Measuring mutual movements, mixing, and mingling among multiple mangrove bays by an important estuarine sea bream (*Archosargus rhomboidalis*)

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ABSTRACT

Quantifying the spatial and temporal aspects of fish residency is needed to understand energy transfer, habitat function, contaminant exposure, and effective design of MPAs in estuarine systems. The spatial and temporal movements of 19 sea bream (*Archosargus rhomboidalis*), an ecologically important species in mangrove estuaries of the western Atlantic, were investigated in multiple bays on a Caribbean Island over two years using surgically implanted acoustic transmitters. Fish were almost continuously monitored (residency index 96–100%) by an array of hydrophones during the 11–13 month battery-life of their transmitters. Individual fish utilized small core areas (mean = 9.8 ha during daytime and 11.0 ha at night), displayed daily site fidelity (mean = 57% overlap in day night core area), showed no evidence of an ontogenetic increase in core habitat size, and many exhibited a change in the bays utilized during winter months which is coincident with suspected spawning. Fish captured from the same bay generally occupied the same spaces within the study area, and in similar proportions, compared to fish captured in adjacent bays. Fish from different bays did not mix and wander throughout the ecosystem even though it is all suitable habitat and is used by different groups of localized individuals. This similarity of occupancy patterns is limited to the spatial scale of bays and temporal scales of weeks or months. When considered at the resolution of individual receivers and hourly time steps, most fish are not in close proximity to one another for the vast majority of the time. Although some pairs of fish had as many as 84% of their hourly detections on the same receivers in the month after tagging, they gradually spent less time near each other, even though their overall pattern of movements was consistent at the scale of whole bays. This highlights the importance of examining movements of fish on multiple spatial scales and time-intervals to understand their interactions.

1. Introduction

Understanding the movements of estuarine fish is needed to inform many aspects of ecosystem management. The size, location, and temporal patterns of fish residency relate to everything from energy transfer (Clark et al., 2009; Hammerschlag et al., 2010a) and nursery function (Huijbers et al., 2015), to contaminant exposure (Taylor et al., 2018) and effective design of MPAs (Aspillaga et al., 2016; Kendall et al., 2017). Fish movements can vary over a range of temporal and spatial scales in response to their requirements for foraging, sheltering, and spawning. Temporal variation may include day versus night, ontogenetic, and seasonal effects (Jadot et al., 2002; D'Anna et al., 2011; Gannon et al., 2015). Spatial variation may include core activity space, home range area, and spawning components that interact with temporal variables (e.g., day vs. night activity area, spawning migration, ontogenetic shifts) (Abecasis et al., 2009; Di Lorenzo et al., 2014; Aspillaga et al., 2016). Even conspecifics in the same area can display different movement patterns due to density dependent factors or plasticity in their response to an environment (Jadot et al., 2006; Abecasis and Erzini 2008; D'Anna et al., 2011; Alós et al., 2012; Di Lorenzo et al., 2016).

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Consequently, in order to obtain a thorough understanding of space requirements, it is important to track movements of many fish comprehensively throughout their potential range and for time periods that span annual cycles. Despite these basic information needs, key gaps remain in research on fish movements for important species in many habitats.

Research on fish movements in mangrove estuaries has focused on a limited number of topics (Faunce and Serafy 2006). For example, mangrove-associated species that are popular fisheries targets or have protected status have received a large proportion of research interest (e. g., Simpfendorfer et al., 2010; Honda et al., 2016; Young et al., 2016; Taylor et al., 2018). In contrast, common fishes often neglected in movement studies include those that are full-time residents, but not subject to fisheries or special conservation needs. Such species can play significant roles in the mangrove ecosystem due to high abundance, position in food webs as primary and secondary consumers, and their role as prey or forage fish (Odum and Heald 1972; Wolff 2006). There is a growing need for information on these important but often less studied fish as management shifts to ecosystem based approaches with the intention of maintaining functional food webs, especially in semi-enclosed bodies of water such as mangrove estuaries (Wolff 2006;

Borges et al., 2017, NOAA Fisheries 2018).

Sea bream (*Archosargus rhomboidalis*) (Sparidae, Linneaus 1758) can be among the most abundant fish in mangrove estuaries of the western Atlantic. They commonly occur in turbid tropical and subtropical bays of continental (Vaughan 1978; Chavance et al., 1984; Hammerschlag and Serafy 2010) and Caribbean estuaries (Acosta and Appeldoorn 1995; Matos-Caraballo et al., 2007; Aiken et al., 2008; Clark et al., 2009; Vaslet et al., 2010) where they omnivorously consume a mixture of algae, seagrass, bivalves, and crustaceans (Vaughan 1978; Nagelkerken and van der Velde 2004; Hammerschlag et al., 2010b). Although they are an abundant species that grows rapidly (2 year lifespan) (Chavance et al., 1986), matures early (~8–9 cm) (Vaughan 1978; Chavance et al., 1986), and attains a small to medium size (~30 cm maximum Total Length) (Robins and Ray 1986), they are not reported as a major fishery species anyplace in their range (Vaughan 1978; Chavance et al., 1984; Carpenter 2002). Their primary ecosystem linkage may be as prey fish and moving energy from softbottom and lower trophic levels in the food web to other parts of the ecosystem and higher trophic levels (Nagelkerken and van der Velde 2004; Clark et al., 2009; Hammerschlag et al., 2010a). Common piscivores large enough to consume them in this habitat include tarpon, green moray eels, and sharks (Kendall et al., 2020;
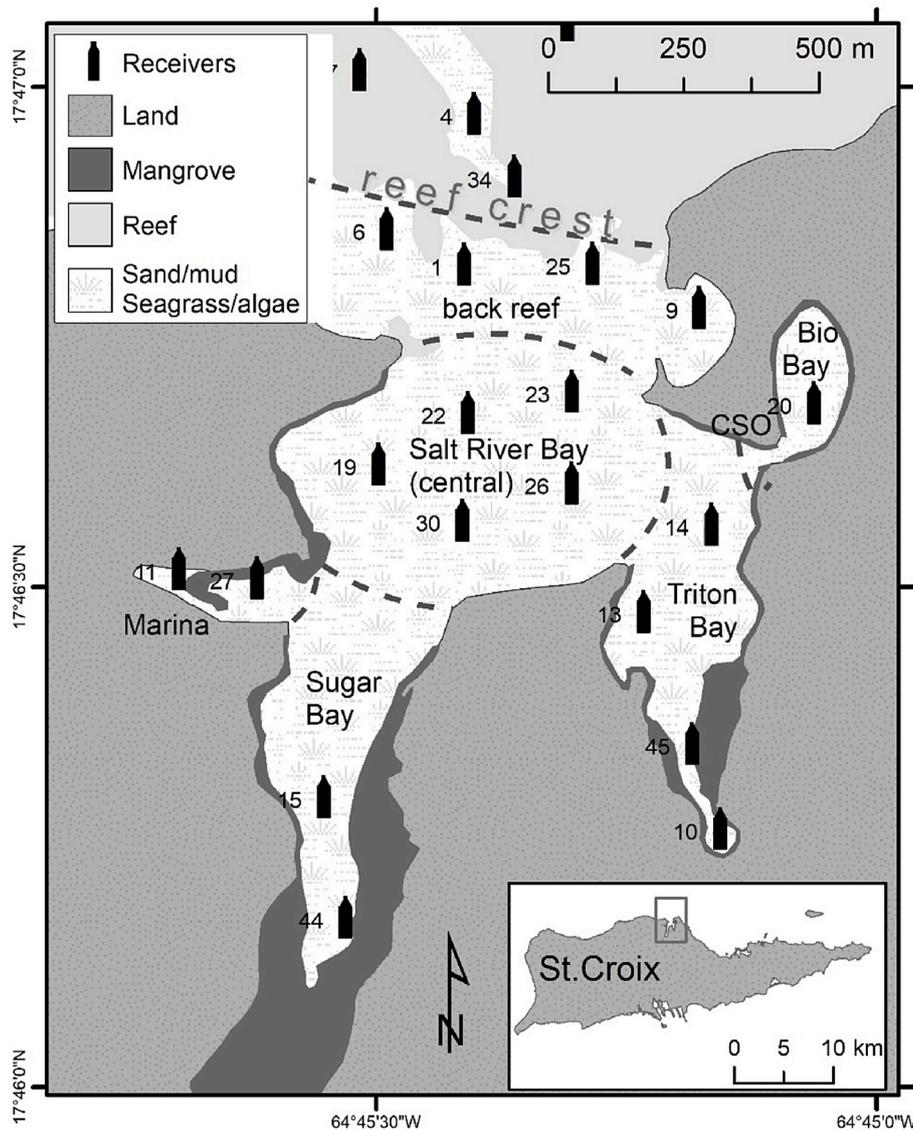

Fig. 1. Salt River Bay study area with site numbers of VR2W telemetry receivers as well as divisions of bays used in summary analyses (dashed lines). Only three of the receivers outside the reef crest are visible in this extent. Rectangle in the inset shows location of Salt River Bay on north coast of St. Croix.

Hammerschlag et al., 2010b). Spawning for this gonochoristic species takes place in winter and spring months in the Gulf of Mexico and Caribbean (Beebe and Tee-Van 1928; Chavance et al., 1984, Garcia-Cagide et al., 1994). Despite its abundance and potentially important role in food webs of mangrove ecosystems, little is known about the movement ecology of these fish beyond this basic life history information.

The objectives of this study were to investigate spatial and temporal aspects of sea bream movements in a mangrove-lined estuary using passive acoustic telemetry. Specifically, we sought to understand the home range size, temporal activity patterns (i.e., diel, lunar, seasonal), and movements of individuals within a multi-bay estuary. In addition, we examined the extent to which fish from various bays shared or overlapped in their home range, shifted to utilize new areas in coincident seasons, and the extent to which they may actually be using the same areas at the same times of the day.

2. Materials and methods

2.1. Study area

Salt River Bay National Historical Park and Ecological Preserve lies on the north central coast of St. Croix, US Virgin Islands (Fig. 1). The estuary is comprised of four smaller bays that lead into a common central basin which is open to the ocean through a natural cut in a fringing reef at the head of the underwater Salt River Canyon (Kendall et al., 2005). Two of the smaller bays are man-made and two are natural. On the eastern side of the estuary lies Bio Bay, a man-made basin dredged in the 1960s as part of a failed hotel development, now the location of the Coastal Studies Outpost (CSO) operated by the National Park Service. This bay has the most restricted water flow compared to the others and possesses a distinctive nighttime ecosystem due to its high concentration of bioluminescent microorganisms (Pinckney et al., 2018). The southeastern bay in the system is Triton Bay, a natural feature surrounded by a very small watershed (~100 ha) with steep, forested hillsides (Oliver et al., 2011). Sugar Bay is to the southwest, another natural bay that differs from Triton in that it is the outflow point of the third largest watershed on St. Croix (~1500 ha) and receives intermittent runoff from a mixed-use mosaic of small farms, forest, residential housing, roads, and small commercial properties (NOAA Office for Coastal Management, 2015). On the western side of the study area is another dredged feature, a small marina that has two narrow openings. All four of these bays are 2–4 m deep, have a mud or sandy bottom, sparse algae or seagrass, and apart from the seawall portion of the marina, all four are almost completely lined with red mangroves (*Rhizophora mangle*) (Kendall et al., 2005). Salt River Bay's central basin is deeper (~5 m), has a sandier bottom, greater seagrass and algae coverage, occasional hardbottom, and a shoreline consisting of sand, rocks, coral rubble, or isolated mangroves. These bay divisions were used to summarize fish positions and tagging locations with the exception of CSO which was only used as a tagging location (Fig. 1).

Temperature (27–29 C) and salinity (35–36 PPT) are similar throughout these bays except during times of heavy rainfall when Sugar Bay receives greater runoff from its large watershed which can reduce salinity on a temporary basis (Kendall et al., 2005). Average oxygen saturation is lowest in the extremities of the bays (65–69%) compared to locations closer to the reef cut (81–84%) whereas turbidity is highest far inside the bays (3–5 nephelometric turbidity units or NTU) compared to the central basin (1–3 NTU) (Kendall et al., 2005). Temperature and salinity loggers were deployed in Triton, Sugar, central bay, and Marina locations while fish were being tracked however, they were part of a bad manufacturing lot and failed to provide useable data.

2.2. Fish tagging

On multiple dates in April–May 2017 and April 2018, fish were captured live using wire fish traps deployed along the mangrove fringe at 1–2 m depth (Table 1). Although various bait types were used in an effort to attract a diversity of fish species for a general tagging study, catch in these bays was dominated by sea bream. Overall sea bream abundance in the catch was ~10:1 over all other species combined, although it varied dramatically among trap sets, even at the same location. Trapped fish were placed into shaded bins filled with local baywater onto the deck of a small research boat. Fish smaller than 20 cm TL were quickly released as being too small to accommodate transmitters. Fish for tagging were haphazardly chosen from remaining fish with the goal to tag roughly equal numbers of fish from each bay. All were well past the size at maturity (length at 50% maturity is 90 cm SL, Chavance et al., 1986). Multiple bins were used to prevent crowding and seawater was changed frequently. Coded acoustic transmitters (VEMCO model V8-4L, random ping delay 130–230 s, ~330 day battery life) were implanted into the body cavity of 27 fish through a ventral incision using well established surgical practices (Reese Robillard et al., 2015). After the 1–2 min surgical procedure, tagged fish were moved to a separate recovery bin for several minutes until normal behaviors resumed and then were released at the point of capture.

2.3. Array design and evaluation

Acoustic receivers (VEMCO, VR2W) were strategically placed throughout the bays and extending offshore into coral reef habitats as part of a general fish telemetry study (n = 18 inside the estuary, n = 18 outside the fringing reef) (Fig. 1). From one to three receivers were needed to monitor the smaller bays depending on their size and morphology, and another nine were moored in the central bay and back reef in a tiered arrangement to detect fish passage. Receivers were spaced approximately evenly (200–250 m apart) inside the bays. Detection range was evaluated by repeated deployments of a range test tag which had a 10 s ping interval and the same size and power specifications as the transmitters used in fish. The tag was deployed for a minimum of 15 min at multiple distances from the receivers at 45 locations throughout the landscape. Range was defined as the distance at which 50% of the expected pings were detected based on a binomial GLM with a logit link function. Range was used as an input parameter for calculating core area sizes. A sentinel tag with the same programming as those used in the fish was fixed to a sand screw inside the bay north of receiver 23 (Fig. 1) to monitor temporal changes in detections due to environmental factors and aid with interpretation of detections from fish. The number of daily detections of the sentinel tag was plotted and day versus night detection rates were compared using the Student's t-test on mean monthly detections. Receivers were retrieved, cleaned, and downloaded every six months and batteries were changed annually.

2.4. Analysis

2.4.1. Geographic and temporal patterns of residency

Data were formatted and organized through the Florida Atlantic Coast Telemetry Network (Young et al., 2020) and the glatos package in R (Krueger et al., 2018). A residency index (RI) was used to determine the proportion of time that each fish was tracked within the acoustic array overall (Alós et al., 2012). This was calculated by dividing the total number of detection days (i.e., a day with a detection anyplace in the array) by the transmitter lifespan (release date to final detection date). The percentages of all detections that occurred in each bay (i.e., Bio Bay, Triton Bay, Sugar Bay, Marina, or central bay) during the day versus night were expressed as stacked bar graphs for each fish. For the purposes of this study, day was defined as 0730–1730 local time, and night was defined as 1930-0530. Crepuscular detections during dawn (0530–0730) and dusk (1730–1930) were excluded since they had no unique patterns and were a transition time between day and night periods which were the focus of the study. The proportions of bay occupancy were compared using non-metric multidimensional scaling

Table 1
Tagging and detection summary for each fish. Detection Days abbreviated as DD.

Fish ID	Total Length (cm)	Tagging location	Date tagged/ released	Last day detected	DD	Residence Index (DD/ Tag Life)	Total Detections	Mean daytime detections	Mean nighttime detections
448	20	Triton	4/27/17	10/12/17	169	0.99	88187	246	178
449	20	Triton	4/27/17	4/18/18	357	1.00	184748	242	186
451	20	Triton	4/27/17	4/18/18	357	1.00	160792	225	143
452	21	Triton	4/27/17	4/18/18	357	1.00	141309	185	140
455	23	Bio Bay	4/27/17	4/23/18	350	0.98	95403	126	114
459	20	Bio Bay	5/24/17	5/6/18	348	1.00	108265	130	125
218	25	Triton	4/19/18	3/15/19	331	1.00	81397	148	50
226	23	Triton	4/20/18	3/15/19	331	1.00	64635	69	100
258	24	Triton	4/20/18	3/16/19	328	0.99	122876	198	112
266	23	Triton	4/19/18	3/15/19	331	0.99	87375	159	59
234	22	CSO	4/23/18	3/19/19	331	1.00	48596	89	45
252	20	CSO	4/23/18	3/19/19	331	1.00	67871	120	61
271	22	CSO	4/23/18	3/19/19	331	1.00	67998	82	84
274	20	CSO	4/23/18	2/28/19	313	1.00	68462	116	73
217	24	Sugar	4/20/18	3/16/19	328	0.99	29466	56	19
225	26	Sugar	4/20/18	3/16/19	330	0.99	68422	122	53
242	24	Sugar	4/20/18	3/16/19	331	1.00	136338	225	114
243	22	Sugar	4/20/18	3/16/19	331	1.00	131501	190	140
265	23	Sugar	4/20/18	3/16/19	329	0.99	32536	62	20

(nMDS). This ordination was based on a Bray Curtis similarity matrix derived from fourth-root transformed percentages to prevent the most used bays from dominating the structure of the nMDS plot (Clarke and Gorley 2006). This was followed by an analysis of similarity (ANOSIM) to determine if fish tagged at the same locations were utilizing the same bays during the day and night time periods (Clarke and Gorley 2006). These analyses were conducted in Primer (v6.1.14).

Seasonal, monthly, and lunar patterns were investigated for each fish using customized abacus plots. Rather than showing all detections at each receiver, we grouped receivers by bay (i.e., Bio Bay, Triton Bay, Sugar Bay, Marina, or central bay) (Fig. 1) and plotted detection days for the ~1 year time series.

The potential influence of lunar cycle on movements was examined using Chi-Square Goodness of Fit Tests (Zar 1999). Specifically, we evaluated if fish spent more time during a particular moon phase in the central bay/backreef areas where spawning has been shown to take place in other systems (Chavance et al., 1984). For this analysis, we summarized the number of detections in the central bay/backreef areas by moon quarter (i.e., new, waxing, full, waning) for each fish and tested the null hypothesis that detections had an equal distribution among lunar quarters (i.e., 1:1:1:1 ratio). Preliminary evaluation of suspected spawning months only (January–June from Chavance et al., 1984) were no different from analysis of all months combined, therefore the entire tracking period of each fish was included in this analysis. Bonferroni adjusted p values (0.05/19 tests = 0.0026) were used to account for conducting multiple tests.

2.4.2. Core area size and coincidence

Several tools are available for evaluating activity space from telemetry data (e.g., Udyawer et al., 2018). In this study, the size of each fish's activity space was calculated as kernel utilization distributions (KUDs) based on the Brownian Bridge Movement Model (Van Winkle 1975), and were created using the adeHabitatHR v.0.4.18 package for R (Calenge 2006). Range of 50% detection efficiency was calculated as 200 m and entered as the sig2 parameter in the kernelbb function. Separate Brownian Bridge KUD estimates were calculated for each fish for day versus night movements by month. A KUD was not calculated for time intervals when only one receiver had detections (this occurred in <2% of possible calculations). Land was masked out from all KUD analyses. We followed other recent research on home range of fishes (defined as 95% KUD volume) and focused on the core area of use (50% KUD) since it represents the most intensively used part of each fish's habitat (Jadot et al., 2006; D'Anna et al., 2011; Di Lorenzo et al., 2014; Gannon et al., 2015; Aspillaga et al., 2016). The core areas of these monthly estimates

were analyzed in several ways. First, we tested whether the size of each fish's core area was different during the day versus night. For this analysis, paired t-tests were used to compare each fish's monthly day versus night core area size. Second, we sought to determine how core area size may change with fish age (i.e., does area size increase with fish age). For this analysis we performed a simple linear regression of the day and night core area sizes by month for the ~1 year period that each fish was tracked. Bonferroni adjusted p values (p = 0.0026) were again used to account for conducting multiple tests.

We next evaluated spatial aspects of fish's core area. Specifically, we determined if the location of each fish's day versus night core area changed. In this analysis, we calculated the percentage of each fish's nighttime core area that was overlapped by its daytime core area for each month that it was tracked. We also calculated the inverse (percentage of daytime core that was overlapped by nighttime) but results were similar. Preliminary evaluation of these results indicated no consistent trends among months and therefore all such monthly differences in core area were averaged for each fish.

The coincident use of space among fish was compared in 1 h intervals to investigate more detailed temporal associations such as using the same part of a bay at approximately the same time of day. For this analysis, we converted all detections into detection hours (presence or absence of a detection any time in each hour) for every fish at every receiver (hereafter called receiver-detection-hours). This enabled us to determine how often pairs of fish were in approximately the same place (within detection range of the same receiver) at approximately the same time (within the same hour). The Jaccard Similarity Index (Jaccard 1912) was used to measure coincident receiver-detection-hours between pairs of fish. This index is the proportion of all receiver-detection-hours of a pair of fish that occurred together. Fish pairs that are seldom detected at the same place and time will have lower similarity values than those fish pairs with higher values. A value of zero indicates no overlap, and 1 indicates complete coincidence of receiver-detection-hours. The Jaccard index is not influenced by mutual absences but does require the same overall monitoring period for appropriate comparisons. Therefore, a few weeks at the beginning and end of some fishes' tag duration were trimmed leaving only the core dates when all fish were present. Fish 448 was excluded from this analysis entirely since it is suspected to have died halfway through its tag life. We calculated the Jaccard Index on a monthly basis in pairs for all fish tagged together and plotted those values by month to examine how pairs of fish may have been found in close proximity to each other through the tracking period.

3. Results

Of the 27 fish tagged over two years at multiple locations within the estuary, 18 provided the full interval of 330 days or more of potential information based on battery life of the transmitters (Table 1). One fish (ID 448) provided 7 months of data before the detections indicated likely mortality. Eight others provided less than one month of useable detections (<10% of the possible total) and were not considered further.

3.1. Sentinel tag

The sentinel tag was affixed to a sand screw in the central bay and provided a consistent reference pattern of detections based on environmental conditions (e.g., more signal interference would result in fewer detections) and additional perspective into the detection patterns of fish (Supplemental Fig. S1). Because surrounding landscape features blocked transmissions or other receivers were too far away, the sentinel tag was only detected on receiver 23. First, detections were generally not influenced by time of day. There was no significant difference in monthly detections of the sentinel tag during the day versus night (p = 0.22). Some months had more detections at night and others during the day, but overall values were similar and within 10% of each other. Therefore, it was not necessary to adjust raw detection numbers during day versus night comparisons for fish. Second, although it was detected on almost every day of both years (>95% of days in 2017, and 100% of days in 2018) and detectability was generally stable for the majority of the study period, detection rates of the sentinel tag became erratic and relatively low during summer months in 2017 (Fig. S1). The definitive cause of this erratic signal blockage is unknown but is suspected to be sound-absorbing macroalgae drifting and accumulating around the receiver and/or sentinel tag during this time. Nuisance levels of sargassum have impacted many Caribbean islands in recent years (Langin 2018) and were observed piled high on the beach northeast of receiver 23 and accumulated on the substrate around receiver 9 during our study (M. Kendall pers. obs.). The pattern of fewer and more intermittent detections in the central bay was observed for fish as well during this time, and could have been interpreted as a change in their behavior were it not for the sentinel tag. The sentinel tag experienced a dramatic increase in both the number and regularity of detections immediately after the passage of Category 5 Hurricane Maria on September 19–20, 2017. We hypothesize that the currents and wave action associated with the storm swept away the drift sargassum from the tag and/or receiver 23 enabling much greater detectability of the sentinel tag for the remainder of the study.

3.2. Geographic and temporal patterns of residency

The residency index indicates that fish were detected in the array for 97–100% of their possible detection days based on battery life of transmitters (11–13 months). None of the sea bream tracked in this study were ever detected on receivers outside the reef crest. Furthermore, no sea bream were ever caught outside the reef crest despite intensive trapping effort. Range tests showed that stations inside the bays had a detection range of ~200 m (based on 50% probability of detection), and therefore provided overlap in detection areas between adjacent receivers and a high degree of bay coverage overall. Collectively, this evidence indicates that sea bream never ventured outside the reef crest or left Salt River Bay and the acoustic array provided nearly continuous monitoring of their activities on a daily basis.

The proportion of time that each fish spent in the various bays was related to their capture location (Fig. 2). For example, fish captured and tagged in Triton Bay had most of their detections in Triton Bay (>90%). Fish tagged at the mouth of Sugar Bay had detections there and also at receivers in the central bay and marina. Overall, the proportions of time spent in each bay were similar during day versus night, but there were a few exceptions. Both fish tagged in Bio Bay (455, 459) spent most of
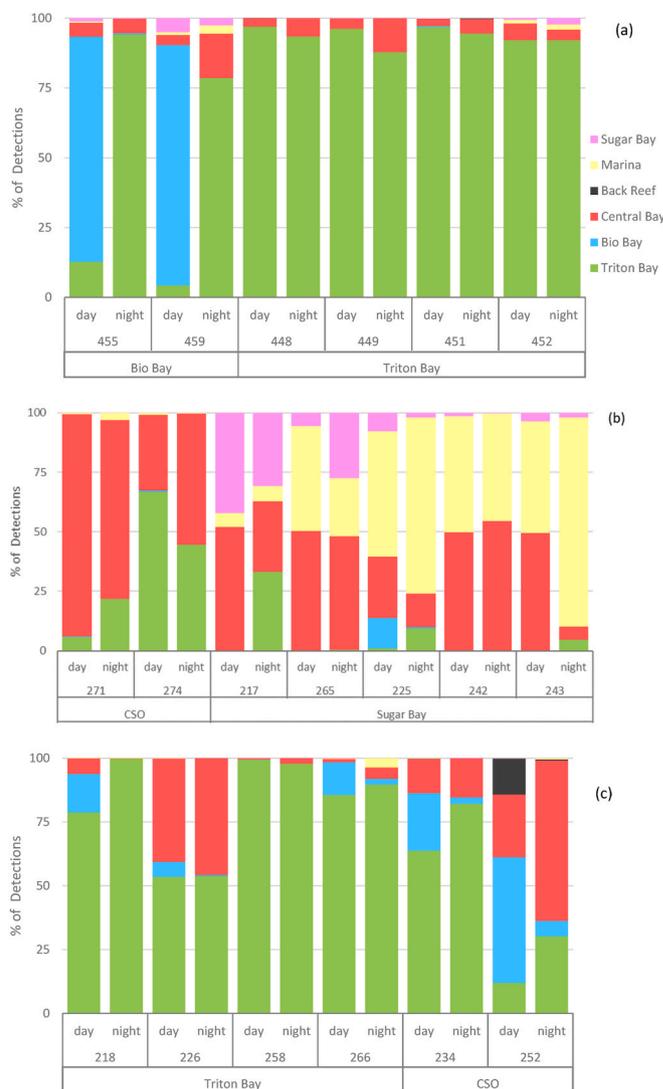

Fig. 2. Percentage of all detections for each fish (three digit unique identification number) among bays calculated during the day and night respectively in (a) 2017, (b) 2018, and (c) 2018 continued. Capture location is listed below each group.

their days in that area, but then shifted to Triton Bay at night. Another fish (252), tagged at the CSO which is next to Bio Bay, had a similar pattern with many more detections in Bio Bay during the day, but then shifting to Triton Bay and Central Bay at night. Two fish tagged in Sugar Bay also showed differences in the locations during day versus night. Both of them spent approximately half their time in the Central Bay during the day, but then spent more time in Triton Bay (217) and the Marina (243) at night.

These patterns were supported by nMDS which plots each fish/day/night combination into ordination space such that points closer together are relatively more similar than those farther apart (Fig. 3). The stress level in this ordination was 0.11 which indicates a good fit in which the overall structure may be interpreted confidently. In general, fish tagged in the same location plotted close to each other, indicating that they generally used the same bays in similar proportions to each other. For example, fish tagged in Sugar Bay had similar overall usage of the various bays during the detection year. Fish tagged in Triton Bay, Bio Bay, and near the CSO also showed this distinct pattern. Also of note, each fish's day versus night points also generally plotted near each other, which indicates that most fish used the same bays in similar proportions in both the day and night. The exceptions to this that were
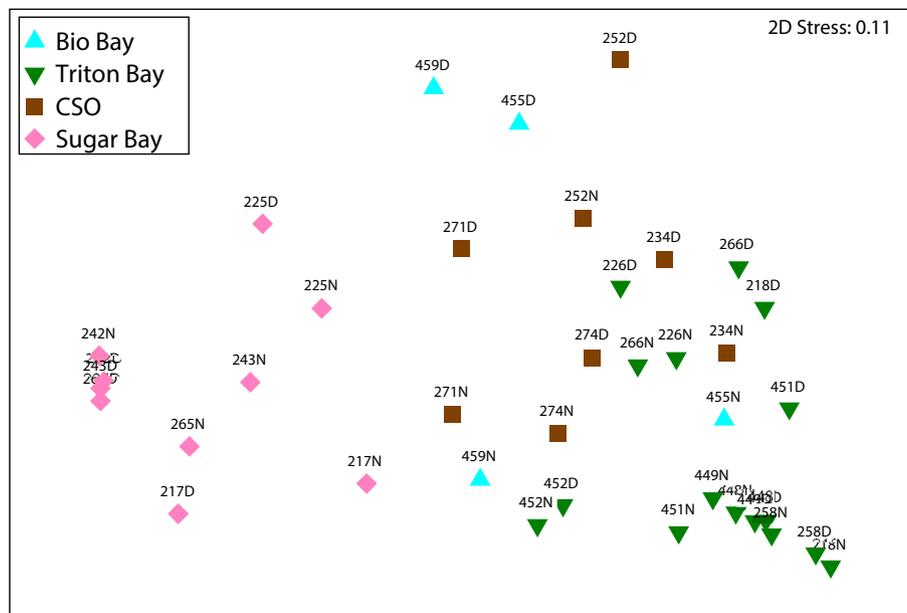
Fig. 3. nMDS based on overall day (D) and night (N) proportions of detections by bay for each fish (i.e., each fish has one point for day and another for night). Point color symbolizes the tagging location of each fish. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

noted in the bar graphs (Fig. 2a) are also evident in the large separation of day versus night points in the nMDS for fish tagged in Bio Bay. During the day these fish plotted separately from most other fish, indicating a relatively different pattern of bay usage, whereas at night their bay usage was similar to the fish tagged in Triton Bay.

The overall ANOSIM indicated that there were significant differences in the overall proportions of bays used by fish based on their location of tagging (R = 0.74, 0 out of 999 permutations >/ = R, p < 0.001). Pairwise tests indicated that each group of fish from a particular tagging location had a significantly smaller within-group difference in bay utilization than all other groups (Table 2).

Temporal patterns in the use of different bays were evident in the abacus plots (Fig. 4a–b). Most fish had very consistent detections primarily in just one or two bays over the course of the entire year, plus intermittent excursions to other bays. Fish tagged in the same bay generally had similar patterns. Departures from this pattern sometimes

Table 2
ANOSIM results and pairwise tests of differences in overall bay use (i.e., proportion of each fish's detections in each bay by day or night) among fish from each tagging location.

Test pairs	R statistic	Possible permutations	Actual permutations	Number >/ = observed	p value
Bio Bay, Triton Bay	0.474	4845	999	13	0.014
Bio Bay, CSO	0.504	495	495	6	0.012
Bio Bay, Sugar Bay	0.828	1001	999	1	0.002
Triton Bay, CSO	0.457	735471	999	0	0.001
Triton Bay, Sugar Bay	0.974	5311735	999	0	0.001
CSO, Sugar Bay	0.943	43758	999	1	0.002

occurred in isolation from other tagged fish and at other times as part of coincident movements shared by multiple individuals. October had an uptick in mobility and use of multiple bays for a few weeks during both years. Winter and spring months also had an increase in the number of bays used by many fish. Onset of this behavior occurred in January in both years and lasted until tags expired in March or April. The passage of Category 5 Hurricane Maria on September 19, 2017 caused no noticeable change in any of the fishes' behavior patterns in the week leading up to, the day of, and following the storm.

Although all fish used the backreef or central bay for at least some time during each moon phase, the number of detections in the backreef or central bay area among lunar phases were significantly different for all fish ($X^2_{(0.05, 3)}$ > critical value, p < 0.001, for all fish) (Table 3). This indicated that the pattern of central bay use among lunar quarters was different from random for all fish, however, the particular phase of highest use was not consistent. The most fish (8/19) had the largest number of their detections in the central bay during the full moon. These fish were captured from Bio Bay, CSO, and Triton Bay. The remaining 11 fish had peak usage of the central bay during other moon phases. None of the fish from Sugar Bay had their peak detections in the central bay during the full moon.

3.3. Core area size and coincidence

Size of each fish's monthly core area was similar during the day and night (Table 3) despite most fish having more detections during the day (Table 1). Overall, core area size among all fish was 9.8 ha (+/- 0.3 SE) during the day and 11.0 ha (+/- 0.3 SE) at night. This core area corresponded roughly to the overlap in detection range of ~3 neighboring receivers in our array. Only 2 out of 19 fish had a significant difference in their day vs night core area size, although the patterns in these differences were not consistent (i.e., fish 243 had a larger core area during the day, 258's was larger at night) (Table 3). Core area size also did not change during the course of the 11–13 month tracking period for most fish. Only 1 out of 19 fish had a significant linear relationship with core area and month (Table 3). Even if all these comparisons used the less conservative non-Bonferroni adjusted p – value (0.05), only 5-6 additional fish out of the 19 fish analyzed would have had significant relationships and the pattern of those relationships was not consistent (e.

Fig. 4a. Abacus plots of individual sea bream (three digit unique identification number) tagged in 2017 by capture location (column at left) and the calendar of detection days colored among the bays in the study area. Time is noted along the X axis as the first letter of each month.

Fig. 4b. Abacus plots of individual sea bream (three digit unique identification number) tagged in 2018 by capture location (column at left) and the calendar of detection days colored among the bays in the study area. Time is noted along the X axis as the first letter of each month.

g., some increasing core area size with age, some decreasing), suggesting that the pattern was spurious.

Spatial overlap of each fish's day and night core area was expressed as the percentage of the nighttime core area by month that was shared with its daytime core area in the same month. A value of 0 indicated no overlap in day versus night core area, and a value of 100% indicated that the nighttime core area had exactly the same footprint or was completely within the extent of the daytime core area. The mean spatial

overlap between daytime and nighttime core areas was 57% (4% SE) with most values being between 44 and 93%. Two fish deviated from this pattern of general overlap in day versus night core area. Both were tagged in Bio Bay and had very little overlap in their nighttime and daytime core areas (10–29%).

The Jaccard Similarity Index for fish pairs plotted by month revealed which fish are most frequently detected in the same area at the same time (i.e., on an hourly basis) and how those associations change over

Table 3
Core area (CA) values and lunar activity summary for each fish. Note that the critical value of p following Bonferroni adjustment is 0.05/19 = 0.0026. P - values below this are noted by (*).

Fish ID	Moon phase with peak central/ backreef activity	avg. Day CA size (ha)	avg. Night CA size (ha)	D/N CA size diff. p - value	CA size vs. fish age regression p - value	% of nighttime CA overlapped by day CA (+/− SE)
448	Full moon	6.3	9.3	0.045	0.209	63 (12)
449	Full moon	5.9	8.7	0.043	0.947	61 (8)
451	Waxing	6.9	9.0	0.223	0.076	58 (8)
452	Full moon	9.1	11.6	0.026	0.004	45 (10)
455	Full moon	10.4	11.6	0.308	0.001*	29 (11)
459	Full moon	9.8	12.3	0.122	0.062	10 (6)
218	New moon	8.4	9.3	0.462	0.351	44 (8)
226	Waxing	11.2	13.2	0.011	0.010	62 (4)
258	Waning	3.1	6.7	<0.0001*	0.919	51 (8)
266	Full moon	7.0	10.9	0.003	0.018	50 (8)
234	Waxing	10.3	10.8	0.398	0.490	62 (6)
252	Waxing	12.1	12.8	0.144	0.424	45 (8)
271	Full moon	13.2	14.4	0.078	0.683	58 (4)
274	Full moon	11.4	11.1	0.333	0.046	71 (4)
217	New moon	13.3	13.8	0.509	0.006	74 (7)
225	New moon	11.7	13.0	0.311	0.227	73 (7)
242	Waning	11.9	11.2	0.037	0.825	93 (2)
243	Waning	12.1	8.4	<0.0001*	0.022	59 (3)
265	Waning	11. 7	11.6	0.976	0.015	88 (4)

the course of the tracking period (Fig. 5a–e). Less than half of fish pairs examined (10 out of the 26 pairs of fish tagged at the same time and location) had low similarity values throughout their tracking period such that only 5–20% of their receiver-detection-hours occurred together even though they were tagged in the same bay. A similar number (11/26) of fish pairs had very high similarity values for at least one or two months after tagging. These pairs of fish had 60–84% of their receiver-detection-hours occurring together in the months after tagging, but then gradually spent less time in proximity to one another such that their similarity values were only 20–30% after 5–8 months. Some fish pairs (6/26) had an increase in similarity values beginning in December/January although they never reached values as high as those experienced in the spring months after tagging.

4. Discussion

The spatial and temporal movements of sea bream, an ecologically important species in mangrove estuaries of the western Atlantic, were investigated in multiple bays over two years. Sea bream were almost continuously monitored by an extensive array of telemetry receivers during the 11–13 month battery-life of their transmitters. Sea bream were found to utilize a small core area, displayed high site fidelity, and have distinct movement patterns that were consistent with the other individuals captured from each bay.

Although there has been scant research on sea bream in the western Atlantic, there have been movement studies using telemetry on other species in the family Sparidae. Fish in this family are primarily coastal or estuarine, they possess a sub-terminal mouth with incisor- and molar-like teeth, and subsist on a benthically focused carnivorous or omnivorous diet. Occupancy of similar ecological niches among sparids makes it

useful to contrast movement patterns. For example, size of the daytime core area of sea bream in St.Croix (i.e., 50% KUD = 9.8 ha) was very similar to that measured in comparable studies for the white sea bream (*Diplodus sargus*) (3.6 ha, Di Lorenzo et al., 2014) (10.6 ha, Aspillaga et al., 2016), salema (*Sarpa salpa*) (4.3–5.1 ha, Jadot et al., 2002, 2006), two-banded sea bream (*Diplodus vulgaris*) (10.1 ha, Alós et al., 2012), and yellowfin bream (*Acanthopagrus australis*) (4.9 ha, Gannon et al., 2015). All these values are similar in magnitude despite differences in sample size, detection span, receiver spacing, and methods used to measure activity space.

There was no difference for most sea bream in the location of their day and night core area in our study, a finding similar to two-banded sea bream (Alós et al., 2012), white sea bream (Aspillaga et al., 2016) and some salema (Jadot et al., 2006). Departure from this pattern was evident for some salema (Jadot et al., 2002) and two sea bream tagged in Bio Bay in this study. These fish spent the majority of their time in Bio Bay during the day, but at night, were located in Triton Bay. By itself this is not necessarily surprising since Triton and Bio Bay are separated by only a narrow channel and if fish reside near this opening even small differences in their day/night location could result in dramatic differences. The pattern becomes more interesting when examined in combination with the six other fish that utilize Bio Bay, all of which preferentially used Bio Bay only during the day. A mere 10% of their Bio Bay detections occur during the night. Bioluminescence may increase the risk of predation, perhaps by outlining their movements, or it may have some other negative influence on sea bream at night resulting in their avoidance of the area.

The omnivorous sea bream feeds almost exclusively during the day (Vaughan 1978) and all but 2 of the fish tracked in this study had a greater number of detections during the day. Individuals of the size we tagged (>20 cm) eat a mixed diet of algae, vascular plants, and epibiotic organisms such as gastropods and tunicates. Daytime foraging is a trait shared by other sparids (Jadot et al., 2006; Gannon et al., 2015), although this is not always readily apparent from telemetry patterns and individual fish show some variability in diel activity (Alós et al., 2012; Aspillaga et al., 2016).

Not only is the basic size of the core area similar for sea bream and several other species of sparids, but site fidelity over time is also typically very high. The small core area and high site fidelity observed here suggest that even small areas such as our study site would be sufficient to protect sea bream. Whereas other sparids have been shown to have similarly high residency index values (i.e., >0.9) and high site fidelity, many of them leave the confines of bays and protected areas for spawning (Alós et al., 2012; Di Lorenzo et al., 2014; Gannon et al., 2015; Aspillaga et al., 2016; Iafrate et al., 2016), something not likely to occur for sea bream based on the continuous detection patterns inside bays in our study.

The spatial arrangement of our receiver array provided nearly continuous detection of sea bream activities on a daily basis throughout the area. This thorough temporal aspect of monitoring, as evidenced by the very high residency index, is suspected to provide robust estimates of core areas based on fish activities for almost an entire year for most fish. However, although representative of the time-span of detection, it is suspected that the core area sizes calculated here overestimate the area actually frequented by the fish. This is due to the large detection range of the receivers and their partial overlap, the uncertainty of knowing where within a large detection range a fish actually is, and the assumptions used in kernel density calculations (Aspillaga et al., 2016). As a result, fine-scale behaviors and sub-hectacre habitat preferences (e.g., Hammerschlag and Serafy 2010) are not addressed.

There was no increase in size of core areas with fish age for sea bream even though we tracked most fish for a period likely to encompass half or a third of their 2–3 year lifespan. Although detection of an increase in core area size may have been obscured by the limitations of the KUD index and our large detection range for receivers, the lack of increase in home range with fish size or age is a finding similar to other sparids
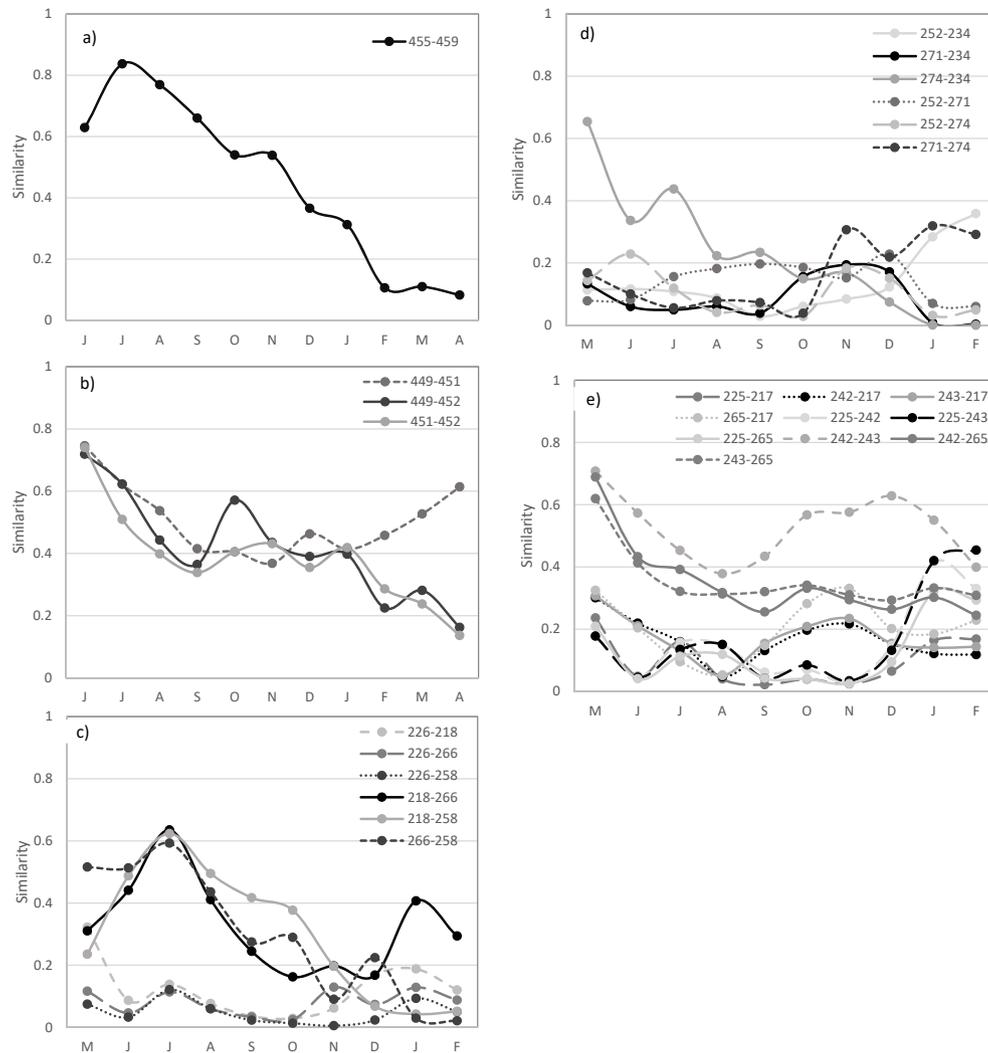
Fig. 5. Monthly Jaccard Similarity Index values for pairs of fish based on coincident receiver-detection-hours tagged in (a) Bio Bay 2017, (b) Triton Bay 2017, (c) Triton Bay 2018, (d) CSO 2018, and (e) Sugar Bay 2018. Pairs are noted by their three digit identification numbers.

(Abecasis and Erzini 2008; Gannon et al., 2015; Aspillaga et al., 2016) and scarids (i.e. parrotfish) (Welsh et al., 2013). Ontogenetic increases in home range size for fish have been documented for many fish and no doubt occur for post settlement and juvenile sea bream. However, all the fish tracked in our study and those of other sparids have been mature individuals. Provided that there is no mediating influence as fish continue to grow after reaching maturity, home range size can stabilize. If nutritional requirements are met, susceptibility to predation remains constant (see Hammerschlag et al., 2010b for smaller sea bream), social dynamics are stable (e.g., territoriality, schooling), and access to reproductive opportunities is sufficient, there is no reason to increase risk or energy expenditure by further enlarging one's home range (Welsh et al., 2013).

There were two periods of synchronized increase in activity among multiple fish, although not necessarily in the same places. One occurred over a two or three week span in October of both years. Given that the pattern occurred in both years (albeit stronger in 2018) it is suspected that some seasonal mechanism was responsible such as an annual foraging opportunity or environmental driver. Unfortunately, the four temperature/salinity loggers that we had deployed at various locations in the system were part of a flawed manufacturing lot and all failed to record useable data. The more striking incidence of increased activity among fish began in January of both years and extended into spring months until tags expired in March and April. Spawning season for sea

bream in the Caribbean is likely January to April (Beebe and Tee-Van 1928; Chavance et al., 1984, Garcia-Cagide et al., 1994). We observed a gravid female on one of our April trips that released eggs while being tagged (M. Kendall pers. obs.). This increase in activity was not spatially constrained to the area near the reef cut (i.e., in the backreef or central bay), as was expected based on an earlier study of sea bream spawning (Chavance et al., 1984). Instead it was more widespread. The increased activity was also not sufficient to significantly increase the size of their core area. Reasons for the diffuse increase in activity could be related to a search for spawning partners, or increased energy demands associated with gametogenesis. Plankton tows, gonadal development indices, and gut content analysis of fish captured from different bays and seasons would be helpful for determining the cause of these movement patterns.

Many fishes exhibit a link between lunar cycles and spawning (Takemura et al., 2009). The relationship between lunar phase and fish activity near the reef cut, where spawning is suspected to take place based on another study (Chavance et al., 1984), was equivocal. A majority of fish tagged in locations farthest from the backreef or central bay (i.e., 8/14 fish tagged in Bio Bay, CSO, and Triton Bay) were more active in the backreef or central bay during the full moon. This could indicate spawning activity during full moons as fish spend more time in spawning habitats. However, the remaining fish tagged in those locations experienced peak activity in the backreef and central bay during other moon phases and none of the fish from Sugar Bay had their peak detections in

the backreef or central bay during the full moon. The Sugar Bay fish include backreef or central bay as parts of their regular home range, and may therefore not have a need to spend additional time in those habitats to accomplish spawning. Indeed, all fish used the backreef or central bay at least some during all moon phases. It is possible that these brief visits are sufficient to accomplish spawning but don't require a long stay during a regular moon phase. Brief spawning migrations or use of backreef and central bay habitats for other activities (e.g., foraging) not aligned to moon phase would confound detection of a spawning migration linked to moon phase. It is also possible, that there is simply not a tight relationship between moon phase and spawning activity for this species or they may be able to utilize more of the bays for reproduction than suspected from the earlier study (Chavance et al., 1984).

Sea bream showed no change in behavior during Hurricane Maria. Throughout the storm, tracked fish were present at the same general suite of stations, and displayed the same diel patterns as in the days before and after the storm. At least above the water's surface, the effects of the storm were severe, and included a large number of boats in the bays being blown off their moorings and piling up on western shores as well as extensive mangrove damage especially on eastern facing canopies (Kendall et al., 2020). Fish (Massie et al., 2019; Bailey and Secor 2016) and sharks (Heupel et al., 2003; Strickland et al., 2020) in riverine and estuarine systems have been documented moving downstream or deeper offshore in response to barometric pressure cues or freshwater flow associated with cyclonic storms. The white sea bream apparently departs from its typical behaviors and seeks deep-water shelter during storms in the Mediterranean (Aspillaga et al., 2016). The lack of apparent response by sea bream at St.Croix is in contrast to these behaviors. This could be due to differences in the ecosystems and options available for fish to seek refuge apart from their typical home range. Perhaps in Salt River Bay there is no alternative but to stay put inside the bays whereas in other systems fish may have the option of moving downstream in a river or deeper to a more favorable habitat to ride out a storm. It could also be that sea bream in this setting just have no need to evacuate. Indeed their behavior on the day of the storm found them largely resident to Triton Bay and Bio Bay with few detections at the mouth of those two bays and in central bay, just as they were immediately before and after the storm. Given the large number of telemetry studies worldwide in locations affected by cyclonic storms (Hussey et al., 2015) and the paucity of studies reporting significant effects, it could be that many fish movements are resilient to storms (i.e., negative results) and are therefore not reported in the literature.

Our results indicate that seabream captured nearby each other generally occupy space within the study area in similar proportions compared to fish captured in adjacent bays. Seabream from the various bays do not mix and wander throughout the ecosystem even though it all appears to be suitable habitat and is used by different groups of localized individuals. This similarity of movements and occupancy patterns is limited to the spatial scale of bays and temporal scales of weeks or months. When considered at the resolution of individual receivers and hourly time steps, it appears that most fish are actually not in close proximity to one another for the vast majority of the time. Although some pairs of fish remained close by each other and shared as many as 84% of their receiver-detection-hours in the month after tagging, they gradually spent less and less time near each other, even though their overall pattern of movements was consistent at the scale of whole bays (i.e., they were in the same bay but not close enough together to be detected at the same receiver within the same hour). This highlights the importance of examining movements of fish on multiple spatial scales and time-intervals to understand the temporal and spatial limits of their associations. Further refinements to studying coincident movements are possible by using high density arrays or constraining detection range or direction of receivers, however, results here indicate that this may not be warranted in the case of sea bream.

It is important to note that fish coincident even at the same receiver and same 1 h time bin are not necessarily schooling together. The time

bin and detection range of receivers instead provides evidence only that they are using the same part of a bay at the same time, and may or may not be in very close proximity. On the other hand, it is also important to recognize that even when an analysis such as this indicates that tagged fish are not together, it does not mean that they are necessarily alone. Of course only a small fraction of the sea bream in the ecosystem were tagged, so any number of fish unknown to us could have been socially interacting with tagged individuals.

The findings of this study fill a basic gap in the knowledge of an abundant estuarine fish of the tropical western Atlantic and highlight their potential as a model organism for studying mangrove ecosystems. Even small bays amenable to protection as MPAs appear sufficient to allow sea bream to complete its life cycle from settlement to spawning. During that time, they transfer energy from their benthic food source to higher trophic levels (Clark et al., 2009; Nagelkerken and van der Velde 2004; Hammerschlag et al., 2010a) as has been suggested for other sparids (Jadot et al., 2006). There is some evidence that eggs and larvae may even be retained in estuarine ecosystems (Chavance et al., 1984) thus encompassing this species entire life history. Sea bream populations, not a focus of fisheries exploitation, may therefore be a useful model for assessing ecosystem health and anthropogenic impacts from habitat degradation and bioaccumulation of contaminants from benthic prey to higher trophic levels (e.g., Taylor et al., 2018).

Author contributions

Kendall: conceptualization, methodology, analysis, writing. Siceloff: conceptualization, methodology, analysis, writing, data curation. Monaco: conceptualization, supervision, editing. Ruffo: investigation, editing. Winship: analysis, editing. Hanna Holloway: methodology, investigation, data curation, editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2021.107254.

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