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Received: 1 March 2026

Accepted: 29 June 2026

Published online: 08 July 2026

Cite this article as: Griffin L.P., Shipley O.N., Adams A.J. *et al.* Discrete foraging landscapes support large scale migrations of a marine fish. *Mov Ecol* (2026). <https://doi.org/10.1186/s40462-026-00677-3>

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Discrete foraging landscapes support large scale migrations of a marine fish

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Abstract

Many marine animals migrate thousands of kilometers, yet the spatial extent of dietary resources acquired along these routes remains poorly understood. Identifying foraging areas across a species' annual cycle is critical for understanding habitat connectivity, aligning conservation with locations essential for sustaining populations, and predicting how environmental variability influences resources. We integrated continental-scale stable isotope assignment modeling (n = 417 individuals) with five years of electronic tagging (n = 85 individuals), using movement data to spatially constrain isotope-based foraging assignments, to identify foraging locations along migration routes of Atlantic tarpon (*Megalops atlanticus*). Distinct

foraging regions emerged across the southeastern United States, including South Florida, the northern Gulf of Mexico, and the Mid-Atlantic Bight. Tissue-specific isotope incorporation rates indicated temporal variation in habitat use, with foraging activity often hundreds of kilometers from capture sites (mean distance to peak probability = 296 ± 188 km). These findings provide a framework for managing foraging habitats essential for highly migratory marine species.

Keywords: Atlantic tarpon, marine conservation, movement ecology, resource acquisition, stable isotope analysis

Introduction

As widespread habitat destruction and climate change continue to redistribute both predators and prey (1), discerning the location of critical foraging grounds used by species throughout their annual cycle is essential for conserving species whose survival and reproductive success necessitate movement across broad scales (2-4). Migration often evolves in response to the temporal and spatial variability of resources, allowing species to exploit peaks in resource abundance while avoiding periods of scarcity (5). In this context, migration is the recurring movements that link habitats during specific phases of the annual cycle, whereas movement more broadly may encompass opportunistic or exploratory displacements, including long-distance travel in search of resources or mates (6). Such migration strategies, often referred to as "surfing resource waves," are well-documented in terrestrial and avian species (7). For example, elk (*Cervus canadensis*), mule

deer (*Odocoileus hemionus*), pronghorn (*Antilocapra americana*), greater white-fronted geese (*Anser albifrons*), and barnacle geese (*Branta leucopsis*) all surf 'green' waves of plant growth to maximize foraging opportunities (7-11), while grizzly bears (*Ursus arctos*), glaucous-winged gulls (*Larus glaucescens*), and rainbow trout (*Oncorhynchus mykiss*) all surf 'red' waves to exploit seasonal pulses of salmon spawning runs (7, 12, 13). In terrestrial ecosystems, the relative ease of tracking species in relation to various environmental cues such as normalized difference vegetation index provides clear examples of how animals synchronize migrations with resource availability throughout their home ranges, allowing for the development of clear and targeted conservation strategies (14).

By contrast, the marine environment presents unique challenges to linking animal movement and resource availability due to its vast spatial scale and dynamic biogeochemical and physical processes. Nonetheless, evidence suggests that resource availability and an animal's ability to track it are equally important for species undergoing oceanic and region-wide migrations (15). For example, little auks (*Alle alle*) migrate thousands of kilometers from East Greenland to the waters off Newfoundland to overwinter in regions of elevated copepod densities, highlighting a tight coupling between migratory movement and zooplankton availability (16). Similarly, blue whales (*Balaenoptera musculus*) closely follow the long-term average phenology of the spring phytoplankton bloom within the California Current Large Marine Ecosystem (17). While resource-driven migration is well-documented in

species reliant on plant-algal phenologies, reconstructing movement patterns in higher trophic-level marine consumers remains challenging due to the vast spatial scales of migration (15), dynamic fine-scale oceanic processes that dictate movement extent (18, 19), and the inherent difficulty of tracking prey distributions that cannot be estimated with remotely sensed data (20).

In recent decades, stable isotope values of consumer tissues combined with spatial interpolations of baseline isotopic variation or 'isoscapes' (21, 22) have greatly advanced retrospective assignments of movement origins and dietary resource use (23, 24). In marine environments, these approaches offer underutilized opportunities to map energetic connectivity between otherwise disparate ecosystems, providing critical insight into how migratory species utilize foraging resources across space. Despite the oceanographic complexity of many marine ecosystems, recent isotopic assignment models based on an expanding set of isoscapes have shown promise for identifying where individual organisms forage. For example, Trueman et al. (24) used jellyfish (*Cyanea capillata*) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isoscapes in the North Sea to determine queen scallop origin (*Chlamys opercularis*) with 90% accuracy achieved within 40% of the isoscape area. Similarly, even when the foraging locations were unknown, the origin of juvenile and adult herring (*Clupea harengus*) were assigned to areas consistent with fisheries survey data, demonstrating the utility of this approach at the basin scale (24).

The integration of known movements from electronic tagging and tracking can further increase assignment accuracy by providing spatial

constraints over which isotopic assignments are performed (25). By restricting assignment areas to locations where individuals were detected during periods corresponding to tissue integration times, movement data help resolve the spatial ambiguities inherent in isotope-based approaches and improve confidence in identifying likely foraging locations. However, while tagging documents movement patterns, it does not provide direct information about resource assimilation, whereas stable isotopes integrate dietary information over tissue-specific time periods. Thus, St. John Glew et al. (26) combined light-based geolocation with $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope values from pelagic seabird feathers to restrict the assignment search area and more accurately determine foraging areas for individuals from across the North Sea. Combining multiple data sources, therefore, can provide nuanced insights into the relative spatial extent of foraging landscapes linked to the full migration extent of a given individual. However, such approaches are underutilized for migratory marine species (27-29) whose conservation status continues to suffer due to widespread environmental shifts and habitat loss (1, 30). This is largely due to a lack of empirically derived isoscapes at spatial and temporal (inter-seasonal and inter-annual) resolutions required to discern sub-regional variation in biogeochemistry that is reflected in the isotopic composition of primary producers (31-33).

Here, we identify the spatial extent of major foraging grounds used by Atlantic tarpon (*Megalops atlanticus*) during their annual migrations. Of conservation concern (34, 35) and known for moving thousands of kilometers

across continental shelf habitats along the Gulf of Mexico (GOM) and the eastern United States (US), tarpon exhibit complex contingent structure with varying movement strategies (36-38). We hypothesized that foraging landscapes would be comprised of discrete regions of an individual's full migration, analogous to 'staging grounds' adopted by highly migratory seabirds (39). We also predicted that tissues with different rates of isotopic incorporation would reveal different regions of an individual's foraging landscape relative to their movement timeline. Finally, we predicted that the location of foraging landscapes would differ between migratory contingents. To test these hypotheses, we identified migration extent and probable origins of dietary resources by integrating separate but extensive stable isotope and electronic tagging datasets. These included $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from multiple tarpon tissues (fin clips and blood plasma), continental shelf-wide isoscapes developed from inshore lizardfish (*Synodus foetens*), a ubiquitous but resident species that inhabits benthic ecosystems along the continental shelf throughout much of the southern and eastern US (33, 40), and five years of tarpon acoustic tracking data (37). Movement data provided spatial constraints, refining isotopic assignments and enabling improved inferences about the timing and location of foraging activity. This integrative framework links migration and foraging information that can be upscaled to test fundamental hypotheses related to energetic connectivity in the marine environment. Ultimately, this will support conservation strategies focused on

protecting critical foraging habitats embedded within large-scale migration corridors.

Results

Continental shelf isoscapes

A total of 534 inshore lizardfish $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were used to develop isoscapes (Shipley et al. 2024) across the southeastern US using Bayesian hierarchical spatial models with integrated nested Laplace approximations. $\delta^{13}\text{C}$ values ranged from -19.8‰ to -12.8‰ (mean $\pm$ SD = -17.5 ± 0.9 ‰), and $\delta^{15}\text{N}$ values ranged from 7.9‰ to 17.0‰ (12.1 ± 1.7 ‰). The reference carbon isoscape indicated the highest $\delta^{13}\text{C}$ values in the northern mid-Atlantic region and along the west coast of Florida. In contrast, the lowest $\delta^{13}\text{C}$ values were observed around the Mississippi Delta and the mid-Atlantic coast, particularly along the coasts of Georgia, South Carolina, and North Carolina (see Fig. S1-S5, and *Continental shelf isoscapes* in supplementary materials (SM)). The reference nitrogen isoscape highlighted the highest $\delta^{15}\text{N}$ values within the western GOM and the northern mid-Atlantic, with generally higher values along the coast, especially around the Mississippi Delta and north of Pamlico Sound. For a detailed discussion of these trends, see Radabaugh et al. (40) and Shipley et al. (33).

Atlantic tarpon

Across the southeastern US (see Fig. S6-S7 and *Tissue collection and processing* in SM), $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of Atlantic tarpon fin tissue ($n = 417$, fork length: 155.9 ± 22.7 cm) ranged from -21.0 to -11.3‰ (-15.2 ± 1.1 ‰)

and from 5.7 to 17.2‰ (14.2 ± 1.5 ‰), respectively. Blood plasma ($n = 30$) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values ranged from -20.0 to -14.8‰ (-17.7 ± 1.3 ‰) and 9.6 to 14.2‰ (12.4 ± 1.0 ‰), respectively.

Foraging assignment models

Based on migratory contingent membership as defined and determined from Griffin et al. (37, 38), a total of 236 Atlantic tarpon sampled for stable isotope analysis were assigned to the Eastern GOM contingent (Figure 1), with their initial search area for geo-assignment encompassing the eastern GOM (South Florida to Louisiana). In contrast, 110 individuals were assigned to the Eastern US Seaboard contingent, with their initial search area along the coast from South Florida to Virginia. Additionally, 71 individuals were captured in South Florida, and their search area for geo-assignment encompassed the entire southeastern US.

Monthly utilization distributions were estimated using dynamic Brownian bridge movement models from 85 acoustically tagged Atlantic tarpon, resulting in 67,557 detections ($6,404.4 \pm 6,705.0$ per individual; median 3,692) with tracking durations from 34 to 2,327 days ($1,280.6 \pm 609.5$ days, median 1,449) (Figure 1). After accounting for typical isotopic incorporation rates of fish fin (~ five months) and blood plasma (~ < three months) (41-44), composite monthly 95% probability contours largely encompassed coastal areas from Louisiana to Delaware. However, composite 95% probability estimates associated with fin samples (set to five-month composites) collected in April ($n = 26$) led to a restriction in the search area

to Florida and South Georgia. Further, if fin tissue samples were collected in March ($n = 2$), April, May ($n = 72$), or June ($n = 116$), composite 95% probability estimates led to search areas excluding coastal areas of Virginia and northward. Only fin samples collected in March and May led to the exclusion of Louisiana. Due to a faster incorporation rate associated with blood plasma (set to three-month composites), 95% probability estimates were more restrictive based on the month of sampling, with individuals captured in January-March having restricted search areas, compared to that of May-December (see Fig S8-S9 and *Search area* in SM). However, all blood samples were taken in April ($n = 12$), May ($n = 10$), June ($n = 6$), and July ($n = 2$).

A generalized additive model with ordinal date as the independent variable predicted the latitude for Atlantic tarpon ($F = 1,150,103.2$, $p < 0.001$, deviance explained = 46%), with high variation observed across different individuals ($F = 648.3$, $p < 0.001$, (Figure 1). The model predicted that Atlantic tarpon would be at higher latitudes during the months of July to October (max latitude: 39.16°N). Corresponding to the assumed incorporation rates for fin (five months) and blood plasma (three months), the 95% confidence intervals (CI) for the predicted latitude ranged from 23.63 to 33.01°N , while the 75% CI ranged from 25.26 to 31.44°N . These latitude predictions further constrained the ‘search areas’ in which to assign foraging landscapes for Atlantic tarpon based on capture date (see Fig. S10 in SM).

South Florida ($< 26.11^{\circ}\text{N}$) was more consistently assigned as the most probable foraging region for Atlantic tarpon, except for those captured in the Mid-Atlantic ($> 29.40^{\circ}\text{N}$, $> -81.50^{\circ}$) (Figure 2). Individuals sampled from this area had the highest assignment probabilities between Georgia and North Carolina ($30.74 - 36.09^{\circ}\text{N}$). Fish sampled from East Florida ($26.0-30.73^{\circ}\text{N}$, $> -81.40^{\circ}$) had the highest assignment probabilities in South Florida as well as in northeastern Florida and Georgia ($29.31 - 31.98^{\circ}\text{N}$). The Northern GOM ($> 29.00^{\circ}\text{N}$, $< -83.30^{\circ}$), including northwest Florida ($28.94 - 30.13^{\circ}\text{N}$), was assigned as a highly probable ($\geq 25\%$) foraging location for fish sampled in the Northern GOM, West Florida ($26.11-30.73^{\circ}\text{N}$, $< -81.79^{\circ}$), and South Florida (Figure 2).

Dependent on location and time of year, assignment probabilities varied among individuals (Figure 3), with the most likely foraging locations ranging from 40.8 to 966.5 km (296.2 ± 188.0 km SD) away from the initial capture location (see Fig. S11 and *Highest probability origin* in SM). Assignment probabilities for blood plasma (158.7 ± 113.7 km SD) were more spatially constrained relative to those from paired fin tissue samples (450.7 ± 205.8 km SD) (Figure 4), and the most probable foraging locations were, on average, closer than those derived from fin ($t = -7.4$, $df = 29$, $p < 0.001$). Sensitivity analysis completed using different trophic discrimination factors (TDFs) between Atlantic tarpon and inshore lizardfish indicated high assignment stability for both fin tissue and blood plasma. Regardless of the TDF, the assignment locations remained highly consistent for 20 out of 30 fin

tissue samples and 13 out of 30 blood plasma samples (see *Isotopic discrimination and sensitivity* in SM).

Discussion

In an era of accelerated environmental change and habitat loss, the effective conservation of highly migratory marine species requires nuanced approaches that can accurately identify the spatial extent of foraging grounds and determine how these vary across time, space, and among conspecifics (45). Our integrative analyses identified discrete foraging landscapes across migration routes that spanned thousands of kilometers for Atlantic tarpon in the southeastern US. The location of foraging landscapes varied by migratory contingents, with Eastern GOM contingent individuals most likely foraging in estuarine systems in the northern GOM, while individuals associated with the Eastern US Seaboard contingent were assigned to probable foraging locations along much of the mid-Atlantic coast. Despite these differences, overlap occurred within contingents, with South Florida emerging as a likely highly utilized foraging ground for both groups. We also observed temporal variation in the scale of foraging migrations by implementing assignment models using tissues with different isotopic incorporation rates. Foraging ranges inferred from blood plasma integrating ~3 months of ecological information were more localized, while those derived from fin clips integrating ~5 months of information often extended hundreds of kilometers from initial sampling locations. Importantly, because tissues integrate diet continuously as individuals move, isotopic values likely represent a spatial

average of resources acquired across more than one foraging area; assignment probabilities should therefore be interpreted as integrated foraging landscapes rather than single points, particularly for the longer-integrating fin tissue. Collectively, these findings provide rare empirical evidence of geographically distinct foraging areas, which may be analogous to avian staging grounds and supports the idea that discrete ecosystems support different stages of migration (46, 47).

Identification of discrete foraging grounds used throughout the migratory cycle of Atlantic tarpon supports foundational migration theory that posits animals optimize energetic costs by using predictable resource-rich habitats and stopover sites en route (11, 48). Although migration is energetically costly, it is critical to sustain fitness (49) and species have evolved strategies to offset these costs (50), such as exploiting environmentally-driven transport systems (e.g., winds, currents) (51, 52) or increasing food intake pre-emptively or along the migration route (53). In this context, identifying consistent foraging grounds used repeatedly by individuals becomes important for conservation and management (54-56), as loss or alteration to these areas may hinder aspects of an individual's life history (3, 57). Our results extend this framework into the marine realm, revealing that highly migratory fish such as Atlantic tarpon depend on a limited set of energetically important foraging areas. Protecting and improving these spatially discrete grounds is essential, as degradation of

even a single key site may compromise broader migratory success, individual fitness, and by extension long-term population viability.

Understanding foraging and habitat use patterns of migratory species like Atlantic tarpon is essential for informing conservation strategies that transcend static management boundaries, particularly as coastal ecosystems face habitat loss, freshwater alteration, and climate-driven shifts (58, 59). For instance, southern Florida, a region that has experienced large-scale habitat degradation from pollution and an altered freshwater flow regime through the Everglades (60, 61), emerged as consistent foraging grounds for individuals across both the Eastern GOM and Eastern US Seaboard contingents. Given their high reliance on this area, conservation efforts should focus on protecting coastal habitats and mitigating the impacts of altered freshwater flows, which can affect the composition and abundance of forage species in estuarine creeks and adjacent wetlands (62, 63). Key prey species for tarpon in southern Florida include mullet (*Mugil* spp.), anchovies (*Anchoa mitchilli*), herrings (*Harengula* spp.), pinfish (*Lagodon rhomboides*), and penaeid shrimp (*Penaeus* spp.) (64, 65). While some of these species are found across diverse habitat types, the continued loss and degradation of seagrass ecosystems due to altered hydrology and freshwater management activities (66-68) may affect habitat quality and prey availability for Atlantic tarpon in this region.

Similarly, both the northern GOM and the mid-Atlantic regions were inferred as probable important seasonal foraging zones. These regions host

productive estuarine ecosystems (69-73) that support various prey sources, including species in the family Clupeidae (74, 75), such as Gulf (*Brevoortia patronus*) and Atlantic (*Brevoortia tyrannus*) menhaden that are important prey for a variety of coastal predators (76, 77). Each year, individuals remain in these northern foraging areas for up to four months (37), reinforcing their role as important energetically-dense foraging grounds (78). Isotopic analyses of Atlantic tarpon eye lenses have further supported annual site fidelity to these northern systems (79), highlighting their role in long-term growth and survival. However, there is growing concern over the management of menhaden stocks (80-82) underscoring the need to explicitly integrate foraging hotspots into ecosystem-based fisheries management frameworks (3).

Methodological Considerations

Accurate assignment of critical foraging areas requires knowledge of the temporal stability of isoscapes and adequate spatial coverage along the migration routes of the focal species. Here, we developed $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isoscapes across the southeastern US using inshore lizardfish and refined isotopic predictions (33, 40) through Bayesian hierarchical models that incorporated spatial dependencies and environmental correlates. While this represents one of the most comprehensive marine isoscape efforts to date for this region, several limitations warrant mentioning. First, this approach assumed relative temporal stability in regional biogeochemical patterns over the sampling period. Although this assumption is supported by studies of the

Southern California Bight (δ^3) and persistent spatial features in continental shelf systems and inshore lizardfish (δ^3), incorporation of sampling year as a temporal effect would strengthen future iterations of this framework, provided sufficient samples exist when partitioned by year and location. Second, isoscape prediction variance varied spatially, with higher uncertainty in sparsely sampled regions (Fig. S5). Our Gaussian Markov random field approach (Fig. S3) explicitly accounted for spatial autocorrelation in the underlying data structure, predictions were constrained to areas within the range of the environmental covariates (δ^4), and our use of acoustic telemetry to constrain search areas helped mitigate assignment patterns reflecting variance structure. Nevertheless, assignment confidence differs across the study area. Baseline sampling was comparatively sparse across portions of southern and eastern Florida and the southeastern Atlantic coast (Georgia and the Carolinas), so assignments in these regions carry greater uncertainty, and expanded spatial coverage of baseline isoscape sampling, along with temporally explicit mapping of assignment confidence, should be priorities for refining future assignments. Third, although our kriging approach extended predictions across our study area, additional inshore lizardfish samples in shallower coastal estuarine habitats would have further constrained errors associated with the assignment probabilities. Moreover, because Atlantic tarpon are euryhaline and our baseline is primarily marine, low-salinity habitat use is not fully captured here; sulfur isotopes ($\delta^{34}\text{S}$) would offer a complementary tracer for distinguishing these sources in future

work. Fourth, some Atlantic tarpon isotope values fell outside predicted isoscape ranges (Fig. S12), likely reflecting trophic position differences, use of very shallow estuarine habitats not well-represented in our inshore lizardfish sampling, or temporal mismatches between tissue integration periods. These individuals have inherently lower assignment confidence. Reported tissue incorporation rates also carry uncertainty; however, because each individual's search area was independently constrained by telemetry, the exact incorporation window may have only limited influence on the assignments. Our sensitivity analysis across 121 TDF combinations (Figs. S13-S15) showed that assignment locations remained stable for most individuals, with consistent regional patterns across tissue types. While assignment probability distributions necessarily encompass broad spatial areas, the emergence of distinct regional patterns (South Florida, northern GOM, and Mid-Atlantic Bight) demonstrates that disparate ecosystems across multiple jurisdictions support different phases of Atlantic tarpon migrations. Despite inherent uncertainty, this regional-scale resolution aligns with spatial scales relevant for fisheries management and habitat conservation across multiple jurisdictions. Finally, it is important to recognize that assignment probability distributions reflect potential foraging locations and areas where prey originated, as prey species often migrate themselves. Despite these challenges, and given the prevalence of stable isotopes (85, 86) and electronic tagging (87) in animal ecology, combining these approaches provides a powerful framework for identifying where animals obtain their

food, especially when movement and foraging data can be paired at the individual level.

Conclusions and Future Directions

Our work highlights how the integration of movement and trophic information can reveal the spatially explicit nature of foraging landscapes relative to migration extent in a highly migratory marine species. While earlier work has focused on the large spatial extent of Atlantic tarpon migrations (37), our findings demonstrate that individuals consistently utilize discrete, energetically important habitats. Refining these approaches through expanded temporal and spatial coverage of baseline isoscapes, paired with continued advances in animal tracking technology, will further improve our ability to identify critical foraging areas for migratory species. These findings underscore the need for spatially explicit conservation strategies that account for migration corridors and the distinct resource hotspots that sustain populations (3). In this context, resolving where Atlantic tarpon forage enables place-based protection that jurisdictionally bounded management often misses. This includes prioritizing the South Florida, northern Gulf of Mexico, and Mid-Atlantic Bight foraging grounds for habitat protection and restoration, coordinating management across the jurisdictions these migrations cross, and integrating these foraging hotspots, and the prey that sustain them, into ecosystem-based fisheries management. This is especially pertinent given the increasing prevalence of marine predator species redistribution and habitat loss (1). When coupled with climate-driven

shifts in oceanographic conditions, these changes can disrupt the persistence of migratory pathways and the resource hotspots. Identifying and prioritizing these areas within the marine environment provides a foundation for more spatially nuanced conservation strategies for migratory marine vertebrates.

Materials and Methods

Generation of continental shelf isoscapes

Inshore lizardfish are ubiquitous across the GOM and Eastern US, and their stable isotope values reflect regional variation in regional ocean biogeochemistry (33, 40). As resident mid-trophic predators with limited movements, they integrate local food-web baselines and serve as a proxy for spatial biogeochemical variation, making them well-suited for constructing isoscapes relevant to higher trophic consumers such as Atlantic tarpon (33). Both inshore lizardfish and Atlantic tarpon are opportunistic foragers (largely piscivores) within coastal ecosystems, and trophic discrimination factors account for differences in trophic position between species and tissue-specific fractionation between Atlantic tarpon tissues (fin, plasma) and inshore lizardfish (see *Isotopic discrimination and sensitivity* in SM). Their ubiquity and site fidelity make them a suitable sentinel for regional isotopic baselines. Inshore lizardfish were collected from continental shelf habitats (mean $\pm$ SD depth: 12.6 ± 25.5 m) that overlap with Atlantic tarpon depth use ($> 80\%$ of their time in ≤ 10 m) (88). We constructed $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isoscapes using 534 (25.70 ± 3.90 cm; maturity ~ 19 cm) inshore lizardfish samples collected across the GOM and Eastern US. We compiled inshore

lizardfish dorsal muscle $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (see *Inshore lizardfish processing* in SM and the complete dataset in SM Data S1) from two published sources (Radabaugh et al. (40), $n = 226$ and Shipley et al. (33), $n = 286$), and collected additional samples ($n = 22$) from anglers and the Florida Fish and Wildlife Research Institute's Fisheries Independent Monitoring Program <https://myfwc.com/research/saltwater/fim/>). To account for spatial autocorrelation and to incorporate uncertainty across the study area, isoscapes were constructed from Bayesian hierarchical spatial models with integrated nested Laplace approximation via the 'R-INLA' package (<http://www.r-inla.org>) (89) (see *Bayesian hierarchical spatial modeling framework* in SM). With $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values as the dependent variables, we constructed two models with sea surface temperature (SST °C), chlorophyll *a* (mg/m^3), and depth (m) as independent variables (see *Environmental and depth data aggregation* in SM). Samples were collected over multiple years, but temporal effects were not modeled due to insufficient sample sizes when partitioned by year and location.

Atlantic tarpon

Approximately 1g of fin tissue (5 mm) was collected from the tip of the anterior lobe of the dorsal fin of each tarpon ($n = 417$; 155.77 ± 17.66 cm). Most samples were placed in 95% ethanol with a subset of duplicate samples ($n = 45$) placed on ice to derive ethanol correction factors (see *Tissue collection and processing* collection in SM). Given its faster rate of isotopic incorporation (41), we collected 5 mL of whole blood and extracted blood

plasma via centrifugation for 15 minutes from a subset ($n = 30$) of Atlantic tarpon (see *Tissue collection and processing* in SM and the complete dataset is in SM Data S2).

Foraging assignment models

Our assignment approach calculated the likelihood that Atlantic tarpon obtained dietary resources from each grid cell within movement-constrained search areas, generating continuous probability distributions across space rather than single-point assignments. A bivariate normal probability function defined the most likely probable foraging spaces of Atlantic tarpon. Assignments were made by estimating the likelihood that Atlantic tarpon $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values fall within a given raster cell and are derived from the isotopic difference between the sample and cell value relative to the total variance in the isoscape. Following that of Vander Zanden et al. (90) and Truemen et al. (2017), the bivariate normal probability function (*Equation 1*):

$$f(x,y|\mu_i, \Sigma) = \frac{1}{(2\pi\sigma_x\sigma_y\sqrt{1-\rho^2})} \times \exp\left(-\frac{1}{2(1-\rho^2)}\left[\frac{(x-\mu_x)^2}{\sigma_x^2} + \frac{(y-\mu_y)^2}{\sigma_y^2} + \frac{2\rho(x-\mu_x)(y-\mu_y)}{\sigma_x\sigma_y}\right]\right)$$

where $f(x,y|\mu_i, \Sigma)$ denotes the likelihood that an individual with adjusted isotopic values ($\delta^{13}\text{C} = x$ and $\delta^{15}\text{N} = y$) originates from a specific cell (i) within the isoscape. Isotopic values were adjusted using trophic discrimination factors that accounted for both trophic position differences between species and tissue-specific fractionation between Atlantic tarpon tissues (fin, plasma)

and inshore lizardfish muscle (see *Isotopic discrimination and sensitivity* in SM). The mean isotopic values for cell i are represented by μ_i , while Σ is the variance-covariance matrix. The correlation between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values across the isoscape is denoted by ρ . The pooled standard deviations for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, σ_x and σ_y , are calculated from the sum of the variances (see *Sum of Variances* in SM). We then extracted the probability estimates for each cell (P) and converted these probabilities into odds ratios using (*Equation 2*):

$$\text{Odds} = \frac{P}{1 - P}$$

This transformation provided the likelihood of an individual with a given isotopic composition originating from a specific cell within the isoscape, providing a more intuitive measure of the relative likelihood of occurrence. We then calculated the maximum odds value and normalized the odds ratios by dividing each by this maximum, enabling a standardized comparison across different cells. This process generates a probability surface across the search area for each individual (Figures 2-4). We refer to these normalized odds ratios, which range from 0 to 1, as 'resource probabilities' hereafter.

The assignment area for each individual was constrained by combining information from telemetry with rates of isotopic incorporation (Figure 1). For example, the incorporation rate defined here as the isotopic half-life (T_{50}) for fin tissue was assumed to be no greater than five months. Therefore, the search window encompassed the previous five months of movement data. Conversely, the incorporation rate for blood plasma was assumed to be no greater than three months (see *Search area* in SM). Atlantic tarpon have

repeatable migratory patterns and form two migratory contingents across the study area, one along the west coast of Florida and northward towards Louisiana, known as the Eastern GOM contingent, and the other along the east coast of Florida and northward towards Virginia, known as the Eastern US Seaboard contingent (37, 38). Depending on the sampling location in this study, we assigned Atlantic tarpon to either the Eastern GOM or Eastern US Seaboard contingents. Then, dependent on contingent membership, we confined our search areas for each sampled fish to corresponding habitat utilization maps derived from Atlantic tarpon satellite telemetry (36). If the sample came from an individual captured in South Florida, where the contingents overlap (37, 38, 91), we could not assign a contingent and extended the search area to the entire extent of the habitat utilization maps from South Florida to Louisiana and Virginia.

Next, we used data collected from an ongoing multi-year Atlantic tarpon acoustic telemetry tracking project that includes data for 85 tagged fish with an mean ($\pm$ SD) fork length of 143.6 ± 17.7 cm (see Griffin et al. (37) for tagging and monitoring details; SM, Table S1). Both isotope-sampled (155.8 ± 22.7 cm, $n = 417$, range: 111.8-208.3 cm) and acoustically tagged (143.6 ± 17.7 cm, $n = 85$, range: 112-183 cm) Atlantic tarpon were above or near maturity (~ 117.5 cm for males, 128.5 cm for females). These data were used to estimate monthly utilization distributions from dynamic Brownian bridge movement models (92, 93) using the 'Actel' (94) and the 'RSP' (95) packages. Dependent on the month of capture, the search area was then

constrained to the corresponding monthly 95% probability contour and the four months prior (five months in total) for fin tissue samples or two months prior (three months in total) for blood plasma samples.

To refine the search area, we determined the likely latitude range of a sampled Atlantic tarpon before capture. Using the ‘mgcv’ package (96), we constructed and validated a generalized additive mixed effects model with latitude as the dependent variable, derived from interpolated tracks using the ‘RSP’ package (95), ordinal date as the independent variable, and individual ID as a random effect. Ordinal date was modeled with a cyclic cubic regression spline smooth with six knots. Model diagnostics were assessed using the *gam.check* function, and the fitted model was then used to predict the potential latitude range for each individual for each day prior to capture (Fig. S10 in SM). Given the shorter incorporation period of blood plasma relative to fin tissue, we used narrower prediction intervals for plasma (75%) to reflect the higher temporal precision of this tissue, while retaining broader 95% intervals for fin, which integrates diet over a longer window. Lastly, we also restricted the search window to areas less than 20 m in depth, corresponding to Atlantic tarpon satellite telemetry data habitat utilization maps (36) and depth use of ≤ 10 m for $> 80\%$ of their time (88). Although Atlantic tarpon primarily occupy shallow coastal habitats, inshore lizardfish samples used here were collected from relatively shallow shelf environments (12.6 ± 25.5 m). As resident mid-trophic predators, inshore lizardfish integrate food-web baselines and capture regional biogeochemical gradients

across the shelf (33), providing an appropriate proxy for spatial isotopic variation relevant to Atlantic tarpon foraging.

Using the information on contingent assignment and space use estimates to define the most likely assignment probability search area, the most likely origin of Atlantic tarpon prey resources was generated for each individual by tissue type and averaged across each sampling region (Northern GOM, West, South, and East Florida, and Mid-Atlantic). Finally, to characterize the spatial scale of foraging relative to capture locations, we calculated the distance from each capture site to the grid cell with the highest assignment probability. We used a Welch Two Sample t-test to test if the distance from the sampling location from blood plasma was significantly different than that from fin tissue. Lastly, we tested the sensitivity of geographic assignment to variable TDFs as recommended for Bayesian isotope mixing models (97) (see *Isotopic discrimination and sensitivity* in SM). To assess the stability of assignment for individuals with paired fin and blood plasma samples, we plotted the change in assignment distance as a function of the discrimination value combination.

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Acknowledgments

We thank the many fishing guides and anglers who assisted with this project's sampling collection, especially Andy Allen, Carl Ball, George Beckwith, Ryan Clase, Court Douthit, Jeff DeBlieux, Danny Flynn, Matt Garrett, Edward Glorioso, Kevin Grubb, Bill Horn, Ben Kurth, Allen Mills, Gabe Nyblad, Kendall Osborne, Sam Pate, Jordan Pate, Cody Pierce, Albert Ponzoa, Cody Rubner, Chris Slattery, Barry Truitt, Andrew Tipler, Newman Weaver, Mark Yanno. We also thank the researchers who helped maintain the many arrays that span both the Gulf of Mexico and the Eastern US and those who shared detection data with us through integrated Tracking of Animals in the Gulf (iTAG), FACT network, Atlantic Cooperative Telemetry (ACT) network, and the Ocean Tracking Network (OTN). Lastly, we thank the Fishery-Independent Monitoring program (Fish and Wildlife Research Institute (FWRI), Florida Fish and Wildlife Conservation Commission (FWC)) for providing assistance with sample collection. In particular, we thank Meagan Schrandt, Jessie Heise, Eric Weather, and Kara Radabaugh from FWRI, FWC for their support related to sample collection and additional data. Portions of text editing and coding support for this manuscript were assisted by ChatGPT

(GPT-5, OpenAI, 2025). Prompts included requests for editing clarity, grammar adjustments, and assistance with R code drafting and troubleshooting.

Funding:

Bonefish & Tarpon Trust

Author contributions:

Conceptualization: LPG, ONS, JWB, SJC, MP, AJD

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Investigation: LPG, ONS, AJS, JWB, SAC, SJC, JJDR, SDN, MP, JW, AJD

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Writing—review & editing: LPG, ONS, AJS, JWB, SAC, SJC, JJDR, SDN, MP, JW, AJD

Ethics approval and consent to participate:

Handling procedures were conducted in accordance with the American Association for Laboratory Animal Science (IACUC protocol 2016-0049, University of Massachusetts). All participants consented to participation.

Consent for publication: All participants consented to publication.

Competing interests:

Authors declare that they have no competing interests.

Availability of data and materials:

All data are available in the supplementary materials.

Figures and Tables:

Fig. 1. Approach to designate assignment area. Assignment search area for each individual was constrained by combining information from telemetry with rates of isotopic incorporation, including from monthly averaged utilization distributions estimated from dynamic Brownian bridge movement models generated from Atlantic tarpon (*Megalops atlanticus*) acoustic telemetry detections (darker colors indicate higher use areas derived by averaging across each individual and month) **(a)**, migratory contingent assignment (adapted from Griffin et al. (37) **(b)**, and predicted latitude range probability based on ordinal date **(c)**.

Fig. 2. Collective resource probabilities. Atlantic tarpon (*Megalops atlanticus*) **(a)** fin tissue sample locations (red), and averaged resource probabilities across regions where samples originated from, including **(b)** Northern Gulf of Mexico, **(c)** West Florida, **(d)** East Florida, **(e)** South Florida, and **(f)** Mid. Atlantic. Brighter colors (yellow) indicate higher resource probabilities, while darker colors (blue) indicate lower resource probabilities.

Fig. 3. Individual resource probabilities. Example resource probability plots of individual Atlantic tarpon (*Megalops atlanticus*) across the Southeastern USA. Each panel includes fish ID, fork length (cm), date of capture, and location of capture (red circle). Brighter colors (yellow) indicate higher resource probabilities, while darker colors (blue) indicate lower resource probabilities.

Fig. 4. Distance to high resource probabilities. Boxplots **(a)** displaying distances to highest probability origins for paired fin tissue and blood plasma samples from individual Atlantic tarpon (*Megalops atlanticus*) across the Southeastern USA. Example resource probability plots of paired individuals **(b-e)**. The top row shows resource probabilities derived from the same individual, with panel **(b)** based on fin tissue and panel **(c)** based on blood plasma. The bottom row also shows probabilities from another individual, with panel **(d)** from fin tissue and panel **(e)** from blood plasma. Each panel includes fish ID, fork length (cm), date of capture, location of capture (red circle), and the highest probability assignment location (arrow). Brighter colors (yellow) indicate higher resource probabilities, while darker colors (blue) indicate lower resource probabilities. The sample location is at the start of the arrow and the point is the highest probability assignment location

Fig. 1

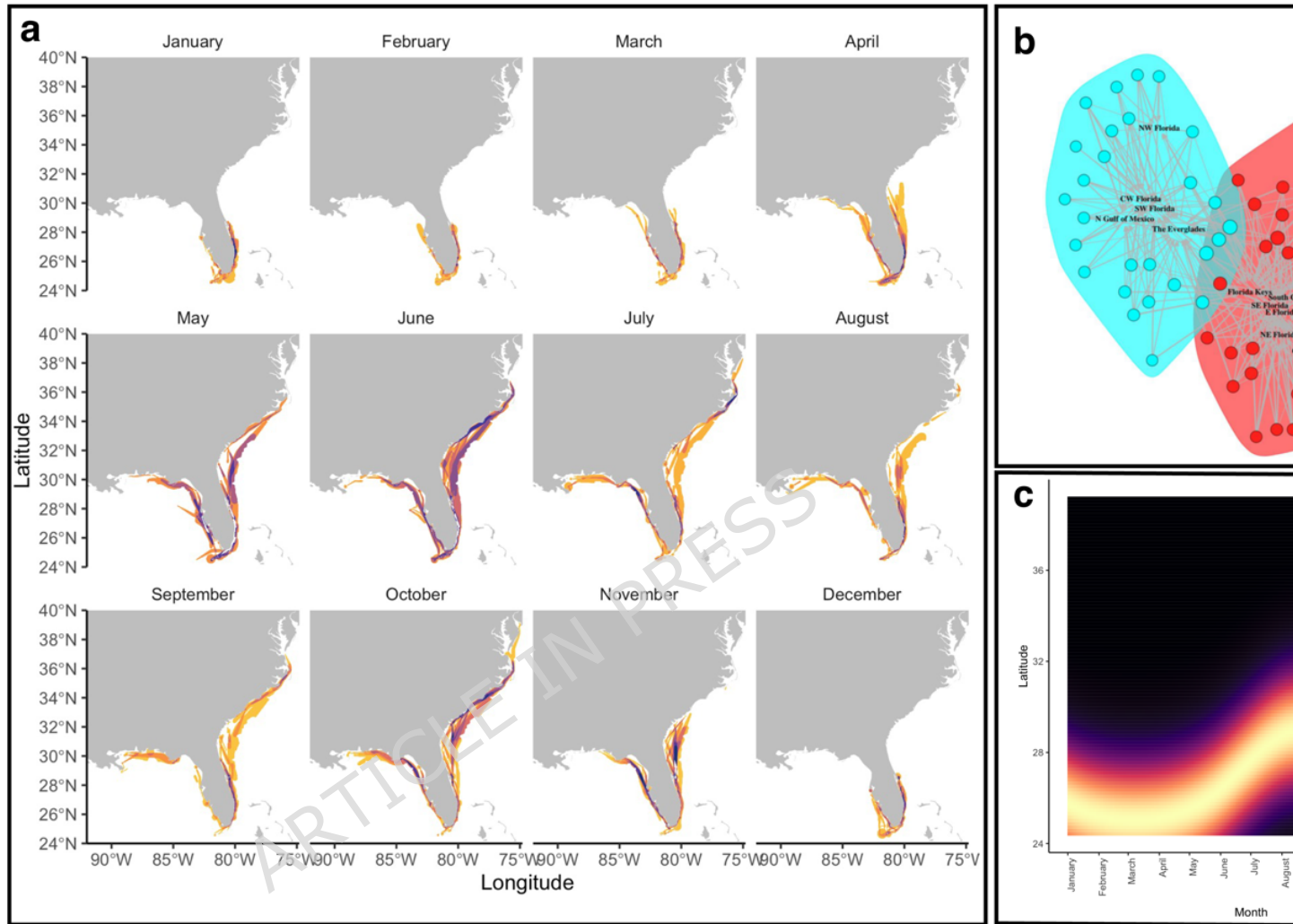


Fig. 2

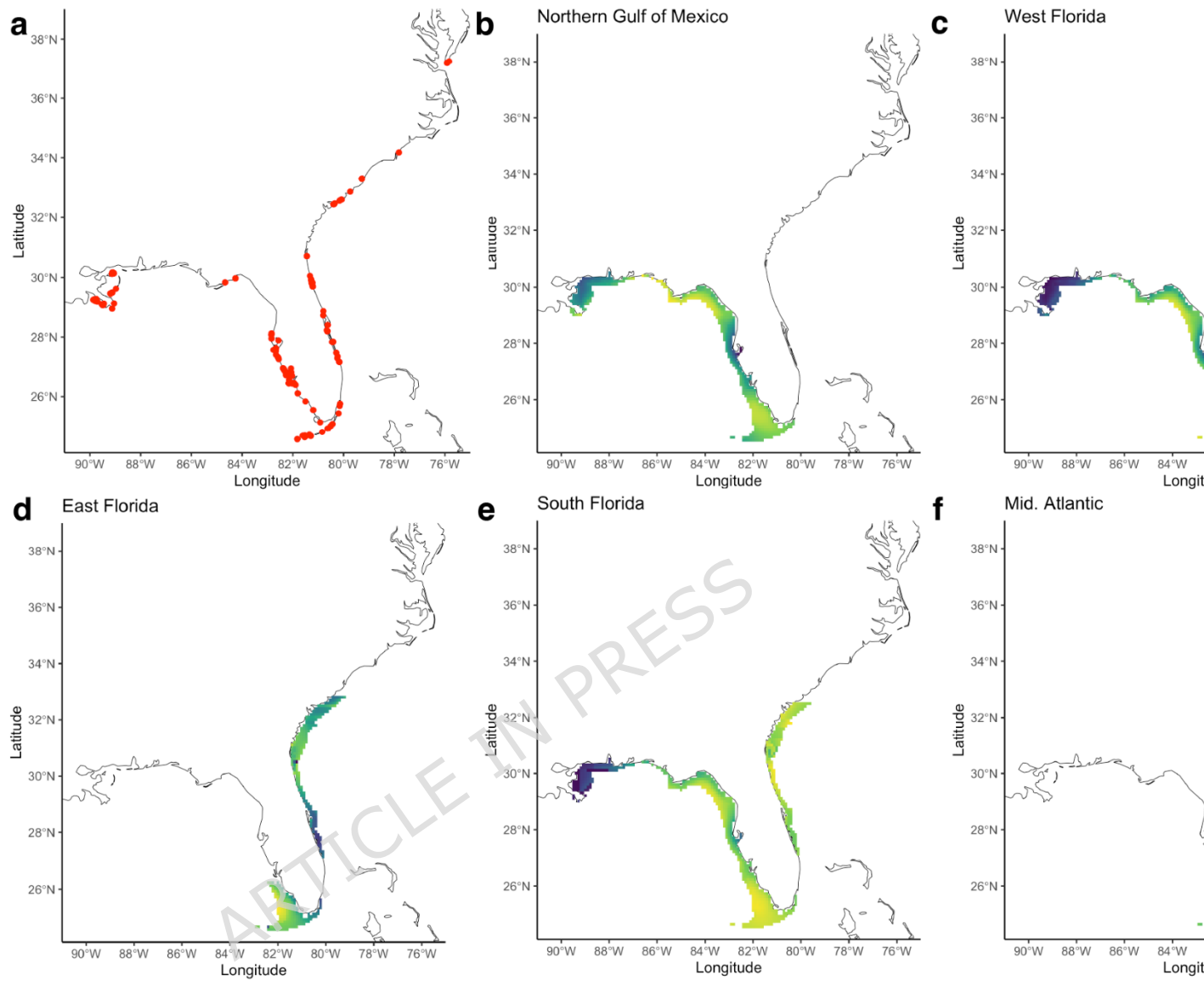


Fig. 3

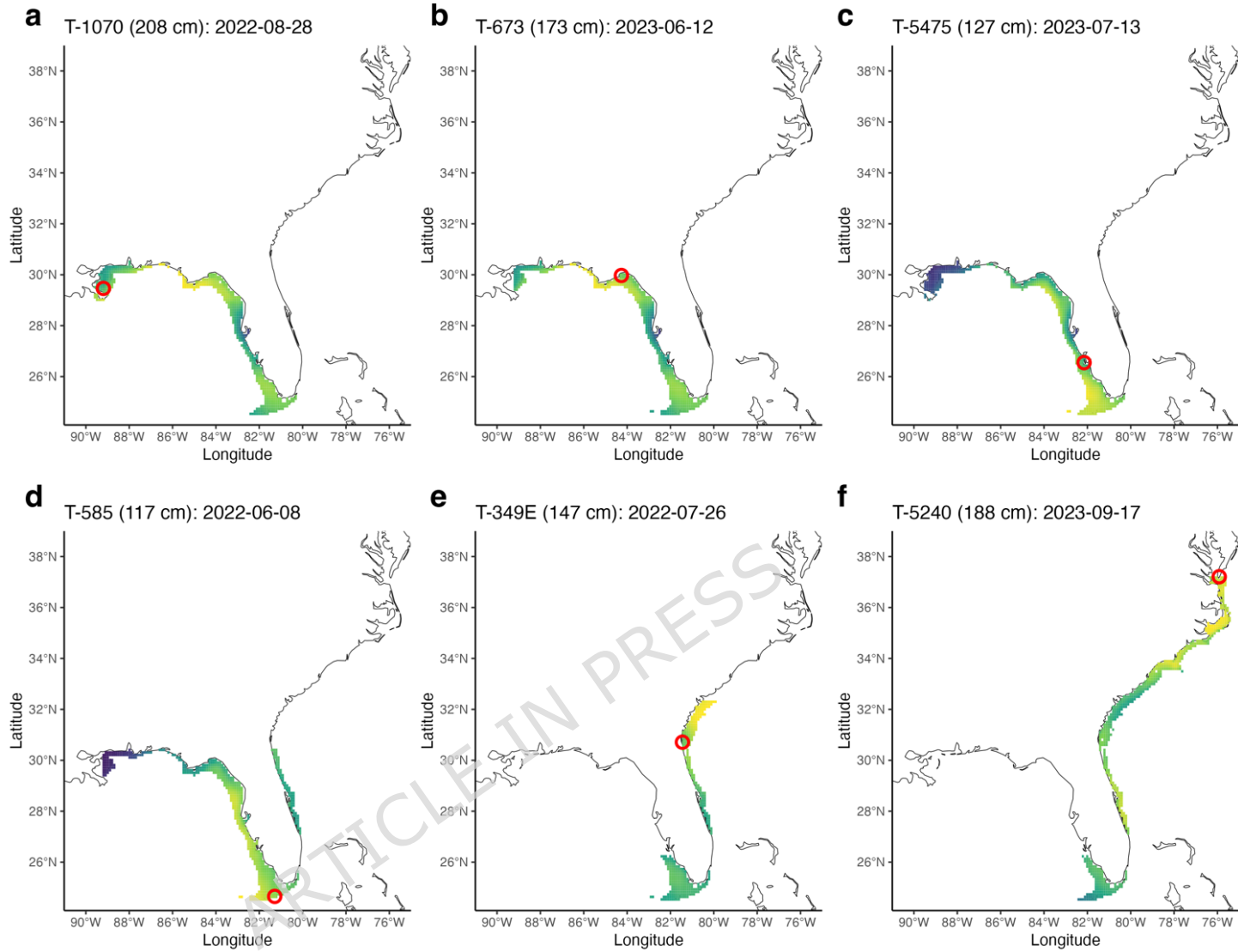


Fig. 4

