


RESEARCH ARTICLE

Seascape heterogeneity and predictability drive movement strategy selection in estuarine predators

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Abstract

1. Animal movement strategies, or suites of correlated traits reflecting how individuals respond to their environment, are often shaped by spatiotemporal heterogeneity and predictability in physicochemical conditions, resources or risk.
2. While movement strategies have been well studied in terrestrial animals using high-resolution satellite telemetry, our understanding of how seascape heterogeneity influences movement strategies in aquatic systems remains limited due to technological constraints.
3. We used a non-gridded passive acoustic telemetry array to identify and classify movement strategies of Common Snook (*Centropomus undecimalis*) and Atlantic Tarpon (*Megalops atlanticus*) within two estuarine systems in Everglades National Park, Florida. We then evaluated how seasonal heterogeneity and environmental predictability influenced movement strategy selection.
4. Using a suite of movement metrics, we identified three statistically distinct movement strategies that varied in movement frequency, home range size and site fidelity. Fish in more homogeneous environments tended to adopt strategies involving frequent movements, larger home ranges and shorter stays in a given location. In contrast, increased seascape heterogeneity was associated with movement strategies characterized by less frequent movements, smaller home ranges and longer residence times. We also found species-level differences in strategy use, with the predictability of dissolved oxygen, salinity and turbidity emerging as key environmental drivers of movement strategy selection.
5. These results demonstrate that seascape heterogeneity and predictability strongly influence the emergence and selection of movement strategies in estuarine predators. Our findings provide a novel approach for identifying movement strategies in aquatic systems using passive acoustic telemetry and highlight the broader importance of seascape complexity in shaping animal behaviour and predicting responses to environmental change.

KEYWORDS

environmental predictability, estuarine predators, movement ecology, movement strategies, passive acoustic telemetry, seascape ecology, seascape heterogeneity

1 | INTRODUCTION

Movement is a universal trait of living organisms that enables them to respond to environmental variability. By moving, individuals can track the distribution of resources, avoid competition or risk and engage in social interactions (Armansin et al., 2020; Nathan et al., 2022). Environmental heterogeneity and predictability, or the spatial variability and temporal constancy of environmental conditions, shape these movements, giving rise to distinct, repeatable movement strategies (Colwell, 1974; Mueller & Fagan, 2008; Nathan et al., 2008; Riotte-Lambert & Matthiopoulos, 2020). Depending on how individuals perceive and respond to environmental cues, strategies can vary from localized residency to wide-ranging nomadism (Abrahms et al., 2017; Spiegel et al., 2017).

Residency tends to be favoured when resources are predictable and spatially structured at fine scales, whereas nomadic or transient movements emerge when resources are unpredictable or vary across broad scales (Fagan et al., 2013; Teitelbaum & Mueller, 2019). For instance, Mongolian Gazelles (*Procapra gutturosa*), often considered the world's most nomadic species, roam extensively across the homogeneous Eastern Steppe in response to unpredictable forage (Olson et al., 2010). In contrast, many White Storks (*Ciconia ciconia*) in the Iberian Peninsula have shifted from historical seasonal migration to residency, exploiting predictable food subsidies from human landfills (Gilbert et al., 2016). These cases highlight how both natural environmental structure and rapid human-driven changes can shape animal movement strategies.

Because movement influences ecological processes such as habitat connectivity, population dynamics, species interactions and even ecosystem function, understanding the relationships between movement strategies and landscape configuration is critical for predicting ecological responses and guiding management (Allen & Singh, 2016; Doherty et al., 2021; Nathan et al., 2008). While much of this work has been conducted in terrestrial systems supported by satellite telemetry and remote sensing (Kays et al., 2015), similar advances in aquatic systems have lagged due to technological constraints and the dynamic nature of seascapes (Hussey et al., 2015). However, recent advancements in aquatic acoustic telemetry technology now allow finer scale aquatic movement analyses and have enabled researchers to quantify increasingly intricate species-habitat relationships, though trade-offs remain between spatial coverage and resolution (Baktoft et al., 2017; Whoriskey et al., 2022). Here, we use passive acoustic telemetry to examine how physicochemical heterogeneity and predictability influence movement strategy selection in two estuarine mesoconsumers.

Globally, estuaries worldwide are undergoing rapid change, particularly due to altered freshwater flow regimes (Chilton et al., 2021). These alterations modify seascape heterogeneity and predictability

(Barbier et al., 2011; Blaber, 2013; Stein et al., 2021). In Florida Bay, USA, historic modifications to the Everglades hydrology have reduced freshwater inflows, with some regions, such as northcentral Florida Bay, now receiving only a quarter of historic levels (Marshall et al., 2014). This reduction has elevated salinities in the region and contributed to mass seagrass die-off events as well as reshaped nekton assemblages (Fredley et al., 2019; Flaherty et al., 2013; Hall et al., 2016; Lee et al., 2016). Yet, despite these changes, the movement responses of estuarine mesoconsumers remain poorly understood.

Here, we focus on Common Snook (*Centropomus undecimalis*, hereafter Snook) and subadult Atlantic Tarpon (*Megalops atlanticus*, hereafter Tarpon), two estuarine-dependent predators with overlapping diets but contrasting physiological tolerances (Kurth et al., 2019; Santos et al., 2025). Tarpon tolerate hypoxic conditions by breathing atmospheric air and often exploit oxygen-poor habitats (Geiger et al., 2000), whereas Snook generally avoid them (Peterson & Gilmore, 1991). This contrast makes the two species ideal for testing how environmental heterogeneity and predictability interact with species traits to influence movement strategies.

Our objectives were as follows: (1) classify distinct movement strategies of Snook and Tarpon using non-gridded passive acoustic telemetry, (2) test how spatiotemporal heterogeneity in physicochemical conditions influences movement strategy selection, and (3) evaluate whether the predictability of specific physicochemical conditions drives interspecific differences. We hypothesize that Snook and Tarpon will exhibit movement consistent with terrestrial resource-tracking studies (i.e. Mueller & Fagan, 2008; Riotte-Lambert & Matthiopoulos, 2020). Specifically, when physicochemical conditions are largely similar across a system (broad-scale heterogeneity), prey distributions should be less predictable, promoting increased transient movements from Snook and Tarpon. Conversely, when fine-scale heterogeneity in physicochemical conditions creates spatially structured habitats, prey distributions may be more predictable, allowing individuals to remain in profitable areas while reducing energetic costs, favouring residency movement (Bastille-Rousseau et al., 2024; Charnov, 1976; Riotte-Lambert & Matthiopoulos, 2020).

We further predict that salinity will be a key driver of strategy selection given its strong influence on estuarine fish communities (Feyrer et al., 2015; Mahoney et al., 2021) and the hypersaline conditions not untypical of our study region (Kiflai et al., 2022). Periods of constant salinity within a system should promote broader, transient movements, whereas variable or unpredictable salinities are expected to reduce within-system movement and favour residency. Finally, we expect interspecific differences in response to dissolved oxygen predictability due to physiological tolerances. Tarpon should increase movement under high dissolved oxygen variability, potentially to exploit oxygen gradients for foraging, while Snook should

reduce movement to avoid the stress of fluctuating or low-oxygen habitats.

2 | MATERIALS AND METHODS

2.1 | Study system

Within Everglades National Park, along the north-central rim of Florida Bay, lie two parallel estuarine lake-chain systems: the Alligator and McCormick (25.181664°N, -80.764714°W). This region has been significantly impacted by the development of South Florida, leading to frequent hypersaline conditions and increased saltwater intrusion from chronic deficits in freshwater inflow (Kiflai et al., 2022; Lee et al., 2006; Price et al., 2019). Each system has a single creek connecting its lakes and a single exit to a southern embayment within Florida Bay (Figure 1). North-to-south environmental gradients exist within both systems, with the northernmost inland

lakes being brackish and the southern bays marine. Additionally, differences in geography result in west-to-east environmental gradients between the systems (Kiflai et al., 2022).

The Alligator System to the west receives less freshwater inflow and has reduced hydrologic connectivity with Florida Bay, resulting in higher, seasonally hypersaline conditions, elevated nutrient concentrations, frequent algal blooms, increased water turbidity and less diverse submerged aquatic vegetation (SAV) cover (Table 3; Eggenberger et al., 2019; Frankovich et al., 2012, 2017; Kiflai et al., 2022). Water residence times in the Alligator System are around 6 months (Price & Frankovich, 2021). In contrast, the McCormick Creek System to the east, with greater freshwater inflow and increased connectivity with Florida Bay, has shorter water residence times of about 4 months (Price & Frankovich, 2021). It features better water quality (i.e. lower nutrients and salinity, and reduced turbidity) and a more diverse SAV community (Frankovich et al., 2012, 2017; Kiflai et al., 2022). Consequently, the Alligator System is generally a more heterogeneous seascape with stronger north-south

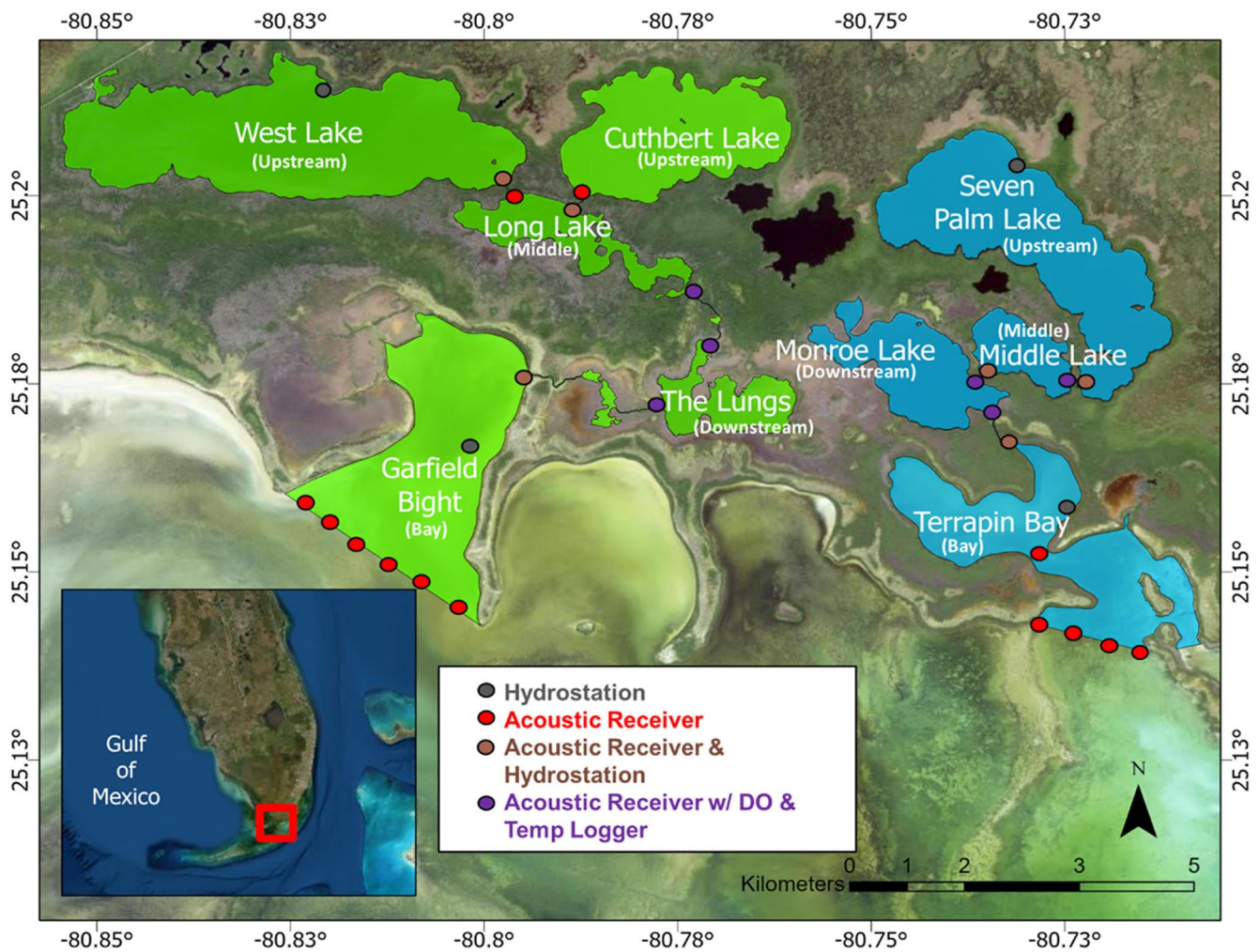


FIGURE 1 The Coastal Everglades Lakes Acoustic Array (CELA²) is located within Northcentral Florida Bay within Everglades National Park. The array consisting of 40 VR2W INNOVASEA acoustic receivers was designed to track Snook and Tarpon movements between the lakes and bays of the Alligator (green) and McCormick (blue) systems. The hydrostations and dissolved oxygen (DO) and temperature loggers were used to construct seasonal biophysical seascapes from July 2016 to April 2021.

physicochemical gradients (Table 3; Eggenberger et al., 2019; Linenfelter et al., 2023). However, seascape heterogeneity varies seasonally in both systems, providing ideal natural settings to study the effects of seascape heterogeneity on predatory fish movement strategy selection.

The seasonality of the Everglades, primarily driven by precipitation and temperature, causes salinity variations in Florida Bay and the coastal Everglades (Abiy et al., 2019; Kelble et al., 2007; Price et al., 2019). We use the average seasonal salinity trends of the Alligator and McCormick Systems as the primary seasonal indicator (Figure S1), defining quarter seasons (hereafter referred to as seasons) as the temporal window for analysing movement strategies and seascape heterogeneity. Within both systems, January to March is early dry season, April to June is late dry season, July to September is early wet season and October to December is late wet season (Figure S1).

2.2 | Study species

Snook are subtropical, euryhaline mesopredators that inhabit freshwater, estuarine and marine systems from Florida to Brazil (Blewett et al., 2006; Boucek et al., 2019). They are diadromous and protandric hermaphrodites, capable of reaching >1000 mm fork length and living up to 21 years (Marshall, 1958; Munyandorero et al., 2020; Taylor et al., 2000). Snook are primarily piscivorous but also feed extensively on invertebrates such as shrimp, crayfish, and crabs (Boucek & Rehage, 2013; Malinowski et al., 2019). Snook are intolerant of hypoxic conditions (<2 mg/L) beyond ~15 cm total length (Peterson & Gilmore, 1991), which constrains their habitat use in estuarine systems.

Tarpon are estuarine-dependent predators that rely on estuaries as nursery habitat (Kurth et al., 2019). Subadult Tarpon (generally less than 117 cm fork length, 13 kg and 10 years of age) are sexually immature but overlap in size, trophic position and prey selection with Snook (Griffin et al., 2022; Kurth et al., 2019; Santos et al., 2025). Unlike Snook, Tarpon tolerate hypoxia due to a modified gas bladder that allows facultative aerial respiration (Geiger et al., 2000). This adaptation enables Tarpon to occupy oxygen-poor habitats, which may reduce predation risk and increase foraging opportunities by limiting prey escape ability in hypoxic waters (Geiger et al., 2000; Heithaus et al., 2009; Kurth et al., 2019).

2.3 | Tracking fish movement

Snook and Tarpon were captured using hook and line, acoustically tagged, and subsequently tracked between the early wet season of 2016 and the early dry season of 2021. Captured fish were surgically implanted with INNOVASEA V-13L acoustic transmitters (i.e. acoustic tag) with a 120-s nominal delay using methodologies described by Eggenberger et al. (2019). With these settings, the acoustic transmitters had an expected battery life of 1500 days

(~4 years). Tagged Snook and Tarpon were tracked throughout the lake systems with the Coastal Everglades Lakes Acoustic Array (CELA²), which is comprised of 40 omnidirectional passive acoustic telemetry receivers (Figure 1; VR2W, INNOVASEA, Bedford, Nova Scotia, Canada). Fish locations were recorded when an acoustically tagged fish swam within the detection range of an acoustic receiver (50–500 m; Eggenberger et al., 2019). Each acoustic tag transmits a unique ultrasonic acoustic signal that receivers detect and record (tag identification, date and time). Detection data were downloaded quarterly throughout the 5 years of tracking. The CELA² receivers were strategically deployed at (a) creek mouth 'choke' points between lakes in a paired 'gated' arrangement, and (b) exit points arranged in a 'curtain' formation in the southern bays (Garfield Bight and Terrapin Bay; Figure 1). The array design was constructed using this methodology that allowed for the tracking of between-lake and bay movements of tagged Snook and Tarpon and did not contain enough receivers to allow for finer scale, within-lake movement tracking. All animal handling procedures were approved by the Florida International University Institutional Animal Care and Use Committee (protocol number: IACUC-18-002-CR02) and conducted in accordance with institutional guidelines. Fieldwork was conducted under permits issued by Everglades National Park (permit number: EVER-2019-SCI-0010).

2.4 | Classifying movement strategies

Before classifying distinct seasonal movement strategies, detection data were cleaned and filtered. First, the acoustic detections of tagged Snook and Tarpon were filtered to exclude (1) the first week of tracking to allow for recovery following capture and tagging and (2) individuals that were only detected in one lake throughout the entirety of their detection history to remove potential mortality events following tagging. Due to the configuration of the acoustic array, gaps in detections were expected when tagged individuals remained within a lake outside of the detection ranges of the adjoining creek mouth receivers. To account for this, it was assumed that the fish remain in the lake they were last detected, but outside of the receiver range during gaps in detections. The validity of this assumption was first assessed during range testing prior to the start of this study (see Eggenberger et al., 2019) but is further verified here by quantifying the number of occurrences where fish were detected in a lake that was not adjacent to the lake of their previous detection (i.e. detection skips).

Movement metrics were selected to be most similar to those utilized by analogous research (Abrahms et al., 2017; Bastille-Rousseau et al., 2024; Brodie et al., 2018; Taylor et al., 2021) that would quantify aspects of an individual's seasonal movements such as the amount of time spent in various locations, between-lake movement frequencies and spatial extent of areas used. Metrics were modified to account for data-type differences such as the spatiotemporal resolution of our passive acoustic telemetry data. Movement metrics centred around movement events (ME) and residence time (RT). A

ME occurs when a tagged fish enters a lake or bay within a system, and RT is the duration of time the fish remains there before moving into another lake or bay. MEs indicate movement frequency or the tendency to explore or shift habitats, while RTs provide insight into how long fish are using a given area, potentially reflecting resource availability, habitat preference or environmental stability (Table 1).

To better capture the multifaceted nature of how Snook and Tarpon interacted with their environment, we incorporated six complementary movement metrics in our analysis, following recommendations for multi-property assessments of space use (Bastille-Rousseau et al., 2024). These metrics are as follows:

1. Average residence time—represents typical patch-use (patches being each lake or bay) duration and may reflect general habitat suitability.
2. Maximum residence time—captures extended use of a lake or bay, possibly indicating high-quality or stable conditions.
3. Minimum residence time—reflects quick transits or exploratory movements and may indicate lake/bay (patch) avoidance or low resource value.
4. Number of movement events—reflects frequency of movements between lakes/bay of a system. This represents the spatial activity level of an individual and can be influenced by environmental heterogeneity and predictability.
5. Proportion of system used—describes the extent to which an individual explores available habitat patches (i.e. lakes and bays), indicating whether it exhibits localized site fidelity or broader use of the system. This metric is calculated as the percentage of lakes visited by an individual during a season relative to the total number of lakes available.
6. Variance in residence times—captures the consistency or variability in the duration of time an individual remains in a given lake or bay, which may reflect differences in foraging behaviour or variability in patch profitability.

Together, these metrics offer a more nuanced characterization of how Snook and Tarpon adjusted their movement in response to seascape conditions, allowing us to distinguish between more resident

behaviour, characterized as strong lake or bay fidelity and more exploratory strategies involving frequent or wide-ranging movements. Fish were considered to have left a system if more than 7 days passed between detections in a bay, ending the RT duration for that ME. If a fish was detected again in the same bay after more than 7 days within the same season, a new ME and RT were recorded. To ensure temporal standardization, only fish detected in a system for at least 45 days within a season (i.e. half of a quarter season) were included in the analysis.

Next, to account for potential interspecific differences in movement tendencies and geomorphological differences between the two systems, seasonal movement metrics were centred and scaled (i.e. z-scored) by system and species. Principal component analysis (PCA) was then used to reduce the dimensionality of the movement data while minimizing information loss, and to assist in the classification of the movement strategy clusters (King & Jackson, 1999). Several clustering approaches, including Partitioning Around Medoid (PAM), Clustering Large Applications (CLARA) and Gaussian Mixture Models (GMM), were explored, but k-means clustering was selected for its balance of interpretability and performance. Following Brodie et al. (2018), k-means clustering was used to assign each fish's seasonal movement metrics into movement strategy groupings. The optimal number of clusters was determined via the gap statistic, which is a goodness-of-fit clustering metric (Tibshirani et al., 2001; Ward & Hook, 1963). Following clustering, Permutational multivariate analysis of variance (PERMANOVA) was used to confirm that movement strategies were statistically distinct (Anderson, 2017). Classification of movement strategies was then based on the centroid values of each k-means cluster, which reflect the relative positioning of movement metrics in multivariate space. These centroid-based classifications were interpreted in conjunction with individual movement histories (Figure S4).

2.5 | Relating movement strategies to internal drivers—Size and sex

To first explore potential drivers of movement strategy selection, we evaluated the role of individual characteristics, particularly body

TABLE 1 The six movement metrics that were used to classify the seasonal movement strategies and their descriptions.

Movement metric	Abbreviation	Description
Average residence time	avg ResidTime	Mean time of a fish's movement event durations
Maximum residence time	max ResidTime	Longest duration between movement events
Minimum residence time	min ResidTime	Shortest movement event duration
Number of movement events	Movement Events	Total number of times a fish moved from one lake or bay to another
Percentage of system used	pct SystUse	Number of lakes (including the bay) a fish visited out of total number of lakes within the system
Variation in residence time	var ResidTime	Variance in the durations of each movement event

size as a proxy for ontogeny. We hypothesized that larger, older individuals might exhibit distinct movement tendencies, such as more resident behaviour due to competitive dominance or to conserve energy. Seasonal body sizes were estimated for each individual using von Bertalanffy growth curves, based on initial length measurements collected at the time of tagging. For Snook, we applied the Gulf Coast growth equation (Munyandorero et al., 2020), and for Tarpon, most of which were not sexed, we used the male-specific growth equation (Crabtree et al., 1997). As protandric (male-first) hermaphrodites, Snook undergo sex reversal at larger sizes and the probability of sex reversal was also estimated based on size following Taylor et al. (2000).

2.6 | Relating movement strategies to external drivers—The physicochemical seascape

The physicochemical seascape was quantified using five covariates: salinity (ppt), temperature (°C), turbidity (Secchi depth in meters), dissolved oxygen (mg/L) and submerged aquatic vegetation cover (SAV; average percent cover of all SAV species in half-metre quadrat replicates). Environmental covariates were sampled at various intervals through eight fixed hydrologic stations operated by Everglades National Park and the United States Geological Survey (see Supporting Information for details and data are available at <https://www.sfwmd.gov/science-data/dbhydro>), along with six PME-miniDOT loggers placed throughout the Alligator and McCormick systems (Figure 1). In addition to this continuous monitoring, extensive seasonal sampling was conducted across each lake and bay using a YSI-2030 and half-metre quadrats to characterize environmental conditions beyond the fixed hydrostations and provide broader spatial coverage of the seascape.

To address potential scale mismatches between the point-based environmental measurements, multiple linear regression (MLR) and linear interpolation were used to estimate the five physicochemical conditions at 1-week intervals within each lake and bay from the early wet season 2016 to early dry season 2021 to match fish detection records. Stepwise AIC backward selection was used to select the best MLR models for each lake and biophysical covariate. Following multiple linear regression, linear interpolation was used to estimate any remaining values.

To evaluate the effects that total physicochemical seascape heterogeneity had on movement strategy selection by Snook and Tarpon, we used a metric common to community ecology: multivariate dispersion. Multivariate dispersion is a multivariate analogue of Levene's test for homogeneity of variance and is often used to assess the variability in community composition among different groups or treatments (Anderson, 2006). Multivariate dispersion is the average distance of group members to the group's spatial centroid. In this study, multivariate dispersion measures the average distance of the weekly values from the five biophysical conditions to their spatial centroid for each system and season. Larger values of multivariate

dispersion signify greater spatiotemporal heterogeneity in a seascape during that season. The weekly values of each biophysical condition were z-scored by system to achieve homoscedasticity, and multivariate dispersions were calculated for each system by season and year using the *betadisper* function in R's Vegan package (version 2.6-4; Anderson, 2006). Then, to relate the multivariate dispersion values to Snook and Tarpon seasonal movement strategies, multinomial log-linear models were fit using the *multinom* function in R's *nnet* package (version 7.3-18).

Finally, to examine relationships between the predictability of individual physicochemical conditions and Snook and Tarpon movement strategies, the coefficient of variation (CV) was calculated for each system, season and year. Smaller CV values indicated reduced variability and thus greater environmental predictability, whereas larger values reflected increased variability and lower predictability. CVs were z-scored to achieve homoscedasticity before conducting boosted regression tree (BRT) analysis using *gbm.auto* (version 2023.8.31; Dedman et al., 2017) in R. BRT analysis is a machine learning technique that is increasingly being used with passive acoustic telemetry data to estimate species' habitat selection, distribution or abundance (Dedman et al., 2015; Froeschke & Froeschke, 2011; Thayer et al., 2017; Viadero et al., 2025). It combines regression trees with boosting to identify breaks in the presence or absence of dependent variables (i.e. the movement strategies) along the range of independent variables (i.e. the biophysical conditions). Boosting is the iterative procedure that averages the various tree outputs and splits to produce a single final model output (Dedman et al., 2015; Elith et al., 2008). BRT offers several advantages over traditional methods, including robustness to multicollinearity, outliers, zero-inflated data, and nonlinear relationships (Elith et al., 2008). A learning rate of 0.001, tree complexity of 5 and a bag fraction of 0.7 were used for all models. Zero-inflated BRT models were applied to the movement strategies that Snook and Tarpon selected least frequently. Model training followed the framework established by Elith et al. (2008). The learning rate determines the degree to which each tree contributes to the model, so decreased learning rates increase the number of trees used in the model. Computational power allowed for the use of smaller (i.e. 0.001) learning rates for our BRTs. Tree complexity is the number of nodes in each tree, and five were chosen to account for variable interactions between our five physicochemical covariates. Finally, the bag fraction sets the percentage of data that will be drawn from at random without replacement to train and test the models (Elith et al., 2008). Model performance was primarily assessed based on balanced accuracy and F1 score. Balanced accuracy is the mean of the true-positive rate (i.e. sensitivity) and the true-negative rate (i.e. specificity) across movement strategy presence and absence. Balanced accuracy was a focal metric of model performance as it accounts for imbalanced datasets and avoids over-emphasis on the majority class. Finally, the F1 score is the harmonic mean of precision and recall and provides a single metric for model performance between 0 and 1, where 1 indicates perfect precision and recall.

3 | RESULTS

3.1 | Acoustic telemetry tracking data

A total of 5.18 million detections were recorded from 133 tagged fish ($n_{\text{snook}}=101$ and $n_{\text{tarpon}}=32$) between July 2016 and April 2021.

TABLE 2 The average, min and max total length (TL), weight and time detected in the array (TIS) for the 92 tagged individuals used in the study.

Species	n	Mean (min-max)		
		TL (mm)	Weight (kg)	TIS (days)
Atlantic Tarpon	23	702 (610-820)	2.8 (1.4-5.1)	522 (74-1504)
Common Snook	69	638 (523-843)	2 (1.1-4.7)	415 (56-1126)

Following the filtering methodology outlined above, seasonal movements from 92 individuals ($n_{\text{snook}}=68$ and $n_{\text{tarpon}}=24$; Figure S2) were included in the analysis, resulting in 326 unique seasonal movement observations (Alligator: $n_{\text{snook}}=128$ and $n_{\text{tarpon}}=75$; McCormick: Alligator: $n_{\text{snook}}=79$ and $n_{\text{tarpon}}=44$; Figure S3). Upon capture, Tarpon were on average larger (greater total length [TL] and weight [WT; kg]; Welch's two sample t -test: $t_{\text{TL}}(42.6)=3.8$, $p=0.0005$ and $t_{\text{WT}}(35.2)=3.8$, $p=0.0005$) than Snook (Table 2). These fish made 12,359 unique movement events ($n_{\text{snook}}=6915$ and $n_{\text{tarpon}}=5444$) over the focal time period with no interspecific difference in total time detected (Welch's two sample t -test: $t_{\text{TIS}}(31.8)=1.3$, $p=0.22$; Table 2). Of these 12,359 unique movement events, only 19 events or 0.15% were classified as skipped detections where a movement event occurred in a lake or bay that was not adjacent to the lake or bay of an individual's previous ME. These results support the notion

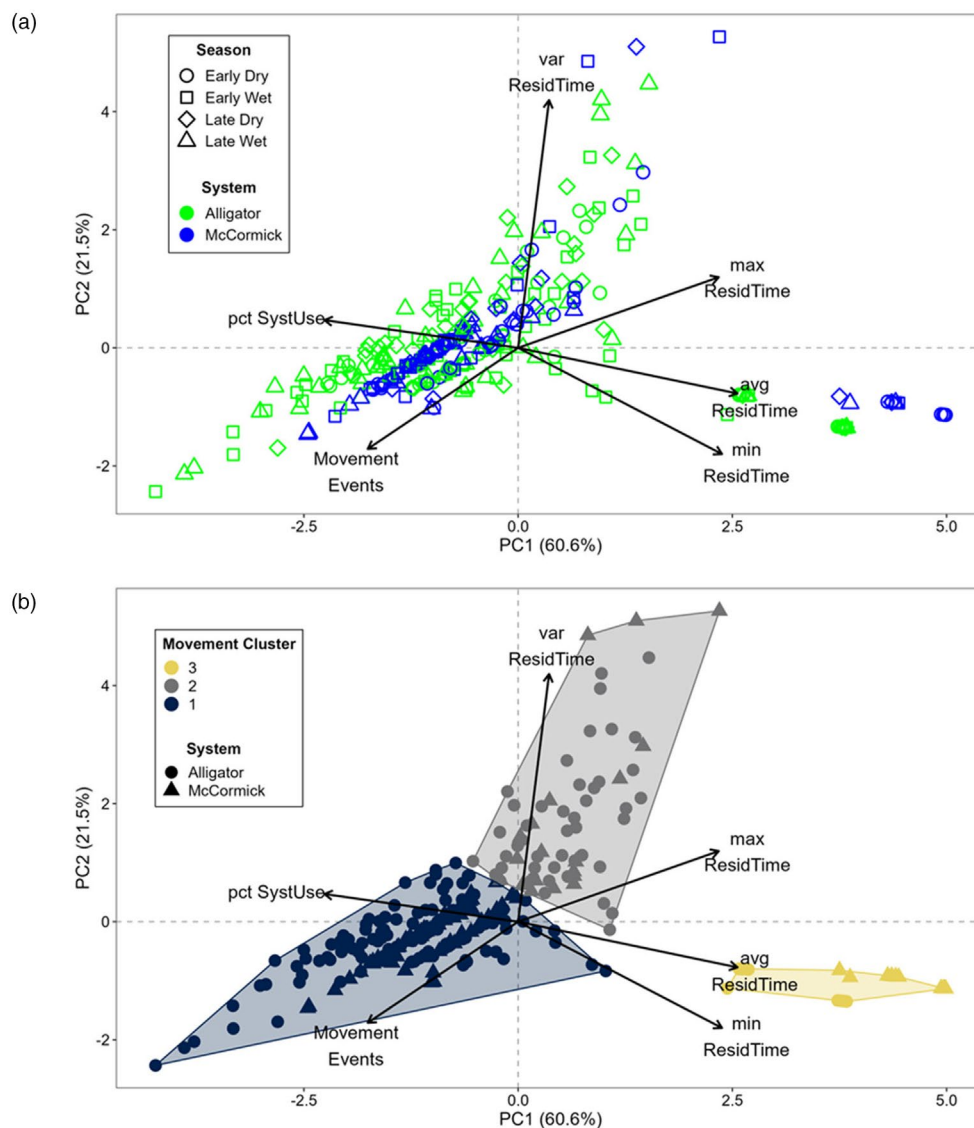


FIGURE 2 (a) Scatterplot of movement metric summaries for the 326 ($n_{\text{snook}}=207$ and $n_{\text{tarpon}}=119$) unique seasonal movements from 92 tagged fish ($n_{\text{snook}}=69$ and $n_{\text{tarpon}}=23$) based on PCA-defined axes with the six movement metrics as vectors. (b) Scatterplot of movement metric summaries based on PCA-defined axes with the movement strategy groupings from k-means clustering ($n_{\text{cluster}_1}=204$, $n_{\text{cluster}_2}=65$, $n_{\text{cluster}_3}=57$). PCA, Principal component analysis.

TABLE 3 Summary table of the biophysical seascape model results by system and lake.

System	Lake	Zone	Mean (min–max)				
			Dissolved oxygen	Salinity	SAV	Temperature	Turbidity
Alligator	West	Upstream	5.1 (0.2–9.6)	14.9 (5.1–26.7)	69 (13.4–99.4)	26.9 (17.8–33.2)	0.5 (0–1)
	Cuthbert	Upstream	6.7 (0.1–12)	13.1 (0.7–50.2)	23.5 (0–100)	28.1 (19.3–34.5)	0.4 (0.2–0.7)
	Long	Middle	4.3 (0.1–11.4)	18.9 (0.8–50.1)	25.4 (0–73.7)	27.6 (18.2–33.8)	0.5 (0.2–0.7)
	Lungs	Downstream	4.8 (0.2–10.7)	23 (0.8–47.3)	57 (2–100)	27.5 (18.5–33.9)	0.5 (0.2–1.2)
	Garfield	Bay	6.3 (0.1–10.1)	33.5 (9.6–50.2)	43.8 (0–97.9)	26.9 (16.6–33.6)	0.4 (0–0.8)
McCormick	Seven Palm	Upstream	5.7 (0.5–8.4)	14.7 (0.8–30.6)	50 (1.2–92.9)	27.8 (18.1–33.8)	0.7 (0.4–1)
	Middle	Middle	4.7 (0.1–11.6)	16.1 (0–36.8)	50.2 (1.5–96.3)	27.4 (17.7–33.5)	0.7 (0.4–0.9)
	Monroe	Downstream	5.1 (0.1–9.7)	21.9 (0–44.4)	46.9 (0–94)	27.2 (17.6–33.4)	0.7 (0–1.2)
	Terrapin	Bay	6.3 (0.2–9.6)	27.6 (2.7–44.9)	24.9 (0–68.1)	27.4 (17.4–34.3)	0.6 (0–1.1)

Note: Covariates were modelled at a 1-week time step from the early wet season 2016 to early dry season 2021.

that the acoustic array design and transmitter settings were highly effective at tracking the between lake/bay movements of the Snook and Tarpon. Further, the observed low rate of skipped detections leveraged support for the assumption that tagged individuals remained in the lake/bay of their last ME during periods of no detection.

3.2 | Classifying movement strategies

The six focal seasonal movement metrics were calculated from the 326 unique seasonal movement records and were then used to construct the PCA (Figure 2a; Eggenberger et al., 2025; dataset available through the Environmental Data Initiative portal). Based on the Kaiser criterion, PC axes one through three were selected for clustering and accounted for a combined 89% of the variance in seasonal movement metric values. k-Means clustering with three groups was determined to be the optimal partitioning method based on sums of squares, average silhouette, and gap statistics (Figure 2b). Movement metric values were significantly different between clusters (PERMANOVA; pseudo- $F_{2,325} = 262.63$, $p = 0.001$). Movement strategy 1 contained 204 seasonal movement observations, followed by 65 seasonal observations of movement strategy 2 and finally 57 observations of movement strategy 3. Based on the centroid values of each k-means cluster (Figure 3), we classified the first cluster as the Transient movement strategy. This strategy was defined by a high number of movement events, extensive system use, and low mean, maximum and minimum residency times, along with low variance in residency time (Figure 3). Conversely, the third movement strategy exhibited the opposite pattern, with high residency across all measures, limited movement events and low system use, consistent with a Resident movement strategy. The second strategy was characterized by intermediate values for most movement metrics but had the greatest variance in residency time among all movement strategies. When evaluated alongside individual movement histories (Figure S4), the second strategy appeared biphasic, with one movement phase of rapid movement throughout a system (similar to those elicited by the Transient movement strategy) and another phase of prolonged residency in one lake or bay (similar

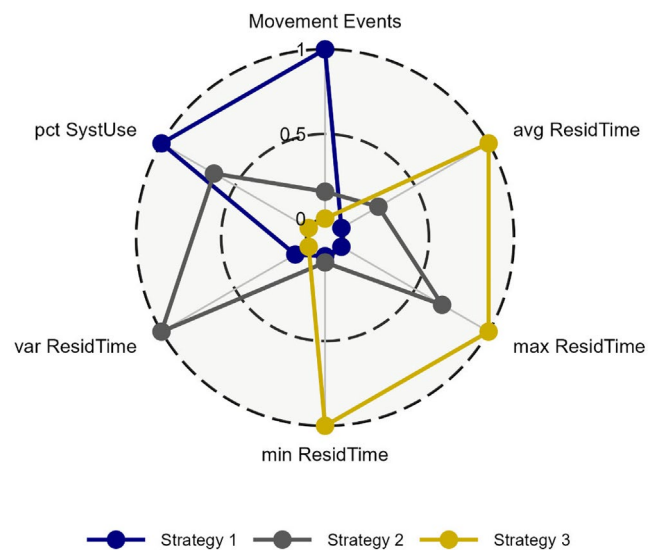


FIGURE 3 Radar plot showing the k-means centroid values for the six movement metrics used in classifying individual movement strategies. For visualization, values were rescaled between 0 and 1. Strategy 1 (blue), characterized by the highest number of movement events and greatest percentage of system use (pct SystUse), was classified as the Transient strategy. Strategy 3 (gold), defined by the longest minimum, maximum and average residence times, was classified as the Resident strategy. Strategy 2 (grey), which exhibited the highest seasonal variation in residence time and intermediate values across other metrics, was classified as the Mixed strategy.

to the Resident movement strategy). Therefore, we classified strategy two as representing a Mixed movement strategy.

3.3 | Quantifying seascape heterogeneity

Forty-two multiple linear regression models were used to estimate the biophysical seascapes of each system at 1-week temporal intervals (Table S1). A 1-week interval was selected to capture seasonal

FIGURE 4 Violin plots showing the seasonal seascape dispersions in the Alligator (green) and McCormick (blue) system. Seascape dispersions were lowest (most homogeneous seascapes) in both systems during the late dry season and the greatest (most heterogeneous) during the late wet season. The Alligator System seascape dispersions were greater (more heterogeneous) than the McCormick System (significant pairwise Wilcoxon test p -values bolded below the system and season comparisons).

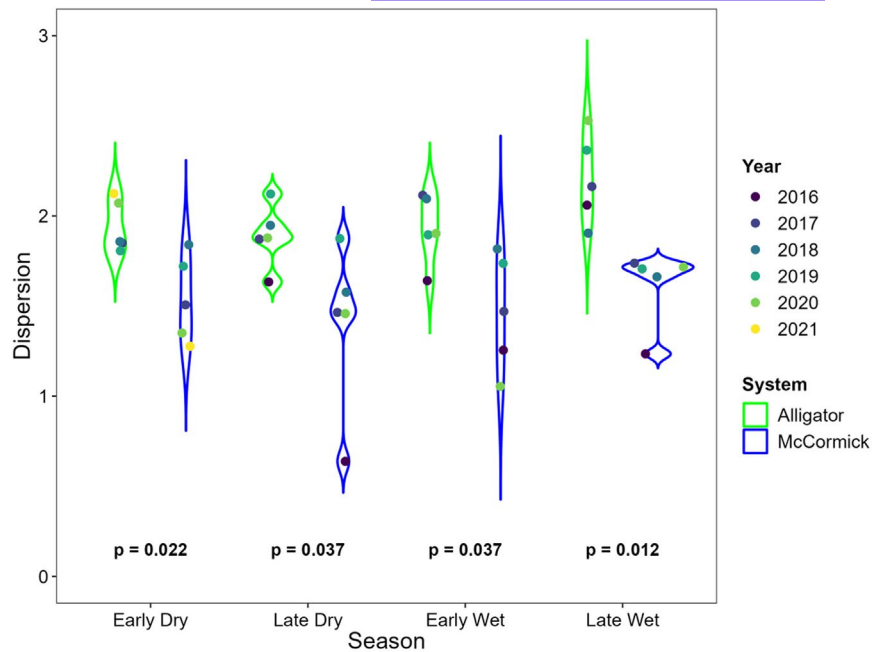


TABLE 4 Results of the multinomial log-linear regression model with the Transient movement strategy and Snook as reference categories.

Predictor	Category	Coefficient	SE	z-Value	p -Value	95% CI (lower)	95% CI (upper)
Mixed	(Intercept)	-3.99	1.08	-3.71	0.00	-6.10	-1.88
Mixed	Multivariate dispersion	1.66	0.61	2.72	0.01	0.46	2.86
Mixed	Atlantic Tarpon	-0.03	0.30	-0.09	0.93	-0.62	0.57
Resident	(Intercept)	-1.82	1.07	-1.70	0.09	-3.92	0.28
Resident	Multivariate dispersion	0.17	0.63	0.27	0.79	-1.07	1.40
Resident	Atlantic Tarpon	0.63	0.30	2.08	0.04	0.04	1.23

Note: Bolded p -values indicate statistically significant effects ($p < 0.05$).

trends and accommodate the sampling rate of the biophysical covariates in each system. Models had an average adjusted R^2 of 0.7, with the models for temperature having the greatest mean adjusted R^2 of 0.98, followed by salinity (0.89), turbidity (0.57) and dissolved oxygen (0.56; see Table S1 for further details). Finally, calculations of total seasonal seascape heterogeneity within the systems using the metric of multivariate dispersion revealed that the Alligator System was generally more heterogeneous (i.e. had larger multivariate dispersion values) than the McCormick System. However, repeated-measures ANOVA revealed no significant effect of season in either system [at the year level: Alligator System— $F(1,4)=0.765$, $p=0.431$; McCormick System— $F(1,4)=0.18$, $p=0.693$; and at the within-year (season) level: Alligator System— $F(3,11)=1.289$, $p=0.327$; McCormick System— $F(3,11)=0.438$, $p=0.73$], indicating that dispersion did not significantly vary between seasons (Table 3; Figure 4).

3.4 | Relating movement strategy to physicochemical seascape heterogeneity and predictability

Multinomial log-linear regression was used to examine the influence of total seascape heterogeneity, quantified as environmental

multivariate dispersion, on Snook and Tarpon movement strategy selection. The Transient movement strategy and Snook were used as the reference categories due to them being the majority classes. Results indicate that both Snook and Tarpon were more likely to select for the movement strategy characterized by increased movement and system use in less heterogeneous (low dispersion) seascapes, while they favoured strategies with reduced movement and system use as seascapes became more heterogeneous (Table 4; Figure 5). Specifically, Snook and Tarpon were most likely to select the Transient movement strategy in homogeneous seascapes (i.e. low multivariate dispersion) and the Mixed movement strategy in heterogeneous seascapes (i.e. high multivariate dispersion; coefficient = 1.66, SE = 0.61, $z=2.72$, $p=0.01$). Seascape heterogeneity did not have a significant effect on the likelihood of Snook and Tarpon selecting the Resident movement strategy (coefficient = 0.168, SE = 0.629, $z=0.267$, $p=0.789$), but Tarpon were more likely to use the Resident movement strategy than Snook (coefficient = 0.632, SE = 0.304, $z=2.08$, $p=0.0375$). Finally, neither the size of Snook and Tarpon nor sex of Snook, estimated based on size due to their protandric hermaphroditism, was significantly associated with movement strategy selection (Figure S6).

BRT models performed well overall with an average balanced accuracy of 0.72 and an F1 score of 0.72 for Snook and an

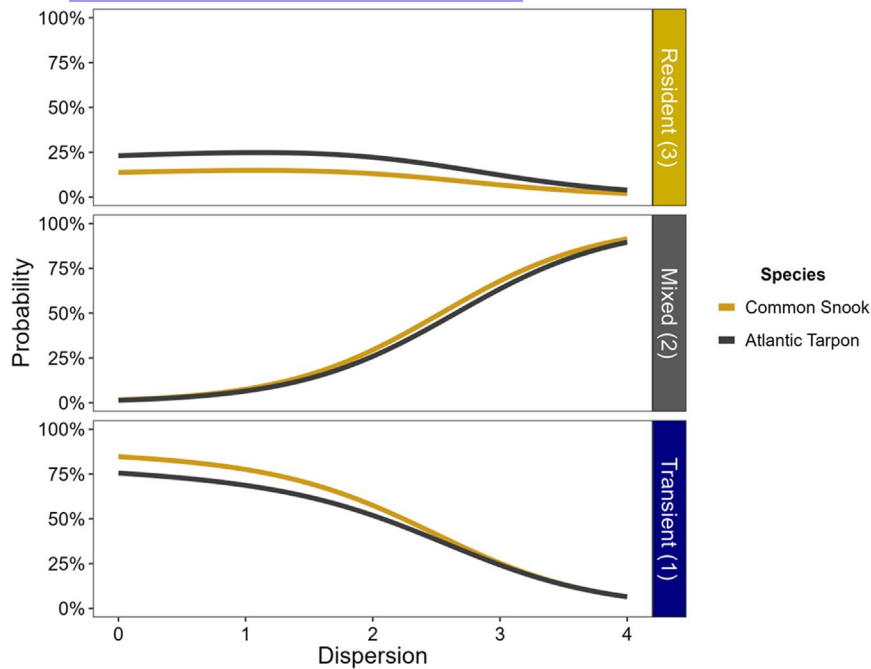


FIGURE 5 Multinomial log-linear model predictions for movement strategy selection by Snook (gold) and Tarpon (silver) across gradients of seascape dispersion. Snook and Tarpon in homogeneous seascapes (dispersion values approaching zero) are predicted to select the Transient movement strategy. As seascapes become more heterogeneous (dispersions approaching four), Snook and Tarpon were expected to use the Mixed movement strategy. Model results suggest that seascape dispersion is not a strong driver of the Resident movement strategy.

average balanced accuracy of 0.82 and an *F1* score of 0.84 for Tarpon (Table 5). Model performance was slightly lower for the Transient strategy compared to the Resident and Mixed strategies, likely due to dataset imbalance, which led to over-selection of the majority class (Elith et al., 2008). Seascape predictability, quantified using the coefficient of variation of the five focal physicochemical conditions, had a variable influence on movement strategy selection in Common Snook and Atlantic Tarpon (Figure 6). For both species, the relative influence of environmental predictability differed by movement strategy, with the strongest effects observed among seasonal movements classified as Resident. In Snook, Residency was most influenced by the predictability of submerged aquatic vegetation (SAV; 25.2%) and temperature (26.4%), whereas Transient and Mixed Snook were most influenced by dissolved oxygen (32.3%). In contrast, Resident Tarpon showed the highest sensitivity to salinity (28.0%) and turbidity (27.3%), while Mixed Tarpon responded most strongly to turbidity variability (35.9%). Across both species, the shape of marginal effects was frequently nonlinear and species-specific, particularly for salinity, SAV and temperature, suggesting that Snook and Tarpon rely on distinct environmental cues when selecting or maintaining movement strategies in response to dynamic seascape conditions.

4 | DISCUSSION

This study aimed to adapt movement strategy theory that had been developed in terrestrial environments, where animals were tracked with higher resolution equipment (e.g. satellite; Mueller & Fagan, 2008; Riotte-Lambert & Matthiopoulos, 2020), to aquatic seascapes with lower-resolution, non-gridded passive acoustic telemetry. Using a suite of movement metrics that quantified

distinct, universal components of movement, we identified three seasonal movement strategies in Common Snook and Atlantic Tarpon: Transient, Mixed and Resident. These strategies differed in frequency and the spatial extent of movement, and our analysis revealed that their prevalence shifted with environmental heterogeneity and predictability.

Our results support theoretical predictions from terrestrial movement ecology, as both Snook and Tarpon exhibited more extensive, Transient movements in homogenized seascapes, where environmental differences between lakes were minimal, and increasingly localized movements as seascape heterogeneity increased at finer spatial scales (i.e. greater differences between adjacent lakes). This reinforces the concept that movement strategies are not fixed traits, but context-dependent responses to environmental structuring (Riotte-Lambert & Matthiopoulos, 2020; Mueller & Fagan, 2008). Notably, individuals switched strategies between seasons, with an average switching probability of 31.5% (Tarpon 41.4% and Snook 27.5%). Additionally, about 20% of individuals (nine Snook and eight Tarpon) used all three movement strategies across their period of record, highlighting behavioural flexibility in response to environmental conditions (Figure S4).

As tropical, euryhaline predators with broad physiological tolerances, Snook and Tarpon are unlikely to experience strong abiotic limitations to movement within these estuarine systems, except under extreme conditions. Known thresholds include temperatures below $\sim 12^{\circ}\text{C}$ (Howells et al., 1990; Mace et al., 2017), prolonged hypersalinity (Adams et al., 2014; Gilmore et al., 1983) or for Snook, hypoxic water (Peterson & Gilmore, 1991). While instances of hypersalinity and hypoxia did occur in some lakes during the late wet or early dry seasons (Figure S2), these events were isolated and infrequent, minimally influencing the overall seascape heterogeneity metric (Figure S1). Furthermore, seascape heterogeneity did not

TABLE 5 Evaluation metrics for movement strategy BRT's.

Statistic	Description	Snook			Tarpon		
		Resident	Mixed	Transient	Resident	Mixed	Transient
Presence	<i>n</i> of presence data used	29	43	135	28	22	69
Absence	<i>n</i> of absence data used	178	164	72	91	97	50
AUC-ROC	Area under the receiver operator (ROC) curve	0.802	0.798	0.783	0.966	0.816	0.825
Specificity	Specificity	0.624	0.616	0.875	0.846	0.546	0.72
Accuracy	Accuracy	0.726	0.727	0.715	0.905	0.773	0.744
Precision	X% of the predictions are right	0.687	0.685	0.816	0.862	0.688	0.733
Recall	Y% of actually existing things are captured	0.828	0.837	0.556	0.964	1	0.768
Balanced accuracy	Balanced accuracy	0.726	0.727	0.715	0.905	0.773	0.744
F1 score	P & R equally rated, score importance depends on project	0.751	0.754	0.661	0.911	0.815	0.75
F2 score	Weighted average of precision and recall	0.795	0.802	0.593	0.942	0.917	0.761
Kappa	Cohen's kappa	0.238	0.306	0.369	0.698	0.308	0.485
Zero inflated	Was zero-inflated model used?	True	True	False	True	True	False
Percent zero	Percentage occurrence of absence from total <i>n</i>	86.0% zeroes	79.2% zeroes	34.8% zeroes	76.5% zeroes	81.5% zeroes	42% zeroes

Note: Models were assigned a learning rate of 0.001, tree complexity of 5 and bag fraction of 0.7. Zero-inflated models were used for the Mixed and Resident movement strategies.

significantly differ across seasons within either system (Figure 4), suggesting that broad seasonal trends in movement strategy selection are unlikely to be driven by extreme physicochemical events alone.

Instead, we suggest that physicochemical heterogeneity may influence movement indirectly by shaping the distribution and composition of prey communities through processes such as environmental filtering (Kraft et al., 2015). Quantifying prey resource seascapes at spatiotemporal scales comparable to the passive acoustic telemetry data was impractical due to time, labour and resource constraints. Although biannual prey sampling was conducted in both systems during peak wet and dry season conditions (see Santos et al., 2025 for details), incorporating this data would have required substantially more computationally intensive modelling and additional assumptions. Nevertheless, results from the prey sampling indicate that greater environmental heterogeneity was associated with higher prey community diversity, supporting the idea that prey heterogeneity and predictability covary with physicochemical heterogeneity and predictability (Figure S7). While a full integration of prey data is beyond the scope of this analysis, future work should investigate these relationships more explicitly. In the meantime, our findings suggest that relatively simple environmental metrics may serve as effective proxies for underlying biotic drivers of movement.

Importantly, we found species-specific responses to seascape predictability, with distinct environmental variables influencing

residency in each species. For Snook, higher predictability in submerged aquatic vegetation cover and temperature was associated with greater site fidelity, likely reflecting a preference for stable, structured habitats that support both consistent prey availability and opportunities for ambush foraging (Blewett et al., 2013; Malinowski et al., 2019). In contrast, Tarpon residency was more closely linked to variability in salinity and turbidity, conditions that reflect their broad environmental tolerance and possible reliance on sensory cues in low-visibility waters (Stephens et al., 2024). These contrasting patterns emphasize the role of behavioural specialization and sensory ecology in mediating species' responses to seascape dynamics.

The broader influence of salinity, turbidity, and dissolved oxygen on movement strategies aligns with established ecological knowledge of estuarine fish behaviour and habitat use. These variables are tightly linked to freshwater inflow regimes, which are increasingly disrupted by coastal development and water management practices (Adams & Van Niekerk, 2020; Barbier et al., 2011; Freeman et al., 2019). For example, salinity fluctuations can cascade through ecosystems by altering dissolved oxygen concentrations and submerged aquatic vegetation distribution (Frankovich et al., 2011; Strazisar et al., 2015). Our findings underscore the potential for hydrological changes to influence not only habitat quality but also animal movement and ecosystem function. Anticipating these responses will be essential as estuarine environments continue to

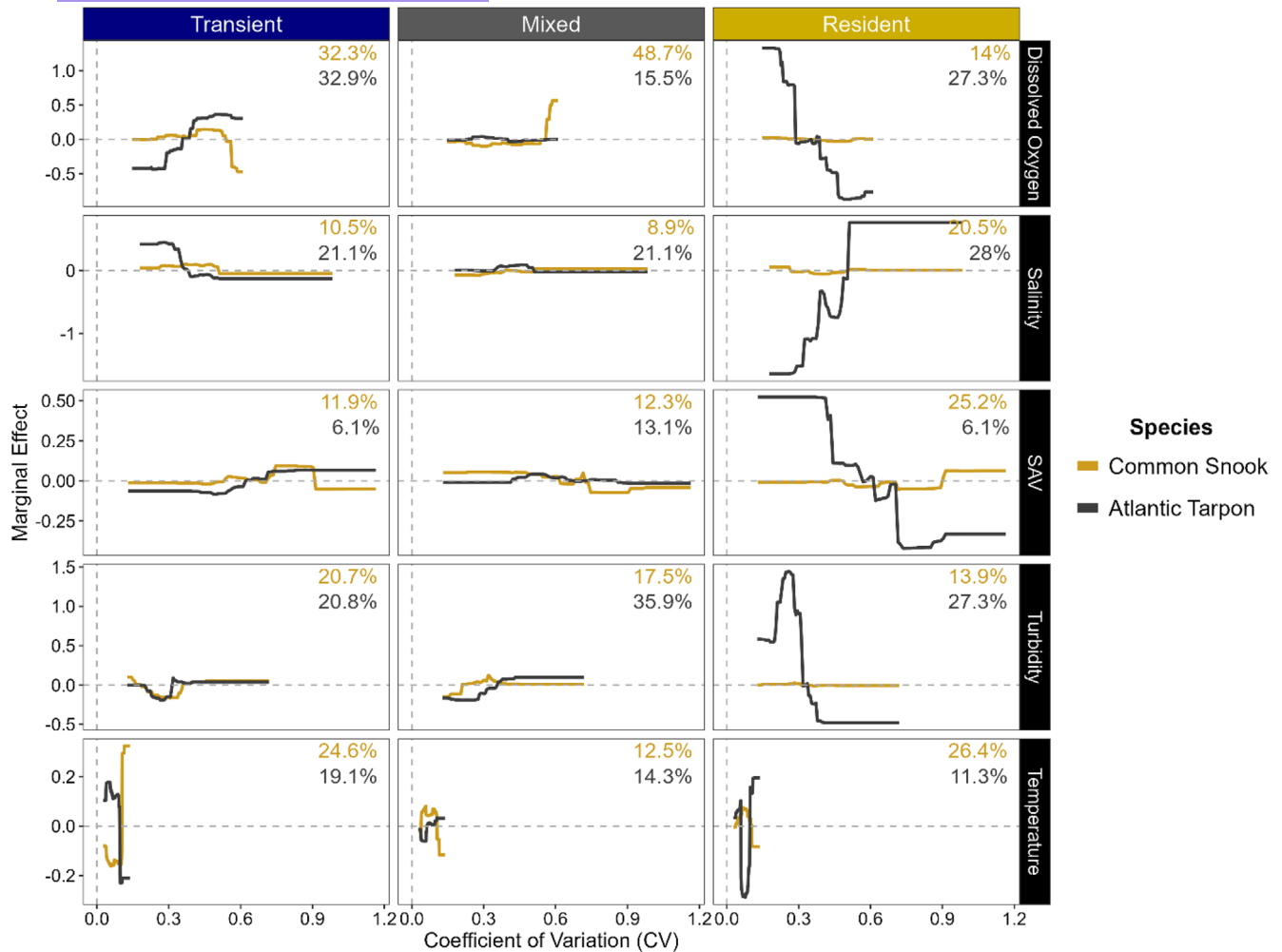


FIGURE 6 Marginal effect plots showing the influence of the coefficient of variation, used as a proxy for seascape predictability in biophysical conditions, on Snook and Tarpon movement strategy selection. The relative influence (%) of this predictor is shown in the top right corner of each panel.

face pressures from sea-level rise, altered precipitation patterns and land-use change.

From a methodological standpoint, the extremely low error rate (0.15%) in skipped movement event detections allowed us to assume lake-level presence between periods of detection, with high confidence. This increased the effective resolution of our non-gridded array and enabled behavioural classification over large estuarine gradients. While this approach lacks the fine-scale positioning capability of gridded arrays with overlapping receiver coverage, which use time-of-arrival differences among multiple receivers to triangulate animal positions with sub-meter accuracy, the design was sufficient for distinguishing broad movement strategies across the brackish-to-marine continuum. However, in systems with more complex connectivity or lower detection coverage, movement strategy classifications would be less reliable.

Our work also highlights the importance of matching spatiotemporal scale to ecological questions. Movement decisions are hierarchical, shaped by risk and reward trade-offs at multiple nested scales (Hutto, 1985; MacArthur & Pianka, 1966). While this study

focused on movements between lakes across seasonal timeframes, finer-scale behaviours, such as within-lake foraging, might follow different patterns. For example, satellite-tracked Tiger Sharks (*Galeocerdo cuvier*) exhibited oriented, directed movements over larger spatial scales (at least 6–8 km), but displayed movement patterns resembling random walks at finer spatial scales (Papastamatiou et al., 2011). Conversely, larger scale movements, such as spawning migrations in Snook and Tarpon, may be driven by cues such as photoperiod, temperature and hydrologic pulses (Griffin et al., 2022; Massie et al., 2022; Trotter et al., 2021; Young et al., 2014). Future work that incorporates higher resolution positional and environmental data, through array reconfiguration, manual tracking or emerging technologies, could offer a more complete understanding of how animals respond to seascape heterogeneity and predictability at various spatial and temporal scales.

Recognizing these challenges of scale, we aligned the environmental data available to us with the resolution of our acoustic array by aggregating thousands of field-based physicochemical measurements collected throughout each lake across multiple

years while also supplementing via fixed hydrologic station data. These data were used in multiple linear regression models to estimate weekly lake-level conditions for each variable. Spatial and temporal averaging of environmental data offered an ecologically meaningful way to estimate weekly lake-level conditions consistent with the spatiotemporal resolution of Snook and Tarpon detections and their movement strategies. While this approach does not offer the high spatial resolution of satellite-based habitat classification methods commonly used in terrestrial systems, such techniques are more difficult to apply in turbid estuarine systems (Topp et al., 2020). Although remote sensing has been used to track submerged aquatic vegetation dynamics in clearer, nearby areas of Florida Bay (Rodemann et al., 2025), the Alligator and McCormick Creek systems are generally turbid and less conducive to these methods.

Finally, despite these efforts to model environmental conditions at the appropriate scale, the metrics we employed to quantify seascape heterogeneity and predictability, multivariate dispersion and the coefficient of variation, primarily captured the magnitude of environmental variability, not its temporal structure. For example, two lakes may exhibit similar coefficients of variation or dispersion values over a season, yet one may undergo gradual shifts while the other experiences frequent, abrupt changes. These temporal dynamics are ecologically important, as they influence how animals perceive and respond to environmental predictability (Riotte-Lambert & Matthiopoulos, 2020). Future work could incorporate additional or alternative metrics, such as autocorrelation or root mean square error (RMSE), to capture the rate and direction of change and provide more nuanced insight into how seascape predictability shapes movement strategies.

5 | CONCLUSIONS

This study contributes to the growing body of research linking environmental heterogeneity and predictability to movement behaviour, particularly in aquatic systems where movement theory has been less explored. By adapting a terrestrial movement strategy framework to passive acoustic telemetry in estuarine seascapes, we classified Snook and Tarpon movements into generalizable behavioural strategies and found that these were influenced by seascape heterogeneity and predictability. Our results suggest that even with relatively coarse environmental and tracking data, broad-scale movement patterns can reveal important behavioural adaptations to dynamic estuarine conditions. This has strong implications for conservation and management: changes to freshwater flow, habitat structure or climate-induced variability may not only shift habitat availability but also alter fundamental movement strategies that underpin population and ecosystem dynamics. Finally, this work provides a foundation for future research applying movement strategy theory in estuarine systems and offers a transferable framework for classifying and predicting fish movement patterns in response to anthropogenic and environmental change.

AUTHOR CONTRIBUTIONS

Cody W. Eggenberger, Rolando Santos and Jennifer Rehage conceived the ideas and designed methodology; Cody W. Eggenberger, Theresa Strazisar and Rene Price collected the data; Cody W. Eggenberger analysed the data; Cody W. Eggenberger led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data are available from the EDI data portal at <https://doi.org/10.6073/pasta/35d9bfabce02883a40744b4f04abdb6e>.

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SUPPORTING INFORMATION

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

Table S1. Multiple linear regression (MLR) results after stepwise AIC backward selection.

Figure S1. Monthly averages with 95% C.I. from the modelled physicochemical covariates across system.

Figure S2. Environmental conditions by lake.

Figure S3. Distribution of movement strategy classifications across seasons by system and species for the 326 unique seasonal movements obtained from 92 tagged individuals ($n_{\text{tarpon}}=23$, $n_{\text{snook}}=69$).

Figure S4. Movement histories with movement strategy categorization for the 92 fish that were included in the analysis.

Figure S5. BRT model results of the relative influence of the coefficient of variation of each environmental conditions by movement strategy for Snook and Tarpon.

Figure S6. Frequency plot of movement strategy classifications by fish total length (mm).

Figure S7. Relationship between multivariate dispersion in physicochemical conditions and prey community of Snook and Tarpon in the Alligator (light and dark green) and McCormick (light and dark blue).

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