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Reproductive Biology and Trophic Niche of Hardhead Catfish in the Northern Gulf of Mexico

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REPRODUCTIVE BIOLOGY AND TROPHIC NICHE OF
HARDHEAD CATFISH IN THE NORTHERN GULF OF MEXICO

A Thesis

Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Master of Science

in

The Department of Oceanography and Coastal Science

by
Lucas G. Pensinger
B.S., University of Delaware, 2017
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Abstract

Generally, marine fishes have very high fecundity with each female producing many small eggs which hatch into small larvae. However, *Ariopsis felis*, a species of marine catfish common to coastal Louisiana, has low fecundity and produces the largest eggs of the teleost fishes. Despite wide range and generally high abundance, we know very little of *A. felis* biology and population. The few existing studies of *A. felis* are older and often have questionable or unclear methodology.

I examined four aspects of *A. felis* reproductive biology: 1) reproductive timing, 2) fecundity, 3) length at first maturity, and 4) mouth brooding. I observed a clear peak of *A. felis* GSI April-June and rarely observed a GSI above 1% outside of these months. I found *A. felis* annual fecundity ranged higher than previously reported. A logistic regression showed an L_{50} of 153mm for female *A. felis*. While I did observe *A. felis* mouth brooding, sampling techniques precluded observing mouth brooding in large enough numbers to draw conclusions.

I then performed stable isotope analysis on white muscle tissue to determine if *A. felis* exhibit an ontogenetic trophic niche shift. I found *A. felis* trophic niche position varied significantly between mature and immature *A. felis*. However, *A. felis* trophic niche width did not vary significantly and mature and immature *A. felis* exhibit a high degree of trophic niche overlap. The insignificant difference in *A. felis* trophic niche width coupled with the high degree of trophic niche overlap is evidence that *A. felis* do not undergo an ontogenetic trophic niche shift in coastal Louisiana. Understanding how abundant coastal fishes reproduce and eat is an important aspect of coastal and estuarine management. This research begins to fill the knowledge gap in *A. felis* reproduction and trophic dynamics in coastal Louisiana.

Chapter 1. Reproductive Biology of *A. felis* in the Northern Gulf of Mexico

1.1. Introduction

Reproductive success in fishes can generally be defined as how likely offspring are to reach sexual maturity and reproduce. Related to that definition, reproductive biology connects the complex biological (and interacting environmental) processes of reproductive strategies to organism growth, size and age at maturity, spatial and temporal range of spawning events, and eventual reproductive success (Lowerre-Barbieri 2009). Teleost fishes have highly diversified strategies of reproduction that include a range of parity (number of lifetime spawning events), fecundity, parental investment, and other aspects of reproduction. Another strategy is spawning frequency; female teleost fishes are either batch spawners, releasing multiple batches or clutches of oocytes within a spawning season, or total spawners, releasing all oocytes at once within a spawning season (Brown-Peterson et al 2011). Regardless of the temporal spawning pattern, annual fecundity measures the total number of oocytes produced, or the spawning capacity, of female fish within a spawning season. Whether batch or total spawners, most marine fishes in environments where food resources are abundant exhibit prolific fecundity and very small oocyte size whereas marine fishes in environments with patchier prey abundance tend to have lower fecundity and larger oocytes (Winemiller and Rose 1993). The size or age at which marine fishes mature (often referred to as size- or age-at-maturity) influences fecundity as fishes that mature early may have more potential seasons during which they can reproduce, but also mature at a smaller size and therefore have less physical space for egg production (Stearns 1989). The former increases potential reproductive success (more occurrences of spawning) while the latter decreases potential reproductive success (less eggs per spawning event). Interestingly, repeat

spawners may also produce more eggs than first time spawners of similar size classes (Trippel 1998), which is a potential additive benefit to early maturation.

The reproductive output of a fish species is critically important in understanding their life history, population dynamics, ecosystem role, and how they will respond to harvest and management (Lambert 2008). Historically, the overall fecundity of an individual fish or total egg production (TEP) of a marine fish population has been considered practically analogous with estimates of spawning stock biomass (SSB) (Lambert 2008). When considering the ecological role and impact of a fish species, an estimation of population size or biomass is necessary and estimating SSB by way of TEP may provide this. However, many studies indicate that not only is the relationship between SSB and TEP less analogous than once believed (Marshall et al. 1998 and Trippel 1999 among others), but the fecundity data to truly test the validity of this relationship is often lacking (Tomkiewicz et al 2003). This lack of data can stem from the complexity of biological and ecological influences on the fecundity of individuals causing high variability in population fecundity estimates. For example, potential fecundity for female Atlantic Cod varies greatly on a population level (150,000 – 25 million eggs), but also varies significantly within fish of the same size class (209,000 – 2.2 million eggs for females in the 60 cm size class) (Lambert et al 2005). Though most population level variation is explained by individual fish size, population level fecundity also varied significantly by year, which may imply an environmental influence (Lambert et al 2005). Another factor leading to a lack of robust fecundity estimates across species is the time and expense required to produce quality fecundity estimates. More recently, however, technological advances have allowed for the development of efficient and inexpensive methods for producing high-quality fecundity data

(Klibansky and Juanes 2007 and Lowerre-Barbieri et al 2011), the collection of which should lead to broader understanding of the ecosystem roles of marine fishes.

Ariopsis felis (Figure 1) 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.

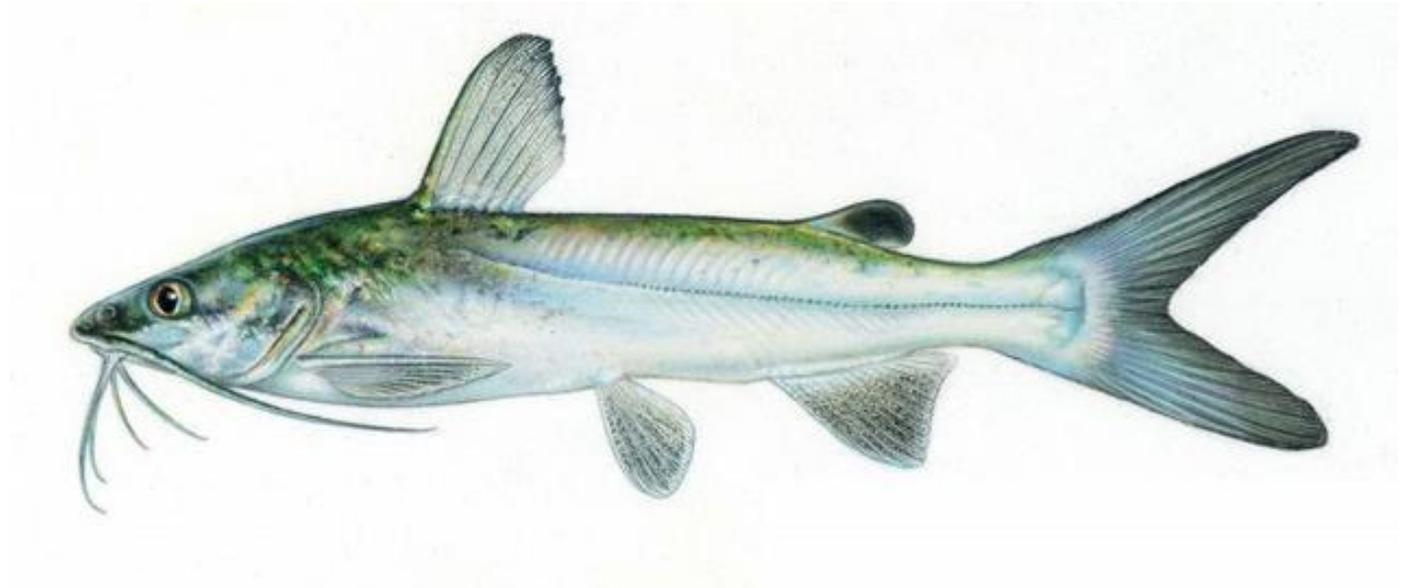


Figure 1. *Ariopsis felis* (Hardhead Catfish) is a marine catfish found in coastal waters from Cape Cod, MA to Yucatan, Mexico. *A. felis* can have extreme local abundance throughout the Gulf of Mexico (illustration © Joseph Tomelleri).

Despite the wide distribution and generally high abundance of *A. felis* we know very little about the species' biology or population. *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). Reports of maximum age vary widely from two years (Benson 1982) to “three to eight growing seasons” (Doerman et al 1977) to 24 (Flinn et al 2019) or 25 years (Armstrong et al 1996). While there have been some studies examining the life history traits 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).

Generally, marine fishes have very high fecundity with each female producing many small eggs that hatch into small larvae allowing reproductive success in highly productive environments (Winemiller and Rose 1993). Fishes with low fecundity tend to be slower growing, less numerous, and more vulnerable species living in environments with patchy prey availability (Winemiller and Rose 1993). *A. felis* has very low fecundity (Ward 1957, Merriman 1940, Yanez-Arancibia and Lara-Dominguez 1988), yet they can have relatively high abundance in the Gulf of Mexico (Armstrong et al 1996, Muncy and Wingo 1983). Gunter (1947) writes of male ariid catfish mouthbrooding large eggs and “helpless [larvae] with large yolks attached” as facts that “have been imperfectly known to ichthyologists for a long time.” In the northern Gulf of Mexico, *A. felis* spawning season is thought to happen from late May through early August (Ward 1957) while spawning season is believed to coincide with the wet season in the southern Gulf of Mexico (Yanex-Arancibia and Lara-Dominguez 1988). Much of the reproductive knowledge of *A. felis* is either incomplete or not definitely applicable to the populations inhabiting the Louisiana coast of the Gulf of Mexico.

Though there is an intrinsic scientific value to basic biological knowledge of any coastal fish species, knowing how coastal fishes reproduce is an important first step understanding their ecological importance. Ecosystem modeling has identified *A. felis* as abundant enough to be one of the more important meso-predators in the Gulf of Mexico (Walters et al 2008), but we know little about how reproductive biology influences abundance and thus ecosystem role for *A. felis*. Considering recent challenges to historic reporting (Armstrong et al. 1996; Flinn et al. 2019) and the general lack of studies on an otherwise abundant species, the objectives of this study are to:

- 1) Comprehensively describe *A. felis* reproductive biology, and
- 2) Evaluate the life history strategy that *A. felis* exhibit in coastal Louisiana.

1.2 Methods

1.2.1 Collection and Processing

All *A. felis* in this study were sampled opportunistically in partnership with the Louisiana Department of Wildlife and Fisheries (LDWF) as a part of their Fishery-Independent Sampling program. Sampling was conducted out of the Lacombe and Bourg LDWF field offices primarily in Coastal Study Areas One (CSA 1, Pontchartrain Basin) and Five (CSA 5, Timbalier/Terrebonne Basin) (Figure 2) between September 2016 and August 2019. LDWF utilizes a variety of 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 shortly after capture, then brought to Louisiana State University for analysis.

A. felis were thawed ($N_{\text{total}} = 1,232$, $n_{\text{female}} = 693$, $n_{\text{male}} = 354$, $n_{\text{indeterminate}} = 185$), and processed for basic biological measurements including total length (TL [mm]), total weight (TW [g]), and gonad weight (GW [g]). The gonadal somatic index was calculated ($\text{GSI} = [\text{GW}/\text{TW}] \times 100$) for each individual and gonadal tissue was preserved in 10% neutral buffered formalin. Histological procedures involved embedding a thin section of gonadal tissue in paraffin, then sectioning embedded gonads to 4- μm thickness.

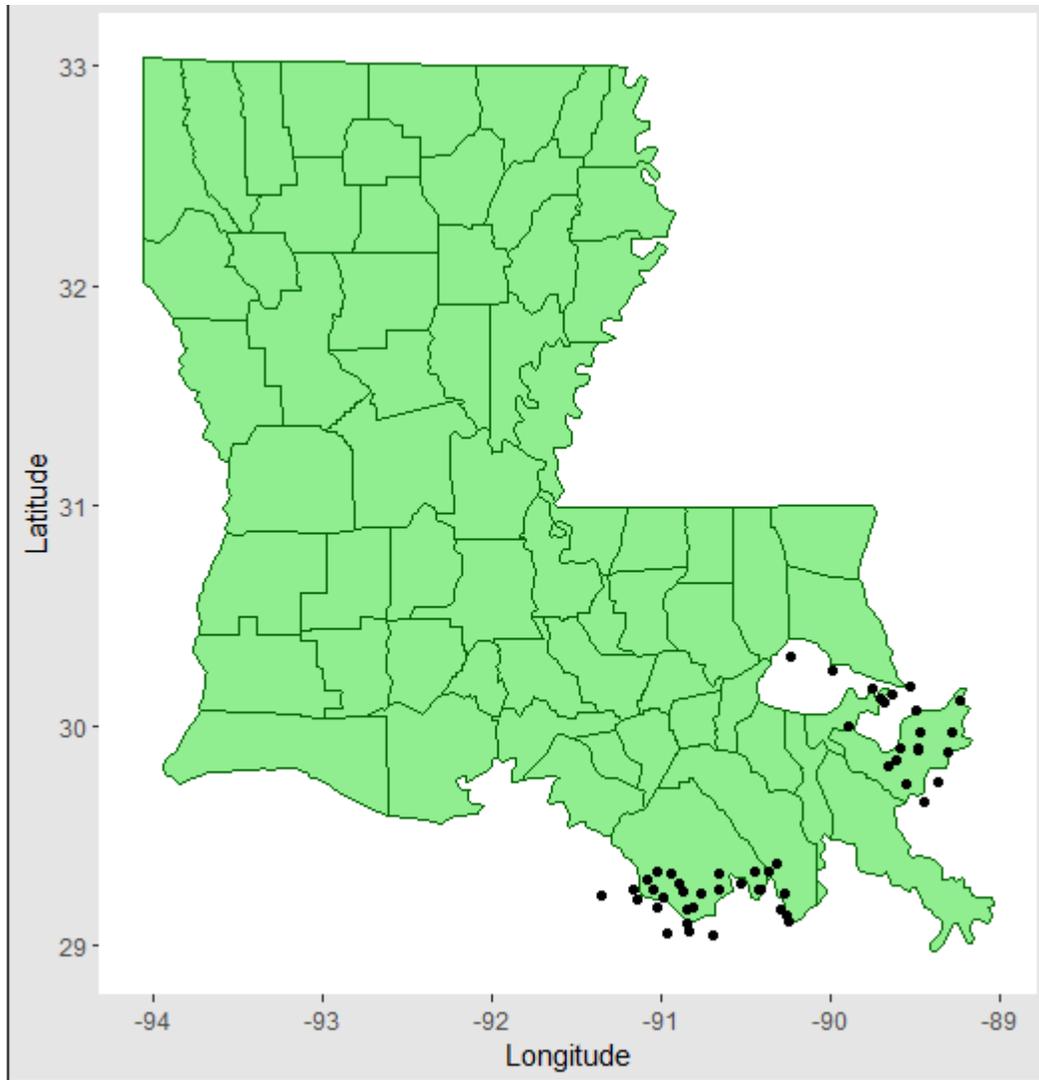


Figure 2. A subset of *A. felis* sampling sites in coastal Louisiana. Uppermost points correspond to Coastal Study Area (CSA) I. Lowermost points correspond to CSA V.

Sections were stained with hematoxylin and eosin and resulting slides were viewed under compound microscopy. I only sectioned a very small subset ($n = 74$) of gonad tissues as the freezing process degraded gonad tissues and subsequent histological examination was not useful in determining gonad stage.

1.2.2 Reproductive Timing

Variations in GSI have long been used as a metric to ascertain the seasonal timing of spawning in fishes (e.g., West 1990, Nieland and Wilson 1993, Jons and Miranda 1997). I determined reproductive timing by examining GSI values of female *A. felis* and examining them by month for any patterns. 1% GSI was almost never exceeded in non-spawning months, therefore we adopted 1% as a cutoff to denote seasonal spawning (Figure 3). In other words, months in which nearly all GSI < 1% were determined to be non-spawning months while months in which GSIs were > 1% were determined to be spawning months.

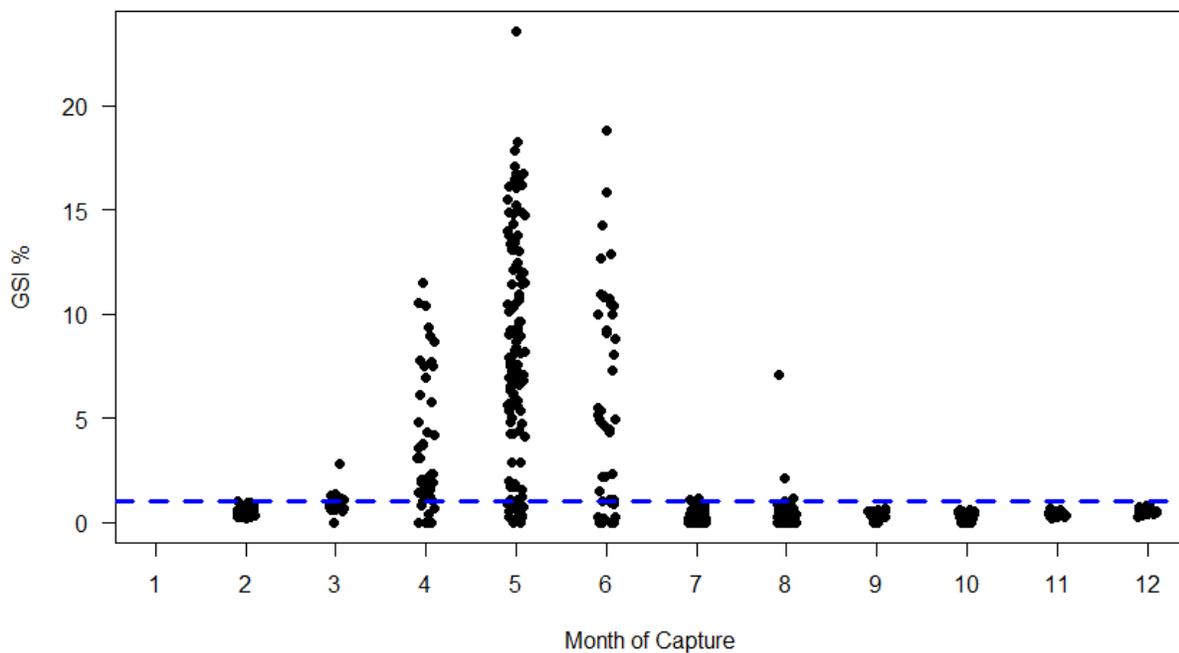


Figure 3. Monthly gonadosomatic index (GSI) values for female *A. felis* show a distinct GSI peak during the months of April, May, and June. In all other months GSI values rarely reach above 1% (dashed blue line).

1.2.3 Fecundity

To estimate fecundity, I subset a random sample of $n = 47$ *A. felis* from females within the spawning season (April – June) as determined by months with GSIs above 1%. From this subset, I followed procedures similar to those developed by Thorsen and Kjesbu (2001) as well as Klibansky and Juanes (2008). The most developed oocytes – oocytes with orange or yellow coloration – were physically removed from each of the 47 individual gonads and imaged utilizing a ZooSCAN system (Hydroptic, 2016). The resulting tagged image file format (TIFF) was converted to an 8-bit image in ImageJ (version 1.52) and the Threshold process was used to eliminate non-oocyte material from the image. Though the threshold range varied, the top end was always the maximum value of 255. The Threshold process changes pixels within the threshold range to black and pixels outside of the range to white. Finally, using the resultant image of black oocytes on a white background, I used the Analyze Particles function with the show overlay option in ImageJ to count and measure a major and minor axis (mm) for each oocyte. The show overlay option simply overlaid a particle count on each oocyte allowing for identification of outliers, which I compared against the original scan for accuracy. Major and minor axes, defined respectively as the largest and smallest axis of each oocyte, were highly correlated ($\rho=0.99$); therefore, I used the major axis of each oocyte to represent oocyte size. The oocyte counts allowed calculation of the fecundity range for *A. felis* as well as mean fecundity and mean oocyte size.

Outside of the spawning season, I observed female *A. felis* with several smaller but still relatively large (most oocytes < 5 mm) oocytes showing inconclusive evidence of atresia. I examined $n = 80$ females distributed as evenly as possible across the remaining eight months of the year (I was not able to sample any fish in January) with at least $n = 10$ females per month. I

examined both number of oocytes and size of oocytes with the same methods detailed in the preceding paragraph in order to clarify gonad activity outside of the spawning season.

1.2.4 Length at First Maturity

The preferred method of determining size or length at first maturity is to determine individual fish maturity through histological examination of gonad development (West 1990, Brown-Peterson et al 2011) and use logistic regression to estimate maturity as a function of fish length (Chen and Palomheino 1994). However, in the absence of confident histological information a GSI cut-off has been found to be an effective method of confirming maturity for some species (Vitale et al 2006 and McPherson et al 2011) and, if the GSI cut-off is determined at the start of the spawning season, has even been found comparable to histological determination of maturity (Flores et al 2014). Because histological examination of gonad tissue was not conclusive in determining oocyte stages, I adopted the previously identified 1% GSI cutoff and applied it to female *A. felis* within the spawning season, in order to determine maturity. A GSI of < 1% almost exclusively corresponded to a fish outside of spawning; therefore, the 1% GSI permitted the application of a binary maturity status (1 = mature, 0 = immature) to female fish within the spawning season. I used logistic regression with the binary maturity status as the response and TL as the predictor:

$$y_i = \alpha + \beta x_i + \varepsilon_i$$

where y_i is the maturity stage (mature or immature) of fish i , α is the intercept parameter, β is the slope parameter, and x_i is the TL for fish i . ε_i represented the residual error. The link function used in estimation was the logit link. An L_{50} estimate (the estimated length at which 50% of the individuals are mature), was calculated as $\frac{-\alpha}{\beta}$. All model estimation was done using the glm function in R (R Core Team, 2019).

1.2.5 Mouthbrooding

Although many of the reproductive strategies of *A. felis* are common to other species, male *A. felis* practice the uncommon habit of mouth brooding. However, likely due to sampling techniques, this was not something I frequently encountered or with a standardized approach to examine more than observationally. When mouth brooding was observed, I counted the eggs or larval *A. felis* and stored the eggs or larvae in 10% neutral buffered formalin within containers labeled with the unique fish identification number corresponding to the paternal *A. felis*.

1.3 Results

1.3.1 General Results

From 2016 to 2018 I sampled $n=1,232$ *A. felis* with sizes ranging between 46–492 mm TL. With the exception of January ($n=2$), sampling was the lowest in March ($n=35$), highest in July and August ($n > 200$ for both months), and generally higher April through October. Representation from CSAs was practically equal with $n=565$ *A. felis* from CSA 1 and $n=561$ *A. felis* from CSA 5. I identified 693 female *A. felis* ($n_F=693$), 354 male *A. felis* ($n_M=354$), and 182 *A. felis* of indeterminate sex ($n_I=182$). To examine *A. felis* maturity, I subset female *A. felis* ($n=222$) during the active reproduction season (April–June). Of this subset of female *A. felis*, 179 were identified as mature ($n_{mature}=179$) and 43 were identified as immature ($n_{immature}=43$). Lengths for the entire subset ranged from 197–455mm TL.

1.3.2 Reproductive Timing

GSI showed a clear peak during April through June (Figure 3). In fact, *A. felis* GSI was rarely greater than 1% outside of these months. This pattern in GSI supports the idea that *A. felis* in coastal Louisiana actively reproduce April through June. Over all samples, GSI ranged from 0.00–23.58% with a mean GSI of 2.32%. Within *A. felis* spawning months of April through June,

GSI for 222 *A. felis* ranged from 0.00–23.58% with a mean of 6.29%, while outside of the spawning months, GSI for 461 *A. felis* ranged from 0.00–10.18% with a mean of 0.44%.

1.3.3 Fecundity

Two *A. felis* categories were examined for fecundity; an in-season fecundity subset ($n=47$) and an out-of-season fecundity subset ($n=80$). *A. felis* size within the in-season fecundity subset ranged from 260–389mm TL. *A. felis* in the out-of-season fecundity subset ranged from 221–435mm TL.

Within the spawning season, I estimated the mean *A. felis* fecundity to be 86 oocytes with a fecundity range of 35 to 196 oocytes. In the oocyte sizes of nearly all individuals, there were two distinct modes (Figure 4). The smaller of the two modes had a wider range of sizes (around 5–10mm mm), which could be evidence for a third and overlapping mode. Two oocyte size classes are evidence that *A. felis* have at least two, but possibly three, batches of oocytes per spawning season.

As expected, GSI values for female *A. felis* outside of the spawning months was low (<1%). However, with such large oocytes (~2–4 mm) observed outside of the spawning months, I wanted to determine whether I was observing slow atresia, months long holdover, or something else. Histological examination of female *A. felis* gonads outside of the spawning season showed possible evidence of atresia, although the freezing of gonadal tissue may also have contributed to the oocyte atresia I observed. Of greater interest was that I observed atretic features for many months and my frozen samples were degraded enough that I could not consider this evidence conclusive.

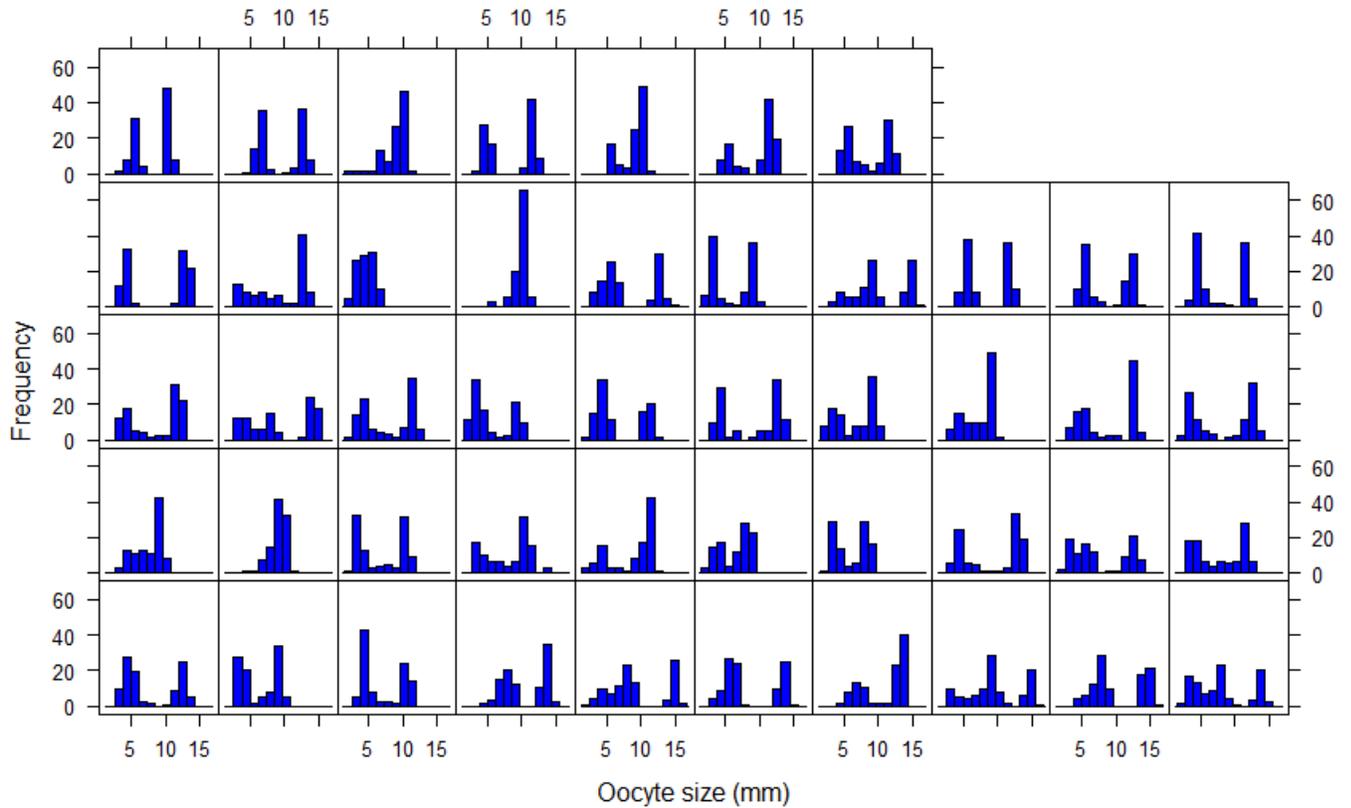


Figure 4. Oocyte size frequencies for individuals from a subset ($n=47$) of female *A. felis* within the spawning season show clear evidence of at least two batches in almost every case. Mean fecundity is 86 oocytes with a range of 35-196 oocytes. Both mean fecundity and fecundity range are larger than previously estimated.

When examining *A. felis* fecundity in months outside the spawning season, I found an out of spawning season oocyte range of 11–184 oocytes with a mean of 90 oocytes and oocyte size ranging from 0.85–14.99 mm with a mean oocyte size of 2.30 mm (Figure 5). In order to estimate the cause of the variability in oocyte size observed (Figure 6), I utilized a mixed model with oocyte size as a function of month of capture and individual fish as a random effect and calculated an intraclass correlation (ICC) of 0.6791. I was unable to discern any trend in oocyte size throughout the low GSI months (Figure 7).

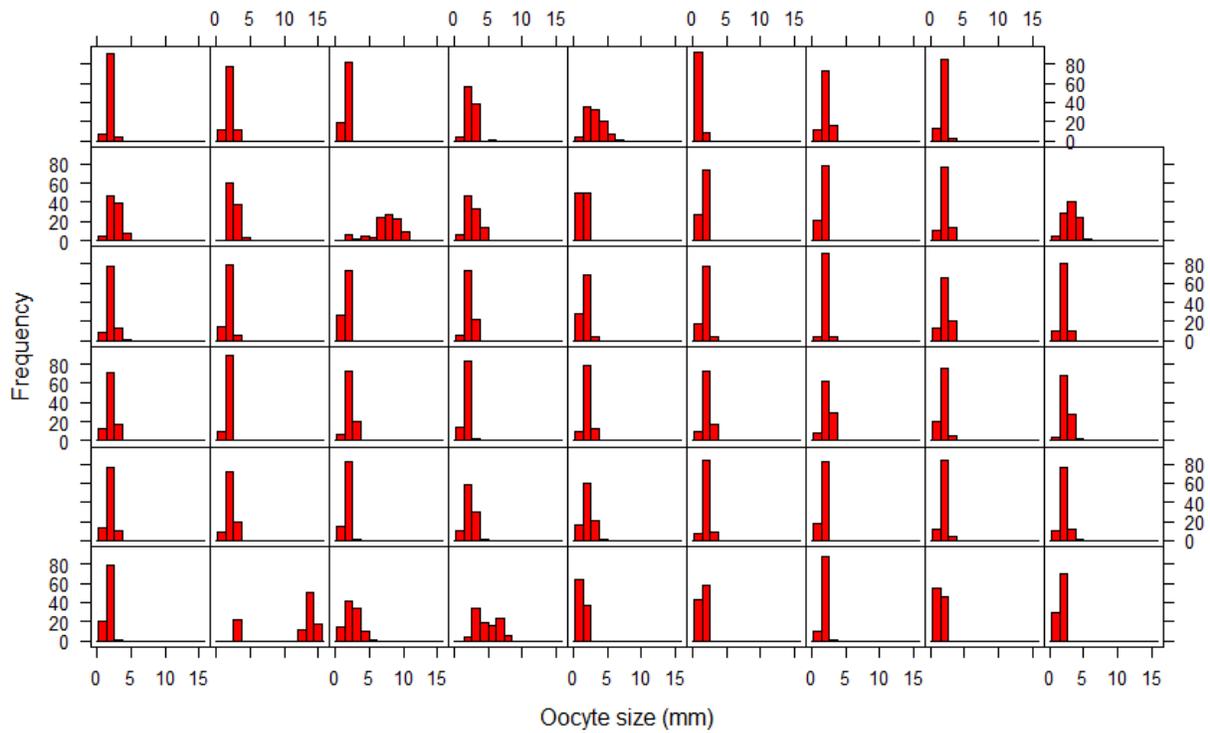


Figure 5. Oocyte size frequencies for a subset of female *A. felis* individuals ($n=53$) outside of the spawning season rarely show oocytes over 5mm. Outside of the spawning season, *A. felis* have an oocyte range of 11-184 oocytes with a mean of 90 oocytes.

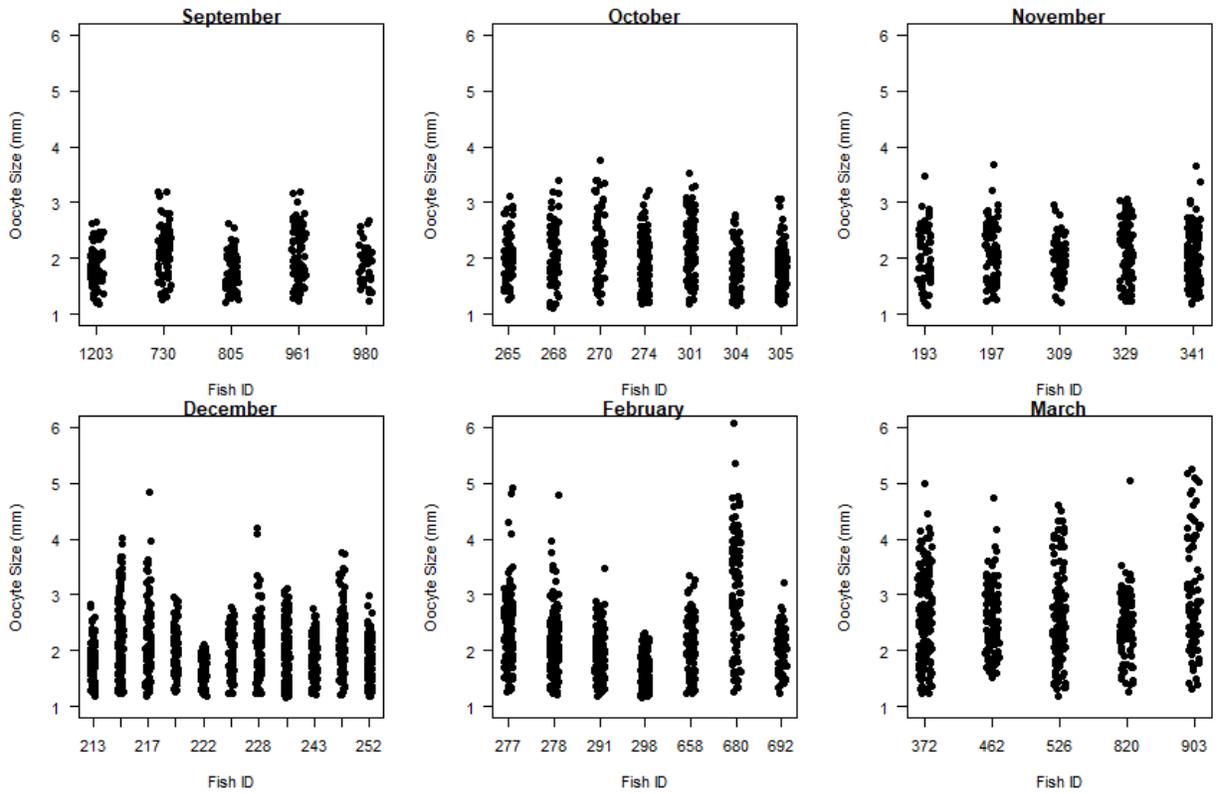


Figure 6. *A. felis* oocyte size separated by individual fish highlights the variability of oocyte sizes for individuals. While there is not a discernable trend in oocyte size throughout the non-spawning months, it does appear variability increases as the spawning season approaches.

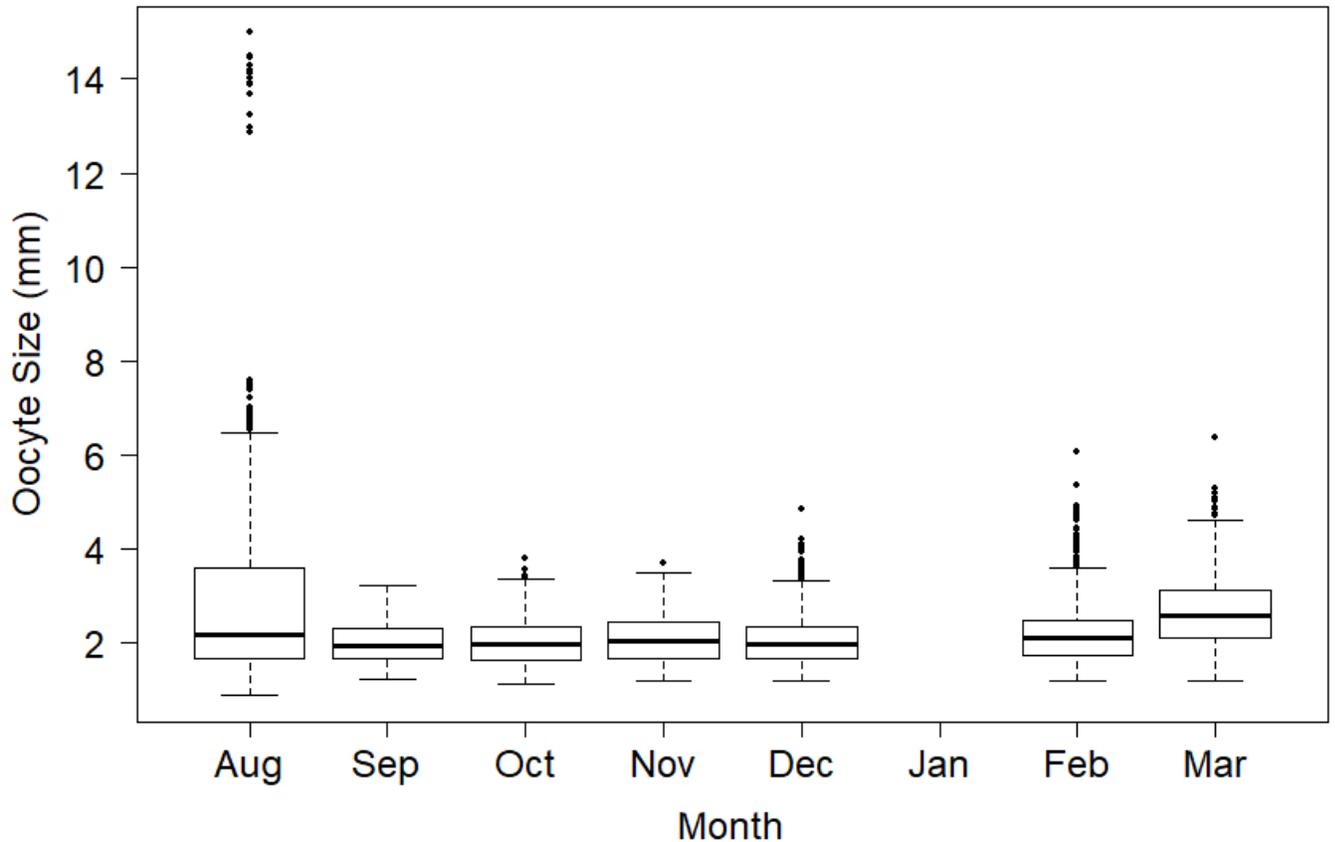


Figure 7. Boxplots of oocyte size each month outside of the *A. felis* spawning season show little evidence of oocyte size changes for at least five months. Though my opportunistic sampling method precluded January *A. felis* samples, it is unlikely January oocyte sizes are dissimilar to December and February meaning there is little to no change in mean oocyte size from August through February. The lower and upper hinges of the boxes represent the first quartile and third quartile respectively while the thick, black line represents the median of each group. Whiskers extend 1.5 times the interquartile range above and below the first and third quartile. Data points outside 1.5 times the interquartile range are shown as individual points.

1.3.4 Length at First Maturity

Absent reliable histological information on maturity, in-season (April–June) *A. felis* were assigned a binary maturity status based on the 1% GSI cut-off described above. With these individual maturity designations, a logistic regression estimated an L_{50} of 253mm TL for female *A. felis* (Figure 8).

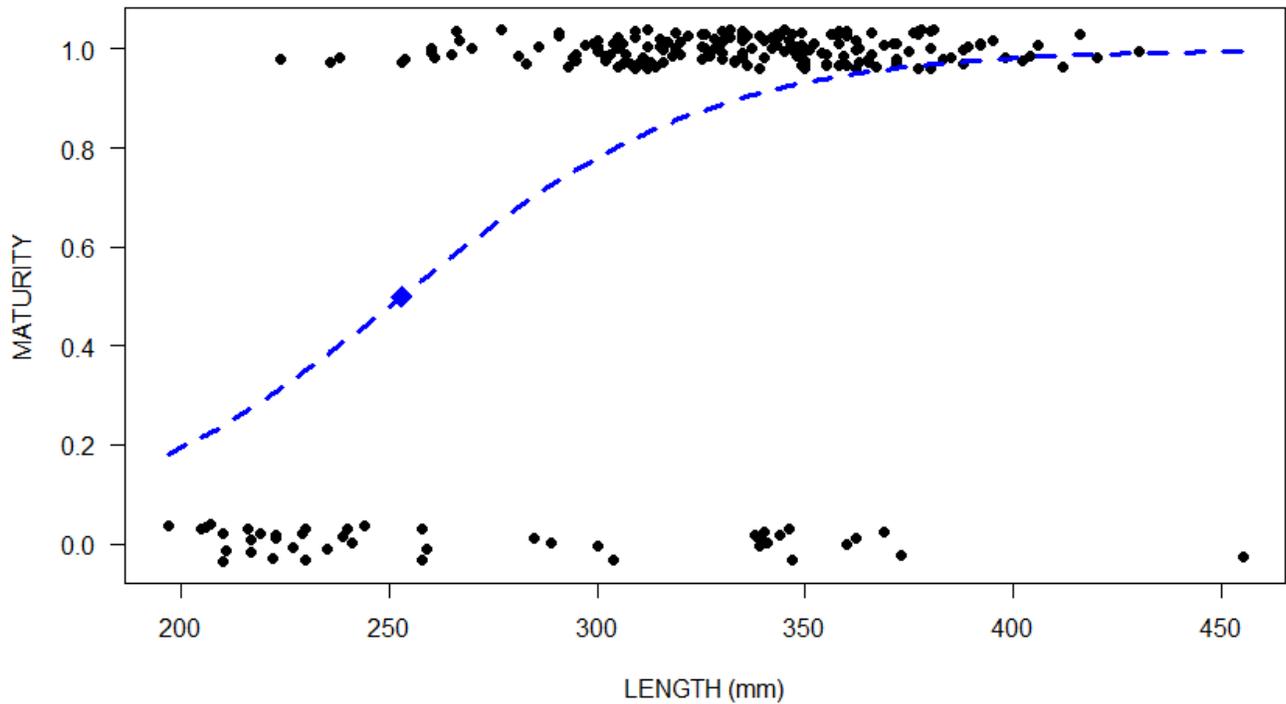


Figure 8. Logistic model (dashed blue line) of female *A. felis* maturity and total length (TL) estimates 50% of females reach one-time sexual maturity (L_{50}) at 253 mm TL (blue diamond). A binary maturity status was assigned to each fish based on GSI within the spawning season. Fish with $GSI \geq 1\%$ were considered mature while fish with $GSI < 1\%$ were considered immature.

The logistic model calculates the probability that an *A. felis* of a given length is mature or immature. The length at which there is a 50% probability that an individual fish is mature corresponds to the length at which 50% of the *A. felis* population will be mature (L_{50}).

1.3.5 Mouth Brooding

I observed $n=12$ *A. felis* males with eggs or larval *A. felis* in their mouths or stomachs ($N_{\text{eggs}} = 6$ and $N_{\text{larvae}} = 6$). The number of eggs per *A. felis* male ranged from 1–23 eggs with a mean of 15 eggs while the number of larvae ranged from 1–11 larvae with a mean of 7 larvae. Male *A. felis* engaged in mouth brooding ranged from 235–390mm TL with a mean of 321 mm TL. All mouth brooding *A. felis* were collected in either July or August. Overall, I collected 94 male *A. felis*

during the months of July and August with a range of 152–390mm TL and a mean of 291mm TL. I observed mouth brooding in approximately 13% of *A. felis* males collected within the same time period I observed mouth brooding fish.

1.4 Discussion

1.4.1 Historic Comparison

My research manages to challenge many of the previous reports on *A. felis* in the northern Gulf of Mexico (Table 1).

Table 1. A comparison of prior research on *A. felis* life history traits to the findings of this research project. My research has managed to challenge much of what was previously believe about *A. felis* reproductive life history traits (1. Muncy and Wingo 1983, 2. Armstrong et al 1996).

Life History Trait	Prior Research	Current Research
Spawning Season	May–August ¹	April–June
Spawning Strategy	Unknown	Batch
Annual Fecundity	<100 ¹	35–196
L ₅₀	100mm TL–250mm SL ^{1,2}	253mm TL

I found the seasonal timing of *A. felis* reproduction in coastal Louisiana beginning earlier and having a shorter duration than previously reported. Similarly, I consistently found higher *A. felis* total fecundity than prior reports, with many *A. felis* females having fecundity well over 100 oocytes. I found strong evidence for *A. felis* batch spawning, with at least two, and potentially three, batches. While previous research has mentioned multiple spawns per season as a possibility (Merriman 1940, Ward 1957), my research provides the first strong evidence of *A. felis* batch spawning. The two or three size modes observed here do not necessarily preclude four or possibly more batches within a single spawning season, but based on the length of the

spawning season (May–June) and the time required for *A. felis* paternal mouthbrooding, the timing of a fourth batch may present challenges. I can infer that two or possibly three batches are much more likely, which corresponds to the observed separation of oocytes sizes.

A. felis mature relatively young ($L_{50} = 253$ mm TL, corresponding to 2–3 years old), which matches up closely with more recent reports of 250 mm TL (Yanez-Arancibia and Lara-Dominguez 1988, Armstrong et al 1996), though many older reports claim a smaller length at maturity (Lee 1937, Merriman 1940). While the accuracy of calculating maturity based entirely on GSI within the spawning season has not yet been confirmed for *A. felis*, the obvious depression in GSI outside of the May through June spawning season lends a high degree of confidence to this method. Reaching lifetime sexual maturity at relatively young ages is similar to other long-lived coastal species such as *Pogonias cromis* (Black Drum) and *Sciaenops ocellatus* (Red Drum), both of which reach maturity around 4 years (Nieland and Wilson 1993, Nieland and Wilson 1994).

I was unable to observe *A. felis* mouth brooding to any great extent; however, additional study could help explain how *A. felis* reproductive behaviors influence population abundance. The mean number of eggs and larvae I observed in the mouths of *A. felis* males were much lower than female *A. felis* fecundity. It is likely most of this mismatch is due to sampling bias inherent in my study design, but mouth brooding in *A. felis*, though widely reported, has been poorly studied. It is unclear whether male *A. felis* carry an entire batch of eggs, a partial batch, or multiple batches from multiple spawning partners.

Outside of the *A. felis* spawning season, I observed what could be evidence of months-long atresia or months long holdover of oocytes. One alternative possibility could be that *A. felis* reproduction is an exceptionally plastic process allowing for a reentry into or an extension of

spawning with favorable environmental conditions. While the GSI values I observed do not support this idea – rarely did I observe any GSI increase outside of the spawning months – it is possible that environmental conditions within the timeframe of my collection did not favor spawning extension. Long oocyte holdover, atresia, or extreme reproductive plasticity are not traits associated with warm-temperate fishes and, as such, should be explored further. Fresh (not frozen) *A. felis* gonad samples would provide valuable insight into out of spawning season oocyte stages and therefore further refine the understanding of *A. felis* reproductive processes.

1.4.3 Comparative Estuarine Reproductive Biology

When comparing *A. felis* reproductive traits with the reproductive traits of similarly sized estuarine species with comparable life histories, such as *Sciaenops ocellatus* (Red Drum), *Pogonias cromis* (Black Drum), and *Paralichthys lethostigma* (Southern Flounder), I found several differences. The most obvious difference is in *A. felis* annual fecundity range which differs by multiple orders of magnitude from the other three species (Table 2 – top four rows). Though all four species are batch spawners, the seasonality of these spawning events differ greatly. *A. felis* spawn in the late spring and early summer, whereas *S. ocellatus*, *P. cromis*, and *P. lethostigma* are fall and winter spawners—a far more common timing for estuarine-dependent species. The eggs *S. ocellatus*, *P. cromis*, and *P. lethostigma* spawn hatch into altricial, or underdeveloped, larvae and adults of these three species exhibit no parental care. *A. felis* larvae are more precocial, or more developed, and *A. felis* males exhibit a higher degree of parental care. By almost every metric, *A. felis* reproductive biology differs from other similarly sized, estuarine dependent fishes.

Table 2. A comparison of *A. felis* life history traits with other longer lived, estuarine dependent species. *A. felis* share many life history traits with elasmobranchs and freshwater catfishes (bottom six rows), but very few life history traits with other estuarine species (top four rows). This is evidence for an *A. felis* life history similar to sharks, rays, and freshwater catfishes. (1. Wilson and Neiland 1993, 2. Davis et al 2015, 3. Powers et al 2012, 4. Corey et al 2017, 5. Tillett et al 2011, 6. Branstetter 1987, 7. Page and Burr 2011, 8. Perry and Carver 1973, 9. Graham 1999, 10. Munger et al 1994).

Species	L_{∞}	L_{50}	A_{50}	Spawning Season	Fecundity Range (Annual)	Spawning Strategy
Black Drum (<i>Pogonias cromis</i>) ^{1,2}	1,549mm TL	610mm TL	4-5 years	January- April	35,000,000– 45,000,000	Batch
Red Drum (<i>Sciaenops ocellatus</i>) ³	1,012mm TL	598mm FL	3-4 years	August- October	20,000,000– 40,000,000	Batch
Southern Flounder (<i>Paralichthys lethostigma</i>) ⁴	514mm TL	303mm TL	1 year	December- January	9,230–18,300,000	Batch
Hardhead Catfish (<i>A. felis</i>)	426mm TL	253mm TL	2-3 years	April-June	35–196	Batch
Bull Shark (<i>Carcharhinus leucas</i>) ⁵	3,119mm TL	1,600mm TL	9-10 years	April-May	1–10	Total (viviparous)
Blacktip Shark (<i>Carcharhinus limbatus</i>) ⁶	1,750mm TL	1,500mm TL	6 years	April-June	1–10	Total (viviparous)
Channel Catfish (<i>Ictalurus punctatus</i>) ^{7,8}	1320mm TL	288mm TL	3 years	April-July	20,000	Batch
Blue Catfish (<i>Ictalurus furcatus</i>) ^{8,9}	1650mm TL	279mm TL	5 years	April-June	30,000-312,000	Batch
Flathead Catfish (<i>Pylodictis olivaris</i>) ^{7,10}	1550mm TL	390mm TL	3 years	May-Aug	3,000-30,000	Batch

Juveniles of all four species are thought to consume similar prey items (Walters et al 2008, Olin et al 2012), therefore the mismatch of seasonal timing with other estuarine dependent species could provide juvenile *A. felis* a competitive advantage in food foraging. Similarly, increased *A. felis* parental investment likely provides a competitive advantage in protection from potential

predators and possibly in foraging for food as well. The advantages provided by increased parental investment compared to other estuarine fishes and a mismatch of spawning seasonality could help explain relatively high *A. felis* abundance in coastal Louisiana despite extremely low *A. felis* fecundity.

Life history comparisons between *A. felis* and other estuarine-dependent teleost species show substantial differences; however, *A. felis* do share several reproductive traits with freshwater catfishes, such as *Ictalurus punctatus* (Channel Catfish), *Ictalurus furcatus* (Blue Catfish), and *Pylodictis olivaris* (Flathead Catfish) as well as coastal and estuarine elasmobranchs, such as *Carcharhinus leucas* (Bull Shark) and *Carcharhinus limbatus* (Blacktip Shark) (Table 2 – bottom six rows). The seasonal timing of *A. felis* spawning is the same as that of both elasmobranch species and all three freshwater catfish species. All six species exhibit a high degree of parental care. *I. punctatus*, *I. furcatus*, and *P. olivaris* females spawn in nests built and protected by males (Page and Burr 2011), *A. felis* are paternal mouthbrooders, and *C. leucas* and *C. limbatus* are viviparous (live young bearers). However, the fecundity of freshwater catfishes is a great deal higher than that of *A. felis*, *C. leucas*, and *C. limbatus* (Table 2). It is possible that increased parental care may help explain *A. felis* abundance in coastal Louisiana. However, both *C. leucas* and *C. limbatus* are listed as “near-threatened” by the International Union for the Conservation of Nature (IUCN), implying that increased parental care alone is not enough to explain *A. felis* abundance. Fishing pressure on *C. leucas* and *C. limbatus* could explain this discrepancy. In 2018, commercial fishers in the western Gulf of Mexico (west of 88° W long) harvested 330.4mt of *C. limbatus* and an additional 93.0 mt of other “large coastal sharks” which includes *C. leucas* whereas there was no targeted, commercial *A. felis* harvest in this same region. Coastal elasmobranchs may also use a wider variety of habitats throughout

their lives, during which they experience higher fishing mortality that *A. felis* do not encounter. However, many equilibrium strategists are sensitive to overfishing (Hoenig and Gruber 1990, Hoff and Musik 1990, King and McFarlane 2003), therefore *A. felis* reproductive and life history traits show that, should a commercial market ever develop, *A. felis* populations could quickly become overfished.

1.4.2 Life History Revised

Generally, the life history traits described here point toward a more complicated life history strategy for *A. felis* than previously believed. Longevity coupled with low fecundity but increased parental investment (and therefore higher juvenile survivorship) are associated with an equilibrium life history strategy (Winemiller and Rose 1992). Other equilibrium strategists are predominately elasmobranchs (sharks and skates), meaning *A. felis* have life history traits – e.g., low fecundity, a high degree of parental investment, relatively large size, and longevity – common to elasmobranchs (King and McFarlane 2003). Equilibrium strategists tend to have low abundance, thus rendering them vulnerable to stressors such as overfishing (Hoenig and Gruber 1990, Hoff and Musik 1990, King and McFarlane 2003) or disease. As equilibrium strategists, *A. felis* likely share similar vulnerability as elasmobranchs to the potential stress of overfishing or disease. Additionally, *A. felis* are an important meso-predator in the Gulf of Mexico (Walters et al 2008) and it is unclear how a possible decline in *A. felis* population would affect the greater ecosystem of the Gulf of Mexico or coastal Louisiana ecosystems.

Although *A. felis* life history might predict low abundance, this does not match up with actual abundance as *A. felis* have relatively high abundance in coastal Louisiana (Armstrong et al 1996, Muncy and Wingo 1983). *A. felis* are not a commercially or recreationally targeted finfish in Louisiana, so this mismatch between life history strategy and abundance could be due to a

lack of fishing mortality and/or an availability of prey, habitat, and other resources that are made available through the removal of several other estuarine species that are heavily fished in coastal Louisiana and the Gulf of Mexico. In a productive environment such as coastal Louisiana with little fishing or predatory pressure, it stands to reason that an equilibrium strategist like *A. felis* with high parental investment (large eggs and paternal mouth brooding) could be locally abundant. However, if fishing pressure were to increase or a disease were to affect *A. felis*, their life history suggests populations could quickly become overfished or threatened (Hoenig and Gruber 1990, Hoff and Musik 1990). Furthermore, because both sexes of *A. felis* appear integral to the success of offspring (females in the production of oocytes and males in the parental care), increased mortality on either sex alone could result in declines. While *A. felis* is not considered a threatened species, populations in South Carolina began to decline in the early 1990s – despite little to no fishing pressure – and to this day are so depressed that South Carolina Department of Natural Resources (SCDNR) declared a moratorium on any *A. felis* harvest in 2007 that continues today (Ballenger 2018). This example underscores both the potential vulnerability of *A. felis* populations as well as the potential obstacles to recovery posed by *A. felis* life history traits. South Carolina could provide a case study for the ramifications of almost entirely removing an abundant meso-predator from an ecosystem.

Chapter 2. Trophic Niche of *Ariopsis felis* in the Northern Gulf of Mexico

2.1 Introduction

Coastal ecosystems are made up of complex and dynamic habitats though 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. Trophic webs are a central pillar in ecology, providing a framework to explain interspecific interactions through energy transfer between trophic levels (Lindeman 1942), and can be used to link localized trophic webs at 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 (Hynes et al 2014). However, many organisms undergo ontogenetic diet changes as they grow or mature (Polis et al 1997), further muddying the waters of coastal trophic webs. The multifaceted, interspecific relationships in coastal ecosystems makes studying trophic webs through more traditional means (e.g. observational studies) impractical and cost prohibitive (Boecklen et al 2011).

Stable isotope analysis (SIA) facilitates the construction of trophic webs in a cost-effective manner by attempting to explain the variation in isotope signatures between consumers and what they are eating as a function of diet and trophic position (Boecklen et al 2011). Specifically, stable isotopes 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 1984) respectively. Generally, as the size of fishes increases, they eat a greater quantity of prey items as well as an increased range of prey item sizes (Reid et al 2007). As such, how fishes interact and affect the ecosystem potentially differs throughout their lifecycles. In a

broad sense, the bivariate mean of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values describes an organism's trophic niche. Given the trophic space in which many species can exist in their lifetime, we might expect coastal fishes to fit into one of three possible trophic niche scenarios: 1) no trophic niche shift or expansion (i.e. fish diet or basal resource use do 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) , or 3) trophic niche shift (i.e. fish occupy a completely different trophic niche with ontogeny) (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 $\delta^{13}\text{C}$ may help uncover which of the three possible trophic niche scenarios describe coastal fishes.

Ariopsis felis (Figure 1) 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. *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). This seasonal trophic niche shift is likely evidence of a seasonal change in *A. felis* habitat use or seasonal differences in nutrient input (Olin et al 2012). Reports of maximum age vary widely from two years (Benson 1982) to “three to eight growing seasons” (Doerman 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 (Flinn et al 2019 and Armstrong et al 1996).

Though there is an intrinsic scientific value to basic biological knowledge of any coastal fish species, knowing how coastal fishes' feeding changes over their lifecycle is an important step 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 (Flinn et al 2019 and Armstrong et al 1996) and the lack of reporting specific to Louisiana coastal ecosystems, the objectives of this study are to:

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

2.2 Methods

2.2.1 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 Fishery-Independent Sampling program. Sampling was conducted out of the Lacombe and Bourg LDWF field offices primarily in Coastal Study Areas One (Pontchartrain Basin) and Five (Timbalier/Terrebonne Basin) (Figure 2) between September 2016 and August 2019. LDWF utilizes a variety of gears in their Fishery-Independent Sampling programing 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 LSU for analysis.

I thawed frozen individual *A. felis* ($N_{\text{total}} = 1232$, $N_{\text{female}} = 693$, $N_{\text{male}} = 354$, $N_{\text{indeterminate}} = 185$), then processed individuals for basic biological measurements of total length (TL [mm]), total weight (TW [g]), and gonad weight (GW [g]). A white muscle tissue (WMT) sample was taken from just posterior to the dorsal fin. I subset $n=126$ *A. felis* WMT samples, and limited sampling to CSA 1 from the months of June, July, and August in 2018, in order to control for temporal and spatial variation in background isotopes for bulk isotope analysis of ratios of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$). I specifically chose to analyze $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ because they act as proxies for habitat use and trophic position, respectively.

2.2.2 Stable Isotope Analysis

WMT samples were freeze dried for > 48 hours at -40°C , ground to a fine powder with a mortar and pestle to homogenize samples and weighed to $0.60\text{g} \pm 0.025\text{g}$ for bulk stable isotope analysis. Tissue was combusted with a Costech 4010 Elemental Analyzer and the resultant gas was run through a Thermo Delta V Isotope Ratio Mass Spectrometer interfaced with a Thermo ConFlow IV. Using the resultant $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, I calculated the C:N ratio. Samples with a C:N ratio > 3.32 from aquatic organisms are lipid heavy and require lipid normalization to analyze, therefore I lipid normalized samples with $\delta^{13}\text{C} > 3.32$ mathematically with the equation:

$$\delta^{13}\text{C}_{\text{normalized}} = \delta^{13}\text{C}_{\text{untreated}} - 3.32 + (0.99 \times \text{C:N}) \text{ (Post 2007).}$$

2.2.3 Statistical Analysis

To determine ontogenetic niche shift for *A. felis* I divided my samples into three classes based on previously determined sex and maturity information (this document Chapter 1): immature (I,

$n=53$), mature male (M, $n=28$), and mature female ($n=45$). *A. felis* do not exhibit sexually dimorphic growth in coastal Louisiana (Flinn et al 2019), however I kept male and female *A. felis* separate to account for any potential feeding differences while male *A. felis* are mouthbrooding. The procedure for determining statistical differences between groups follows.

I used linear regression to determine if univariate $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values changed with *A. felis* length. I used δ stable isotope value as the response and TL as the predictor:

$$y_i = \alpha + \beta x_i + \varepsilon_i$$

where y_i is the stable isotope value for fish i , α is the intercept parameter, β is the slope parameter, and x_i is the TL for fish i . and ε_i represented the residual error. All model estimation was done using the `lm` function in R (R Core Team, 2019).

I examined niche position of each group through multivariate and univariate analysis of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in a Frequentist framework (Hammerschlag-Peyer et al 2011). Niche position is examined by calculating the mean Euclidean distance (MED) between centroid means of each group (Turner et al 2010) (Figure9). If the absolute value of the med was significantly different than zero, the groups were considered to have different niche positions (Hammerschlag-Peyer 2011). I further examined significant differences in multivariate niche position through univariate analysis of variance (ANOVA) of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ respectively to determine the isotopic driver of niche position.

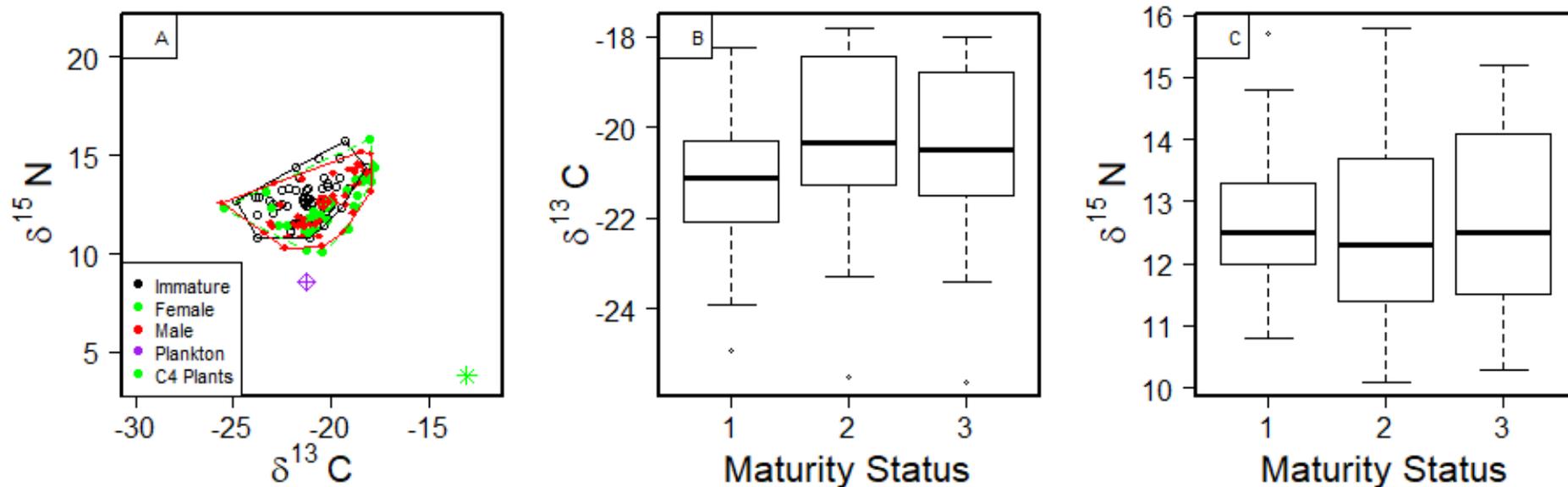


Figure 9. Bivariate $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ plot with convex hulls representing trophic niche width and position (A). Open, black circles and solid, black line represent immature *A. felis*, closed, green circles and dashed green line represent mature, female *A. felis*, and closed, red circles and solid red line represent mature, male *A. felis*. Centroid means are represented by open circles bisected by solid lines. The mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values vary significantly between immature *A. felis* and both mature male and mature female *A. felis*. Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ do not vary significantly between mature, male *A. felis* and mature female *A. felis*. Isotopic signatures for C4 plants (green asterisk) and plankton (red diamond) are included for reference. Panels B and C show the distribution in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ respectively, separated into the same maturity groupings as Panel A. The lower and upper hinges of the boxes represent the first quartile and third quartile respectively while the thick, black line represents the median of each group. Whiskers extend 1.5 times the interquartile range above and below the first and third quartile. Data points outside 1.5 times the interquartile range are shown as individual points.

I examined niche width in both Frequentist (Hammerschlag-Peyer et al 2011) and Bayesian (Jackson et al 2011) frameworks. 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 Euclidian distance between each individual sample within a group and the group's centroid mean (Hammerschlag-Peyer et al 2011 and Turner et al 2010). In the Bayesian framework I used standard ellipse areas (SEA) to examine trophic niche between groups (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 and the Bayesian estimate of niche overlap, I calculated SEA encompassing 95% of data points. Using posterior probabilities (pp) I compared each group to all other groups. Posterior probabilities allowed me to calculate the difference between estimated posteriors in two groups and then examine the probability of whether a posterior value from one group would be less than all posterior values from the comparison group. Significant differences in niche width were further explored through univariate analysis of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ utilizing Bartlett's Test to determine isotopic driver of niche width.

Finally, I examined potential niche overlap by constructing 95% standard ellipses (Figure 3) for immature, male, and female *A. felis* and calculating the percent of area overlap between *A. felis* groups in both directions (Jackson et al 2011). This process shows whether there is evidence of a trophic niche expansion. A 95% standard ellipse area (95% SEA) is simply a Bayesian estimation of the area of an ellipse that contains 95% of the data points within a group. All statistical analyses were performed in R (R Core Team 2019). R code for tests for dispersion and central tendency can be found in the Appendix of Turner et al (2010) while Bayesian ellipses

were estimated following the SIBER package (Jackson et al 2011) for RStudio guide. SEA overlap was calculated using the NicheRover package (Lysy et al 2014) for RStudio. Significance level for Frequentist statistics was determined prior to statistical analysis at the 95% confidence level ($\alpha \leq 0.05$) for all tests.

2.3 Results

2.3.1 Trophic Niche Position

Univariate, linear regression of *A. felis* stable isotope value and *A. felis* TL showed significant differences in $\delta^{13}\text{C}$ with *A. felis* size ($F(1,124) = 20.33, p < 0.01$). However, I found no significant difference in *A. felis* $\delta^{15}\text{N}$ values with *A. felis* size ($F(1,124) = 1.195, p = 0.20$).

Multivariate analysis of trophic niche position found a significant difference in niche position between immature *A. felis* and mature male *A. felis* ($\text{MED} = 0.8627, p = 0.02$) and between immature *A. felis* and mature female *A. felis* ($\text{MED} = 1.0726, p = 0.02$). There was no difference in trophic niche position ($\text{MED} = 0.2192, p = 0.91$) between mature male *A. felis* and mature female *A. felis*. Univariate analysis of trophic niche position through ANOVA of $\delta^{13}\text{C}$ showed a significant difference between groups ($F = 6.701, \text{df} = 1, p = 0.01$) while univariate analysis of trophic niche position through ANOVA of $\delta^{15}\text{N}$ showed no significant difference between groups ($F = 0.046, \text{df} = 1, p = 0.83$).

2.3.2 Trophic Niche Width and Overlap

Frequentist, multivariate analysis of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ between immature, mature male, and mature female *A. felis* groups showed a significant variation in trophic niche width between immature *A. felis* and mature male *A. felis* ($\text{MDC} = 0.5090, p = 0.01$) as well as a significant difference in trophic niche width between immature *A. felis* and mature female *A. felis* ($\text{MDC} = 0.6169, p < 0.01$). However, there was no significant difference in trophic niche width ($\text{MDC} = 0.1079,$

$p=0.668$) between mature male *A. felis* and mature female *A. felis*. Bayesian, 95% SEAs of bivariate means overlap at 95% credible intervals for immature, mature male, and mature female *A. felis* (Figure 10).

Similarly, univariate analysis of homogeneity of variance using Bartlett's Test found no significant difference in $\delta^{13}\text{C}$ between groups ($K^2=5.01$, $df=2$, $p=0.08$) or $\delta^{15}\text{N}$ between groups ($K^2=4.47$, $df=2$, $p=0.11$). The trophic niche of immature *A. felis* overlaps with the trophic niche of mature male *A. felis* 74.10%. Immature *A. felis* trophic niche overlaps with *A. felis* mature female trophic niche 80.83%. Mature male *A. felis* trophic niche and mature female *A. felis* trophic niche overlap with the trophic niche of immature *A. felis* at 93.09% and 92.75% respectively. Mature male *A. felis* trophic niche overlaps with mature female *A. felis* trophic niche 93.77% while mature female *A. felis* trophic niche overlaps with the trophic niche of mature male *A. felis* 88.70% (Figure 10).

2.4 Discussion

What coastal fishes eat and the habitats they utilize are important factors influencing how these fishes interact with coastal ecosystems. Describing the trophic niche of a coastal fish species begins to unpack 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 $\delta^{13}\text{C}$ can be used to describe trophic position or shifts (Peterson and Fry 1987 and Minagawa and Wada 1984) and habitat or resource use (Peterson and Fry 1987 and France and Peters 1997) respectively. Examining ontogenetic shifts through simultaneous analysis of trophic position ($\delta^{15}\text{N}$) and habitat use ($\delta^{13}\text{C}$) allows for a more quantitative understanding of the ecosystem role of fish species (Hammerschlag-Peyer et al 2011). I would expect coastal fishes to fit into one of

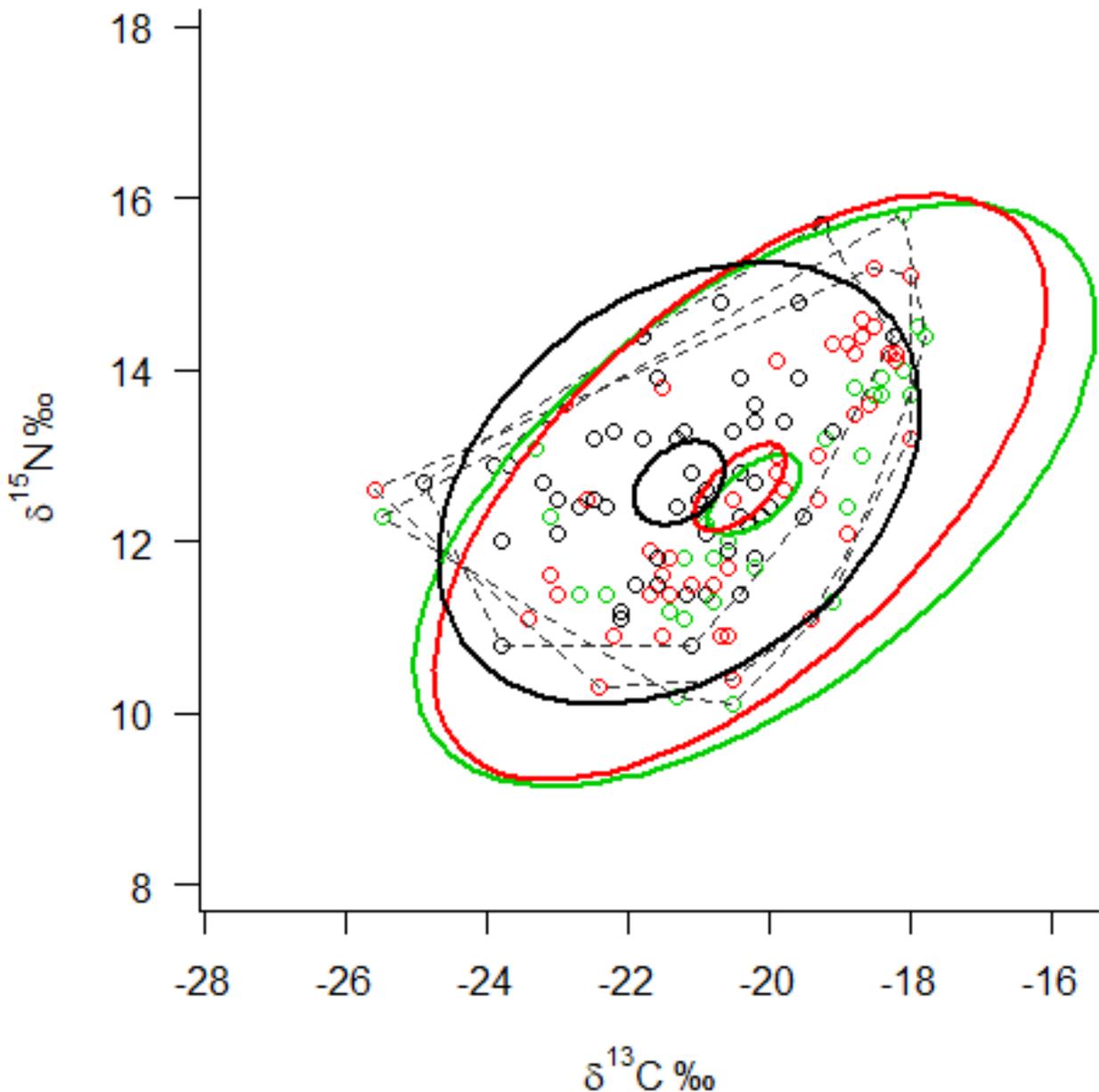


Figure 10. Bivariate $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ plot of convex hulls for immature (open, black circles) and mature, male (open, red circles), and mature, female (open, green circles) *A. felis* overlaid with 95% Bayesian ellipses of trophic niche (larger circles) and 95% Bayesian ellipses of bivariate means (smaller circles). Bivariate means of mature and immature *A. felis* are not significantly different (overlap of all three groups at 95% credible intervals). The lowest percent overlap trophic niche as measured by 95% Bayesian SEAs is 74.10% (immature *A. felis* overlap with mature, male *A. felis*) while the highest percent overlap is 93.77% (mature, male *A. felis* overlap with mature, female *A. felis*).

three possible trophic niche scenarios: 1) no trophic niche shift or expansion, 2) trophic niche expansion, but no niche shift, or 3) trophic niche shift (Hammerschlag-Peyer et al 2011).

A. felis in coastal Louisiana appear to exhibit the first trophic niche scenario. Though immature *A. felis* have significantly different ontogenetic trophic niche positions than that of either mature male or mature female *A. felis*, whether *A. felis* trophic niche width varies ontogenetically depends on the statistical metric used. Frequentist, multivariate analysis (mean distance to centroid or MDC) shows immature *A. felis* trophic niche width is significantly difference from both mature male and mature female *A. felis* trophic niche width. Both Bayesian, multivariate analysis of trophic niche width (SEA) and univariate analysis of the potential drivers of trophic niche width (Barlett's Test) find no significant difference between groups. Immature *A. felis* trophic niche and mature *A. felis* trophic niche overlap to a high degree (93.09% overlap immature to mature male, 92.75% overlap immature to mature female). Mature *A. felis* trophic niche and immature *A. felis* trophic niche have a lesser, but still large, percent overlap (74.10% overlap mature male to immature, 80.83% overlap mature female to immature). The degree of two way percent overlap – immature to mature and mature to immature – coupled with no significant ontogenetic difference in *A. felis* trophic niche width is evidence that *A. felis* diet in coastal Louisiana does not change with ontogeny (Hammerschlag-Peyer et al 2011 and Werner and Gilliam 1984). U nivariate analysis of trophic position does show a small, but significant difference in mean $\delta^{13}\text{C}$ values, implying *A. felis* might use a slightly wider variety of base resources or habitat later in their lifecycle, but generally eat similar prey items regardless of maturity status or size.

There are a variety of non-dietary factors which could influence *A. felis* isotopic signatures. Generally, WMT is thought to have a turnover rate measured in weeks to months

(Winter et al 2019 and Busst and Britton 2018). As paternal mouthbrooders, the timing of my *A. felis* subsample (July—August) could lead to male *A. felis* isotopic signatures influenced by fasting during mouthbrooding. The influence of fasting on male *A. felis* isotopic signatures could mask potential differences between either male and female *A. felis* or male and immature *A. felis*. 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 I attempted to control for as many non-dietary factors influencing the isotopic signatures of *A. felis* WMT, I cannot definitively say none of these factors mask possible ontogenetic differences in *A. felis* trophic niche position, width, or overlap.

In marine and estuarine environments, $\delta^{13}\text{C}$ isotopic signatures are largely influenced by plankton and C4 plants with C3 plants having a lesser impact (Peterson and Fry 1987). *A. felis* are considered estuarine generalist feeders (Muncy and Wingo 1983 and Merriman 1940) but appear to feed predominately on prey items derived from plankton (Figure 9, Panel A). This also provides evidence for *A. felis* using a variety of habitats throughout their lifecycle. As *A. felis* mature, their trophic niche expands slightly, but broadly, *A. felis* are using similar habitats and eating similar prey items regardless of size or maturity status. Such generalist feeding and habitat use could partially explain the apparent mismatch between *A. felis* life history and abundance.

Most 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 the trophic niche portion of this study ranged from 46mm TL to 432mm TL, an increase of nearly a factor of ten, while mass varied by nearly a factor of 100 (0.723g to 690g). 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 *A. felis* could have large enough mouths (mouth gape) that prey size for immature *A. felis* is not limited by mouth gape leading to similar stable isotope signatures for immature and mature *A. felis*. However, horizontal mouth gape of *A. felis* appears comparable to many other marine fishes (Scharf et al 2000), so mouth gape seems an unlikely explanation for the similar isotope signatures of immature and mature *A. felis*.

A. felis have isotopic signatures 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) (Figure 5). The $\delta^{13}\text{C}$ range of *A. felis* does not overlap with that of *S. ocellatus*, but does overlap with the four other species, while the $\delta^{15}\text{N}$ range of all five species overlaps (Winemiller et al 2007). The amount of overlap in isotopic signatures supports evidence (Olin et al 2012, Walters et al 2008) that *A. felis* competes directly for prey items with 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, how *A. felis* trophic niche, abundance, and their effect on other estuarine fishes are important factors in the management of healthy coastal ecosystems.

A. felis is an important mesopredator in the Gulf of Mexico (Walters et al 2008) and eat varied prey items throughout their lifecycle. Mature *A. felis* utilize 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 outsized influence on ecosystem connectivity in coastal

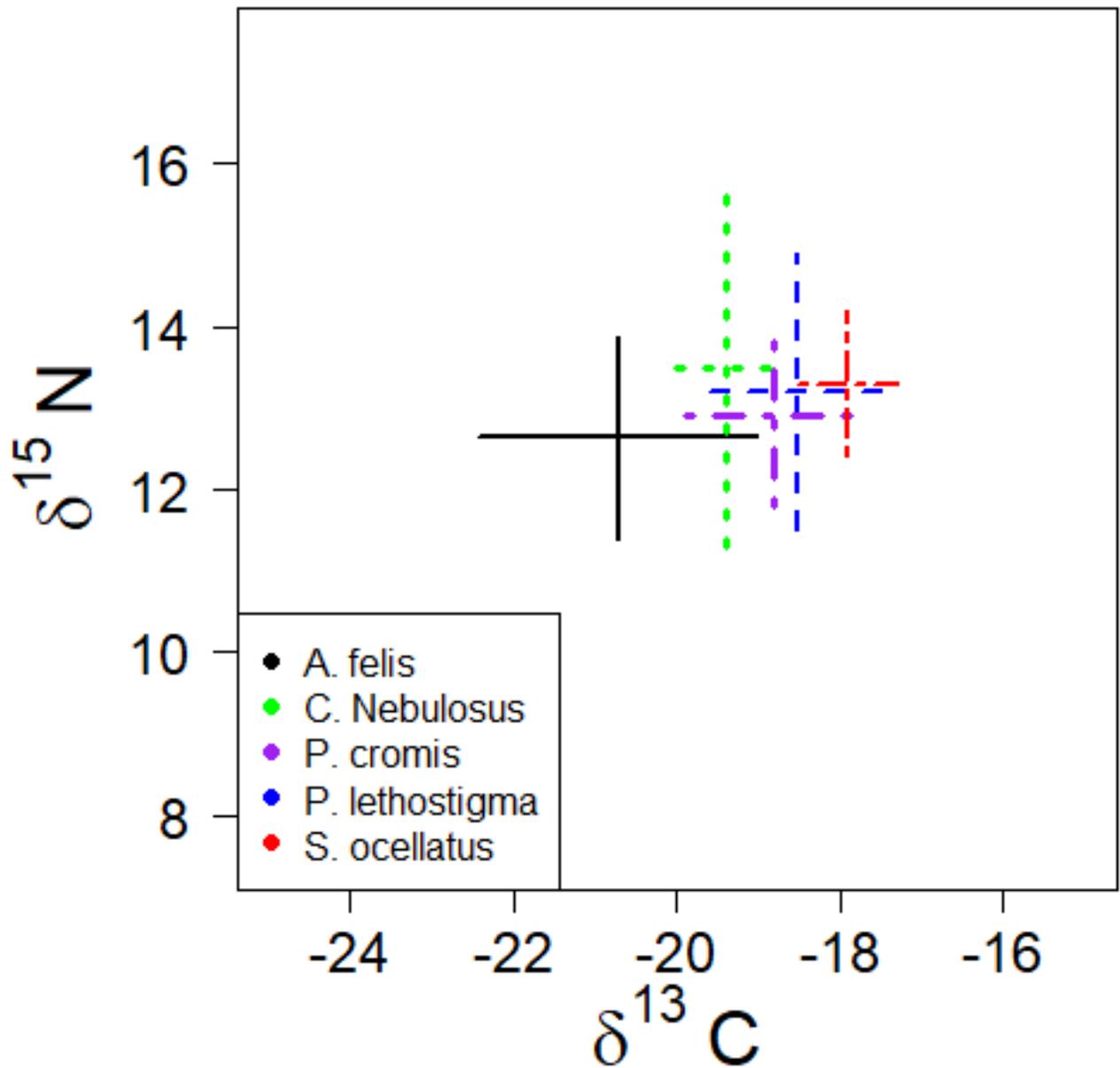


Figure 11. A comparison of mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopic signatures plus standard deviation for *A. felis* and four other estuarine predators common to the Gulf of Mexico (*A. felis* = solid, black line; *Cynoscion nebulosus* = green, dotted line; *Pogonias cromis* = purple, dashed/dotted line, *Paralichthys lethostigma* = blue, dashed line; and *Sciaenops ocellatus* = red, two-dashed line). Values for *A. felis* come from this study while all other values are from Winemiller et al (2007). *A. felis* isotopic range overlaps with all other species except for the $\delta^{13}\text{C}$ range of *S. ocellatus*, though *S. ocellatus* isotopic range overlaps with *C. nebulosus*, *P. lethostigma*, and *P. cromis*. This is evidence that all five species occupy similar estuarine trophic niches.

Louisiana due to local abundance. Lack of fishing pressure plus the consumption of a wide variety of prey items independent of ontogeny could possibly explain the seeming mismatch between *A. felis* life history traits and abundance (see Chapter 1). 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 due to stressors, such as the decrease seen in South Carolina beginning in the early 1990s (Webster et al 2013), could decouple an important trophic link between coastal ecosystems in the Gulf of Mexico. Historic catch data in South Carolina could provide insight into the implications of the removal of an abundant meso-predator from coastal ecosystems, though the scope of such an examination is likely beyond the breadth of this research. This research does represent important first steps in understanding how *A. felis* life history and trophic niche affect abundance and ecosystem role in coastal Louisiana.

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