Seasonal variation in the phenology of Atlantic tarpon in the Florida Keys: migration, occupancy, repeatability, and management implications

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ABSTRACT: Atlantic tarpon *Megalops atlanticus* are important mesopredators in the western Atlantic Ocean, and the focus of a popular recreational fishery that targets them throughout their annual migration in the Gulf of Mexico and southeastern USA. Using 4 years of acoustic telemetry data, we quantified the seasonal variation in phenology of arrival and departure, and occupancy for subadult and adult *M. atlanticus* in the Florida Keys, USA. While detection profiles of subadult *M. atlanticus* (n = 11) varied in residency and dispersal patterns, all adult *M. atlanticus* detection profiles (n = 47) exhibited seasonal residency. The median spring–summer residence period of adult *M. atlanticus* ranged from 40 to 60 d, with a mean of 51 d across years. At the individual level, repeatability in the timing of arrival and duration were high across years, suggesting that photoperiod may be an important migratory cue. Further, the repeatability in the timing of arrival to the Florida Keys for individuals was not associated with sea surface temperature (SST). At the population level, residency corresponded with the spawning season, with the majority of adult *M. atlanticus* arriving in April once SST reached 26°C, and then departing in June (27–29°C). Highest occupancy probabilities for adult *M. atlanticus* occurred in May (26–28°C) and lowest between August and October. Large aggregations of *M. atlanticus* that occur during the spawning season (April–June) are potentially vulnerable to the effects of habitat degradation and angling-related mortality and behavioral changes. These data on *M. atlanticus* phenology provide insights for implementing science-based strategic management plans.

KEY WORDS: *Megalops atlanticus* · Movement ecology · Migratory · Behavioral consistency · Repeatability · Spawning · Conservation · Recreational fisheries

1. INTRODUCTION

Migration, a common behavior in fishes, has evolved to maximize growth, survival, and reproductive suc-

cess (Leggett 1977, Gross et al. 1988, Roff 1988), balancing biological and ecological benefits against numerous costs, such as increased physiological demands and predation risk (Brönmark et al. 2008,

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Tamario et al. 2019). Further, the recurring seasonal timing of migratory events (i.e. migration phenology) may determine the ability of an organism to complete life cycle events that have important implications related to their fitness (Forrest & Miller-Rushing 2010). For example, the migrations of fish to spawning areas, and their timing, should provide the optimal abiotic and biotic conditions that lead to the greatest survival and development of fertilized eggs and hatched larvae (Jørgensen et al. 2008, Lowerre-Barbieri et al. 2017, Tamario et al. 2019). Conversely, if migration phenology becomes decoupled from critical abiotic conditions and biotic resources (i.e. mismatch), life history strategies (e.g. spawning, foraging) may be disrupted or altered, leading to potential demographic changes (Miller-Rushing et al. 2010, Chmura et al. 2019). To avoid a mismatch, the timing of these events has likely evolved from a complex interaction between genetic and environmental cues, such as temperature, photoperiod, lunar cycle, and resource availability (Forrest & Miller-Rushing 2010, Wang et al. 2010, McNamara et al. 2011, Anderson et al. 2013). If stimuli become reliable indicators for successful life history decisions (e.g. migratory/spawning timing), they could emerge as repeatable at the individual level and hence be selected for (Forsythe et al. 2012, Otterå et al. 2012).

To maximize population fitness, there is often individual diversity in behavioral and ecologically variable traits. Referred to as the 'portfolio effect' (Figge 2004), this diversity spreads risk across an unpredictable environment resulting in increased reproductive success. An example of this is partial migration, which is common in fishes, and refers to migratory and resident contingents within the same population (Jonsson & Jonsson 1993, Chapman et al. 2012). Similar to migratory timing, individual status (resident vs. migrant) can be influenced by genetic makeup, age, sex, body condition, and environmental mechanisms (Chapman et al. 2011, 2012, Secor et al. 2020). Overall, understanding both individual level repeatability/variability and population-level trends in migratory behaviors should help to answer questions surrounding individual fitness, population dynamics, and trophic web dynamics, especially if migrants fill important predator/prey niches (Edwards & Richardson 2004, Chapman et al. 2011, 2012, Gillanders et al. 2015). Such questions may also shed light on best management practices and on the ability for a species to persist in the face of large-scale environmental perturbations, such as climate change (Killen et al. 2016, Tamario et al. 2019, Crear et al. 2020, Langan et al. 2021). For example, Peer & Miller

(2014) demonstrated that the arrival timing of striped bass *Morone saxatilis* to spawning grounds were largely driven by springtime water temperatures, and thus, static seasonal fishing closures disproportionately targeted egg-bearing females in some years due to climate-induced variability in fishing mortality. Considering that migratory fish may face compounding anthropogenic disturbances that can impede their migratory success (e.g. dams, harvest, prey exploitation, and habitat degradation) (Robinson et al. 2009), implementing effective conservation and management strategies for migrant species remains challenging (Weng et al. 2008, Block et al. 2011, Heupel et al. 2015, Hays et al. 2016, 2019). Identifying the seasonal use, variation, and function of migrant habitats across life stages should help to prioritize management and conservation strategies to ensure life history needs are met (Pressey et al. 2007, Runge et al. 2014, Pratt et al. 2019, Lowerre-Barbieri et al. 2021).

The Atlantic tarpon *Megalops atlanticus*, a migratory mesopredator, is found along the coasts of the eastern and western Atlantic Ocean, including the Gulf of Mexico (GOM) and the Caribbean Sea (McMillen-Jackson et al. 2005). While little is known on the ecology of *M. atlanticus*, recent efforts have begun to highlight the wide regional connectivity and seasonal distributions of adult *M. atlanticus* within the northwest Atlantic (Griffin et al. 2018, Luo et al. 2020, Friess et al. 2021). Within the northern hemisphere, specifically in the GOM and southeastern USA, many *M. atlanticus* are believed to undergo annual spawning migrations in the early spring and summer. After migrating to pre-spawning areas, adult *M. atlanticus* are believed to first form pre-spawning aggregations 2–5 km offshore (Crabtree et al. 1992), and then move to spawning areas that likely occur 200–250 km offshore along continental slopes at depths of 100–200 m surrounding spring and summer new or full moons (Crabtree et al. 1992, Crabtree 1995, Shenker et al. 2002, Luo et al. 2020). Following the spawning migration, the majority of adult tarpon are believed to then migrate northward in the summer and early fall, likely to forage in areas surrounding productive estuarine systems (Luo et al. 2020, Drymon et al. 2021). Migrant *M. atlanticus* then move south as sea surface temperatures (SSTs) begin to decrease in the fall (Griffin et al. 2018, Luo et al. 2020, Friess et al. 2021).

As a prized gamefish, this migratory species supports a fishery that is estimated to generate millions of dollars in economic revenue across the GOM and the southeastern USA (Steinback et al. 2004, Fedler 2011, 2013). Prior to *M. atlanticus* moving offshore to

spawn, recreational anglers across southern Florida target large schools of hundreds to thousands of *M. atlanticus* that form within passes, cuts, and deep channels. Two of the most common locations to target these seasonal aggregations occur around Boca Grande on the west coast of Florida and around the Florida Keys archipelago on the southern tip of Florida (Camp et al. 2018). Similarly, anglers are increasingly targeting *M. atlanticus* along their coastal migratory corridors and northern foraging areas (Barbieri et al. 2008). In addition to the economic contributions of the fishery, *M. atlanticus* provide cultural identity to many stakeholders (Kokomoor 2010, Mill et al. 2010, Davis 2017) and, characteristic of migrant species, likely provide essential ecosystem services such as energy transfer and trophic interactions (Bauer & Hoye 2014). However, *M. atlanticus* are currently listed as 'Vulnerable' on the International Union for Conservation of Nature Red List due to habitat degradation, bycatch mortality, and consumptive fisheries (Adams et al. 2014, 2019). The wide distribution and seasonality of this species has made implementing management strategies at the proper spatiotemporal scales difficult (Barbieri et al. 2008), underlining the complexity associated with protecting and conserving migrant *M. atlanticus* populations.

Specifically, within the Florida Keys during the early spring and summer months, catch-and-release anglers target *M. atlanticus* on or near shallow water flats (<3 m depth), and, along with the permit *Trachinotus falcatus* and bonefish *Albula vulpes* fisheries, support a fishery with an annual economic impact estimated at $465 million (Fedler 2013). This archipelago (approximately 400 km in length), and its nearshore habitats, consists of mangrove forest islands, expansive seagrass flats, a 580 km barrier reef, and over 1000 shipwrecks providing artificial reef structure (National Oceanic & Atmospheric Administration 2016), with over 9500 km^2 managed by the National Oceanic and Atmospheric Administration and The Florida Fish and Wildlife Commission as the Florida Keys National Marine Sanctuary (www.floridakeys.noaa.gov). This area supports both adult and subadult *M. atlanticus*, along with a wide diversity of other vertebrate and invertebrate species (Suman et al. 1999, Sawaya et al. 2019). However, the archipelago is affected by multiple anthropogenic threats, including freshwater flow alterations through the Florida Everglades, water quality and habitat degradation, climate change effects, damage from boat use, and overfishing (Krusczynski 1999, Lapointe et al. 2004, Keller & Causey 2005, Hallac et al. 2012, Brownscombe et al. 2019a).

While adult *M. atlanticus* in this area are well-established as seasonal migrants (Lowerre-Barbieri et al. 2021), little is known about tarpon phenology, its cues, behavioral plasticity, and/or intrinsic individual variation. Understanding these behaviors is critical to predicting how resilient this important species will be to the regional stressors the Florida Keys is undergoing. As such, the objectives of our study were to (1) describe general subadult and adult occupancy (e.g. arrival and departure timing, duration), (2) determine if patterns (arrival/departure dates/SSTs and duration) were repeatable at the individual level, and (3) at the population level, assess the temporal and environmental variability (time of year, SST, lunar cycle) associated with *M. atlanticus* arrivals to, departures from, and abundance patterns within the Florida Keys. With the shallow-water habitat use by *M. atlanticus* (>80% of their time in water depths ≤10 m; Luo & Ault 2012), we capitalized on an extensive acoustic telemetry array in the Florida Keys. In addition, the small size and extended battery life of acoustic telemetry transmitters also allowed for a wide size range of *M. atlanticus* to be tagged and monitored for multiple years. Overall, this effort was the first to examine the phenology of *M. atlanticus* migration in the Florida Keys at a resolution that can broadly inform habitat and resource management, as well as conservation needs (Cooke et al. 2004, Hussey et al. 2015).

2. MATERIALS AND METHODS

2.1. Fish capture and tagging

Megalops atlanticus for this study were captured from May 2016 to August 2019, using recreational fishing gear. Sampling locations included the Florida Keys, FL (24.61° N, 81.48° W), Charlotte Harbor, FL (26.72° N, 82.2° W), Tampa Bay, FL (27.61° N, 82.67° W), Apalachicola, FL (29.65° N, 84.93° W), southern Georgia (30.84° N, 81.42° W), and central South Carolina (33.06° N, 79.33° W). Once landed, all *M. atlanticus* were revived by either slowly idling the boat forward with the fish submerged or by holding the fish stationary while supporting its weight under the pelvic fins and allowing uninhibited buccal pumping. Acoustic transmitters (V16, 69 kHz, 16 mm diameter, 98 mm length, 17.3 g in air, min and max delay times 60–120 s, estimated battery life 1910 d; Amirix) were inserted into the coelomic cavity after making a 3–4 cm incision with a scalpel through the muscle wall. When wave action was manageable, predator

density/predation threat was low, and individual tarpon were moderately unimpaired, incisions were closed using a single suture (PDS-II monofilament absorbable, 3-0, model Z497G; Ethicon); otherwise, no suture was used. Fork length (FL, cm) and girth (cm) were used to estimate weight (kg) (Ault & Luo 2013).

2.2. Tracking system

During our study, over 200 autonomous fixed acoustic receivers (VR2RW and VR2Tx models; Amirix) were deployed in the Florida Keys. Receivers were deployed to support projects affiliated with the University of Massachusetts Amherst, Carleton University, Bonefish & Tarpon Trust, and the Florida Fish & Wildlife Conservation Commission (offices St. Petersburg and Marathon). Due to the extent of the large study area and multiple project goals, receivers were deployed using a point-of-interest arrangement rather than a grid formation (Brownscombe et al. 2019b). Receivers were fixed to 1 m of rebar and were cemented within heavy mooring stands (30–50 kg) placed on the seafloor. 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 (VRT2Tx model; Amirix) at 8 unique sites within the Florida Reef Tract (Brownscombe et al. 2020).

In addition to detections on receivers in the Florida Keys, detections from *M. atlanticus* were also collected through collaborative institutional networks (integrated Tracking of Animals in the Gulf, Florida Atlantic Coast Telemetry, and Atlantic Cooperative Telemetry). These networks include 1000+ acoustic receivers spanning the GOM and coastal southeastern USA enabling the tracking of migratory animals beyond a single array (Griffin et al. 2018, Ellis et al. 2019, Bangley et al. 2020, Friess et al. 2021, Lowerre-Barbieri et al. 2021). The Ocean Tracking Network (Iverson et al. 2019) also provided support through receiver loans and data sharing facilitation between researchers.

2.3. Data analysis

2.3.1. Data filtering and descriptive statistics

All statistical analyses were conducted using R 3.6.2 (R Core Team 2019). *M. atlanticus* detection data

were examined between May 2016 and August 2020. Multiple data filters were applied to all *M. atlanticus* acoustic detection data prior to analysis and visualizations. Filters identified potential false detections arising from code mutations or collisions (Simpfendorfer et al. 2015) using 3 criteria: (1) consecutive detections that occurred within a time period less than the minimum tag delay (defined here as 60 s), (2) unrealistic detections (movements) at >10 m s^{-1} (a higher rate was chosen when considering variable detection ranges), and (3) singular detections occurring within a specific time frame (defined here as 120 min). Due to post-release survival concerns (Guindon 2011, Luo et al. 2020), only *M. atlanticus* with detections >1 station and detected over 14 d after tagging were used for data analysis and visualization. All stations with *M. atlanticus* detections were collapsed into 2 separate array types: (1) detections occurring within the Florida Keys and (2) detections occurring outside the Florida Keys. If detections occurred at stations in proximity (~20 km) to the Florida Keys, including stations located on nearby shipwrecks and reefs, they were considered within the array (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m684 p133_supp.pdf). We assigned nearby detections from Florida Bay, the Everglades, Biscayne Bay, and the Dry Tortugas as outside of the Florida Keys array due to the limited detection coverage, spatial extent, and generalized habitat differences. To increase the interpretability of space use across the Florida Keys, detections were also assigned to nodes based on their geographic position and habitat types (e.g. flats/channels, Florida Reef Tract, shipwrecks). Stations that were within similar habitat types and relatively close together were grouped into the same node (Fig. S2).

Within the study area, and in general, subadults have been shown to be residents, while adults are seasonal migrants (Lowerre-Barbieri et al. 2021). However, marine fish typically exhibit complex relationship between size, maturity, and movement patterns. Thus, to further evaluate these patterns, *M. atlanticus* were classified as either adults, potential adults, or subadults using FL measurements and observed movement patterns, e.g. broad scale movements, net square displacement. Based on *M. atlanticus* sexual maturity estimates for Florida (117.5 cm FL for males and 128.5 cm FL for females; Crabtree et al. 1997), all *M. atlanticus* ≥128.5 cm FL were considered adult. Considering that *M. atlanticus* growth rates and sexual maturity estimates vary (Ault et al. 2008) and some tagged *M. atlanticus* may be smaller adult males, we also examined and reported movement data of all *M. atlanticus* with FLs >100 cm and <128.5 cm to

identify any individuals that were potentially mis-categorized. We reclassified larger individuals that were <128.5 cm as 'potential adults' if they exhibited distinct migratory behaviors with north–south seasonal movements and were >100 cm. In addition, if we observed a clear ontogenetic shift occur during an individual's tracking duration that also coincided with potentially reaching size of maturity, we reclassified subsequent detections as belonging to this new category. As demonstrated by Kurth et al. (2019) and Woodcock & Walther (2014), due to additional food requirements, late-stage subadults are expected to shift from estuarine-like habitats to coastal waters prior to joining spawning populations. Unless explicitly stated, all analyses specifically focused on adult *M. atlanticus* include this category of 'potential adult'.

We examined a variety of metrics at the month level for subadult and adult (including 'potential adult' category) *M. atlanticus* within the Florida Keys to describe individual movements. These metrics included individual mean number of detections at the receiver level, individual mean sum residence time (minutes) at the node level, individual mean sum distance traveled (km) at the node level, and ID count (i.e. number of unique individuals) across month at the Florida Keys array level. To calculate residence (minutes present) at the node level, we first summarized the detection data into events using the 'events' function via the 'glatos' package (Holbrook et al. 2020), and subsequently calculated the residence period for individuals within each event as the time difference between the event's first detection and its last detection. The function defines a new event occurring when an individual is detected at a different location (e.g. station, node, or array type) or if a certain user-defined time threshold is reached with no consecutive detections at the same location. Here, the 'events' function used nodes as the location and a threshold of 60 min.

The 'events' function was subsequently used to generate arrival and departure dates for individual *M. atlanticus* at the array level, i.e. entering or exiting the Florida Keys. Events were defined when consecutive *M. atlanticus* detections from an individual indicated that an *M. atlanticus* entered or left the Florida Keys or when 30 d passed with no new detections. To avoid generating artificial arrival dates (e.g. the arrival date as the tagging date), we eliminated all arrival events that occurred less than 30 d within their tagging date. Further, to reduce tagging biases surrounding departure timing, we eliminated departure events that occurred within 14 d of their tagging date. Since an individual detection log may contain

multiple arrivals and departures into or out of the Florida Keys throughout a given year or season, we derived cutoff periods to estimate the first arrival and the last departure event of a given season. Here, the constructed spring–summer season was defined as 1 March to 31 August and the fall–winter season as 1 September to 28 February. The dates surrounding the spring–summer season were aimed to capture the annual spawning migration by *M. atlanticus* to the Florida Keys, while the dates surrounding the fall–winter season were aimed to capture the post-northerly migration period or the overwintering phase of *M. atlanticus*. 'To' and 'from' movements between the nodes were summed and plotted to highlight areas of high use within the Florida Keys. The mean arrival and departure dates in the spring–summer season over all individuals were computed and plotted with 95% confidence intervals (CI). Further, to classify if an *M. atlanticus* visited or overwintered within the Florida Keys, we examined arrival and departure dates of individuals between December and February.

SST data were extracted at the daily level across the study through the NOAA ERDDAP server, Simons & Mendelssohn 2012; dataset ID: jplMURSST41) using the 'rerddap' (Chamberlain et al. 2019), 'xtrac-tomatic' (Mendelssohn 2018), and 'rerddapXtracto' (Mendelssohn 2019) packages. An average daily SST was extracted from an area that spanned all stations within the Florida Keys (latitude max. = 25.07°, latitude min. = 24.43°, longitude max. = −82.23°, longitude min. = −80.31°) and were subsequently assigned to corresponding *M. atlanticus* detections.

2.3.2. Time-to-event analysis for duration, arrival, and departures of *M. atlanticus* within the Florida Keys

Time-to-event analysis, also known as survival analysis (Miller 2011), was implemented for adult (including potential adult) *M. atlanticus* to examine (1) duration of time, here, estimated as the number of days *M. atlanticus* spent within the Florida Keys between first arrival and last departure dates, (2) when *M. atlanticus* first arrived in the Florida Keys, and (3) when *M. atlanticus* last departed the Florida Keys. These metrics were generated earlier from the 'events' function, and analyses were only applied for adults and for the spring–summer (1 March to 31 August) season, which corresponds with the annual tarpon spawning period and with their highest abundance. Since some *M. atlanticus* overwintered in the Florida Keys, their arrival date for the spring–sum-

mer season was adjusted accordingly to reflect this discrepancy. By examining abacus plots at the individual level, we identified which *M. atlanticus* individuals overwintered for an extended period directly prior to the spring–summer season and subsequently used their prior fall–winter arrival date. In addition, considering *M. atlanticus* are often not continuously detected within the Florida Keys, even with some individuals temporarily leaving the array, it should be noted that duration is estimated by taking the number of days between the first arrival and last departure date.

To compare arrival and departure time-to-event metrics across years, we used 1 September as a benchmark date for each season, i.e. in a given year, how many days since 1 September were logged until an arrival or departure event occurred. This day was chosen so that the arrival dates of individuals that overwintered prior to the spring–summer season could also be included. All analyses were plotted by year with median time-to-event displayed across all individuals. The median for each spring–summer/year combination (including the overwintering individuals) and its 95% CI were also extracted and converted to a month–day calendar day format. The 95% CIs were not reported for time-to-event analysis involving 2017 due to limited data. Time-to-event analyses were implemented using the 'survival' (Therneau & Lumley 2014) and 'survminer' (Kassambara et al. 2017) packages.

2.3.3. Behavioral consistency

To examine whether differences among adult individuals in phenology patterns were consistent across years, we first generated 5 separate metrics, including arrival ordinal date, arrival SST, departure ordinal date, departure SST, and duration (days from first arrival to last departure). Again, arrival dates were adjusted for individuals that overwintered directly prior to the spring–summer season (1 March to 31 August) and duration encapsulating the overall number of days within our study area, regardless of whether *M. atlanticus* temporarily left or were not detected. Subsequently, for fish with detections in >1 year, we estimated repeatability (R) (Rohlf & Sokal 1981, Lessells & Boag 1987) using linear mixed modeling (Dingemanse & Dochtermann 2013) with individual as a random effect. In total, 5 linear mixed models were constructed with each metric as a response variable and individual ID as the random effect alone. The estimation of R is the proportion of total variation in a behavior trait within and between indi-

viduals. An R of 1 indicates that an individual's observed behavior trait is consistent across all repeated measures. Conversely, an R value of 0 indicates that the behavior trait is completely random across repeated measures (Rohlf & Sokal 1981, Lessells & Boag 1987). Estimations for R and the statistical significance (likelihood ratio test) were computed with the 'lme4' package (Bates et al. 2015) and the 'rptR' package (Stoffel et al. 2017), and 95% CIs were derived from 1000 parametric bootstraps. Considering some individuals had only 2 years of observations and to decrease singular fitting when deriving 95% CI via parametric bootstraps, we performed these estimations on 2 separate samples: one containing individuals with >1 year of observations, and the other a subset containing individuals with >2 years of data.

2.3.4. Predicting *M. atlanticus* arrivals, departures, and occupancy patterns in the Florida Keys

Random forest, a type of machine learning algorithm, aims to optimize predictive accuracy while reducing variance and avoiding model overfitting (James et al. 2013, Hengl et al. 2018). Based on binary recursive partitioning, random forest increases model performance and reduces overfitting by constructing multiple data trees using randomly selected data and predictor subsets and building ensemble predictions (Breiman 2001). Here, we implemented random forest models to understand what best predicts the arrivals, departures, and daily occupancy of adult *M. atlanticus* within the Florida Keys. In total, we constructed 3 separate datasets for each random forest model: 1 for arrivals, 1 for departures, and 1 for daily occupancy. For the first 2 datasets, we derived arrivals and departures from the 'events' function; however, arrivals and departures to/from the Florida Keys were measured on a regular basis rather than first and last occurrence. As 2 separate datasets, they contained daily dates that spanned the first to the last event across all individuals (arrival or departure, respectively). Again, the same criteria for eliminating arrival or departure dates near the tagging period were applied. All dates of the new datasets were marked as either 'present' or 'absent', meaning if 1 or more *M. atlanticus* arrived or departed on that date it would be labeled as 'present', otherwise 'absent'. Subsequently, using these arrival/departure classifications as the response variables, we constructed 4 explanatory variables including month, SST, lunar cycle, and year. The lunar cycle of each date was computed using the 'lunar' package (Lazaridis 2014).

Lastly, the third separate dataset was constructed to examine daily occupancy. While duration reflected the time spent by individual *M. atlanticus* in the Florida Keys, here, daily occupancy highlights the numerical abundance of *M. atlanticus* on a given day. Rather than classification (present vs. absent), as was done for arrival and departure random forest models, daily occupancy was implemented using daily counts of *M. atlanticus*. Since tagging began in 2016, we only included daily counts from 2017 to 2020. If no *M. atlanticus* were detected during a given day within the Florida Keys, the daily count was listed as 0. Lastly, when predicting daily occupancy, this was constrained to the observed data set and provides a relative measure of abundance rather than an absolute measure.

All models were implemented using the 'mlr' (Bischl et al. 2016) and 'ranger' packages (Wright & Ziegler 2017) and interpreted using the 'iml' package (Molnar et al. 2018). For each random forest model (using 1000 trees), we first evaluated a series of hyperparameter values to determine which values led to the greatest overall model improvement (Lovelace et al. 2019). Based on inputs, our selected hyperparameters control how many predictors that can be used in each tree, the percentage of observations in each tree, and the minimum number of observations a terminal node within a tree should have (Probst et al. 2019). To find the optimal values for each final model, we ran a 5-fold cross-validation procedure with 50 hyperparameter combinations (250 models in total) (Lovelace et al. 2019, Probst et al. 2019). Since random forest models are designed to optimize predictive accuracy, classification models (arrival and departures) were biased in predicting the majority class (absences) compared to the minority classes (presences). To overcome this common issue associated with random forest and imbalanced datasets, we manually assigned model weights to each class by trial and error until sensitivity (true positive rate; accurately predicted presences) and specificity (true negative rate; accurately predicted absences) performance metrics were similar (Brownscombe et al. 2021). In addition to sensitivity and specificity, additional performance metrics (0 being poor performance and 1 being perfect performance) included overall accuracy, fall-out (false positive rate; inaccurately predicted presences), miss rate (false negative rate; inaccurately predicted absences), and precision (positive predictive value; accurately predicted presences to the total number of presences). For the regression-based random forest model (daily occupancy), we extracted the mean of absolute error, root mean square error, mean of square error, and coefficient of determination (R^2).

Subsequently, for each predictor in each model, we constructed partial dependency plots, using the 'pdp' package (Greenwell 2017), to evaluate their marginal effect on the predicted outcome, also known as ŷ (expected probability for arrival or departure events) or predicted (expected daily occupancy number of *M. atlanticus*). Year, as 1 of the 4 created explanatory variables, was not evaluated since it was included to control for variation across years rather than as an interpretable explanatory predictor. All 2-way interactions, except with year, were also assessed using partial dependency plots.

3. RESULTS

3.1. Descriptive statistics

After applying detection filters, we used 58 633 detections ranging from May 2016 to August 2020 for 57 *Megalops atlanticus* across 34 receiver nodes within the Florida Keys. The overall tracking duration for *M. atlanticus* ranged from 20 to 1500 d (633 ± 407 d [SD]) (Table S1). At tagging, 42 individuals were considered mature (≥128.5 cm FL) and 15 were considered immature (<128.5 cm FL). However, 4 large subadults (>100 cm FL) demonstrated distinctive migratory patterns as assessed by movement tracks and net squared displacement, and were re-classified as 'potential adults' (Table S1). In addition, 1 individual (ID 16678, 107 cm FL at tagging) shifted to a migratory pattern following the first year of monitoring (Figs. S3−S5), and subsequent detections from this fish were reclassified as a potential adult and was used in adult-only analyses. Thus, a total of 47 adult (including the 'potential adult' category) *M. atlanticus* detection profiles were analyzed.

The remaining 10 subadults (Figs. S6−S8) that were not reclassified as potential adults (excluding the 1 fish that exhibited an ontogenetic shift) exhibited high year-round residence periods, with 7 never being detected outside the Florida Keys (Fig. 1). Of the 3 that did disperse from the Florida Keys, ID 15889 (94 cm FL) moved to Tampa Bay in the winter and was subsequently detected in the Everglades in the fall. ID 15902 (114 cm FL) moved to Tampa Bay in early summer and was subsequently detected in the Florida Keys for the following year. Lastly, ID 16677 (107 cm FL), tagged in the lower Florida Keys, moved between the Florida Keys, rivers within the Everglades, and across northwest
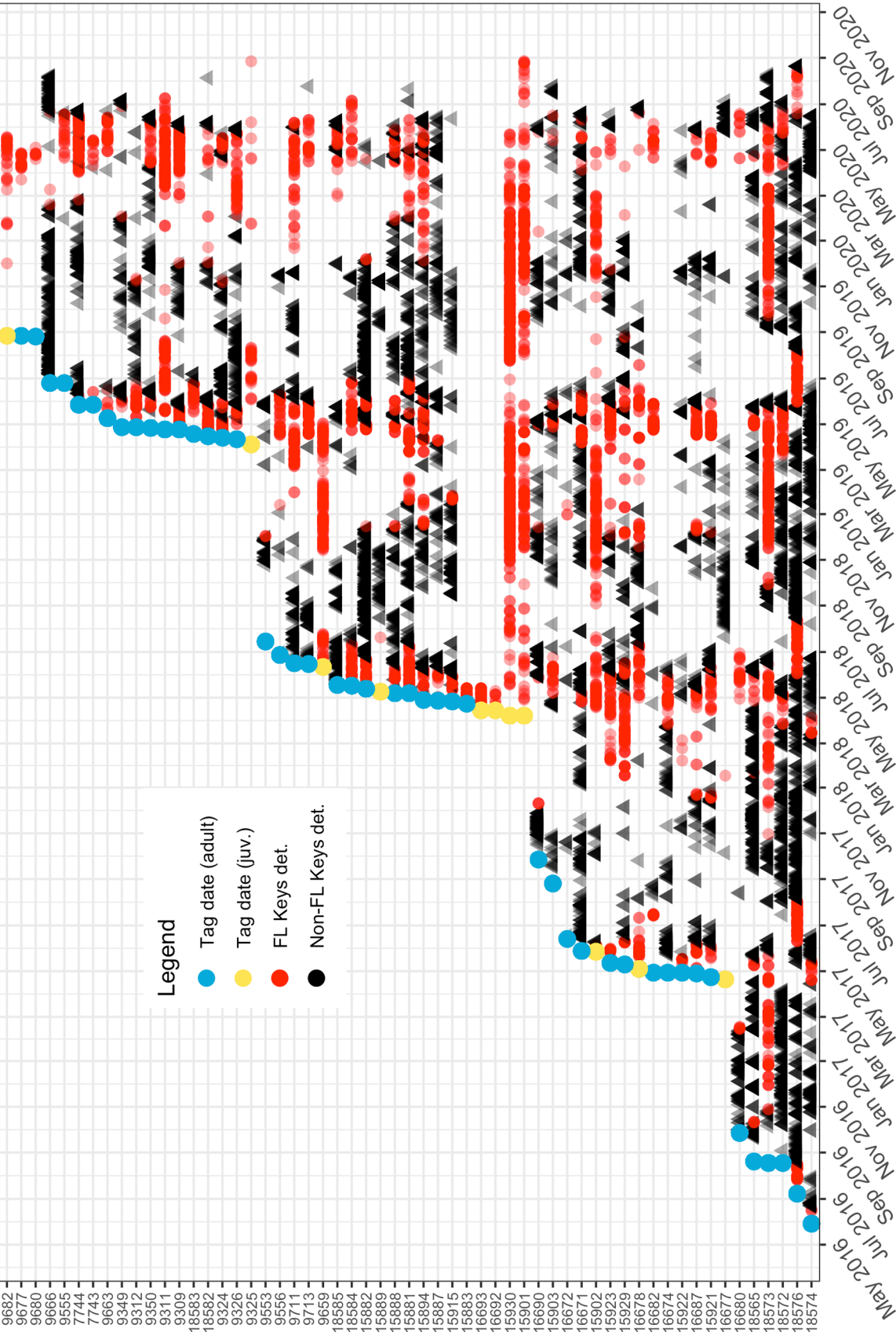
Fig. 1. Atlantic tarpon *Megalops atlanticus* IDs and their detections across time. The locations of detections, i.e. within vs. outside of the Florida Keys (FL Keys), are represented by semi-transparent red circles and black triangles, respectively. The capture dates are shown in blue or yellow, indicating whether the individual was deemed an adult (including potential adults/migrant subadults) or a subadult, respectively. ID 16678 was labeled as a subadult here due to the apparent ontogenetic shift occurring after the first year of tracking

Florida Bay. Of the *M. atlanticus* classified as subadults (now including the individual that exhibited an ontogenetic shift), 10 were tagged within the Florida Keys and 1 (ID 9682, 114 cm FL) was tagged near the Georgia/Florida state line (Table S1). While our criteria classified ID 9682 as a subadult, it is possible that this fish was a potential adult based on its size, distant/northern capture location, and limited detection history (i.e. Florida Keys between December and June). Of the *M. atlanticus* detected within the Florida Keys, the greatest number of subadult individuals were detected in the spring (April–June) (Fig. 2a), the individual mean number of detections were greatest in January, December, and March but lowest in June and July (Fig. 2b). Further, individual mean subadult residence time was greatest between November and February (Fig. 2c), with subadults traveling their greatest distances within the Florida Keys between March and May (Fig. 2d).

All detection profiles from adult *M. atlanticus* were seasonal residents with only 4 out of the 47 adults detected exclusively in the Florida Keys array (Fig. 1). However, these 4 individuals had substantial gaps in their detection histories and/or were limited by tracking duration. While the greatest number of individuals and detections for adult *M. atlanticus* were in the spring (April–June) (Fig. 2a), 27 of the 47 adult *M. atlanticus* were detected at least once within the Florida Keys during the winter months (December–February) (Fig. S9a). Individual mean number of detections for adult *M. atlanticus* were highest in April, May, July, and December and lowest in September, October, and November (Fig. 2b). Further, individual mean adult residence time was greatest in the spring months, March and April, followed by December (Fig. 2c), with adults traveling their greatest distances within the Florida Keys between April and August (Fig. 2d). The highest space use by adult tarpon occurred within shal-
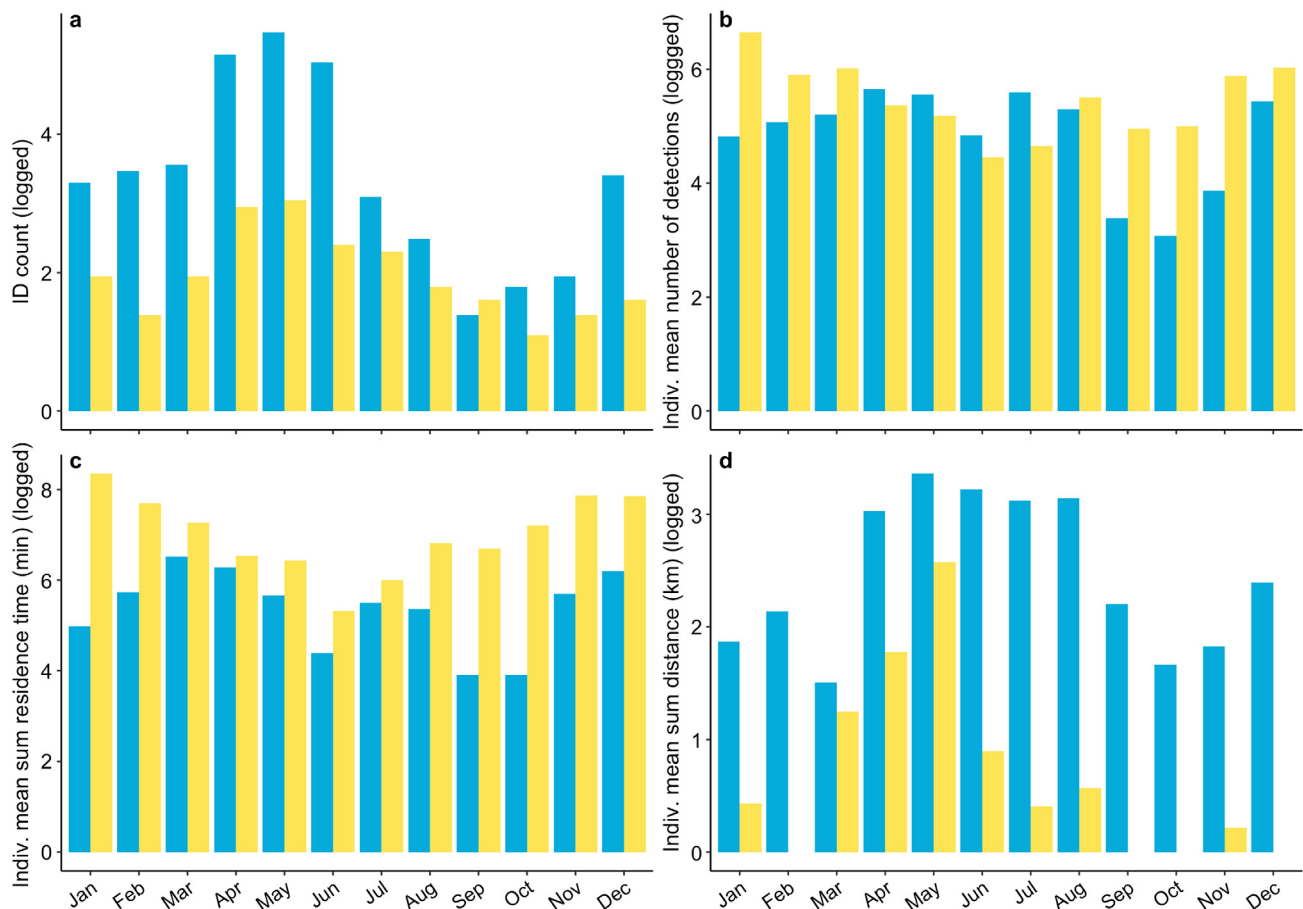

Fig. 2. Atlantic tarpon *Megalops atlanticus* space use metrics within the Florida Keys, including (a) sum ID count, (b) individual mean number of detections at the receiver level, (c) individual mean sum residence time (in minutes) across month at the node level, and (d) individual mean sum distance (km) across months at the node level. All values were logged (i.e. log-transformed), and blue and yellow bars indicate adults (including potential adults) and subadults, respectively

low water areas on the Atlantic side of the Florida Keys (Fig. 3).

For the spring–summer season (March–August) and with all individuals aggregated, the mean arrival/departure dates were 25 April (19 April–1 May, 95% CI) for arrivals and 6 June (1–12 June, 95% CI) for departures (Fig. 4). Across all adult detections and each season independently, *M. atlanticus* detections had a mean of 26.9°C in the spring, 30.4°C in the summer, 27.1°C in the fall, and 23.6°C in the winter (Fig. S9b)

3.2. Time-to-event analysis for duration, arrival, and departures

Using survival analysis to explore seasonal phenology, we subset the dataset by the spring–summer season and importantly included the arrival dates for individuals that arrived in earlier months (e.g. overwintering). Results indicated that *M. atlanticus* remained within the Florida Keys for a median of 40 d in 2017, 60 d (40–114 d, 95% CI) in 2018, 48 d (41–67 d, 95% CI) in 2019, and 56 d (44–73 d, 95% CI) in 2020 (Fig. 5, Table 1). The average median duration for all years combined was 51 d. Median arrival dates were 28 April in 2017 (no CI due to data limitation), 14 April (14 March–7 May, 95% CI, wide CI likely due to data limitation) in 2018, 17 April (12–27 April, 95% CI) in 2019, and 15 April (11–21 April,

95% CI) in 2020 (Table 1). Median departure dates were 31 May in 2017, 7 June (29 May–22 June, 95% CI) in 2018, 31 May (29 May–9 June, 95% CI) in 2019, and 5 June (29 May–14 June, 95% CI) in 2020 (Table 1).

3.3. Behavioral consistency

Repeatability estimates ranged from 0.16 to 0.55 and from 0.11 to 0.88 for individuals with more than 1 and 2 years of observations, respectively (Table 2). Other than differences in arrival SSTs, all R values across the 2 groups were significant, indicating that *M. atlanticus* exhibited repeatable phenology patterns from year to year. Specifically, R estimates for arrival dates (indicative of photoperiod, i.e. day length) and duration period were highest in both groups, i.e. individuals with >1 year of observations (n = 13, n = 11, respectively) vs. individuals with more than 2 years of observations (n = 13, n = 12, respectively) (Fig. 6).

3.4. Predicting *M. atlanticus* arrivals, departures, and occupancy patterns in the Florida Keys

For the arrival and departure random forest models, we modeled 131 arrival presences vs. 1131 arrival absences and 147 departure presences vs. 1290 de-
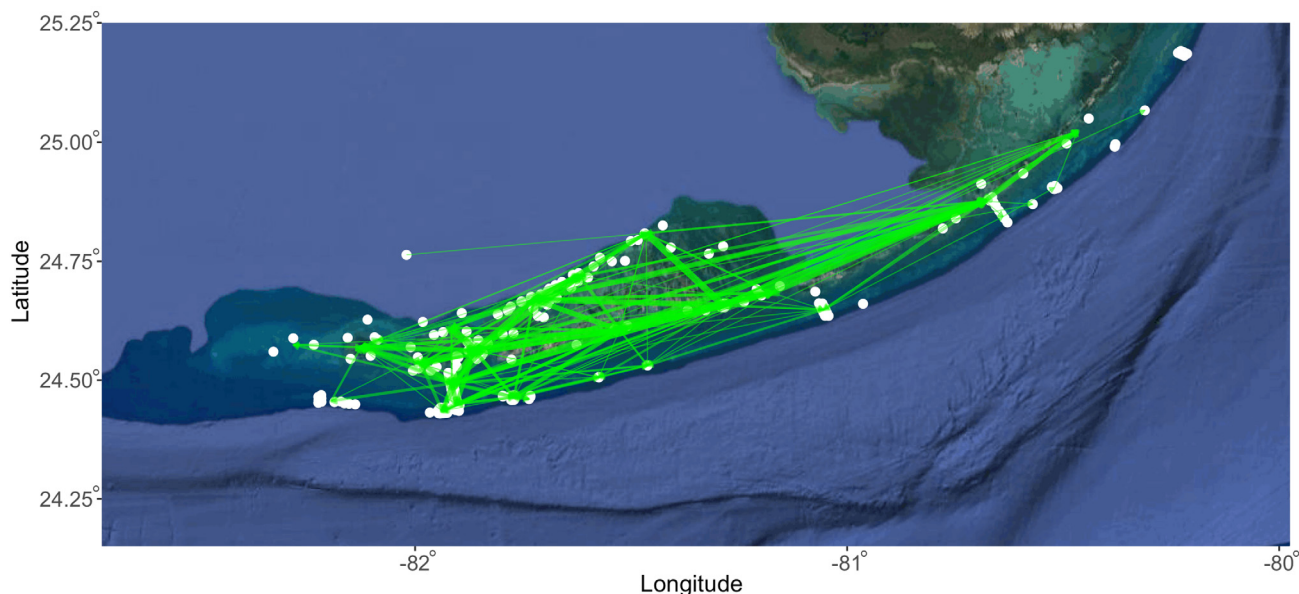

Fig. 3. Adult Atlantic tarpon *Megalops atlanticus* movement pathways across nodes highlighted in green across the Florida Keys (base map from Google Maps). Receivers (white dots) were grouped into nodes based on receiver proximity and by habitat characteristics. Thicker connections between nodes indicate a higher number of movements relative to thinner connections
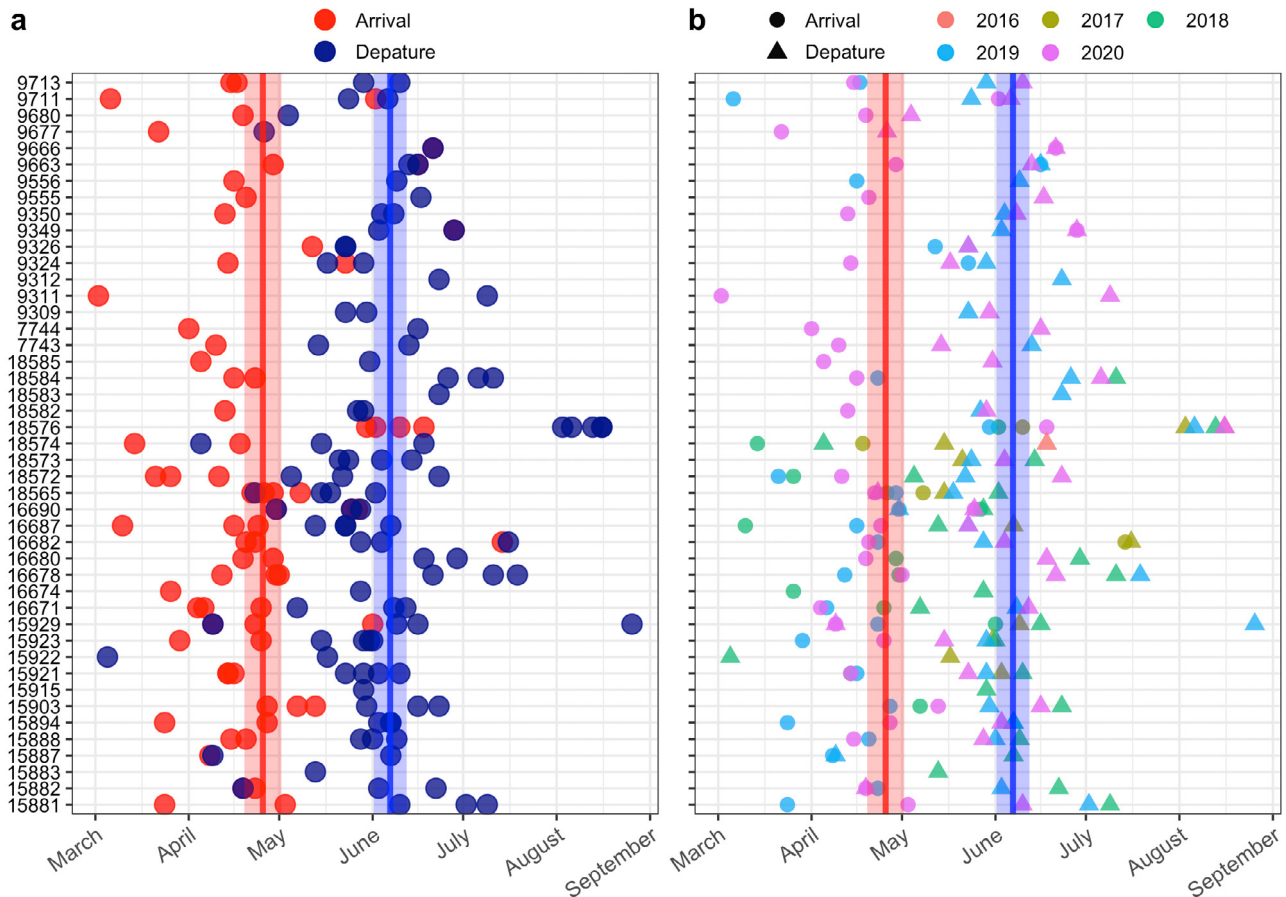
Fig. 4. Mean arrival and departure events and 95% confidence internals (shaded area) to and from the Florida Keys of tagged adult Atlantic tarpon *Megalops atlanticus* between 1 March and 31 August (spring–summer season). (a) All arrival (red dots) and departure (blue dots) events across years grouped; and (b) arrivals (circles) and departures (triangles) by year level as indicated by different colors. Each point represents the first arrival and last departure during the spring–summer season

parture absences. Accuracy for both models was 0.87, true positive and negative rates were between 0.88 and 0.87, false positive and negative rates were between 0.12 and 0.13, and precision for both models was 0.44 (Table 3a). Partial dependency plots for arrivals indicated that the ŷ values (probabilities) most notably began to increase during April when SSTs reach 26°C and continued into May and June when SSTs are less than 28°C (Fig. 7). Further, arrival events were likely to occur across all observed SSTs (22–25°C) in December (Fig. 7). The likelihood of departures began to also increase in April when SSTs reached 27°C and were greatest in May and June when SSTs were between 27 and 29°C (Fig. 8).

The performance metrics of the daily occupancy random forest model indicated a fairly accurate model with an R^2 value of 0.77 (Table 3b). The model inputs consisted of 569 days with no *M. atlanticus* detected, 376 days with 1 detected, 124 days with 2 detected, and 254 days with ≥3 (with a maximum of

17) *M. atlanticus* being detected. Partial dependency plots for daily occupancy indicated that most *M. atlanticus* were expected to be present starting in April when SSTs were ≥26°C. Further, *M. atlanticus* expected occurrence was greatest in May when temperatures reached 26–28°C and began to decrease in June with the lowest values between August and October (Fig. 9). For all 3 models, lunar cycle had little to no effect on tarpon arrival or departure timing, as well as on daily occupancy.

4. DISCUSSION

Using 4 yr of acoustic telemetry data, we examined subadult and adult Atlantic tarpon *Megalops atlanticus* phenology patterns within the Florida Keys. Of the 11 subadults, 7 were detected only within the Florida Keys, 3 were detected outside with far-ranging movements to Tampa Bay, Charlotte Harbor, the
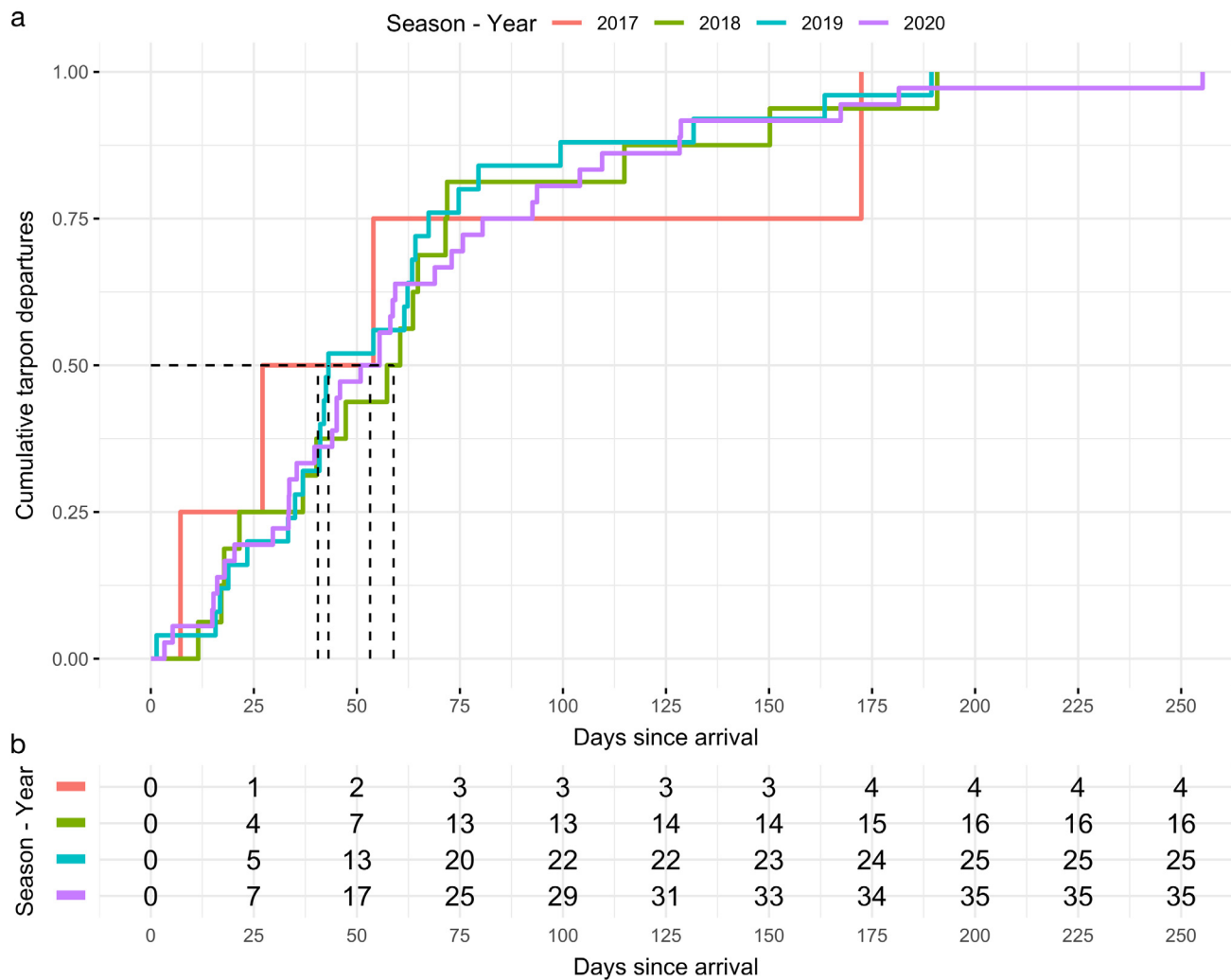
Fig. 5. Time-to-event analysis showing the time (days) that adult Atlantic tarpon *Megalops atlanticus* spent within the Florida Keys during the spring–summer season (1 March–31 August), including the arrival dates prior to the season if individual fish visited or overwintered within the Florida Keys. (a) Cumulative *M. atlanticus* departures (0–1) by days since arrival at the year level and medians displayed (dashed and color matching lines); (b) number of individuals vs. days since arrival at the year level

Everglades, and Florida Bay regions, and 1 appeared to undergo an ontogenetic shift, switching to adult-like migratory patterns. With some subadults traveling hundreds of kilometers, our results highlight individual-level differences in subadult residence and dispersal behaviors. While the extent was not captured and individuals were <100 cm FL, Duffing Romero et al. (2021) similarly documented variable subadult *M. atlanticus* (mean = 83.7 cm FL, range = 61–95 cm FL) residency behaviors in the US Virgin Islands. Regardless of whether subadult *M. atlanti-cus* dispersed or remained within the Florida Keys, these data highlight the potential functional importance of the region for recruitment and/or as developmental habitats. While the Florida Keys lack major sources of freshwater, marshes, and upper estuarine habitat, commonly identified as essential juvenile

Table 1. Time-to-event analysis results for Atlantic tarpon *Megalops atlanticus* arrival and departure dates to and from the Florida Keys during the spring–summer season (1 March–31 August), including the arrival dates prior to the season, if individual fish visited or overwintered within the Florida Keys. Median dates and 95% confidence intervals (CI) are displayed at the year level; NA: not applicable

Year	Event	Median date	Lower date (CI 95%)	Upper date (CI 95%)
2017	Arrival	28 April	NA	NA
2017	Departure	31 May	NA	NA
2018	Arrival	14 April	14 March	7 May
2018	Departure	7 June	29 May	22 June
2019	Arrival	17 April	12 April	27 April
2019	Departure	31 May	29 May	9 June
2020	Arrival	15 April	11 April	21 April
2020	Departure	5 June	29 May	14 June

Table 2. Repeatability (R) estimates with 95% confidence intervals (CI) for Atlantic tarpon *Megalops atlanticus* individuals with >1 year of observations (full dataset) and a subset of individuals with >2 years of observations (subset dataset). ID count indicates the number of individuals per dataset, and the p-value was derived from the likelihood ratio test (no symbol: p = 0.1–1.0; ***p < 0.001). SST: sea surface temperature

Metric	Dataset	ID count	R	Lower R (CI 95%)	Upper R (CI 95%)	p
Arrival date	Full	25	0.48	0.16	0.71	***
Arrival SST	Full	25	0.16	0.00	0.44	
Departure date	Full	32	0.43	0.16	0.62	***
Departure SST	Full	32	0.36	0.10	0.57	***
Spring–summer duration	Full	25	0.55	0.26	0.75	***
Arrival date	Subset	12	0.88	0.68	0.95	***
Arrival SST	Subset	12	0.11	0.00	0.45	
Departure date	Subset	18	0.48	0.15	0.68	***
Departure SST	Subset	18	0.46	0.13	0.67	***
Spring–summer duration	Subset	12	0.64	0.29	0.81	***

habitat for early-stage *M. atlanticus* juveniles (Kurth et al. 2019, Wilson et al. 2019), it has been reported that *M. atlanticus* can recruit to marine/ hypersaline waters as well (Brown & Severin 2008, Rohtla & Vetemaa 2016). Alternatively, our data may highlight when sub-adult *M. atlanticus* move from proximal estuarine habitats (e.g. the Everglades) to coastal habitats for either increased foraging opportunities or to eventually join adult populations (Woodcock & Walther 2014, Seeley & Walther 2018, Kurth et al. 2019, Navarro-Martínez et al. 2020).

Conversely, all adult *M. atlanticus* exhibited seasonal residency to the Florida Keys, with the majority arriv-
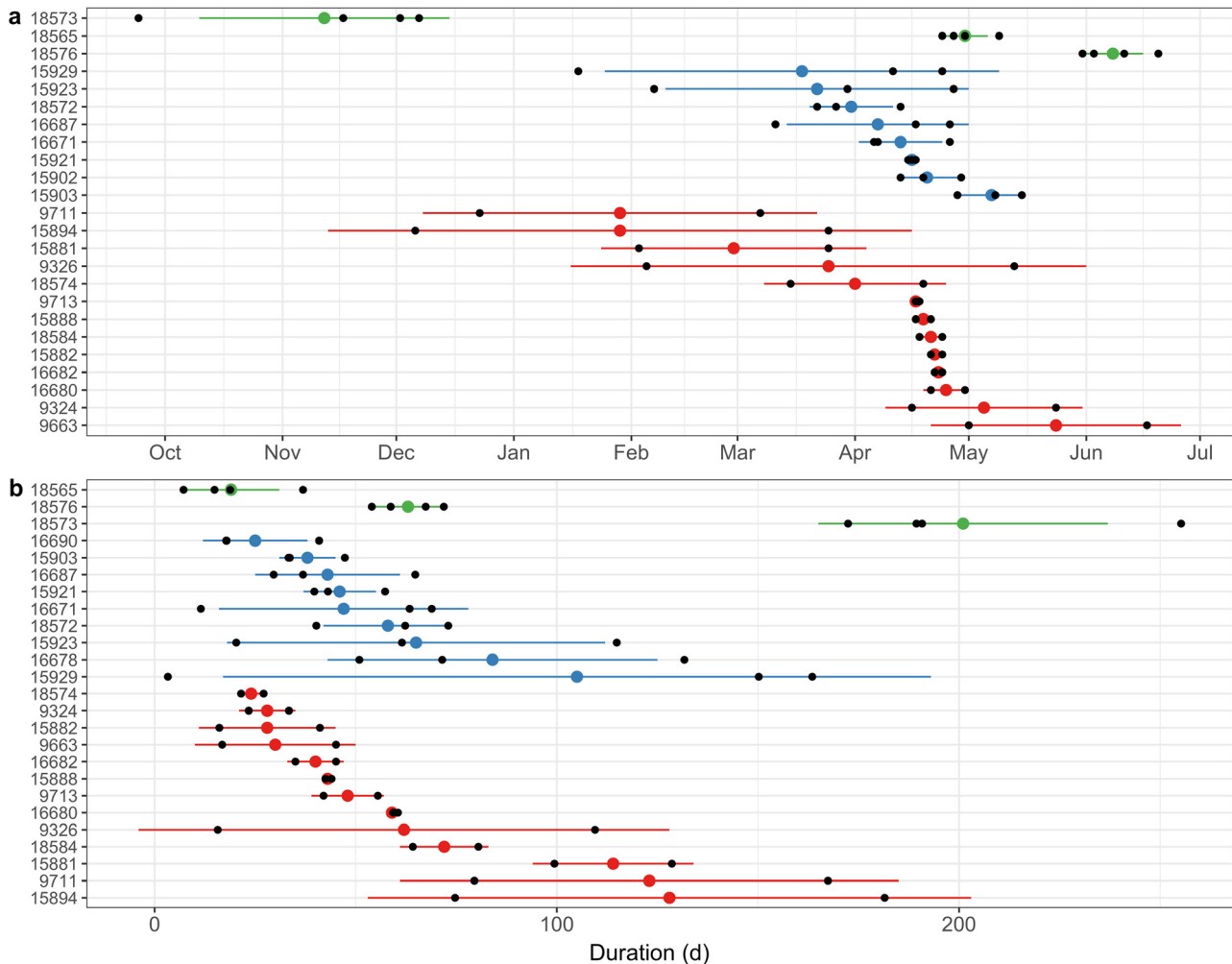

Fig. 6. Repeatability of tarpon arrivals and duration. The mean and standard deviation of (a) the first arrival ordinal dates and (b) duration (using the first arrival and last departure) is shown for each adult Atlantic tarpon *Megalops atlanticus* ID with multiple years of tracking data as indicated by color. Black dots show the observed arrival dates or duration, respectively, for each *M. atlanticus*

Table 3. Performance metrics from random forest models that classified (a) Atlantic tarpon *Megalops atlanticus* arrival and departure events and (b) daily *M. atlanticus* occupancy counts within the Florida Keys

(a) Event	Accuracy	Sensitivity (true positive rate)	Specificity (true negative rate)	Fall-out (false positive rate)	Miss rate (false negative rate)	Precision (positive predictive value)
Arrival	0.87	0.88	0.87	0.13	0.12	0.44
Departure	0.87	0.87	0.87	0.13	0.13	0.44

(b) Event	Mean of absolute errors	Root mean squared error	Mean of squared errors	Coefficient of determination (R^2)
Occupancy	0.76	1.14	1.31	0.77

ing in late April and departing in late May or early June (approximately 50 d of residency). While partial migration may occur within *M. atlanticus* populations (as suggested by Luo et al. 2020), our data provided no evidence for year-round adult residents in the Florida Keys. Overall, across all individuals and at the population level, our models that examined arrival/departures on a regular basis (rather than their first and last seasonal occurrence) indicated that *M. atlanticus* arrival/departure timing and occupancy were closely connected to time of year (month) and SST. Again, at the population level, *M. atlanticus* were most likely to arrive in April when SSTs were between 26 and 28°C and depart in May–June when SSTs were between 27 and 29°C. Consistent with arrivals and departures, occupancy increased in April, was greatest in May, and began to decrease in June as SST increased. Occupancy across all individuals was lowest from mid-summer and into the fall.

M. atlanticus anglers in the GOM and southeastern USA have long recognized the potential relationship between SST and the presence of *M. atlanticus* (Babcock 1951, Mill et al. 2010, White & Brennen 2010, Spotte 2016). Indeed, isotherms of approximately 26°C have been linked to the onset of spring and fall *M. atlanticus* migrations (Luo & Ault 2012, Luo et al. 2020). In support of these studies, we found that *M. atlanticus* were, overall, most likely to arrive in the Florida Keys as temperatures reached and exceeded 26°C in the spring. However, at the individual level, when examining the annual repeatability of each individual's first arrival and last departure to the region, we found that *M. atlanticus* consistently arrived at similar dates and remained within the Florida Keys for approximately the same duration from year to year. This result highlights that embedded within the population are a diversity of individual-level consistent movement strategies even with most *M. atlanticus* arriving to the Florida Keys just prior to putative spawning events but with

others arriving months earlier. Similarly, Tibblin et al. (2016) reported that while individual northern pike *Esox lucius* underwent repeatable breeding migrations, the arrival timing among individuals was significantly different from one another.

In this study, when examining the repeatability at the individual level, all measured metrics were significantly repeatable, except for arrival SSTs. Further, departure SSTs had the second lowest repeatability scores. While temperature was important in helping to characterize tarpon arrivals and departures at the population level, these analyses at the individual level suggested that the repeatable patterns in migration phenology surrounding the Florida Keys were more linked to photoperiod (i.e. daylength) than temperature. Photoperiod, indicative of time of year, has been shown to stimulate changes in endocrine systems that can act as a strong cue for migration and reproduction in fish (Baggerman 1962, Peter & Crim 1979, Cowan et al. 2017), as well as in other taxa (Bradshaw & Holzapfel 2007, Bauer et al. 2011). In other long-lived iteroparous fish species, photoperiod has been linked as a repeatable and potential cue for the spawning and migration timing for lake sturgeon *Acipenser fulvescens* (Forsythe et al. 2012) and Arctic char *Salvelinus alpinus* (Jensen et al. 2012, 2020). Considering the wide distribution of *M. atlanticus*, relying on photoperiod at the individual level, rather than on temperature, may help facilitate their collective arrival for spawning when traveling from different and distant locations. Specifically, photoperiod may have been selected for, to ensure that an individual's seasonal phenology coincides with the formation of nearshore pre-spawning aggregations prior to moving hundreds of kilometers offshore to spawn during new/full moons (Crabtree 1995, Luo et al. 2020).

While individual-level arrival dates and durations for *M. atlanticus* were highly repeatable among years and indicative of photoperiod, they were also likely
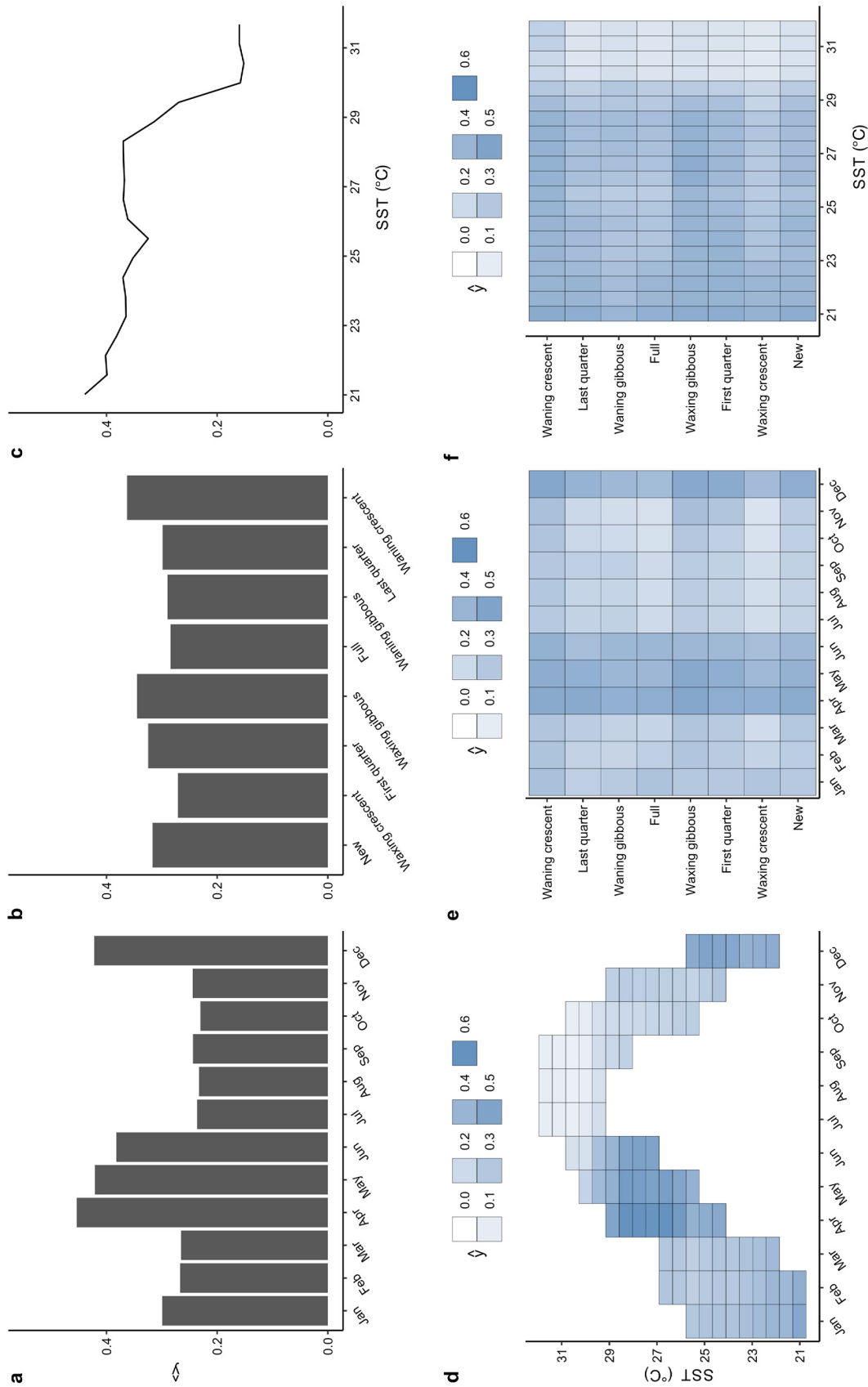
Fig. 7. Random forest partial dependency output plots highlighting relationships between environmental variables and arrival timing of adult Atlantic tarpon *Megalops atlanticus* within the Florida Keys. Probabilities (ŷ) of *M. atlanticus* departing with predictors (a) month, (b) lunar cycle, (c) sea surface temperature (SST), (d) SST and month, (e) lunar cycle and month, and (f) lunar cycle and SST
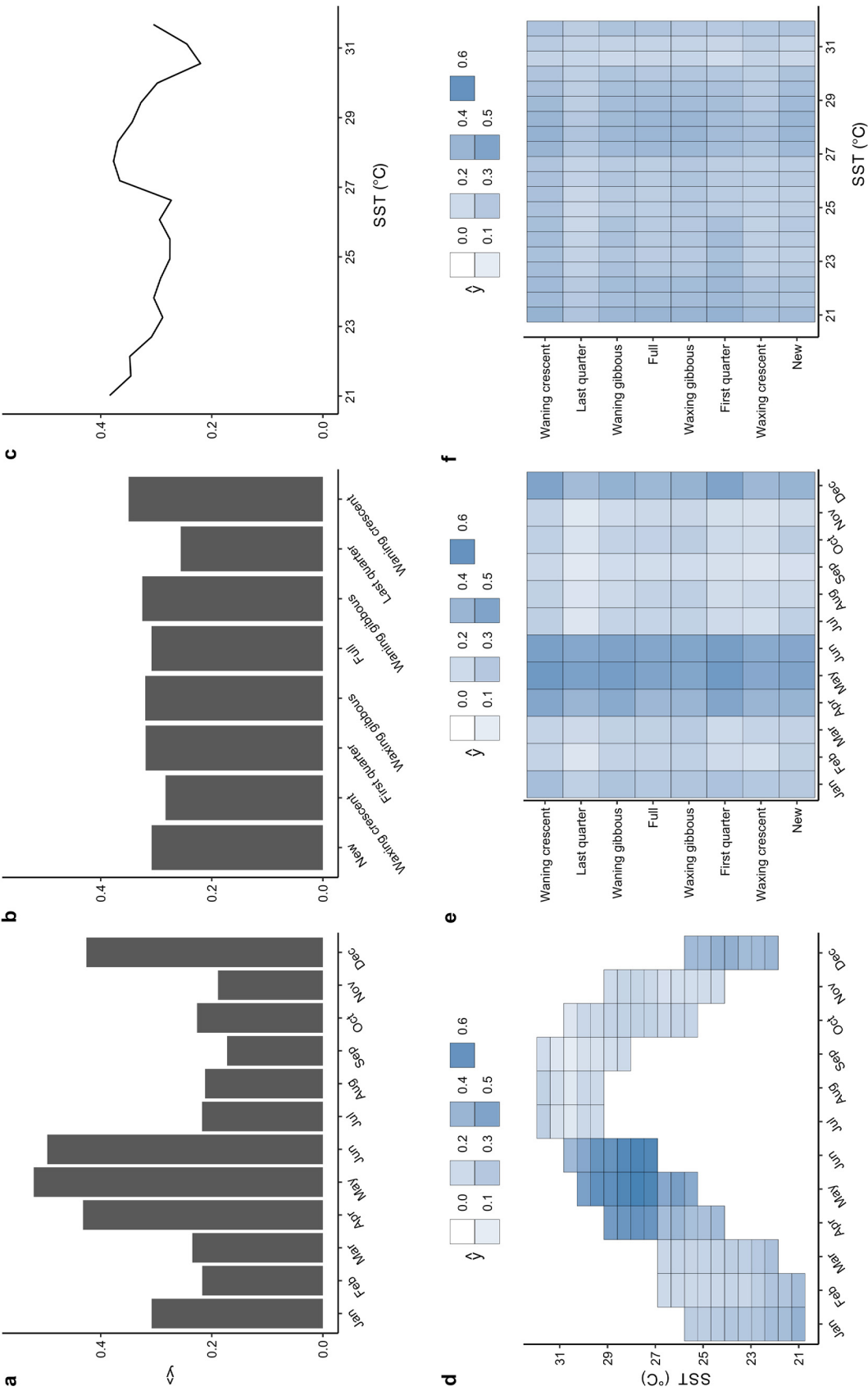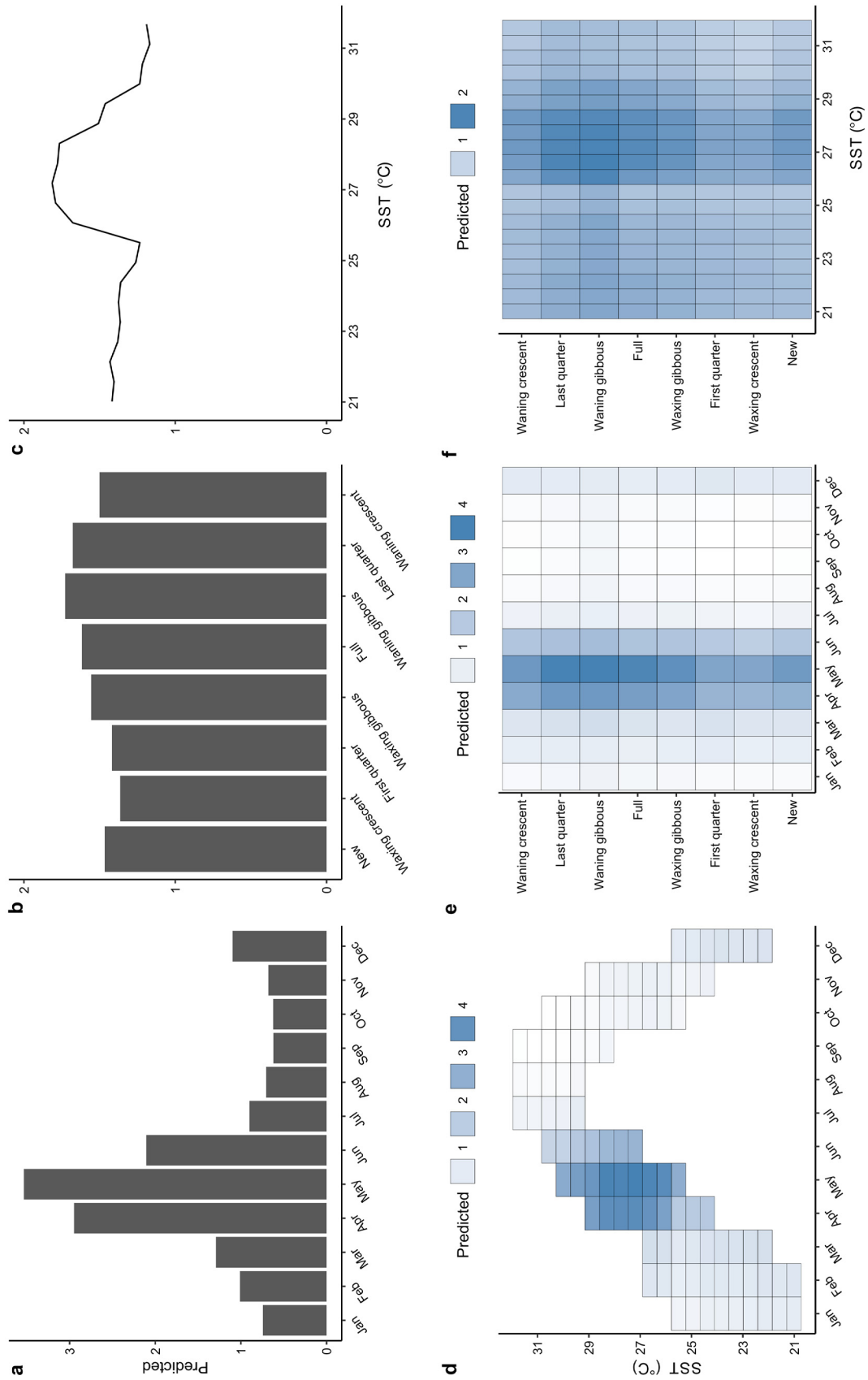
Fig. 8. As in Fig. 7, but for departure timing

Fig. 9. As in Fig. 7, but for daily occupancy counts. Plots show predicted counts

driven by a combination of additional external stimuli (e.g. wind direction and persistence, temperature) to some extent as reflected by the observed variation from year to year (Lower Keys Guide Association pers. comm.). Most research on the phenology of fish migration and individual-level repeatability has been on freshwater and anadromous species (Brodersen et al. 2012, Forsythe et al. 2012, Tibblin et al. 2016, Eldøy et al. 2019, Jensen et al. 2020), rather than purely marine fishes (but see Thorsteinsson et al. 2012). Ultimately, understanding trait repeatability of ecologically important events in wild fish, such as spawning migration timing, should help to inform and forecast the effects of environmental change (e.g. climate change) on fishes and their capacity to adapt to disturbance (Killen et al. 2016).

Geographically, the Florida Keys represent the most southern contiguous piece of shallow-water habitats in the southeastern USA. Many *M. atlanticus* migrate to this remote area and remain through the spring for an extended period of time and subsequently migrate sometimes many hundreds of kilometers away (Griffin et al. 2018, Luo et al. 2020), which implies that these habitats may be functionally important for specific *M. atlanticus* life history stages and strategies. Given the absence of abundant prey sources compared to higher-latitude estuarine systems (Pikitch et al. 2014), it is unlikely that *M. atlanticus* migrate to the Florida Keys in the spring for foraging purposes but rather to form the pre-spawning aggregations that subsequently move offshore for spawning activities (Crabtree 1995, Crabtree et al. 1997, Luo et al. 2020). Consistent with this suggestion, using stable isotope analysis with *M. atlanticus* eye lenses, Kurth et al. (2019) observed consistent basal-resource dependence within individual *M. atlanticus* and speculated that feeding in the spring and early summer was most likely associated with gonadal growth and increased metabolism during migrations rather than that of growth occurring in the late summer and fall.

Within Florida, including other pre-spawning aggregation locations (e.g. Boca Grande), spawning periods are likely to occur a few days to a week around a new or full moon (Crabtree 1995, Shenker et al. 2002, Luo & Ault 2012, Luo et al. 2020); hence, it would be appropriate to expect higher departure probabilities around new or full moons in the months of April, May, or June. However, this lack of signal and in combination with the lower repeatability estimates for departure dates suggests that *M. atlanticus* may begin to gradually move towards and aggregate near the Florida Reef Tract prior to spawning in the

Florida Straits (Luo et al. 2020). While the formation of aggregations has been reported as absent in recent years for unknown reasons, in agreement, local fishing guides have noted large aggregations of *M. atlanticus* in proximity to the Florida Reef Tract (T. Holeman & B. Holeman pers. comm.). Further, considering that Florida Keys anglers in the spring occasionally note large schools of *M. atlanticus* quickly moving away from nearshore deeper channels and towards offshore areas, additional research (e.g. increased receiver coverage) is warranted in the area to examine fine-scale spawning-related movements (Lowerre-Barbieri et al. 2021). Ultimately, *M. atlanticus* departures may be difficult to capture if *M. atlanticus* spawn twice or display more indiscriminate 'wandering' tendencies (either within nearshore or offshore waters) than direct non-random spawning-oriented movements. Indeed, fishing guides have also reported *M. atlanticus* far offshore beyond the Florida Reef Tract in large numbers (T. Holeman & B. Holeman pers. comm.), further complicating our understanding of tarpon spawning behaviors.

Lastly, departures may also be linked to broader and more complex climatic and oceanographic processes (e.g. Loop Current and Florida Current) that, in turn, drive the formation of variable and seasonal mesoscale eddies and tidal bores in the Florida Keys/Florida Strait (Lee et al. 1995, D'Alessandro et al. 2007). While these patterns have been linked as dispersal and larval settlement mechanisms for reef fishes in the Florida Keys (D'Alessandro et al. 2007), they may also, in part, help to explain *M. atlanticus* spawning behaviors.

Within Florida, *M. atlanticus* angling is catch-and-release only; however, they can be susceptible to depredation and post-release mortality due to predation or physiological exhaustion (Guindon 2011, Hammerschlag et al. 2012, Luo et al. 2020). Thus, catch-and-release as a management practice alone may not be enough to meet conservation endpoints for this species, especially if individuals are removed from the population prior to moving offshore to spawn. Based on our findings, this fishery relies on the same adult individuals each year, and the loss of highly fecund females that have yet to spawn could prove detrimental at the population level over time (Adams et al. 2014). Considering that *M. atlanticus* population connectivity is mediated through both the movement of individuals and larval dispersal via currents (E. Wallace et al. unpublished), protecting mature fish from depredation (Griffin et al. in press) and post-release mortality (Guindon 2011, Hammerschlag et al. 2012, Luo et al. 2020) in these areas should

help to maintain population connectivity across the southeastern USA and the GOM, where similar catch-and-release fisheries are expanding. In addition to increased efforts to protect adults surrounding the spawning season (e.g. gear and angling modifications, education, temporary closures), conservation measures should be implemented to mitigate local and regional habitat degradation and water quality issues (e.g. altered freshwater flows, pollution, and habitat loss; see Brownscombe et al. 2019a) that further threaten subadult and adult seasonal habitats (Adams et al. 2014). Lastly, with no formal stock assessment, this fishery remains data poor and lacks information on estimates of size structure and mortality and trends in fishery performance (e.g. catch rates). Future management strategies should incorporate and address tangential effects including depredation, post-release mortality, and changes in fishing effort that interact with habitat- and water quality-related challenges. This is especially important as the human population of, and tourism in, the Florida Keys continues to grow, with concomitant increase in the above-mentioned threats. Thus, new management strategies that incorporate these dynamics, as informed by this and similar studies, are essential.

5. CONCLUSION

The Florida Keys represent critical habitat for subadult and adult *Megalops atlanticus* life history stages. The occupancy of adult *M. atlanticus* in the Florida Keys appears to be intrinsically linked with pre-spawning activities, first aggregating in near-shore waters and subsequently moving offshore to spawn. Overall, at the population level and coinciding with their spawning season, the combination of SST and time of year were the strongest predictors of their phenology. However, at the individual level, we demonstrate adult *M. atlanticus* displayed consistent and repeatable migration patterns and suggest that photoperiod is an important migratory cue. Ultimately, considering that these habitats are functionally important for multiple *M. atlanticus* life stages, we suggest management to promote habitat protection at both the local level (e.g. wastewater runoff mitigation) and regional level (e.g. Florida Bay/the Everglades water flow regime restoration). Further, since the fishery relies on the same individuals from year to year, it is essential to develop and apply education or policy (gear use/time area closures) strategies to mitigate post-release mortality and depredation events. Given that the Florida Keys are linked

with subadult life history phases and pre-spawning activities, habitat protection and reducing angling-related mortality will be imperative for the fishery and for the population to persist.

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