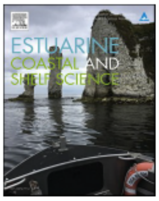
Estuarine, Coastal and Shelf Science 278 (2022) 108130

Contents lists available at ScienceDirect

Estuarine, Coastal and Shelf Science

journal homepage: www.elsevier.com/locate/ecss



Otolith stable isotope micro-sampling to discriminate poorly studied stocks: Crevalle Jack in the eastern gulf of Mexico

Carissa L. Gervasi[a,*], James A. Nelson[b], Peter K. Swart[c], Rolando O. Santos[a], Ryan J. Rezek[d], W. Ryan James[a], Amanda E. Jefferson[e,f], J. Marcus Drymon[e,f], Jessica Carroll[g], Ross E. Boucek[h], Jennifer S. Rehage[a]

[a] *Florida International University, Institute of Environment, 11200 SW 8th St, Miami, FL, 33199, USA*
[b] *University of Louisiana at Lafayette, Department of Biology, 410 E St Mary Blvd, Lafayette, LA, 70503, USA*
[c] *University of Miami, Department of Marine Geosciences, Rosenstiel School of Marine and Atmospheric Science, 4600 Rickenbacker Causeway, Miami, FL 33149, USA*
[d] *Coastal Carolina University, Department of Marine Science, 100 Chanticleer Drive East, Conway, SC, 29526, USA*
[e] *Mississippi State University, Coastal Research and Extension Center, 1815 Popps Ferry Rd., Biloxi, MS, 39532, USA*
[f] *Mississippi-Alabama Sea Grant Consortium, 703 East Beach Dr, Ocean Springs, MS, 39564, USA*
[g] *Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute, 100 8th Ave. SE, St. Petersburg, FL, 33701, USA*
[h] *Bonefish & Tarpon Trust, 2937 SW 27th Ave, Suite 203, Miami, FL, 33133, USA*

ARTICLE INFO

Keywords:
Stable isotopes
Otolith microchemistry
Otolith micro-sampling
Crevalle jack
Population connectivity

ABSTRACT

Developing conservation and management strategies for species with complex life histories, broad spatial distributions, and long lifespans is notoriously difficult. Too often managers cannot identify critical habitats nor vulnerable life stages because of the sheer scale of migration or uncertainty about connectivity among populations. Advancements in otolith stable isotope analysis, and specifically sampling of discrete otolith layers, have provided opportunities to assess lifetime migrations and connectivity without extensive, long-term field sampling. Here, we compared carbon and oxygen stable isotope values in discrete otolith layers for Crevalle Jack (an unregulated and data-poor species) captured in two isotopically distinct regions (Alabama and the Florida Keys). Our goal was to address vital questions about how broad-scale movement patterns through ontogeny differ between the two regions and whether connectivity occurs throughout the life history. Our results revealed that Crevalle Jack appear to inhabit inshore nursery areas at age-0, before migrating to coastal/offshore habitats between age-1 and age-2. Comparisons between fish collected in northeastern and southeastern Gulf of Mexico regions revealed significant differences in the patterns of stable isotope values throughout the life history and in otolith $\delta^{13}C$ values. Despite these differences that suggest a separation of the two populations, individual variability was significant, hindering our ability to determine whether fish from the two regions represent separate, self-recruiting stocks. Our research illustrates the potential of otolith stable isotope micro-sampling as a tool for examining broad-scale movement and migration patterns of fishes, and informing future research and management.

1. Introduction

The understanding of population connectivity and dispersal pathways is essential to effective fisheries management. Knowledge of connectivity patterns in particular is crucial for delineating appropriate spatial scales of management and for specifying vital subareas to protect from exploitation (Fogarty and Botsford, 2007). Misaligned stock assessment and population boundaries can have severe consequences, including over-exploitation and localized depletion (Berger et al., 2021; Ying et al., 2011). Additionally, successful implementation of marine protected areas requires that the size and location match the spatial distribution and habitat use of the species of interest (Kramer and Chapman, 1999; Moffitt et al., 2009). However, population connectivity (specifically ecological connectivity) can occur over multiple spatio-temporal scales and can therefore be challenging to assess. Ecological connectivity is defined as the exchange of individuals among local populations that can affect population dynamics and demographics (Sale et al., 2010). This exchange can occur over multiple life history

---

[*] Corresponding author.
E-mail address: cgerv002@fiu.edu (C.L. Gervasi).

https://doi.org/10.1016/j.ecss.2022.108130
Received 20 October 2021; Received in revised form 14 October 2022; Accepted 19 October 2022
Available online 23 October 2022

stages, and includes larval dispersal, juvenile recruitment and retention, and large-scale movements of sub-adults and adults. Ecological connectivity is the basis of metapopulation ecology (Levins, 1968) and contingent theory (Hjort, 1914; Secor, 1999), paradigms that are increasingly being used to explain empirical observations of fisheries dynamics (Cadrin and Secor, 2009).

Despite increasing recognition of the importance of ecological connectivity and metapopulation processes in fisheries, many stock assessments are unable to account for complex population structures, often assuming that a fish stock is a single, spatially homogeneous population stemming from a single larval pool (Archambault et al., 2016). Spatially-explicit population models are becoming increasingly common, but studies of population connectivity mainly focus on early life history stages (e.g., Hinrichsen et al., 2011; Miller, 2007). Juvenile and adult-mediated connectivity is largely understudied, despite research showing that adult movements can significantly affect metapopulation structure and dynamics (Frisk et al., 2014). It is therefore crucial that population connectivity of exploited fishes is assessed at all life history stages, and that this spatial structure is incorporated into population models and stock assessments.

Assessment of population connectivity throughout the life history of a species is challenging, often requiring extensive, long-term field studies (e.g., routine fisheries-independent sampling or tag-recapture/animal tracking projects) to examine movement/dispersal patterns of the different life stages. However, advances in otolith microchemistry provide opportunities to rapidly examine movement patterns over the entire life history of an individual. Otoliths remain the most common structure used to age fishes, since clear growth bands are evident for most species (Campana, 2001). Additionally, because otoliths are inert, trace elements and isotope ratios are incorporated into otoliths as a fish grows, affected by ambient water concentrations. If a fish resides in a certain body of water for a portion of its life, the chemical signature of that water body will be retained in the section of the otolith corresponding with that period of the fish's life (Walther and Limburg, 2012). Because of these attributes, otoliths have been used in fisheries science to reconstruct environmental histories (Campana, 1999; Walther and Limburg, 2012).

The applications of otolith chemical composition are numerous and include identifying nursery areas or natal origin (Gerard and Muhling, 2010; Thorrold et al., 2001), reconstructing migration patterns (Avigliano et al., 2021; Sturrock et al., 2012; Walther and Limburg, 2012), retrospectively assigning adults to areas of origin (Gerard et al., 2015), and determining stock structure (Tanner et al., 2016). Furthermore, changes in chemical composition over the lifetime of an individual fish can be discerned via sampling of discrete otolith layers (i.e., micro-sampling; Jamieson et al., 2004). Stable isotope micro-sampling throughout the entire otolith is a relatively recent approach that has distinct advantages, including establishing environmental histories of individual fish, examining partial migration, and comparing life history patterns among populations (Høie et al., 2004a; Jamieson et al., 2004; Kawazu et al., 2020; Wang et al., 2021; Weidman and Millner, 2000). More often though, studies concentrate on broad regions of the otolith (e.g., core vs. edge) corresponding to different life history stages (e.g., birth vs. age at collection), potentially missing critical transition periods or periods of connectivity throughout the entire life history.

The purpose of this study was to examine lifetime migration patterns of Crevalle Jack (*Caranx hippos*) captured from two distinct regions of the eastern Gulf of Mexico (the Florida Keys and Alabama). The Crevalle Jack is an important part of the recreational fishery in both these areas, yet is currently unregulated and there is evidence that population abundance may be declining (Gervasi et al., 2022). Specifically, our study aimed to determine whether otolith micro-sampling could be used to distinguish between fish from each region based on differences in stable isotope values throughout otoliths. If separation in isotope values is evident throughout the life history, it would suggest a lack of mixing between the two areas, which has implications for stock assessment and management. By comparing stable isotope chemistry in discrete otolith layers between the two groups, our research addresses vital questions about how broad-scale movement patterns through ontogeny differ between the two regions. In addition to aiding in conservation and management, our results demonstrate the potential of otolith stable isotope micro-sampling as a tool for assessing lifetime population connectivity of fishes that can better inform future population models and stock assessments.

2. Material & methods

2.1. Study species

The Crevalle Jack is a large marine fish native to the Atlantic coast of North America and the Gulf of Mexico (GOM; Smith-Vaniz and Carpenter, 2007). The species is targeted by both commercial and recreational anglers (Kwei, 1978) but is unregulated in all coastal U.S. states within the species range and is considered data-poor (i.e., there is not enough information available to estimate relative stock status and appropriate reference points). In recent years, a decline in population abundance has been observed in the Florida Keys region (Gervasi et al., 2022) but the extent of the decline is unknown. Knowledge of migration patterns and population connectivity is, therefore, crucial for conservation and management of the species. However, little research has been conducted to date on Crevalle Jack biology and ecology, and critical questions remain about stock structure and life history.

Spawning is suspected to occur in subtropical and tropical waters, but in the Western Atlantic, it has only been observed at Gladden Spit, Belize, a promontory reef that serves as a multi-species spawning aggregation site (Heyman and Kjerfve, 2008). Although other species in the Carangidae family have been observed spawning in continental shelf edge habitats throughout the GOM (Heyman et al., 2019), only indirect evidence (courtship behavior and color changes) of Crevalle Jack spawning has been observed at a marine sanctuary in the northwestern GOM (Helies et al., 2016). However, Crevalle Jack larvae have been observed throughout the GOM, mostly in the spring and summer months (Ditty et al., 2004; Flores-Coto and Sanchez-Ramirez, 1989). Post-larval fish have also been observed in offshore waters in the summer and fall (Mohan et al., 2017). Young-of-the-year Crevalle Jack are found in coastal estuaries throughout the Atlantic and GOM (Flaherty et al., 2013; McBride and McKown, 2000; Nelson, 1992), but the linkages between these juvenile nursery habitats and adult populations are unknown. McBride and McKown (2000) examined seasonal abundance and size structure of Crevalle Jack from New York to Florida. Their findings suggested that larvae spawning at subtropical and tropical latitudes are dispersed via ocean currents up the Atlantic coast and into temperate estuarine habitats, and at least some individuals can migrate back down to the tropics and return to the spawning sites. This suggests that Crevalle Jack throughout the Atlantic coast of the U.S. may represent a single stock, but evidence is limited and connectivity with Gulf of Mexico, Caribbean, and South American populations is unknown. Veteran fishing guides in the Florida Keys have observed that large, adult Crevalle Jack appear to migrate seasonally into and out of the south Florida region, but where these individuals go is unknown (Gervasi et al., 2022). Previous research estimates that Crevalle Jack age at 50% maturity is about 3–4 years, but maturation data comes from a single population in the Caribbean (Caiafa et al., 2011). Adult Crevalle Jack are found in a variety of habitats, including coastal flats, coral reefs, artificial reefs, channels, and canals (Smith-Vaniz and Carpenter, 2007), but again, movement and migration patterns of adults is currently unknown.

2.2. Focal populations and alternative hypotheses

Adult Crevalle Jack were collected from two coastal regions: the Florida Keys (FK) and coastal Alabama (AL; Fig. 1). These regions were selected for several reasons. First, there is evidence that several

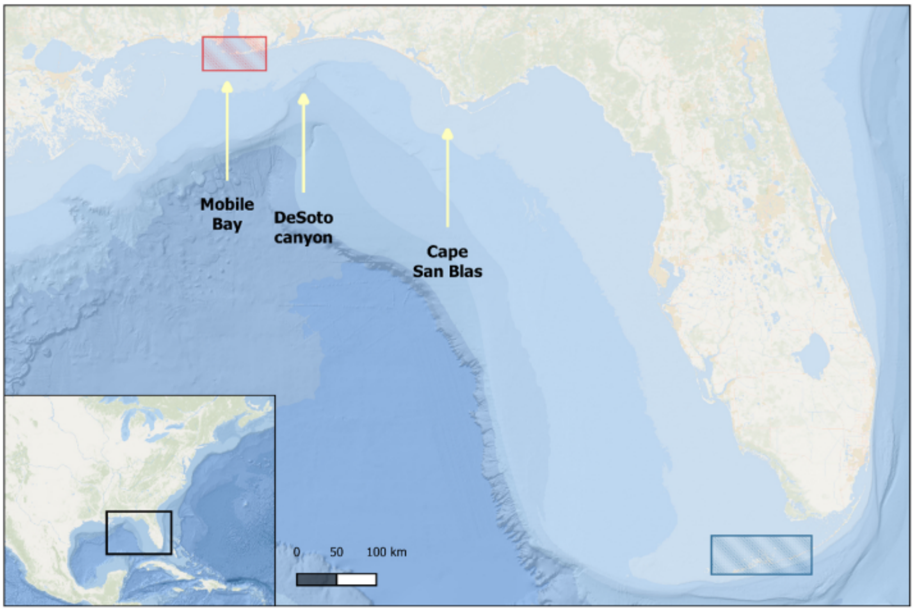


Fig. 1. Approximate capture locations of Crevalle Jack in Alabama (red hashed box) and Florida (blue hashed box) sampled for otolith stable isotope analysis. Exact GPS coordinates of capture locations were not recorded. Yellow arrows point to Mobile Bay, the DeSoto canyon, and Cape San Blas, areas that may serve as zoogeographic divides in the northern Gulf of Mexico. Inset map highlights study area in the southeastern United States. Map credit Esri, GEBCO, NOAA, National Geographic, DeLorme, HERE, Geonames.org, and other contributors. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

ecological and faunal divides exist in the northern GOM. Studies have suggested that zoogeographic breaks occur at Mobile Bay (Drymon et al., 2020), the DeSoto Canyon at the eastern edge of the Mississippi River basin (Defenbaugh, 1976; Gallaway, 1981; Ward, 2017), and at Cape San Blas at the eastern end of the Florida panhandle (Estes, 2016; Zieman and Zieman, 1989). Fish and invertebrate assemblages have been shown to differ on either side of these boundaries, suggesting that AL and FK Crevalle Jack may represent distinct populations. Secondly, according to Marine Recreational Information Program data (MRIP; NOAA, 2021), out of all coastal Atlantic and GOM states, recreational catch of Crevalle Jack from 2000 to 2021 was highest in Florida, followed by Alabama. Total catch from Alabama was more than twice the next highest-ranking state (North Carolina). Assuming recreational landings are a proxy for fish abundance, the MRIP data suggest that the Florida and Alabama regions may encompass centers of abundance for the species within the U.S. The Florida Keys was specifically chosen because previous research found evidence of a decline in Crevalle Jack abundance in the area, prompting management concerns (Gervasi et al., 2022). To successfully manage the population in Florida, it is important to understand if connectivity between Florida and other management jurisdictions exists. Finally, AL and FK represent two isotopically distinct regions, with both δ^{18}O and δ^{13}C values of water samples, sediments, and primary producers varying substantially. Coastal areas near the large rivers of the north-central GOM receive substantial inputs of freshwater depleted in ^{18}O, with average δ^{18}O of river samples ranging from −2.2‰ to as low as −6.6‰ in the Mississippi River (Wagner and Slowey, 2011), and terrestrial carbon depleted in ^{13}C, with values near −27‰ (Fry, 1983). In the Florida Keys, limited freshwater input combined with high rates of evaporation lead to ^{18}O-enriched waters (1.7‰ in the Upper Florida Keys; Sternberg and Swart, 1987), and abundant ^{13}C-enriched seagrasses and macroalgae (δ^{13}C ~ −10 to −15‰) grow in nearshore areas and are exported offshore (Fry, 1983).

Oxygen stable isotope values in the ocean are influenced by evaporation and freshwater input, and correlate with salinity (Epstein and Mayeda, 1953). During incorporation into biominerals (i.e., aragonite and calcite in shells and otoliths), stable isotopes of oxygen are fractionated and the magnitude of fractionation is directly related to water temperature according to the following equation (Trueman and St. John Glew, 2019):

$$\delta^{18}O_{otolith} - \delta^{18}O_{water} = B - A(T), \tag{1}$$

where T is water temperature and A and B are species-specific coefficients. Average annual sea surface temperature from NOAA sea surface temperature satellite data from 2010 to 2020 was about 25 °C in the northeastern GOM and about 27 °C in the southeastern GOM (Huang et al., 2015). This temperature difference is minor compared to the differences in $\delta^{18}O_{water}$ values between regions, so we expected to observe higher $\delta^{18}O_{oto}$ values in FK fish than in AL fish at least in the otolith edge region (point of capture).

The carbon isotope composition of fish otoliths is much more complex than the oxygen isotope composition, and is deposited in disequilibrium with the surrounding environment (Martino et al., 2020). Carbon isotopes in otoliths are a combination of dissolved inorganic carbon (DIC) in the aquatic environment and oxidized organic carbon derived from the diet of the fish (Solomon et al., 2006). Studies have estimated that the majority of otolith isotope composition is derived from DIC (~80%) with the remaining 20% derived from the diet (Høie et al., 2003; Nelson et al., 2011; Solomon et al., 2006; Tohse and Mugiya, 2007; Weidman and Millner, 2000). However, $\delta^{13}C_{DIC}$ values in coastal waters exhibit a fairly limited range (approximately −2‰–2‰), with ^{13}C often more depleted in estuarine and freshwater systems than in marine systems (Bouillon et al., 2011). Metabolism also affects $\delta^{13}C_{oto}$ values, as an increase in respiration and metabolic carbon dioxide increases the proportion of metabolically sourced carbon in the blood, which is deposited into the otolith (Martino et al., 2020). There is an inverse relationship between $\delta^{13}C_{oto}$ values and temperature, as temperature is a primary driver of metabolic rate (Martino et al., 2020). Due to the minor difference in average temperatures between GOM regions, we expected that changes in metabolic rate through ontogeny would be similar among all sampled Crevalle Jack, regardless of the region where they were collected. And since $\delta^{13}C_{DIC}$ values in coastal waters are rather homogeneous, we therefore expected that any difference in $\delta^{13}C_{oto}$ values between AL and FK fish would be mainly attributed to the δ^{13}C values of basal organic material. Therefore, we expected that FK Crevalle Jack would have higher $\delta^{13}C_{oto}$ values than AL Crevalle Jack at least in the otolith edge region.

If juveniles exhibited local recruitment (i.e., if the two populations represented separate, self-recruiting stocks), we expected the $\delta^{13}C_{oto}$ and $\delta^{18}O_{oto}$ values of FK fish to be significantly different than the values for AL fish throughout the otoliths (H1; Fig. 2). Alternatively, if recruitment to both adult locations was from common nursery grounds, we would expect an overlap in the $\delta^{13}C_{oto}$ and $\delta^{18}O_{oto}$ values in the

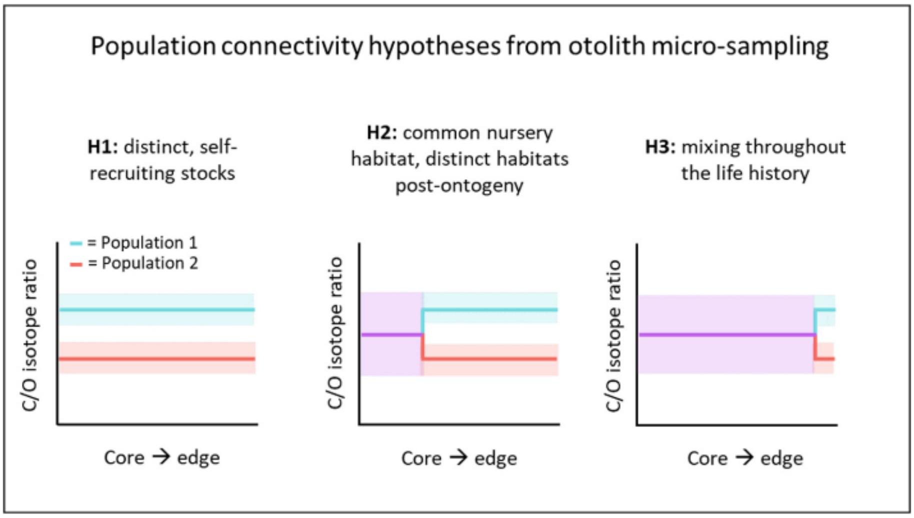


Fig. 2. Hypotheses concerning population connectivity between Florida Keys (blue lines) and Alabama (red lines) Crevalle Jack. Diagrams show simplified expected otolith stable isotope results corresponding to each hypothesis, with shaded regions denoting expected ranges of individual transects. If the two populations represent distinct, self-recruiting stocks (H1), we would expect $\delta^{18}O_{oto}$ and $\delta^{13}C_{oto}$ values to differ between populations throughout the otolith, regardless of the actual isotope ratio values, with no overlap between individuals from the distinct regions. If there are common nursery habitats but distinct habitats post-ontogeny (H2), we would expect overlap in the $\delta^{18}O_{oto}$ and $\delta^{13}C_{oto}$ values at earlier ages, with potentially substantial individual variability indicative of random distribution amongst juvenile habitats, followed by a divergence to different values post-ontogeny. If mixing between populations occurs throughout the life history (H3), we would expect overlap in $\delta^{18}O_{oto}$ and $\delta^{13}C_{oto}$ values everywhere except the otolith edge (point of capture), with substantial variability amongst individual fish. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

juvenile regions, followed by a divergence to either the FK or AL adult habitats (H2; Fig. 2). Adult connectivity would be evidenced by an overlap in the isotope values throughout adult ages (H3; Fig. 2). Otolith micro-chemistry has been previously used to test similar hypotheses about migratory patterns and connectivity of other fish species (Avigliano et al., 2021).

All FK fish were collected opportunistically in cooperation with local charter boat captains and recreational fishermen between 2019 and 2021. Otoliths from AL fish were collected by Mississippi State University (MSU) scientists from fish harvested by recreational anglers during the annual Alabama Deep Sea Fishing Rodeo from 2017 to 2019. Exact coordinates of capture locations were not recorded for most fish, but the broad area of capture was documented in all cases (Fig. 1). We aimed to analyze otoliths from the oldest fish possible so we could capture the full time series of movements for each population. However, in Florida, fish over 4-years old were rarely encountered by charter boat captains, so we limited our analyses to fish 4–5 years old. A total of 12 otolith samples were collected for analysis per population ($n = 24$ total; Supplementary, Table S1), with multiple transects milled per otolith for stable isotope analysis ($n = 426$ total transects).

2.3. *Otolith sectioning and aging*

The left and right otoliths from each fish were embedded, sectioned, and mounted to microscope slides for further analysis, with the left otoliths used for aging and the right otoliths used for stable isotope analysis. We first embedded both otoliths in epoxy using a silicone mold and a two-part epoxy resin. Once solidified, embedded otoliths were sectioned through the nucleus using an Isomet low-speed diamond bladed saw with four blades separated by spacers to produce three thin sections per otolith. For the left otoliths, a 0.5 mm spacer was used, such that resulting thin sections were approximately 0.5 mm thick for aging. For the right otoliths, a 0.6 mm spacer was used to produce thin sections approximately 0.6 mm thick. These thicker sections were used for stable isotope analysis as they provided a bit more otolith material for analysis. All thin sections were rinsed with water or 95% ethanol and adhered to clear microscope slides using a toluene-based mounting medium. Slides were allowed to dry for a minimum of 48 h before further analysis.

Using the left otolith, opaque zones were counted from the core to the edge using a stereomicroscope following standard aging protocols (VanderKooy et al., 2020). Age class was determined based on the number of opaque zones and summer annulus deposition (Snelson, 1992), i.e., age was determined as the number of opaque zones unless the fish was collected between January 1 and July 31 and the margin code was 3 or 4. In this case, age was assigned as the number of opaque zones plus one. Each fish from the Florida Keys was read with at least two blind reads at the Florida Fish and Wildlife Conservation Commission Fish and Wildlife Research Institute (FWRI) in St. Petersburg, FL. If the two reads disagreed, then a third read was conducted, and the final age was determined from the consensus age of the three reads. Each fish from Alabama was aged by two readers at MSU. If the two readers disagreed on an age assignment, a third reader aged the otolith and final age was assigned if two out of the three readers agreed. If all three readers disagreed, then the first two readers consulted with each other and either reached an agreement or deemed the otolith unreadable.

2.4. *Stable isotope analysis*

Oxygen and carbon stable isotopes can be used to examine spatial connectivity since stable isotope values vary predictably across the Gulf of Mexico as a function of climate and nutrient regimes (McMahon et al., 2013; Trueman et al., 2012). Sectioned otoliths not used for aging (right sagittal) were first photographed using a high-resolution camera affixed to a stereomicroscope. Using ImageJ software (Abràmoff et al., 2004), the approximate width of each growth band in mm was measured. Otoliths were then sampled using a New-Wave micromill in the University of Miami Stable Isotope Laboratory (Fig. 3). With the micromill system used in this study, the user manually traces transects across the sample region of interest on an image of the otolith on the computer screen. The computer then interpolates between two transects at a fixed distance with the material from each pass being milled on the advancing edge of the cutting blade. Transects were milled starting from the otolith edge and moving in towards the core in 0.05 mm increments for a maximum of 21 transects per otolith (range = 16–21). Increments of 0.05 mm between transects were chosen to maximize temporal resolution while ensuring enough material was available for analysis (at least 0.04 mg of powder per transect was required). Powdered material was collected in glass vials for subsequent analysis. The $\delta^{18}O_{oto}$ and $\delta^{13}C_{oto}$ values of the multiple transects of each analyzed otolith were measured using a ThermoQuest Finnigan Delta Plus Mass Spectrometer (Thermo Fisher Scientific, Inc., Bremen, Germany) attached to a Kiel III automated carbonate device. Internal standards (six within each run)

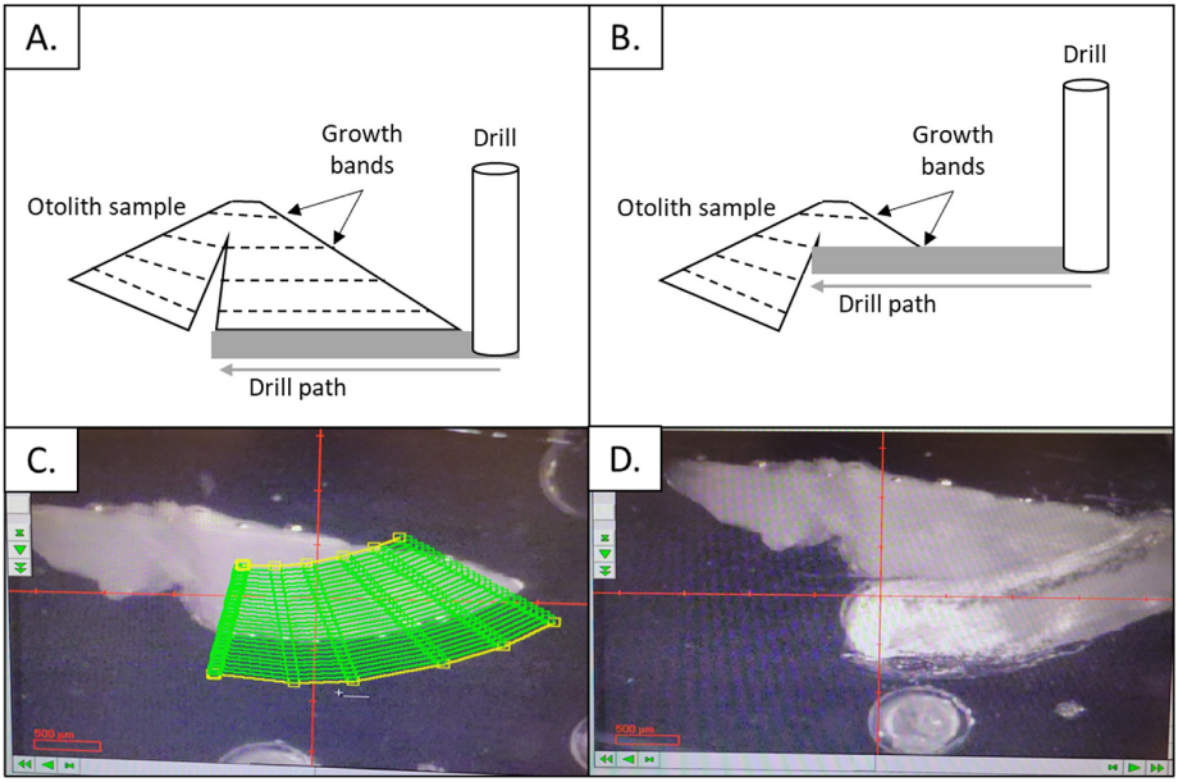


Fig. 3. Simplified schematic diagram of the micromilling system used in this study. The initial drill path runs parallel to the edge of the otolith section (A). Powdered sample is collected, and the drill is moved up the sample towards the core in increments of 0.05 mm until the entire otolith has been sampled. Drill path partway through the otolith (B). Image of the user-drawn initial and final drill paths (yellow lines) and computer interpolated drill paths (green lines) (C). Image of the otolith sample with the initial drill path completed (D). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

calibrated to NBS-19 (National Bureau of Standards) were processed along with a batch of 40 samples. The measured values were corrected for the usual isobaric interferences and are reported relative to Vienna Pee Dee Belemnite (V-PDB) using the conventional notation. Standard deviations determined on the standards were less than 0.05‰ for $\delta^{13}C$ and less than 0.1‰ for $\delta^{18}O$.

2.5. Statistical analysis

According to independent 2-group t-tests for each growth band, there were no significant differences in growth band widths between the two groups of Crevalle Jack ($p > 0.05$ for all *t*-tests). We therefore assumed growth rates were approximately the same between AL and FK and transect numbers corresponded to the same time in each fish's life. A series of regression models were fit to the carbon and oxygen data, with $\delta^{18}O_{oto}$ or $\delta^{13}C_{oto}$ values as the dependent variable. The goal of the regression modeling was to examine the typical trends in $\delta^{18}O_{oto}$ and $\delta^{13}C_{oto}$ values throughout the life history of Crevalle Jack and determine if isotopic profiles differed significantly between fish captured in isotopically distinct regions. Regression models were employed in a similar study that examined broad scale migration patterns of the Red-throat Emperor, *Lethrinus miniatus*, using otolith stable isotope chemistry (Currey et al., 2014). The authors used models to test for significant differences in isotope signatures throughout otoliths by latitude, similar to how our study aimed to test for differences by region.

We initially fit several simple generalized linear models (GLMs; Nelder and Wedderburn, 1972) to the isotope data (linear, logarithmic, quadratic, and cubic), with $\delta^{18}O_{oto}$ or $\delta^{13}C_{oto}$ values as the dependent variable and transect number (proxy for fish age) as the only independent variable. Residuals and q-q plots were used to assess normality and homogeneity of variance assumptions. For all models, the residuals did not appear to follow a normal distribution, thus violating the model assumptions. Linear models assume that there is a linear relationship between continuous dependent (Y) and independent (X) variables. However, this is not always the case. Real relationships in nature can have many different shapes that are not necessarily linear (Marrie et al., 2009). From an ecological point of view, it makes sense that the relationship between fish age and otolith stable isotope values may not be linear, since movement patterns of fishes are known to vary at different life stages (Kurth et al., 2019). Generalized additive models (GAMs; Wood, 2006) provide a robust way to model nonlinear trends. GAMs are basically extensions of GLMs that allow the expected independent variable to vary smoothly with a continuous dependent variable (Knape, 2016). Furthermore, GAMs can be extended to incorporate random variables in a mixed model format (GAMM). Hanson et al. (2013) used GAMM models to reconstruct marine life-history strategies of Atlantic salmon, *Salmo salar*, L., from otolith stable isotopes. Following a similar methodology, GAMM models were fit in this study to Crevalle Jack $\delta^{18}O_{oto}$ and $\delta^{13}C_{oto}$ data using the mgcv package in R (Wood, 2004).

Several models were fit and compared using Akaike's Information Criterion (AIC; Akaike, 1973). First, a simple model was fit with transect as the only independent variable (model 1). Two additional models were fit to the data that incorporated population information; model 2 with transect and location as independent variables, and model 3 with transect, location, and a transect by location interaction term. All three models were compared using AIC and the model with the lowest AIC was selected as the best fitting base model. Data points taken from the same individual are likely to be correlated. To account for non-independence of the data and incorporate individual variability into the model, we then fit one additional model (model 4) that expanded upon the best fitting base model by including fish ID as a random variable in the form of a random intercept term. All analyses were conducted using R version

4.0 (R Core Team, 2021).

3. Results

A total of 24 Crevalle Jack otoliths were analyzed, 12 from coastal Alabama and 12 from the Florida Keys. All fish were collected between 2017 and 2021 and ranged in age from 4 to 5 years old, with 16 fish age-4 and 8 fish age-5 (Supplementary, Table S1). The number of transects milled per otolith ranged from 16 to 21, depending on the age of the fish and timing of collection. The average number of transects milled per otolith was 19.3, and the total sample size was 426 transects. As there were no significant differences in growth band widths between the two groups, the average estimated growth band widths from all fish were used to assign the following approximate ages to each transect: Transects-1-3 were assigned to age-0, transects-4-7 to age-1, transects-8-11 to age-2, transects-12-15 to age-3, transects-16-19 to age-4, and transects-20-21 to age-5 (Table 1).

3.1. Model selection

For both the $\delta^{18}O_{oto}$ and $\delta^{13}C_{oto}$ data, GAMM models including transect, location, a transect location interaction term, and fish ID as a random intercept were the best fitting models according to AIC (Table 2). The model formula therefore took the following form:

$$y_i = \beta_0 + \beta_1 Location_i + f_1(Transect_i)Location_i + FishID_i + \varepsilon_i \quad (2)$$

where y is either $\delta^{18}O_{oto}$ or $\delta^{13}C_{oto}$, $\beta_0 + \beta_1 Location$ is the parametric part of the linear predictor, *Location* and *Transect* are predictor variables, f_1 is a smooth function, and *FishID* is the random intercept term.

3.2. Lifetime stable isotope patterns

The random variable *Fish ID* was significant in both models, revealing significant individual variability in lifetime stable isotope profiles (Supplementary, Tables 2 and 3). Most fish exhibited relatively low $\delta^{13}C_{oto}$ and $\delta^{18}O_{oto}$ values at age-0 followed by an increase in both $\delta^{13}C_{oto}$ and $\delta^{18}O_{oto}$ values between ages-1 and -2. Across both groups, $\delta^{13}C_{oto}$ and $\delta^{18}O_{oto}$ values remained relatively stable throughout the remainder of the transects for most individuals. However, there were individuals that deviated from these common trends. For AL fish, the $\delta^{13}C_{oto}$ and $\delta^{18}O_{oto}$ values for fish #AL 2, AL 7, AL 8, and AL 12 did not increase from age-0 to age-3, instead remaining relatively constant throughout the life history (Fig. 4). Additionally, fish #AL 4 and #AL 6 showed much more variability in isotope values over time, with several peaks and valleys. FK fish showed slightly less individual variability than AL fish, with the general pattern described above being evident for each fish except fish #FK 12 (Fig. 5). There was instead a substantial dip in both $\delta^{13}C_{oto}$ and $\delta^{18}O_{oto}$ values at age-3 for this individual.

Table 1
Mean and standard error of growth band widths measured using ImageJ, approximate number of transects milled within each age band (each transect was 0.05 mm), and transect numbers assigned to each age. Age-4 growth bands were only measured for fish aged to be 5 years old since the entire age-4 band may not have been present at the time of collection for 4-year-old fish. Growth band widths were not measured for age 5, since age-5 fish were culled at varying times during year 5, and thus remaining transects were assigned to age-5.

Growth band (age)	Mean width (mm)	Std. error	No. transects	Assigned transects
0	0.148	0.013	3	1–3
1	0.213	0.012	4	4–7
2	0.211	0.021	4	8–11
3	0.190	0.017	4	12–15
4	0.183	0.003	4	16–19
5	–	–	2	20–21

Table 2
Adjusted R^2, AIC, and ΔAIC for each of the GAM models fit to the $\delta^{13}C_{oto}$ and $\delta^{18}O_{oto}$ data. Bolded terms indicate the best models selected.

$\delta^{18}O_{oto}$	Variables	Adjusted R^2	AIC	ΔAIC
Model 1	Transect	0.342	1471	86
Model 2	Transect, Location	0.350	1467	82
Model 3	Transect, Location, Transect x Location	0.378	1452	67
Model 4	**Transect, Location, Transect x Location, FishID (random intercept)**	**0.491**	**1385**	**0**
$\delta^{13}C_{oto}$	Variables	Adjusted R^2	AIC	ΔAIC
Model 1	Transect	0.386	1679	198
Model 2	Transect, Location	0.406	1665	184
Model 3	Transect, Location, Transect x Location	0.456	1632	151
Model 4	**Transect, Location, Transect x Location, FishID (random intercept)**	**0.637**	**1481**	**0**

3.3. Geographic variation

The best fitting GAMM models revealed that the two smooth curves for AL and FK fish were significantly different from zero ($p < 0.001$; Supplementary, Tables 2 and 3). In order to test whether the two curves were significantly different from each other, we fit additional models using difference curves, where one of the factor levels are taken as a reference level, a smooth is fit to the reference level, and then difference curves are fit to remaining factor levels (Baayen et al., 2018). The difference between the AL and FK curves was significant for both the $\delta^{13}C_{oto}$ ($edf = 4.8$, $F = 58.2$, $p < 0.001$) and $\delta^{18}O_{oto}$ ($edf = 4.4$, $F = 29.9$, $p < 0.001$) models. So, despite significant individual variability, GAMM model results revealed a significant difference in trends between AL and FK fish (Fig. 6). Furthermore, by plotting the difference smooths (Rij et al., 2022) between AL and FK for both models, we observed some significant differences between the regions at certain transect values (Fig. 7). A difference smooth is the difference between the smooths of two conditions, or levels of a factor. When the difference smooth 95% confidence interval does not contain zero, it reveals a significant difference between the two factor levels at the $\alpha = 0.05$ level. At age-0, the $\delta^{13}C_{oto}$ values for AL fish were significantly higher than for FK fish. Then from age-2 to age-5, $\delta^{13}C_{oto}$ values were significantly higher for FK fish than for AL fish. There was much more overlap in $\delta^{18}O_{oto}$ values between the two regions, but $\delta^{18}O_{oto}$ values were significantly higher for FK fish than for AL fish at the end of the transects (ages 4 and 5). $\delta^{18}O_{oto}$ values were also generally lower for FK fish than AL fish at age-0, similar to the $\delta^{13}C_{oto}$ data. AL fish, in general, showed more homogeneous lifetime stable isotope profiles than FK fish.

4. Discussion

Stable isotope micro-sampling of fish otoliths can provide a wealth of information about habitat use throughout the life-history of a species, which is critical information for fisheries management and conservation (Compton et al., 2012; Galaiduk et al., 2017; Nagelkerken et al., 2015). Our research showed the potential of this approach for assessing lifetime migration patterns and connectivity of data-poor populations with wide-ranging distributions. In the eastern GOM, there is a substantial difference in environmental stable isotope values of carbon and oxygen between northern and southern coastal aquatic habitats (Fry, 1983; Vander Zanden et al., 2015). The main goal of our research was to determine whether otolith stable isotope micro-sampling could be used to distinguish between individual fish captured from both regions of the

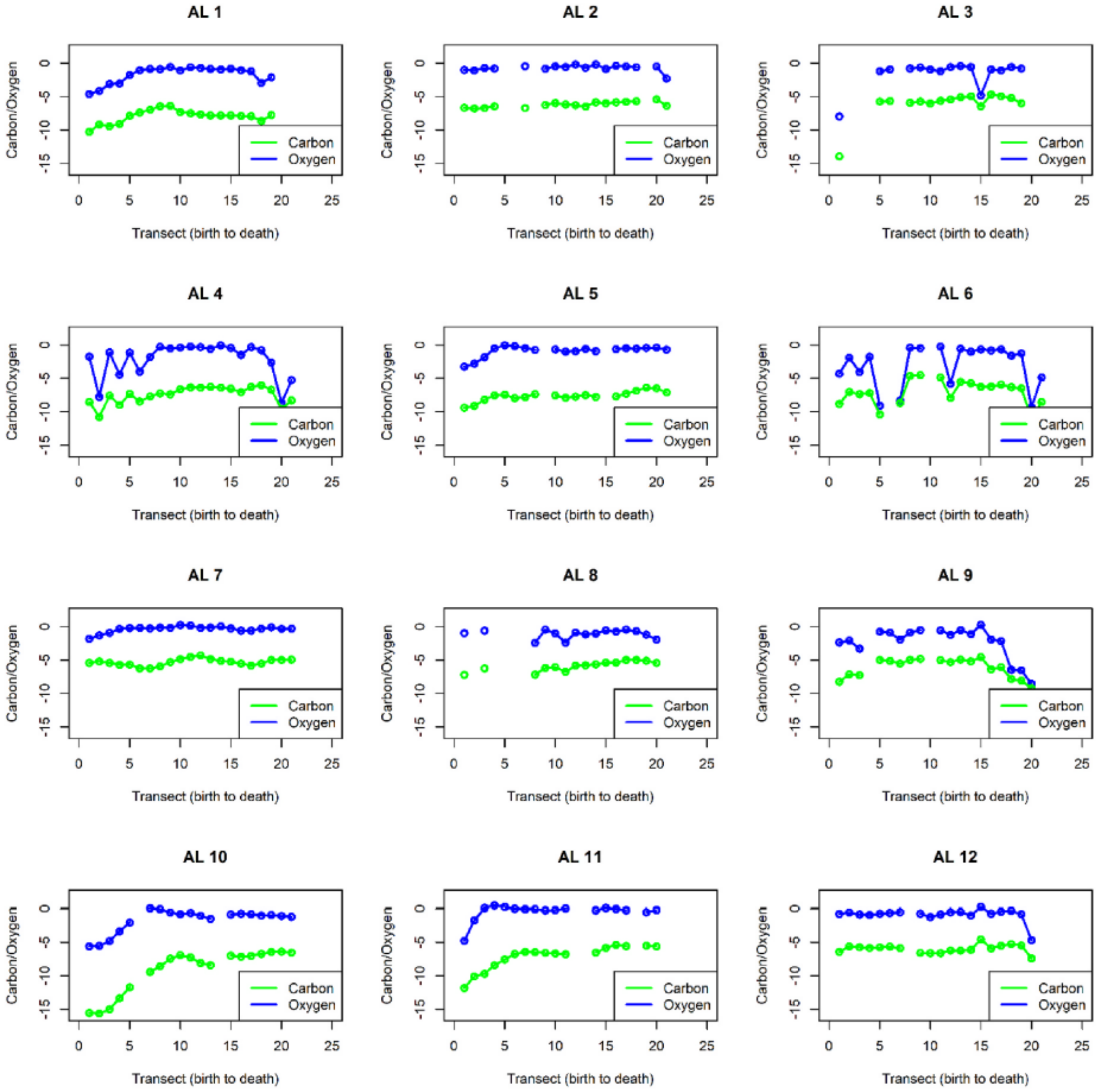


Fig. 4. Individual $\delta^{18}O_{oto}$ (oxygen) and $\delta^{13}C_{oto}$ (carbon) transects for each Crevalle Jack from Alabama (AL). Some transects have missing values due to instrument error or small sample size.

GOM (northeastern and southeastern), and whether fish from the two regions exhibited similar lifetime migration patterns. Our model results suggested that isotopic profiles of Crevalle Jack from Alabama and the Florida Keys were significantly different, but followed similar patterns of increasing $\delta^{13}C_{oto}$ and $\delta^{18}O_{oto}$ values from the otolith core to edge. However, there was overlap in stable isotope values between some individuals from the two regions, that could be attributed to inter-annual variability in environmental stable isotope values (as fish were collected over multiple years), or individual variability in movement patterns of Crevalle Jack, with potential connectivity between the northeastern and southeastern GOM regions. Our results did not appear to support any of our original hypotheses (Fig. 2), but instead supported a fourth hypothesis, that there is a difference in Crevalle Jack habitat use from age-0 to age-5 between the two regions, but that some level of connectivity may occur due to individual variability. The results of this study serve as a first step towards elucidating broad-scale movement patterns of an important sportfish species in the GOM.

4.1. *Lifetime migration patterns*

In our study, most Crevalle Jack otoliths displayed the same trend of increasing $\delta^{18}O_{oto}$ values from age-0 to about age-3 regardless of the region where they were collected (AL or FK). Among individual fish, the average difference between minimum and maximum $\delta^{18}O_{oto}$ values throughout the otoliths was 5.27‰ for AL fish and 4.50‰ for FK fish (Supplementary, Table S4). Research has shown that temperature-induced $\delta^{18}O_{oto}$ varies by approximately 1‰ per 4 °C (Høie et al., 2004b). According to NOAA sea surface temperature satellite data, water temperature varies by less than 10 °C seasonally in the Florida Keys region and by less than 15 °C seasonally in the Alabama region (Huang et al., 2015). These seasonal temperature ranges are not enough to explain the full range of $\delta^{18}O_{oto}$ values measured in individual Crevalle Jack otoliths. However, fish migrating among seawater, brackish estuaries, and freshwater environments can display much larger variations in $\delta^{18}O_{oto}$ values (Hsieh et al., 2019). Open ocean seawater has measured $\delta^{18}O_{water}$ values close to 0‰, while freshwater is typically depleted in ^{18}O, with $\delta^{18}O_{water}$ values as low as −10‰ (Kendall and Coplen, 2001; Lin et al., 2011). Previous research has additionally

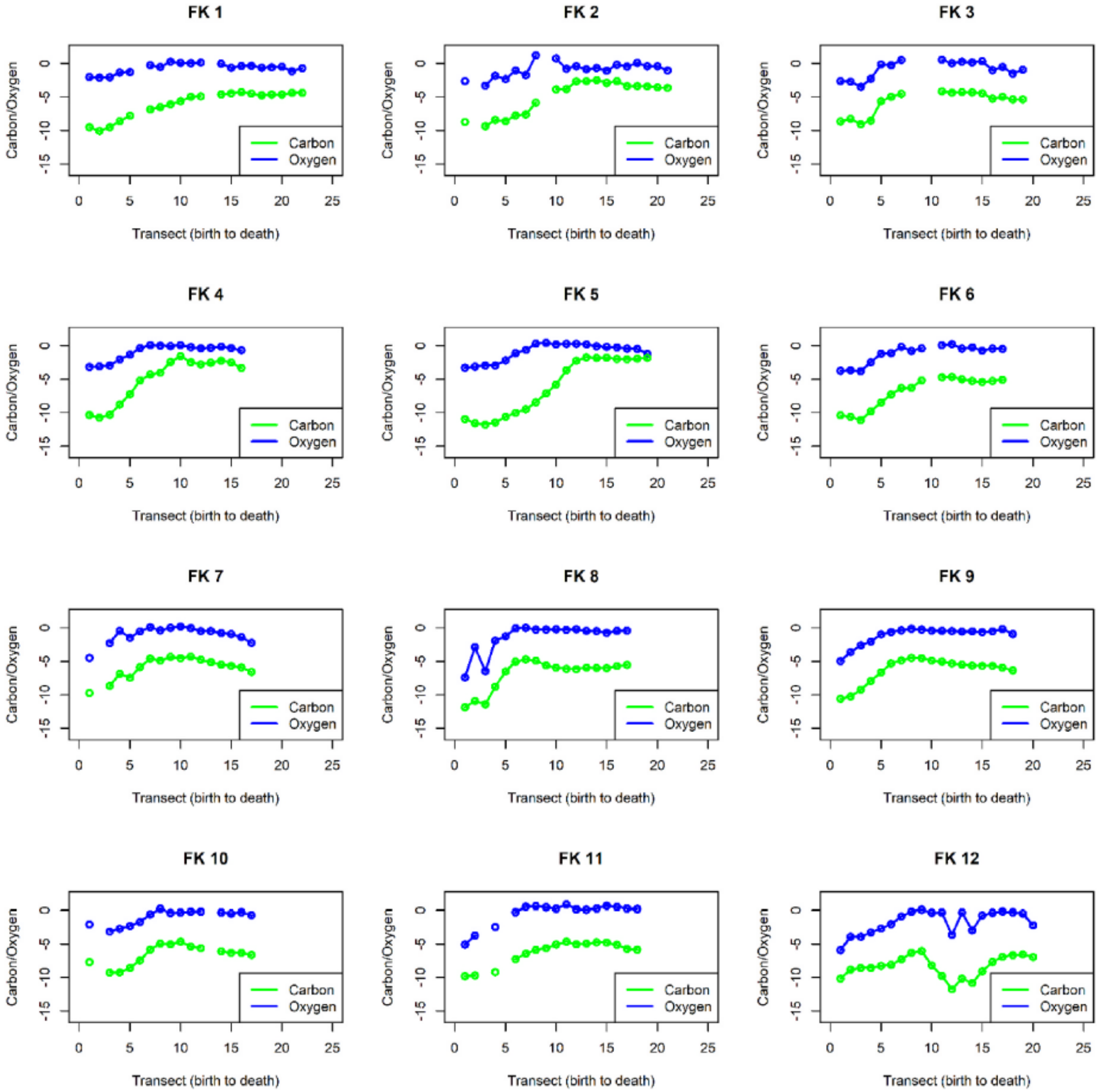


Fig. 5. Individual $\delta^{18}O_{oto}$ (oxygen) and $\delta^{13}C_{oto}$ (carbon) transects for each Crevalle Jack from the Florida Keys (FK). Some transects have missing values due to instrument error or small sample size.

shown a positive correlation between $\delta^{18}O$ values in fish otoliths and salinity (Hsieh et al., 2019; Pruell et al., 2012; Shirai et al., 2018). The increase in $\delta^{18}O_{oto}$ values from age-0 to age-3 observed in most Crevalle Jack otoliths likely reflects some combination of a decrease in water temperature and increase in salinity, which could be explained by an ontogenetic migration from warm, shallow water inshore habitats to cooler, higher salinity coastal habitats.

Measured $\delta^{13}C_{oto}$ values also increased from age-0 to age-3 for most fish. Among individual fish, the average difference between minimum and maximum $\delta^{13}C_{oto}$ values throughout the otoliths was 4.68‰ for AL fish and 6.44‰ for FK fish (Supplementary, Table S4). The increase we observed in Crevalle Jack $\delta^{13}C_{oto}$ values over time is likely predominantly due to a decrease in size-specific metabolism during ontogeny, which research has shown is the main driver of changes in $\delta^{13}C_{oto}$ values (Chung et al., 2019; Høie et al., 2004a). For instance, Chung et al. (2019) showed that changes in metabolism associated with changing foraging and predation dynamics are clearly encapsulated in $\delta^{13}C_{oto}$ values. As juveniles, fish metabolism and oxygen consumption are higher than at adult stages, as juveniles have higher predation risk, and increased pressure to grow (Trueman et al., 2016; Wurster and Patterson, 2003). As such, lifetime profiles of $\delta^{13}C$ in fish otoliths commonly display increases due to ontogenetic changes in metabolism (Kalish, 1991). Besides metabolic changes, there are other factors that could contribute to the observed pattern in $\delta^{13}C_{oto}$ values, including ontogenetic migration between habitats with distinct $\delta^{13}C_{DIC}$ values, a shift in diet, possibly from a more terrestrial source (low $\delta^{13}C$ values) to a more marine source (high $\delta^{13}C$ values; Peterson and Fry, 1987), and/or a shift in trophic position, as $\delta^{13}C$ values typically increase by 1‰ for every increase in trophic level (Peterson and Fry, 1987). Additionally, there is an inverse relationship between $\delta^{13}C_{oto}$ values and temperature, as temperature is a primary driver of metabolic rate (Martino et al., 2020). Future studies should investigate the external and internal mechanisms that regulate Crevalle Jack fractionation, to more specifically examine the drivers of changing $\delta^{13}C_{oto}$ values over time. Due to the complexity of $\delta^{13}C$ fractionation in fish otoliths, we cannot make any conclusions about Crevalle Jack migration through ontogeny solely based on the $\delta^{13}C_{oto}$ data. However, the observed increase in $\delta^{18}O_{oto}$ values through ontogeny combined with the observed increase in $\delta^{13}C_{oto}$ values do suggest an ontogenetic migration between ages-0 and -3.

This ontogenetic migration hypothesis aligns with previous

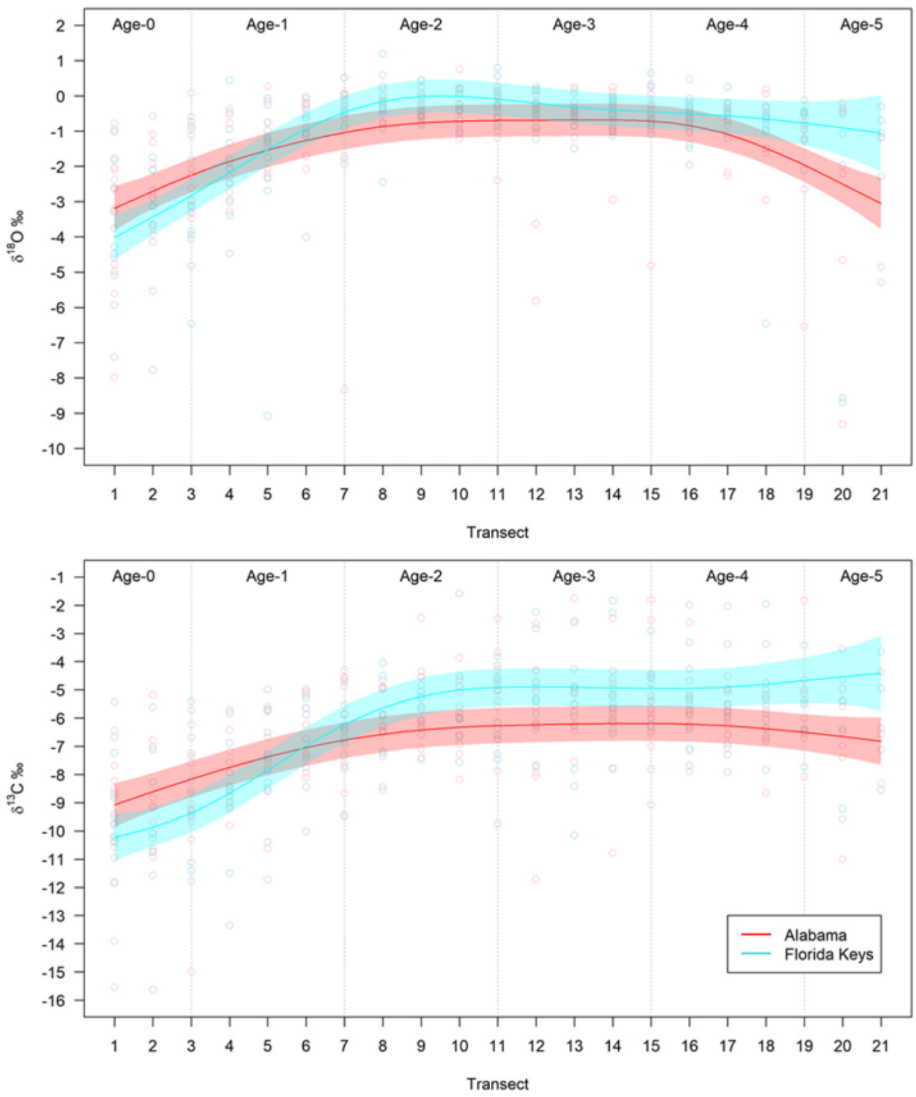


Fig. 6. GAMM model predictions (lines) for $\delta^{18}O_{oto}$ (top) and $\delta^{13}C_{oto}$ (bottom). Red dots are raw data points and shaded red regions are 95% confidence intervals corresponding to Alabama Crevalle Jack (AL). Blue dots are raw data points and shaded blue regions are 95% confidence intervals corresponding to Florida Crevalle Jack (FK). Gray dotted vertical lines are estimated age transition points, and numbers 0–5 across the top are estimated ages corresponding to each range of transects. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

observations of Crevalle Jack habitat use as well as previous literature. The Florida Fish and Wildlife Conservation Commission (FWC) conducts regular 183-m seine fisheries-independent monitoring (FIM) surveys in shallow, coastal estuaries. In all Gulf coast estuaries sampled between 1996 and 2018, length-frequency distributions of the catch showed that age-0 Crevalle Jack were most abundant, with few fish captured older than age-1 (FWC, 2021). Previous otolith micro-sampling research also attributed similar increases in both $\delta^{18}O_{oto}$ and $\delta^{13}C_{oto}$ values over time observed in Chum Salmon (*Oncorhynchus keta*) to ontogenetic movement from inshore nurseries to more marine habitats (Wang et al., 2021). Ontogenetic migrations from inshore, estuarine nursery habitats to coastal and offshore subadult/adult habitats have been observed for several sportfish species in the GOM, including Red Drum (*Sciaenops ocellatus*; Winner et al., 2014) and Atlantic Tarpon (*Megalops atlanticus*; Kurth et al., 2019). Morphology and behavior change as fish grow, which often necessitates a change in habitat to meet energetic requirements and resource needs (Huijbers et al., 2015). Movement from juvenile to adult habitats may specifically be associated with reproduction or habitat shifts reflecting changing ratios of mortality risk and growth rates (Gillanders et al., 2003). Typically, individuals will reside in areas of low mortality risk as juveniles, when they are most susceptible to predation, and move to areas with higher mortality risk but better access to food resources as they grow and become less susceptible to predation. These ontogenetic habitat shifts therefore often involve trade-offs between fitness and survival that can impact physiological processes like growth (Higgins et al., 2015). Knowledge of these changes in habitat niche requirements over the life history of a species is crucial for understanding how community composition is structured across a mosaic of habitats (Compton et al., 2012; Nagelkerken et al., 2015). This in turn aids in multispecies spatial management (Galaiduk et al., 2017).

Although most Crevalle Jack otoliths exhibited an increase in $\delta^{18}O_{oto}$ and $\delta^{13}C_{oto}$ values from age-0 to age-3, there were a few individuals (all AL fish), for which isotope values did not increase (Fig. 4). Fish #AL 2, AL 7, AL 8, and AL 12 had relatively constant $\delta^{18}O_{oto}$ and $\delta^{13}C_{oto}$ values from age-0 to age-3. This result does not necessarily preclude ontogenetic migration, as it is possible these individuals simply moved between nursery and adult habitats that had similar isotopic profiles. The influence of the large river systems in the northern GOM extends out into the coastal environment, leading to substantial mixing between inshore and coastal areas that varies seasonally and annually (Sanial et al., 2019). This mixing could explain the relatively homogeneous stable isotope profiles of some AL Crevalle Jack even if they engaged in migration behavior, as oxygen stable isotope profiles would look homogeneous whether the fish was in inshore or coastal environments. We also noted individual variability in the range of $\delta^{18}O_{oto}$ and $\delta^{13}C_{oto}$ values present throughout the otoliths of fish from both regions. Research has shown that variability in intrinsic factors such as body condition and sex can influence animal behavior and lead to substantial individual variability

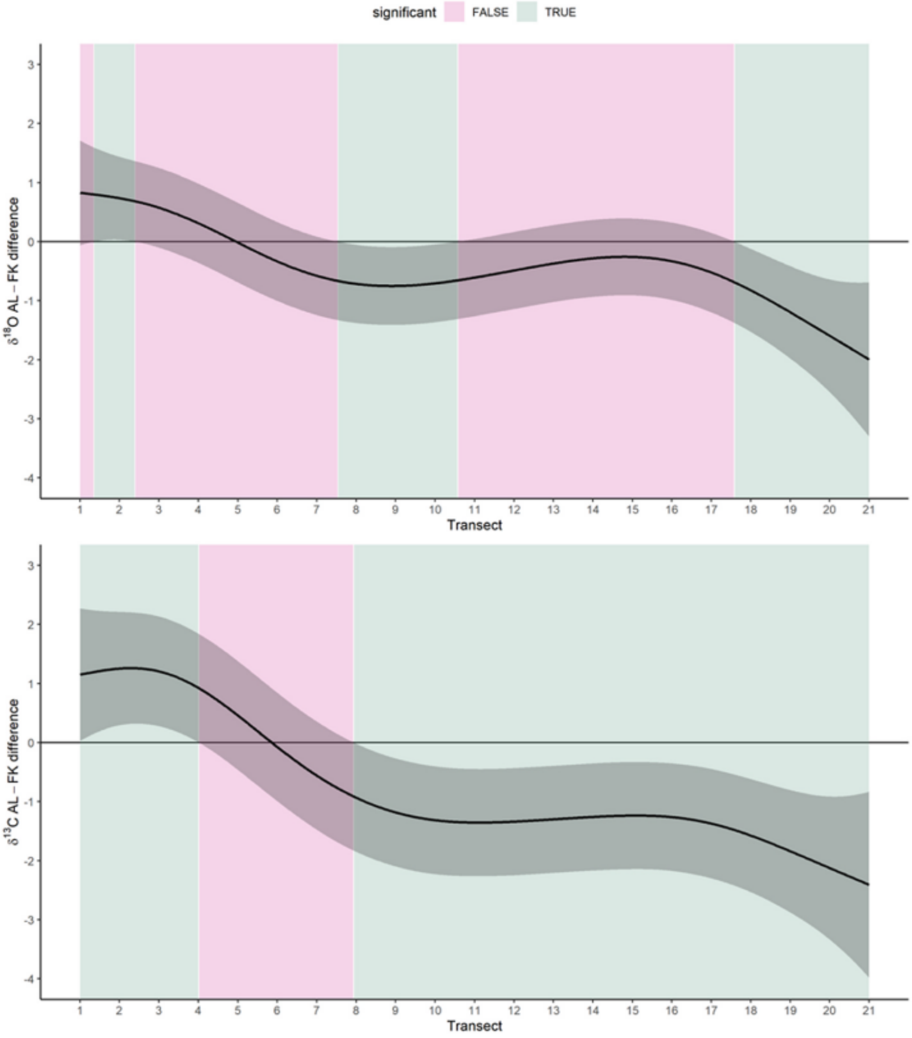


Fig. 7. Difference smooths for the $\delta^{18}O_{oto}$ (top) and $\delta^{13}C_{oto}$ (bottom) models between the levels of factor Location (AL and FK). Transects where the difference smooth is significantly different from zero are highlighted in green and transects where the difference smooth is not significantly different from zero are highlighted in pink. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

in lifetime movement and migration patterns within populations (Bolnick et al., 2011; Sih et al., 2004). Understanding the drivers and consequences of individual variability in movement patterns through ontogeny is important for understanding how environmental changes affect individual fitness of valuable species (Matich and Heithaus, 2015). Future research that more closely examines individual variability in movement patterns of Crevalle Jack, using higher resolution methods such as acoustic telemetry, would help determine the extent and possible causes of individual variability in the population.

By age-3, Crevalle Jack appeared to have completed their ontogenetic migration, which coincides with estimated age at sexual maturity in the Caribbean (Caiafa et al., 2011), though age at maturation has been shown to vary significantly between populations of the same species, e.g., for Bonefish (*Albula vulpes*; Rennert et al., 2019). $\delta^{18}O_{oto}$ and $\delta^{13}C_{oto}$ values remained relatively constant to age-5. It is difficult to make any conclusions regarding movement patterns from age-3 to age-5 based solely on the $\delta^{13}C_{oto}$ values due to the variety of factors that influence carbon fractionation in fish otoliths. But for several individuals, $\delta^{18}O_{oto}$ values declined from age-3 to age-5, suggesting movement to an isotopically distinct habitat, perhaps lower salinity and/or warmer waters. The observed decrease in $\delta^{18}O_{oto}$ values from age-3 to age-5 could feasibly represent a gradual movement towards the species preferred temperature (Fry, 1947). Adult Crevalle Jack occupy a range of habitats, including canals, deep-water reefs, and shallow-water flats (Smith-Vaniz and Carpenter, 2007). High-resolution stable isotope analysis of the older bands of the otoliths coupled with oceanographic data and other methods like acoustic telemetry (Ajemian et al., 2020), could increase our understanding of these fine-scale movement patterns post-ontogeny.

4.2. Geographic variation

Overlap in individual stable isotope profiles between AL and FK fish precludes concluding that fish from the two regions represent distinct, self-recruiting populations with no mixing. However, there was a difference between the otolith stable isotope values of AL and FK Crevalle Jack, with GAMM models revealing a significant difference in trends between regions. The aforementioned substantial mixing between inshore and coastal regions in the northeastern GOM might explain why we saw different lifetime stable isotope patterns between regions in our GAMM models. We might expect that nursery habitats in the northeastern GOM would have similar stable isotope values as nearby offshore habitats due to the substantial mixing. But in the southeastern GOM, nursery habitats may have more distinct stable isotope values than nearby offshore areas. This could explain why lifetime stable isotope profiles of AL fish were generally more homogeneous than those of FK fish.

At the point of capture (age-4 or age-5) $\delta^{18}O_{oto}$ and $\delta^{13}C_{oto}$ values were significantly higher in FK fish than AL fish. In the GOM, numerous studies have examined spatial heterogeneity of $\delta^{18}O$ and $\delta^{13}C$ values in coastal water, primary producers, fish muscle tissue, and fish otoliths. Compared to the southeastern GOM (Florida Keys), where $\delta^{18}O_{water}$ values in marine environments are relatively high (~1.7‰) due to high rates of evaporation (Sternberg and Swart, 1987), in the northeastern GOM (Alabama), influxes of freshwater from large river systems lead to relatively low $\delta^{18}O_{water}$ values ranging from −2.2 to −6.6‰ (Wagner and Slowey, 2011). This pattern has also been observed in fish otoliths. Gerard and Muhling (2010) examined $\delta^{18}O_{oto}$ values for juvenile Gray Snapper (*Lutjanus griseus*) in the Florida Keys region, with mean values around 0‰. Similarly, Patterson et al. (2014) examined $\delta^{18}O_{oto}$ values in juvenile Red Snapper (*Lutjanus campechanus*) and Lane Snapper (*Lutjanus synagris*) in coastal Alabama waters, and mean $\delta^{18}O_{oto}$ values were about −1.8‰ and −1.2‰, respectively. Vander Zanden et al. (2015) created a $\delta^{13}C$ value isoscape for the Eastern Gulf of Mexico region using loggerhead scute tissue that showed clear $\delta^{13}C_{scute}$ value enrichment in south Florida coastal waters (~−13 to −8‰) compared to the northern GOM (~−20 to −15‰). Fry (1983) compared $\delta^{13}C_{muscle}$ values in several species of shrimp throughout coastal GOM waters and had similar findings as Vander Zanden et al. (2015). The authors found a significant difference between the south Florida coast and the Louisiana and North Texas coasts, with lower $\delta^{13}C_{muscle}$ values in shrimp from the latter regions (~−13 to −11‰ in Florida compared to ~ −19 to −16‰ in Louisiana). This previous research aligns with our results and confirms that the spatial heterogeneity of $\delta^{18}O$ and $\delta^{13}C$ values in the eastern GOM is apparent in the tissues and biominerals of several aquatic organisms. Our results further highlight that otolith microchemistry can be a useful tool for assessing fish population dynamics in the region. As metabolic carbon comprises about 20% of fish otoliths, the difference of around 5–10‰ between $\delta^{13}C$ values observed in loggerhead scute tissue and shrimp muscle tissue in the northeastern and southeastern GOM could explain the approximate 0.6–1.5‰ difference between $\delta^{13}C_{oto}$ values of AL and FK Crevalle Jack post-ontogeny. Since $\delta^{13}C_{oto}$ values for FK fish remained significantly higher than for AL fish from age-3 to age-5, it suggests most fish in this age range remained in their respective regions (northeastern or southeastern GOM), but some individuals may have moved between regions.

The significant difference in $\delta^{13}C_{oto}$ values between AL and FK fish at age-0 (Fig. 7) suggests that these two groups of fish may have utilized geographically distinct nursery habitats. The difference in $\delta^{13}C_{oto}$ values between nurseries could be due to differences in estuarine vegetation. In the GOM, salt marshes and mangroves are the predominant intertidal habitats, and there is a north-south transition with salt marshes ranging from 25 to 45°N (IFAS, 2016), and mangrove habitats dominating latitudes 30°N to 30°S (Giri et al., 2011). Therefore, south Florida mainly consists of mangrove intertidal habitats while Alabama is dominated by salt marsh habitats. Mangroves are predominantly C_3 plants and salt marshes contain predominantly C_4 plants (Baker et al., 2021). Numerous studies have shown that $\delta^{13}C$ values are significantly higher in C_4 plants than C_3 plants (Baker et al., 2013; Bouillon et al., 2008; Cerling et al., 1997; Currin et al., 1995), with $\delta^{13}C$ values of C_4 plants being around −12‰ and $\delta^{13}C$ values of C_3 plants being around −24‰ to −30‰ (Bouillon et al., 2011). This regional difference in the base of the estuarine food web could explain why the $\delta^{13}C_{oto}$ values were significantly lower in age-0 FK fish than in age-0 AL fish. If this is the case, it suggests most fish may have recruited from inshore juvenile habitats to coastal habitats within the same region of the GOM.

4.3. Study limitations

An assumption of our study was that growth rates did not vary significantly among all the sampled Crevalle Jack, and therefore each transect corresponded to the same region of the otolith. There were slight differences in measured growth band widths among otoliths (Table 1), but the differences were minor, suggesting that growth rates were similar among the individuals. Furthermore, there were no significant differences in growth band widths between the two populations (AL and FK) based on independent 2-group t-tests for each growth band. Nevertheless, the slight differences in growth band widths likely explain some of the variance in $\delta^{13}C_{oto}$ and $\delta^{18}O_{oto}$ values per transect among fish from the same region, and this variation also means that the groups of transects assigned to each age are approximate. Another potential source of variation is due to sampling of Crevalle Jack otoliths over multiple years (2017–2021). Carbon stable isotope values in the ocean can vary annually due to changes in productivity, and oxygen stable isotope values can vary with changes in runoff, evaporation, and precipitation. This variability can thus effect $\delta^{13}C_{oto}$ and $\delta^{18}O_{oto}$ values (Trueman et al., 2012). Finally, while lifetime isotopic profiles were only examined through age-5, the Crevalle Jack is a relatively long-lived species with a maximum recorded age of 20 years (Jefferson et al., 2021). Therefore, movements beyond age-5 remain unknown. However, a challenge with micromilling otoliths from very old fish is that growth band width decreases with age as somatic growth slows. Transects at these older bands would therefore likely reflect the combined isotopic environment experienced over an entire year, or even multiple years, possibly obscuring migrations. Studies that combine otolith stable isotope analysis with other techniques like acoustic telemetry (Crossin et al., 2017) or genetics (Ovenden, 2013) can help further elucidate lifetime movement and migration patterns and connectivity of important species.

5. Conclusions

The results of our research provide previously unknown information about Crevalle Jack migration patterns through ontogeny and revealed a distinction between individuals captured in the Florida Keys and coastal Alabama that aligns with known isotopic variations between the two regions. These findings suggest that most Crevalle Jack may recruit from inshore estuaries to coastal habitats within the same broad region of the GOM and remain in either the northeastern or southeastern GOM regions through to at least age-5. However, there was substantial individual variability, suggesting that some individuals may move between regions during ontogeny (i.e., recruit to inshore nurseries at age-0 in one region but migrate to sub-adult habitats in the other region). Alternatively, the individual variability may instead be attributed to interannual differences in environmental stable isotope values within each region, as fish were collected over a period of several years. Unfortunately, there were no environmental stable isotope data available over the time period of our study for us to test this theory. Long-term monitoring of stable isotope values in water, sediment, and primary producer samples over broad spatial-temporal scales would aid in interpreting the results of studies such as this one, enhancing the utility of otolith stable isotope micro-sampling in the future. The information gained in this study about Crevalle Jack movement and migration patterns is critical for spatial management of the species and will aid in future conservation efforts. Micro-sampling of otoliths allowed us to assess changes in movement and migration throughout the life history quickly and easily, with only a limited number of samples collected over a short time. Even though we had little *a priori* knowledge of Crevalle Jack migration patterns and population connectivity, well-known isotopic gradients in the Gulf of Mexico afforded us the opportunity to examine migration and connectivity without extensive, long-term sampling. As scientists continue to map isoscapes of marine and coastal environments and assess seasonal and annual variability, stable isotope research will further aid in understanding and managing important fish stocks. Our research serves as a case study for the potential applications of otolith stable isotope micro-analysis to assessing species ecology, population dynamics, and connectivity. Future work analyzing stable isotopes of Crevalle Jack juvenile otoliths from a range of nursery habitats could help identify linkages between juvenile and adult habitats, further elucidating stock structure. Furthermore, the methods outlined in this manuscript can be applied to any fish species and may be especially useful for future studies on migration and connectivity of data-poor species with broad spatial distributions.

CRediT authorship contribution statement

Carissa L. Gervasi: Writing – review & editing, Writing – original draft, Visualization, Software, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **James A. Nelson:** Writing – review & editing, Validation, Conceptualization. **Peter K. Swart:** Writing – review & editing, Validation, Supervision, Resources, Methodology, Formal analysis, Conceptualization. **Rolando O. Santos:** Writing – review & editing, Conceptualization. **Ryan J. Rezek:** Writing – review & editing, Conceptualization. **W. Ryan James:** Writing – review & editing, Conceptualization. **Amanda E. Jefferson:** Writing – review & editing, Resources, Methodology, Investigation. **J. Marcus Drymon:** Writing – review & editing, Resources, Investigation. **Jessica Carroll:** Writing – review & editing, Resources, Methodology. **Ross E. Boucek:** Writing – review & editing, Resources, Funding acquisition, Conceptualization. **Jennifer S. Rehage:** Writing – review & editing, Validation, Supervision, Project administration, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgments

The authors would like to acknowledge the recreational fishing guides who assisted with sample collection, including N. LaBadie, D. Kilpatrick, J. Hoover, Z. Routman, A. Tipler, J. Gagliardini, and J. Carlson, as well as the coordinators and participants of the Alabama Deep Sea Fishing Rodeo. Special thanks go to K. Rynerson and the rest of the age and growth lab at FWRI for assistance with otolith sectioning and aging. Much appreciation goes to the two anonymous reviewers for comments that improved the manuscript. This study was developed in collaboration with the Florida Coastal Everglades Long-Term Ecological Research program under National Science Foundation Grant No. DEB-1832229 and this work was reviewed and deemed exempt by Florida International University's Institutional Animal Care and Use Committee (IACUC protocol exemption #IACUC-19-005, 8 January 2019). Funding was provided by the Lower Keys Guides Association, private donation, the Everglades Foundation FIU ForEverglades Graduate Scholarship, the American Fisheries Society Steven Berkeley Marine Conservation Fellowship, and the FIU University Graduate School Doctoral Evidence Acquisition Fellowship. This is contribution #1497 from the Institute of Environment at Florida International University.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2022.108130.

References

Abràmoff, M.D., Magalhães, P.J., Ram, S.J., 2004. Image processing with imageJ. Biophot. Int. 11, 36–41. https://doi.org/10.1201/9781420005615.ax4.

Ajemian, M.J., Drymon, J.M., Hammerschlag, N., Wells, R.J.D., Street, G., Falterman, B., McKinney, J.A., Driggers, W.B., Hoffmayer, E.R., Fischer, C., Stunz, G.W., 2020. Movement patterns and habitat use of tiger sharks (*Galeocerdo cuvier*) across ontogeny in the Gulf of Mexico. PLoS One 15, 1–24. https://doi.org/10.1371/journal.pone.0234868.

Akaike, H., 1973. Maximum likelihood identification of Gaussian autoregressive moving average models. Biometrika 60, 255–265. https://doi.org/10.1093/biomet/60.2.255.

Archambault, B., Le Pape, O., Baulier, L., Vermard, Y., Véron, M., Rivot, E., 2016. Adult-mediated connectivity affects inferences on population dynamics and stock assessment of nursery-dependent fish populations. Fish. Res. 181, 198–213. https://doi.org/10.1016/j.fishres.2016.03.023.

Avigliano, E., Pisonero, J., Bouchez, J., Pouilly, M., Domanico, A., Sánchez, S., Clavijo, C., Scarabotti, P., Facetti, J.F., Caffetti, J.D., del Rosso, F.R., Llamazares Vegh, S., Volpedo, A.V., 2021. Otolith Sr/Ca ratio complements Sr isotopes to reveal fish migration in large basins with heterogeneous geochemical landscapes. Environ. Biol. Fish. 104, 277–292. https://doi.org/10.1007/s10641-021-01074-y.

Baayen, R.H., van Rij, J., de Cat, C., Wood, S., 2018. Autocorrelated errors in experimental data in the language sciences: some solutions offered by generalized additive mixed models. In: Speelman, D., Heylen, K., Geeraerts, D. (Eds.), Mixed-Effects Regression Models in Linguistics, Quantitative Methods in the Humanities and Social Sciences. Springer International Publishing, Cham, pp. 49–69. https://doi.org/10.1007/978-3-319-69830-4_4.

Baker, R., Abrantes, K., Feller, I.C., 2021. Stable isotopes suggest limited role of wetland macrophyte production supporting aquatic food webs across a mangrove-salt marsh ecotone. Estuar. Coast 44, 1619–1627. https://doi.org/10.1007/s12237-021-00895-5.

Baker, R., Fry, B., Rozas, L.P., Minello, T.J., 2013. Hydrodynamic regulation of salt marsh contributions to aquatic food webs. Mar. Ecol. Prog. Ser. 490, 37–52. https://doi.org/10.3354/meps10442.

Berger, A.M., Deroba, J.J., Bosley, K.M., Goethel, D.R., Langseth, B.J., Schueller, A.M., Hanselman, D.H., 2021. Incoherent dimensionality in fisheries management: consequences of misaligned stock assessment and population boundaries. ICES J. Mar. Sci. 78, 155–171. https://doi.org/10.1093/icesjms/fsaa203.

Bolnick, D.I., Amarasekare, P., Araújo, M.S., Bürger, R., Levine, J.M., Novak, M., Rudolf, V.H.W., Schreiber, S.J., Urban, M.C., Vasseur, D.A., 2011. Why intraspecific trait variation matters in community ecology. Trends Ecol. Evol. 26, 183–192. https://doi.org/10.1016/j.tree.2011.01.009.

Bouillon, S., Connolly, R.M., Gillikin, D.P., 2011. Use of stable isotopes to understand food webs and ecosystem functioning in estuaries. Treatise Estuar. Coast. Sci. 7, 143–173. https://doi.org/10.1016/B978-0-12-374711-2.00711-7.

Bouillon, S., Connolly, R.M., Lee, S.Y., 2008. Organic matter exchange and cycling in mangrove ecosystems: recent insights from stable isotope studies. J. Sea Res. 59, 44–58. https://doi.org/10.1016/j.seares.2007.05.001.

Cadrin, S.X., Secor, D.H., 2009. Accounting for spatial population structure in stock assessment: past, present, and future. In: Beamish, R., Rothschild, B. (Eds.), The Future of Fisheries Science in North America. Springer Science+Business Media B.V., pp. 405–426. https://doi.org/10.1007/978-1-4020-9210-7

Caiafa, H.I., Narváez, B.J., Borrero, F.S., 2011. Algunos aspectos de la dinámica poblacional del jurel *Caranx hippos* (pisces: carangidae) en Bocas de Ceniza, Caribe colombiano. Rev. MVZ Córdoba 16, 2324–2335.

Campana, S.E., 2001. Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. J. Fish. Biol. 59, 197–242. https://doi.org/10.1006/jfbi.2001.1668.

Campana, S.E., 1999. Chemistry and composition of fish otoliths: pathways, mechanisms and applications. Mar. Ecol. Prog. Ser. 188, 263–279.

Cerling, T.E., Harris, J.M., MacFadden, B.J., Leakey, M.G., Quade, J., Eisenmann, V., Ehleringer, J.R., 1997. Global vegetation change through the Miocene/Pliocene boundary. Nature 389, 153–158. https://doi.org/10.1038/38229.

Chung, M.T., Trueman, C.N., Godiksen, J.A., Holmstrup, M.E., Grønkjær, P., 2019. Field metabolic rates of teleost fishes are recorded in otolith carbonate. Commun. Biol. 2, 1–10. https://doi.org/10.1038/s42003-018-0266-5.

Compton, T.J., Morrison, M.A., Leathwick, J.R., Carbines, G.D., 2012. Ontogenetic habitat associations of a demersal fish species, *Pagrus auratus*, identified using boosted regression trees. Mar. Ecol. Prog. Ser. 462, 219–230. https://doi.org/10.3354/meps09790.

Crossin, G.T., Heupel, M.R., Holbrook, C.M., Hussey, N.E., Lowerre-Barbieri, S.K., Nguyen, V.M., Raby, G.D., Cooke, S.J., 2017. Acoustic telemetry and fisheries management. Ecol. Appl. 27, 1031–1049. https://doi.org/10.1002/eap.1533.

Currey, L.M., Heupel, M.R., Simpfendorfer, C.A., Williams, A.J., 2014. Inferring movement patterns of a coral reef fish using oxygen and carbon isotopes in otolith carbonate. J. Exp. Mar. Biol. Ecol. 456, 18–25. https://doi.org/10.1016/j.jembe.2014.03.004.

Currin, C.A., Newell, S.Y., Paerl, H.W., 1995. The role of standing dead *Spartina alterniflora* and benthic microalgae in salt marsh food webs: considerations based on multiple stable isotope analysis. Mar. Ecol. Prog. Ser. 121, 99–116. https://doi.org/10.3354/meps121099.

Defenbaugh, R., 1976. A Study of the Benthic Macroinvertebrates of the Continental Shelf of the Northern Gulf of Mexico. Ph.D. dissertation. Texas A&M University, College Station TX.

Ditty, J.G., Shaw, R., Cope, J.S., 2004. Distribution of carangid larvae (Teleostei: carangidae) and concentrations of zooplankton in the northern Gulf of Mexico, with illustrations of early *Hemicaranx amblyrhynchus* and *Caranx* spp. larvae. Mar. Biol. 145, 1001–1014. https://doi.org/10.1007/s00227-004-1381-z.

Drymon, J.M., Dedman, S., Froeschke, J.T., Seubert, E.A., Jefferson, A.E., Kroetz, A.M., Mareska, J.F., Powers, S.P., 2020. Defining sex-specific habitat suitability for a northern Gulf of Mexico shark assemblage. Front. Mar. Sci. 7, 35. https://doi.org/10.3389/fmars.2020.00035.

Epstein, S., Mayeda, T., 1953. Variation of O^2 content of waters from natural sources. Geochem. Cosmochim. Acta 4, 213–224.

Estes, C., 2016. Comparison of Reef Fish Communities East and West of Cape San Blas in Northeast Gulf of Mexico. Thesis. Florida State University, Tallahassee, FL.

Flaherty, K.E., Matheson, R.E., McMichael, R.H., Perry, W.B., 2013. The influence of freshwater on nekton community structure in hydrologically distinct basins in northeastern Florida Bay, FL, USA. Estuar. Coast 36, 918–939. https://doi.org/10.1007/s12237-013-9614-3.

Flores-Coto, C., Sanchez-Ramirez, M., 1989. Larval distribution and abundance of carangidae (pisces), from the southern Gulf of Mexico, 1983-1984. Gulf Res. Rep. 8, 117–128. https://doi.org/10.18785/grr.0802.04.

Fogarty, M.J., Botsford, L.W., 2007. Population connectivity and spatial management of marine fisheries. Oceanography 20, 112–123. https://doi.org/10.5670/oceanog.2007.34.

Frisk, M.G., Jordaan, A., Miller, T.J., 2014. Moving beyond the current paradigm in marine population connectivity: are adults the missing link? Fish Fish. 15, 242–254. https://doi.org/10.1111/faf.12014.

Fry, B., 1983. Fish and shrimp migrations in the northern Gulf of Mexico analyzed using stable C, N, and S isotope ratios. Fish. Bull. 81, 789–801.

Fry, F., 1947. Effects of the environment on animal activity. Publ. Ont. Fish. Res. Lab. 68, 1–62.

FWC (Florida Fish and Wildlife Conservation Commission), 2021. Fisheries-independent monitoring using stratified-random sampling [WWW Document]. https://myfwc.com/research/saltwater/reef-fish/monitoring/fim-stratified-random-sampling/. (Accessed 17 September 2021).

Galaiduk, R., Radford, B.T., Saunders, B.J., Newman, S.J., Harvey, E.S., 2017. Characterizing ontogenetic habitat shifts in marine fishes: advancing nascent methods for marine spatial management. Ecol. Appl. 27, 1776–1788. https://doi.org/10.1002/eap.1565.

Gallaway, B.J., 1981. An ecosystem analysis of oil and gas development on the Texas-Louisiana continental shelf. U.S. Fish and Wildlife Service, Office of Biological Services, Washington, D.C.. FWS/OBS-81/27. 89pp.

Gerard, T., Malca, E., Muhling, B.A., Mateo, I., Lamkin, J.T., 2015. Isotopic signatures in the otoliths of reef-associated fishes of southern Florida: linkages between nursery grounds and coral reefs. Reg. Stud. Mar. Sci. 2, 95–104. https://doi.org/10.1016/j.rsma.2015.08.014.

Gerard, T., Muhling, B., 2010. Variation in the isotopic signatures of juvenile gray snapper (*Lutjanus griseus*) from five southern Florida regions. Fish. Bull. 104, 98–105.

Gervasi, C.L., Santos, R.O., Rezek, R.J., James, W.R., Boucek, R.E., Bradshaw, C., Kavanagh, C., Osborne, J., Rehage, J.S., 2022. Bottom-up conservation: using translational ecology to inform conservation priorities for a recreational fishery. Can. J. Fish. Aquat. Sci. 79, 47–62 https://doi.org/dx.doi.org/10.1139/cjfas-2021-0024.

Gillanders, B.M., Able, K.W., Brown, J.A., Eggleston, D.B., Sheridan, P.F., 2003. Evidence of connectivity between juvenile and adult habitats for mobile marine fauna: an important component of nurseries. Mar. Ecol. Prog. Ser. 247, 281–295.

Giri, C., Ochieng, E., Tieszen, L.L., Zhu, Z., Singh, A., Loveland, T., Masek, J., Duke, N., 2011. Status and distribution of mangrove forests of the world using earth observation satellite data. Global Ecol. Biogeogr. 20, 154–159. https://doi.org/10.1111/j.1466-8238.2010.00584.x.

Hanson, N.N., Wurster, C.M., Todd, C.D., 2013. Reconstructing marine life-history strategies of wild Atlantic salmon from the stable isotope composition of otoliths. Mar. Ecol. Prog. Ser. 475, 249–266. https://doi.org/10.3354/meps10066.

Helies, F., Jemison, J., Heyman, W., Gallaway, B., 2016. Prediction and Verification of Snapper-Grouper Spawning Aggregation Sites on the Offshore Banks of the Northwestern Gulf of Mexico, Final Report. NOAA/NMFS Award Number NA 14NMF4270039, Tampa, FL.

Heyman, W.D., Grüss, A., Biggs, C.R., Kobara, S., Farmer, N.A., Karnauskas, M., Lowerre-Barbieri, S., Erisman, B., 2019. Cooperative monitoring, assessment, and management of fish spawning aggregations and associated fisheries in the U.S. Gulf of Mexico. Mar. Pol. 109, 103689 https://doi.org/10.1016/j.marpol.2019.103689.

Heyman, W.D., Kjerfve, B., 2008. Characterization of transient multi-species reef fish spawning aggregations at Gladden Spit, Belize. Bull. Mar. Sci. 83, 531–551.

Higgins, R.M., Diogo, H., Isidro, E.J., 2015. Modelling growth in fish with complex life histories. Rev. Fish Biol. Fish. 25, 449–462. https://doi.org/10.1007/s11160-015-9388-8.

Hinrichsen, H.H., Dickey-Collas, M., Huret, M., Peck, M.A., Vikebø, F.B., 2011. Evaluating the suitability of coupled biophysical models for fishery management. ICES J. Mar. Sci. 68, 1478–1487. https://doi.org/10.1093/icesjms/fsr056.

Hjort, J., 1914. Fluctuations in the great fisheries of northern europe. Rapp. Procès-Verbaux 20, 1–228.

Høie, H., Andersson, C., Folkvord, A., Karlsen, 2004a. Precision and accuracy of stable isotope signals in otoliths of pen-reared cod (*Gadus morhua*) when sampled will a high-resolution micromill. Mar. Biol. 144, 1039–1049. https://doi.org/10.1007/s00227-003-1275-5.

Høie, H., Folkvord, A., Otterlei, E., 2003. Effect of somatic and otolith growth rate on stable isotopic composition of early juvenile cod (*Gadus morhua* L) otoliths. J. Exp. Mar. Biol. Ecol. 289, 41–58. https://doi.org/10.1016/S0022-0981(03)00034-0.

Høie, H., Otterlei, E., Folkvord, A., 2004b. Temperature-dependent fractionation of stable oxygen isotopes in otoliths of juvenile cod (*Gadus morhua* L.). ICES J. Mar. Sci. 61, 243–251. https://doi.org/10.1016/j.icesjms.2003.11.006.

Hsieh, Y., Shiao, J.C., Lin, S., wood, Iizuka, Y., 2019. Quantitative reconstruction of salinity history by otolith oxygen stable isotopes: an example of a euryhaline fish Lateolabrax japonicus. Rapid Commun. Mass Spectrom. 33, 1344–1354. https://doi.org/10.1002/rcm.8476.

Huang, B., Banzon, V., Freeman, E., Lawrimore, J., Liu, W., Tc, P., Smith, T., Thorne, P., Woodruff, S., Zhang, H.-M., 2015. NOAA Extended Reconstructed Sea Surface Temperature (ERSST), Version 4, 2.1.22. NOAA National Centers for Environmental Information. https://doi.org/10.7289/V5KD1VVF [Dataset ID: nceiErsstv4].

Huijbers, C.M., Nagelkerken, I., Layman, C.A., 2015. Fish movement from nursery bays to coral reefs: a matter of size? Hydrobiologia 750, 89–101. https://doi.org/10.1007/s10750-014-2162-4.

IFAS (University of Florida Institute of Food and Agricultural Sciences Extension), 2016. Gulf coast salt marshes [WWW document]. https://soils.ifas.ufl.edu/wetlandextension/types/gulfcoastmarsh.htm. (Accessed 8 July 2021).

Jamieson, R.E., Schwarcz, H.P., Brattey, J., 2004. Carbon isotopic records from the otoliths of Atlantic cod (*Gadus morhua*) from eastern Newfoundland, Canada. Fish. Res. 68, 83–97. https://doi.org/10.1016/j.fishres.2004.02.009.

Jefferson, A., Jargowsky, M., Ivec, G., Cooper, P., Carroll, J., Gervasi, C., Rehage, J., Mareska, J., Powers, S., Drymon, J., 2021. Age, growth, and diet of crevalle jack (Caranx hippos) in the Gulf of Mexico. Fish. Manag. Ecol.

Kalish, J.M., 1991. Oxygen and carbon stable isotopes in the otoliths of wild and laboratory-reared Australian salmon (Arripis trutta). Mar. Biol.

Kawazu, M., Tawa, A., Ishihara, T., Uematsu, Y., Sakai, S., 2020. Discrimination of eastward trans-Pacific migration of the Pacific bluefin tuna *Thunnus orientalis* through otolith δ^{13}C and δ^{18}O analyses. Mar. Biol. 167, 1–7. https://doi.org/10.1007/s00227-020-03723-9.

Kendall, C., Coplen, T.B., 2001. Distribution of oxygen-18 and deuteriun in river waters across the United States. Hydrol. Process. 15, 1363–1393. https://doi.org/10.1002/hyp.217.

Knape, J., 2016. Decomposing trends in Swedish bird populations using generalized additive mixed models. J. Appl. Ecol. 53, 1852–1861. https://doi.org/10.1111/1365-2664.12720.

Kramer, D.L., Chapman, M.R., 1999. Implications of fish home range size and relocation for marine reserve function. Environ. Biol. Fish. 55, 65–79. https://doi.org/10.1023/a:1007481206399.

Kurth, B.N., Peebles, E.B., Stallings, C.D., 2019. Atlantic Tarpon (*Megalops atlanticus*) exhibit upper estuarine habitat dependence followed by foraging system fidelity after ontogenetic habitat shifts. Estuar. Coast Shelf Sci. 225, 106248 https://doi.org/10.1016/j.ecss.2019.106248.

Kwei, E.A., 1978. Food and spawning activity of *Caranx hippos* (L.) off the coast of Ghana. J. Nat. Hist. 12, 195–215. https://doi.org/10.1080/00222937800770081 org/10.1080/00222937800770081.

Levins, R., 1968. Evolution in Changing Environments: Some Theoretical Explorations. Princeton University Press, Princeton, NJ.

Lin, I.T., Wang, C.H., Lin, S., Chen, Y.G., 2011. Groundwater-seawater interactions off the coast of southern Taiwan: evidence from environmental isotopes. J. Asian Earth Sci. 41, 250–262. https://doi.org/10.1016/j.jseaes.2011.03.001.

Marrie, R.A., Dawson, N.V., Garland, A., 2009. Quantile regression and restricted cubic splines are useful for exploring relationships between continuous variables. J. Clin. Epidemiol. 62 https://doi.org/10.1016/j.jclinepi.2008.05.015.

Martino, J.C., Doubleday, Z.A., Chung, M.T., Gillanders, B.M., 2020. Experimental support towards a metabolic proxy in fish using otolith carbon isotopes. J. Exp. Biol. 223 https://doi.org/10.1242/jeb.217091.

Matich, P., Heithaus, M.R., 2015. Individual variation in ontogenetic niche shifts in habitat use and movement patterns of a large estuarine predator (*Carcharhinus leucas*). Oecologia 178, 347–359. https://doi.org/10.1007/s00442-015-3253-2.

McBride, R.S., McKown, K.A., 2000. Consequences of dispersal of subtropically spawned crevalle jacks, *Caranx hippos*, to temperate estuaries. Fish. Bull. 98, 528–538.

McMahon, K.W., Hamady, L.L., Thorrold, S.R., 2013. A review of ecogeochemistry approaches to estimating movements of marine animals. Limnol. Oceanogr. 58, 697–714. https://doi.org/10.4319/lo.2013.58.2.0697.

Miller, T.J., 2007. Contribution of individual-based coupled physical-biological models to understanding recruitment in marine fish populations. Mar. Ecol. Prog. Ser. 347, 127–138. https://doi.org/10.3354/meps06973.

Moffitt, E.A., Botsford, L.W., Kaplan, D.M., O'Farrell, M.R., 2009. Marine reserve networks for species that move within a home range. Ecol. Appl. 19, 1835–1847. https://doi.org/10.1890/08-1101.1.

Mohan, J.A., Sutton, T.T., Cook, A.B., Boswell, K.M., Wells, R.J.D., 2017. Influence of oceanographic conditions on abundance and distribution of post-larval and juvenile carangid fishes in the northern Gulf of Mexico. Fish. Oceanogr. 26, 526–541. https://doi.org/10.1111/fog.12214.

Nagelkerken, I., Sheaves, M., Baker, R., Connolly, R.M., 2015. The seascape nursery: a novel spatial approach to identify and manage nurseries for coastal marine fauna. Fish Fish. 16, 362–371. https://doi.org/10.1111/faf.12057.

Nelder, J.A., Wedderburn, R.W.M., 1972. Generalized linear models. J. R. Stat. Soc. Ser. Gen. 135, 370–384.

Distribution and abundance of fishes and invetebrates in Gulf of Mexico estuaries volume I: data summaries. In: Nelson, D. (Ed.), 1992. ELMR Report Number 10. NOAA/NOS Strategic Environmental Assessments Division, Rockville, MD.

Nelson, J., Hanson, C., Koenig, C., Chanton, J., 2011. Influence of diet on stable carbon isotope composition in otoliths of juvenile red drum *Sciaenops ocellauts*. Aquat. Biol. 13, 89–95. https://doi.org/10.3354/ab00354.

NOAA (National Oceanic and Atmospheric Administration), 2021. About the marine recreational information program. https://www.fisheries.noaa.gov/recreational-fishing-data/about-marine-recreational-information-program. (Accessed 9 September 2021).

Ovenden, J.R., 2013. Crinkles in connectivity: combining genetics and other types of biological data to estimate movement and interbreeding between populations. Mar. Freshw. Res. 64, 201–207. https://doi.org/10.1071/MF12314.

Patterson, W.F., Barnett, B.K., Sluis, M.Z., Cowan, J.H., Shiller, A.M., 2014. Interspecific variation in juvenile snapper otolith chemical signatures in the northern Gulf of Mexico. Aquat. Biol. 21, 1–10. https://doi.org/10.3354/ab00567.

Peterson, B.J., Fry, B., 1987. Stable isotopes in ecosystem studies. Annu. Rev. Ecol. Systemat. 18 18, 293–320. https://doi.org/10.1146/annurev.es.18.110187.001453.

Pruell, R.J., Taplin, B.K., Karr, J.D., 2012. Spatial and temporal trends in stable carbon and oxygen isotope ratios of juvenile winter flounder otoliths. Environ. Biol. Fish. 93, 61–71. https://doi.org/10.1007/s10641-011-9890-3.

R Core Team, 2021. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Rennert, J.J., Shenker, J.M., Angulo-Valdés, J.A., Adams, A.J., 2019. Age, growth, and age at maturity of bonefish (*Albula species*) among Cuban habitats. Environ. Biol. Fish. 102, 253–265. https://doi.org/10.1007/s10641-018-0836-x.

Rij, J. van, Wieling, M., Baayen, R.H., Rijn, H. van, 2022. Itsadug: Interpreting Time Series and Autocorrelated Data Using GAMMs. R package version 2.4.1.

Sale, P., Van Lavieren, H., Ablan Lagman, M., Atema, J., Butler, M., Fauvelot, C., Hogan, J., Jones, G., Lindeman, K., Paris, C., Steneck, R., Stewart, H., 2010. Preserving reef connectivity: a handbook for marine protected area managers. In: Connectivity Working Group, Coral Reef Targeted Research & Capacity Building for Management Program. UNU-INWEH.

Sanial, V., Shiller, A.M., Joung, D.J., Ho, P., 2019. Extent of Mississippi River water in the Mississippi Bight and Louisiana Shelf based on water isotopes. Estuar. Coast Shelf Sci. 226, 106196 https://doi.org/10.1016/j.ecss.2019.04.030.

Secor, D.H., 1999. Specifying divergent migrations in the concept of stock: the contingent hypothesis. Fish. Res. 43, 13–34. https://doi.org/10.1016/S0165-7836(99)00064-8.

Shirai, K., Koyama, F., Murakami-Sugihara, N., Nanjo, K., Higuchi, T., Kohno, H., Watanabe, Y., Okamoto, K., Sano, M., 2018. Reconstruction of the salinity history associated with movements of mangrove fishes using otolith oxygen isotopic analysis. Mar. Ecol. Prog. Ser. 593, 127–139. https://doi.org/10.3354/meps12514.

Sih, A., Bell, A., Johnson, J.C., 2004. Behavioral syndromes: an ecological and evolutionary overview. Trends Ecol. Evol. 19, 372–378. https://doi.org/10.1016/j.tree.2004.04.009.

Smith-Vaniz, W., Carpenter, K.E., 2007. Review of the crevalle jacks, *Caranx hippos* complex (teleostei: carangidae), with a description of a new species from west africa. Fish. Bull. 105, 207–233.

Snelson, F., 1992. Biological studies of crevalle jack (*Caranx hippos*) in Florida. In: Final Report Submitted to Marine Research Institute. Florida Marine Research Institute. Florida Marine Research Institute, St. Petersburg. Orlando, FL.

Solomon, C.T., Weber, P.K., Cech, J.J., Ingram, B.L., Conrad, M.E., Machavaram, M.V., Pogodina, A.R., Franklin, R.L., 2006. Experimental determination of the sources of otolith carbon and associated isotopic fractionation. Can. J. Fish. Aquat. Sci. 63, 79–89. https://doi.org/10.1139/f05-200.

Sternberg, L. da S.L., Swart, P.K., 1987. Utilization of freshwater and ocean water by coastal plants of southern Florida. Ecology 68, 1898–1905.

Sturrock, A.M., Trueman, C.N., Darnaude, A.M., Hunter, E., 2012. Can otolith elemental chemistry retrospectively track migrations in fully marine fishes? J. Fish. Biol. 81, 766–795. https://doi.org/10.1111/j.1095-8649.2012.03372.x.

Tanner, S.E., Reis-Santos, P., Cabral, H.N., 2016. Otolith chemistry in stock delineation: a brief overview, current challenges and future prospects. Fish. Res. 173, 206–213. https://doi.org/10.1016/j.fishres.2015.07.019.

Thorrold, S.R., Latkoczy, C., Swart, P.K., Jones, C.M., 2001. Natal homing in a marine fish metapopulation. Science 291, 297–299. https://doi.org/10.1126/science.291.5502.297.

Tohse, H., Mugiya, Y., 2007. Sources of otolith carbonate: experimental determination of carbon incorporation rates from water and metabolic CO_2, and their diel variations. Aquat. Biol. 1, 259–268. https://doi.org/10.3354/ab00029.

Trueman, C.N., Chung, M.-T., Shores, D., 2016. Ecogeochemistry potential in deep time biodiversity illustrated using a modern deep-water case study. Philos. Trans. R. Soc. B Biol. Sci. 371, 20150223 https://doi.org/10.1098/rstb.2015.0223.

Trueman, C.N., Mackenzie, K.M., Palmer, M.R., 2012. Identifying migrations in marine fishes through stable-isotope analysis. J. Fish. Biol. 81, 826–847. https://doi.org/10.1111/j.1095-8649.2012.03361.x.

Trueman, C.N., St John Glew, K., 2019. Isotopic tracking of marine animal movement. In: Hobson, K., Wassenaar, L. (Eds.), Tracking Animal Migration with Stable Isotopes. Elsevier Science & Technology, Cambridge, MA, pp. 137–172.

Vander Zanden, H.B., Tucker, A.D., Hart, K.M., Lamont, M.M., Fujisaki, I., Addison, D.S., Mansfield, K.L., Phillips, K.F., Wunder, M.B., Bowen, G.J., Pajuelo, M., Bolten, A.B., Bjorndal, K.A., 2015. Determining origin in a migratory marine vertebrate: a novel method to integrate stable isotopes and satellite tracking. Ecol. Appl. 25, 320–335.

A practical handbook for determining the ages of Gulf of Mexico fishes. In: VanderKooy, S., Carroll, J., Elzey, S., Gilmore, J., Kipp, J. (Eds.), 2020. Publication Number 300. Gulf States Marine Fisheries Commission. Ocean Springs, MS.

Wagner, A.J., Slowey, N.C., 2011. Oxygen isotopes in seawater from the Texas-Louisiana shelf. Bull. Mar. Sci. 87, 1–12. https://doi.org/10.5343/bms.2010.1004.

Walther, B.D., Limburg, K.E., 2012. The use of otolith chemistry to characterize diadromous migrations. J. Fish. Biol. 81, 796–825. https://doi.org/10.1111/j.1095-8649.2012.03371.x.

Wang, J., Gao, Y., Liu, W., Zhang, H., Dettman, D.L., 2021. The life history and populations of chum salmon (*Oncorhynchus keta*) in China: an otolith isotopic investigation. Appl. Geochem. 127, 104903 https://doi.org/10.1016/j.apgeochem.2021.104903.

Ward, C.H., 2017. Habitats and biota of the Gulf of Mexico: before the deepwater horizon oil spill. In: Water Quality, Sediments, Sediment Contaminants, Oil and Gas Seeps, Coastal Habitats, Offshore Plankton and Benthos, and Shellfish, vol. 1. Springer, New York, NY.

Weidman, C.R., Millner, R., 2000. High resolution stable isotope records from North Atlantic cod. Fish. Res. 46, 327–342. https://doi.org/10.1161/CIRCRESAHA.111.260943.

Winner, B.L., Flaherty-Walia, K.E., Switzer, T.S., Vecchio, J.L., 2014. Multidecadal evidence of recovery of nearshore red drum stocks off west-central Florida and connectivity with inshore nurseries. N. Am. J. Fish. Manag. 34, 780–794. https://doi.org/10.1080/02755947.2014.920737.

Wood, S., 2006. Generalized Additive Models: an Introduction with R. CRC Press, Boca Raton, FL.

Wood, S.N., 2004. Stable and efficient multiple smoothing parameter estimation for generalized additive models. J. Am. Stat. Assoc. 99, 673–686. https://doi.org/10.1198/016214504000000980.

Wurster, C.M., Patterson, W.P., 2003. Metabolic rate of late Holocene freshwater fish: evidence from δ13C values of otoliths. Paleobiology 29, 492–505. https://doi.org/10.1666/0094-8373(2003)029<0492:MROLHF>2.0.CO;2.

Ying, Y., Chen, Y., Lin, L., Gao, T., 2011. Risks of ignoring fish population spatial structure in fisheries management. Can. J. Fish. Aquat. Sci. 68, 2101–2120. https://doi.org/10.1139/F2011-116.

Zieman, J., Zieman, R., 1989. The ecology of the seagrass meadows of the west coast of Florida: a community profile. U S Fish Wildl. Serv. Biol. Rep. 85 (7.25).