



Spatial-temporal patterns of Permit (*Trachinotus falcatus*) habitat residency in the Florida Keys, USA

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Abstract Permit (*Trachinotus falcatus*) occupy a variety of coastal marine habitats and support valuable recreational fisheries in their home region of the Caribbean Sea. As an aggregate spawning species, Permit require careful management in locations such as the Florida Keys where they experience substantial fishing pressure. We used acoustic telemetry to examine Permit residency patterns over 4 years amongst 12 high-residency sites that are likely important

spawning (natural or artificial reefs) or foraging (seagrass flats) habitats. Residency was highest in artificial reefs, supporting previous research that suggests Permit have high fidelity to these habitats compared to seagrass flats and natural reefs on the Florida Reef Tract, which are highly connected. Residency peaked in the spring and summer months in most sites, with a marked decline in the late fall, suggesting potential undetected movement outside the region during that period. Permit exhibited high residency at an important spawning site in March, indicating that this spawning aggregation is vulnerable to fishing pressure with current regulations, which protect Permit from April through July. Seagrass flats in close proximity (<10 km) to spawning locations are likely of high importance to Permit as a food source during the extensive spawning season. Permit residency was generally consistent amongst water temperatures, although residency patterns varied with temperature amongst sites. Residency at natural reef spawning sites increased leading up to the full moon, which is a potential spawning cue for this species. These findings build on a body of recent research on Florida Keys Permit, providing residency information over space and time that may help to further guide the development of marine protected areas and fisheries regulations.

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Introduction

Coastal marine ecosystems are subject to numerous anthropogenic threats and are therefore changing rapidly, necessitating conservation-oriented management actions such as designation of marine protected areas and fisheries regulations such as harvest closures or no-fishing zones (De Mitcheson and Colin 2012; Rassweiler et al. 2012). Such measures are particularly relevant for species that are vulnerable to overexploitation, such as aggregate spawning fishes, whose aggregations often form in predictable locations and times (Erisman et al. 2011). As such, it is essential to understand the spatial-temporal patterns of fish space use to guide these key management actions including the timing and locations of protection measures. Indeed, well-designed spatial-temporal fishing closures surrounding fish aggregations have been effective at restoring historically overfished populations (Erisman et al. 2017; Waterhouse et al. 2020). Importantly, there is growing evidence that fishes often rely on a mosaic of habitat types during their spawning period, which may include a variety of habitat functions (e.g., spawning staging areas, intermittent foraging), in addition to sites specific to spawning events (Danylchuk et al. 2011; Boucek et al. 2017). To date, much of these data were derived from visual observations; however, telemetry now offers a technological approach to remotely monitor fish occupancy simultaneously at many specific locations, which may serve a variety of functions to focal fish species, over many years (e.g., Rudolfson et al. 2021). This enables exploration of how a wide range of spatial-temporal factors (e.g., season, temperature, lunar phase, habitat structure) influence fish habitat use using modeling techniques (Brownscombe et al. 2021). This can support more informed and finely tuned resource management actions, as well as predictions into the rapidly changing oceanic conditions in the future due to factors such as climate change, to generate proactive, adaptive management strategies.

The Permit (*Trachinotus falcatus*) is a fish species in the Carangidae family that occupies a wide range of habitat types and supports valuable fisheries at diverse locations throughout their range in the Western Atlantic Ocean, Caribbean Sea, and Gulf of Mexico (Adams and Cooke 2015). In the Florida Keys, USA, Permit occupy shallow nearshore seagrass flats (1–3 m) primarily to feed, and offshore

adjacent natural/artificial reefs to spawn (Brownscombe et al. 2020a, b). Previous research has shown high connectivity by Permit between the expansive Florida Keys seagrass flats and reefs on the Florida Reef Tract; however, Permit in regions further offshore in the Gulf of Mexico and west of the Florida Keys appear to remain primarily offshore, relying on offshore algae-based prey (Brownscombe et al. 2022). Permit support popular recreational fisheries amongst these shallow nearshore and offshore habitat types, including flats fisheries that generally exhibit relatively low catch rates and high rates of catch-and-release, and rarely experience angling-related predation (Holder et al. 2020). Conversely, in offshore reef habitats, Permit aggregate in larger numbers (>100 individuals) and are targeted more easily by anglers that exhibit higher catch rates, a greater tendency to prioritize Permit harvest, and depredation of angler-hooked Permit by sharks, which can exceed 50% in some locations (Holder et al. 2020). Since angling effort on offshore habitats coincides with Permit spring and summer offshore spawning aggregations, the increased catch rates and angling-related mortality make them especially vulnerable and are of conservation concern (Brownscombe et al. 2019).

Recognizing the need to protect Permit spawning aggregations from overexploitation, fishing regulations currently prohibit Permit harvest in the months of April through July in South Florida within a spatially designated area, the Special Permit Zone (SPZ; <https://myfwc.com/fishing/saltwater/recreational/permit/>). However, due to high densities of opportunistic shark predators, catch-and-release is also unsustainable at certain locations where depredation can be exceedingly high (Holder et al. 2020). This, in part, led to the recent (2021) formation of a no-fishing zone in the region surrounding Western Dry Rocks (WDR) in the months of April through July (<https://myfwc.com/fishing/saltwater/recreational/wdr/>). WDR has been identified as the most important aggregation site in the Lower Florida Keys for spawning Permit (Brownscombe et al. 2020a, b) that historically experienced high fishing pressure (Holder et al. 2020). While this new regulation was an important step for Permit conservation, little is known about numerous additional likely Permit spawning aggregation sites in proximity to the Florida Keys (Brownscombe et al. 2020b). This is a clear informational need to continue

to develop effective Permit fishing regulations in this region.

Previous research has established Permit habitat connectivity (Brownscombe et al. 2020a), identification of Permit spawning sites (Brownscombe et al. 2020b), and Permit resource ecology (Brownscombe et al. 2022) in the Florida Keys; however, spatial-temporal patterns of residency have yet to be explored. We therefore aimed to assess the spatial-temporal patterns and environmental correlates of Permit residency at important locations in the region, which include likely spawning locations in proximity to reefs, as well as foraging locations on seagrass flats (Brownscombe et al. 2020a, b, 2022). The findings are applicable for the assessment and further development of current Permit management practices through measures such as spatially and temporally defined marine protected areas.

Methods

Data collection

Permit site occupancy was measured using acoustic telemetry. Acoustic receivers (VR2W and VR2Tx, Vemco Inc, Halifax, NS, Canada; $n=60$) were deployed at locations throughout the coastal region of the Florida Keys in 2015, and the array grew to 100 receivers by May 2019 (Fig. 1). Permit tracking was also aided by an additional 1000+ receivers deployed in the region, 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 Brownscombe et al. 2020b for details on receiver deployments). Permit ($n=150$ permit; 68 ± 10 cm fork length [mean \pm SD], 46–98 mm range) were captured via angling from March 2016 to May 2019, at a range of locations throughout the Florida Keys, from west of the Marquesas to Biscayne Bay, and northward 60 km into the Gulf of Mexico. Captured fish were tagged with acoustic transmitters V13-1x (high power, 80- to 160-s delay, 653-day life, 9.2 g, 13×30.5 mm, Vemco Inc), V13A-1x (low power, 80- to 160-s delay, 355-day life, 9.2 g, 13×30.5 mm, Vemco Inc), or V16-4x (high power, 60- to 120-s delay, 1910-day life, 24 g, 16×68 mm, Vemco Inc) via surgical implantation. Extensive details on

tracking system deployment and permit tagging are reported in Brownscombe et al. (2020a, b, 2022).

Data analysis

All statistical analyses were conducted in 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 ggmap (Kahle and Wickham. 2013). Permit detections via acoustic telemetry were filtered to remove potential false detections by first removing detections by individual tags that occurred prior to tag deployment, duplicate detections, which included those that occurred within a period less than the minimum tag delay (i.e., 60 s). Lastly, any single detection that occurred within a 24-h period at a receiver station was considered unreliable and was removed. Filtered Permit detections ($n=1,896,740$) were then aggregated into 43 spatially distinct locations (see Brownscombe et al. 2020b). Twelve of these locations had substantive permit occupancy rates (i.e., were detected on >100 days by >10 individuals) and were included in this analysis to examine spatial-temporal patterns of site occupancy. These sites included two natural reef habitats on the Florida Reef Tract; five artificial reef habitat sites spanning the Florida Reef Tract, the Gulf of Mexico, and west of the Marquesas; and five seagrass flats habitats spanning from the Upper Florida Keys to the Marquesas (general location maps included below in the “Results” section). At each site, a daily Permit detection dataset was generated; days were included for each site when receivers were deployed at that location (see Appendix S1). This included a range of time periods amongst sites (1091 ± 303 days; mean \pm SD; 709- to 1475-day range). For each day in the dataset, a Permit residency index (RI) was calculated by multiplying the number of Permit detections by the number of individuals detected. RI was then scaled between 0 and 1, dividing these values by the maximum daily value in the dataset. Each daily residency value was assigned a water temperature from in situ measurement via acoustic receivers (Innovasea VR2Tx) or Hobo Temperature Pro loggers (Onset Computer Corporation, Bourne, Massachusetts), taken as the daily mean of hourly measurements. Temperatures were assigned either from the acoustic receiver node

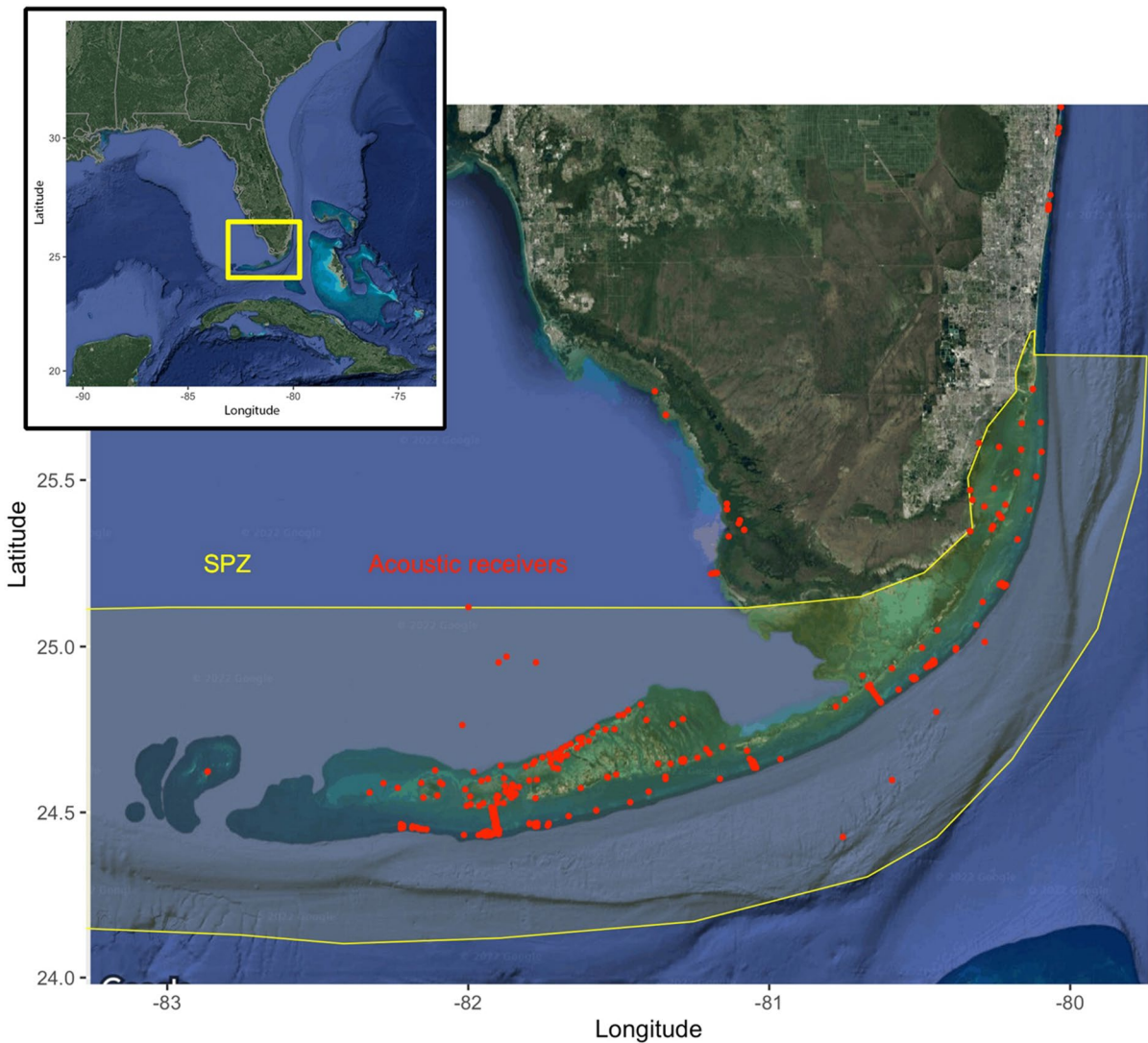


Fig. 1 Study location map showing acoustic receiver deployment locations (red) and the boundary of the Special Permit Zone (yellow). Top left: location of the study site at the southern edge of Florida, focused on the Florida Keys

of focus or from the closest node with similar habitat characteristics.

To examine spatial-temporal patterns in Permit RI, a random forests (RF) model was used with the randomForest package (Liaw and Wiener 2002). RF is a machine learning algorithm that fits classification and regression trees, which recursively create binary partitions in the data using available predictors to optimize accurate prediction of the response variable (Breiman et al. 1984; De’Ath and Fabricius 2000). RF fit a series of classification and regression trees models using random subsets of data and predictors

in order to improve prediction accuracy and reduce the potential for overfitting of the training dataset (Breiman 2001). Data were subset into training (70%; $n=9165$) and test (30%; $n=3929$) data to assess model fit. A RF was fit to daily permit RI at each site in the training dataset, with study day (1–1516), site (1–12), region (Upper Keys flats, Lower Keys flats, Atlantic western, gulf, reef tract), habitat type (natural reef, artificial reef, flats), month of the year, water temperature ($^{\circ}\text{C}$), and lunar phase (new, waxing crescent, first quarter, waxing gibbous, full, waning gibbous, last quarter, waning crescent) as predictors. RF were

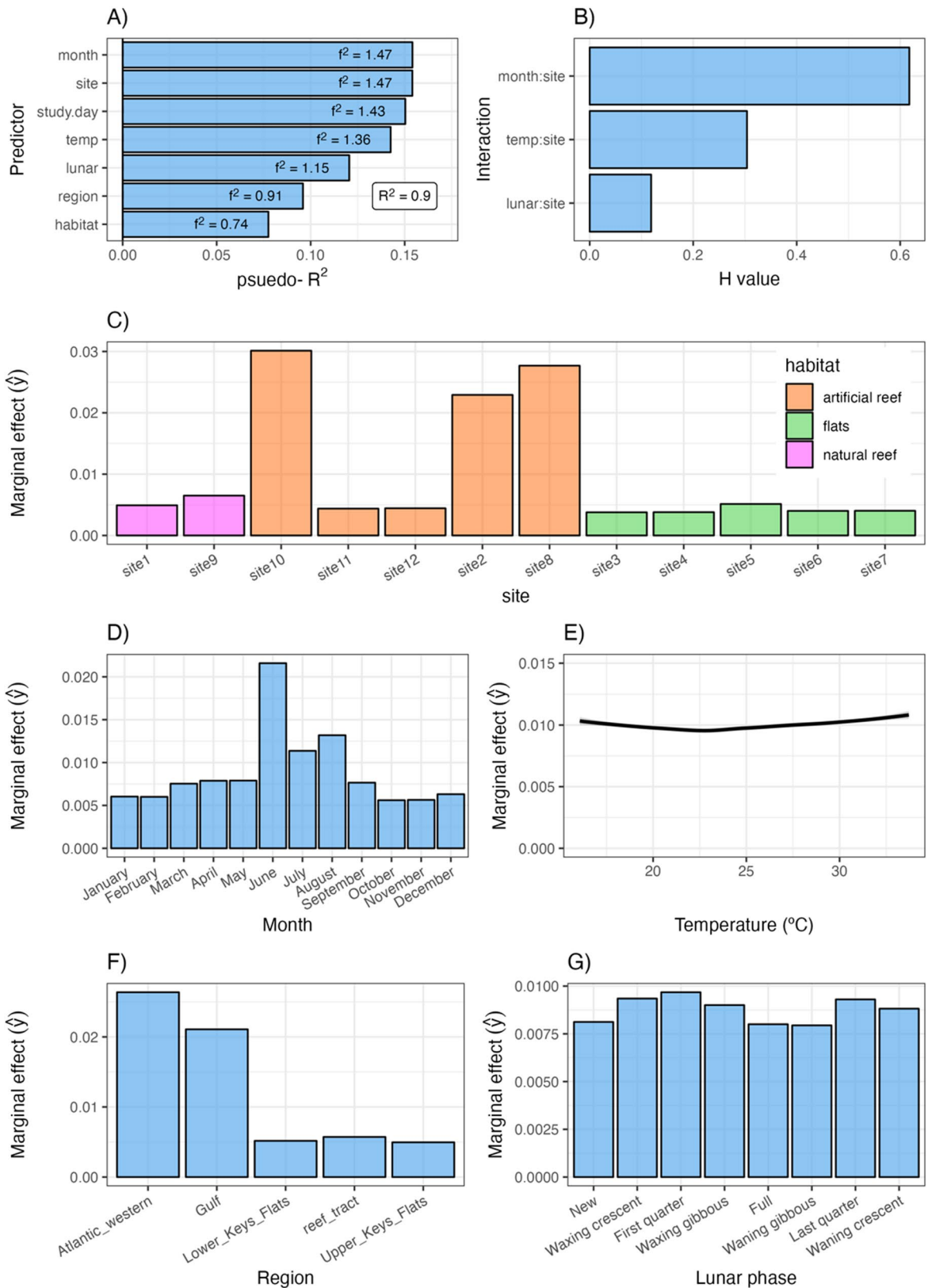
fit with 1000 trees, and the default *mtry* setting as the square root of the number of predictors. Model fit was assessed by calculating R^2 from model predictions to the test dataset using the *caret* package (Kuhn et al. 2019). Patterns in residuals in relation to fitted values, amongst predictors, across time and space were assessed via visual diagnostic plots following (Zuur et al. 2017), and all indicated strong model fit. Predictor importance was assessed with the % increase in mean squared error (%IncMSE), which was calculated by comparing the MSE of fitted trees that contained the variable to those that did not. These values were used to estimate the variance explained by each predictor with a pseudo- R^2 value, calculated by scaling %IncMSE values to 0–1, and multiplying them by the total model R^2 in test data. Effect sizes for each predictor were estimated using Cohen's f^2 (Cohen 1988), calculated as $f^2 = dR^2 / (1 - R^2_{\text{full}})$, where dR^2 is the difference in pseudo- R^2 between trees with and without the predictor, and R^2_{full} is that of the full model predicted on test data. Partial dependencies (i.e., the relationship between the predictor and the response with other predictors held constant at their mean) were calculated with the “*pdp*” package (Greenwell 2017). Variable interactions were assessed with the H-statistic (standardized range from 0=no interaction, 1=strong interaction) using the “*iml*” package (Molnar 2019).

Results

Of the 150 Permit tagged with acoustic transmitters, 127 (680 ± 10 cm fork length; mean \pm SD; 46–98 cm range) generated 1,896,740 reliable detections from 2016-03-17 to 2020-12-04, with variable tracking periods amongst these individuals (332 ± 214 days; mean \pm SD; 1–930 day range). At the 12 unique sites where Permit occupancy was examined, there was major variation in permit occupancy over space and time across coastal regions of the Florida Keys (Fig. 2). The RF model predictions were able to explain $R^2=0.9$ of the variation in true RI values in test data (Fig. 2A). RF identified important temporal variation, with month of the year being the strongest predictor of permit space use; followed by site, study day, and water temperature; then lunar phase and region; and lastly, habitat type (Fig. 2A). All predictors explained $>7\%$ of variation in the

data, and all had large effect sizes ($f^2 > 0.35$; Cohen 1988). Permit residency was substantially higher at three artificial reef sites; otherwise, there were similar overall levels of residency amongst other sites spanning natural reef and flats habitats (Fig. 2D). Overall, permit residency was highest in the summer months (June, July, August; Fig. 2D), although occupancy was consistent amongst water temperatures in the region (Fig. 2E). Regional variation was also considerable, where Atlantic western and Gulf of Mexico regions had higher residency than other regions (Fig. 2F). Permit occupancy was relatively high in the moon phases surrounding the first quarter and last quarter moons, although variability amongst phases was relatively low.

The effects of individual predictors described above must be taken in context of important interactions, which were assessed in relation to site, along with its interaction with temperature and lunar phase (Fig. 2B). Of these, the site:month interaction was by far the most important, with variable patterns of monthly occupancy amongst sites across the Florida Keys (Fig. 3). Permit occupied natural reef sites most frequently from March to August, with the highest occupancy at site 9 in March and April and site 1 in April through July. Permit occupied artificial reef sites in a similar pattern, with high occupancy in spring and summer months, although with varied windows of occupancy amongst sites (Fig. 3). Site 8 was the only offshore reef site where Permit exhibited relatively high occupancy throughout the year. Permit exhibited a wide range of monthly occupancy patterns in flats habitat sites, with sites 5 and 7 exhibiting high occupancy in the spring/summer spawning season, and other sites exhibiting the opposite monthly pattern (Fig. 3). Notably, the axis scales in Fig. 3 are variable to illustrate the temporal patterns; occupancy was generally higher at most artificial reef sites, followed by natural reef sites, and then flats habitats (Fig. 4). Patterns of Permit site occupancy in relation to lunar phase were also variable amongst sites (Fig. 5). Natural reef sites were occupied most frequently in the periods leading up to the full moon, but lunar phase patterns were highly variable amongst artificial reef and flats sites. Similarly, patterns of Permit site occupancy amongst water temperatures were highly variable amongst sites (Fig. 6), which largely reflect the monthly patterns of Permit site occupancy (Fig. 3).



◀**Fig. 2** **A** Predictor importance scores (pseudo- R^2) and Cohen's f^2 effect sizes for predictors of permit residency index with a random forests model; **B** predictor interaction scores (Friedman's H-statistic); and the marginal effects of **C** site, **D** month, **E** water temperature, **F** region, and **G** lunar phase on permit residency index at locations in proximity to the Florida Keys

Discussion

Permit exhibited a range of residency patterns amongst the 12 sites examined here with acoustic telemetry in the coastal region of the Florida Keys. Residency at offshore artificial reef sites was markedly higher than natural reefs and flats habitats, supporting previous research that suggests these Permit have high site fidelity and rarely move to other habitats (Brownscombe et al. 2022). Meanwhile, seagrass flats and Florida Reef Tract experience a high degree of Permit connectivity and therefore lower overall residency at individual locations. Residency at sites across the region was generally highest in the spring and summer months, with a marked decline in the late fall, indicating there were likely undetected movements (likely due to incomplete tracking system coverage in the open ocean) outside of the region during this period. The regions and habitats that Permit occupy outside of current tracking system coverage, especially in the fall season, are a current knowledge gap in Florida Keys Permit ecology.

Peaks in Permit residency during the spawning period were evident at most of their putative spawning sites (identified in Brownscombe et al. 2020a). Of note is that Permit exhibited some of the highest residency rates in the month of March at Site 9, which is a previously identified important spawning location, where both catch-and-release and harvest are currently only restricted in the months of April through July. Otherwise, Permit residency at natural and artificial reef sites generally peaked in April through July (extending into August and September at some locations), with varied timing in peak residency within this month range amongst sites. This corresponds closely with the Permit reproductive period (Crabtree et al. 2002). Permit exhibit an extensive and varied spawning period throughout their range, with studies reporting March to September in Cuba (Garcia-Cagide et al. 2001) and February to October in Belize (Graham and Castellanos 2005). Our findings suggest that the Permit

spawning period is similar in the Florida Keys to that of Cuba, from March through August, but with peak spawning in April to July amongst diverse sites. There is clearly some flexibility in the timing, extent, and location of Permit spawning, which has potential to shift over time, especially with altered oceanic conditions due to climate change, to which habitat and fisheries management strategies may need to adapt.

Previous research has established that seagrass flats are important sources of food for Permit (Brownscombe et al. 2020a, 2022). We found that seagrass flats sites exhibited more variable monthly patterns of Permit residency, with some corresponding to the spawning period, and others having high residency outside the spawning period. Examining these patterns over space (Fig. 4), the seagrass flats sites in close proximity to spawning locations experience high residency during the spawning period. This likely indicates that Permit that spawn on the Florida Reef Tract rely on nearby seagrass flats habitats (<10 km away) for food intermittently during their extended spawning period, especially during peak spawning months (i.e., March to June). This observation is consistent with that of Boucek et al. (2017), who found that common snook (*Centropomus undecimalis*) and spotted seatrout (*Cynoscion nebulosus*) rely on a combination of interconnected spawning and foraging habitats during their spawning periods in the coastal Tampa Bay, Florida. This highlights the need to consider fish habitat as a matrix of biogeographically connected features that support spawning, as opposed to the specific spawning habitat alone, which is likely especially relevant to species that have extended spawning periods, and hence require energy intake to sustain themselves. Outside the peak spawning period, Permit expanded their range to occupy seagrass habitats further from spawning sites more frequently, likely taking advantage of available food resources. This is consistent with the ecology of bonefish in the region, who migrate between distinctive spawning and productive foraging habitats (Boucek et al. 2019). Movement to flats further from spawning sites may also be partially driven by predation risk, as predators (mainly sharks) have a tendency to aggregate around fish spawning aggregations (De Mitcheson and Colin 2012; Mourier et al. 2016), which is evident for Permit in the Florida Keys (Holder et al. 2020).

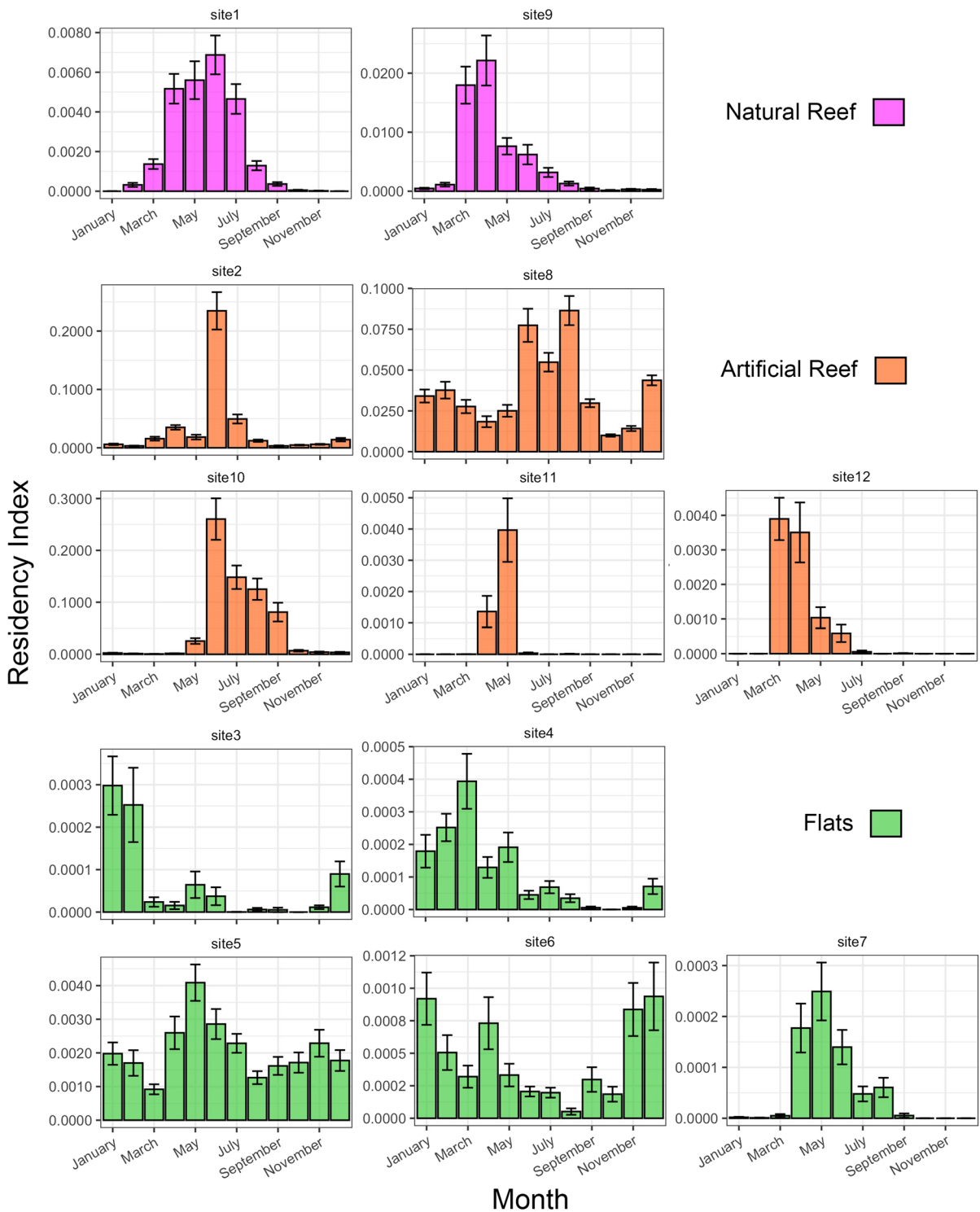


Fig. 3 Permit residency index amongst unique sites (1–12) ranging amongst natural reef, artificial reef, and flats habitats in proximity to the Florida Keys by month of the year. Bars represent means \pm standard error

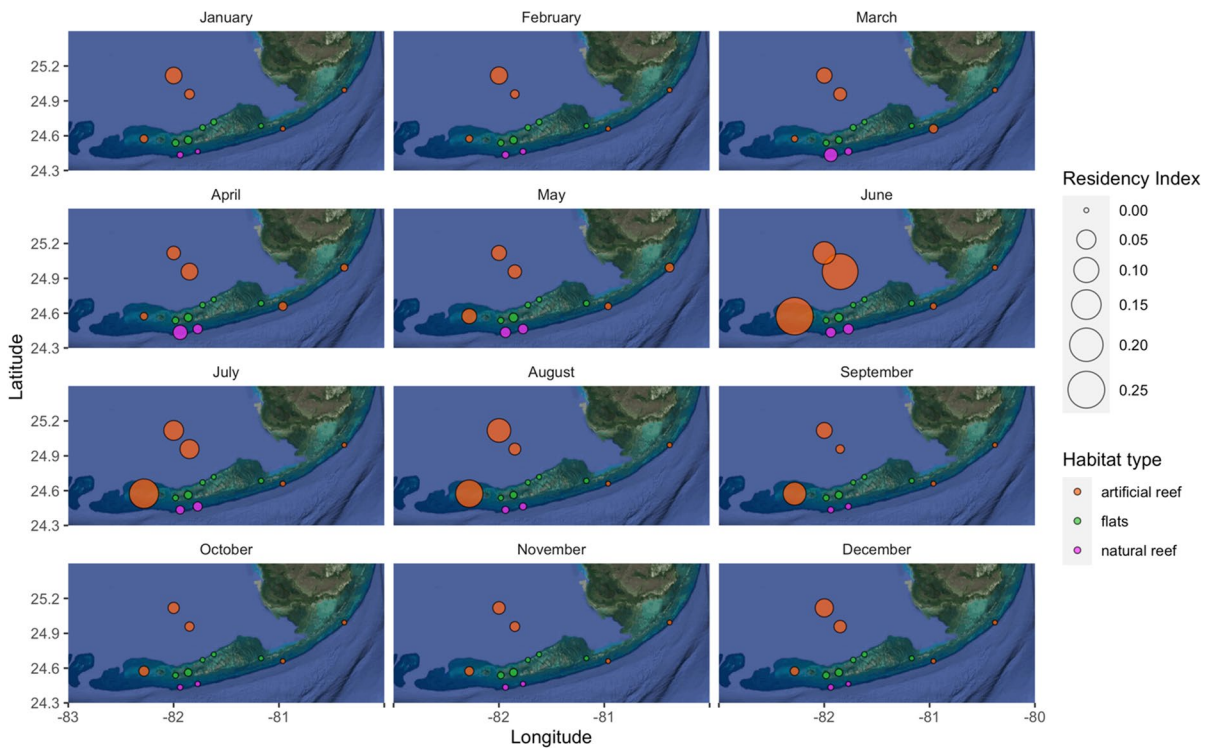


Fig. 4 Maps of mean permit residency index at twelve key sites spanning artificial reefs, natural reefs, and flats habitats in proximity to the Florida Keys by month of the year

Temperature and lunar periodicity also had large effect sizes on permit residency in the Florida Keys, but variability amongst these factors was relatively low compared to other predictors. Permit residency was overall fairly consistent amongst temperatures, but showed highly variable patterns amongst sites. Cooling temperatures in the fall season may be a cue used by Permit that initiates the apparent movement outside the Florida Keys. However, Permit residency increased in the winter months with cold temperatures at many flats and artificial reef sites, and there was generally little evidence that Permit were avoiding cold or warm thermal extremes in this region. Hence, Permit appear to be tolerant of a range of ecologically relevant temperatures within the current thermal regime of the Florida Keys. Regarding lunar phase, natural reef sites exhibited a consistent pattern of permit occupancy in the periods leading up to the full moon, which is the period where Permit spawning (as well as other carangid fish species) has been observed in similar habitat types in

Belize (Graham and Castellanos 2005), as well as in Cuba (Garcia-Cagide et al. 2001). These associations, including broad thermal tolerances and spawning activity surrounding the full moon, are key considerations for how Permit may shift their seemingly flexible spawning strategy with future changing conditions.

Overall, our findings provide insights into the functional role of various sites for Permit in the Florida Keys and the timing and potential drivers of their habitat use, which is relevant for their management. Moderate-high Permit occupancy of spawning sites occurred from March through September, with the highest residency in April to July at diverse spawning sites. As an aggregate spawning species, protection of Permit spawning aggregations from fishing pressure is an important management action. A key finding is that Permit are occupying an important spawning site, site 9, in March when they are currently vulnerable to angling pressure (<https://myfwc.com/fishing/saltwater/recreational/wdr/>). Additionally, the

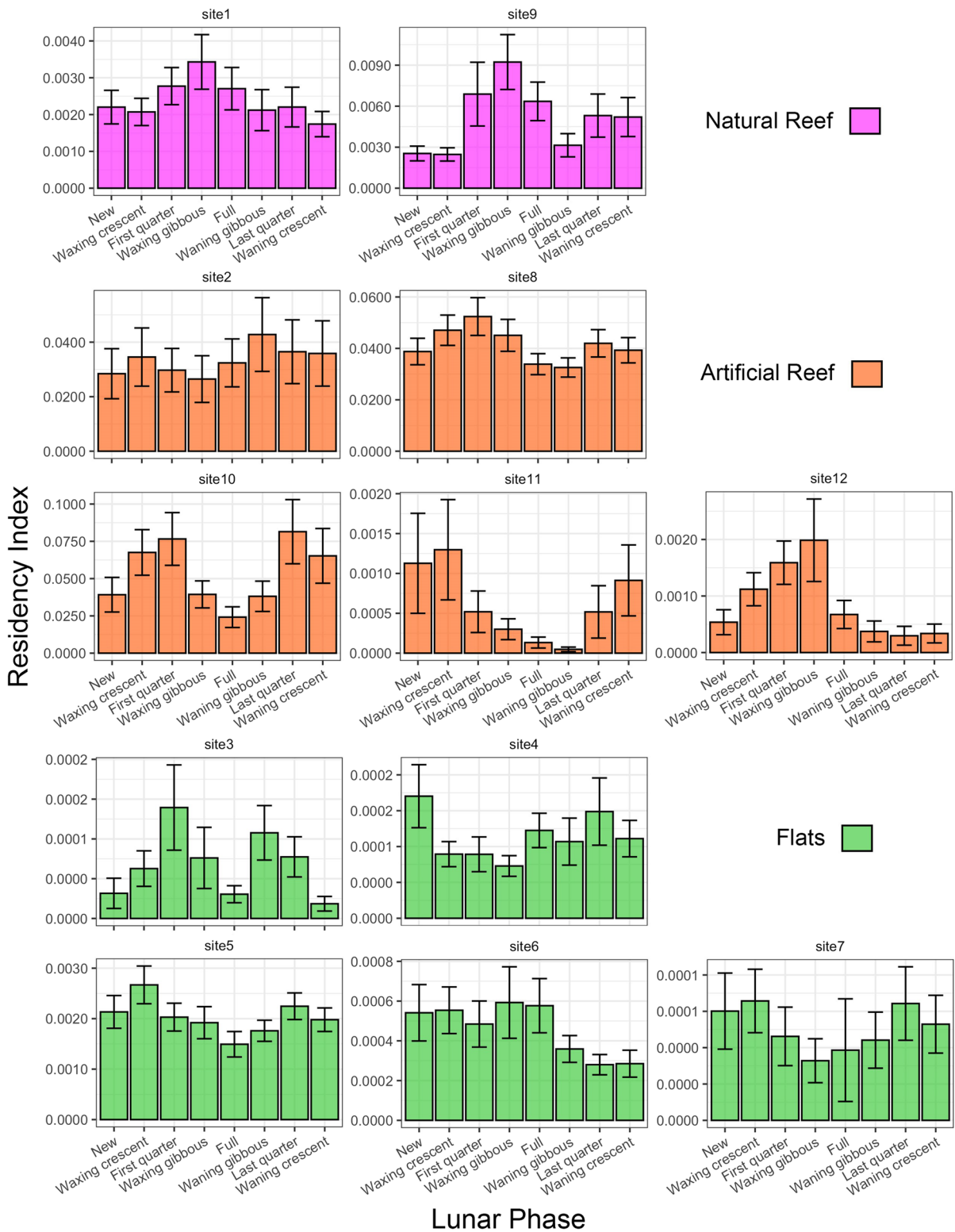


Fig. 5 Permit residency index amongst unique sites (1–12) ranging amongst natural reef, artificial reef, and flats habitats in proximity to the Florida Keys by lunar phase. Bars represent means \pm standard error

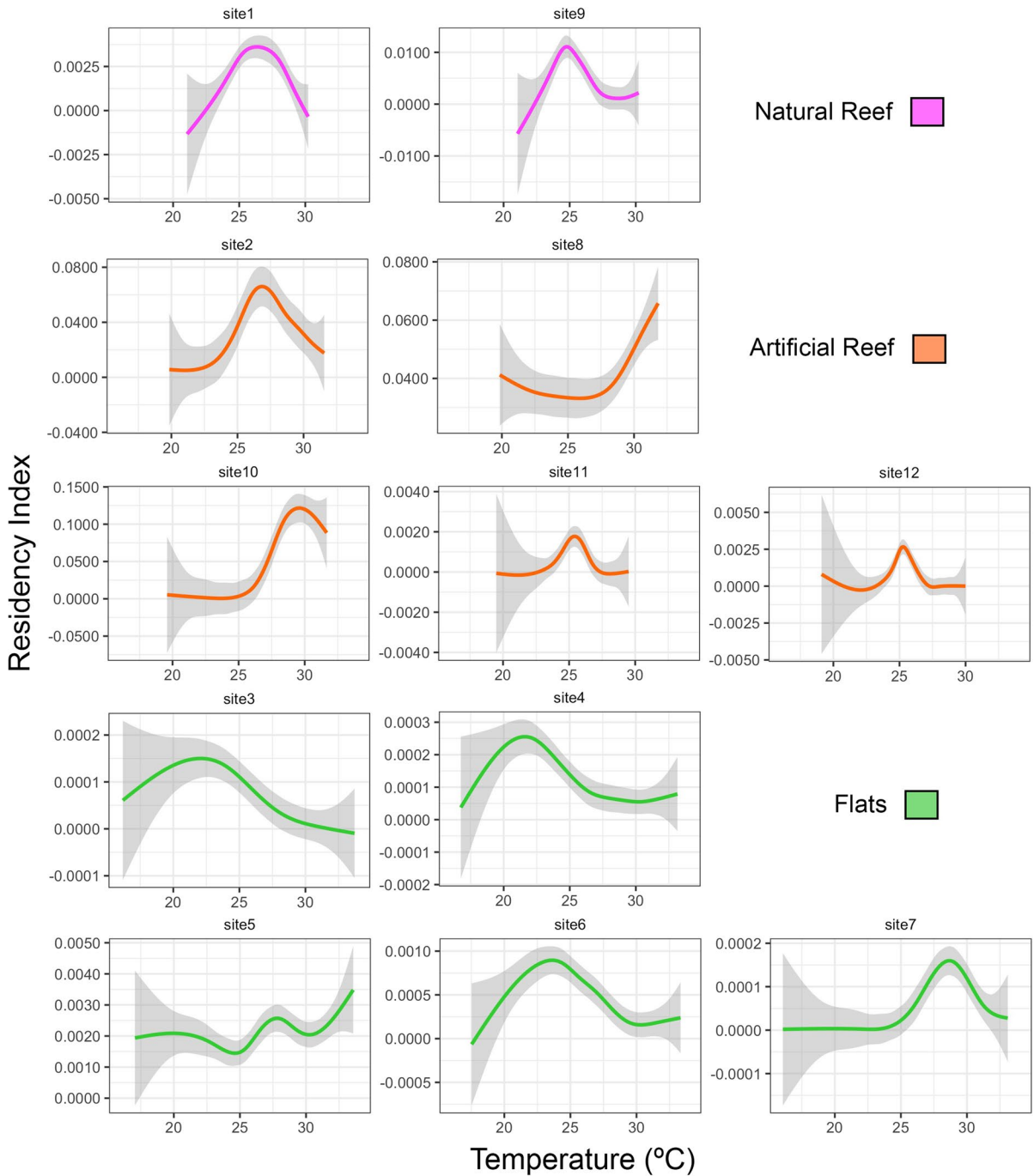


Fig. 6 Permit residency index amongst unique sites (1–12) ranging amongst natural reef, artificial reef, and flats habitats in proximity to the Florida Keys by water temperature. Data are represented with a generalized additive model smoother \pm 95% confidence interval

high occupancy of seagrass flats in close proximity (<10 km) to spawning sites on the Florida Reef Tract suggests that these sites are of especially high value to spawning fish as a key food source during

their extensive spawning period. Hence, Permit conservation should consider their critical habitat as a mosaic of reef and seagrass flats.

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Data availability Data associated with this work will be made available upon reasonable request. Because these data describe the space use of an exploited species, it is prudent to restrict access to raw data.

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