



Ontogenetic stability in the trophic niche of a common Gulf of Mexico fish, *Ariopsis felis*

Lucas G. Pensinger · Michael J. Polito ·
Stephen R. Midway 

Received: 8 September 2020 / Accepted: 20 April 2021 / Published online: 14 May 2021
© The Author(s), under exclusive licence to Springer Nature B.V. 2021

Abstract *Ariopsis felis* (Hardhead Catfish) is an abundant yet understudied estuarine fish species in the US Atlantic and Gulf of Mexico. Very little is known about the species' trophic role and place in coastal food webs. This study was designed to provide baseline information on *A. felis* stable isotope values and to examine for any ontogenetic changes. $n = 126$ *A. felis* were sampled in the summer of 2018 in Terrebonne Bay, LA, USA, and muscle tissue was analyzed for stable carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) values. Overall, we found little evidence for any ontogenetic trophic niche shifts, expansions, or contractions; mature males and females have similar isotopic values and little to no differences were detected between immature and mature fish. Ultimately, *A. felis* occupy a trophic niche similar to that of other common estuarine fishes; however, the lack of any ontogenetic change in trophic position suggests that *A. felis* may be occupying a more stable and long-term place in coastal food webs.

Keywords Hardhead catfish · Stable isotope · $\delta^{13}\text{C}$ · $\delta^{15}\text{N}$

Introduction

Coastal ecosystems are made up of complex and dynamic habitats, yet we often define these ecosystems by homogeneous physical and biological characteristics. Teasing apart the complex, interspecific interactions within coastal ecosystems can provide clarity for how organisms interact with and use coastal habitats. Food webs are a central pillar in ecology, providing a framework to explain interspecific interactions through energy transfer between trophic levels (Lindeman 1942), and food webs can be used to connect localized interactions to the greater ecosystem level through the crossing of spatial habitat boundaries by predator, prey, or nutrients (Polis et al. 1997).

Nektonic, coastal fishes provide one such pathway for the movement of resources both as consumers and as prey for larger predators (Hyndes et al. 2014). Generally, as the size of fishes increases, so does the quantity and size range of prey items (Reid et al. 2007). As such, how fishes interact and affect the ecosystem potentially differs throughout their lifecycle. Many organisms undergo ontogenetic diet changes as they grow or mature (Polis et al. 1997), which further muddies the waters of coastal trophic webs. The multifaceted, interspecific relationships in coastal ecosystems make studying food webs through more traditional means (e.g., observational studies) impractical and cost prohibitive (Boecklen et al. 2011).

L. G. Pensinger · M. J. Polito · S. R. Midway (✉)
Department of Oceanography and Coastal Sciences,
Louisiana State University, Baton Rouge, 70803, LA, USA
e-mail: smidway@lsu.edu

Stable isotope analysis (SIA) facilitates the study of food webs in a cost-effective manner as variation in the stable isotope values of consumers is a function of diets and trophic position (Boecklen et al. 2011). Specifically, stable isotope values of nitrogen ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$) are used as a proxy for trophic position (Minagawa and Wada 1984) and habitat use, through base level, organic diet inputs (Peterson and Fry 1987), respectively.

In a broad sense, the bivariate mean and variance of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values, also referred to as the isotopic niche (Newsome et al. 2007), describes an organism's trophic niche (Turner et al. 2010). Given the trophic space in which many species can exist in their lifetime, we might expect coastal fishes to fit into one of four possible ontogenetic scenarios: (1) no trophic niche shift or expansion/contraction (i.e., fish diet or basal resource use does not change with ontogeny), (2) trophic niche expansion or contraction, but no niche shift (i.e., fish utilize a wider or smaller variety of prey items or basal resources with ontogeny), (3) trophic niche shift (i.e., fish occupy a completely different trophic niche with ontogeny), or (4) both a trophic niche shift and expansion (Hammerschlag-Peyer et al. 2011). This framework expands upon the theoretical scenarios by Layman et al. (2007) and allows for robust statistical analysis of trophic niche (Turner et al. 2010; Hammerschlag-Peyer et al. 2011). Multivariate analysis of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values can be used to help uncover which of the four possible trophic niche scenarios describe coastal fishes (Hammerschlag-Peyer et al. 2011). In addition, direct calculations of trophic position and the relative importance of basal carbon sources can be made from consumer $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values to further elucidate ontogenetic scenarios (Post 2002; Quezada-Romegialli et al. 2018b).

Ariopsis felis (Hardhead Catfish) is a species of marine catfish found in coastal waters from Cape Cod, MA, USA, to Yucatan, Mexico (Muncy and Wingo 1983) and is common in the coastal waters of Louisiana; however, we know very little about the species' biology or population status. *A. felis* are considered opportunistic feeders that feed on detritus, crustaceans, other fish (Lee et al. 1980), and potentially even target the scales of live fish (lepidophagy) (Hoese 1966). In southern Florida lagoons, *A. felis* showed no evidence of body size-related shifts in trophic niche, but trophic niche did vary significantly with season (Olin et al. 2012). That study sampled

$n = 63$ *A. felis* over two seasons and two estuaries, although stable isotope values were very similar between estuaries. The seasonal trophic niche shift observed by Olin et al. (2012) is likely evidence of a seasonal change in *A. felis* habitat use or seasonal differences in nutrient input. Reports of maximum age vary widely from 2 years (Benson 1982) to “three to eight growing seasons” (Doermann et al. 1977) to 24 (Flinn et al. 2019) or 25 years (Armstrong et al. 1996), with the strongest evidence supporting longevity >20 years. While there have been some studies examining the life history traits and feeding behavior of *A. felis* in the northern Gulf of Mexico and southern Florida, there remain large gaps in our knowledge of this abundant coastal fish and recent studies have challenged some of the little reporting available (Armstrong et al. 1996; Flinn et al. 2019).

Though there is an intrinsic scientific value to basic biological knowledge of any coastal fish species, knowing how coastal fishes' feeding changes over their lifetime is an important step toward understanding their ecological importance. Ecosystem modeling has predicted *A. felis* as abundant enough to be one of the more important meso-predators in the Gulf of Mexico (Walters et al. 2008), but despite that abundance, we know little of the trophic niche of *A. felis* in coastal Louisiana. Determining possible ontogenetic dietary shifts of *A. felis* in Louisiana informs their trophic niche which, in turn, informs the role of *A. felis* in coastal ecosystems and is the basis of understanding predator-prey relationships. Considering recent challenges to historic reporting (Armstrong et al. 1996; Flinn et al. 2019) and the lack of reporting specific to Louisiana coastal ecosystems, the objectives of this study were to:

- 1) establish *A. felis* trophic niche in coastal Louisiana, and
- 2) determine which trophic niche scenario best describes *A. felis* ontogeny in coastal Louisiana.

Methods

Collection and processing

A. felis used in this study were sampled opportunistically in partnership with the Louisiana Department of Wildlife and Fisheries (LDWF) as a part of their routine Fishery-Independent Sampling program.

Sampling was conducted out of the Lacombe and Bourg LDWF field offices primarily in Coastal Study Areas (CSA) 5 (Terrebonne Basin) (Fig. 1) between June and August, 2018. LDWF uses a variety of collection gears in their fishery-independent sampling program, including bag seines, gill nets, trammel nets, and trawls. For more information on this program, see LDWF’s Marine Fisheries Section Independent Sampling Activities (2017). Whole fish were frozen, then collected by Louisiana State University for analysis.

A total of $n = 126$ *A. felis* were taken to represent Terrebonne Basin from the summer months (June, July, and August, 2018). Samples were individually thawed and processed for basic biological measurements of total length (TL [mm]) and total weight (TW [g]). A white muscle tissue (here-after muscle) sample was taken slightly posterior to the dorsal fin for stable isotope analysis. We specifically chose to analyze carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotope values because they act as proxies for habitat use and trophic position, respectively (Minagawa and Wada 1984; Peterson and Fry 1987; Boecklen et al. 2011).

Stable isotope analysis

Muscle tissue samples were freeze dried for > 48 h at -40°C , ground to a fine powder with a mortar and pestle to homogenize samples, and weighed to $0.60\text{ mg} \pm 0.025\text{ mg}$ for bulk stable isotope analysis. Tissue was combusted with a Costech 4010 Elemental Analyzer

and the resultant gas was analyzed through a Thermo Scientific Delta V Isotope Ratio Mass Spectrometer interfaced with a Thermo Scientific ConFlow IV.

Stable isotope values were normalized using a two-point system with glutamic acid reference material (USGS-40 and USGS-41). Sample precision based on repeated reference material was 0.1‰ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. Stable isotope values were calculated with the following equation and are expressed in standard delta (δ) notation in per mil units (‰):

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000 \quad (1)$$

where X is ^{13}C or ^{15}N and R is the corresponding ratio $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$. The R_{standard} values were based on Vienna Pee Dee Belemnite (VPDB) for $\delta^{13}\text{C}$ and atmospheric N_2 (AIR) for $\delta^{15}\text{N}$ values.

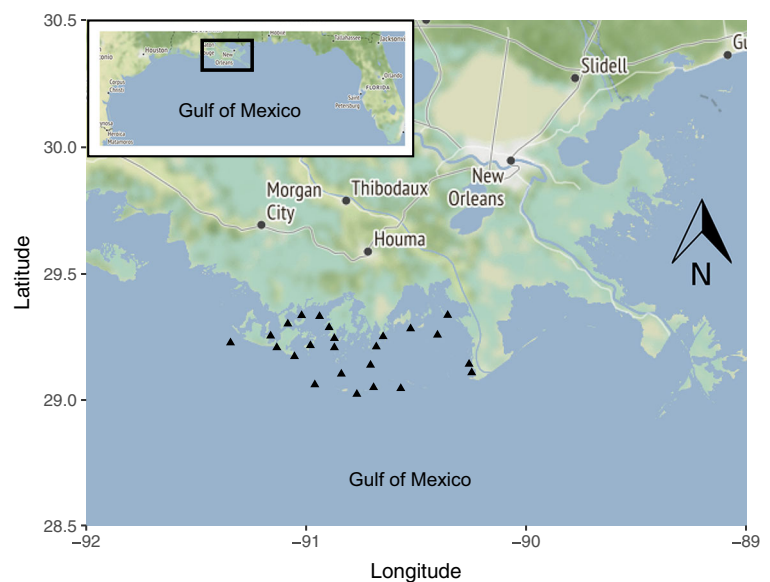
Samples with a C:N ratio > 3.32 from aquatic organisms require lipid normalization to analyze $\delta^{13}\text{C}$; therefore, we normalized samples with C:N values > 3.32 with the equation (Post et al. 2007):

$$\delta^{13}\text{C}_{\text{normalized}} = \delta^{13}\text{C}_{\text{untreated}} - 3.32 + (0.99 \times \text{C} : \text{N}) \quad (2)$$

Statistical analysis

To determine ontogenetic niche shift for *A. felis*, we divided the samples into three classes based on previously determined sex and maturity information (Pensinger et al. 2021): immature ($n = 53$), mature

Fig. 1 *A. felis* sampling sites in Terrebonne Bay, coastal Louisiana



male ($n = 28$), and mature female ($n = 45$). Sex and maturity were determined from visual inspection of the gonads (for sex) and based on spawning season gonadosomatic index (for maturity). *A. felis* do not exhibit sexually dimorphic growth in coastal Louisiana (Flinn et al. 2019); however, male and female *A. felis* were kept separate to account for any potential feeding differences while male *A. felis* are mouthbrooding. The procedure for determining statistical differences between groups follows.

A linear regression was used to determine if univariate $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values changed with *A. felis* length. The δ value was modeled as the response (y) and size (TL) as the predictor:

$$y_i = \beta_0 + \beta_1 \times TL_i + \epsilon_i \quad (3)$$

where y_i is the δ value for fish i , β_0 is the intercept parameter, β_1 is the slope parameter, and TL_i is the total length for fish i . ϵ_i represented the residual error. All model estimation was done using the `lm` function in R (R Core Team 2019).

Niche position of each group was examined through multivariate and univariate analysis of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in a Frequentist framework (Hammerschlag-Peyer et al. 2011). Niche position is examined by calculating the mean Euclidean distance (ED) between centroid means of each group (Turner et al. 2010). If the absolute value of ED was significantly different than zero, the groups were considered to have different niche positions (Hammerschlag-Peyer et al. 2011). We also examined significant differences in multivariate niche position through univariate analysis of variance (ANOVA) of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, respectively, to determine the isotopic driver of niche position.

Niche width was evaluated within two common frameworks: Frequentist (Hammerschlag-Peyer et al. 2011) and Bayesian (Jackson et al. 2011). In the Frequentist framework, niche width is measured by the dispersion between samples calculated by comparing the mean distance to centroid (bivariate mean; MDC) of each group. In other words, the Euclidean distance between each individual sample within a group and the group's centroid mean (Hammerschlag-Peyer et al. 2011; Turner et al. 2010). In the Bayesian framework, we used standard ellipse areas (SEA_b) to examine trophic niche between groups using Markov Chain Monte Carlo simulations implemented in the Stable Isotope Bayesian Ellipses in R (SIBER) package (Jackson et al. 2011). Bayesian standard ellipses

describe the mean covariance of bivariate data and are generally calculated encompassing 40% of data points (Jackson et al. 2011). However, to maintain consistency between SEA_b and the Bayesian estimate of niche overlap, we calculated SEA_b encompassing 95% of data points. For SIBER analyses, we used 5 chains of 10,000 iterations with a burn-in of 1000 and thinning of 10. Using posterior probabilities (PP), we compared SEA_b of each group to all other groups, with $PP > 0.95$ used as a measure of significant differences. Posterior probabilities allowed us to calculate the difference between estimated posteriors in two groups and then examine the probability of whether posterior SEA_b values from one group are less than the posterior SEA_b value from the comparison group. Significant differences in multivariate niche width were further explored through univariate analysis of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values utilizing Bartlett's test to determine which element drove the observed multivariate difference in niche width between ontogenetic groups (Hammerschlag-Peyer et al. 2011).

We examined trophic niche overlap among groups relative to the SEA_b of immature, male, and female *A. felis* estimated to contain 95% of the data points within each group (Jackson et al. 2011). Trophic niche overlap was calculated as the probability of one species falling into the niche area (i.e., SEA_b) of another using a Bayesian model with Markov Chain Monte Carlo simulations implemented in the NicheRover package in R (Swanson et al. 2015). For NicheRover analyses, we used 5 chains of 10,000 iterations with a burn-in of 1000 and thinning of 10. The resulting pairwise trophic niche overlap values (%) are presented as median values with 95% credible intervals. Trophic niche overlap comparisons provided additional ability to assess potential ontogenetic niche shifts and expansions or contractions among groups.

Finally, to further complement the isotopic niche analyses described above, we estimated trophic position and the relative importance of basal carbon sources α to *A. felis* using a Bayesian model from the package `tRophicposition` (Version 0.7.5) implemented in R (Quezada-Romegialli et al. 2018b). This package employs a Bayesian formulation of the TP equations outlined in Post (2002) coupled with Markov Chain Monte Carlo simulations (Quezada-Romegialli et al. 2018a). This model was parameterized using reported literature stable isotope values of basal carbon sources for the Terrebone Basin, LA, collected in August

and September of 2016 (Nelson et al. 2019). Specifically, a two baseline model with trophic fractionation was examined with the C4 grass *Spartina alterniflora* used as a proxy for terrestrial carbon sources ($\delta^{15}\text{N}$: $6.6 \pm 0.6\text{‰}$; $\delta^{13}\text{C}$: $-14.5 \pm 0.3\text{‰}$) and water column particular-organic matter (POM) used as a proxy for aquatic carbon sources ($\delta^{15}\text{N}$: $6.7 \pm 0.8\text{‰}$; $\delta^{13}\text{C}$: $-22.5 \pm 0.8\text{‰}$). Prior to incorporation in the model, 100 points were randomly generated from the mean and standard deviation of each basal resource contributions (James et al. 2020). All models incorporated an assumed mean trophic fractionation ($\Delta^{13}\text{C} = 0.39 \pm 1.30$; $\Delta^{15}\text{N} = 3.4 \pm 0.98$) per trophic transfer (Post 2002). These values represent the average trophic discrimination calculated across a range of aquatic consumers (Post 2002), and as such provide a measure of the mean \pm SD trophic discrimination factors across all steps/species in the food web leading up to *A. felis*. For all models, we used 5 chains of 10,000 iterations with a burn-in of 1000 and thinning of 10. Resulting TP and α metrics are presented as median values with 95% credibility intervals. An α value of 1 represents a 100% use of aquatic carbon sources (i.e., 0% use of terrestrial carbon sources). Similar to SEA_b comparisons above, we used PP to compare trophic

position and α metrics of each group, with $PP > 0.95$ used as a measure of significant differences.

All statistical analyses were performed in R (R Core Team 2019). Model-checking was performed by calculating Gelman–Rubin diagnostic to assess convergence and by comparing posterior estimates of the mean and standard deviation of TP and α to their corresponding naive and time-series Markov Chain Monte Carlo (MCMC) errors to assess precision (Gelman et al. 2013). For all models, point estimates of the potential scale reduction factor (R_c) were < 1.01 and below or equal to their corresponding upper confidence limits ($R_{95\%}$) indicating model convergence. In addition, both naive and time-series MCMC errors were less than 5% of their corresponding standard deviations (i.e., standard deviations were >20 times larger than MCMC errors) indicating model precision.

Results

Trophic niche position

Univariate, linear regression of *A. felis* stable isotope values and TL found a significant, positive effect of

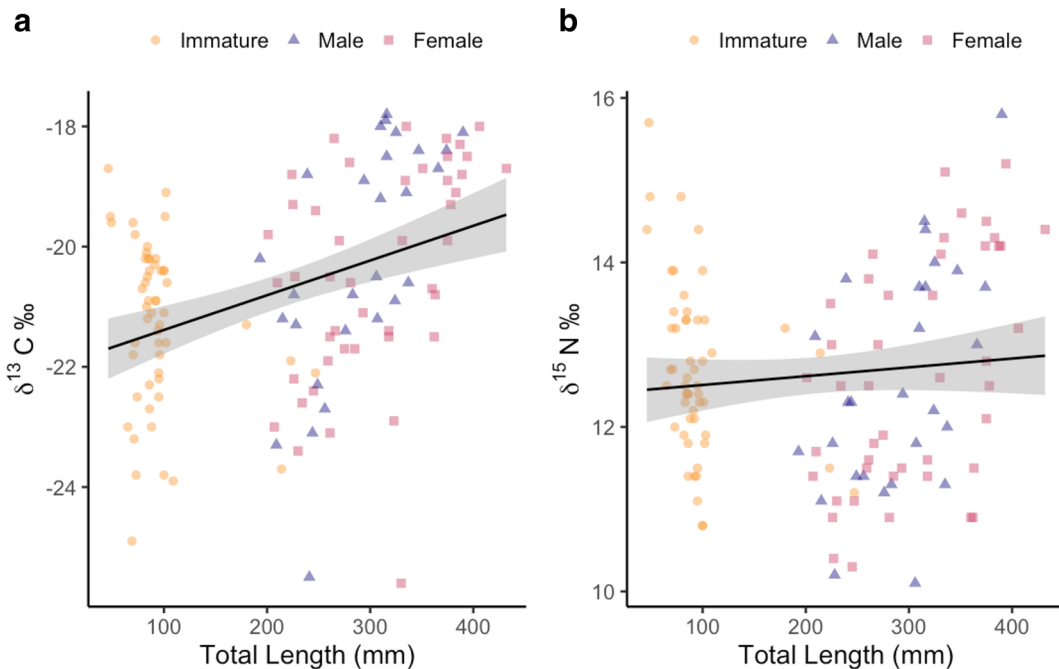


Fig. 2 $\delta^{13}\text{C}$ (A) and $\delta^{15}\text{N}$ (B) values plot against total length (mm). Filled orange squares represent immature *A. felis*, filled red circles represent mature female *A. felis*, and filled purple

triangles represent mature male *A. felis*. The black line (a) represents the regression and the gray shaded region represents the confidence interval for the regression

size on $\delta^{13}\text{C}$ values ($\beta_1 = 0.006$, $SE = 0.001$, $p < 0.05$; Fig. 2). However, no significant effect of size was found on $\delta^{15}\text{N}$ values ($\beta_1 < 0.0001$, $SE < 0.0001$, $p = 0.28$).

Multivariate analysis of trophic niche position found a significant difference in niche position between immature and mature male *A. felis* ($ED = 0.8627\%$, $p = 0.02$) and between immature and mature female *A. felis* ($ED = 1.0726\%$, $p = 0.02$). There was no difference in trophic niche position ($ED = 0.2192\%$, $p = 0.91$) between mature male and mature female *A. felis*. ANOVA of trophic niche position of $\delta^{13}\text{C}$ values showed a significant difference between groups ($F = 6.701$, $df = 1$, $p = 0.01$). Tukey Honest Significant Difference pairwise tests (Midway et al. 2020) found that immature fish $\delta^{13}\text{C}$ values were 1.1‰ lower than adult males ($p = 0.02$) and 0.9‰ lower than adult females ($p = 0.02$). ANOVA for the response $\delta^{15}\text{N}$ values showed no significant difference between groups ($F = 0.046$, $df = 1$, $p = 0.83$; Table 1).

Trophic niche width

Frequentist, multivariate analysis of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values between immature, mature male, and mature female *A. felis* groups showed a small, but significant (absolute) difference in trophic niche width between immature and mature males ($MDC_{immature} - MDC_{male} = 0.5090\%$, $p = 0.01$) as well as a small, but significant difference in trophic niche width between immature and mature females ($MDC_{immature} - MDC_{female} = 0.6169\%$, $p < 0.01$). However, there was no significant difference in

trophic niche width between mature male and mature female *A. felis* ($MDC_{male} - MDC_{female} = 0.1079\%$, $p = 0.668$). Our second proxy of niche width ($SEAb$) did not differ among immature, mature male, and mature female *A. felis* (all $PP < 0.95$, Table 1). Similarly, univariate analysis of homogeneity of variance using Bartlett's test found no significant difference in $\delta^{13}\text{C}$ values between groups ($\chi^2 = 5.01$, $df=2$, $p = 0.08$) or $\delta^{15}\text{N}$ values between groups ($\chi^2 = 4.47$, $df=2$, $p = 0.11$).

Trophic niche overlap

The trophic niche of immature individuals overlaps with the trophic niche of mature male *A. felis* by 74% (95% CI = 57–89%). Immature *A. felis* trophic niche overlap with mature female trophic niche by 80% (95% CI = 67–92%). The mature male trophic niche and mature female trophic niche overlap with the trophic niche of immature *A. felis* by 93% (95% CI = 83–99%) and 92% (95% CI = 81–99%) respectively. Mature male trophic niche overlaps with mature female trophic niche by 93% (95% CI = 84–99%), while the mature female trophic niche overlaps with the trophic niche of mature males by 89% (95% CI = 74–97%; Fig. 3).

Trophic position and basal carbon sources

Bayesian analysis of trophic position estimated a median trophic position of 2.75 for immature *A. felis*. Estimates of median trophic position of mature male and mature female *A. felis* are 2.74 and 2.72 respectively. Credible intervals for all three groups overlap

Table 1 Sample size (n), total length (mm) range, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ means, standard ellipse areas ($SEAb$), trophic position, and α and broken down by immature, mature male, and mature female *A. felis* included in this study

Metric	Immature	Male	Female
sample size (n)	53	28	45
Total length (mm)	46–247	193–390	201–432
$\delta^{13}\text{C}\text{‰} \pm \text{SD}$	-21.3 ± 1.4	-20.2 ± 2.0	-20.4 ± 1.8
$\delta^{15}\text{N}\text{‰} \pm \text{SD}$	12.7 ± 1.0	12.5 ± 1.4	12.6 ± 1.4
$SEAb\text{‰}^2$ [95% CI]	5.8 [3.8,8.2]	6.4 [4.6,8.3]	4.4 [3.2,5.7]
Trophic position [95% CI]	2.75 [2.59,2.92]	2.74 [2.56,2.94]	2.72 [2.51,2.95]
α [95% CI]	0.99 [0.96,1.00]	0.96 [0.89,1.00]	0.94 [0.84,1.00]

Uncertainty is included in the form of standard deviation (SD) or 95% credible interval (95% CI)

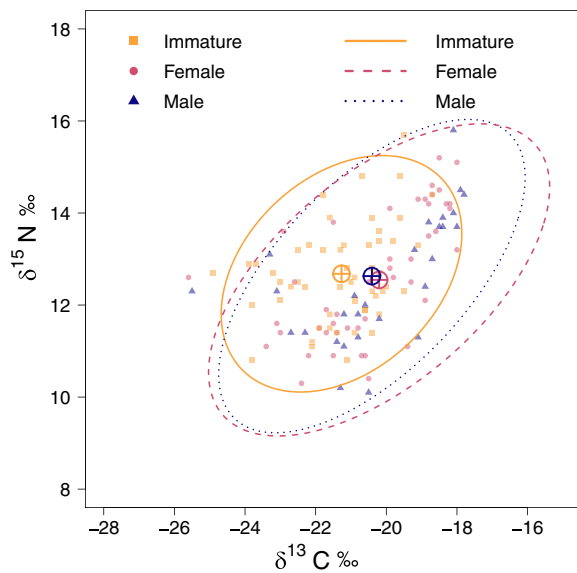


Fig. 3 Bivariate $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values plotted with 95% standard ellipses for *A. felis* (with colors following those presented in Fig. 2). Centroid means are represented by open circles bisected by solid crosshairs

at 95% and all PP < 0.95, indicating that trophic position was similar among groups (Table 1). The median α for immature *A. felis* is estimated at 0.99. Median α for male *A. felis* is estimated as 0.96 and median α for female *A. felis* is estimated as 0.94. Similarly, there is no significant difference in α among groups (all PP < 0.95) with 95% credible intervals overlapping among immature, mature male, and mature female *A. felis* (Table 1).

Discussion

What coastal fishes eat and the habitats they use are important factors influencing how these fishes interact with coastal ecosystems. Describing the trophic niche of a coastal fish species begins to elucidate the complicated nature of these interactions (Werner and Gilliam 1984) allowing for more effective ecosystem and fisheries management. Differences in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values can be used to describe trophic position or shifts (Peterson and Fry 1987; Minagawa and Wada 1984) and habitat or resource use (Peterson and Fry 1987; France and Peters 1997), respectively. Examining ontogenetic shifts through simultaneous analysis of trophic position ($\delta^{15}\text{N}$ values) and

habitat use ($\delta^{13}\text{C}$ values) allows for a more quantitative understanding of the ecosystem role of fish species (Hammerschlag-Peyer et al. 2011). Entering this study, we expected fish to fit into one of four possible trophic niche scenarios: (1) no trophic niche shift or expansion/contraction, (2) trophic niche expansion, but no niche shift, (3) trophic niche shift, or (4) both a trophic niche shift and expansion (Hammerschlag-Peyer et al. 2011).

We found mixed statistical results when testing for possible trophic niche shifts with ontogeny in *A. felis* in coastal Louisiana. First, we found a positive relationship with body size (TL) and muscle tissue $\delta^{13}\text{C}$, but not $\delta^{15}\text{N}$ values. In addition, while the multivariate, frequentist proxy of trophic niche position (ED) differed between immature and mature fish, univariate analysis identified differences in $\delta^{13}\text{C}$ values, but not $\delta^{15}\text{N}$ values, as the proximate cause. These results suggest no change in the trophic position of *A. felis* with ontogeny, but rather a possible shift in basal carbon sources between ontogenetic groups. However, the differences in $\delta^{13}\text{C}$ values found between immature and mature *A. felis* were small ($\sim 1.0\text{‰}$) relative to the range of basal carbon sources found in their environment. For example, in estuarine environments, $\delta^{13}\text{C}$ values of consumers are largely influenced by suspended particulate organic matter such as phytoplankton ($-21.5 \pm 0.8\text{‰}$) and C4 plants ($-14.5 \pm 0.3\text{‰}$), with C3 plants ($-28.6 \pm 1.3\text{‰}$) having a lesser impact (Peterson et al. 1985; Peterson and Fry 1987; Nelson et al. 2019). In our study, *A. felis* and basal resources (i.e., POM and C4) were collected in the same season (June–September) and region (Terrebonne Bay basin) but different years (2016 vs. 2018). If the stable isotope values of these two basal resources differed between these two years, they could impact our median estimates of trophic position and/or basal carbon source use in *A. felis*. However, if such interannual variation occurred, it would not alter the results of our relative comparisons of trophic position and basal carbon source use among adult and immature *A. felis*. Specifically, in addition to finding no significant differences in calculated trophic position among groups, the predicted use of aquatic (POM) vs. terrestrial (C4 plants) basal carbon sources also did not differ among immature and mature *A. felis* (Table 1). In combination, these results suggest a general stability with ontogeny in the trophic niche position of *A. felis* in coastal Louisiana, at least over the transition

to maturity during the season examined here. Even so, given the observed relationship between TL and muscle tissue $\delta^{13}\text{C}$, it may be worthwhile in future studies to examine this question over multiple seasons using a broader size range of *A. felis* that includes individuals near this species' maximum body size (>400 mm; Flinn et al. 2019).

We also found little support for a trophic niche expansion or contraction with ontogeny in *A. felis* in coastal Louisiana. Specifically, while the multivariate, frequentist proxy of trophic niche width (*MDC*) indicated small, but significant differences among immature and mature *A. felis*, subsequent univariate analyses (Bartlett's test) found no differences in the degree of variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ with ontogeny. In addition, our Bayesian proxy of trophic niche width *SEA_b* did not differ among immature, mature male, and mature female *A. felis* (Table 1). Similarly, the degree of niche overlap among immature and mature fish was constantly high (74–93%) and 95% credibility intervals around niche overlap estimates overlapped among all comparisons. Finally, 95% credibility intervals around median estimates of trophic position and the relative use of aquatic vs. terrestrial basal carbon sources (α) were broadly similar. In combination, these results suggest a general stability in the trophic niche width of *A. felis* over the transition to maturity. Given these findings *A. felis* in coastal Louisiana most likely fall under the first of the four possible ontogenetic scenarios: no trophic niche shift or expansion/contraction (i.e., fish diet or basal resource use does not appreciably change with ontogeny).

There are a variety of non-dietary factors which could influence *A. felis* isotopic signatures. Generally, white muscle tissue is thought to have a turnover rate measured in weeks to months (Winter et al. 2019; Busst and Britton 2018). As paternal mouthbrooders, the timing of our *A. felis* subsample (July–August) could produce male stable isotope values influenced by fasting during mouthbrooding. The influence of fasting on male stable isotope values could mask potential differences between either males and females or males and immature individuals. Similarly, mature *A. felis* of both sexes are thought to move offshore in the winter months (Muncy and Wingo 1983). It is unclear whether juvenile *A. felis* exhibit this same behavior, which potentially introduces a seasonal isotopic difference driven by ontogeny. While

we attempted to control for as many non-dietary factors as possible that may influence the stable isotope values of *A. felis* white muscle, we cannot definitely say none of these factors mask possible ontogenetic differences in *A. felis* trophic niche position, width, or overlap. Seasonal effects on stable isotopes in *A. felis* have been reported elsewhere in Gulf of Mexico estuaries (Olin et al. 2012), and the same study also reported very similar $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values to what we observed.

A. felis are considered estuarine generalist feeders (Muncy and Wingo 1983; Merriman 1940) and, based on our results, there does not appear to be a meaningful ontogenetic shift in this feeding pattern between immature and mature fish. *A. felis* are likely using similar habitats and eating similar prey items regardless of size or maturity status. The 95% CI of calculated trophic positions for *A. felis* in this study were slightly lower than the estimation from FishBase using the TROPH routine (trophic position = 3.0; Froese and Pauly 2000). This may be due to the use of primary producer (trophic position = 1) stable isotope values as opposed to representative aquatic and terrestrial primary consumers (trophic position = 2) as basal sources for the Bayesian model and/or an artifact of the specific trophic discrimination factors employed (Post 2002; Quezada-Romegialli et al. 2018a). The $\delta^{13}\text{C}$ values observed in this study suggest that *A. felis* rely on a wide range of food resources primarily derived from water column production as opposed to marsh grass production (Nelson et al. 2019). Such generalist feeding and habitat patterns use could partially explain the apparent mismatch between *A. felis* life history and abundance, whereby their low fecundity and relatively high abundance are not well understood.

Many organisms undergo ontogenetic trophic niche shifts, especially when transitioning from larvae to juvenile or juvenile to adult (Werner and Gilliam 1984). However, *A. felis* does not appear to undergo such an ontogenetic trophic niche shift in coastal Louisiana. *A. felis* sampled for this study ranged from 46-mm TL to 432-mm TL, an increase of nearly a factor of ten, while mass varied by nearly a factor of 100 (0.723 to 690 g). It seems counterintuitive that a species exhibiting such a wide range in body size does not shift its trophic position as body size increases. Theoretically, immature fish could have large enough mouths (i.e., gape width) that prey size for imma-

ture *A. felis* is not limited by mouth size—leading to similar stable isotope values for immature and mature groups. However, horizontal mouth gape of *A. felis* appears comparable to many other marine fishes (Scharf et al. 2000), and as such mouth gape seems an unlikely explanation for the similar isotope signatures of immature and mature *A. felis*.

A. felis have stable isotope values similar to other large-bodied, estuarine-dependent fishes such as *Sciaenops ocellatus* (Red Drum), *Paralichthys lethostigma* (Southern Flounder), *Pogonias cromis* (Black Drum), and *Cynoscion nebulosus* (Spotted Seatrout) (Fig. 4). The range of $\delta^{13}\text{C}$ values in *A. felis* does not overlap with that of *S. ocellatus*, but does overlap with the three other species, while the $\delta^{15}\text{N}$ values of all five species overlap (Winemiller et al. 2007). One caveat is that fish $\delta^{13}\text{C}$ values in Wine-miller et al. (2007) were not normalized to account for lipid content which has the potential to lower $\delta^{13}\text{C}$ values (Post et al. 2007). Even so, amount of overlap in stable isotope values supports evidence (Olin et al. 2012; Walters et al. 2008) that *A. felis* has the potential to compete for prey items with

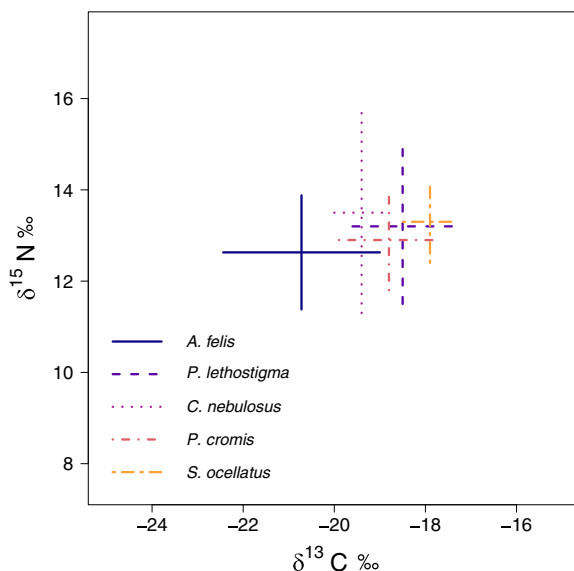


Fig. 4 A comparison of mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotope values plus standard deviation for *A. felis* and four other estuarine predators common to the Gulf of Mexico. Values for *A. felis* come from this study while all other values are from Wine-miller et al. (2007). *A. felis* stable isotope values overlap with all other species except for the $\delta^{13}\text{C}$ values of *S. ocellatus*, though *S. ocellatus* stable isotope values overlap with *C. nebulosus*, *P. lethostigma*, and *P. cromis*

other, more commercially desirable estuarine fishes. Competition for resources is an important factor to consider when examining ecosystem level interactions and modeling (Walters et al. 2008). As such, *A. felis* trophic niche, abundance, and their effect on other estuarine fishes are important factors in the management of healthy fish populations and coastal ecosystems.

A. felis is an important mesopredator in the Gulf of Mexico (Walters et al. 2008) and they eat varied prey items throughout their lifetime. Mature *A. felis* use a variety of coastal and marine habitats, which, especially when combined with localized abundance, likely make *A. felis* an important vector in the transfer of energy across ecosystem boundaries as both predator and prey. In fact, *A. felis* may have an out-sized influence on ecosystem connectivity in coastal Louisiana due to their local abundance. Lack of fishing pressure plus the consumption of a wide variety of prey items independent of ontogeny could possibly explain the apparent mismatch between *A. felis* life history traits and abundance that was mentioned earlier. However, as previously discussed, *A. felis* life history traits suggest potential vulnerability to stressors such as overfishing or disease. A decrease in *A. felis* abundance—such as the substantial decline seen in South Carolina beginning in the early 1990s (Ballengier 2018)—could decouple an important trophic link between coastal ecosystems if that same decline were to occur in the Gulf of Mexico. Historic catch data in South Carolina could provide insight into the implications of the removal of an abundant mesopredator from coastal ecosystems. This study represents an important first step in understanding *A. felis* trophic niche in coastal Louisiana.

Acknowledgements We thank the Louisiana Department of Wildlife and Fisheries for assistance in collecting the fish.

Data availability Data will be made available upon reasonable request.

Compliance with Ethical Standards

Ethical approval This work examined only previously deceased organisms that were collected by those outside the author group under appropriate permits.

Conflict of interest The authors declare no competing interests.

References

- Armstrong M, Murphy M, Muller R, Harshany D, Crabtree R (1996) A stock assessment of hardhead catfish, *Arius felis*, and gafftopsail catfish, *Bagre marinus*, in Florida waters. Report to the Florida Marine Fisheries Commission
- Ballenger JC (2018) Contributions to the biology of Red Drum, *Sciaenops ocellatus*, in South Carolina: continuation of mark–recapture studies and abundance estimates. Tech rep., South Carolina Department of Natural Resources, Charleston
- Benson NG (1982) Life history requirements of selected finfish and shellfish in Mississippi Sound and adjacent areas. U.S. Fish and Wildlife Service
- Boecklen WJ, Yarnes CT, Cook BA, James AC (2011) On the use of stable isotopes in trophic ecology. *Annu Rev Ecol Evol Syst* 42:411–440
- Busst GM, Britton JR (2018) Tissue-specific turnover rates of the nitrogen stable isotope as functions of time and growth in a cyprinid fish. *Hydrobiologia* 805(1):49–60
- Doermann J, Huddleston D, Lipsey D, Thompson S (1977) Age and rate of growth of the sea catfish, *Arius felis*, in Mississippi coastal waters. *J Tenn Acad Sci* 52:148
- Flinn S, Midway S, Ostrowski A (2019) Age and growth of hardhead catfish and gafftopsail catfish in coastal Louisiana, USA. *Mar Coast Fish* 11(5):362–371
- France R, Peters R (1997) Ecosystem differences in the trophic enrichment of ^{13}C in aquatic food webs. *Can J Fish Aquat Sci* 54(6):1255–1258
- Froese R, Pauly D (2000) FishBase 2000: concepts designs and data sources, vol 1594. WorldFish, Penang
- Gelman A, Carlin JB, Stern HS, Dunson DB, Vehtari A, Rubin DB (2013) Bayesian data analysis. CRC press, Boca Raton
- Hammerschlag-Peyer CM, Yeager LA, Araújo MS, Layman CA (2011) A hypothesis-testing framework for studies investigating ontogenetic niche shifts using stable isotope ratios. *PLoS ONE* 6(11):e27104
- Hoese HD (1966) Ectoparasitism by juvenile sea catfish, *Galeichthys felis*. *Copeia* 1966(4):880–881
- Hyndes GA, Nagelkerken I, McLeod RJ, Connolly RM, Lavery PS, Vanderklift MA (2014) Mechanisms and ecological role of carbon transfer within coastal seascapes. *Biol Rev* 89(1):232–254
- Jackson AL, Inger R, Parnell AC, Bearhop S (2011) Comparing isotopic niche widths among and within communities: Siber–Stable Isotope Bayesian Ellipses in R. *J Animal Ecol* 80(3):595–602
- James WR, Lesser JS, Litvin SY, Nelson JA (2020) Assessment of food web recovery following restoration using resource niche metrics. *Sci Total Environ* 711:134801
- Layman CA, Quattrochi JP, Peyer CM, Allgeier JE (2007) Niche width collapse in a resilient top predator following ecosystem fragmentation. *Ecol Lett* 10(10):937–944
- Lee DS, Gilbert CR, Hocutt CH, Jenkins RE, McAllister DE, Stauffer JR Jr (1980) Atlas of North American freshwater fishes. North Carolina State Museum of Natural History
- Lindeman RL (1942) The trophic-dynamic aspect of ecology. *Ecology* 23(4):399–417
- Merriman D (1940) Morphological and embryological studies on two species of marine catfish, *Bagre marinus* and *Galeichthys felis*. *Zoologica* 25(13):221–248
- Midway S, Robertson M, Flinn S, Kaller M (2020) Comparing multiple comparisons: practical guidance for choosing the best multiple comparisons test. *PeerJ* 8:e10387
- Minagawa M, Wada E (1984) Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between $\delta^{15}\text{N}$ and animal age. *Geochim Cosmochim Acta* 48(5):1135–1140
- Muncy RJ, Wingo WM (1983) Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Gulf of Mexico): Sea catfish and gafftopsail catfish. Tech. rep. U.S. Fish and Wildlife Service, Division of Biological Services
- Nelson JA, Lesser J, James WR, Behringer DP, Furka V, Doerr JC (2019) Food web response to foundation species change in a coastal ecosystem. *Food Webs* 21:e00125
- Newsome SD, Martinez del Rio C, Bearhop S, Phillips DL (2007) A niche for isotopic ecology. *Front Ecol Environ* 5(8):429–436
- Olin JA, Rush SA, MacNeil MA, Fisk AT (2012) Isotopic ratios reveal mixed seasonal variation among fishes from two subtropical estuarine systems. *Estuaries Coasts* 35(3):811–820
- Pensinger L, Brown-Peterson NJ, Green CC, Midway SR (2021) Reproductive biology of hardhead catfish *Ariopsis felis*: Evidence for overwintering oocytes. *Journal of Fish Biology*
- Peterson BJ, Fry B (1987) Stable isotopes in ecosystem studies. *Annu Rev Ecol Syst* 18(1):293–320
- Peterson BJ, Howarth RW, Garritt RH (1985) Multiple stable isotopes used to trace the flow of organic matter in estuarine food webs. *Science* 227(4692):1361–1363
- Polis GA, Anderson WB, Holt RD (1997) Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annu Rev Ecol Syst* 28(1):289–316
- Post DM (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology* 83(3):703–718
- Post DM, Layman CA, Arrington DA, Takimoto G, Quattrochi J, Montana CG (2007) Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. *Oecologia* 152(1):179–189
- Quezada-Romegialli C, Jackson A, Harrod C (2018a) tRophic-Position: Bayesian trophic position calculation with stable isotopes. R Package Version 0.7.5
- Quezada-Romegialli C, Jackson AL, Hayden B, Kahilainen KK, Lopes C, Harrod C (2018b) tRophicPosition, an R package for the Bayesian estimation of trophic position from consumer stable isotope ratios. *Methods Ecol Evol* 9(6):1592–1599
- R Core Team (2019) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>
- Reid WD, Clarke S, Collins MA, Belchier M (2007) Distribution and ecology of *Chaenocephalus aceratus* (Channichthyidae) around South Georgia and Shag Rocks (Southern Ocean). *Polar Biol* 30(12):1523–1533
- Scharf FS, Juanes F, Rountree RA (2000) Predator size-prey size relationships of marine fish predators: interspecific variation and effects of ontogeny and body size on trophic-niche breadth. *Mar Ecol Prog Ser* 208:229–248
- Swanson HK, Lysy M, Power M, Stasko AD, Johnson JD, Reist JD (2015) A new probabilistic method for quantifying

- n*-dimensional ecological niches and niche overlap. *Ecology* 96(2):318–324
- Turner TF, Collyer ML, Krabbenhoft TJ (2010) A general hypothesis-testing framework for stable isotope ratios in ecological studies. *Ecology* 91(8):2227–2233
- Walters C, Martell SJ, Christensen V, Mahmoudi B (2008) An Ecosim model for exploring Gulf of Mexico ecosystem management options: implications of including multistanza life-history models for policy predictions. *Bull Mar Sci* 83(1):251–271
- Werner EE, Gilliam JF (1984) The ontogenetic niche and species interactions in size-structured populations. *Annu Rev Ecol Syst* 15(1):393–425
- Winemiller KO, Akin S, Zeug SC (2007) Production sources and food web structure of a temperate tidal estuary: integration of dietary and stable isotope data. *Mar Ecol Prog Ser* 343:63–76
- Winter ER, Nolan ET, Busst GM, Britton JR (2019) Estimating stable isotope turnover rates of epidermal mucus and dorsal muscle for an omnivorous fish using a diet-switch experiment. *Hydrobiologia* 828(1):245–258

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.