









RESEARCH ARTICLE

Application of telemetry and stable isotope analyses to inform the resource ecology and management of a marine fish

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Abstract

1. Animal movement and resource use are essential considerations for effective environmental management, but they are challenging to quantify in expansive natural ecosystems such as oceans.
2. We used a novel combination of fish tracking with expansive acoustic telemetry networks, stable isotope analysis and integrated modelling techniques to characterize the spatial and trophic ecology of a marine fish species, permit *Trachinotus falcatus*, and to address specific resource management needs in the Florida Keys.
3. Tracking-based movement patterns indicated that permit remained primarily within the designated fisheries management unit (92% of individuals), but they moved frequently among distinct habitat types and fisheries. Movement metrics from 109 individuals were integrated into Bayesian isotope mixing models, revealing variable reliance on seagrass- versus offshore/pelagic-based energy channels amongst individuals. Variance was driven mainly by fish habitat use and home range size (km²).
4. A telemetry-based regional isoscape, informed by individual-level estimates of resource use (% seagrass reliance; median = 70%, 29%–100% range), illustrated connectivity among habitats and fisheries. Specifically, seagrass flats were highly connected with the Florida reef tract, with frequent movements between these habitat types and a high reliance on seagrass-based prey. There was a distinction between these fish and those occupying artificial reefs, with the latter showing high use of pelagic/offshore (i.e. planktonic) energy channels.
5. *Synthesis and applications.* This study used a novel combination of telemetry, stable isotope analysis and integrated modelling techniques to identify two distinct ecotypes of a nearshore fish species, permit, in the Florida Keys. Of the two ecotypes, nearshore Florida Keys permit support multiple valuable fisheries; for these fish management should prioritize conservation of seagrass flats as

a key permit food source, as well as fisheries protection measures at spawning sites on the Florida reef tract. This study highlights the capacity for integrated telemetry-isotope models to provide key insights into animal ecology that has direct implications for applied environmental management.

KEYWORDS

acoustic telemetry, Bayesian mixing models, conservation, environmental management, movement ecology, resource ecology, stable isotope analysis

1 | INTRODUCTION

An understanding of animal spatial and resource ecology is essential for effective environmental management. For example, the scale of animal space use dictates the effective spatial extent of protected areas (Burgess et al., 2014; Lea et al., 2016), a growing conservation strategy in diverse ecosystems world-wide (Agardy et al., 2011; Agardy & Tundi Agardy, 1994). Mobile animals require access to a variety of habitats, which serve a range of specific functional roles such as supporting foraging and/or reproduction (Foley et al., 2010; McLeod et al., 2009; Shipley et al., 2021). In addition, spatial-temporal habitat use is highly relevant for other aspects of environmental management, such as designing harvest regulations to reduce the potential for overexploitation, especially at times when species are most vulnerable (e.g. during spawning aggregations; Lowerre-Barbieri et al., 2017). Animal spatial and resource ecology is also highly relevant to ecosystem ecology. For example, the transfer of nutrients across habitats by mobile animals is an important aspect of ecosystem function (Allgeier et al., 2013; Archer et al., 2015; McCauley et al., 2012). Therefore, this type of knowledge is key for ecosystem-based management (Pikitch et al., 2004; Slocombe, 1993) focused on maintaining functional, healthy ecosystems.

Despite its relevance to environmental management, the spatial and resource ecology of mobile animals is challenging to quantify, especially in large, open systems such as oceans. Fortunately, there are a growing suite of tools to address knowledge gaps. Of these, telemetry applications are growing rapidly, with networks of acoustic receivers placed throughout aquatic ecosystems across the globe, enabling tracking of a diversity of aquatic animals at spatial-temporal scales never before possible (Crossin et al., 2017; Hussey et al., 2015; Iverson et al., 2019). Stable isotope techniques have also advanced, whereby the isotopic composition of animal tissues can be compared with that of ecosystem biota (i.e. isotopic endmembers) to inform space use, as well as organismal functional roles (Newsome et al., 2012; Shipley & Matich, 2020). Both tools provide unique insights into animal spatial and resource ecology, but each has its own caveats. Acoustic telemetry provides continuous long-term monitoring of specific locations, but logistical constraints often result in incomplete tracking system coverage, leaving animal space use unknown for large areas and periods of time (Brownscombe, Ledee, et al., 2019). Additionally, acoustic telemetry approaches fail

to provide information on resource assimilation. Isotopic techniques can provide a non-lethal, time-integrated evaluation of animal diet and habitat use where temporal windows are dictated by the isotopic incorporation rate of the analysed tissue (Thomas & Crowther, 2015; Vander Zanden et al., 2015b). Yet, rarely can estimates be quantified across the entire lifetime of the focal taxa, and are often limited to a period of a few months (Shipley & Matich, 2020). When combined, however, acoustic telemetry and isotopic approaches provide a complementary and holistic understanding of animal spatial and resource ecology (Ceriani et al., 2012; Madigan et al., 2014; Speed et al., 2012; Vander Zanden et al., 2015a). For example, Shipley et al. (2021) used nitrogen stable isotopes to predict the timing of habitat shifts in juvenile sand tiger sharks *Carcharias taurus* and validated the models using acoustic telemetry data, while Harrison et al. (2017) were able to link differences in individual movement behaviours to dietary specializations. However, direct integration of the two data sources using modelling techniques has rarely been accomplished and may provide greater insights into the nature of space and resource use.

Spatial and resource ecology is highly relevant environmental management, and is particularly important for coastal marine fishes, which live in highly diverse and dynamic habitats that are often under heavy pressure from growing human populations (Halpern et al., 2008; Worm et al., 2006). Many coastal marine fish populations are subjected to recreational fishing activity including both harvest and catch-and-release (Coleman et al., 2004). Permit *Trachinotus falcatus*, a member of the Carangidae family, occupy coastal marine habitats in the western Atlantic, Caribbean Sea and Gulf of Mexico (Adams & Cooke, 2015) and support multiple, highly valuable recreational fisheries in Florida (Fedler, 2013). In south Florida, permit occupy a variety of habitat types, foraging mostly on benthic invertebrates in shallow, nearshore flats (<5 m depth; Brownscombe, Griffin, Morley, Acosta, Hunt, Lowerre-Barbieri, Crossin, et al., 2020) and spawning in the spring and summer months in proximity to natural and/or artificial reefs (Brownscombe, Griffin, Morley, Acosta, Hunt, Lowerre-Barbieri, Adams, et al., 2020). Despite being located in the Florida Keys Marine Sanctuary, the expansive seagrass flats and coral reefs in the region are subject to extensive degradation from a variety of anthropogenic pressures (De Freese, 1991; Lapointe & Clark, 1992; McIvor et al., 1994). On the flats, individuals are commonly targeted by recreational anglers in a predominantly catch-and-release fishery. During spawning,

permit form aggregations, often numbering in the hundreds to thousands, when they can be more easily targeted by anglers and more commonly harvested (Brownscombe, Adams, et al., 2019). For this reason, permit harvest is prohibited during the primary spawning season (April through July, Brownscombe, Adams, et al., 2019) within the Special Permit Zone (SPZ; <https://myfwc.com/fishing/saltwater/recreational/permit/>) in south Florida. However, shark depredation on angled permit at spawning locations can exceed 50% in some locations (Holder et al., 2020), rendering this regulatory approach insufficient in some cases.

The diverse habitats that permit occupy and multiple fisheries they support make the species a valuable case study for understanding habitat connectivity and resource use, with the information having direct applications for management. Yet, there are inherent challenges associated with generating comprehensive measures of space use and trophic interactions of wild animals such as permit. Specifically, previous studies have identified permit spawning sites and varied levels of connectivity among habitats with telemetry (Brownscombe, Griffin, Morley, Acosta, Hunt, Lowerre-Barbieri, Adams, et al., 2020; Brownscombe, Griffin, Morley, Acosta, Hunt, Lowerre-Barbieri, Crossin, et al., 2020), but comprehensive assessments of habitat connectivity and resource use require further investigation. To that end, we conducted a 5-year study combining acoustic telemetry and stable isotope values for 109 adult and subadult permit in south Florida. To characterize their level of connectivity among habitat types and reliance upon primary prey resource pools, we used modelling techniques that integrated the two data sources, providing key insights for permit management. More broadly, the described approach should serve as a model for combining tracking and isotopic data to reveal the nature of a broad suite of ecological processes, the understanding of which is critical to the environmental management in diverse contexts.

2 | MATERIALS AND METHODS

2.1 | Data collection

A total of 150 permit (681 ± 97 mm fork length; mean \pm SD; 457–978 mm range) were captured for sampling via recreational angling from March 2016 to May 2019 across the Florida Keys, from Biscayne Bay to west of the Marquesas, northward up to 60 km into the Gulf of Mexico (Appendix S1; Figure S1). Captured fish were tagged immediately with acoustic transmitters 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 delay, 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) via surgical implantation (see Brownscombe, Griffin, Morley, Acosta, Hunt, Lowerre-Barbieri, Crossin, et al. (2020) for more details on tagging procedures). Prior to release, a 5-mm fin clip was taken from the tip of the dorsal fin for stable isotope analysis, which was either stored on ice temporarily (<10 h) prior to freezing, or immediately placed in 95% reagent grade ethanol prior to further

analysis as described in Appendix S1. Tagged permit were tracked with acoustic receivers (VR2W and VR2Tx, Innovasea Inc). Starting in 2015, 60 receivers were established specifically to track permit, and this number grew to 100 by May 2019. An additional 1000+ receivers were also deployed in adjacent coastal regions throughout the study by other research groups, with data sharing facilitated by the Florida Atlantic Coastal Telemetry network (FACT), integrated Tracking of Animals in the Gulf of Mexico network (iTAG) and the Ocean Tracking Network (OTN; see Appendix S1; Figure S2 for map of receiver locations). All procedures were conducted in accordance with the Carleton University Animal Care Committee (application 11473), as well as the American Association for Laboratory Animal Science (IACUC protocol 2013-0031, University of Massachusetts Amherst).

2.2 | Quantitative statistical analyses

2.2.1 | Acoustic telemetry data

All statistical analyses were conducted in the R (R Core Team, 2019) via RStudio (RStudio Team, 2016), with data processing and plotting conducted with packages dplyr (Wickham et al., 2021), ggplot2 (Wickham, 2016) and gmap (Kahle & Wickham, 2013). Permit acoustic telemetry detections were aggregated over 5 years from 2016 to 2020. Prior to analysis, permit detections were filtered to remove potentially false detections, which often occur due to a variety of environmental and technological factors (Brownscombe, Ledee, et al., 2019; Simpfendorfer et al., 2015). Firstly, detections that occurred within a time period shorter than the minimum tag delay (60 seconds), as well as any that occurred for a given tag prior to its deployment were removed. Secondly, any single detections of an individual transmitter that occurred at a receiver within a 24-h time period were removed. Filtering resulted in 1,896,740 reliable detections from 127 individual permit at 314 individual receiver stations from 17 March 2016 to 12 April 2020 (see Appendix S1; Figure S3; Table S1 for fish tracking details). Detections were further aggregated by receiver nodes, which represented distinct locations (e.g. a reef, shipwreck or area of nearshore flats; $n = 47$; Appendix S1; Figure S4). Each node was characterized as a specific habitat type. Flats were considered nearshore areas with a depth < 5 m, with extensive seagrass coverage. Reef tract represents the habitat of the Florida Reef Tract, and it included both natural and artificial reefs. Artificial reefs included shipwrecks or other anthropogenically sourced structures (e.g. communication towers) in areas geographically separate from the reef tract. Each node was assigned as inside or outside the SPZ—a region that encompasses the southern tip of Florida, extending out to the Dry Tortugas, where permit recreational fishing harvest is more restricted for conservation purposes (<https://myfwc.com/fishing/saltwater/recreational/permit/>). Permit detections, residency periods and movements were quantified within and between receiver nodes to characterize the

level of residency and movements between nodes, habitat types and the SPZ, with the resulting data integrated into the stable isotope models described below. Individual residency periods were calculated as continuous periods where <1 h lapsed between detections at a receiver node (as per Brownscombe, Griffin, Morley, Acosta, Hunt, Lowerre-Barbieri, Adams, et al., 2020). Movements were considered when reliable detections of an individual occurred subsequently among receiver nodes. Home range size (km²) was calculated with minimum convex polygons using the *adehabitatHR* package (Calenge, 2006). In cases where home ranges were <1 km², they were set to 1 km² due to the spatial resolution of acoustic telemetry tracking, where detection ranges of acoustic receivers can reach up to 500 m (Brownscombe et al., 2020).

2.2.2 | Stable isotope mixing models

Stable isotope mixing models were implemented in the R package *MixSIAR* (Stock et al., 2018; Stock & Semmens, 2016). The approach allows for the integration of continuous, fixed and random effects into a Bayesian modelling framework (Stock et al., 2018). We used an isotopic endmember approach (e.g. Madigan et al., 2015; McCauley et al., 2012; Shipley et al., 2019) to establish the reliance of individual permit on two major energy channels: seagrass- and pelagic offshore-derived production. Specific endmembers were selected based on stomach content data available (discussed in Brownscombe, Griffin, Morley, Acosta, Hunt, Lowerre-Barbieri, Crossin, et al., 2020). Although permit can be found proximate to coral reefs, there is little evidence suggesting that individuals rely upon a considerable proportion of reef-associated forage (Brownscombe, Griffin, Morley, Acosta, Hunt, Lowerre-Barbieri, Crossin, et al., 2020). To isotopically categorize seagrass and pelagic offshore endmembers, site faithful consumer species that are assumed to be at isotopic steady state with each energy channel were gathered from the published literature (see Appendix S1; Table 2). We used 100 resampling iterations from the published means and standard deviations, assuming a normal distribution, to generate a carbon and nitrogen isotope mixing space for each energy channel (see approaches described by Shipley et al., 2021). Resampling resulted in $n = 1,600$ and $n = 2,200$ prey baseline isotope values for seagrass ($\delta^{13}\text{C} = -12.7 \pm 1.3\text{‰}$ and $\delta^{15}\text{N} = 5.2 \pm 1.7\text{‰}$) and offshore/pelagic prey ($\delta^{13}\text{C} = -18.4 \pm 1.1\text{‰}$ and $\delta^{15}\text{N} = 7.9 \pm 3.1\text{‰}$) respectively. A full breakdown of the baseline organisms can be found in Appendix S1 and Table S2.

Appropriate parameterization of Bayesian isotope mixing models requires that all consumer data [corrected for trophic discrimination factors (TDFs)] fall within the bounds of the mixing space (Phillips et al., 2014; Smith et al., 2013). For models with greater than two sources, the condition is typically validated through the simulation of mixing polygons (Smith et al., 2013). Here the approach was not appropriate because of the use of a two-end member mixing model. Therefore, to validate the efficacy of the linear mixing space, we

first assigned all consumer stable isotope data TDFs of $\Delta^{13}\text{C} = 3.0\text{‰}$ and $\Delta^{15}\text{N} = 3.5\text{‰}$ based on a recent meta-analysis of fish fin TDFs (Canseco et al., 2021). All individuals that fell beyond the 2.5th and 97.5th percentiles of the carbon ($\delta^{13}\text{C} = -10.9\text{‰}$ to 20.3‰) and nitrogen ($\delta^{15}\text{N} = 2.2\text{‰}$ – 13.1‰) isotope values of either end members were subsequently removed from further analyses. Use of the criterion resulted in the removal of $n = 7$ individuals comprising ~6% of the sampled population.

Movement metrics (inferred through passive acoustic telemetry) with paired carbon and nitrogen stable isotope data were available for $n = 109$ individuals. We ran five candidate models to identify the potential drivers of permit resource use and compared results with those of a null model. Predictor variables included animal body size (fork length, mm), as well as telemetry-based metrics, home range (HR, km²) and dominant habitat of occupancy (highest residency values; categorical – reef tract, flats or artificial reefs). Temporal factors were not included in the model because there were no significant seasonal patterns detected in the data (Appendix S1; Figure S5), which was expected due to slow fin tissue turnover rates (~3–6 months) relative to the seasonal sampling period. A set of models were run that explored the effects of a single predictor variable only, then a second set of models were run that combined the effects of the dominant habitat occupied with each of the continuous predictor variables. The most likely model was evaluated through leave-one-out cross validation (LOOic) scores and Akaike weights (Stock et al., 2018). Mixing models were run across three Markov chains for 50,000 iterations with a burn in of 25,000 and a thinning interval of 25. Model convergence was examined based on Gelman diagnostics, where all parameter estimates should fall below 1.05 (Stock et al., 2018). All models were run with a residual*process error structure and uninformative priors (Stock et al., 2018; Stock & Semmens, 2016). Due to low tracking days for some individuals, we compared mixing model outputs from the full dataset ($n = 109$) to a 'trimmed' dataset including individuals with tracking durations >100 days ($n = 90$). We used TDFs of $\Delta^{13}\text{C} = 3.0\text{‰}$ and $\Delta^{15}\text{N} = 3.5\text{‰}$ (see above) both of which were assigned a conservative standard deviation of 1.0‰, given the suite of environmental and physiological factors that can drive variability in TDFs (Caut et al., 2009; Shipley & Matich, 2020) but could not be quantified for permit sampled in this study.

2.2.3 | Telemetry-based isoscape

The best fitting stable isotope mixing model was used to generate a telemetry-informed isoscape, which was estimated by applying the fitted seagrass reliance probability values for each individual from the mixing model to estimates of the mean spatial position of the fish from the tracking data. These values were used to generate continuous predictions of proportional seagrass reliance using kriging on a 0.01×0.01 latitude/longitude raster grid (~1.23 km² cells) using the *autoKrige* function from the 'automap' package (Hiemstra et al., 2008).

3 | RESULTS

3.1 | Spatial ecology

Acoustic telemetry data showed that, of the permit with reliable (filtered) tracking data ($n = 127$), the majority were detected only within the SPZ (92%), with eight individuals detected north of the SPZ in either the Gulf of Mexico or the Atlantic Ocean (Figure 1; see Appendix S1; Figure S7 for details on specific movement locations). However, a high level of permit movement occurred within the SPZ in proximity to the Florida Keys (Figure 1a). There were high levels of movement detected within habitat types, especially in the flats and the reef tract (Figure 1b). There was also a high level of connectivity between the flats and the reef tract, but a relatively low level of movement between artificial reefs and any other habitat type, including between individual artificial reefs (Figure 1b).

3.2 | Resource ecology

Stable isotope data from permit fin tissues ranged from -17.3% to -7.9% and from 6.4% to 14.9% for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ respectively (Figure 2). Bayesian isotope mixing models revealed that dominant habitat and home range best explained variability in permit resource use (Table 1), based on the lowest LOOic score (LOOic = 408.9) and

highest Akaike weight ($w = 64\%$). Individuals detected most frequently near artificial reefs showed a strong reliance upon pelagic energy channels (median = 70%), whereas individuals with larger home ranges on reef tract and flats habitats were more heavily reliant upon seagrass-derived energy (median = 76% and 81% respectively; Figure 3). Further, across all habitats, individuals with larger home ranges were more reliant on seagrass-derived energy and individuals with smaller home ranges exhibiting greater reliance on pelagic-derived energy (Figure 3).

Based on Akaike weights, two additional models cannot be discounted in terms of explaining permit resource use. The model containing only the effect of habitat yielded the second highest LOOic score and Akaike weight (LOOic = 410.7, $w = 26\%$, Table 1). Secondly, the model containing the effects of habitat + size on permit resource use carried 11% of the Akaike weight (LOOic = 412.5, Table 1). Here, exponential relationships were observed between increasing body size and reliance upon offshore-derived energy, a trend that was consistent across all three habitats (Figure 3). Across these three models, multiplicative error terms were higher for $\delta^{13}\text{C}$ ($\xi_{\text{C}} = 3.1\text{--}3.7$) compared with $\delta^{15}\text{N}$ ($\xi_{\text{N}} = 0.6\text{--}0.7$), suggesting some potential variability remained unaccounted regarding permit $\delta^{13}\text{C}$ values (Table 1; Stock & Semmens, 2016; Stock et al., 2018). We observed negligible differences between mixing models run using the full and trimmed (tracking periods > 100 days) datasets (Appendix S1; Tables S3 and S4).

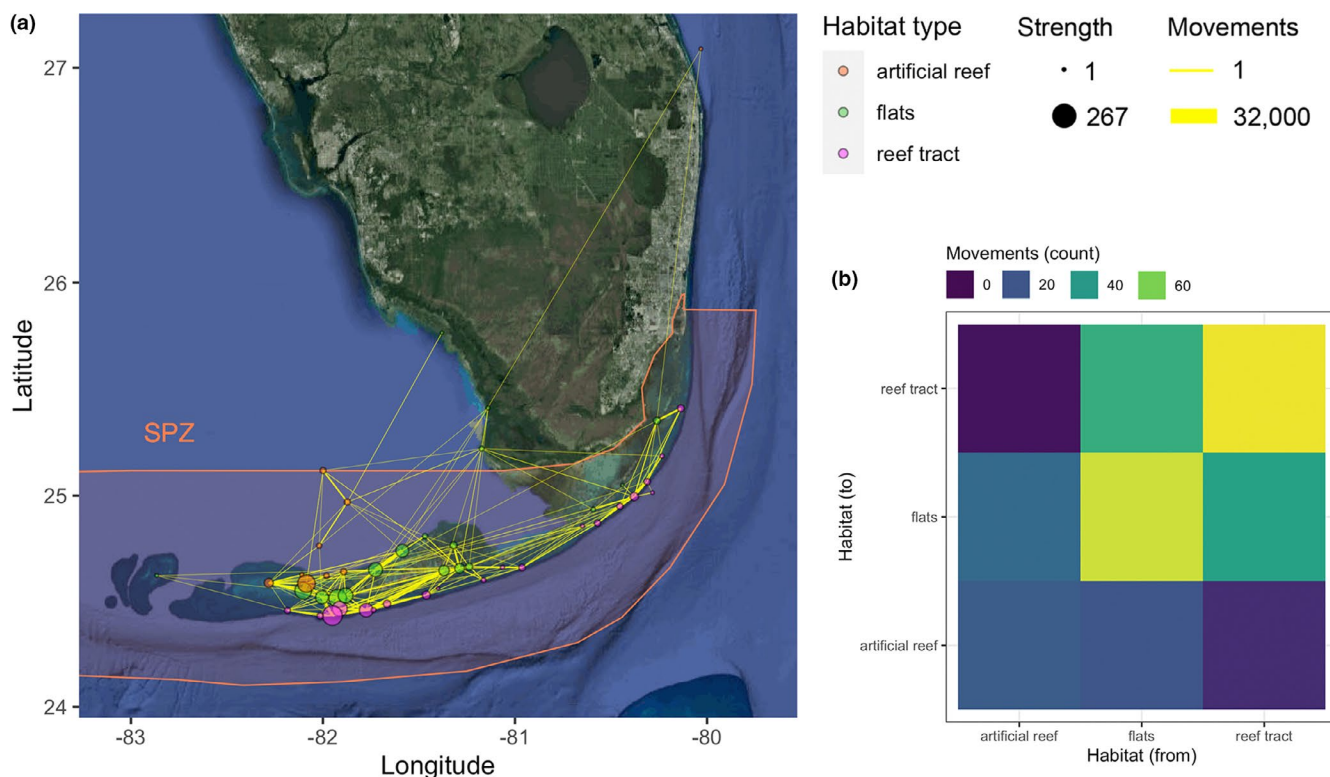


FIGURE 1 (a) Movement patterns of permit ($n = 127$) derived from acoustic telemetry tracking, aggregated by individual receiver nodes ($n = 47$) in South Florida. Nodes are coloured by habitat type, and the size of the circle indicates node strength (the number of connections to other nodes). Movements are indicated by the yellow lines, with the width denoting the number of movements. (b) Tile mosaic indicating the number of permit movements among distinct habitat types

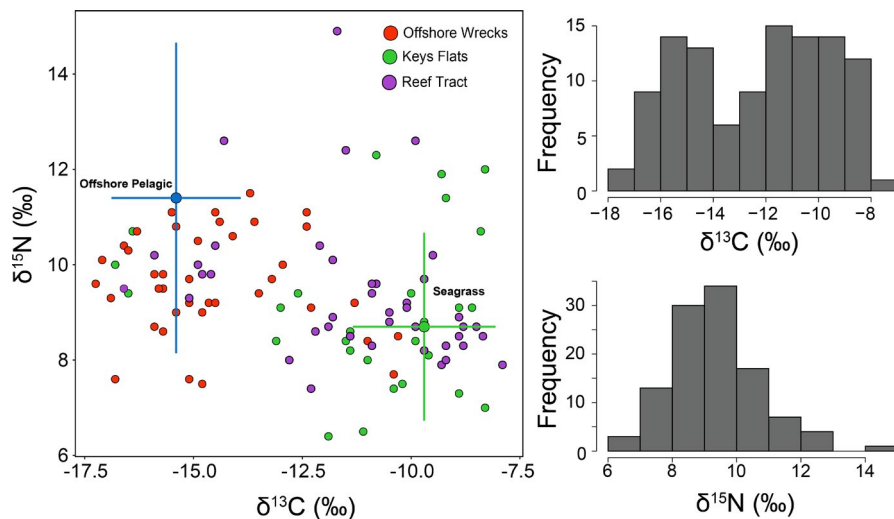


FIGURE 2 Stable isotope mixing space relative to seagrass and pelagic/offshore baselines (mean \pm SD) for permit categorized by three predominant habitats of detection: artificial reefs (red circles), flats (green circles) and reef tract (purple circles). Permit isotope value are corrected for trophic discrimination. Right panels are histograms of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for the sampled population ($n = 109$)

TABLE 1 Summary statistics comparing six candidate Bayesian stable isotope mixing models to evaluate the drivers of resource use in permit. Models are ordered based on LOOic scores and associated Akaike weights (w_i). Table also highlights LOOic standard error (SE), the difference in LOOic between subsequent models (ΔLOOic) and the associated standard error. ξ_j represent multiplicative error terms for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, which are lowest for the best fitting model

Model	LOOic	SE (LOOic)	ΔLOOic	SE (ΔLOOic)	w_i	ξ_C	ξ_N
Habitat + HR	409	24.8	0	NA	0.62	3.1	0.6
Habitat	410.8	24.1	1.8	2.6	0.25	3.3	0.7
Habitat + Size	412.1	23.6	3.1	5.1	0.13	3.7	0.6
Size	421.2	21.8	12.2	11.2	0.00	5.6	0.5
HR	437.7	19.1	28.7	12	0.00	5.5	0.6
Null	439.9	18.7	30.9	12.1	0.00	5.6	0.7

3.3 | Telemetry-based isoscape

The best fitting stable isotope model, including the predominant habitat type of fish residency and fish home range size, indicated distinct spatial patterns of permit reliance on seagrass-based prey (Figure 4a). The isoscape, generated by telemetry-informed stable isotope modelling, illustrates the interconnectivity among the flats-reef tract habitats by permit, which rely heavily on seagrass-based prey (Figure 4b). However, permit residing primarily on artificial wrecks and in the Gulf of Mexico and west of the Marquesas were rarely detected outside that habitat type and exploited food resources associated with offshore phytoplanktonic-based production.

4 | DISCUSSION

Here we combined acoustic telemetry and Bayesian stable isotope mixing models to elucidate the habitat and resource use of permit in the coastal region of south Florida. We determined that permit throughout the coastal Florida Keys region exhibit a high level of connectivity between the flats and Florida Reef Tract, relying heavily on seagrass-based prey. Therefore, these fish likely use the flats and reefs for foraging and spawning respectively. Conversely, permit that occupy artificial reefs (predominantly shipwrecks) further

offshore in the Gulf of Mexico and west of the Florida Keys remain primarily in these habitats and exploit offshore pelagic-based prey. However, there was a significant effect of permit body size on resource use, where smaller sized fish were heavily reliant on seagrass-based prey, with larger fish shifting more towards offshore, phytoplanktonic-based resources. Below, we discuss these findings in terms of their relevance for permit conservation, which highlights the value of combining these two information sources through integrating modelling techniques. We then discuss how the combined telemetry-informed stable isotope approach could be further refined and applied to other study systems and questions.

The apparent distinction between flats-reef tract permit and offshore artificial reef permit observed here may indicate that these fish could be considered separately in management contexts, such as recreational fishing regulations and MPA development. However, the observed pattern of resource use among permit of different body sizes is relevant, as offshore fish relied on seagrass-based prey at smaller sizes, and permit in all habitat types showed a general shift away from seagrass towards pelagic-based prey at large adult sizes (Figure 3). This is consistent with permit life history, as juvenile permit larvae settle onto sandy beach shoreline and juveniles occupy shallow nearshore flats habitats (Adams et al., 2006). Permit age of maturity is ~ 500 mm (Crabtree et al., 2002), at which point they migrate to offshore spawning locations near natural or artificial reefs

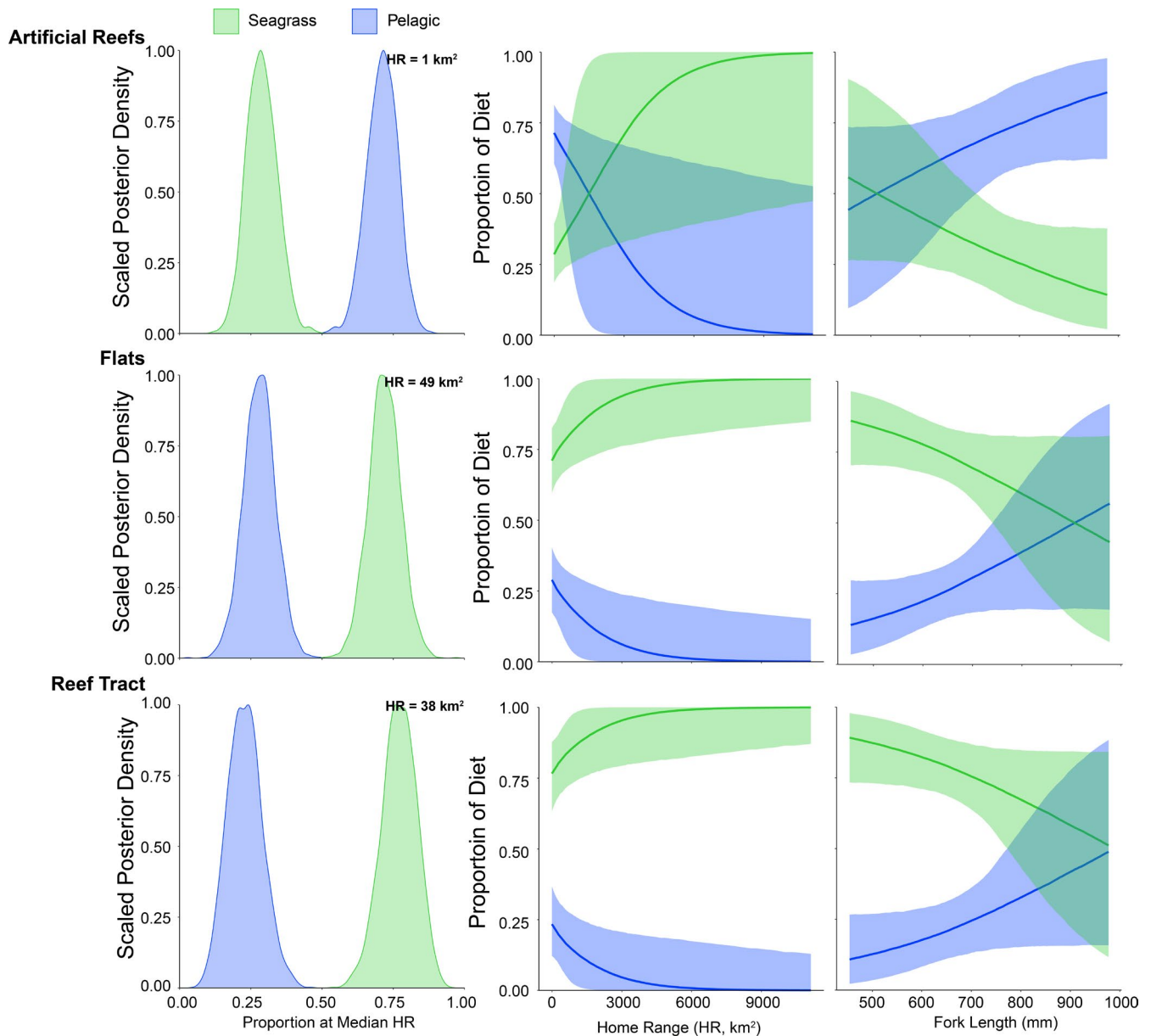
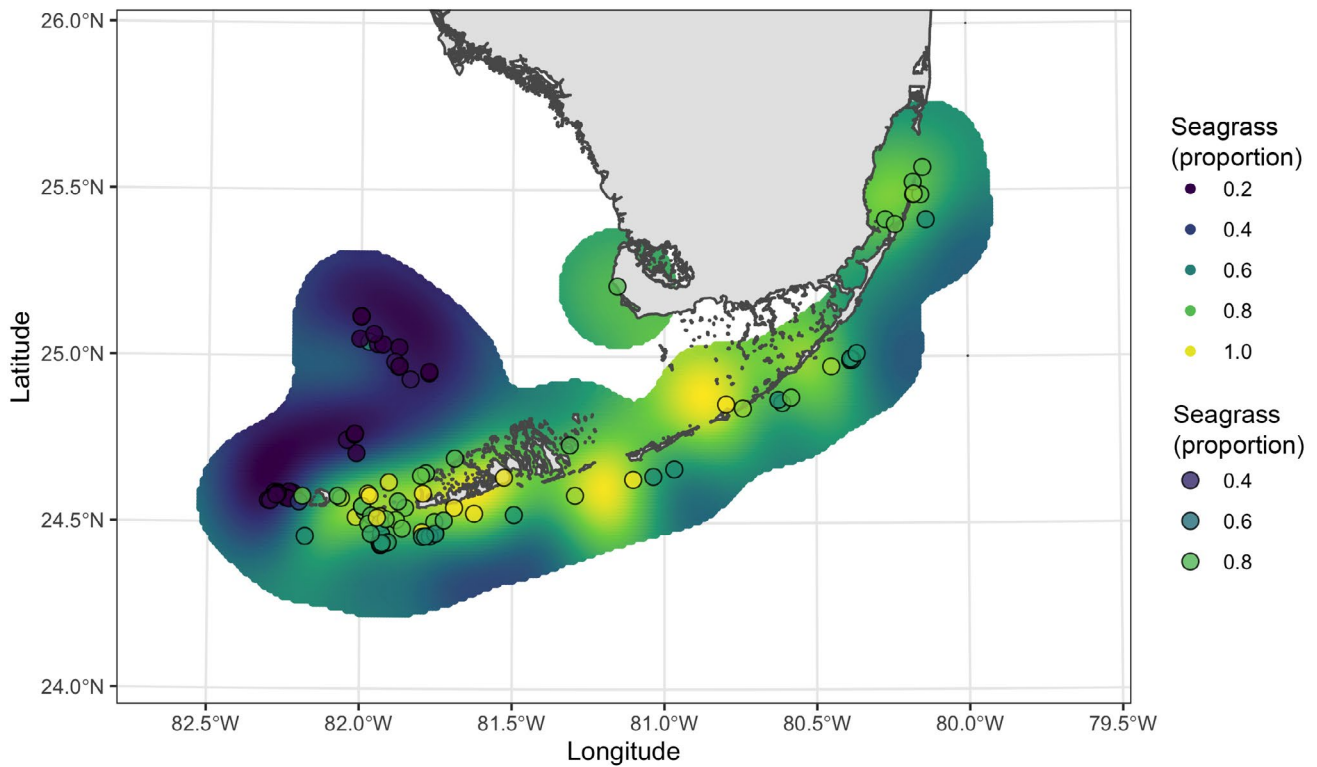


FIGURE 3 Posterior density distributions highlighting the reliance of permit on seagrass versus pelagic energy channels from individuals preferentially utilizing artificial reef, flats and reef tract habitats. Estimates are extracted from the most likely model based on LOOic criteria (site + HR) and represent relative proportions for permit at the median home range size. Middle panels show changing reliance upon seagrass and pelagic energy channels across home range. Right panels are extracted from habitat + size, which are also a strong model based on LOOic criteria, showing shifting reliance upon energy channel reliance across animal fork length

(Brownscombe, Griffin, Morley, Acosta, Hunt, Lowerre-Barbieri, Crossin, et al., 2020). Pelagic-based permit and prey also exhibited higher $\delta^{15}\text{N}$ values, indicating a different ^{15}N baseline composition and/or trophic position. This suggests that larger adults may exploit offshore prey more effectively, perhaps larger invertebrates such as swimming crabs, which were the bait used almost exclusively to catch permit for this study, and were commonly observed offshore. Once larger permit become less reliant on seagrass flats for food, they may be able to avoid energetically costly long-distance migrations to the flats to feed, enabling them to move among offshore habitats, including to artificial reefs.

Combined, the movement patterns and size-specific resource ecology of permit could be indicative of a broader life-history shift from reliance on nearshore flats at earlier life stages to an existence further offshore as larger adults. There was a higher level of movement from the Florida reef tract to offshore artificial reefs than vice versa, although connectivity to offshore reefs was generally low (Figure 1). It is, however, unlikely that a broad life-history shift in habitat use would be highly detectable when tracking periods for individual permit averaged 371 days, and their life span can exceed 20 years (Crabtree et al., 2002). There were large adults captured and tracked among all habitat types, so if such a shift exists it may occur in a subset of individuals, with a

(a) Telemetry-based isoscape - Fish positions



(b) Telemetry-based isoscape - Habitat locations

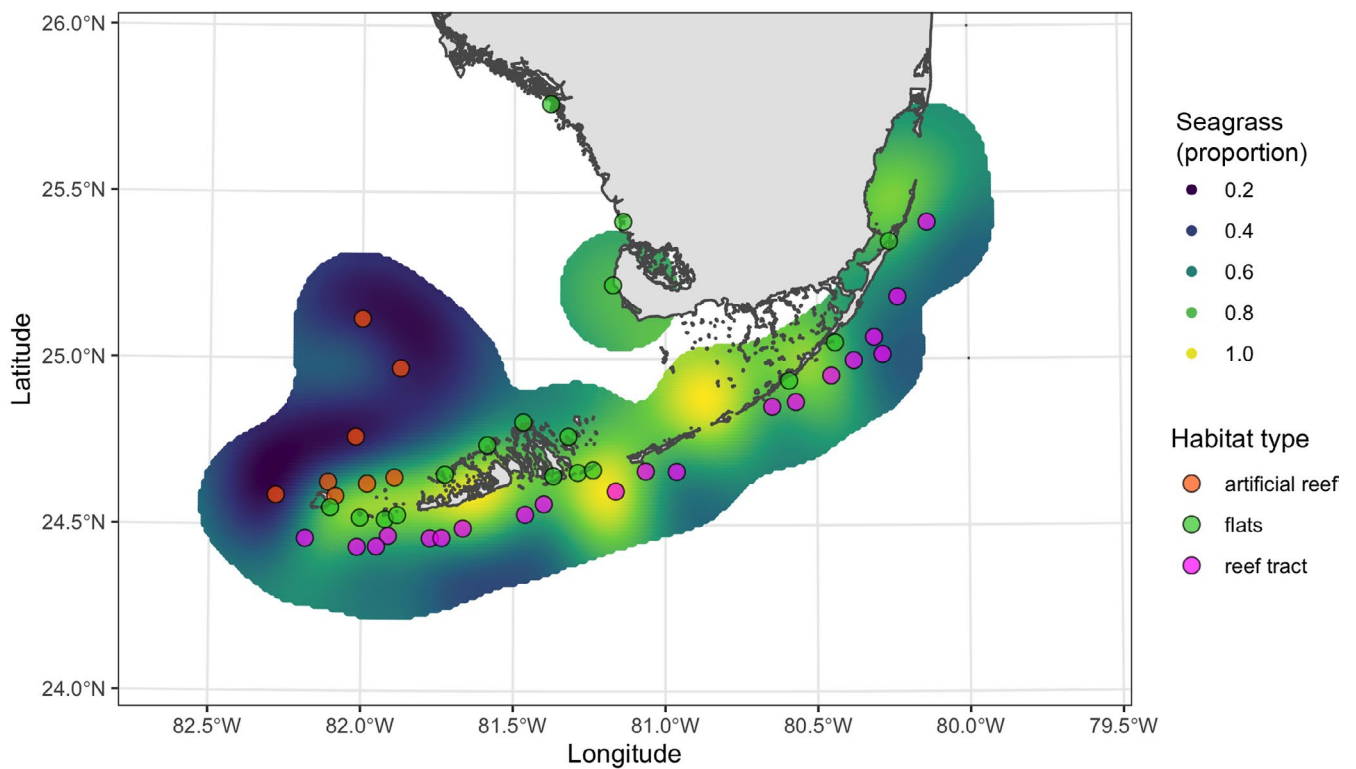


FIGURE 4 Spatial patterns of permit reliance on seagrass-based prey (proportion) generated from telemetry and isotope-based mixing models, with (a) mean fish positions from acoustic telemetry, and (b) habitats where acoustic receivers were located for fish tracking

range of permit life-history ecotypes across their life history. Overall, there is clearly a distinction between flats–reef tract and offshore reef permit in the subadults and adults studied here, although at the population level there may be some functional connectivity related to ontogenetic movements. In this case, the conservation of offshore reef-based permit is still of relevance to the flats–reef tract permit and vice versa. This was only made visible from examining both telemetry-based movement and stable isotope data, integrated with modelling techniques.

Permit in proximity to the Florida Keys that move between the flats and the reefs rely on a wide range of habitats that suffer from degradation issues, and support multiple fisheries on flats and the Florida reef tract (Brownscombe, Griffin, Morley, Acosta, Hunt, Lowerre-Barbieri, Crossin, et al., 2020; Holder et al., 2020). Ecologically, permit likely play a key role as mesopredators, impacting their prey and predators in multiple habitats, and distributing nutrients among seagrasses and reefs. Economically, permit support multiple, high-value fisheries. Their combined ecological and economic importance emphasizes the need for effective fisheries management to avoid overexploitation. In particular, due to high rates of angler hooking success and shark depredation in spawning sites (Holder et al., 2020), the most pertinent conservation action for Florida Keys permit may be to protect key spawning aggregations from fishing pressure, including catch-and-release. Indeed, there is much evidence of the negative population impacts of overexploiting fish spawning aggregations, and the conservation benefits of protecting them (Aguilar-Perera, 2006; Erisman et al., 2011; Waterhouse et al., 2020). Our findings combined with Brownscombe, Griffin, Morley, Acosta, Hunt, Lowerre-Barbieri, Adams, et al. (2020) indicate that permit observed in flats and Florida Reef Tract habitats are the same individuals, moving from seagrass flats foraging habitats to reef tract spawning habitats, and supporting unique fisheries in these two habitat types in the process. Therefore, the protection of permit spawning sites on the Florida reef tract are of the highest priority for protection due to their role in supporting not only the offshore fishery, but the highly valuable flats fishery. Indeed, one important reef tract spawning site, Western Dry Rocks, was recently designated as a no-fishing MPA during the permit spawning season (<https://myfwc.com/fishing/saltwater/recreational/wdr/>). Permit would surely benefit from extending this approach to other spawning sites, which were identified in Brownscombe, Griffin, Morley, Acosta, Hunt, Lowerre-Barbieri, Adams, et al. (2020). The reliance of permit on seagrasses, especially at earlier life stages, highlights a major need to protect and restore degraded seagrass in the coastal regions of south Florida (Hall et al., 1999; Lapointe et al., 1994).

The integration of comprehensive, telemetry-based space use metrics as predictors in Bayesian stable isotope mixing models provided valuable insights into permit ecology and conservation. This approach has rarely been applied to date and is likely to be fruitful in many other ecological contexts. It is noteworthy that substantial effort is required to combine these techniques, underscoring the uniqueness of the data presented in this study. However, the value is apparent, as in this case it helped to reveal a potential ontogenetic shift in habitat and resource use that would not have been apparent

otherwise. Further, applying these advanced models to generate a telemetry-based isoscape (Figure 4) provided a clearer picture of probable species' ecology relevant for communication and decision-making purposes by resource managers. Specifically, this isoscape makes clear the connection between Florida reef tract spawning sites and the valuable flats fishery, indicating the need to conserve those spawning aggregations. There are many potential approaches to integrate these two data sources in mixing models—we utilized a fairly simple set of telemetry-based predictors, but there are many of potential relevance, such as site or habitat connectivity from network analysis metrics (Brownscombe, Ledee, et al., 2019; Whoriskey et al., 2019). The study design used here involved sampling fish tissues for stable isotope analysis at the time of capture and telemetry tagging, meaning the isotope data reflect fish space/resource use in the months prior to capture, and telemetry-based space use was quantified in subsequent months/years. This mismatch is not ideal and forces the assumption that the fish exhibited consistent patterns of space and resource use before and after sampling/tagging, which may not always be the case, especially in proximity to ontogenetic shifts. Studying fish, especially those in large systems such as open oceans, rarely allows for recapture of the same individuals, but this may be possible in certain cases (e.g. fish with small home ranges or in small, closed aquatic systems). Despite some challenges, the use of this type of combined telemetry-isotope study approach will undoubtedly continue to evolve to generate important insights into animal ecology and management in the coming decades.

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CONFLICT OF INTEREST

None.

AUTHORS' CONTRIBUTIONS

J.W.B. contributed to study design, data acquisition, analysis and interpretation, article drafting and revision; O.N.S. contributed to data analysis, article drafting and revision; L.P.G., D.M. and R.B. contributed to study design, data acquisition, article drafting and revision; A.A., A.J.A., A.J.D. and S.J.C. contributed to study design, article drafting and revision. M.P. contributed to study design, data acquisition and analysis, article drafting and revision.

DATA AVAILABILITY STATEMENT

Data are available via Zenodo <https://doi.org/10.5281/zenodo.5850251> (Brownscombe et al., 2022).

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