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Reproductive biology of hardhead catfish *Ariopsis felis*: evidence for overwintering oocytes

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Abstract

Hardhead catfish *Ariopsis felis* are a common marine catfish in the coastal waters of the Gulf of Mexico (GOM). The low economic value of this species has depressed interest and research, and although the species is known for its extremely low fecundity and large oocytes, little else is known about this catfish species. A total of 1230 samples across all months of the year from 2016 to 2018 resulted in 681 females, and analysis of gonado-somatic index (I_G) revealed 1% to be a clear cut-off indicating maturity. Females are considered capable of spawning from April to June when I_G averaged 4–8%. Both atresia and post-ovulatory follicles were present in July, suggesting that spawning ends in July in the northern GOM. The 1% I_G cut-off was used to designate maturity, and from that an L_{50} of 253 mm was estimated. Batch fecundity from 41 females estimated a mean batch size of 36 oocytes. Perhaps the most interesting finding was the presence of secondary growth stage oocytes (*e.g.*, cortical alveoli) from July through November, well outside the spawning capable period. Furthermore, 78% of females had some early vitellogenic oocytes present during the non-spawning season, and the distribution of these relatively large (2–5 mm) oocytes did not change over time. The results here are not only important as reproductive biology information for a common and abundant species, but also present interesting and unusual patterns of non-spawning season oocyte development that is not commonly seen in Western Hemisphere subtropical fish species.

KEYWORDS
fecundity, gonado-somatic index, Louisiana, mouth-brooding

1 | INTRODUCTION

The diversity and complexity of biological processes and reproductive strategies inherent to fishes have been increasingly studied over the past several years, leading to an expansion in interest and understanding of fish reproductive biology (Lowerre-Barbieri *et al*., 2011). Interest in reproductive biology has been motivated by everything from desires to understand basic biological functions (Poortenaar *et al*., 2004) to enhanced information for population assessment and harvest (Midway & Scharf, 2012) to maximizing productivity in aquaculture settings (Blawut *et al*., 2018). Recent advances in fish reproductive biology have moved towards holistic ways of considering suites of traits that govern reproductive strategies (Murua & Saborido-Rey, 2003) and ultimately influence life history (Winemiller & Rose, 1992). In fact, understanding a species' life history may be useful in management settings when other, more specific reproductive information is not available (King & McFarlane, 2003). The importance of reproductive biology is further underscored by the

need to understand how fishes — both harvested and non-harvested species — will respond to climate change and other large-scale stressors (Poloczanska *et al*., 2016; Whitney *et al*., 2016).

Hardhead catfish *Ariopsis felis* (Linnaeus 1766) is a marine species found in coastal waters from Cape Cod, MA, USA, to Yucatan, Mexico (Muncy & Wingo, 1983) and is common in the coastal waters of Louisiana, USA. Despite the wide distribution and locally high abundance of *A. felis*, relatively little is known about the species' biology or life history. *A. felis* are considered opportunistic feeders on detritus, crustaceans and other fish (Lee *et al*., 1980), and potentially even target the scales of live fish (lepidophagy; Hoese, 1966). For many years, their published longevity estimate ranged from 2 years (Benson, 1982) to "three to eight growing seasons" (Doermann *et al*., 1977); nonetheless, recent work documented *A. felis* aged to an estimated 24 years (Flinn *et al*., 2019). In the northern Gulf of Mexico (GOM), the *A. felis* spawning season is thought to happen from late May through early August (Ward, 1957), whereas in the southern GOM the spawning season is believed to coincide with the wet season (June to September; Yáñez-Arancibia & Lara-Domínguez, 1988). Although the spawning season is not well studied, the limited information available suggests that *A. felis* do not exhibit a winter spawning strategy, which is very common in temperate coastal fishes (*e.g*., Taylor *et al*., 2009). Although there have been a few studies examining the life-history traits of *A. felis* in the northern GOM and southern Florida, there remain large knowledge gaps concerning this abundant coastal fish. For example, *A. felis* are considered very abundant in many parts of their range, whereas they are nearly extirpated in the US Southeast Atlantic (Ballenger, 2018), and no cause has been advanced.

Generally, marine fishes have very high fecundity with mature females producing many small eggs that hatch into small larvae, allowing reproductive success in highly productive environments (Winemiller & Rose, 1993). Fishes with low fecundity tend to be slower growing, less numerous and more vulnerable species that live in environments with patchy prey availability (Winemiller & Rose, 1993). Although Winemiller and Rose (1993) classified *A. felis* as an equilibrium strategist, the species appears to exhibit life-history traits that are not entirely compatible with known clusters of traits for this type of strategy. For instance, *A. felis* fecundity has been reported to be extremely low (around 100 offspring in a season; Merriman, 1940; Muncy & Wingo, 1983; Ward, 1957), yet their (relative) abundances have been anecdotally reported as high in many parts of their range, and they are a very commonly known fish species to coastal anglers throughout the northern GOM. *A. felis* also exhibit mouth-brooding, which is often associated more with freshwater fishes than marine fishes. Gunter (1947) wrote on male ariid catfish mouth-brooding large eggs and "helpless (larvae) with large yolks attached" as facts that "have been imperfectly known to ichthyologists for a long time." Furthermore, the Winemiller and Rose (1993) classification as an equilibrium strategist is based on models of life-history traits in aggregation. This interpretation may change with additional field and empirical data.

Although there are many fish species that lack specific studies on their reproductive biology, it is curious that very little is known about *A. felis* – a species that is both widely distributed and locally abundant. Further underscoring their ubiquity and importance, ecosystem modelling has identified *A. felis* as one of the more important mesopredators in the GOM (Walters *et al*., 2008). Given the species' low fecundity, high abundance, fast growth rate (Flinn *et al*., 2019) and other life-history traits that are seemingly incongruous, the objectives of this study were to (a) document reproductive seasonality, (b) estimate the size at first maturity, (c) quantify batch fecundity and (d) describe any observed mouth-brooding.

2 | MATERIALS AND METHODS

2.1 | Collection and processing

2.1.1 | Ethical statement

This study complied with all ethical requirements of the *Journal of Fish Biology* and local authorities. Hardhead catfish were killed during regular routine monitoring operations carried out independently by the Louisiana Department of Wildlife and Fisheries (LDWF) or donated as deceased samples. Animal welfare laws, guidelines and policies were not applicable.

Sampling was conducted monthly out of the Lacombe and Bourg, LA, LDWF field offices primarily in Coastal Study Areas One (Pontchartrain Basin) and Five (Timbalier/Terrebonne Basin; Figure 1) between September 2016 and August 2018. A majority (>95%) of *A. felis* in this study were sampled by LDWF as a part of their Fishery-Independent Sampling programme. A small sub-set of fish (5%) used in the current study originated from coastal Mississippi, USA, and were donated from fishery-dependent sources and used exclusively for summer and fall (July to October) gonadal histology. This small sub-set of fish is not part of the primary data set and is referred to

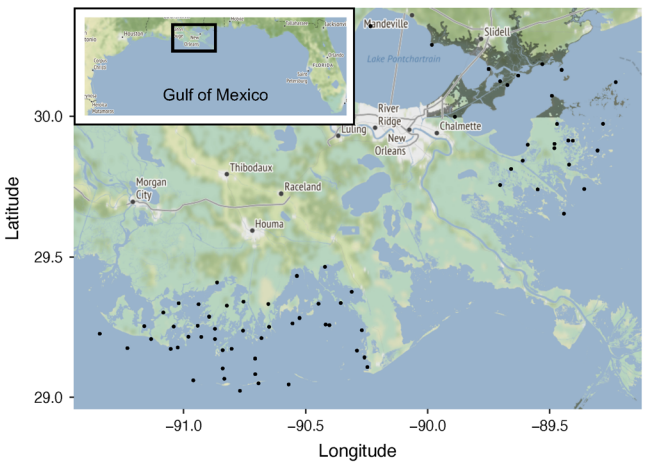

FIGURE 1 *Aris felis* sampling sites (black dots) in Terrebonne Bay (southern cluster of points) and Pontchartrain coastal area (eastern cluster of points), coastal Louisiana, USA. Samples were collected from 2016 to 2018

only in specific methods and results. LDWF uses a variety of gears in its Fishery-Independent Sampling programme, including bag seines, gillnets, trammel nets and trawls. For more information on this programme, see LDWF's Marine Fisheries Section Independent Sampling Activities (LDWF, 2018).

Whole fish were frozen shortly after capture and then transported to Louisiana State University for analysis. Thawed *A. felis* were processed for basic biological measurements including total length [TL (mm)], total mass [TM (g)] and gonad mass [GM (g)]. The gonadosomatic index (I_G) was calculated for each individual using the equation:

$$I_G = \frac{GM}{TM} \times 100.$$

The entire gonad was then preserved in 10% neutral buffered formalin (NBF) for a minimum of 1 week, and a small (2 mm) section was taken from the middle of a randomly selected ovarian lobe for histological analysis. Histological processing followed standard techniques including dehydration, clearing, paraffin embedment (Paraplast, Leica) and sectioning at 4 μm. Sections were stained with haematoxylin (560 MX, Leica) and eosin (Phloxine 515, Leica), and the resulting slides were viewed using a compound microscope. Large-format digital images of histology preparations were created by merging multiple low magnification image captures to create a single (mosaic) image file. Reproductive phases (immature, developing, spawning capable, regressing and regenerating) and oocyte stages [primary growth, cortical alveolar (CA), vitellogenic (VO) and atretic] were identified following Brown-Peterson *et al.* (2011). The authors of this study define reproductively active females as those in the developing and spawning capable phases and reproductively inactive females as those in the immature, regressing and regenerating phases.

Preliminary histological sections showed chatter and other characteristics that compromised the quality and readability of the samples, which was likely attributable to prior freezing as well as the large size of VO oocytes. Based on the nature of sampling, freezing was required; therefore, to fix gonad samples without prior freezing, the authors collected a small (n= 37), fisheries-dependent sample during summer and fall 2019. This small sub-set was not a complete substitution for other year-round samples, but rather reflected an opportunity to analyse additional histological samples that were not frozen. These samples were fixed within 12 h of capture in 10% NBF and processed for histological examination as above. Because these samples were outside the expected spawning season, the authors preliminarily observed and classified only CA and VO oocytes as well as atresia, and post-ovulatory follicle (POF) features. For each ovarian section, each of the above four features was assigned a relative abundance of *none*, *few*, *moderate* or *many* to assist with quantifying the observations of this study. *None* was defined as a feature being absent, *few* was defined as covering 1–10% of the section (or a small number of features), *moderate* was defined as 10–25% of the section and *many* was defined as >25% of the section or anything that was in great abundance.

2.2 | Reproductive seasonality

The authors used I_G as an indicator of reproductive timing, which allowed them to greatly increase the size of the available samples because of the lack of quality histological samples. Variations in I_G have long been used as a metric to ascertain the seasonal timing of spawning in fishes (*e.g.*, Jons & Miranda, 1997; Nieland & Wilson, 1993; West, 1990). In addition, the large oocyte sizes found in *A. felis* lead to large I_G values, and the resulting variability in this metric made it easy to identify monthly changes in I_G. The authors determined reproductive timing by examining mean I_G values by month and used an I_G value <1% as the cut-off for non-spawning season months.

2.3 | 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 gonadal development (Brown-Peterson *et al.*, 2011; West, 1990) and use logistic regression to estimate maturity as a function of fish size (Chen & Paloheimo, 1994). Nonetheless, in the absence of confident histological information, an I_G cut-off has been found to be an effective method of confirming maturity in other species (Brown-Peterson *et al.*, 2019; McPherson *et al.*, 2011; Vitale *et al.*, 2006). If the I_G cut-off is determined at the start of the spawning season, results are comparable to histological determination of maturity (Flores *et al.*, 2015). Because the histological examination of gonadal tissue was not conclusive in determining oocyte stages, the authors adopted the 1% I_G cut-off and assumed that any female *A. felis* during the spawning season (April to June) with I_G < 1% was immature. Thus, using the 1% I_G cut-off permitted the application of a binary maturity status (1 = *mature*, 0 = *immature*) to female fish within the spawning season. The authors 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 status (mature or immature) of fish i, α is the intercept parameter, β is the slope parameter, x_i is the TL for fish i and ε_i is the residual error. The link function used in estimation was the logit link. An L_{50} estimate (the estimated TL at which 50% of the individuals are mature) was calculated as $\frac{-\alpha}{\beta}$. All model estimation was performed using the **glm** function in R (R Core Team, 2019), which uses iteratively reweighted least squares to estimate parameters.

2.4 | Fecundity

A random sample of n = 47 female *A. felis* was identified from the months of highest I_G. Fecundity procedures were similar to those developed by Thorsen and Kjesbu (2001) as well as Klibansky and Juanes (2008). Individual ovaries were sliced open, and oocytes were

physically removed with gentle scraping. In some samples, an apparent thin film of very small, soft oocytes remained adhered to the ovarian wall and could not be removed without damage. Despite this, oocyte sizes were generally large, and the vast majority of oocytes easily dissociated from the ovary and from each other. Each of the 47 samples was separately imaged using a ZooSCAN system. 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. Although 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, the *Analyze Particles* function was used 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 was then 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 (ρ = 0.99); therefore, the authors used the major axis of each oocyte to represent oocyte size in millimetres. The oocyte counts allowed the calculation of the total number of oocytes in each individual *A. felis* as well as mean batch fecundity and mean oocyte size.

The authors estimated *batch fecundity* (F_B) by sub-setting only oocytes ≥10 mm from females sampled in April to June. Because few oocytes were observed above 15 mm, the authors think that F_B was best described by oocytes in the upper size range, 10–15 mm, and therefore most likely to be an upcoming batch. Relative batch fecundity (F_{RB}) was calculated as

$$F_{RB} = \frac{F_B}{TM - GM}$$

to enable the comparison of F_B across different-sized fish.

The authors tested for an effect of fish TL on fecundity because larger fish are documented to have greater fecundity counts in other fish species (Barneche *et al*., 2018). To test for this relationship, they used a generalized linear model with a Poisson distribution because fecundity counts are integer data. The model is represented as follows:

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

where y_i is the integer count of batch fecundity from fish i, α is the intercept parameter, β is the slope parameter, x_i is the TL for fish i and ε_i is the residual error. The link function used in estimation was the log link. All model estimation was performed using the **glm** function in R (R Core Team, 2019), which uses iteratively reweighted least squares to estimate parameters.

Preliminary evaluation of females in the non-spawning months revealed ovaries with relatively large (2–5 mm) oocytes, but with I_G < 1%. To better understand year-round fecundity and oocyte dynamics, the authors examined an additional n = 53 females over the eight regressing and regenerating phase (*i.e*., reproductively inactive) months (January was not included because of a lack of overall samples). Oocyte extraction was identical to the methods described earlier, with the notable difference that no (visible) oocytes were left behind during the removal of the oocytes from the ovary (oocytes were entirely removed from the ovary such that only the ovarian wall remained). The authors examined both total number of oocytes and oocyte size with the same methods detailed for the spawning season fecundity counts and used a linear mixed model to examine the effect of month on oocyte size. A random effect for individual fish was included to account for the non-independence of oocyte measurements from the same fish. (Modelling only the mean oocyte diameter per fish was a possibility but would have aggregated all fish into one diameter value and potentially lost information.) In addition, the authors excluded the months of July and August, in which some fish still exhibited large oocytes that were not characteristic of the vast majority of oocytes in non-spawning months. Excluding these July and August fish still provided 6 months of data, which the authors believed was sufficient to characterize the regenerating phase oocyte dynamics. A Tukey HSD test (Midway *et al*., 2020) was used to evaluate group differences for any appropriate models with significant results.

2.5 | Mouth-brooding

Although many of the reproductive strategies of *A. felis* are common to other species, male *A. felis* practice the uncommon habit of mouth-brooding. When mouth-brooding was observed, the authors counted the eggs or larval *A. felis*. Analyses of male mouth-brooding in *A. felis* were limited to basic biological characteristics, such as TL and mass.

3 | RESULTS

The authors sampled a total of 1230 *A. felis* from 2016 to 2018, of which 182 were sexually immature (and sex could not be determined *via* gross visual examination), 354 were male and 681 were female. Individuals ranged in size from 46 to 492 mm TL. Although only two fish were sampled in January, the other 11 months ranged between 35 samples (March) and 261 samples (August). Sampling location was also very balanced in representation; 565 *A. felis* came from the Pontchartrain basin and 562 *A. felis* came from the Timbalier-Terrebonne basin. The majority of the analyses of this study took place on 681 females.

3.1 | Reproductive seasonality

Mean I_G values by month were calculated to determine months with elevated I_G that would indicate oocyte development and spawning capability. *A. felis* produce large oocytes that result in I_G values in April, May and June that are both large and very distinct from the

remaining 9 months of the year (Figure 2a). Although no female samples were collected in January, it is likely that I_G values were low during this month, similar to those in December and February. Mean I_G values in April, May and June were 3.5, 7.8 and 5.4%, respectively, whereas the mean I_G values of all other months ranged between 0.19 and 0.94% (Figure 2a; although Figure 2a does not display means, the median values that are displayed are nearly identical values to the means). Based on these clear findings, the authors established April, May and June as the spawning season when fish would be in the developing and spawning capable phases (*i.e.*, reproductively active), whereas the remaining 9 months were considered the non-spawning season, with fish in the regressing and regenerating phases (*i.e.*, reproductively inactive).

The authors detected no effect of *year* or *location* (estuarine basin) on I_G. To examine for an effect of year the authors examined monthly mean I_G across sample years. Although not every year represented in the data provided complete monthly sampling, when months were broken down by year the overall patterns in I_G remained. In other words, regardless of the year, all months of April, May and June had large mean I_G values (>1%), and all other months had small I_G values (<1%). Similar to year, no effect of location was detected as monthly I_Gs between the two estuaries were consistent and I_G values were almost entirely overlapping.

Although ovarian samples prepared histologically failed to produce slides of sufficient quality for analysis, the authors were able to observe several large oocytes and putative VO oocytes well outside the spring spawning season. Histological analysis of freshly preserved ovarian tissue (n = 37) from late summer and fall 2019 showed the presence of CA oocytes in every sample, with most having a relative abundance of moderate or many (Table 1; Figure 3a–c). VO oocytes (Figure 3b,d) were in 78% of samples, although typically at few to moderate relative abundance and were only observed in the primary VO stage. Atresia was only present in 33% of fish (9 of 37), and although generally low in relative abundance, atresia was common in July fish at the end of the known spawning season (Figure 3c). POFs were also present in 9 of 37 fish (Figure 3a), which were most commonly seen in July samples, although not always in the exact same samples as those with atresia. Thus, although I_G values were low in July, based on the presence of POF spawning likely continued in July. Furthermore, these data suggest that despite low I_G values from July through October, female *A. felis* continue to support CA and VO oocytes. Histological analysis of the four males captured in July, September and October showed that all were reproductively inactive, with testes undergoing spermatogonial proliferation and no residual spermatozoa present. This suggests that males do not continue to invest energy in gametogenesis after the spawning season, unlike evidence for females.

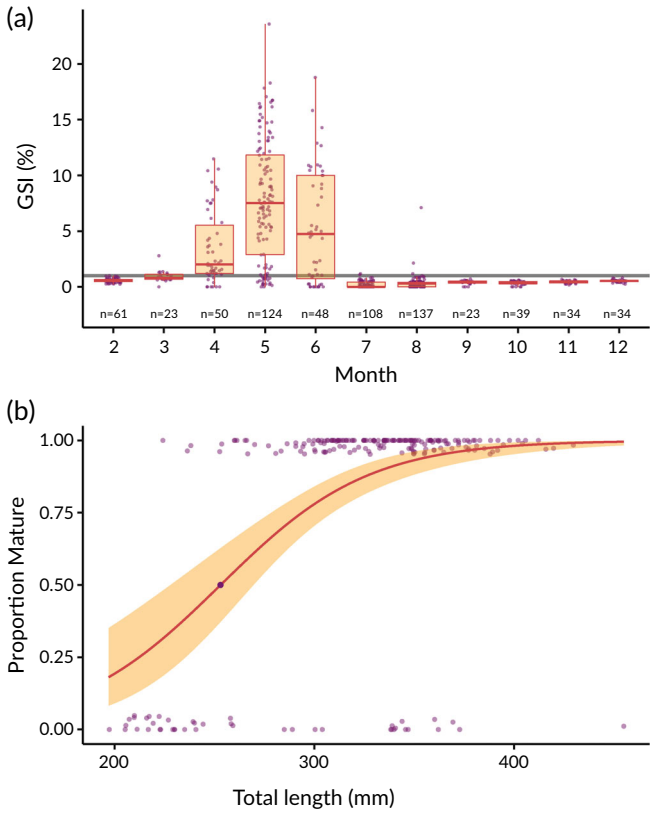

FIGURE 2 Reproductive parameters of female *Aris felis* in coastal Louisiana, USA, from 2016 to 2018. (a) Monthly gonado-somatic index (I_G) values. For each boxplot, the box represents the interquartile range (IQR), the middle line represents the median value and the whiskers extend to 1.5 times the IQR. The grey horizontal line is a reference line at I_G that equals 1%, which was the cut-off between spawning season months and non-spawning season months. Monthly sample sizes are found below the boxes and above the enumerated months on the *x*-axis. (b) Maturity ogive. Females were considered mature if their I_G was >1% during the months of April through June. Individual data points are represented in the purple jittered points. The curved line and shaded uncertainty region represent the fitted logistic regression model with the L_{50} estimate represented by the black dot at TL = 253 mm

3.2 | Length at first maturity

Of the 222 females sampled from April to June which were used for maturity analysis, 179 were mature and the remaining 43 were

TABLE 1 Percentage of non-spawning season female *Aris felis* (by month) exhibiting cortical alveolar (CA), vitellogenic (VO), atresia and post-ovulatory follicles (POF) based on histological analysis of fresh (not frozen) gonadal tissue

	July	August	September	October
Sample size	9	13	9	6
CA (%)	100	100	100	100
VO (%)	44	54	67	67
Atresia (%)	33	15	33	17
POF (%)	78	8	11	0

Note. For this table, *few*, *moderate* or *many* oocytes (the classifications described in the text and applied to each sample) were collapsed into present, whereas the classification *none* was considered absent.

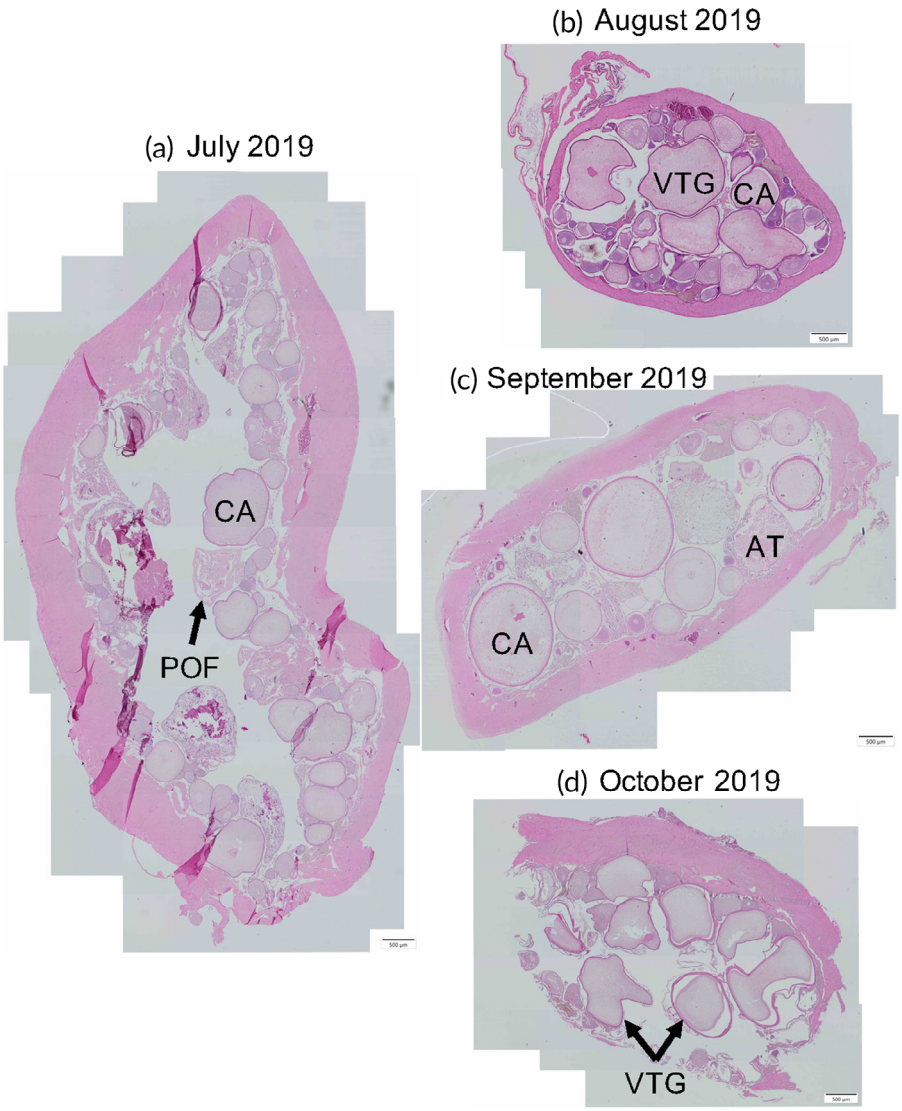

FIGURE 3 Four examples of gonadal histology from *Aris felis* outside the spawning season. Months of capture are included on the individual section panels, a–d. AT: atretic oocyte; CA: cortical alveoli stage oocyte; POF: post-ovulatory follicle; VTG: vitellogenic oocyte. Total lengths of the four fish from which these samples were taken ranged from 374 to 485 mm

immature based on the 1% I_G cut-off of this study. The maturity ogive of this study (Figure 2b) fit the data well and estimated an L_{50} of 253 mm TL. Similar to evaluating reproductive seasonality, the authors also looked at the possible effect of *year* and *location* (estuarine basin) on length at first maturity. For both breakdowns of year and estuarine basin, the L_{50} estimates were similar (*i.e.*, within a few millimetres), and the model estimates and uncertainty were largely overlapping. From these comparisons, the authors found no evidence for an effect of time or location on female *A. felis* length at first maturity.

3.3 | Fecundity

Female *A. felis* were split into two categories for fecundity work. April–June individuals were considered together as those females exhibiting batch fecundity (F_B) during the reproductively active phases. Similarly, July–March individuals were grouped together to examine the number of oocytes present (F_i) in the reproductively inactive phases.

3.3.1 | Reproductively active season

The 47 females sampled for fecundity during April to June ranged in size from 260 to 389 mm TL and were approximately equally represented among the 3 months. Examining n = 41 females between April and June for F_B estimates (including only oocytes ≥10 mm, which removed six fish), batch sizes ranged from 1 to 51 with a mean of 36 (and median of 40). Batch fecundity was significantly and positively related to fish size (P-value < 0.001; Figure 4a), and therefore F_{RB} was used to look at changes in fecundity across months. Overall, mean F_{RB} was 0.11 eggs g^{-1} ovary-free body weight (standard deviation = 0.04) and was similar from April and May, with a slight increase in June. The range of F_{RB} was similar for all months and not statistically significant among months (P-value = 0.07; Figure 4b). The authors also found counts of all oocytes >2.5 mm to be higher in May (mean = 83 oocytes) than in April (mean = 113 oocytes) or June (mean = 74 oocytes) (Supporting Information Figure S1), suggesting additional recruitment of oocytes between April and May. An ANOVA provided more evidence for these monthly differences (P-value < 0.01) and a

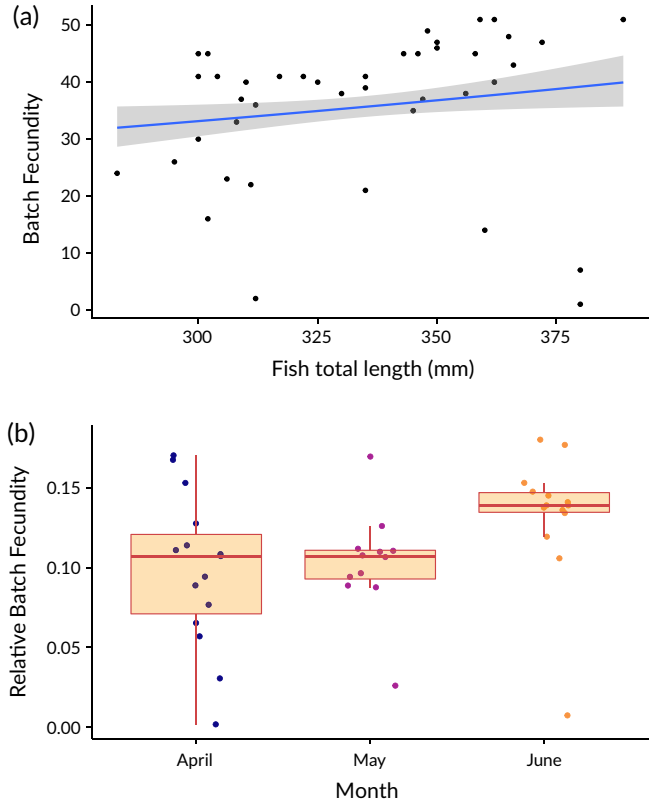

FIGURE 4 Fecundity of *Aris felis* in coastal Louisiana, USA, sampled in 2016–2018. (a) The relationship between total length (TL, mm) and batch fecundity for n= 41 fish from April to June based on oocytes ≥10 mm. Points represent individual fish. The blue line and grey uncertainty region represent the fitted model (Poisson GLM) and show a significant increase in batch fecundity with fish TL. (b) Relative batch fecundity by month during April, May and June. For each boxplot, the box represents the interquartile range (IQR), the middle line represents the median value and the whiskers extend to 1.5 times the IQR. Months are not significantly different from each other (see text for details)

Tukey HSD test confirmed that total oocyte counts in May differed from both April and June (whereas April and June did not differ from each other).

When individual distributions of oocyte sizes were considered, it was clear that fish in each month exhibited multiple distinct oocyte diameters (Figure 5). The range of oocyte diameters that the authors observed was 1.97–16.16 mm, with a mean of 8.25 mm. The oocyte size distributions also made it clear that multiple size class modes of oocytes were present in every month (Figure 5), often with complete separation between size distributions of the batches. The occurrence of small diameter oocytes in the ovary throughout the reproductive season suggests that *A. felis* exhibits indeterminate fecundity, as oocytes are continuously recruited throughout the spawning season. Further support for indeterminate fecundity may come from the decrease in relative total fecundity in June and July at the end of the spawning season and subsequent increase in the months up to and including the early part of the spawning season (Supporting Information Figure S2). Thus, although it is tempting to suggest that an individual female can spawn two to three times in a season based on the number of oocyte modes, this may not be accurate because of oocyte recruitment dynamics in indeterminate spawners.

3.3.2 | Reproductively inactive season

The 53 females sampled for oocyte counts during July to March ranged in size from 221 to 435 mm TL. Oocyte counts ranged from 11 to 184 with a mean of 90. The vast majority of fish during these months showed a single but distinct distribution of oocytes that ranged between 2 and 5 mm in diameter (Figure 6). Only two fish showed any oocytes >10 mm in diameter, both of which were sampled in July and August at the end of the spawning season. Results of the linear mixed model to test for the effect of month on oocyte size found the random effect for fish accounted for 20% of the residual error. The effect of month in the model was estimated to be 0.11 (S.E. = 0.03). Although the **lmer** function the authors used to fit this model does not provide *P*-values, both the ratio of the estimate to the S.E. and the general visual of oocyte diameters over time (Figure 7) suggest strong evidence that oocytes outside of the spawning season increase in diameter from September to March.

3.4 | Mouth-brooding

The authors observed n = 12 *A. felis* males with eggs or larvae in their mouths or stomachs (six holding eggs and six holding larvae found in July and August). The number of eggs carried per male ranged from 1 to 23 with a mean of 15, whereas the number of larvae ranged from 1 to 11 with a mean of 7. The TL of males engaged in mouth-brooding ranged from 235 to 390 mm with a mean of 321 mm. All mouth-brooding males were collected in either July or August. Overall, 94 male *A. felis* were collected during the months of July and August with a size range of 152–390 mm TL and a mean of 291 mm TL. These results suggest that mouth-brooding males are among the larger of the typical males the authors sampled, although they remained uncommon as the authors observed only 13% of the males collected within the time period (July and August) mouth-brooding.

4 | DISCUSSION

4.1 | Updated reproductive information

This study provides new and updated reproductive information for a widely distributed and locally abundant coastal fish species. Reproductive seasonality of *A. felis* in the GOM was previously reported from May to August with an annual fecundity of <100 oocytes (as reviewed in Muncy & Wingo, 1983). Nonetheless, the current study identified the spawning season for *A. felis* as April through June in the north central GOM, with only very few individuals showing high I_G values after June. Although I_G values decreased by July, the authors

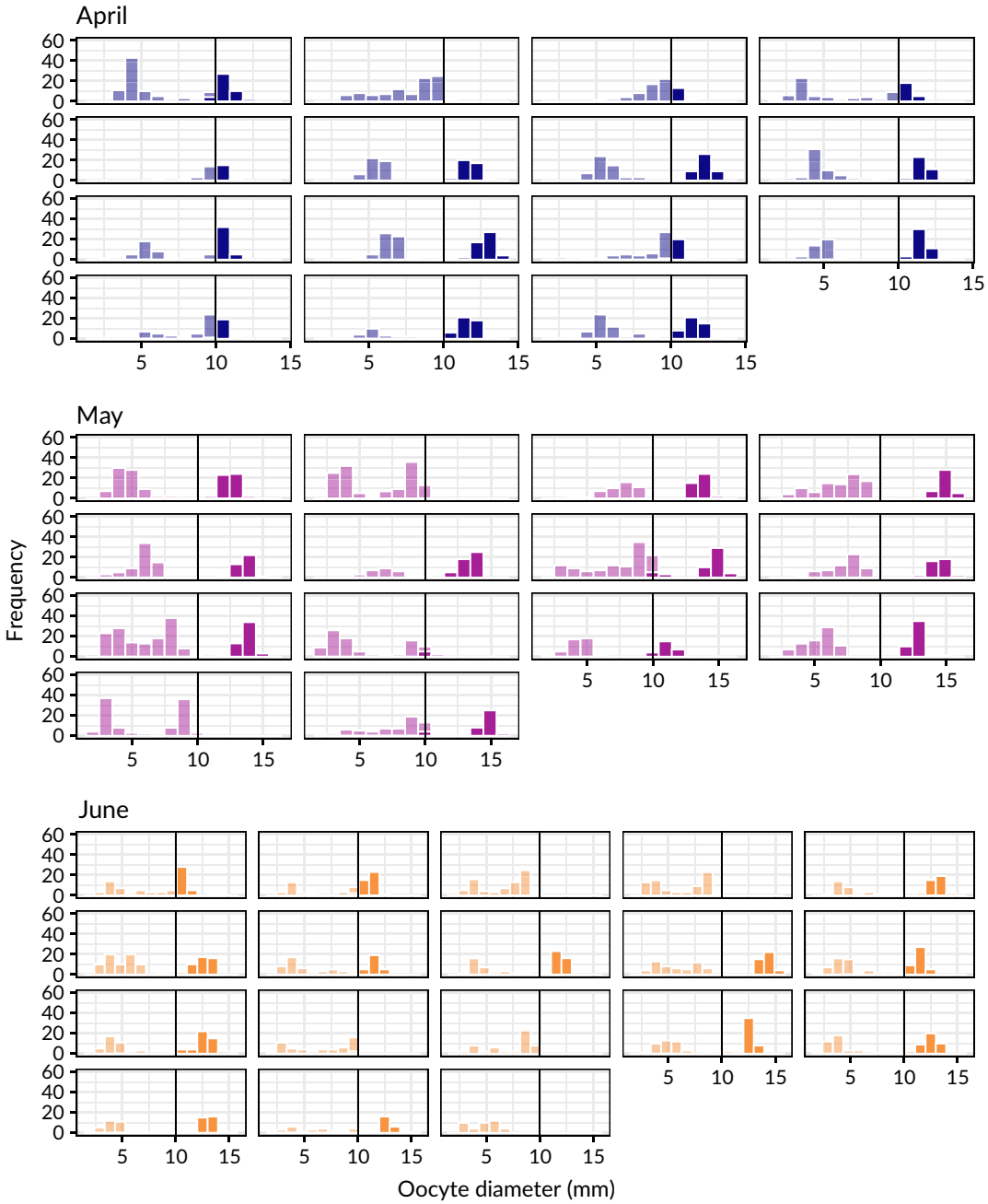

FIGURE 5 Histograms of oocyte counts by oocyte diameters for $n = 49$ *Aris felis* in coastal Louisiana, USA, during April, May and June. Individual plots represent individual fish, although there is no chronology of samples within month. The vertical lines within each panel represent a reference to 10 mm, which is the cut-off size applied for fecundity estimation. Similarly, oocytes less than 10 mm are in a lighter hue, whereas oocytes greater than 10 mm are in a darker hue

did observe POFs in July, which supports the idea that the spawning season may extend to July and be slightly offset (delayed) from a spawning season determined exclusively by I_G. Additional evidence that the spawning season may be longer than inferred from I_G values was the capture of males brooding embryos in July, suggesting spawning also occurred in July.

Although this species has a relative longevity (up to 24 years; Flinn *et al.*, 2019), the L_{50} of 253 mm TL that the authors estimated corresponds to a young age – around age 2 or 3. The estimate of size-at-maturity in this study is largely consistent with other published estimates (Yáñez-Arancibia & Lara-Domínguez, 1988), but does disagree with much older reports of smaller size-at-maturity (Lee, 1937; Merriman, 1940). The authors also recognize that using I_G to determine individual maturity is not a perfect substitute for histology. Nonetheless, the high I_G values the authors observed during the spawning season – particularly in comparison to the consistently low

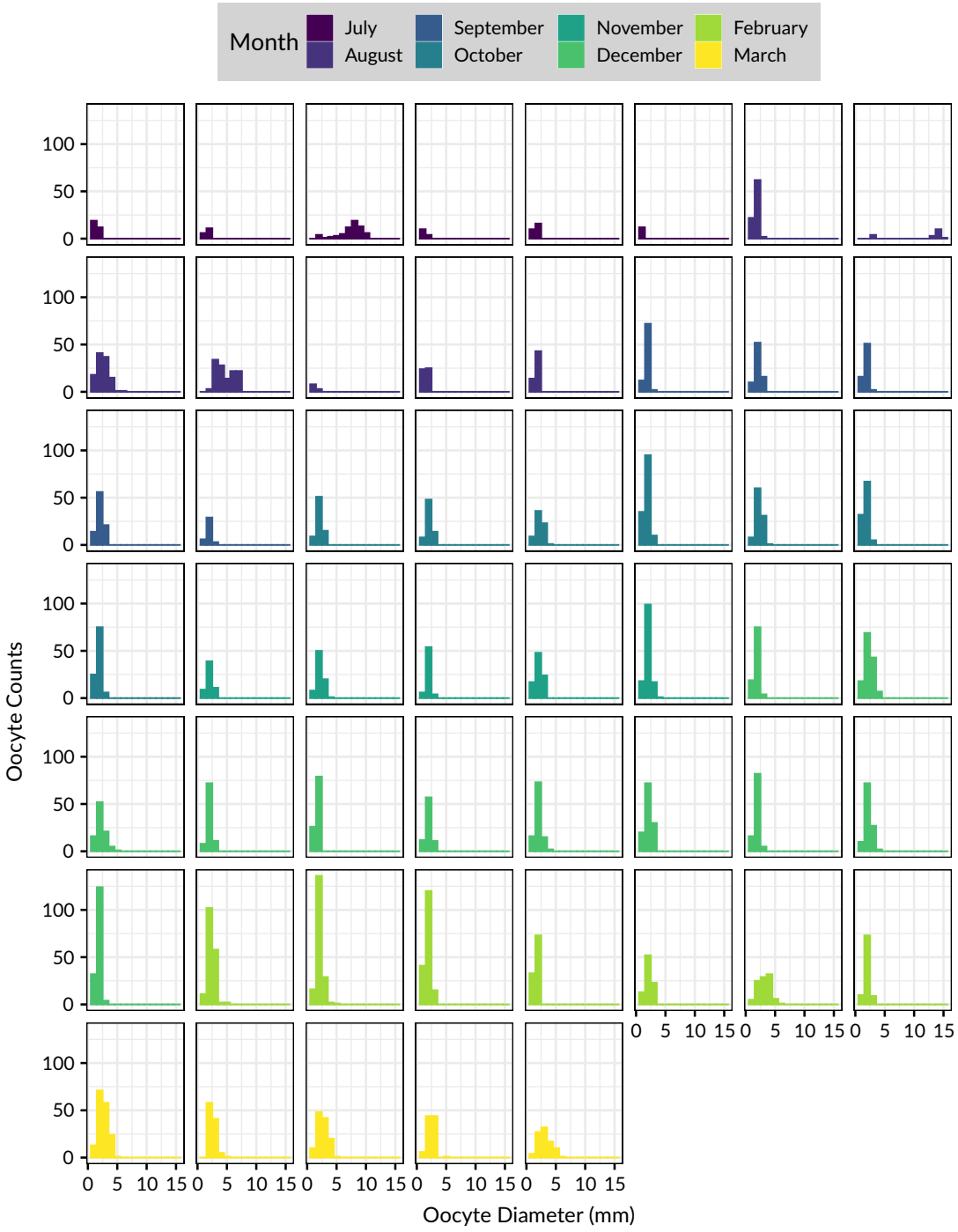

FIGURE 6 Histograms of oocyte counts by oocyte diameters for *Aris felis* in coastal Louisiana, USA, during the non-spawning season months. Individual plots (53 panels) represent individual fish, which are ordered by summer months at the top, sequentially to winter months at the bottom

I_G during the majority of the year – helped provide confidence that what they observed in I_G was a reflection of ovarian development and thus sexual maturity.

Previous work (Merriman, 1940; Ward, 1957) has noted the possibility of multiple spawns (batches) in *A. felis*, and the present work contributes to this claim with the multiple size class distributions of oocytes the authors measured. The mean F_B estimate of 36 of this study is lower than previous fecundity estimates (Merriman, 1940; Muncy & Wingo, 1983; Ward, 1957), although those estimates counted all oocytes present in the ovary. Indeed, the numbers of all oocytes present in the ovary during the spawning season reported here are similar to these earlier reports of *A. felis* fecundity. Because the observed oocyte distribution data during the reproductive season suggest that *A. felis* has indeterminate fecundity (Ganias *et al.*, 2015),

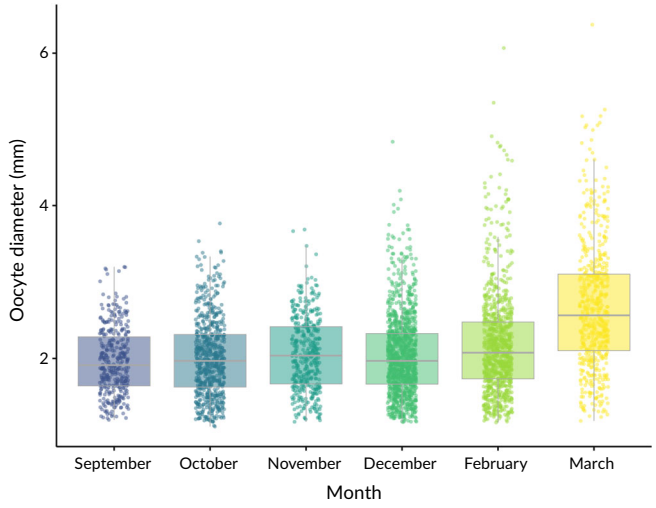

FIGURE 7 Individual oocyte diameters by month for 53 *Aris felis* sampled during the non-spawning season. Although multiple oocytes for each fish are included here, a linear mixed effects model accounting for individual fish estimated a positive effect of month, suggesting that oocyte diameters increase during the non-spawning season. Boxplots are overlaid to show the median (centre of box), interquartile range (extent of the box) and vertical lines extending to 1.5× the interquartile range

it is impossible to determine a total annual fecundity for the species without knowledge of the spawning interval and total number of spawning events. Although the authors observed at least two to three oocyte size classes in most fish during the spawning season, it is unlikely that these oocyte modes represent the only batches because oocytes develop and recruit into VO oocytes at any time during the reproductive season in fish with indeterminate fecundity (Murua & Saborido-Rey, 2003). Often, the smaller of the multiple size classes had a wide range of sizes (around 5–10 mm), which could be evidence for a third size class that has not yet differentiated in size. Mendoza-Carranza and Hernández-Franyutti (2005) reported two batches in female gafftopsail catfish *Bagre marinus* (Mitchill 1815) based on oocyte distribution, which is another Ariidae catfish found in the GOM. Male *A. felis* brooding embryos have been reported as early as May in the northern GOM (W. Dempster, University of Southern Mississippi, pers. comm.), suggesting that females spawn multiple batches from May through July. Further research to gain a better understanding of spawning frequency in the Ariidae is necessary to provide accurate annual fecundity estimates.

Mouth-brooding of eggs as a parental investment strategy has been described as one of four corroborated synapomorphies for the Family Ariidae (Acero & Betancur-R, 2007). Unfortunately, the authors were unable to observe mouth-brooding to any great extent; it is likely that sampling methods may have agitated fish in such a way that they released any eggs or larvae. Indeed, the number of eggs and larvae observed in the average mouth-brooding male was lower than the F_B estimates of this study. This discrepancy in numbers can likely be attributed to some loss of mouth-brooding eggs and larvae that were released during sampling.

4.2 | Arrested development?

One of the most interesting observations that the authors found was the consistent presence of secondary growth oocytes (in the CA or early VO stages) in fish well outside of the spawning season. The authors' expectation of annual oocyte dynamics for a warm-temperate coastal fish species would be the reproductively active fish that they observed during the spawning season (April through June), followed by a large reduction in I_G and atretic and primary growth stage oocytes during the non-spawning season. The authors observed both a large reduction in I_G after June in combination with atresia after the spawning season months, and atresia at low levels through October. Nonetheless, primary growth oocytes were not the only oocyte stage present during the reproductively inactive period. The authors found CA and early VO oocytes throughout summer and fall sampling, with 100% of fish sampled from July to October containing CA oocytes. Although histological samples of frozen tissue taken during the spawning season did not allow for reliable interpretation, histology of freshly preserved ovarian tissue during summer and fall 2019 allowed a better understanding of oocyte development during the non-spawning season.

The authors can consider at least four explanations for the appearance of apparently viable, developing oocytes in non-spawning season *A. felis*. The first possible explanation is that developing oocytes provide nutrition to mouth-brooding males. Gunter (1947) first posited this idea, and although the authors found no evidence of it, they did not sample in an optimal way to observe this and therefore cannot rule it out. Regardless, the slight increase in size over the fall and winter months of the arrested oocytes provides some evidence against their consumption. A second possible explanation is that *A. felis* are year-round spawners, but with a peak in the spring. The authors consider this explanation to be very unlikely based on their evidence. First, none of the 53 females they studied in July to March had oocyte sizes >10 mm diameter that they observed during the spawning season, and they saw no evidence of late-developing VO oocytes in their limited sample of non-spawning females. The authors also did not sample any individuals outside the spawning season that had I_G values comparable to fish during the spawning season. The third possible explanation for the appearance of viable, developing oocytes outside the spawning season is that the oocytes undergo a very slow or delayed atresia, despite the fact that atresia occurs more rapidly in warmer waters. Although the authors acknowledge that their histological samples are from limited and opportunistic sampling, they did examine 37 females captured from July to October and widespread atresia was not common in any samples, including those with some atresia. The authors do not rule out the possibility that some atresia was occurring, or that atresia might be delayed until the winter months; nonetheless, such a dynamic of delayed atresia would be unusual for a warm-temperate species (Brown-Peterson *et al*., 2011). The possibility of late atresia is further challenged by the fact that *A. felis* are spring spawners, and mass atresia of oocytes from a previous spawning season is uncommon in ovaries containing developing oocytes preparing for the next spawning season. The authors also

document a small but measurable increase in oocyte size over non-spawning months, suggesting an investment in oocyte growth.

The fourth and final explanation the authors considered was that non-spawning season oocytes were overwintering for the following spawning season, as has been shown for flatfishes living in deep or cold water (Hunter *et al*., 1992; Simonsen & Gundersen, 2005). This phenomenon appears unlikely based on observed oocyte dynamics in comparable fish from comparable locations; in other words, warm-temperate coastal fishes are not documented to overwinter oocytes. Nonetheless, for a number of reasons, this explanation might have the most support. First, the oocyte sizes (and numbers) the authors observed throughout the non-spawning months were consistent and appeared to slightly increase in size between June and October. It is unlikely that the authors would consistently observe a small stock of slow-growing oocytes over many months, only for atresia to then take place at the time they are most needed. Another consideration for this explanation is that *A. felis* may not be a typical warm water coastal fish on which the authors base expectations but may be more like other tropical and sub-tropical catfishes around the world. In fact, Wallace and Selman (1981) even noted that "oocytes which have terminated vitellogenesis may be recruited into maturation," citing the Asian stinging catfish *Heteropneustes fossilis* (Bloc, 1794; Goswami & Sundararaj, 1971) as a species that arrests oocyte development in late vitellogenesis only to later re-recruit those oocytes. Another study on the yellow catfish *Pelteobagrus fulvidraco* (Richardson, 1846) by Cao *et al*. (2009) reported that females returned to stage II (the *early developing* stage as defined by Heins & Baker, 1993) for overwintering and waited until March to progress to stage III (late developing). Although less relevant to overwintering oocytes, Mollah (1986) reported in the broadhead catfish *Clarias macrocephalus* (Günther, 1864) evidence for two distinct spawning seasons within the same year, *i.e*., spawning seasons that were months apart. Perhaps the most compelling comparison comes with the species *Arius manillensis* (Valenciennes, 1840), a marine catfish found in the Philippines. Ramos and Alfonso (2019) reported that *A. manillensis* had low I_G values (*c*. 1%) from October through February, while also having a substantial percentage (21–63%) of oocytes in the endogenous-vitellogenesis stage (*i.e*., CA or early vitellogenesis) and measuring 2.9–6.5 mm. The non-spawning season oocyte dynamics and growth in *A. manillensis* appear similar to what the authors observed in *A. felis*, both represented within the Family Ariidae and using mouth-brooding as a form of parental investment. Although the phenomenon of apparently viable oocytes throughout the non-spawning season certainly warrants more investigation, it is curious that the most similar examples the authors found also involved catfishes. It could be that because so many catfish species have relatively large oocytes and low fecundity, a variety of strategies have evolved to avoid complete atresia and resorption of energetically valuable tissue. In addition, this "ready stock" of CA and early VO oocytes allow complete oocyte development and maturation of very large oocytes during the relatively short *A. felis* spawning season.

4.3 | Life history

The life-history traits described here and in other recent work on *A. felis* suggest a more complicated life-history strategy than previously believed. Longevity over 20 years coupled with low fecundity and increased parental investment are associated with an equilibrium life-history strategy (Winemiller & Rose, 1992); indeed, these authors suggested that *A. felis* is an equilibrium strategist. Other equilibrium strategists are characteristically elasmobranchs (sharks and skates), suggesting that *A. felis* may have life-history traits common to elasmobranchs. Nonetheless, equilibrium strategist also tends to mature at older ages, which *A. felis* do not (Flinn *et al*., 2019). Although fecundity type of equilibrium strategists has not been examined, the Gulf Pipefish (*Syngnathus scovelli*), a member of the Syngnithadae that have been defined as equilibrium strategists (Winemiller, 2005), has indeterminate fecundity (Kornienko, 2001), similar to *A. felis*.

Equilibrium strategists tend to have low abundance, thus rendering them vulnerable to stressors such as overfishing (Hoenig & Gruber, 1990; King & McFarlane, 2003) or disease. Although life-history theory might predict low abundance for *A. felis*, that prediction does not match up with the observed abundance in the GOM. *A. felis* are not a commercially or recreationally targeted finfish in Louisiana (or elsewhere in their range), so the mismatch between life-history strategy and abundance could be because of a near-complete lack of fishing mortality combined with an availability of prey, habitat and other resources that are made available by the removal of several other estuarine species that are heavily fished in coastal Louisiana and the GOM. Being in a productive environment such as coastal Louisiana combined with low fishing or predatory pressure, it stands to reason that an equilibrium strategist like *A. felis* could be locally abundant. Nonetheless, if fishing pressure were to increase or a disease were to affect the population, life-history theory suggests that populations could quickly become overfished or threatened. Because both sexes of *A. felis* appear integral to the success of offspring (*i.e*., females in the production of oocytes and males in the parental care), increased mortality on either sex alone could result in declines. Furthermore, *A. felis* are thought to be an important mesopredator in the GOM (Walters *et al*., 2008), and it is unclear how a possible population decline might affect the greater GOM or coastal Louisiana ecosystems. Although *A. felis* is not considered a threatened species in the GOM, populations in South Carolina began to decline in the early 1990s – despite little to no fishing pressure – and to this day populations are so depressed that South Carolina Department of Natural Resources maintains a moratorium (dating back to 2007) on any *A. felis* harvest (Ballenger, 2018). Although the cause of the decline remains unknown, the example of *A. felis* in South Carolina waters underscores both the potential vulnerability of populations and the potential obstacles to recovery posed by species exhibiting equilibrium life-history traits.

5 | CONCLUSIONS

The reproductive output of a fish species is critically important in understanding their life history, population dynamics, ecosystem

role and how they respond to harvest and management (Lambert, 2008). Hardhead catfish were once a ubiquitous species along two North American coasts, most notable for their very large eggs and mouth-brooding strategy, but understudied because of lack of commercial or recreational interest. With increasing studies, the authors are learning more about *A. felis*, and the results presented here provide clear information about their size-at-maturity, spawning seasonality and fecundity, while at the same time reporting possible evidence for the rare trait of overwintering developing oocytes. The decline and near-disappearance of *A. felis* along the US southeast Atlantic coast remind us that a ubiquitous species can quickly disappear, and that we should take advantage of the species' current abundance to further understand its life-history dynamics.

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AUTHOR CONTRIBUTIONS

All authors contributed equality to the study design, data generation, data analysis and manuscript preparation.

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SUPPORTING INFORMATION

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

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