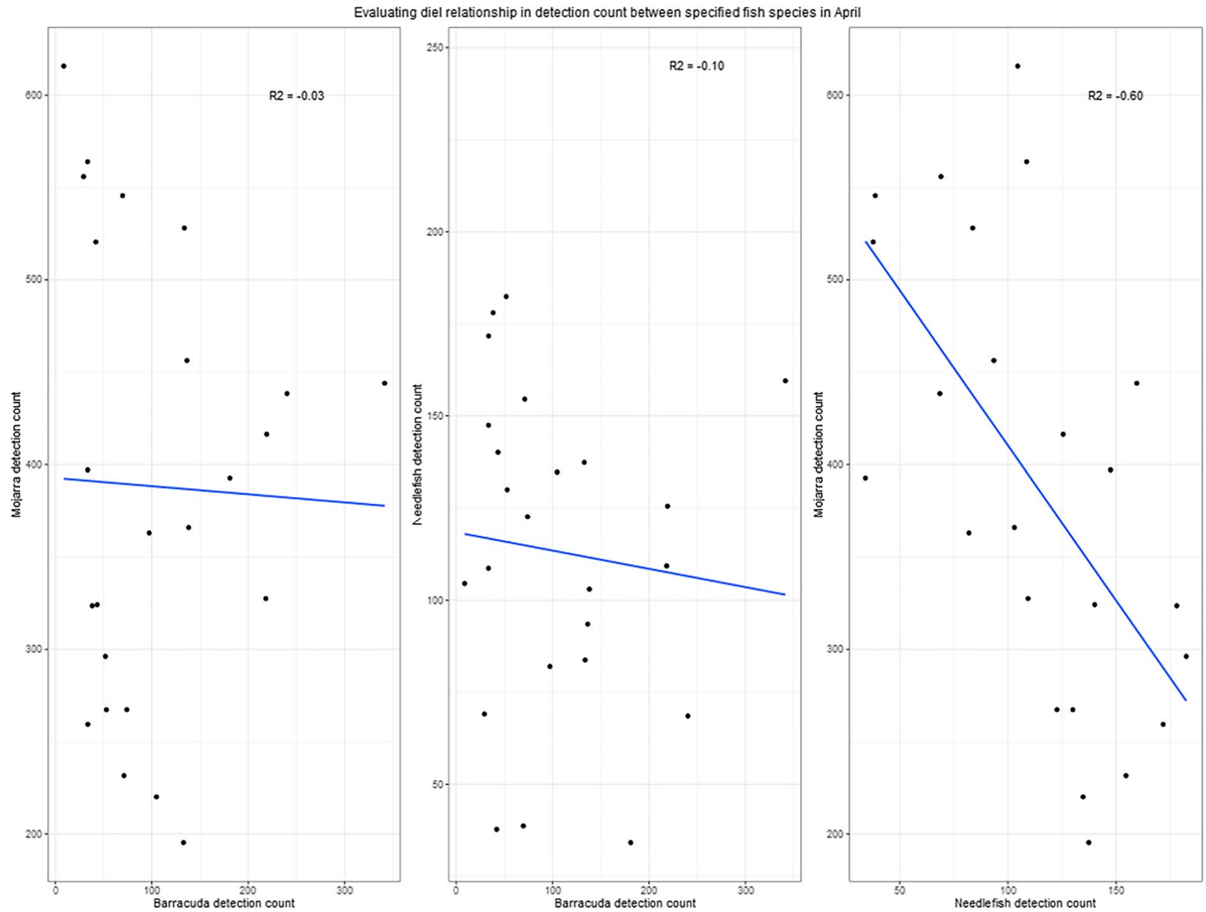

Fig. 6 Detection count correlation between specified fish species in April 2016

they use for both foraging and to avoid predators (Nagelkerken et al. 2000).

All 19 yellowfin mojarra tagged in April were successfully tracked for a mean of 12 days (range 6–16 days), and detected more often and more consistently (during that short period) than the other three species showing the highest levels of residency (Figs. 2, 3 and 5, Table 1). Greater than 60% of detection (116,663) occurred on a single receiver (receiver 2; Figs. 3 and 5); this receiver was 120 m away from the mojarra release site. Receiver 2 was deployed in 0.6 m of water with soft sand and very sparse *Halodule* (Fig. 3). More than 15,000 detections were recorded on receivers 3 and 13, which were the next closest receivers to receiver 2 (Fig. 3). Receiver 3 was an adjacent shallow water receiver in 0.5 m water, with soft sand, *Batophora, Halodule*, and *Laurencia* present. Receiver 13 was a deep-water receiver in 1.7 m of water, with a hard silty substrate containing *Batophora* and *Laurencia*.

All 21 needlefish tagged during the April array deployment were detected (Fig. 2), however residency decreased relatively consistently over the tracking period (Fig. 5). Two tagged needlefish were detected more frequently than other tagged needlefish (Fig. 2, Table 1). Detection counts were highly variable among receivers, although receiver 12 had ~ 50% of total detections (Figs. 3 and 5); this is the same receiver with high levels of barracuda detections. Given that juvenile barracuda (Hammerschlag et al. 2010) and needlefish (Arceo-Carranza et al. 2004; Day et al. 2016) are piscivorous and prey on small baitfish, this could account for similarities in their space use. Both species are known to use nearshore marine habitats, often in or near-high-structure environments such as mangroves (Murchie et al. 2015).

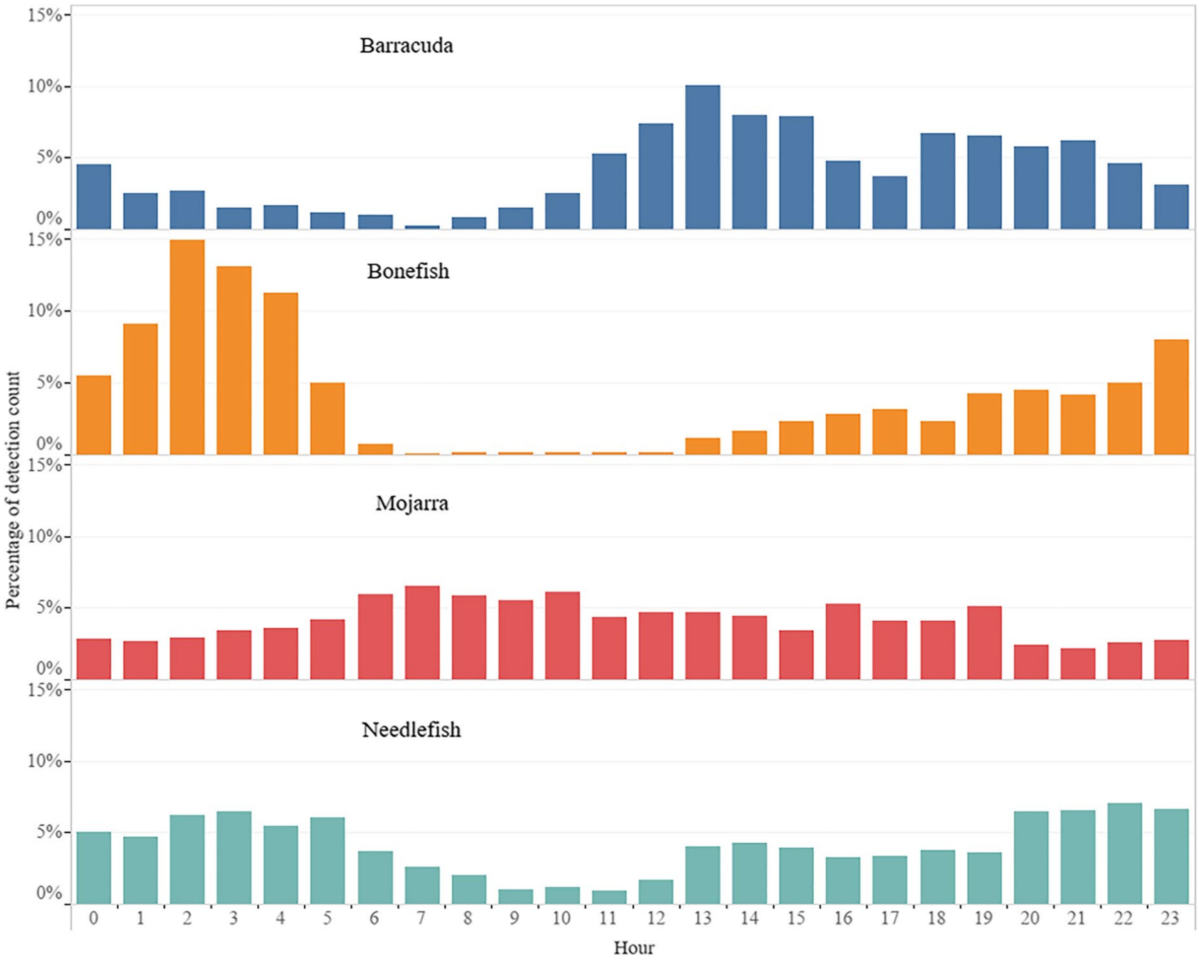

Fig. 7 Percent diel detection counts of barracuda, bonefish, mojarra, and needlefish using data available from February to April 2016

Overall, there was a moderately negative correlation between daily mojarra detection count and needlefish detection count $r^2 = -0.60$), while there were slightly negative relationships between barracuda detection count and mojarra detection count ($r^2 = -0.03$), and between barracuda detection count and needlefish detection count (−0.10) in April and during April (Fig. 6). However, the mojarra we tagged were all larger than those that would likely be consumed by the tagged juvenile needlefish given gape limitations. Nonetheless, the larger mojarra that we tagged often schooled with even smaller mojarra which could contribute to the relationship we observed here.

Across the four species, diel variation in space use and residency was apparent. Bonefish were predominantly detected at night (Fig. 7). Barracuda were detected regularly throughout the afternoon, night, and early morning, and less during the morning (Fig. 7). Needlefish exhibited patterns somewhat similar to barracuda in that residency was lowest during the morning and higher during other parts of the day and night (Fig. 7). Yellowfin mojarra were detected consistently throughout the day and night (Fig. 7). Diel patterns of space use often reflect variation in environmental conditions (e.g. temperature), food availability and predation risk. Because all the fishes studied here are small-bodied, they would all be subject to predation risk from predatory fish (e.g. juvenile lemon sharks, adult barracuda, adult redfin needlefish), as well as raptors and wading birds. We did not study larger predators here but anecdotally we did encounter putative predators

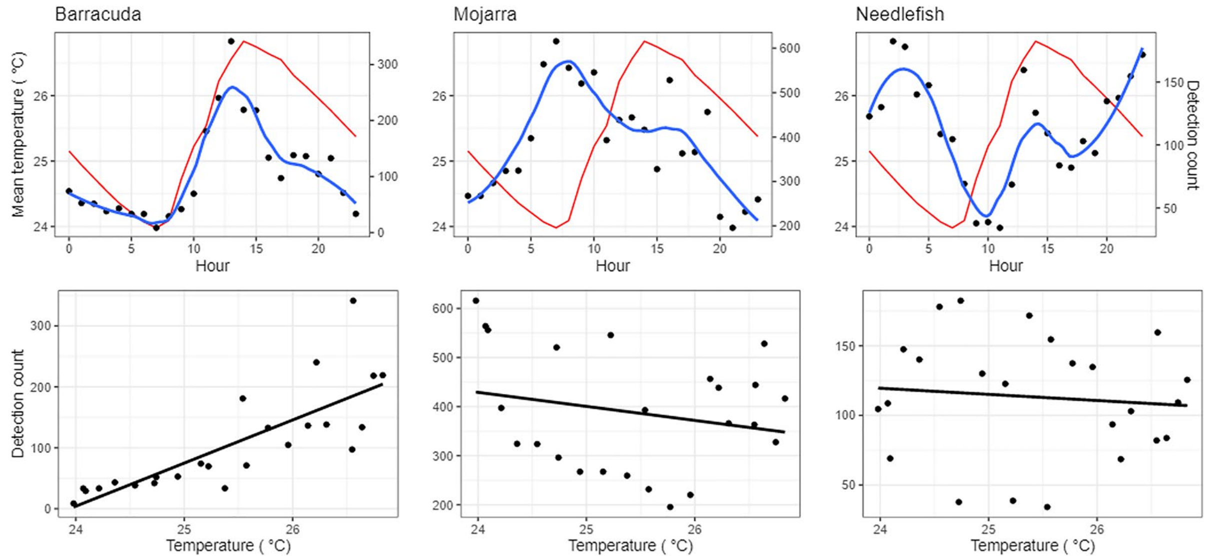

Fig. 8 Correlation between water temperature and detection count of the different fish species, and pairwise comparison in detection count between the fish species using April data only. To account for variability in the number of fish that were detected through the days, we divided that by the number of different fish that were detected in each hourly period. On the top graphs, the red lines inform the diel mean hourly temperature, the black dots inform the total detection count, while the blue line illustrates the best fit line done with a loess smoothing of span 0.5. The bottom graphs inform the relationships between mean temperature and detection count

frequenting the array during daylight periods when they could be easily observed. Previous studies of juvenile lemon sharks, the most omnipresent predator in the study area, revealed that they cruise nearshore areas during both day and night (Murchie et al. 2010), but tend to be more active during nocturnal periods (Nixon and Gruber 1988). We did not study food availability but given that these were highly productive areas, we do not believe food to be limiting. All of the species we studied here are opportunistic and eat a range of invertebrate and vertebrate prey items.

Table 2 Results of linear mixed effects model with detection count dependent on temperature (fixed effect) and fish ID as a nested random effect given its species

Random effects			
Groups	Name	Variance	Std. dev
Fish ID: Species	Intercept	471.76	21.720
Species	Intercept	21.83	4.673
Residual		3,846.75	62.022
Number of obs: 4741, groups: fish ID: species, 59; species, 3			
Fixed effects			
	Estimate	Std. error	*T*-value
Intercept	−74.7913	18.8813	−3.961
Temperature	4.4762	0.7275	6.153

Environmental conditions are the most likely contributor to the diel variation in residency that we observed in our study. We were unable to obtain reliable data on tide but the region has semidiurnal tides which have dramatic effects on water depth and temperature. However, in the area where we conducted our research, solar radiation is the primary determinant of water temperature such that clear diel patterns of water temperature independent of tide conditions are observed. The approximate average surface water temperature for the duration of the study was 23 °C, with March having a lower average temperature of approximately 20 °C and April having a higher average temperature of approximately 25 °C (Fig. 8, Table 2). Given that most of the detections across the species occurred in April, the analysis of temperature as a driver of space use and movement was confined to that month.

Water temperature tended to be lowest in early morning (e.g. 7 am) and warmest in late afternoon (e.g. 15:00) with typical minimum temperatures of 24 °C and highs of 27 °C (Fig. 8). Although this is a

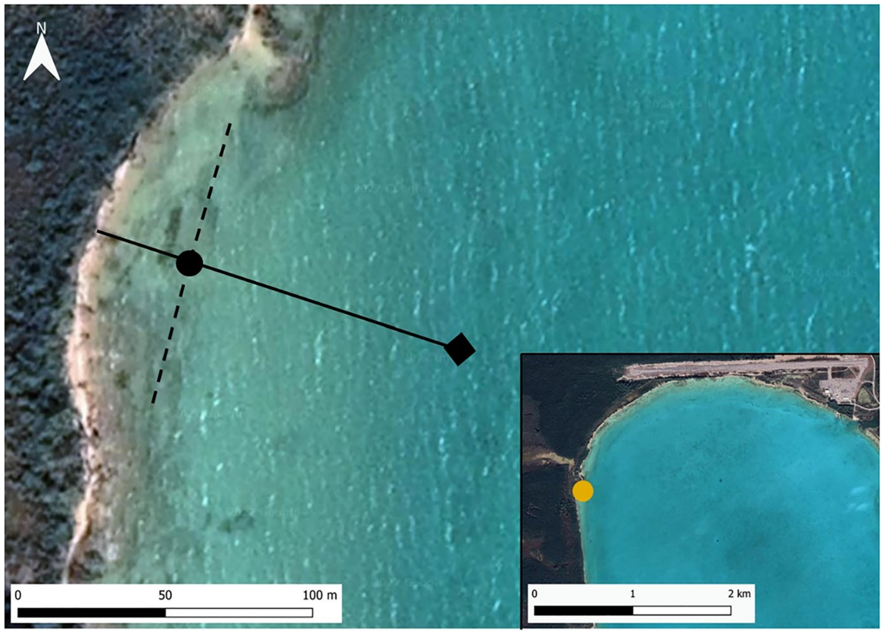

Fig. 9 Map of the range testing completed pre-study on February 16, 2016. The black dot denotes the location of the shallow receiver, deployed horizontally and facing shore, whereas the black diamond denotes the deep-water receiver and was deployed vertically. The hashed line is the northeast and southwest transect, whereas the solid line to the left of the dot is the northwest transect, and to the right of the dot (between the dot and diamond) is the southeast transect

relatively small range in temperatures, water temperature is regarded as the master factor influencing the biology of fish (Brett 1971; Brett and Groves 1979) such that even 1 °C can have a major influence on physiology and behaviour (Fry 1947). Indeed, temperature is considered the main factor on why juvenile bonefish were not present in habitats they had been previously during the March attempts, and why the study was ended in March to wait for warmer temperatures and lower intensity winds in April (although juvenile bonefish were still not captured in April).

We assessed relationships between hourly water temperature and residency for all four species and noted a strong positive correlation for juvenile barracuda whereby the diel pattern of detections (i.e. residency) closely tracked that of water temperature (Fig. 8). Conversely, for juvenile redfin needlefish and yellowfin mojarra also tracked in April, there was a slight negative correlation between water temperature and residency (Fig. 8). We acknowledge that environmental conditions and predator–prey dynamics can interact in complex ways in nearshore systems (DiGirolamo et al. 2012) but our data do not allow us to explore that further. For barracuda, there was a significantly positive correlation between temperature and detection count with a Spearman correlation value of 0.9 and p-value of 2.69×10^{-6} (Fig. 8). For mojarra, there was a slightly negative but non-significant correlation between temperature and detection count with a Spearman correlation value of -0.18 and p-value of 0.40 (Fig. 8). For needlefish, there was a slightly negative but non-significant correlation between temperature and detection count with a Spearman correlation value of -0.11 and p-value of 0.62 (Fig. 8). Based on the output of the Linear Mixed Effects Model, we observe that temperature explains some of the variation in detection count as informed by the greater model estimate (4.4762) compared to the standard error (0.7275; Table 2). However, even while accounting for measured random effects, the unexplained variation in the detection count remains high.

Another interesting finding encountered throughout this project is one related to the diel infestation of a common gnathiid isopod on nearshore reef fish (Sikkel et al. 2006; Coile and Sikkel 2013). Tagging of many of the needlefish used in the current study occurred at night. Following anaesthesia and tagging, fish were left to recover in flow-through net pens for an hour, as had been done with the other tagged fish. However, researchers noticed that although needlefish appeared to be fine post-surgery, several of them showed signs of impairment within 20 min following surgery, and some ($n = 4$) died following these impairments. Researchers recovered the fish to retrieve their tags and noticed

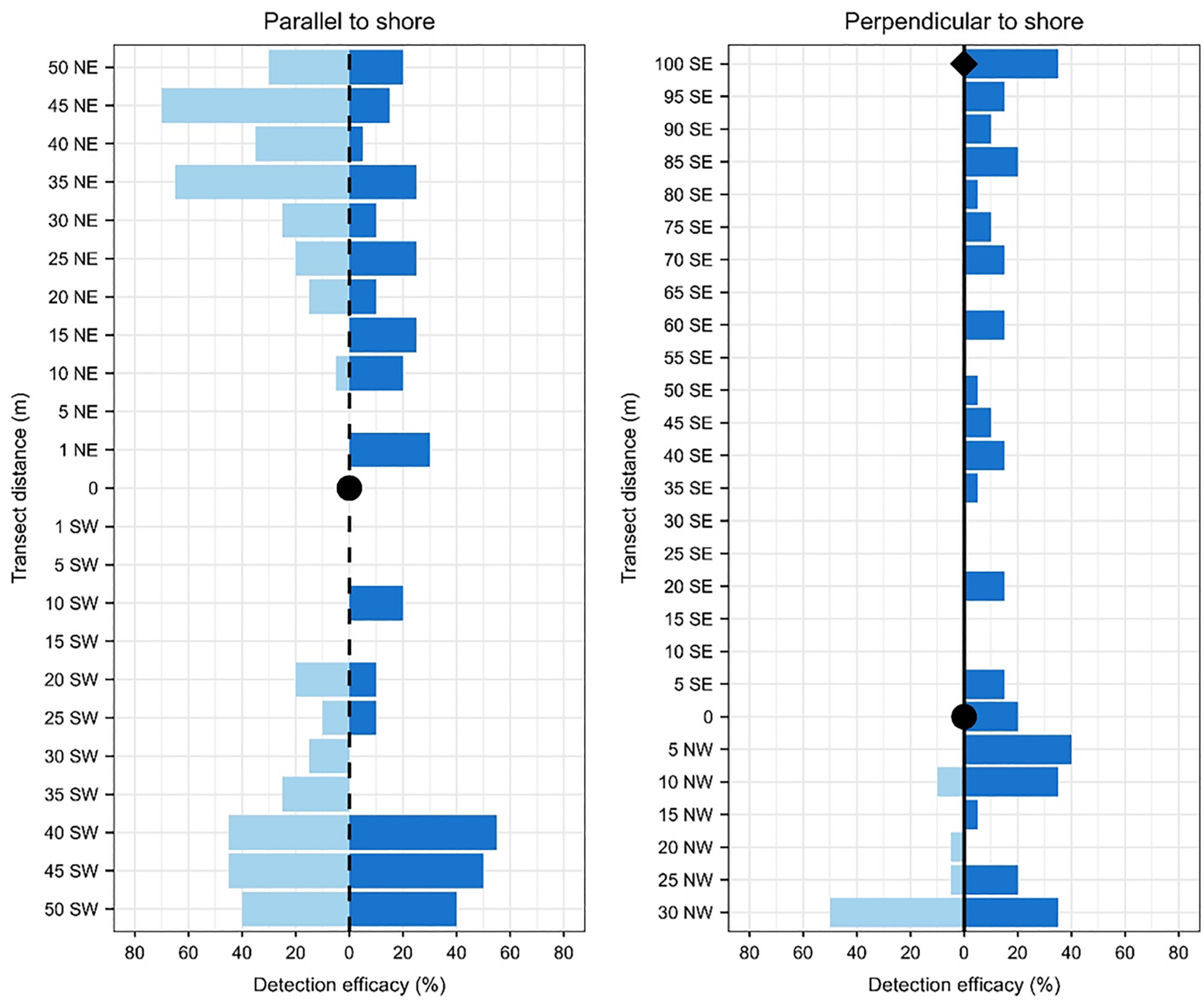

Fig. 10 The deep (dark grey/dark blue) and shallow (light grey/light blue) receiver detections along the southwest and northeast transect (parallel to shore), and southeast and northwest transect (perpendicular to shore). The detection efficacy is presented on the *x*-axis, with the left-side bars (light blue) denoting the shallow receiver detections, and the right-side bars (dark blue) denoting the deep-water receiver detections along the respective transects. The *y*-axis is the distance from the shallow receiver to the test tag (though tag was detected by the deep receiver as well). The hashed line (parallel to shore) and the solid line (perpendicular to shore) are illustrated on the map in Fig. 9 for ease of presentation; the black circle denotes the location of the shallow receiver, and the diamond denotes the location of the deep receiver (coinciding with the range test map in Fig. 9)

that the fish had been consumed by these gnathiid isopods. The gnathiids were accessing the body cavity through the sutured incision sites. Once researchers retrieved the dead needlefish, the only thing remaining was the tag that had been surgically implanted, with all other organs having been consumed by the gnathiids. An outcome of this project learning was to only leave fish to recover in flow-through net pens during the day and to avoid tagging fish into the evenings; this is also a recommendation for any other researchers looking to complete similar works. Though the project findings did not specifically look at fish movement in relation to diel parasitism, barracuda and mojarra were detected least during the night, and avoidance of these nearshore reef fish parasites could be a possible driver of these patterned movements (Fig. 7).

Range testing was completed prior to the commencement of the current study (Fig. 9, Fig. 10). The range testing was completed using a receiver in shallow water (e.g. same depth as receivers 1–12) and another in deep water (e.g. same depth as receivers 19 and 20). The purpose was to determine the detection ranges and efficiencies of both receiver orientations and depths. The tag was tested parallel to shore in shallow water (NE and SW; Fig. 9), and then perpendicular to shore, between shore and the deep receiver (in a NE direction; Fig. 9). Due to the water depth in the shallow area, the receiver was oriented horizontally to the substrate, with the hydrophone tip facing the shore, while the deeper water receiver was anchored to the bottom vertically, with the hydrophone tip facing upwards. Even for the testing completed along shore, the deep-water receiver detected the tag; thus, results show the detection for both shallow and deep-water receivers at all points during the range testing (i.e. NE and SW for both shallow and deep receivers; Fig. 10).

The deep receiver had detections in all transect orientations (i.e. perpendicular to shore in both directions, and from shore to the deep receiver; Fig. 10). During the NE and SW transects parallel to shore, both the shallow and deep receivers performed relatively well (max detection efficacy < 70%), though the shallow receiver struggled to detect the tag when it was closer to the receiver (Fig. 10). The largest limitation appeared to occur when the tag was moved from the shore in the NE direction (perpendicular to shore) and passed behind the shallow water receiver. The shallow water receiver did not detect the tag whatsoever once it was behind the hydrophone tip (Fig. 10). Conversely, the deep receiver with a vertical orientation in the water was able to detect the tag in 5 cm of water against the shore, a little over 130 m away (Fig. 10).

The results of this range test determined that horizontal receivers (i.e. on their side, facing shore) had limitations in what they were able to successfully detect, though this was an accepted trade-off in the current study to allow for finer scale nearshore detections. The results of this range test also support that likely most detections in the current study made by receivers 1–12 would have been either detected between the receivers and shore, or alongside the receivers as in the parallel transects of the range test (NE and SW). The vertical, deep water (~ 2 m) receiver performed considerably better, although detection efficacies were fairly low to moderate throughout. These detection efficacies were only considered for 60 s (i.e. 20 possible detections) at a time and were stationary for that time; it is likely that a moving fish, in the water and within range of the receiver for greater duration than 60 s would offset some of the low to moderate detection efficacies during this range test.

Unfortunately, it is impossible to tease apart changes in fish distribution and detection efficiency in a detailed manner. Nonetheless, given that we used acoustic telemetry in a hostile environment, it is remarkable that we were able to track fish over time and in a range of conditions suggesting that with additional performance assessments this could be a valuable tool for the study of fish in dynamic nearshore habitats. Overall, we conducted one of the first acoustic telemetry studies of multiple juvenile and/or small-bodied fishes in a tropical or subtropical flats fish community. Even with the limitations of the technology used, low sample size for some species, and the challenging environment, our study was able to provide insights into the space use of four species, as well as the role of water temperature as a driver of their spatial ecology. The findings presented here provide important natural history data on the ecology of poorly studied fishes and should be useful for generating testable hypotheses about the interaction of small-bodied fish in coastal flats systems. Future studies would benefit from using a larger array that extended further offshore, longer-lasting tags, and efforts to assess seasonal variation in space use. Using high-resolution 2-dimensional positioning would enable more detailed assessments of movement and habitat use.

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Data availability Data have been uploaded to the Ocean Tracking Network data warehouse (https://members.oceantrack.org/OTN/projects) where we adhere to their data policy (https://members.oceantrack.org/data/policies) which is intended to serve as a long-term repository with the goal of enabling data reuse.

Declarations

Ethics approval and consent to participate Research permits were kindly provided by the Bahamas Department of Marine Resources, whereas animal care approvals were secured from the Carleton University Animal Care Committee and conformed with the guidelines of the Canadian Council on Animal Care.

Conflict of interest The authors declare no competing interests.

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