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Predator–prey landscapes of large sharks and game fishes in the Florida Keys

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Abstract

Interspecific interactions can play an essential role in shaping wildlife populations and communities. To date, assessments of interspecific interactions, and more specifically predator–prey dynamics, in aquatic systems over broad spatial and temporal scales (i.e., hundreds of kilometers and multiple years) are rare due to constraints on our abilities to measure effectively at those scales. We applied new methods to identify space-use overlap and potential predation risk to Atlantic tarpon (*Megalops atlanticus*) and permit (*Trachinotus falcatus*) from two known predators, great hammerhead (*Sphyrna mokarran*) and bull (*Carcharhinus leucas*) sharks, over a 3-year period using acoustic telemetry in the coastal region of the Florida Keys (USA). By examining spatiotemporal overlap, as well as the timing and order of arrival at specific locations compared to random chance, we show that potential predation risk from great hammerhead and bull sharks to Atlantic tarpon and permit are heterogeneous across the Florida Keys. Additionally, we find that predator

encounter rates with these game fishes are elevated at specific locations and times, including a prespawning aggregation site in the case of Atlantic tarpon. Further, using machine learning algorithms, we identify environmental variability in overlap between predators and their potential prey, including location, habitat, time of year, lunar cycle, depth, and water temperature. These predator–prey landscapes provide insights into fundamental ecosystem function and biological conservation, especially in the context of emerging fishery-related depredation issues in coastal marine ecosystems.

KEYWORDS
acoustic telemetry, conservation, machine learning, predator–prey dynamics

INTRODUCTION

Predator–prey interactions: background

Populations, communities, and ecosystems are shaped largely by how species interact with one another (Berlow et al., 2009; Poisot et al., 2015; Vandermeer, 1969; Werner & Peacor, 2003; Wootton, 1994, 2002). Interactions involving predators and their prey are an especially important driver of population dynamics, animal behavior, and individual space use through predation or nonlethal predator effects (trait-mediated or risk effects) (Ives et al., 2005, Preisser et al., 2005; Wirsing et al., 2007a; Creel & Christianson, 2008; Heithaus, Wirsing, et al., 2008; Jorgensen et al., 2019). Predation risk landscapes will influence the spatiotemporal patterns of both predators and prey, with their overlap affecting encounter and predation rates (Lima & Dill, 1990; Sabal et al., 2021; Sih, 2005). In turn, these predation risk landscapes can have substantial impacts within an ecosystem. For example, within the marine environment, tiger shark (*Galeocerdo cuvier*) presence modifies space-use or foraging patterns of green turtles (*Chelonia mydas*), bottlenose dolphins (*Tursiops aduncus*), dugongs (*Dugong dugong*), and sea snakes (*Disteria major*, *Hydrophis elegans*), mainly through nonlethal effects, potentially altering seagrass communities (Heithaus & Dill, 2006; Heithaus, Frid, et al., 2007; Kerford et al., 2008; Wirsing et al., 2007a, 2007b; Wirsing & Heithaus, 2009). Similarly, killer whale (*Orcinus orca*) presence alters space use of white sharks (*Carcharodon carcharias*) at elephant seal (*Mirounga angustirostrous*) haul-out sites, redistributing predation pressure and risk on seal colonies (Jorgensen et al., 2019). With many apex and mesopredator populations in decline, their loss may result in long-lasting ecosystem-wide shifts, including trophic cascades (Crooks & Soulé, 1999; Estes et al., 2011; Estes et al., 2016; Ferretti et al., 2010; Heithaus, Frid, et al., 2008; Heupel et al., 2014; Nowicki et al., 2021; Ripple et al., 2016).

Given the relevance of predator–prey relationships to population stability and ecosystem function, it is important to understand the environmental variability (e.g., seasonality, temperature, time of day, habitat, lunar cycle) that may influence the spatiotemporal overlap of predators and their potential prey. However, monitoring long-term predator–prey overlap is challenging since many large predators, such as sharks, often have wide-ranging movements and large home ranges and occur at low densities (Heithaus & Vaudo, 2012; Simpfendorfer & Heupel, 2012). With recent advances in electronic tracking technology (Hussey et al., 2015; Kays et al., 2015), it is possible to examine the potential relationships between predators and their prey at much finer scales. For example, both active and passive acoustic telemetry show that sharks select for habitats with higher prey abundance and increased foraging success (Heithaus et al., 2002), even when that prey source is seasonal (Meyer et al., 2010). Further, tracking data have highlighted predator–prey dynamics operate at multiple spatiotemporal scales, including diel and tidal patterns as well as horizontal and vertical habitat selection (Barnett et al., 2010; Guttridge et al., 2012).

It becomes increasingly difficult to examine such relationships when both predators and prey are highly mobile marine species because there is a need for high-resolution multispecies data to assess potential encounters. For example, using satellite telemetry data collected from bull sharks (*Carcharhinus leucas*) and their prey, Atlantic tarpon (*Megalops atlanticus*; referred to hereafter as tarpon), Hammerschlag et al. (2012) found that tarpon modified their swimming behavior (location, speed, and path tortuosity) in areas of high bull shark density, suggesting potential avoidance behavior by tarpon from predation risk. However, characteristic of satellite telemetry, this study was limited by sample size (including shark size range), monitoring period, and geopositioning error and, thus, did not assess whether shark migrations

were driven by tarpon or vice versa. Ultimately, more robust spatiotemporal data sources and methods are needed to fill fundamental and applied knowledge gaps on predator–prey interactions, particularly in marine systems (Friess et al., 2021; Lowerre-Barbieri, Kays, et al., 2019).

Sharks and their prey in the Florida Keys

The coastal habitats surrounding the Florida Keys represent a complex patchwork of heterogeneous habitats for marine fish of all life history stages (Acosta et al., 2007; Burke et al., 2012). This area of >8000 km^2 encompasses shallow mangrove forest islands and seagrass flats (<3 m deep), a 580-km-long barrier reef (Florida Reef Tract), and over 1000 known shipwrecks. While this area and its surrounding habitats have received extended protection through multiple sanctuary, national park, and wildlife refuge designations (e.g., Florida Keys National Marine Sanctuary, Biscayne National Park, Everglades National Park), continued anthropogenic pressures, such as overfishing, habitat degradation, and lack of freshwater flow through the Everglades into Florida Bay, continue to alter the ecosystem as a whole (Bartholomew et al., 2008; de Freese, 1991; Jackson, 1997; Lapointe et al., 1994; Lapointe & Clark, 1992; Maliao et al., 2008; McIvor et al., 1994).

Of particular note, shark abundance and species composition in the Florida Keys has substantially declined due to overexploitation since the 1920s (Heithaus, Burkholder, et al., 2007, NOAA/NMFS Highly Migratory Species Division, 2006). However, despite these changes, recreational fishing guides and anglers throughout the southeastern United States report frequent and increasing issues with shark depredation (i.e., fish consumed by sharks prior to landing). This growing unrest in the community over a perceived overabundance of sharks, which can negatively affect fishing opportunities (Adams et al., 2019), has been the focus of management meetings at both the federal and state (Florida) levels (May 2020 and September 2020 Meetings of the NOAA Atlantic Highly Migratory Species Advisory Panel, December 2020 Meeting of the Florida Fish and Wildlife Conservation Commission). Depredation occurs in a number of coastal fisheries, including those targeting two prized game fish, tarpon and permit (*Trachinotus falcatus*). While both tarpon and permit are considered natural prey for these shark species (A. J. Adams, unpublished data; Castro, 2010; Roemer et al., 2016), recreational angling has exacerbated predation events when fish are exposed to capture stress, including extended fight times (Ault et al., 2007; Guindon, 2011). A common time for anglers to target both tarpon and permit in the Florida Keys is before and during spawning events when they aggregate in large schools ranging from hundreds to thousands of individuals in the spring and summer (tarpon: Luo et al., 2020; Griffin et al., 2022; permit: Brownscombe, Griffin, Morley, et al., 2019). Indeed, Holder et al. (2020) documented that depredation rates of angled permit by bull and great hammerhead (*Sphyrna mokarran*) sharks exceeded 30%–50% of hooked fish at certain sites, and, most troubling, depredation rates were particularly high at permit spawning aggregation sites. Similarly, approximately 15% of all tarpon hooked within an aggregation at one specific location during the spawning season resulted in depredation by great hammerheads (G. A. Casselberry, unpublished data). Considering both of these recreational species, along with bonefish (*Albula vulpes*), have a $465 million annual economic impact in the Florida Keys (Fedler, 2013), identifying high-risk areas for anglers to potentially avoid or to enact protective measures, ranging from heavier fishing tackle requirements to reduce fight time to temporary fishing closures, is critical for effective fisheries management.

Objectives

Given the importance of sharks as predators in coastal marine ecosystems and growing conflicts with recreational fisheries, it is imperative to understand the ecology of sharks and their prey within the Florida Keys in greater detail. Using a 3-year acoustic telemetry data set, we (1) tested whether great hammerheads and bull sharks were nonrandomly arriving when potential prey were present at specific sites and (2) used machine learning to examine the broad spatiotemporal patterns of predator–prey relative overlap and their variability across environmental predictors (e.g., time of year, location, habitat type, lunar cycle, temperature). This approach, using acoustic telemetry, represents an advance in characterizing broad spatiotemporal patterns in predator–prey dynamics. Further, the findings provide important insights into predation risk landscapes and are relevant for resolving the growing human–wildlife conflict over recreational fishery depredation in the region.

METHODS

Data collection

Acoustic receivers

Between 2015 and 2019, nearly 300 autonomous fixed acoustic receivers (VR2W, VR2Tx, and VR2AR models, Vemco Inc., Halifax, NS, Canada) were deployed to

support projects affiliated with the University of Massachusetts Amherst, Carleton University, Bonefish & Tarpon Trust, University of Miami, University of Florida (Gainesville), and Florida Fish and Wildlife Conservation Commission (FWC, offices in St. Petersburg and Marathon). In addition, the Ocean Tracking Network (OTN) provided loaned receivers to support coverage across the Florida Keys receiver locations, which spanned the Florida Keys (approximately 300 km in distance), ranging from the northernmost portion of Biscayne Bay to the Marquesas Keys. Receivers were affixed (transducer upright) to 1 m rebar that was cemented within heavy mooring stands (30–50 kg) placed on the seafloor. Owing to the large study area and multiple project goals, receivers were deployed using a point-of-interest arrangement rather than a grid formation (Brownscombe, Lédée, Raby, et al., 2019). Further, receivers were grouped into nodes based on proximity to one another and habitat classification (Figure 1, Appendix S1: Table S1). Acoustic receiver performance (i.e., detection range and efficiency) was assessed using reference tags at 9 different receivers across several distinctive habitats within the flats and

by using environmental noise data collected from 39 acoustic receivers (Vemco VR2Tx and VR2AR models) at eight unique sites within the Florida Reef Tract (Brownscombe, Griffin, Morley, et al., 2019).

Acoustic tagging

All animals were tagged internally with Vemco V13 (80–120 s delay), V13A (80–120 s delay), or V16 (delays of 30–90 s, 50–130 s, 60–90 s, 60–120 s, 90–150 s, 140–220 s, 150–360 s) transmitters (InnovaSea Systems Inc., Halifax, NS, Canada), with the exception of some hammerheads that received external V16 tags at the base of the dorsal fin to reduce handling times, since this species exhibits high capture stress responses (Gulak et al., 2015, Jerome et al., 2018). Sharks were captured and tagged in the Florida Keys, Florida (FL), Biscayne Bay, FL, and Bimini, The Bahamas (see Appendix S2 for further details). Tarpon were primarily captured and tagged within the Florida Keys, as well as waters surrounding Apalachicola, FL, Tampa Bay, FL, Charlotte Harbor, FL,
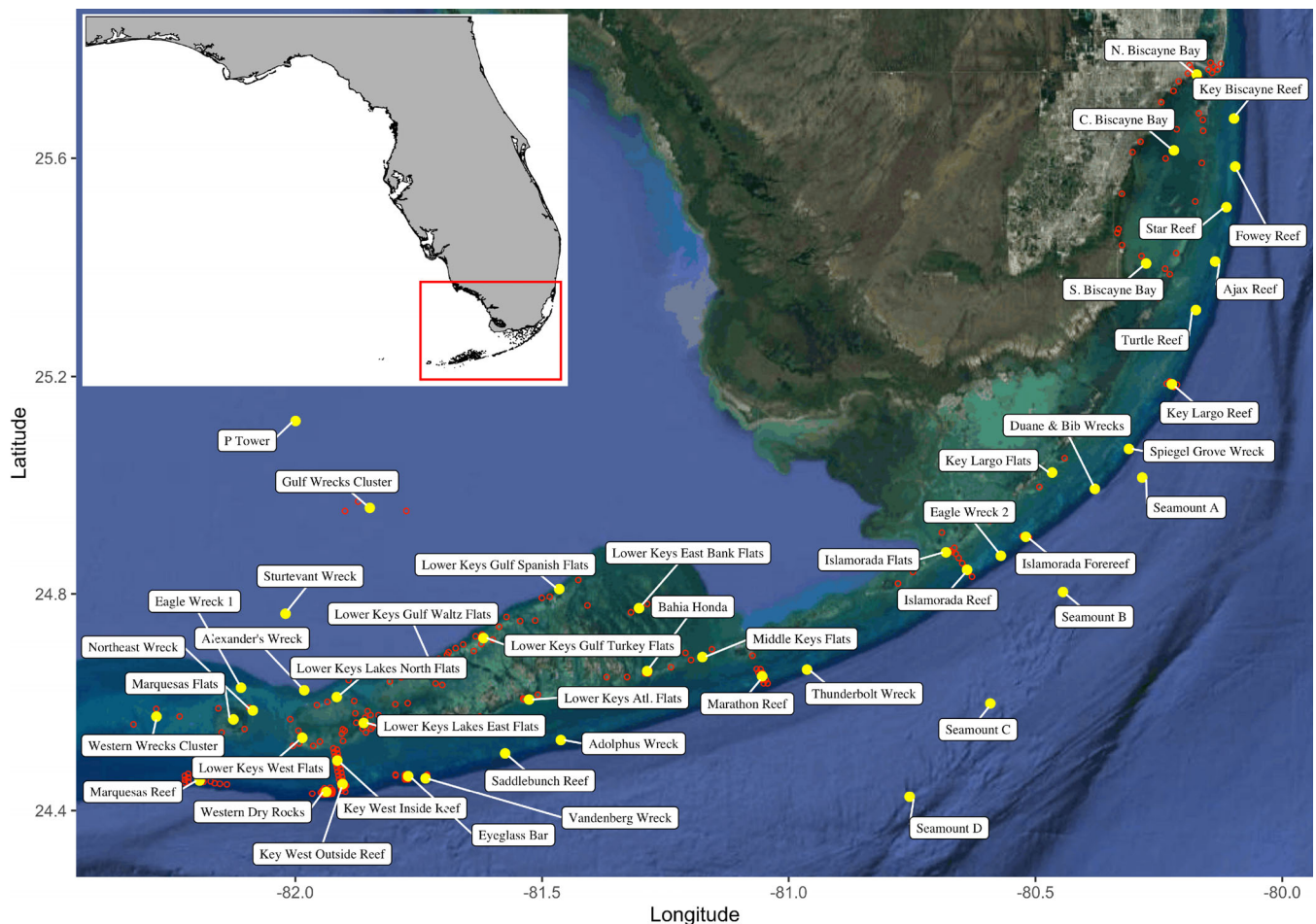
FIGURE 1 Node positions (yellow closed circles) and labels plotted on top of receiver positions (red open circles)

Amelia Island, FL, Cumberland Island, FL, and George-town, South Carolina. Permit were captured and tagged in proximity to the Florida Keys.

Data analysis

Data organization and filtering

This database builds on that used in Lowerre-Barbieri et al. (2021). To examine species overlap between tarpon and both shark species individually as well as the overlap between permit and both shark species individually, data were collected between 1 August 2016 and 25 June 2020 from all available receivers within the defined study area for tarpon, permit, great hammerhead sharks, and bull sharks. Because of mismatched download periods by each institution, data were included from the Biscayne Bay area for almost 1 year longer (August 2019–June 2020) than in the Florida Keys in the south. Data from this extended period were included because permit were not regularly detected within Biscayne Bay until later in the study period due to later tagging efforts in that general area. Because all models were based on presence/absence at the receiver aggregate, that is, node level, many of the issues related to imbalanced sampling times were negated. Here, nodes are defined as aggregate receiver groups ($n = 48$) based on both receiver geographic position (mean $2.85 \pm$ SD 4.28 km apart) and habitat type, that is, receivers close to one another with similar habitat types would be aggregated into the same node (Figure 1, Appendix S1: Table S1).

To ensure that the sharks were large enough to pose a predatory threat to both adult permit and tarpon via natural predation or depredation, we included all tagged sharks greater than 2 m in total length (TL) at the time of tagging ($n = 28$ bull sharks and $n = 42$ great hammerhead sharks). A TL of 2 m has been identified as a significant length threshold where sharks begin incorporating larger prey items, like chondrichthyans, into their diets (Lucifora et al., 2009). Further, evidence suggests that sharks, regardless of size, are not gape limited, consuming prey both in pieces and whole across a broad size range (Lucifora et al., 2009). Additionally, three bull sharks that were classified as mature based on published size at maturity estimates (Natanson et al., 2014) (size range: 188–196 cm TL) were included in the data set to account for a lack of significant differences in diet and trophic level between large subadult and mature bull sharks based on previous stable isotope analyses (Abrantes et al., 2018). These cutoffs removed six sharks from the data set (bull shark $n = 4$, great hammerhead $n = 2$). Further, tarpon with a tracking duration of fewer

than 14 days were removed in case postrelease mortality occurred, a common caveat of tarpon angling (Guindon, 2011) and tagging due to fish exhaustion or shark predation. Subsequently, detection data were filtered to remove false detections (Brownscombe, Griffin, Chapman, et al., 2019; Simpfendorfer et al., 2015), including (1) any detections occurring before the tag was deployed; (2) duplicate detections (when identified, the first detection of the duplicate pair was retained); (3) detections that occurred within 60 s of each other for a given individual; (4) unrealistic detections (movements), here defined as movements (considering variable detection ranges) greater than 3 m/s; and (5) singular detections occurring within a given time frame, here defined as 24 h.

Interspecific differences in space use

Descriptive plots were generated to examine interspecific differences in space use at the array and node levels separately. For each species and month, we calculated detection count, mean detection count, and mean residence time (daily) in the study area (array level). Additionally, spatial plots were generated to explore detection counts of tarpon and permit relative to great hammerheads and bull sharks at the node level.

Predator–prey hourly overlap events and predator arrival times

To first compare areas of general space use to areas of hourly predator–prey overlap, we constructed hourly presences (defined as one or more detections in a binned hour) for each species and each node. Nodes with overlapping hourly presences between a given prey and shark species were also generated. The total number and proportion of nodes detected/overlapped at the hourly level were also derived.

To explore whether synchronous movements related to predator–prey relationships existed between tarpon or permit and sharks (i.e., if sharks were more likely to arrive when tarpon or permit were already present), we examined the arrival times of both shark species separately at the node level compared to tarpon or permit presence/absence (Appendix S1: Figure S1). First, hourly presence and absence (here, defined as no detections) data from tarpon and permit were assigned across all study hours and at each node when receivers within nodes were operational and detecting. Then the arrival timing for great hammerheads and bull sharks were subsequently compared to tarpon and permit presence

or absence at the node and hourly level. Overlapping events, or presences, and associated metrics, including number of detections, total shark arrival count (number of times sharks arrived at a node), shark overlap arrival count (number of times when sharks arrived and tarpon or permit were already present), and shark overlap arrival percentage (proportion of times when sharks arrived and tarpon or permit were already present), were then examined for only nodes where overlap occurred (i.e., relative rather than absolute) (Appendix S1: Figure S1).

Finally, using the aforementioned metrics, we tested whether shark overlap arrival counts were due to random chance (randomly arriving at a given node regardless of tarpon or permit presence). We resampled (i.e., randomly generated) the observed shark arrival counts for a given species at a given node 100 times and compared the mean simulated shark overlap arrival counts to the observed shark overlap arrival counts with a one-sample t-test (using an α of 0.05 as the cutoff for significance) and Cohen's D test (with 95% confidence intervals) for effect size. Shark tagging occurred nonrandomly before and during the study period, resulting in more sharks being available for detection at the end of the study period ($n = 73$) than the beginning ($n = 1$), which in turn resulted in an increased probability of shark detection and arrival with time. We included a conditional probability statement within the resampling process to account for this. First, we separately calculated the cumulative number of great hammerhead and bull shark tags that were available for detection based on tagging dates. Subsequently, to account for unequal probabilities of shark detection, the random draws of zeros and ones were generated with the proportion of observed shark arrivals (base probability) multiplied by the proportion of sharks available for detection (adjusted probability) (Appendix S1: Figure S1).

Drivers and environmental variability of predator–prey relative daily overlap events

To explore the environmental variability and potential drivers of tarpon and permit daily overlaps with great hammerheads and bull sharks, we first constructed a presence/absence data frame containing all the dates when receivers were operational at each specific node. If at least one individual of a given shark or prey species was detected at a given node, then that node–date combination was marked as present. When completed for each species, we were able to identify those date–node combinations that contained daily overlaps between tarpon and each shark species and between permit and each shark

species separately. To improve model performance and to reduce zero inflation, we removed dates when both species of the predator–prey pairing of interest were not detected somewhere within the array and removed nodes where no overlap between sharks and the given species of interest occurred. Thus, by removing locations and certain dates with no registered overlap events, these analyses examined the relative daily overlap between sharks and tarpon and permit.

We used random forest (RF) models to assess the potential drivers of daily overlaps for each predator–prey species combination. RF, a popular machine learning algorithm, minimizes variance and overfitting while maximizing accuracy (Breiman, 2001). Compared to frequently employed analytical methods, such as generalized linear models, RFs are able to overcome common challenges associated with data sets with unbalanced data, correlated predictors, and complicated predictor interactions (Breiman, 2001; Cutler et al., 2007; Liaw & Wiener, 2002). Based on binary recursive partitioning, these models fit multiple data trees with randomly selected predictor subsets to find the best fitting model.

Daily species overlap (i.e., absence vs. presence at a given node), regardless of number of unique individuals, was the response variable and node, habitat type, month, lunar cycle, depth, and temperature were included as predictors. Habitat type was categorized with a generalized habitat classification surrounding a given node, which included artificial reef (sunken and wrecked ships), flats (shallow <3 m habitats), reef tract, or seamount. The lunar cycle of each date was computed using a lunar package (Lazaridis, 2014). Temperature data from over 50 loggers (Onset HOBO Water Temperature-v2; Bourne, Massachusetts) and VR2Tx receivers (Vemco Inc., Halifax, NS, Canada) that were deployed across the study area were used to derive the average daily water temperature at the node level. When temperature data were absent for a node, those collected at the nearest node with a similar depth and habitat structure were used.

All RF models were implemented in the randomForest package (Liaw & Wiener, 2002) using an 8-fold cross-validation procedure and by constructing 1000 trees per fold. Each fold used a random subset of seven eighths of the data to train the model, while the holdout data set, the one eighth not used, was used to evaluate and test model performance using a wide range of metrics. Performance metrics included classification accuracies (i.e., positive and negative prediction values) and overall model accuracy, sensitivity to indicate the true positive classification rate, specificity to indicate the true negative classification rate, and the kappa statistic to compare the observed accuracy with expected accuracy (random chance). Further, an F1-score was generated to indicate the weighted average

between precision (ratio of correctly predicted positive class observations to the total predicted positive class observations) and balanced accuracy was generated to indicate the average proportion of correct classifications.

Since many absences existed within each prey–predator daily overlap data frame, RF models designed to optimize overall model accuracy were biased to predicting absences over presences. To overcome the tendency for RF models to weight the importance of predicting absences over presences, owing to the imbalanced structure of the data, we manually assigned model weights to each category/class to penalize misclassification of the minority class (presences) (Chen et al., 2004). The assignment of model weights was accomplished by trial and error until satisfactory accuracies, meaning relatively balanced error rates between classes, were achieved for both response categories (absences and presences). Feature importance (i.e., predictor importance) was assessed using mean decrease accuracy, which is the loss in model accuracy in trees where the predictor was not included. Partial dependency plots (PDPs) were constructed using the pdp package in R (Greenwell, 2017) for each variable to evaluate their marginal effect on the predicted outcome ($\hat{y}$). Further, we evaluated all spatiotemporal two-way interactions (excluding correlated interactions between depth and temperature, depth and node habitat type, and temperature and node habitat type). Relative PDPs were generated for the top five interactions, as indicated by the H-statistic value (Friedman & Popescu, 2008) and was calculated using the iml package (Molnar et al., 2018).

RESULTS

Interspecific differences in space use

Detections were collected and analyzed for 68 tarpon (59 adult, 9 juvenile), 116 permit (105 adult, 11 juvenile), 42 adult great hammerheads, and 31 bull sharks (Appendix S1: Figure S2, Table 1, Appendix S1: Table S2). Detection count, mean detection count per species, and residence time varied considerably among species, individuals, and life stages (Figure 2). Generally, detections were greatest in the spring for mature tarpon, winter for juvenile tarpon, fall–winter for bull sharks, late summer–early winter for great hammerhead sharks, and spring–early summer for both mature and juvenile permit. There was a high level of space-use overlap at sites within the Florida Keys when comparing tarpon and permit to great hammerheads and bull sharks (Figure 3), and residence varied both in space and time for all species. Tarpon had the highest residence levels in shallow water habitats with the most extensive space use occurring between April and June and least extensive between August and November (Appendix S1: Figure S3). Permit appeared to use both deep and shallow water habitats across all months, with highest residence values occurring along the reef tract between March and July (Appendix S1: Figure S4). Bull sharks resided largely in deep water habitats (i.e., natural reef and artificial reef), particularly north of the Florida Keys within the Gulf of Mexico between June and August, but also appeared to have the highest residence periods in specific shallow water locations, including the Bahia Honda and North Biscayne nodes (Appendix S1:

TABLE 1 Tagging and tracking descriptive information for Atlantic tarpon, bull sharks, great hammerheads, and permit. Number tagged, tracking duration, animal size, number of detections, and station count (number of receivers detected on) are shown across columns. Atlantic tarpon and permit were measured at the fork length, and shark species were measured at their total lengths

Species	Maturity	No. tagged	Mean tracking duration	SD tracking duration	Mean size	SD size	Mean detection	SD detection	Mean station count	SD station count
Atlantic tarpon	Mature	59	398.08	404.51	143.25	18.92	727.08	1036.74	21.00	18.83
Atlantic tarpon	Subadult	9	204.67	213.45	80.43	11.85	2600.00	6147.40	9.78	13.51
Bull shark	Mature	30	685.92	445.13	239.37	21.64	2472.57	6373.72	23.50	23.40
Bull shark	Subadult	1	904.00	NA	215.00	NA	71.00	NA	25.00	NA
Great hammerhead	Mature	40	262.58	363.09	296.65	36.90	225.30	366.93	15.85	15.59
Great hammerhead	Subadult	2	1.85	1.62	210.50	10.61	7.50	0.71	1.50	0.71
Permit	Mature	105	274.04	167.62	70.14	8.56	12,598.80	23,217.11	15.12	17.89
Permit	Subadult	11	214.77	191.87	52.02	3.58	4906.27	5541.04	5.82	6.62

Abbreviation: NA, not available.
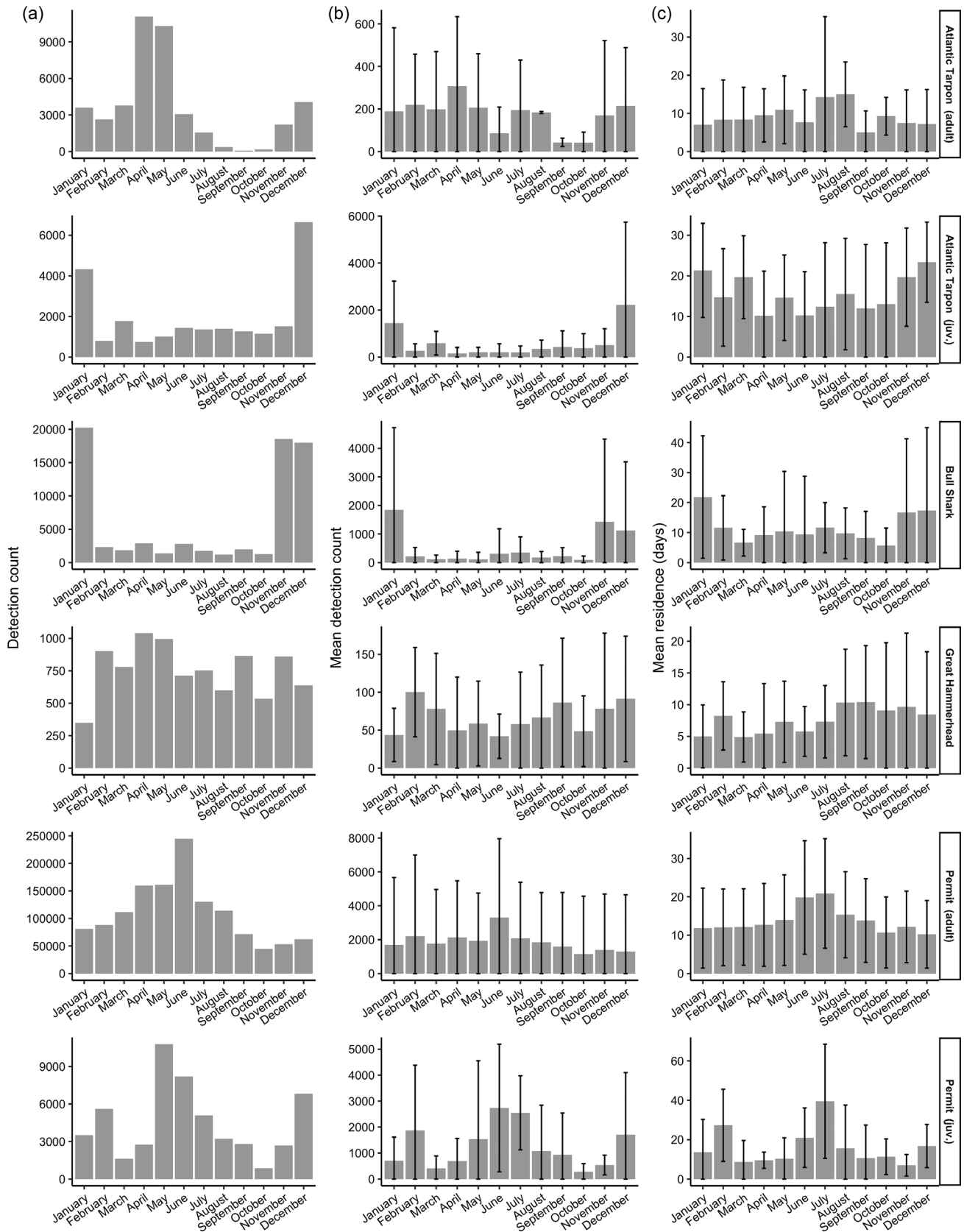
FIGURE 2 (a) Sum detention count, (b) mean detection count, and (c) daily mean residence time at array level for adult and juvenile Atlantic tarpon, bull sharks, great hammerheads, and adult and juvenile permit. Standard deviation for mean detection and residence time are indicated by error bars
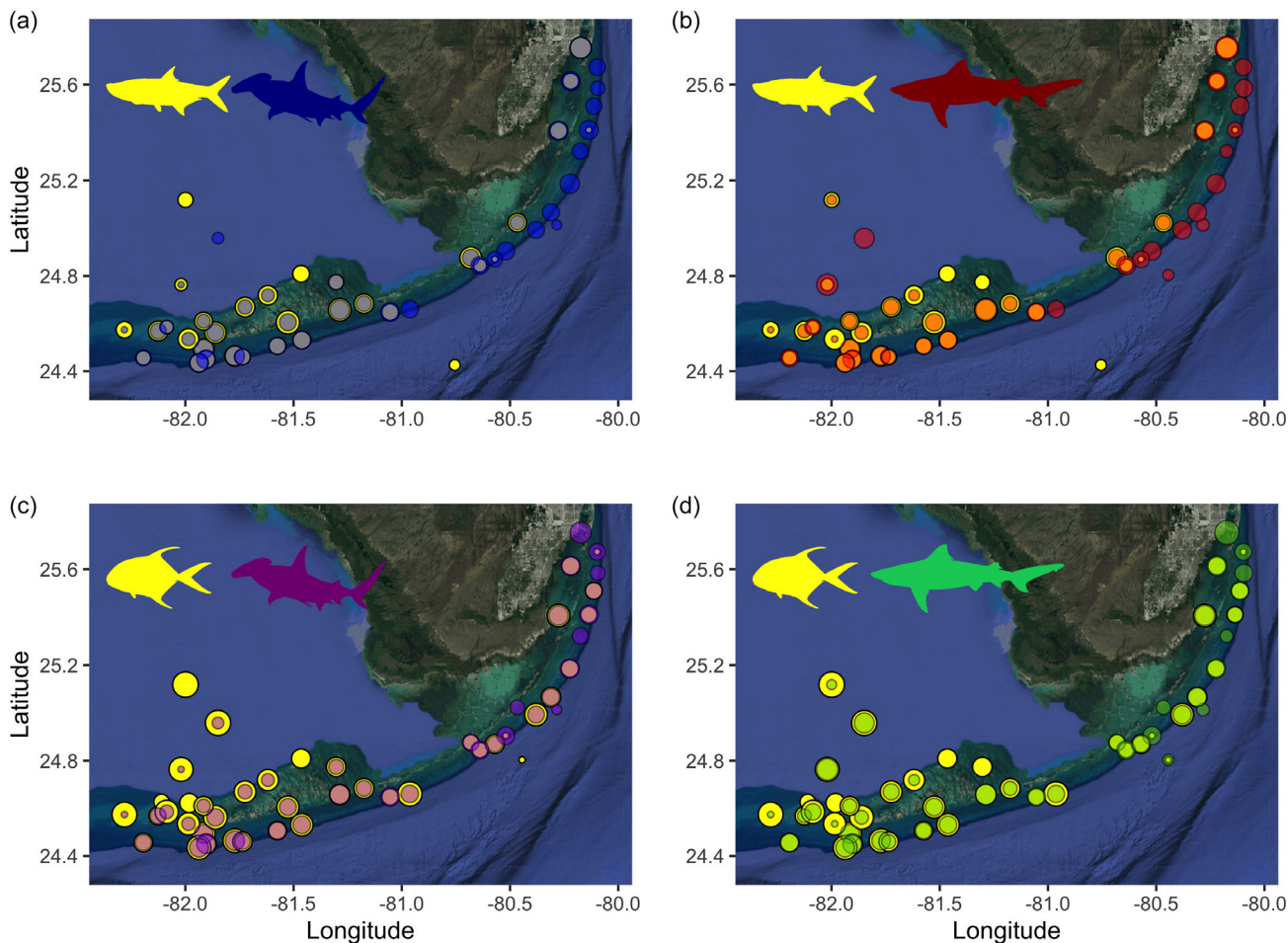
FIGURE 3 Detections logged across nodes for (a) Atlantic tarpon (yellow) and great hammerheads (blue), (b) Atlantic tarpon (yellow) and bull sharks (red), (c) permit (yellow) and great hammerheads (purple), and (d) permit (yellow) and bull sharks (green). Shark detections are plotted on top of tarpon and permit detections (yellow), as indicated by overlaid colors. Due to transparency of colors associated with shark detections, multiple shades may appear when overlapped with potential prey detections (yellow) (e.g., in panel (a), blue overlaid on yellow appears gray)

Figure S5). At Bahia Honda, residence was highest between April and June, while residence was highest at the North Biscayne node between November and February (Figure 1, Appendix S1: Figure S5). Great hammerheads were also located most often in deep water habitats, natural reef, and artificial reef. While hammerheads were detected across shallow water habitats year round in Biscayne Bay, south of Biscayne Bay they were primarily detected in shallower habitats only between April and June (Appendix S1: Figure S6). Further, great hammerhead residence was largely restricted to the Miami and Biscayne Bay areas during December.

Predator–prey hourly overlap events and predator arrival times

Of the total 48 nodes within the study area, tarpon were detected at 33 (69%), permit at 41 (85%), hammerheads at 41 (85%), and bull sharks at 42 (88%) (Appendix S1: Figure S7). For tarpon and permit, hourly overlaps with hammerheads occurred at 7 (15%) and 11 (23%) nodes and with bull sharks at 3 (6%) and 16 (33%) nodes, respectively (Appendix S1: Figure S7). After constructing hourly presence and absence bins for tarpon and permit at the node level and comparing those with shark arrival events, we found hammerheads arrived when prey were already present at 6 nodes for tarpon and at 11 nodes for permit (Appendix S1: Table S3). Bull sharks arrived when tarpon were already present at 3 nodes and when permit were already present at 16 nodes (Appendix S1: Table S3). Great hammerheads arrived when tarpon were already present on 56 (shark overlap arrival count) per 793 arrivals (total shark arrival count) (7.1%, shark overlap arrival percentage) (Figure 4a), bull sharks arrived when tarpon were already present on 154 per 2729 arrivals (5.6%) (Figure 4b), great hammerheads arrived when permit were already present on 44 per 476 arrivals
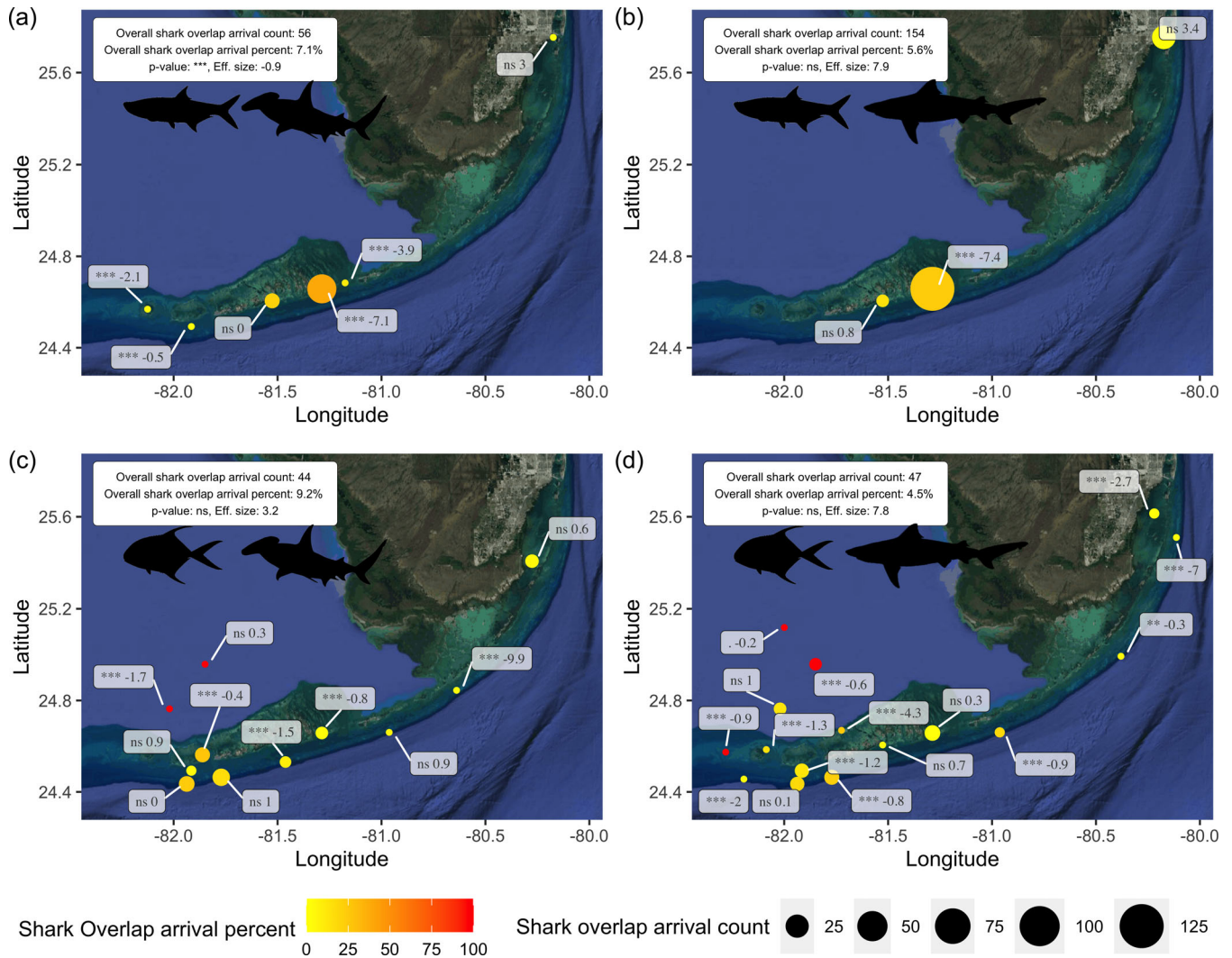
FIGURE 4 Predator–prey hourly overlap events and predator arrival times for (a) Atlantic tarpon and great hammerheads, (b) Atlantic tarpon and bull sharks, (c) permit and great hammerheads, and (d) permit and bull sharks. Overlap events and associated metrics were only examined for locations where overlap events occurred; these overlap locations were also grouped together to examine overall overlap metrics. To test whether shark overlap arrival counts were due to random chance, we resampled the observed shark arrival counts (using a conditional probability statement for shark availability) for a given species and location 100 times and compared the mean simulated shark overlap arrival counts to the observed shark overlap arrival counts with a one-sample t-test; p-values are defined as follows: 0–0.001 = ***, 0.001–0.01 = **, 0.01–0.05 = *, >0.05 = no symbol. The circle size represents the shark overlap arrival count (log) (i.e., shark arrival when prey were already present), and the color indicates the shark overlap arrival percentage (i.e., the proportion between total shark arrival counts and shark overlap arrival counts). Each node is annotated with calculated p-value and effect size (via Cohen's D). Overall shark overlap arrival count, shark overlap arrival percent, p-value, and effect size are also displayed in upper left of each panel

(9.2%) (Figure 4c), and bull sharks arrived when permit were already present on 47 per 1037 arrivals (4.5%) (Figure 4d).

When grouping all nodes that had at least one overlapping event for the species of interest, great hammerheads arrived at locations when tarpon were present significantly more often than randomly (one-sample t-test). However, we found that bull sharks did not arrive when tarpon were present significantly more often than randomly across all nodes. Neither shark species was

found to arrive when permit were present significantly more often than randomly (Appendix S1: Table S3). However, at the node level, numerous locations had sharks arriving when prey species were present significantly more often than randomly. For great hammerheads and tarpon, four of the six overlapping nodes were significant, while for bull sharks and tarpon, one of the three nodes was significant. For great hammerheads and permit, 5 of the 16 nodes were significant, and 12 of 16 nodes were significant for bull sharks and permit.

Drivers of predator–prey daily overlap events

The top three node locations where tarpon and great hammerheads overlapped daily were Bahia Honda ($n = 35$), North Biscayne Bay ($n = 21$), and Lower Keys Atlantic Flats ($n = 18$), while permit and great hammerheads overlapped at Eyeglass Bar ($n = 16$), Key West Inside Reef ($n = 15$), and Western Dry Rocks ($n = 15$) (Appendix S1: Table S4). The top three locations where tarpon and bull sharks overlapped were North Biscayne Bay ($n = 80$), Bahia Honda ($n = 78$), and Lower Keys Atlantic Flats ($n = 12$), and permit and bull sharks overlapped in Bahia Honda ($n = 17$), Key West Inside Reef ($n = 17$), and Eyeglass Bar ($n = 16$) (Appendix S1: Table S4).

In predicting spatiotemporal drivers of overlap, overall RF model accuracy varied (0.61–0.85, Appendix S1: Table S5) with the model involving tarpon and bull sharks having the highest overall accuracy value (0.85). Examining the factors that influenced species overlaps, RF found spatial and temporal patterns, with spatial characteristics (i.e., location, habitat type, and depth) as consistently important predictors among all species (Figure 5). Month also had an important impact on all species overlaps except for permit and bull sharks (Figure 5). PDPs highlighted varying relative two-way interaction ŷ values for daily overlaps between species. In relative terms, tarpon and great hammerheads (Figure 6a) overlapped more often in spring (April–June) and during November at specific nodes. Specifically, in May, Bahia Honda followed by North Biscayne had the highest interaction ŷ value. August and September produced minimal ŷ values across all locations. Further, interactions including lunar cycles were in the top five interacting variables for each species, specifically, days within the waning crescent lunar phase (excluding tarpon and bull shark PDP) produced relatively high ŷ values. Tarpon and bull sharks (Figure 6b) had little to no likelihood of overlap at any depth or any location in February, July, August, and September. Bahia Honda and North Biscayne Bay in the spring and late fall/early winter produced high ŷ values, specifically at water temperatures between 22°C and 31°C. Permit and great hammerheads (Figure 7a) overlapped more often in the spring and summer and at both shallow locations (e.g., Bahia Honda, South Biscayne Bay), shipwrecks (e.g., Adolphus Wreck), and natural reef (e.g., Eyeglass Bar, Key West Inside Reef, Western Dry Rocks) locations. Permit and bull sharks (Figure 7b) overlapped more often at Bahia Honda and across multiple wrecks and reef locations during the spring and summer. Relative to locations where overlap occurred, both shark species were more likely to overlap with permit during the waning crescent lunar phase in the spring and summer and at deeper depths.

DISCUSSION

While general space use by species was widespread across a diversity of habitats in coastal regions in the Florida Keys, overlap between predators and prey were highly specific in both location and time. A subset of these sites was significant with respect to nonrandom and synchronous overlap of sharks and game fish, suggesting these sites are likely places where predation risk may be higher for tarpon and permit if sharks are returning to these sites to actively pursue them. In addition to these nonrandom locations, other sites were high in overlap but not significant, suggesting that sharks may be generally overlapping with permit and tarpon in highly productive areas, potentially with a large and more diverse prey base. While co-occurrence does not equate to foraging success, it does highlight increased chances of predation risk for both tarpon and permit in areas of high overlap with sharks. With the extensive spatiotemporal data available, we were able to explore the aspects of the environmental variability that influence the overlap of these species. Here, we discuss the relevance of these findings and considerations for applying this type of approach to understanding predation landscapes, with a variety of potential applications.

Ecological implications

Our findings suggest co-occurrence and predation risk for tarpon and permit from great hammerhead and bull sharks occurs heterogeneously across the Florida Keys. Additionally, predation risk for tarpon and permit was elevated at known aggregation sites related to prespawning and spawning behaviors. For example, both shark species arrived significantly more often than by random chance, and with large effect sizes, when tagged tarpon were present at Bahia Honda, a well-known tarpon prespawning aggregation site. In contrast, neither shark species deviated from the random use of North Biscayne Bay, a location with high individual tarpon residence, but a site not believed to be a prespawning aggregation site.

Surprisingly, for permit, although we did observe variable levels of overlap across locations, we did not detect nonrandom synchronous overlap for shark species or permit at Western Dry Rocks, a known permit spawning ground (Brownscombe et al., 2020; Brownscombe,
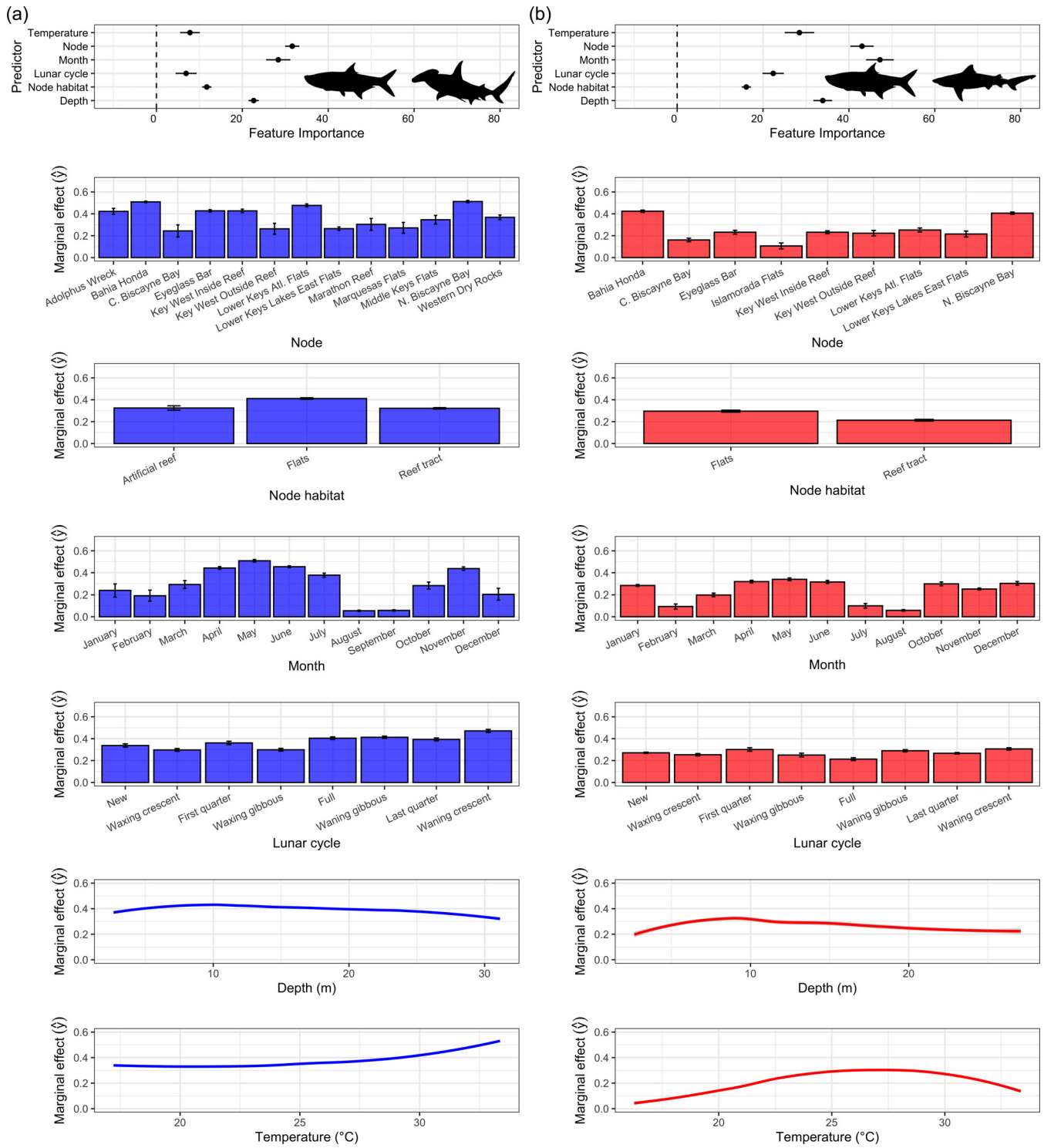
FIGURE 5 Daily overlap random forest model results for (a) Atlantic tarpon and great hammerheads, (b) Atlantic tarpon and bull sharks, (c) permit and great hammerheads, and (d) permit and bull sharks. The top panel indicates feature importance followed by partial dependency plots (marginal effects) for node, node habitat, month, lunar cycle, depth, and temperature. Means and 95% confidence intervals are displayed for each panel

Griffin, Morley, et al., 2019). Specifically, while high over-lap at Western Dry Rocks did occur for permit with both great hammerhead and bull sharks (24.2% and 18.8%, respectively), nonrandom overlap was not detected at this

location, potentially because of the numerous species that are also believed to form spawning aggregations here, including mutton (*Lutjanus analis*) and gray snapper (*Lutjanus griseus*; Lindeman et al., 2000), as well as black
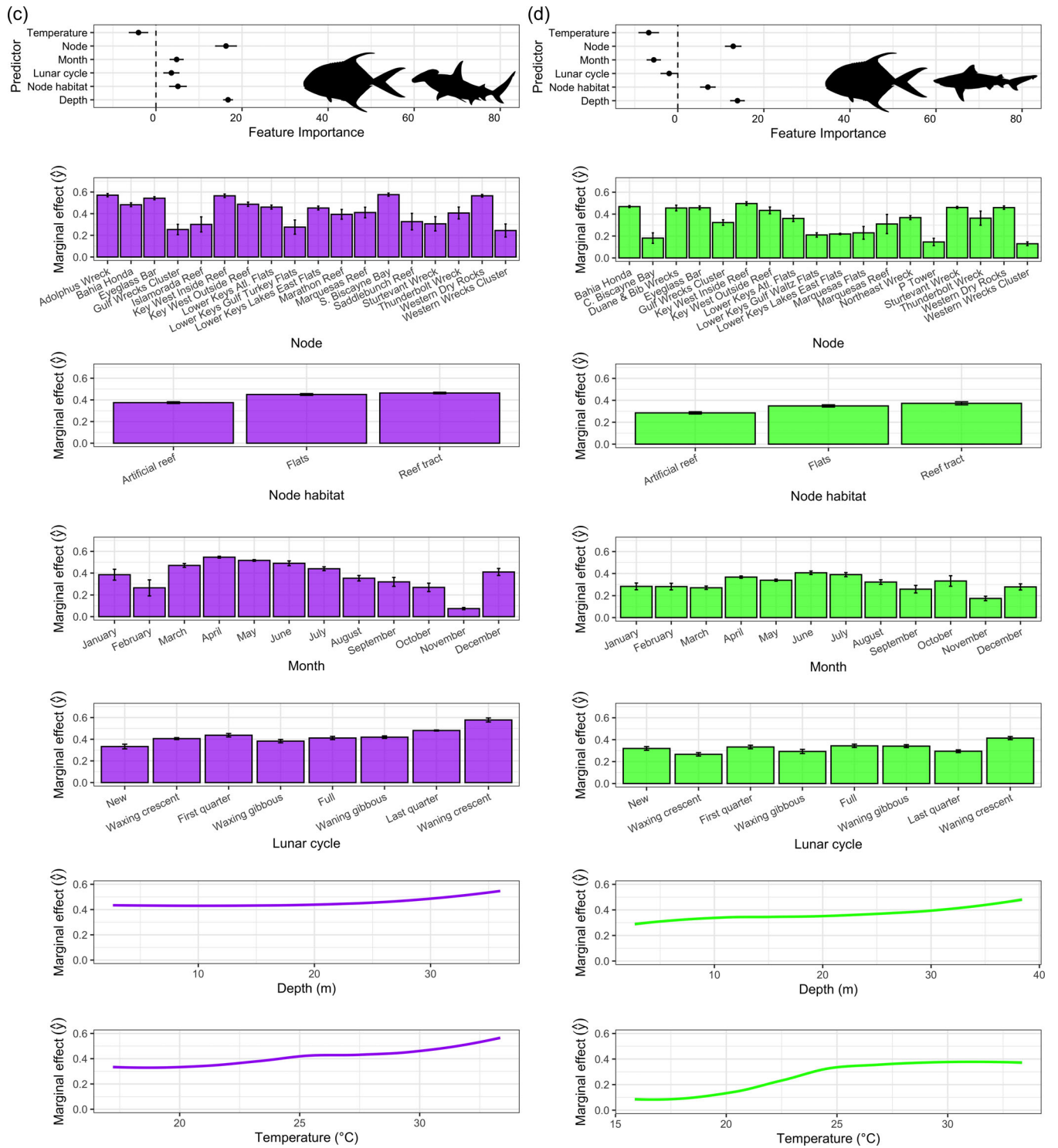
FIGURE 5 (Continued)

(*Mycteroperca bonaci*), Nassau (*Epinephelus striatus*), gag (*Mycteroperca microlepis*), and yellowfin (*Mycteroperca venenosa*; Keller et al., 2020) groupers. For some, these spawning aggregations occur outside the spring and summer permit spawning months, with grouper in particular believed to spawn there in the winter months (Keller et al., 2020). Since Western Dry Rocks attracts multiple

spawning aggregations, sharks may be generally targeting this area as a location of potentially high foraging success regardless of when permit spawn. Additionally, non-random predator arrivals were spread more broadly throughout the study area in locations specific to permit compared to tarpon because they likely have numerous spawning/prespawning aggregation sites in the Florida
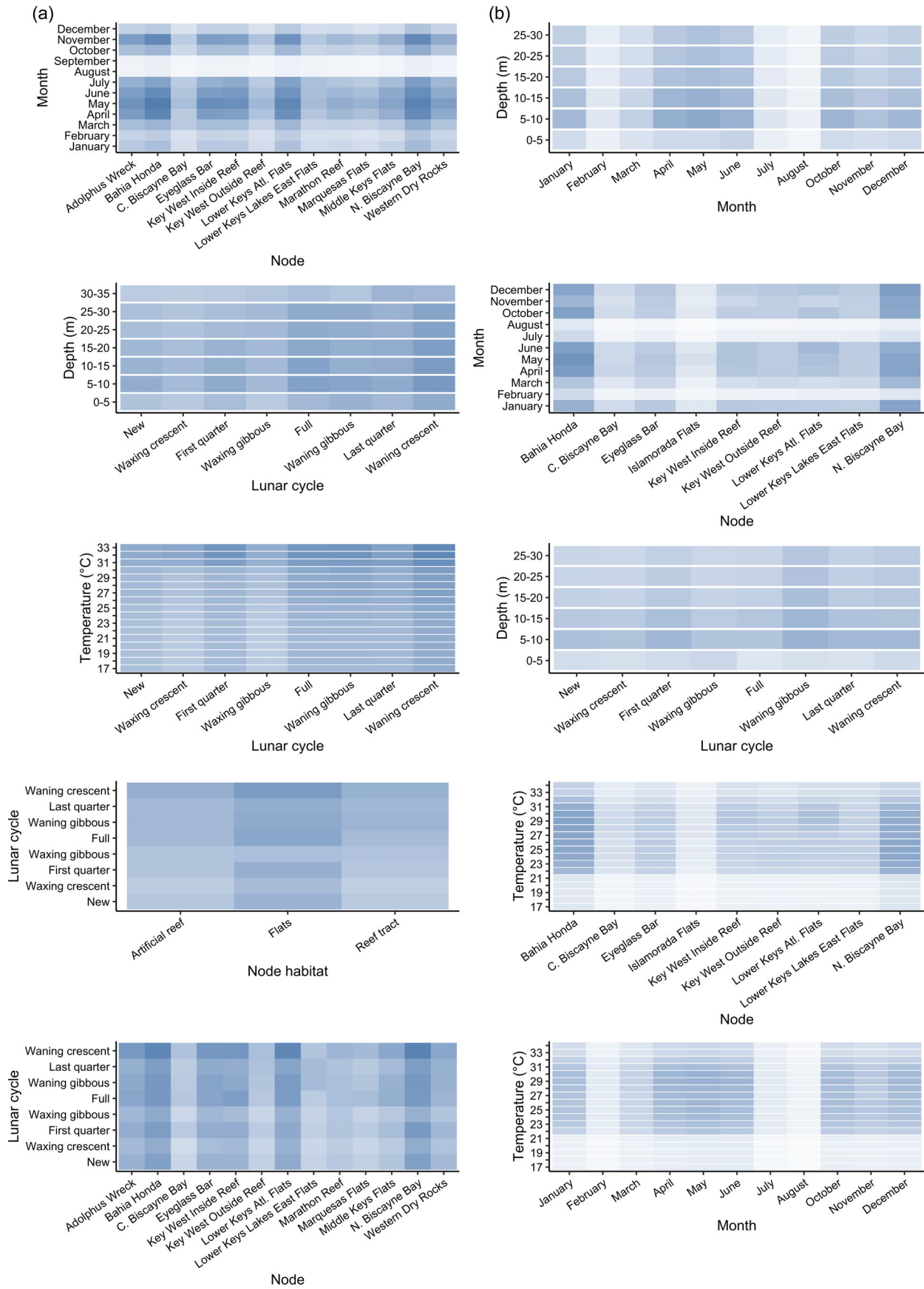
FIGURE 6 Top five two-way interactions (ordered from top to bottom) displayed from daily overlap random forest models for (a) Atlantic tarpon and great hammerheads and (b) Atlantic tarpon and bull sharks. The relative mean marginal effects (ŷ) are shown in each two-way interaction partial dependency plot (darker blue equates to higher relative ŷ). September is missing from Figure 5b panels including month due to ŷ = 0
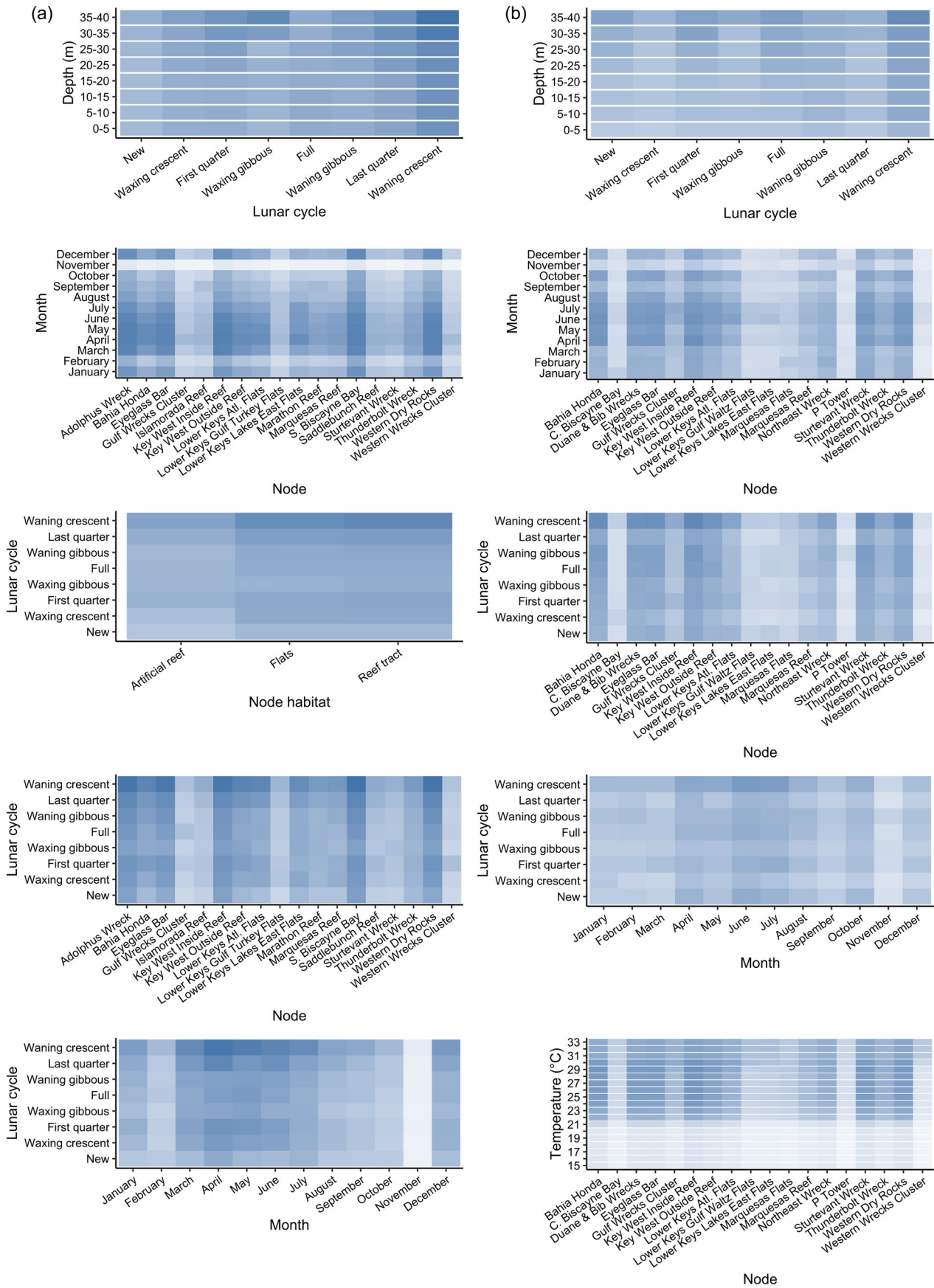
FIGURE 7 Top five two-way interactions (ordered from top to bottom) displayed from daily overlap random forest models for (a) permit and great hammerheads and (b) permit and bull sharks. The relative mean marginal effects (ŷ) are shown in each two-way interaction partial dependency plot (darker blue equates to higher relative ŷ)

Keys other than Western Dry Rocks (Brownscombe et al., 2020).

The repeated return of sharks to areas where potential prey are present and where foraging could be more successful thanks to a large aggregated prey base suggests these sharks may be relying on a memory of successful foraging attempts at specific locations in the Florida Keys. Indeed, models of foraging behavior across heterogeneous landscape scales show that, in heterogeneous landscape models, the inclusion of memory of successful foraging events and locations improves foraging success (Bracis et al., 2015). While the precise mechanisms connecting shark memory to successful foraging behavior in the wild remains difficult to unravel, spatial learning, memory retention, and response to classical conditioning have been documented in sharks across taxa (Guttridge et al., 2009; Schluessel & Bleckmann, 2012). Individuals from multiple reef-associated shark species reliably arrive at and prey upon fish spawning aggregations elsewhere in tropical marine environments (Mourier et al., 2016; Olsen & LaPlace, 1979; Pickard et al., 2016; Rhodes et al., 2019). Further, the repeated return of highly migratory sharks to prey aggregations has been documented globally (Guttridge et al., 2017; Hacohen-Domené et al., 2015; Jorgensen et al., 2010; Schilds et al., 2019; Skomal et al., 2017), suggesting a potential link between memory and successful foraging events. Within the study site and across consecutive years, individual great hammerheads, identified by external tags or unique fin morphologies, have been observed feeding on tarpon or recaptured at known tarpon prespawning aggregation sites (G. A. Casselberry, unpublished data; K. Grubb, B. Spano, and N. Wheeler, personal communication). Diet studies for both shark species throughout the study area, through direct stomach content or stable isotope analyses, would improve our understanding of these sharks' seasonal reliance on game fish aggregations.

Examining predator–prey overlap at the broader daily level revealed more frequent cases of overlap spanning additional locations across the study area, including movement corridors and foraging grounds for tarpon and permit, in addition to spawning and prespawning aggregations. There was a strong seasonal component to daily overlap for both prey species, in combination with other environmental parameters (habitat type, lunar cycle, depth, and temperature) coinciding with tarpon and permit spawning seasons, as well as tarpon and bull sharks overwintering in the Florida Keys. Specifically, the interaction between lunar phase and other environmental variables was important in explaining predator–prey daily overlap. Interestingly, great hammerheads with tarpon and permit, and bull sharks with permit, were more likely to overlap during the waning crescent lunar phase when combined with certain locations or specific times of year. Considering spawning periods occur a few days to a week surrounding a new or full moon for tarpon (Crabtree, 1995; Crabtree et al., 1997; Luo & Ault, 2012) and permit (Bryan et al., 2015; Graham & Castellanos, 2005), we hypothesized that predators would overlap during or just prior to when aggregations were most abundant and vulnerable. However, given that both tarpon and permit likely rely heavily on vision to avoid potential predators (Miyazaki et al., 2000; Schweikert & Grace, 2018), the waning crescent lunar phase may provide an optimal tradeoff for predators between prey presence and vulnerability, if foraging at night.

Management implications

A key component of the successful conservation and management of any species is a fundamental understanding of its spatial ecology, which includes identifying foraging grounds (Anadón et al., 2011; Barnett et al., 2012; Hays et al., 2019). Quantifying the movement dynamics of sharks and their teleost prey can improve decision-making in the context of potential seasonal harvest closures or the establishment of protected areas to preserve ecologically important habitats (Daly et al., 2018; Gilman et al., 2019; Lowerre-Barbieri, Catalán, et al., 2019; Micheli et al., 2004). The potential shark foraging grounds identified herein are located primarily within the Florida Keys National Marine Sanctuary boundaries, which relies heavily on spatial ecosystem-based management (Office of National Marine Sanctuaries, 2019). Further fine-scale investigation (e.g., minimum convex-polygons, kernel density estimates, Brownian bridge movement models) may be specifically warranted to quantify the ecological importance of these sites, including how spawning seasons and related aggregations of tarpon or permit (or other spawning species) are spatially and temporally linked with predator presence/abundance. Pending the results of future studies, these areas should likely be considered in management plans for the sanctuary. Further, identifying and examining foraging locations related to other prey species is recommended since both sharks prey upon a wide range of species in addition to tarpon and permit (Gallagher & Klimley, 2018; Snelson Jr. et al., 1984).

The severity of shark population declines within the Northwest Atlantic and Gulf of Mexico has been debated (Baum et al., 2005; Burgess, Beerkircher, Cailliet, Carlson, Cortes, et al., 2005b; Burgess, Beerkircher, Cailliet, Carlson, Cortés, et al., 2005a; Jiao et al., 2009); however, in some regions, conservation practices are succeeding and coastal shark populations are increasing (Carlson

et al., 2012; Curtis et al., 2014; Peterson et al., 2017; Pondella & Allen, 2008). Though populations have likely not returned to historic abundance levels in the Florida Keys (Froeschke et al., 2012; Heithaus, Burkholder, et al., 2007; Tinari & Hammerschlag, 2021; Ward-Paige et al., 2010), increasing shark populations in conjunction with increased human use of the ocean has the potential to lead to increased human–wildlife conflict and highlights the need to proactively manage human behavior to account for larger predator populations (Carlson et al., 2019). Indeed, within our study area and throughout the state of Florida, some fishing boat captains, guides, and anglers have noted increased conflict with sharks and believe that they are a threat to their catch (Drymon & Scyphers, 2017, Casselberry et al. 2022). To reduce predation events of prized game fish, some are calling for altering existing shark species protections and increasing shark bag limits.

Considering sharks actively pursue potential foraging opportunities, as this study supports, sharks may also be able to identify advantageous foraging grounds that also overlap with areas of high recreational fishing pressure, leading to successful prey capture before landing (depredation) or postrelease. While shark conditioning to angler activities is widely believed to exist among angler groups, the degree to which it occurs remains uncertain (Mitchell, McLean, Collin, & Langlois, 2018). Associative learning by sharks to angling activities is largely undocumented (Mitchell et al., 2020); however, such behaviors have been observed in some shark-related ecotourism ventures (Bruce & Bradford, 2013; Brunnschweiler & Barnett, 2013; Fitzpatrick et al., 2011; Johnson & Kock, 2006). Because anglers and sharks co-occur at the same fish aggregations, conditioned or not, localized depredation and postrelease mortality events are likely a function of opportunistic foraging strategies that occur when sharks become attracted to angling activity through auditory (e.g., boat noise, injured fish), olfactory (e.g., bait chum, physiological distress signals), visual, or electrical cues (Mitchell, McLean, Collin, & Langlois, 2018).

Our results show high overlap for sharks and their prey in two regions known to have high recreational fishing pressure and to suffer from depredation and postrelease mortality: Bahia Honda for tarpon (G. A. Casselberry, unpublished data) and Western Dry Rocks for permit (Holder et al., 2020). These aggregations—associated with prespawning/spawning behaviors—are often heavily fished owing to the high likelihood of successfully hooking one of these prized game fish. Following optimal foraging theory, that is, the energetic tradeoff between energy gained or expended by foraging behaviors (Pyke et al., 1977), it would be expected that sharks would engage in depredation or postrelease predation opportunities since they provide a means of high energy gains while minimizing energy expenditure by capitalizing on distressed or exhausted prey (Madigan et al., 2015; Mitchell, McLean, Collin, & Langlois, 2018). Thus, anglers that target tarpon and permit spawning migrations likely alter natural predation landscapes by increasing mortality risk and decreasing antipredator responses, which ultimately has large implications for management and conservation efforts (Sabal et al., 2021).

As with many recreationally important game fish, tarpon and permit lack adequate stock assessments, perhaps under the false assumption that catch-and-release fishing mortality is minimal. The Florida permit stock has not been assessed in over two decades (Addis et al., 2019; Armstrong et al., 1996), and tarpon lack assessment despite being highly migratory, crossing state and, likely, international borders, where they are less regulated (Griffin et al., 2018; Luo et al., 2020). Further, while depredation mortality is infrequently accounted for in stock assessments (Kneebone et al., 2021; Peterson & Hanselman, 2017; Sippel et al., 2017; Tixier et al., 2020), it may be essential to incorporate for the management of recreationally important fish stocks. Indeed, quantifiable hook-and-line recreational depredation rates have been difficult to acquire (Mitchell, McLean, Collin, Taylor, et al., 2018). Within the Florida Keys, in some areas depredation rates as high as 15% for tarpon (G. A. Casselberry, unpublished data) and up to 90% for permit (Holder et al., 2020) have been estimated. While postrelease mortality (due to stress or predators) is believed to be low for permit (Holder et al., 2020), tarpon postrelease mortality estimates range from 13% to 27% throughout the Atlantic, Gulf of Mexico, and Caribbean (Guindon, 2011; Luo et al., 2020). Regardless of current estimates, depredation and postrelease mortality rates should continue to be monitored since they may increase, especially if sharks nonrandomly pursue/co-occur with these game fish aggregations, as this study suggests. Ultimately, such data combined with these findings are critical to ensuring that effective management measures are enacted in areas of increased predation risk such as spatial, temporal, or species-specific fishing closures, species-specific tackle requirements (heavier and stronger rods) to reduce fight time, or the application of emerging shark deterrent technologies.

The approach and considerations

Although we could not quantify predation risk directly, nor infer predation events from the analyses presented in this study, we do highlight locations with nonrandom overlap of predators and their prey and, thus, elevated levels of potential predation risk. While this has been explored in the marine environment to some degree, it is

typically limited to seabirds and other much larger predators (e.g., marine mammals, basking sharks) that feed on much smaller fish and plankton (Benoit-Bird et al., 2013; Davoren, 2013; Sims et al., 2006). Within marine systems, studies that involve the monitoring of free-ranging predator and prey movements are often hindered by small spatial scales or short-term, asynchronous temporal scales relative to the species of focus (Hammerschlag et al., 2012, 2015; McMahan et al., 2013). Our application of acoustic telemetry and combining tag data from multiple simultaneous research projects (via Integrated Tracking of Aquatic Animals in the Gulf of Mexico [iTAG], The Florida Atlantic Coast Telemetry [FACT] networks) allowed us to overcome such hurdles and ultimately provide insights into the nonrandom and heterogeneous predation risk of two shark species and their prey across the broader Florida Keys landscape.

We also implemented machine learning algorithms, that is, RF, to examine potential environmental variability in daily predator–prey overlap. When compared to frequently employed statistical inferences (e.g., generalized linear models), this approach overcame common challenges associated with data sets with zero-inflated data, correlated predictors, and complicated predictor interactions (Breiman, 2001; Cutler et al., 2007; Liaw & Wiener, 2002). However, in this case, as is common with severely unbalanced data sets (i.e., few presences, many absences), our models and their performance metrics still indicated overall relatively poor accuracy in the non-training data. Here, we utilized class weighting (Chen et al., 2004) to help balance the data set and to dramatically reduce the misclassification of true positives (i.e., proportion of predator–prey overlaps correctly classified). This conservative approach increased true positive classification error rates (also known as sensitivity; see Molnar, 2019) and, in turn, worsened false positive classification rates (also known as specificity; see Molnar, 2019) that is, incorrectly predicted false predator–prey overlaps. The use of class weighting will directly affect the tradeoff between sensitivity and specificity model fit metrics, and the choice between which metric to prioritize in relation to overall accuracy will depend on the context of the question. For example, Brownscombe et al. (2020) prioritized sensitivity (proportion of presences accurately classified) over specificity (proportion of absences accurately classified) to search for all potential permit spawning locations in the Florida Keys. This precautionary approach (i.e., lower true positive error at a cost of higher false positive error) was also the most appropriate and applicable method to inform conservation strategies surrounding depredation concerns.

Conclusion

Spatiotemporal patterns in species interactions, such as predator–prey dynamics, have important implications for ecosystem function and biological management decisions (Hunsicker et al., 2011). This is particularly the case in the Florida Keys because of the high fish species diversity (Jeffrey, 2001), including predatory sharks (Heithaus, Burkholder, et al., 2007) and the growing conflicts with recreational fishery mortality. Because co-occurrence and predator–prey landscapes may be disproportionate at certain times and locations, the predator–prey daily overlaps projected by our models may help to guide management efforts focused on megafauna conservation and the sustainability of recreational fisheries. We suggest that marine ecologists should find an increasing utility of acoustic telemetry and machine learning techniques to overcome analytical challenges associated with monitoring mobile species across multiple spatial and temporal scales. Ultimately, this study and its methods extend the field of predator–prey dynamics and provide important insights on the landscape of megafauna occupying apex and mesopredator roles in the ecosystem.

CONFLICT OF INTEREST
The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT
The data that support the results in this study were shared through iTAG and are archived through the Ocean Tracking Network (OTN, https://members.oceantrack.org/OTN/projects). OTN dictates data be released after 2 years following the expiration of any given tag. Additional support and access can be provided directly via tag owners: tarpon, permit, and great hammerheads tagged by UMass and Carleton U (https://members.oceantrack.org/OTN/project?ccode=BTTFLK), great hammerheads and bull sharks tagged by BBFSF (https://members.oceantrack.org/OTN/project?ccode=V2LBBFSF), and great hammerheads and bull sharks tagged by U. Miami (https://members.oceantrack.org/OTN/project?ccode=V2LURB).

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