Received: 25 July 2019 | Accepted: 10 December 2019
DOI: 10.1111/jfb.14227

REGULAR PAPER

JOURNAL OF FISH BIOLOGY fsbi

Seasonal occupancy and connectivity amongst nearshore flats and reef habitats by permit *Trachinotus falcatus*: considerations for fisheries management

Jacob W. Brownscombe[1,2] | Lucas P. Griffin[3] | Danielle Morley[4] | Alejandro Acosta[4] | John Hunt[4] | Susan K. Lowerre-Barbieri[5,6] | Glenn T. Crossin[2] | Sara J. Iverson[2] | Ross Boucek[7] | Aaron J. Adams[7,8] | Steven J. Cooke[1] | Andy J. Danylchuk[3]

[1]Fish Ecology and Conservation Physiology Laboratory, Department of Biology, Carleton University, Ottawa, Ontario, Canada

[2]Department of Biology, Dalhousie University, Halifax, Nova Scotia, Canada

[3]Department of Environmental Conservation, University of Massachusetts Amherst, Amherst, Massachusetts, USA

[4]South Florida Regional Lab, Florida Fish and Wildlife Conservation Commission, Marathon, Florida, USA

[5]Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute, St. Petersburg, Florida, USA

[6]Fisheries and Aquatic Science Program, School of Forest Resources and Conservation, University of Florida, Gainesville, Florida, USA

[7]Bonefish and Tarpon Trust, Miami, Florida, USA

[8]Florida Atlantic University Harbor Branch Oceanographic Institute, Fort Pierce, Florida, USA

Correspondence
Jacob W. Brownscombe, Fish Ecology and Conservation Physiology Laboratory, Department of Biology, Carleton University, 1125 Colonel By Drive, Ottawa, Ontario K1S 5B6, Canada.
Email: jakebrownscombe@gmail.com

Funding information
This project was funded by Bonefish and Tarpon Trust with support from Costa Del Mar, The March Merkin Fishing Tournament, private donations and Hell's Bay Boatworks. Additional support was provided by a NASEM Gulf Research Program through a hurricane recovery grant and the acoustic receiver array was supported by a loan from the Ocean Tracking Network. J.W.B. is supported by a Banting postdoctoral fellowship, Dalhousie University, Carleton University and Bonefish and Tarpon Trust

Abstract

We used acoustic telemetry to quantify permit *Trachinotus falcatus* habitat use and connectivity in proximity to the Florida Keys, USA, and assessed these patterns relative to current habitat and fisheries management practices. From March 2017 to June 2018, 45 permit tagged within 16 km of the lower Florida Keys were detected at stationary acoustic receivers throughout the south Florida region, the majority of which remained within the Special Permit Zone, where more extensive fisheries harvest regulations are implemented. There was a high level of connectivity between nearshore flats (*i.e.*, <3 m water depth) and the Florida reef tract (FRT; 15–40 m water depth), with 75% of individuals detected in both habitats. These locations probably function primarily as foraging and spawning habitats, respectively. Permit occupancy on the FRT peaked during the months of March–September, with the highest number of individuals occurring there in April and May. Specific sites on the FRT were identified as potentially important spawning locations, as they attracted a high proportion of individuals that exhibited frequent visits with high residency durations. There were also significant positive relationships between seasonal habitat-use metrics on the FRT and an empirical permit gonadosomatic index. Large aggregations of permit at spawning sites on the FRT are potentially vulnerable to the effects of fishing (including predation during catch and release) at a critical point in their life cycle. These data on permit space use and movement, coupled with knowledge of stressors on their ecology, provide insights for implementing science-based strategic management plans.

KEYWORDS
conservation, marine biology, movement ecology, permit, recreational fisheries, *Trachinotus falcatus*

1 | INTRODUCTION

Animal movement patterns and habitat use are essential considerations for environmental management and conservation strategies (Allen & Singh, 2016; Anthony & Blumstein, 2000; Blumstein & Fernández-Juricic, 2010). For example, animal home range dictate the spatial scale at which habitats must be conserved and human activities managed. Habitat use and function are also highly relevant when prioritising environmental management actions (Law & Dickman, 1998). With marine fishes, a particular emphasis is often placed on conserving essential spawning habitats and protecting spawning individuals from anthropogenic threats (Koenig *et al*., 2000; Lewis *et al*., 1996). These considerations are especially pertinent to the conservation of coastal marine fishes that have the potential to move between diverse habitats at vast spatial and temporal scales and have often complex larval distribution patterns (Allison *et al*., 1998; Crowder & Norse, 2008; Kramer & Chapman, 1999). Furthermore, many nearshore marine fish species support recreational and commercial fisheries and are therefore at greater risk of overexploitation (Arlinghaus *et al*., 2007; Cooke & Cowx, 2004). Fish movement patterns and spawning site fidelity play key roles in fisheries stock structure and productivity and are therefore highly relevant to fisheries management (Lowerre-Barbieri *et al*., 2016, 2017). Historically, there has been much uncertainty in the spatial, behavioural and physiological ecology of wild marine fishes, but recent development of advanced tracking technologies has enabled major insights into these fields that are relevant to diverse aspects of ecosystem and fisheries management (Cooke *et al*. 2016; Crossin *et al*. 2017; Lowerre-Barbieri *et al*. 2019).

The coastal marine environments surrounding the Florida Keys archipelago represent a complex case for environmental management because there is a unique combination of high levels of habitat heterogeneity, fish species diversity and conservation threats (Bartholomew *et al*., 2008; Burke *et al*., 2012; Maliao *et al*., 2008; Weil, 2004). This region consists of large networks of mangrove forests, shallow-water (<3 m) seagrass flats, a 580 km long barrier reef (the Florida reef tract; FRT) and over 1000 known shipwrecks that function as artificial reefs (NOAA, 2016). These nearshore marine habitats are managed by the Florida Keys National Marine Sanctuary (FKNMS; www.floridakeys.noaa.gov), Everglades National Park (www.nps.gov/ever), Biscayne National Park (www.nps.gov/bisc) and numerous wildlife refuges (www.fws.gov/refuges). However, this region still faces many anthropogenic threats, including alterations to freshwater flow through the Florida Everglades, inputs of nutrients and other contaminants, climate change, extreme weather events, invasive species, boating disturbance, habitat degradation or loss and overfishing (Brownscombe *et al*., 2019a; De Freese, 1991; Lapointe & Clark, 1992; McIvor *et al*., 1994). Numerous vertebrate and invertebrate species utilise many of these habitats for a part or the entirety of their life cycle (Acosta *et al*., 2007; Ault *et al*., 2013; NOAA, 2016) including diverse fish species, many of which support the US $8 billion saltwater recreational fishing industry in Florida (NMFS, 2018). One such species is the permit *Trachinotus falcatus* (L. 1758), which, combined with bonefish *Albula vulpes* (L. 1758) and Atlantic tarpon *Megalops atlanticus* Valenciennes 1847, support a predominantly catch-and-release (C&R) flats (<3 m water depth) fishery with an estimated $465 million annual economic value in the Florida Keys (Fedler, 2013). Permit also occupy deeper-water structures including reefs and shipwrecks that are used for spawning (Bryan *et al*., 2015; Graham & Castellanos, 2005). In these deeper-water habitats, permit support another recreational fishery operated by boat fleets that have a greater tendency to harvest permit than the flats fishery (Brownscombe *et al*., 2019b). Further, high densities of opportunistic predators around deeper-water structures can result in high predation rates (Holder *et al*., 2020; B. Binder, unpubl. data). Permit may be especially vulnerable to these combined effects during their spawning period, when they aggregate in large schools at predictable locations where anglers can easily target them.

Given the general lack of scientific knowledge regarding permit ecology and population trends, the Florida Fish and Wildlife Conservation Commission (FWC) established the special permit zone (SPZ; www.myfwc.com/fishing/saltwater/recreational/Permit/) in 2011 based on reports from fishing guides about declining permit fishing opportunities. The SPZ extends south from Cape Florida in the Atlantic Ocean to Cape Sable in the Gulf of Mexico, including state and federal waters encompassing the Florida Keys, extending westward beyond the Dry Tortugas. Within the SPZ, permit harvest is more restricted than northern regions of Florida and originally included a harvest prohibition period during the months of May–July. However, preliminary fish tracking data showed that permit were forming putative spawning aggregations before this period and in 2018 the harvest prohibition period was extended to include April (Brownscombe *et al*., 2019b). There is clear recognition that permit require protection during this important period in their annual life cycle, but the extent to which permit move between habitat types and fisheries and the seasonal timing and locations of spawning have not been scientifically established. Therefore, our objectives were to examine seasonal occupancy and connectivity between nearshore flats and the FRT and identify important spawning locations for permit in the Florida Keys.

2 | MATERIALS AND METHODS

This research was conducted with permission of the Florida Keys National Marine Sanctuary under permit # FKNMS-2013-040-A2 and the Florida Fish and Wildlife Conservation Commission under permit # SAL-16-1205. All handling procedures were conducted in accordance with the Carleton University Animal Care Committee (application 11,473), as well as the American Association for Laboratory Animal Science (IACUC protocol 2013–0031, University of Massachusetts Amherst).

2.1 | Tracking system

In August 2015 an array of 60 acoustic receivers (VR2W, Vemco Inc.; www.vemco.com) was established to track permit movement patterns and habitat use. Receivers were placed in proximity to the nearshore flats throughout the Florida Keys and by May 2018, the receiver array was expanded to include 84 acoustic receivers, thanks to support from the NASEM Gulf Research Program and the Ocean Tracking Network (www.oceantrackingnetwork.org; Supporting Information Figure S1). Each receiver was moored to the seabed, attached to a 1 m rebar stand connected to a 30–50 kg cement base (heavier moorings were used on hard substrates where movement was more probable). Owing to the nature of the ecosystem, which consists of an expansive >8000 km^2 area of shallow (<3 m) flats, traditional grid-style receiver arrangement was deemed unlikely to detect tagged fish effectively and a point-of-interest arrangement was used (Brownscombe *et al.* 2019c). Acoustic receivers were placed adjacent to popular fishing locations on the Florida Keys flats, which were informed by consultation with local fishing guides. An additional 117 receivers were established in 2014–2016 at diverse locations along the FRT (Supporting Information Figure S1) aimed at tracking a range of fish species, providing essential coverage of potential permit spawning habitats. To monitor variability in acoustic receiver performance (*i.e.*, their ability to detect proximity of tagged fish effectively), reference tags were placed in proximity to nine receivers in flats habitats (Brownscombe *et al.*, 2019d; Supporting Information Figure S2). These data were unavailable for receivers on the FRT, but measures of environmental noise were available from 39 acoustic receivers (Vemco VR2Tx and VR2AR models) at eight unique sites (Supporting Information Figure S3). The causes of variation in acoustic receiver performance can be highly diverse (Kessel *et al.* 2014); however, in coral-reef habitats, environmental noise (including physical sources such as wind and biological sources such as fish and invertebrates) is often the major factor affecting performance (Cagua *et al.*, 2013; Mathies *et al.*, 2014; Stocks *et al.*, 2014). Supplementing these receiver arrays, another 1000+ acoustic receivers were deployed by other researchers throughout the south-eastern USA aimed at tracking diverse marine organisms. Sharing of permit detection data from these receivers was facilitated through the Florida Acoustic Telemetry network, integrated Tracking of Animals in the Gulf of Mexico network and the Ocean Tracking Network.

2.2 | Fish tagging

From March 1, 2016 to May 1, 2018, 101 permit were tagged in the general region surrounding the Florida Keys with either V13-1x (high power, 80–160 s delay, 653 day life, 6.2 g in water; Vemco Inc), V13A-1x (low power, 80–160 s, 355 day life, 6.2 g in water; Vemco Inc), or V16-4x (high power, 60–120 s delay, 1910 day life, 11.7 g in water; Vemco Inc) acoustic transmitters. Permit were captured *via* recreational angling with a range of gear types, from medium strength fishing rods and 6.8 kg break strength braided Dacron line and 1–2 m fluorocarbon leaders, to heavy fishing rods with 22.7 kg break strength line, as well as 10 wt fly fishing rods with 5.4 kg strength fluorocarbon tippet. Lighter gear was used in shallow water flats and heavier gear in offshore habitats where structures and predators posed challenges to fish capture. Upon capture, permit were held in either a 1 m^3 floating net pen alongside a boat, or in a 300 l livewell for 5 to 20 min before tagging with acoustic transmitters.

For tagging, permit were held in the supine position with their head submerged in water. A 3–4 cm incision was made with a scalpel through the muscle wall into the coelomic cavity, *c.* 4 cm from the ventral midline, *c.* 8 cm anterior to the anal fin. Transmitters were inserted toward the anterior portion of the fish's body and the incision was closed with three simple interrupted sutures with absorbable monofilament material (Ethicon 3–0 PDS II, Johnson and Johnson; www.jnj.com). Individuals were retained for 5–20 min before release, depending on fish condition and perceived predation risk of the environment, ensuring that equilibrium and tail grab reflexes were intact (Brownscombe *et al.* 2017). In some cases, permit were relocated up to 1 km from the capture site beforer release when predators were observed. All surgical equipment (scalpels, tweezers, haemostats, sutures) and transmitters were disinfected with 10% povidone-iodine solution before the tagging procedure. All surgery was conducted by the same experienced person while wearing nitrile gloves.

2.3 | Data analysis

A series of data filters were applied to permit acoustic detection data before further analysis and visualisation. Detections were examined in the period between March 1, 2017 and May 31, 2018, when a minimum of four individual permit were detected in each month and before the last major acoustic receiver download. Individuals that were detected by acoustic receivers within this time period and were tagged before May 1, 2018 were included in further data analysis (n = 45; Supporting Information Figure S4 and Table S1). Potentially false detections (resulting from code mutations or collisions; Simpfendorfer *et al.* 2015) were filtered out of the dataset using the criterion that a minimum of two detections must occur at a receiver within a 2 h time period. False or duplicate detections were also filtered out of the dataset when multiple detections were logged on the same or multiple receivers within a shorter time period than the minimum tag transmission delay (60 s). Permit detections at acoustic receivers were then aggregated by unique sites and these data were mapped to examine movement patterns in relation to the boundaries of the SPZ. To examine seasonal patterns of permit movement and habitat use, detection data were further filtered to include habitats (*i.e.*, nearshore flats and the FRT) where there was acoustic receiver coverage for the entire time period (Supporting Information Figure S5). Permit residency time (h) was calculated at each unique site, where individuals were considered to be resident at a site within the time period when a maximum of 1 h lapsed between detections. Detection metrics examined here included permit residency, the number of detection events (unique residency periods) and the number of individuals detected. Raw detection metrics were corrected to account for the number of tagged permit in the system at the daily level using $D_C = D(T_d T_\mu^{-1})^{-1}$, where D_C is corrected values, D is raw detection values, T_d the number of tagged fish in the system on a given day and T_μ the overall mean number of fish tagged in the system over the study period. Corrected values were plotted seasonally at each site in relation to recreational fisheries harvest prohibition periods and permit gonadosomatic index (I_{GS} = 100(gonad mass / (total mass − gonad mass)) data from Crabtree *et al*. (2002). Due to the sensitive nature of these data, generic names for sites were used to avoid any negative influence on permit conservation (*i.e*., anglers using this information to target spawning permit); specific location data can be made available upon reasonable request. To elucidate potential spawning habitats, linear models were used to examine the relationship between monthly permit I_{GS} (both sexes combined) and permit residency, detection events and indvidual count in each habitat type (flats and FRT). Measures of acoustic receiver performance (*i.e*., reference tag detections in flats habitats and environmental noise in FRT habitats) were plotted seasonally to assess whether it affecte seasonal patterns in permit habitat use. All data analysis was conducted using RStudio (RStudio Team, 2016) in R (R Core Team, 2018).

3 | RESULTS

During the period of March 1, 2017 and May 31, 2018, 45 individual tagged permit were detected 79,823 times at 128 acoustic receivers (Supporting Information Figure S6 and Table S1). Only one individual was detected outside of the SPZ near Fort Pierce, 420 km north-east of its tagging location (Figure 1). The other 44 individuals were detected in closer proximity to the Florida Keys, 75% of which moved

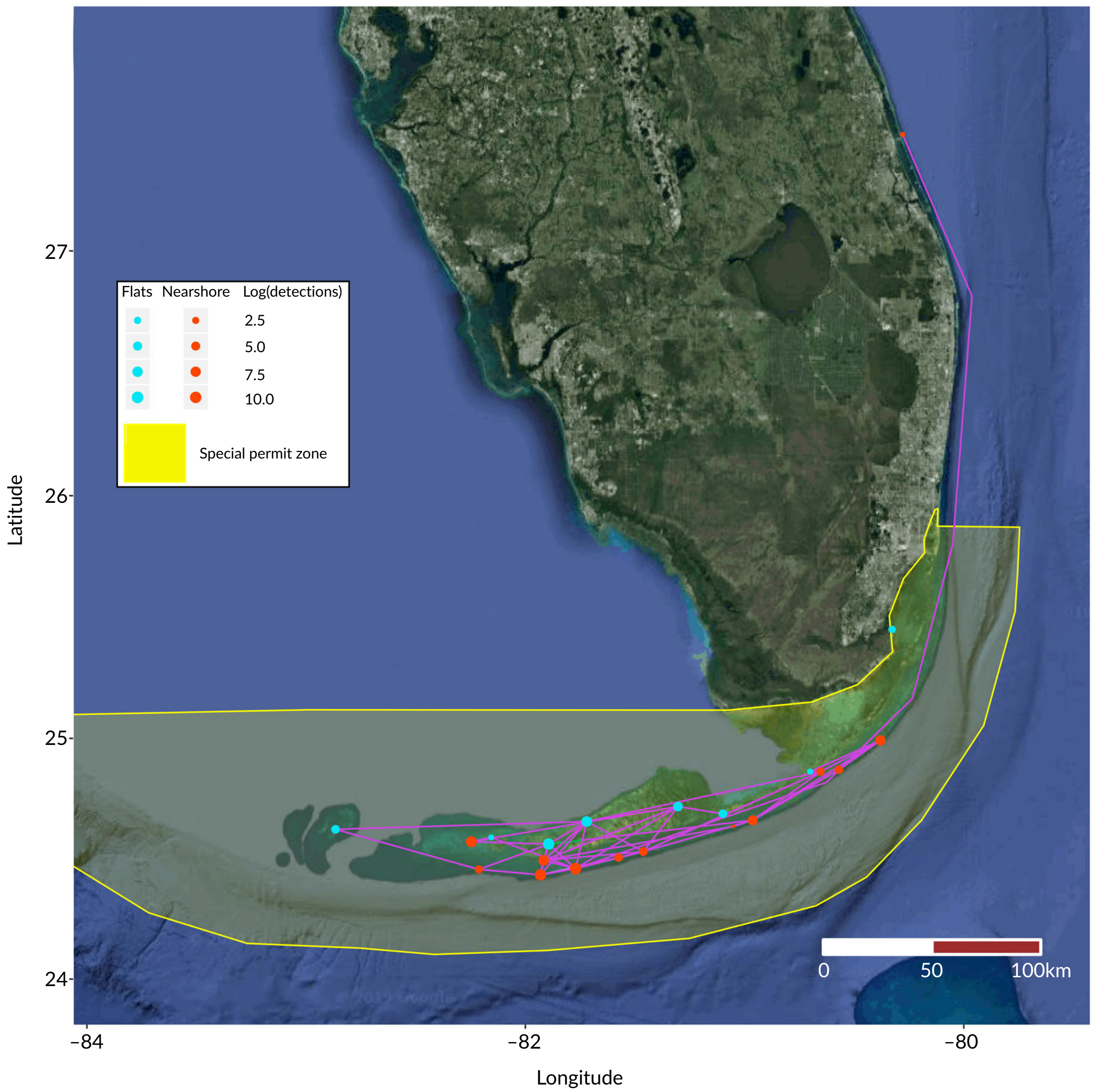

FIGURE 1 Map of *Trachinotus falcatus* detections at general locations, categorised by flats (●) and nearshore (●, includes the Florida reef tract and shipwreck) sites. The size of the circle indicates the log+1 transformed total number of *T. falcatus* detections at each location. ——, *Trachinotus falcatus* movements between sites; □, the special permit zone (SPZ), which extends south from Cape Florida in the Atlantic Ocean to Cape Sable in the Gulf of Mexico, including state and federal waters

TABLE 1 Summary statistics for permit detections at acoustic receivers (grouped by site) in the Florida Keys. Corrected values account for the number of *Trachinotus falcatus* in the system at the daily level. Intra-habitat and inter-habitat movements indicate movements within and between the flats and reef tract habitat categories, and Fish ID count indicates the number of individual *T. falcatus* detected

Site	Tagging	Raw detection values					Corrected detection values				Fish movements		
	Fish tagged (*n*)	Detections (*n*)	Residency (h)	Detection events	Mean residency (h)	Fish ID count	Detections (*n*)	Residency (h)	Detection events	Mean residency (h)	Intra-habitat	Inter-habitat	Inter-habitat ID count
Flats													
Flats1	16	15,407	3602.71	592	6.09	26	14,242.87	3183.74	567.03	5.61	48	51	21
Flats2	8	2887	611.84	172	3.56	12	3469.89	771.07	238.59	3.23	47	12	9
Flats3	4	390	77.34	48	1.61	8	309.97	51.63	40.59	1.27	4	1	5
Flats4	0	93	4.92	8	0.61	2	48.77	2.58	4.20	0.61	0	0	1
Flats5	0	73	4.32	2	2.16	2	66.57	4.03	1.71	2.36	1	1	2
Flats6	0	16	1.80	1	1.80	1	8.39	0.94	0.52	1.80	0	0	0
Flats7	0	5	0.09	3	0.03	1	6.85	0.09	4.70	0.02	0	2	1
Flats8	0	4	0.13	2	0.07	1	2.10	0.07	1.05	0.07	0	0	1
All flats sites	28	18,875	4341.68	797	5.45	36	18,220.05	4089.41	827.38	4.94	100	67	27
Reef tract													
FRT1	0	35,872	5401.29	425	12.71	19	40,644.70	6036.56	462.76	13.04	22	8	12
FRT2	11	18,148	3159.47	259	12.20	24	14,177.32	2447.71	221.30	11.06	46	29	17
FRT3	0	3297	504.12	110	4.58	24	2847.56	437.70	110.27	3.97	51	19	19
FRT4	0	2191	198.42	83	2.39	1	3505.17	307.41	124.05	2.48	4	1	1
FRT5	4	1035	56.38	8	7.05	3	1996.31	95.44	10.73	8.90	2	1	3
FRT6	0	119	9.98	9	1.11	8	100.29	7.98	7.18	1.11	6	3	7
FRT7	0	96	14.65	5	2.93	1	102.98	15.71	5.36	2.93	1	0	1
FRT8	0	88	5.15	6	0.86	4	48.34	2.78	3.69	0.75	5	0	3
FRT9	0	56	5.57	8	0.70	3	74.23	6.79	10.63	0.64	4	1	3
FRT10	0	44	4.04	10	0.40	6	49.49	4.39	11.40	0.39	2	3	6
FRT11	0	2	0.03	1	0.03	1	2.15	0.03	1.07	0.03	1	0	1
All FRT sites	15	60,948	9505.63	858	11.08	36	63,799.31	9521.89	907.99	10.49	144	65	27

between the shallow nearshore flats and the FRT (Figure 1 and Table 1). Flats1 site had the highest residency rates on the flats, number of individuals detected and level of connectivity to other sites on the flats and FRT sites (Table 1). Flats2 and Flats3 sites also had high levels of these metrics relative to lower levels in the remaining flats sites. On the FRT, two sites (FRT1 and FRT2) had the highest permit

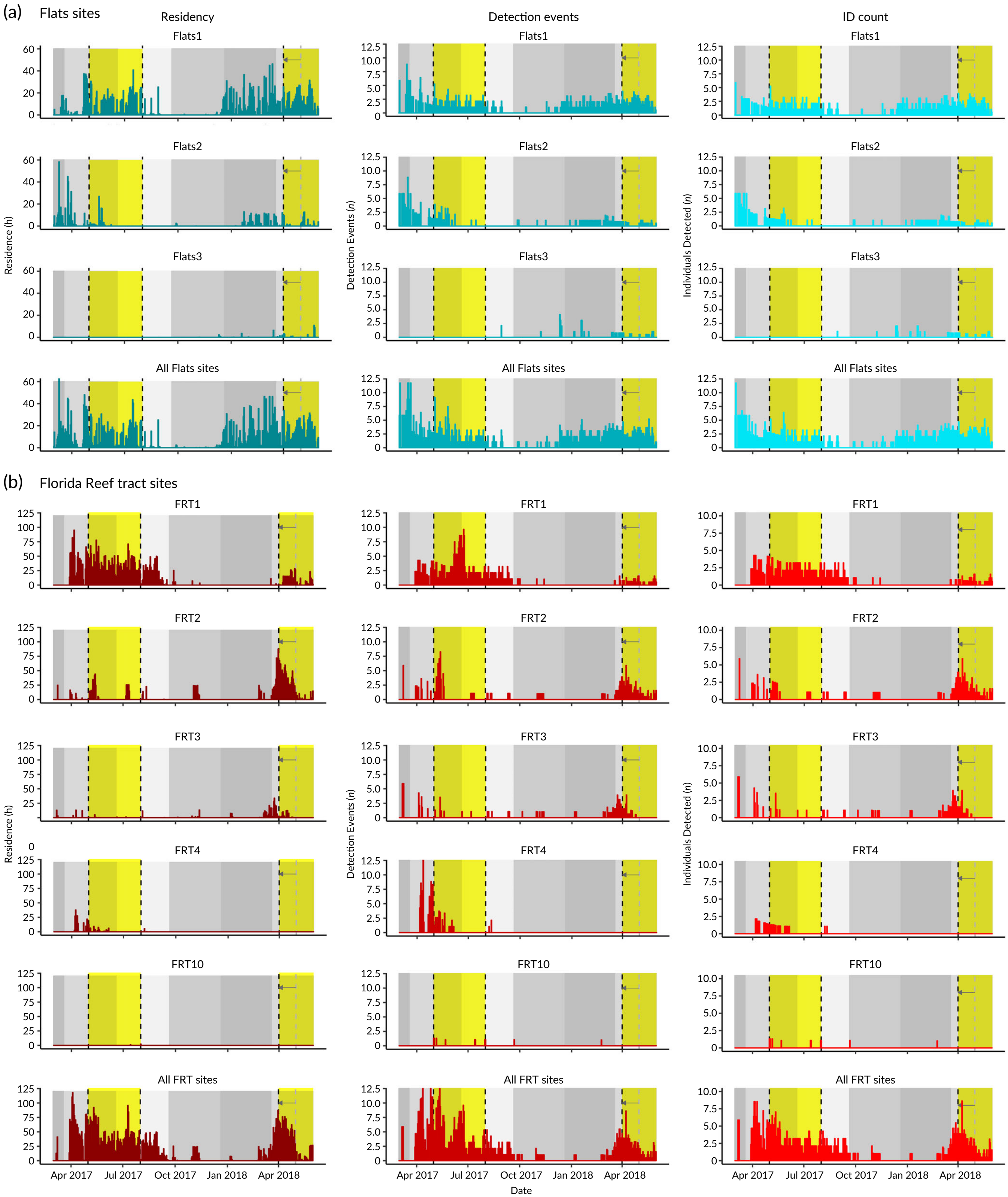

FIGURE 2 (a) Corrected *Trachinotus falcatus* space use including residency (h), detection events (*n*), and individual permit detected (ID count *n*) at flats sites (■) and (b) Florida Reef Tract sites (■), from March 2017 to June 2018. ■, The time periods where *T. falcatus* harvest was prohibited in the special permit zone (SPZ), which was May through July in 2017, extended to include April in 2018. Only sites that have ≥10 total detection events are shown. Season: (■) Winter, (■) Spring, (□) Summer, and (■) Fall. (■) Closed Harvest Period

residency rates of all sites, while FRT3, a gate of receivers stretching from Key West to the edge of the FRT, also detected many permit with high frequency, but lower mean residency values (Table 1). Permit residency and detection events were highest at FRT1 of all FRT sites, but a lower number of individuals were detected there (42%) than at FRT2 and FRT3 (53%). Of the distinct FRT sites (excluding FRT3, which was a gate of receivers spanning a large distance), FRT2 had the highest level of connectivity to the flats, with 17 of 24 (71%) of permit detected there, making a total of 29 movements between this location and the flats (Table 1). FRT2 also exhibited high connectivity to other reef sites, with 46 total movements to other reef sites, compared with 22 movements from FRT1 to other reef sites.

Examining temporal patterns of permit space use at sites with the highest residency, individuals visited multiple flats sites year-round, with a distinct decline in occupancy in the autumn, which coincided with Hurricane Irma on September 10, 2017 (Figures 2a and 3a). Permit were also detected on the FRT least commonly in autumn, followed by the winter months, with the highest occupancy, unique visits (detection events) and number of individuals from March–September (Figures 2b and 3a). Acoustic receiver detection efficiency of reference transmitters was generally consistent amongst months in flats habitats (Supporting Information Figure S2), but acoustic receiver noise measures were higher in all FRT sites in summer months and lower in winter months (Supporting Information Figure S3), which may have resulted in underestimation (rather than misestimation) of the observed seasonal patterns in permit occupancy of the FRT.

Crabtree *et al.* (2002) reported the highest permit I_{GS} values in the months of March–September, with a peak in April (Figure 3). Comparing monthly permit detection metrics with I_{GS} from Crabtree *et al.* (2002), there was a significant positive relationship between permit I_{GS} and permit residency in FRT sites ($F_{1,8}$ = 6.09, P < 0.05; Figure 3b), but not the flats ($F_{1,8}$ = 3.17, P > 0.05). This pattern was consistent with detection events (FRT: $F_{1,8}$ = 10.05, P < 0.01; flats: $F_{1,8}$ = 1.72, P > 0.05) and the number of individuals detected (FRT: $F_{1,8}$ = 68.74, P < 0.001; flats: $F_{1,8}$ = 1.01, P > 0.05).

4 | DISCUSSION

Here we explored the movement patterns of 45 permit tagged in proximity (<16 km) to the lower Florida Keys to assess their space use patterns and connectivity between nearshore flats and the FRT in the context of current habitat and fisheries management. We found that the majority of the 45 tracked permit remained within the nearshore marine habitats of the FKNMS and the SPZ where additional protection from harvest is provided for this species compared to regions

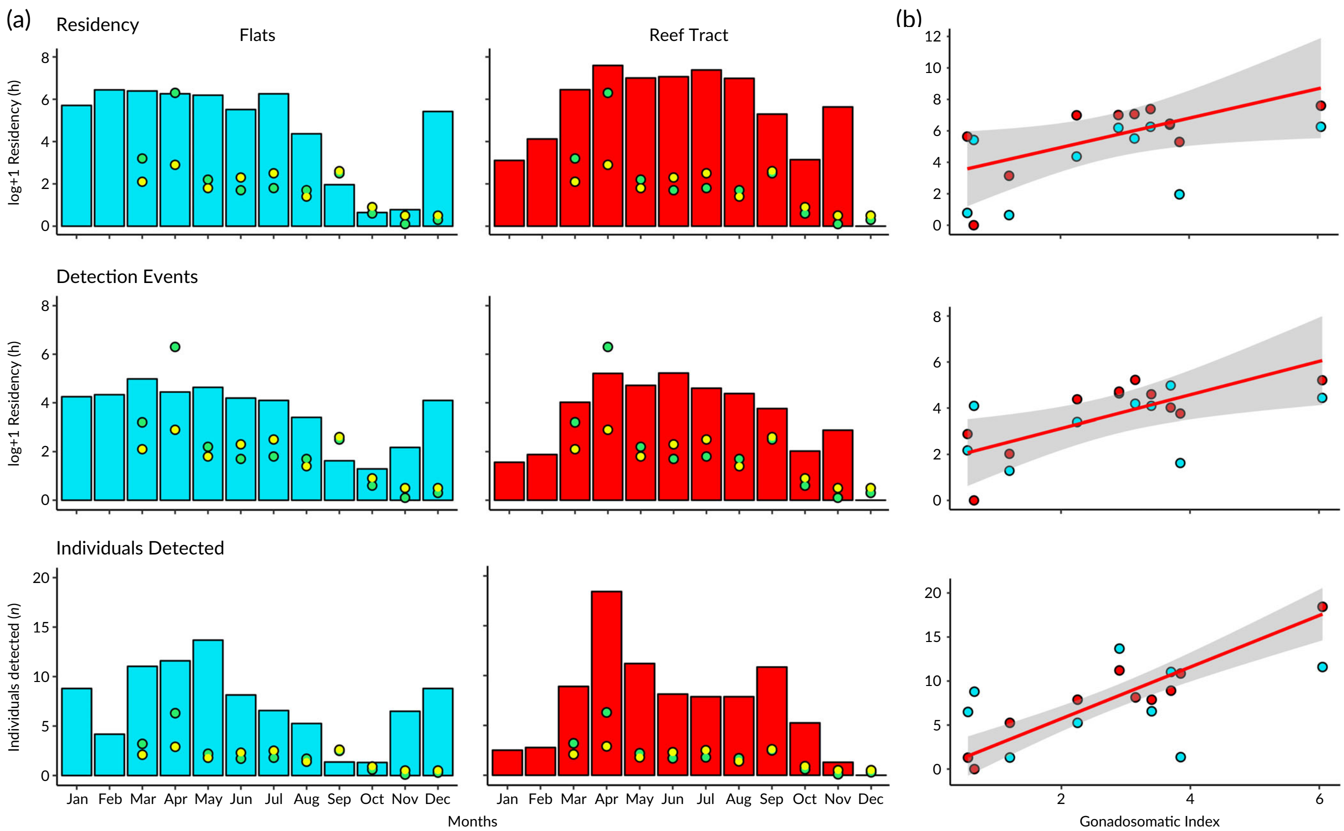

FIGURE 3 (a) Corrected *Trachinotus falcatus* detection metrics summarised by month (■, flats; ■, reef tract sites), and permit mean gonadosomatic index (I_{GS}; ●, males; ●, females; data from Crabtree *et al.*, 2012) and (b) the mean (—, ± SD) relationship between *T. falcatus* I_{GS} and *T. falcatus* detection metrics summarised by month. All detection metrics were corrected for the number of individuals in the system and the number of detection days in each month that data were collected

farther north in Florida. Although most permit remained within the vicinity of the Florida Keys, they frequently moved between the flats and the FRT (75% of individuals), forming connections between distinct habitat types and recreational fisheries.

Specific sites on the FRT have been long thought to be permit spawning habitats, with large aggregations forming starting in spring months (Brownscombe *et al*., 2019b; Bryan *et al*., 2015). Although actual spawning activity has not been documented on the FRT, it has been observed in proximity to reef promontories in Belize (Graham & Castellanos, 2005). The significant relationships between empirical monthly permit I_{GS} from Crabtree *et al*. (2002) and permit residency, detection events and individual count on the FRT strongly support the notion that permit spawn at specific sites on the FRT. Unlike the FRT, there were no significant relationships between monthly permit I_{GS} and detection metrics on the flats. The shallow-water nearshore seagrass flats of the Florida Keys represent highly productive habitats for invertebrates (Stoner, 1980; Williams & Heck, 2001) that are probably permit prey. Although not reported here, permit fin-tissue stable-isotope signatures indicate that the majority of individuals in this region rely heavily on prey based in seagrasses (J.W.B., unpubl. data). With the majority of individuals moving between these habitats, it is likely that permit in the Florida Keys utilise flats habitats primarily for foraging and undertake multiple trips farther offshore to structures such as reef promontories on the FRT for spawning during the months of March through September. However, permit were detected on the FRT year-round and some individuals were not detected moving between habitats. Therefore, it is possible that a smaller proportion of the permit population specialises on a certain habitat type; *e.g*., remaining on the FRT for the majority of their adult lives.

When interpreting seasonal permit habitat-use patterns measured using passive acoustic telemetry, it is important to consider that variability in acoustic receiver performance (*i.e*., detection range) may influence findings. In flats habitats, reference-tag detection efficiency was fairly consistent amongst months (Supporting Information Figure S2; Brownscombe *et al*., 2019d) and probably had limited influence on permit seasonal occupancy patterns in this habitat. However, there was a strong seasonal pattern in acoustic receiver-derived measures of environmental noise on the FRT, with the highest noise in the summer months and lowest in the winter at all FRT sites at which it was measured (Supporting Information Figure S3). Permit generally occupied the FRT more in the summer than winter; therefore, system performance variation may have resulted in the underestimation of this general seasonal pattern, rather than confounding it. In coral reef habitats, environmental noise is probably the greatest source of variability in receiver performance (Cagua *et al*., 2013; Stocks *et al*., 2014). However, it is unclear to what degree acoustic receiver performance influences the various habitat-use metrics examined here, particularly the number of individuals detected by month. For example, would a two-fold decrease in receiver performance result in half as many individuals being effectively detected? This seems unlikely in the case of permit aggregating near FRT structures for extended periods to spawn. As methods continue to develop to measure and correct for acoustic receiver performance (Brownscombe *et al*., 2019d; Kessel *et al*., 2014), further consideration of how it influences relevant ecological metrics is warranted.

Although the relationship between monthly permit I_{GS} and residency on the FRT was examined with all FRT sites aggregated, these detection data were driven primarily by two specific sites on the FRT that had by far the highest residency, detection events and individuals detected (FRT1 and FRT2). These two sites are probably important spawning locations for permit in the Florida Keys. Because permit form large spawning aggregations in particular locations at predictable times, they are especially vulnerable to capture by recreational fisheries and may also attract high densities of predators (Holder *et al*., 2020). To date, recreational fishing regulations have focused on limiting permit harvest, but allowing C&R, during the spawning period (www.myfwc.com/fishing/saltwater/recreational/Permit/). Yet, when high densities of opportunistic predators are also present, C&R may result in high rates of depredation (Raby *et al*. 2014), rendering this conservation strategy less effective.

The locations and timing of permit spawning are also highly relevant to population connectivity due to complex spatial patterns of larval dispersal. For example, particle drift models suggest that a large proportion of bonefish larvae that settle in south Florida may be sourced from other regions such as Cuba (Zeng *et al*., 2018); therefore, the context of bonefish conservation may be larger than south Florida. However, bonefish have a longer larval development period than permit. Similar models have suggested that permit spawning offshore of the Dry Tortugas, west of the Florida Keys, may be a major source of permit larvae in the region due to oceanic currents (Bryan *et al*., 2015), yet the temporal patterns in permit larval settlement suggest larvae are also sourced from other regions (Adams *et al*., 2006). Larval dispersal and settlement patterns of reef fishes in the Florida Keys are complex due to the influences of the timing of fish spawning and oceanic current patterns, including the formation of mesoscale eddies and tidal bores in the region between the FRT and the Florida Keys (Berger *et al*., 2004; D'Alessandro *et al*., 2007). The seasonal timing of permit spawning on the FRT appears to coincide closely with the presence of mesoscale eddies and tidal bores in the region (Berger *et al*., 2004; D'Alessandro *et al*., 2007) and may be a mechanism for higher self-recruitment than would be expected otherwise. Like bonefish, permit occupy diverse regions of the Caribbean Sea and the level of population connectivity amongst broader regions, as well as the degree of self-recruitment in south Florida is relevant to permit conservation and worthy of future research. To this end, exploration of the timing of permit spawning in relation to relevant factors such as mesoscale eddies and lunar phases would be valuable. Further, the attributes of spawning sites (*e.g*., structure relief, water currents) would inform why permit select particular spawning sites, enabling predictions of additional potential locations in the region.

Both within and outside of the spawning period, permit in the Florida Keys occupy seagrass flats frequently and as discussed previously, stable-isotope signatures indicate that seagrass-based prey are a major food source (J.W.B., unpubl. data). There is limited information on permit diet, but data from Belize showed that permit feed on invertebrates including predominantly urchins and various species of mollusc (R Clarke, unpubl. data). Permit diet in the Florida Keys is a knowledge gap that is relevant to their conservation, especially in relation to anthropogenic influences on seagrass flats. Pollution and alterations to freshwater flows in the Everglades have caused declines in seagrass densities and changes to species composition (Hall *et al*., 1999, 2016; Lapointe *et al*., 1994) and boating activity has caused widespread damage to seagrass meadow integrity (Kruer, 2017; Sargent *et al*., 1995; Zieman, 1976). Knowledge on the extent to which these stressors are affecting permit prey availability would be predicated on knowledge of permit diet.

When interpreting the findings reported here, it is important to note that although permit were tagged at diverse sites throughout the flats, reefs and nearshore shipwrecks, the majority of permit were tagged in proximity to the lower Florida Keys, which is in the westernmost region of the broader Florida Keys. Hence, the importance of both flats and reef habitats in the middle and upper Florida Keys are probably underrepresented for permit in those regions, where large aggregations of permit have been observed by the authors and local fishing guides. Another important caveat is that acoustic receiver coverage in the region is incomplete and hence there may be additional important spawning sites without receiver coverage not identified here. Indeed, the low number of permit detections in all habitats in the fall of 2017 indicates that permit moved to regions without receiver coverage during this period, which could have been, at least in part, a response to Hurricane Irma in September 2017.

In summary, the majority of permit in the Florida Keys (with an emphasis on the lower Keys) rely on nearshore seagrass flats for foraging throughout the year and move farther offshore to structures including reef promontories on the FRT for spawning from March through September, with a peak during April and May. Permit also aggregated on the FRT in late March, during which current fisheries regulations allow for harvest. The interconnectedness of these two habitat types means that ecologically, permit probably serve as a prey source to top predators in diverse habitats and play an important role as invertivores on seagrass flats, distributing nutrients to coral reefs. From a fisheries perspective, the two unique fisheries on the flats and deeper-water structures are largely supported by the same individual fish moving amongst habitats and should be considered in management contexts as a single interconnected group. For example, declines in the permit flats fishery could be related to stressors acting on these fish in reef habitats, or *vice versa*. Current habitat and fisheries management appears to function at a sufficient spatial scale, at minimum for the permit that predominantly occupy the lower Florida Keys. However, the vulnerability of permit spawning aggregations to fishing pressure, combined with opportunistic predators, may compromise the efficacy of harvest prohibition alone to protect spawning permit from overexploitation. Consideration should be given to providing more extensive protection for permit spawning aggregations at specific reef sites, two of which were identified here, but reported under generic site names for the purposes of permit conservation in keeping with principles needed to restrict access of sensitive data that could enable exploitation (Cooke *et al*., 2017). Specific site details can be made available upon reasonable request and have already been shared with relevant resource managers. Research on permit diet in relation to changes in prey availability due to ongoing alterations to seagrass densities and compositions, the factors that influence the timing and locations of spawning and the prevalence of recreational fishing-related permit depredation in spawning aggregations are also important avenues for future research.

ACKNOWLEDGEMENTS

The acoustic receiver array was supported by a loan from the Ocean Tracking Network. We thank the fishing guides and anglers who assisted with the telemetry array design and Permit tagging for this project including Captains Travis and Bear Holeman, Will Benson, Rob Kramarz, Zack Stells, Brandon and Jared Cyr, Chris Trosset, Nathaniel Linville, Ian Slater, Augustine Moss, Sandy Horn, Ted Margo, Richard Berlin and Jeff Rella. We also thank the researchers that shared permit acoustic telemetry detection data with us through integrated Tracking of Animals in the Gulf (iTAG) and Florida Acoustic Telemetry Network (FACT), in particular Harold 'Wes' Pratt of Mote Marine Laboratory, funded by The Shark Foundation/Hai Stiftung and Mike McAllister.

CONTRIBUTIONS

J.W.B. contributed to study design, data collection and analysis and manuscript preparation. L.P.G, D.M. and R.B. contributed to study design, data collection and manuscript preparation. A.A, A.J.A., J.H., S.K.L.-B., G.T.C., S.J.I., S.J.C. and A.J.D. contributed to study design and manuscript preparation.

ORCID

Jacob W. Brownscombe https://orcid.org/0000-0003-2496-8764

REFERENCES

Acosta, A., Bartels, C., Colvocoresses, J., & Greenwood, M. F. D. (2007). Fish assemblages in seagrass habitats of the Florida keys, Florida: Spatial and temporal characteristics. *Bulletin of Marine Science*, *19*, 1–19.

Adams, A. J., Wolfe, R. K., Kellison, G. T., & Victor, B. C. (2006). Patterns of juvenile habitat use and seasonality of settlement by permit, *Trachinotus falcatus*. *Environmental Biology of Fishes*, *75*, 209–217.

Allen, A. M., & Singh, N. J. (2016). Linking movement ecology with wildlife management and conservation. *Frontiers in Ecology and Evolution*, *3*. www.frontiersin.org/articles/10.3389/fevo.2015.00155/full.

Allison, G. W., Lubchenco, J., & Carr, M. H. (1998). Marine reserves are necessary but not sufficient for marine conservation. *Ecological Applications*, *8*, S79–S92.

Anthony, L. L., & Blumstein, D. T. (2000). Integrating behaviour into wildlife conservation: The multiple ways that behaviour can reduce N(E). *Biological Conservation*, *95*, 303–315.

Arlinghaus, R., Cooke, S. J., Lyman, J., Policansky, D., Schwab, A., Suski, C., … Thorstad, E. B. (2007). Understanding the complexity of catch-and-release in recreational fishing: An integrative synthesis of global knowledge from historical, ethical, social and biological perspectives. *Reviews in Fisheries Science*, *15*, 75–167.

Ault, J. S., Smith, S. G., Bohnsack, J. A., Luo, J., Zurcher, N., McClellan, D. B., … Causey, B. (2013). Assessing coral reef fish population and community changes in response to marine reserves in the Dry Tortugas, Florida, USA. *Fisheries Research*, *144*, 28–37.

Bartholomew, A., Bohnsack, J. A., Smith, S. G., Ault, J. S., Harper, D. E., & McClellan, D. B. (2008). Influence of marine reserve size and boundary length on the initial response of exploited reef fishes in the Florida keys National Marine Sanctuary, USA. *Landscape Ecology*, *23*, 55–65.

Berger, T., Lee, T. N., Atkinson, L., Williams, E., & Leaman, K. (2004). Florida current meanders and gyre formation in the Southern Straits of Florida. *Journal of Geophysical Research*, *100*, 8607.

Blumstein, D. T., & Fernández-Juricic, E. (2010). *A primer of conservation behavior*. Sunderland, MA: Sinauer Associates.

Brownscombe, J. W., Adams, A. J., Young, N., Griffin, L. P., Holder, P. E., Hunt, J., … Danylchuk, A. J. (2019b). Bridging the knowledge-action gap: A case of research rapidly impacting recreational fisheries policy. *Marine Policy*, *104*, 210–215.

Brownscombe, J. W., Danylchuk, A. J., Adams, A. J., Black, B. D., Boucek, R. E., Power, M., et al. (2019a). Bonefish in South Florida: Status, threats and research needs. *Fisheries Research*, *102*, 329–348.

Brownscombe, J. W., Danylchuk, A. J., Chapman, J. M., Gutowsky, L. F. G., & Cooke, S. J. (2017). Best practices for catch-and-release recreational fisheries–angling tools and tactics. *Fisheries Research*, *186*, 693–705.

Brownscombe, J. W., Griffin, L. P., Chapman, J. M., Morley, D., Acosta, A., Crossin, G. T., … Danylchuk, A. J. (2019d). A practical method to account for variation in detection range in acoustic telemetry arrays to accurately quantify the spatial ecology of aquatic animals. *Methods in Ecology and Evolution*. https://doi.org/10.1111/2041-210X.13322.

Brownscombe, J. W., Ledee, E., Raby, G. D., Struthers, D. P., Gutowsky, L. F. G., Nguyen, V. M., et al. (2019c). Conducting and interpreting fish telemetry studies: Considerations for researchers and resource managers. *Reviews in Fish Biology and Fisheries*, *29*, 369–400.

Bryan, D. R., Luo, J., Ault, J. S., McClellan, D. B., Smith, S. G., Snodgrass, D., & Larkin, M. F. (2015). Transport and connectivity modeling of larval permit from an observed spawning aggregation in the Dry Tortugas, Florida. *Environmental Biology of Fishes*, *98*, 2263–2276.

Burke, J. S., Kenworthy, W. J., Viehman, T. S., McDonough, V. L. & Degan, B. (2012). *Biodiversity and ecosystem function of shallow bank systems within Florida Keys National Marine Sanctuary (FKNMS)*. Marine Sanctuaries Conservation Series ONMS-12-03. https://repository.library.noaa.gov/view/noaa/13452.

Cagua, E. F., Berumen, M. L., & Tyler, E. H. M. (2013). Topography and biological noise determine acoustic detectability on coral reefs. *Coral Reefs*, *32*, 1123–1134.

Cooke, S. J., & Cowx, I. G. (2004). The role of recreational fishing in global fish crises. *Bioscience*, *54*, 857–859.

Cooke, S. J., Martins, E. G., Struthers, D. P., Gutowsky, L. F. G., Power, M., Doka, S. E., … Krueger, C. C. (2016). A moving target—incorporating knowledge of the spatial ecology of fish into the assessment and management of freshwater fish populations. *Environmental Monitoring and Assessment*, *188*, 239.

Cooke, S. J., Nguyen, V. M., Kessel, S. T., Hussey, N. E., Young, N., & Ford, A. T. (2017). Troubling issues at the frontier of animal tracking for conservation and management. *Conservation Biology*, *31*, 1205–1207.

Crabtree, R. E., Hood, P. B., & Snodgrass, D. (2002). Age, growth and reproduction of permit (*Trachinotus falcatus*) in Florida waters. *Fishery Bulletin*, *100*, 26–34.

Crossin, G. T., Heupel, M. R., Holbrook, C. M., Hussey, N. E., Lowerre-Barbieri, S. K., Nguyen, V. M., … Cooke, S. J. (2017). Acoustic telemetry and fisheries management. *Ecological Applications*, *27*, 1031–1049.

Crowder, L., & Norse, E. (2008). Essential ecological insights for marine ecosystem-based management and marine spatial planning. *Marine Policy*, *32*, 772–778.

D'Alessandro, E., Sponaugle, S., & Lee, T. (2007). Patterns and processes of larval fish supply to the coral reefs of the upper Florida keys. *Marine Ecology Progress Series*, *331*, 85–100.

De Freese, D. E. (1991). Threats to biological diversity in marine and estuarine ecosystems of Florida. *Coastal Management*, *19*, 73–101.

Fedler, T. (2013). Economic Impact of the Florida Keys Flats Fishery, *32608*, 25.

Graham, R. T., & Castellanos, D. W. (2005). Courtship and spawning behaviors of carangid species in Belize. *Fishery Bulletin*, *103*, 426–432.

Hall, M., Furman, B., Merello, M., & Durako, M. (2016). Recurrence of *Thalassia testudinum* Seagrass die-off in Florida bay, USA: Initial observations. *Marine Ecology Progress Series*, *560*, 243–249.

Hall, M. O., Durako, M. J., Fourqurean, J. W., & Zieman, J. C. (1999). Decadal changes in seagrass distribution and abundance in Florida bay. *Estuaries*, *22*, 445.

Holder, P. E., Griffin, L. P., Adams, A. J., Danylchuk, A. J., Cooke, S. J., & Brownscombe, J. W. (2020). Stress, predators and survival: Exploring permit (*Trachinotus falcatus*) catch-and-release fishing mortality in the Florida keys. *Journal of Experimental Marine Biology and Ecology*, 524 (online).

Kessel, S. T., Cooke, S. J., Heupel, M. R., Hussey, N. E., Simpfendorfer, C. A., Vagle, S., & Fisk, A. T. (2014). A review of detection range testing in aquatic passive acoustic telemetry studies. *Reviews in Fish Biology and Fisheries*, *2014*, 199–218. https://doi.org/10.1007/s11160-013-9328-4.

Koenig, C. C., Coleman, F. C., Grimes, C. B., Fitzhugh, G. R., Scanlon, K. M., Gledhill, C. T., & Grace, M. (2000). Protection of fish spawning habitat for the conservation of warm-temperate reef-fish fisheries of shelf-edge reefs of Florida. *Bulletin of Marine Science*, *66*, 593–616.

Kramer, D. L., & Chapman, M. R. (1999). Implications of fish home range size and relocation for marine reserve function. *Environmental Biology of Fishes*, *55*, 65–79.

Kruer, C. R. (2017) *Florida Keys Shallow Water Boating Impact Analysis and Trends Assessment-Mapping Summary Report*.

Lapointe, B. E., & Clark, M. W. (1992). Nutrient inputs from the watershed and coastal eutrophication in the Florida keys. *Estuaries*, *15*, 465.

Lapointe, B. E., Tomasko, D. A., & Matzie, W. R. (1994). Eutrophication and trophic state classification of seagrass communities in the Florida keys. *Bulletin of Marine Science*, *54*, 696–717.

Law, B. S., & Dickman, C. R. (1998). The use of habitat mosaics by terrestrial vertebrate Fauna: Implications for conservation and management. *Biodiversity and Conservation*, *7*, 323–333.

Lewis, C. A., Lester, N. P., Bradshaw, A. D., Fitzgibbon, J. E., Fuller, K., Hadanson, L., & Richards, C. (1996). Considerations of scale in habitat conservation and restoration. *Canadian Journal of Fisheries and Aquatic Sciences*, *53*, 440–445.

Lowerre-Barbieri, S., DeCelles, G., Pepin, P., Catalán, I. A., Muhling, B., Erisman, B., … Paris, C. B. (2017). Reproductive resilience: A paradigm shift in understanding spawner-recruit systems in exploited marine fish. *Fish and Fisheries*, *18*, 285–312.

Lowerre-barbieri, S. K., Kays, R., Thorson, J. T. & Wikelski, M. (2019) The ocean' s movescape: Fisheries management in the bio-logging decade (2018–2028). *ICES Journal of Marine Science*, *76*(2), 477–488.

Lowerre-Barbieri, S. K., Walters Burnsed, S. L., & Bickford, J. W. (2016). Assessing reproductive behavior important to fisheries management: A case study with red drum, *Sciaenops ocellatus*. *Ecological Applications*, *26*, 979–995.

Maliao, R. J., Turingan, R. G., & Lin, J. (2008). Phase-shift in coral reef communities in the Florida keys National Marine Sanctuary (FKNMS), USA. *Marine Biology*, *154*, 841–853.

Mathies, N. H., Ogburn, M. B., McFall, G., & Fangman, S. (2014). Environmental interference factors affecting detection range in acoustic telemetry studies using fixed receiver arrays. *Marine Ecology Progress Series*, *495*, 27–38.

McIvor, C. C., Ley, J. A., & Bjork, R. D. (1994). Changes in freshwater inflow from the Everglades to Florida bay including effects on biota and biotic processes: A review. In S. Davis & J. C. Ogden (Eds.), *Everglades: The Ecosystem and Its Restoration*. Boca Raton, FL: CRC Press, Taylor Francis Group.

National Marine Fisheries Service. (2018) *Fisheries of the United States*, 2017.

NOAA. (2016) *National Oceanic and Atmopheric Administration - Florida Keys National Marine Sanctuary*. Retrieved from http://floridakeys.noaa.gov/about/welcome.html?s=about.

R Core Team. (2018). *R: A language and environment for statistical computing* (Vol. 2018). Vienna, Austria: R Foundation for Statistical Computing.

Raby, G. D., Packer, J. R., Danylchuk, A. J., & Cooke, S. J. (2014). The understudied and underappreciated role of predation in the mortality of fish released from fishing gears. *Fish and Fisheries*, *15*, 489–505.

Sargent, F. J., Leary, T. J., Crewz, D. W. & Kruer, C. R. (1995) Scarring of Florida's Seagrasses: Assessment and management options. *Florida Marine Research Institute Technical Reports* 37.

Simpfendorfer, C. A., Huveneers, C., Steckenreuter, A., Tattersall, K., Hoenner, X., Harcourt, R., & Heupel, M. R. (2015). Ghosts in the data: False detections in VEMCO pulse position modulation acoustic telemetry monitoring equipment. *Animal Biotelemetry*, *3*, 482–492.

Stocks, J. R., Gray, C. A., & Taylor, M. D. (2014). Testing the effects of near-shore environmental variables on acoustic detections: Implications on telemetry Array design and data interpretation. *Marine Technology Society Journal*, *48*, 28–35.

Stoner, A. W. (1980). The role of seagrass biomass in the organization of benthic macrofaunal assemblages. *Bulletin of Marine Science*, *30*, 537–551.

Team, R. S. (2016). *RStudio: Integrated development for R* (p. 2016). Boston, MA: RStudio, Inc.

Weil, E. (2004). Coral reef diseases in the wider Caribbean. In: E. Rosenberg & Y. Loya (eds.), *Coral health and disease*. Berlin, Heidelberg: Springer, 35–68.

Williams, SL, Heck Jr., KL, 2001. Seagrass community ecology. In: Bertness, MD, Gaines, SD, Hay, ME (Eds) Marine Community Ecology. Sunderland, Massachusetts: Sinauer Associates, 317–337.

Zeng, X., Adams, A., Roffer, M., & He, R. (2018). Potential connectivity among spatially distinct management zones for bonefish (*Albula vulpes*) via larval dispersal. *Environmental Biology of Fishes*, *102*, 233–252.

Zieman, J. C. (1976). The ecological effects of physical damage from motor boats on turtle grass beds in southern Florida. *Aquatic Botany*, *2*, 127–139.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

How to cite this article: Brownscombe JW, Griffin LP, Morley D, et al. Seasonal occupancy and connectivity amongst nearshore flats and reef habitats by permit *Trachinotus falcatus*: considerations for fisheries management. *J Fish Biol*. 2020;96:469–479. https://doi.org/10.1111/jfb.14227