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Argulus from the Pascagoula River, MS, USA, with an Emphasis on Those of the Threatened Gulf Sturgeon, *Acipenser oxyrinchus desotoi*

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Abstract: Species of *Argulus* (Branchiura Thorell, 1864) are common ectoparasites of freshwater, estuarine, and marine fishes. Argulid identification and taxonomy is often confusing because many species are reported to parasitize multiple host species, have similar morphological characters, and come from various salinity regimes. Gulf sturgeon is an anadromous fish natal to drainages in the north-central Gulf of Mexico, and as with many endangered species, has a poorly documented parasite community. During Gulf sturgeon tagging and monitoring studies (2016–2019) in the Pascagoula River, MS, USA, species of *Argulus* were collected from Gulf sturgeon as well as other incidentally captured fishes. *Argulus flavescens* Wilson, 1916 was found on Gulf sturgeon and flathead catfish, *Argulus americanus* Wilson, 1902 on bowfin, and *Argulus bicolor* Bere, 1936 on Atlantic stingray. We provide morphological details and measurements for these species as well as the first confirmed 28S rDNA molecular data. *Argulus flavescens* was more abundant and prevalent on larger Gulf sturgeon and on sturgeon captured in freshwater rather than estuarine habitats. Our results indicate that *A. flacescens* may not tolerate estuarine salinities and that the anadromous life-history pattern of Gulf sturgeon could help rid them of *A. flavescens* when they emigrate from their riverine habitats.

Keywords: Branchiura; parasites; fish louse; anadromous; diadromous; 28S; bowfin; stingray

1. Introduction

Species of subclass Branchiura Thorell, 1864 are ectoparasites of aquatic vertebrates, but overwhelmingly of fishes [1,2] and freshwater fishes more so than saltwater fishes [3]. Argulidae Leach, 1819 is the sole extant family and contains four genera: *Argulus* Müller, 1785, *Chonopeltis* Thiele, 1900, *Dipteropeltis* Calman, 1912, and *Dolops* Audouin, 1837; with *Argulus* being the most specious genus with ca. 160 species [4]. Argulids are commonly referred to as carp lice or fish lice (but the latter common name can also refer to some species of copepods).

Argulids are capable of moving freely about their hosts, can swim to new host individuals (or host species), and females will leave a host to lay eggs on hard substrate, debris, or vegetation [2,5,6]. This behavior, along with their relatively large size, distinctive sucker-like maxillules, and compound eyes, makes individuals rather easy to spot with the naked eye. Argulid identification can be difficult because of overlapping morphological characters, the ability of some freshwater and marine species to overlap in estuarine habitats, and many species are only known from their original descriptions [2,4,7]. The three best studied species in terms of their distribution, lifecycle, host use, and ecology are *Argulus coregoni* Thorell, 1865, *Argulus foliaceus* (Linnaeus, 1758), and *Argulus japonicus* Thiele, 1900 (reviewed in [6]), the latter of which has been introduced throughout the world [8]. Eighteen freshwater species of *Argulus* have been reported from North America [1] and 10 species have been reported from the Gulf of Mexico [9], with no species reported from the Pascagoula River, MS, USA.

Gulf sturgeon, *Acipenser oxyrinchus desotoi*, is an anadromous species distributed in the north-central Gulf of Mexico, with seven natal drainages distributed from the Pearl River, LA/MS, USA, in the west, and the Suwanee River, FL, in the east [10]. Their pattern of anadromy is rather unique in that both spawning and non-spawning individuals of all size classes immigrate into riverine habitats each Spring and emigrate to estuarine and marine habitats in late Fall. Gulf sturgeon reside in stretches of the river called holding areas [11] during the late Spring (April–May) through late Fall (Oct–Nov), and seem to cease feeding during this time as well [10,12]. Interestingly, these fish also congregate in holding areas with many individuals found in relatively short (<2 river kilometers; rkm) stretches. The parasite fauna of Gulf sturgeon is poorly known. Only two studies have documented any parasites of Gulf sturgeon; one documenting Gulf sturgeon as a host for the glochidia of the purple bankclimber mussel [13] and an unpublished study that lists some ecto- and endoparasites, including an unidentified species of *Argulus* [14].

Species of *Argulus* can either directly or indirectly (increased susceptibility to secondary infection) cause fish mortality in aquaculture settings [6,15] where fish are crowded and stressed, but generally cause few problems in the wild (although some instances have occurred see [16] and references therein). Conceivably, when Gulf sturgeon are concentrated in their holding area habitats during the warmer months of the year while also fasting they could be more prone to fish lice. Therefore, the first objective of this study was to identify species of *Argulus* from Gulf sturgeon and other event-collected fishes from the Pascagoula River to document some of the argulid diversity present in this drainage and to provide morphological and molecular data for those species. Our second objective was to understand the ecology of a species of *Argulus* parasitizing Gulf sturgeon; in particular to determine patterns of fish lice infestation on Gulf sturgeon.

2. Materials and Methods

2.1. Collection and Specimen Preparation

All fish were captured in the Pascagoula River, MS, USA (Figure 1). Fish were targeted at three Gulf sturgeon holding areas (Dead Lake: DL, Paper Mill Camp: PMC, and Cumbest Bluff: CB), a migratory choke-point in the river (Census Site: Cen), and four locations in the Pascagoula River estuary (PRE). All fishing occurred between August 2016 and September 2019 as part of ongoing tagging studies for Gulf sturgeon. Fish were captured using anchored gill nets of varying sizes (1.2 m high × 45.7 m or 91.4 m long with 5.1 cm, 6.4 cm, 10.2 cm, or 12.7 cm bar mesh) that were fished between 30 min and 2 h depending on water temperature (<1 h when water temperatures were ca. 30 °C to minimize stress). Once captured, Gulf sturgeon (Table 1, Appendix A) were transported to shallow water where the following data collection occurred: sturgeon were measured for fork length (FL), total length (TL), weighed, examined for tags, and then visually examined for external parasites along the length of the body, on fins, around the mouth, and in the mouth. Non-sturgeon fishes (Table 2) were measured for TL and beginning in 2018 were quickly examined for external parasites. In nearly all cases, parasites were removed from the host fish and stored in 70% ethanol. After handling all fish were released.

Individual *Argulus* were cleared in lactic acid. Measurements were made using a compound microscope equipped with a differential interference contrast and calibrated digital software (iSolutions Lite Version 8.2 ©, IMT Inc., Vancouver, BC, Canada). All measurements are in micrometers unless otherwise stated and are displayed as the mean followed by the range in parentheses.
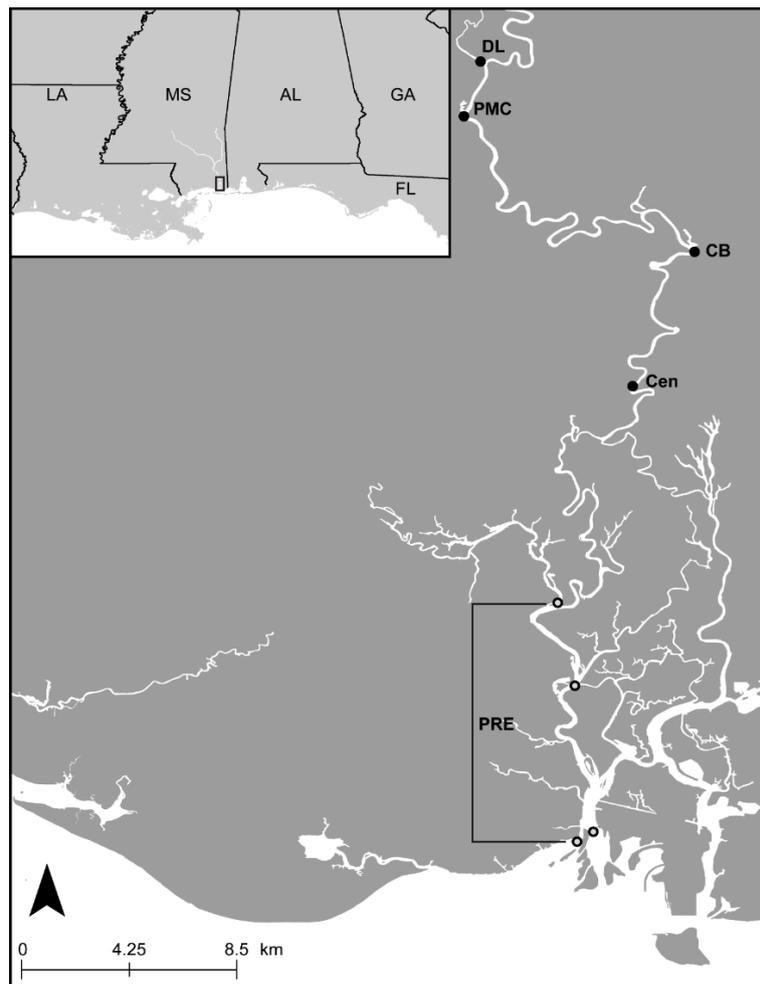
Figure 1. Spatial extent of the sampling locations in the Pascagoula River, MS, USA. Insert map displays the broader southeastern US and the rectangle denotes the study area. Closed circles denote Gulf sturgeon capture locations in the non-estuarine reaches of the river; open circles denote capture locations grouped as estuarine locations. Abbreviations from South to North: PRE: Pascagoula River Estuary (rkm 0–12); Cen: Census site (rkm 26); CB: Cumbest Bluff (rkm 38); PMC: Paper Mill Camp (rkm 55); DL: Dead Lake (rkm 58).

Table 1. Number of Gulf sturgeon examined for argulids from 2016–2019 by size class and location.

Size Class	Estuary	Census Site	Cumbest Bluff	Paper Mill Camp	Dead Lake
2016					
Juvenile	0	5	2	0	6
Subadult	0	7	22	1	2
Adult	0	4	12	0	0
2017					
Juvenile	0	0	1	0	7
Subadult	2	0	4	5	3
Adult	0	0	0	2	3
2018					
Juvenile	0	1	10	1	2
Subadult	1	0	28	4	5
Adult	0	0	9	1	1
2019					
Juvenile	8	0	5	0	1
Subadult	2	0	18	5	2
Adult	0	0	12	2	3

Table 2. Species, size range (total length in cm), and number of each from each location examined for argulids from 2018–2019. Fishes were identified based on keys in [17]. Abbreviations PRE: Pascagoula River Estuary; Cen: Census site; CB: Cumbest Bluff; PMC: Paper Mill Camp; DL: Dead Lake.

Common Name	Scientific Name	Size Range	PRE	Cen	CB	PMC	DL
2018							
Atlantic stingray	*Hypanus sabinus*	25.0–37.8 [†]	10	0	0	0	0
bowfin	*Amia calva*	86.5	0	0	1	0	0
spotted gar	*Lepisosteus oculatus*	70.0–136.0	0	0	1	8	0
longnose gar	*Lepisosteus osseus*	84.2–143.8	17	0	0	2	1
Gulf menhaden	*Brevoortia patronus*	19.0–21.0	6	0	0	0	0
gizzard shad	*Dorosoma cepedianum*	35.6–42.0	0	0	0	7	0
striped anchovy	*Anchoa hepsetus*	11.4	1	0	0	0	0
quillback	*Carpiodes cyprinus*	37.2	0	0	1	0	0
small mouth buffalo	*Ictiobus bubalus*	31.0–72.4	0	0	14	8	6
hardhead catfish	*Ariopsis felis*	39.5–41.1	2	0	0	0	0
gafftopsail catfish	*Bagre marinus*	52.1–60.6	3	0	0	0	0
blue catfish	*Ictalurus furcatus*	57.2–100.0	0	0	7	0	0
channel catfish	*Ictalurus punctatus*	49.5	0	0	1	0	0
flathead catfish	*Pylodictis olivaris*	52.6–78.6	0	0	5	1	0
southern flounder	*Paralichthys lethostigma*	37	1	0	0	0	0
freshwater drum	*Aplodinotus grunniens*	57.2–68.8	0	0	5	3	0
sand seatrout	*Cynoscion arenarius*	20.4–30.2	19	0	0	0	0
black drum	*Pogonias cromis*	37.8–90.8	4	0	0	0	0
sheepshead	*Archosargus probatocephalus*	52.4–55.6	2	0	0	0	0
2019							
longnose gar	*Lepisosteus osseus*	101.2	0	0	0	1	0
gizzard shad	*Dorosoma cepedianum*	31.4–44.0	0	0	5	7	0
quillback	*Carpiodes cyprinus*	29.8	0	0	0	1	0
small mouth buffalo	*Ictiobus bubalus*	61.4–70.2	0	0	0	4	0
grass carp	*Ctenopharyngodon idella*	110.5	0	0	0	1	0
channel catfish	*Ictalurus punctatus*	39.4–59.2	0	0	3	0	0
flathead catfish	*Pylodictis olivaris*	59.0–79.2	1	0	2	0	0
freshwater drum	*Aplodinotus grunniens*	67.2	0	0	0	1	0

[†] Disc width (cm).

2.2. Genetic Techniques and Comparison

Individual specimens of *Argulus* chosen for sequencing were first examined under a stereomicroscope in deionized water and sinistral thoracopods 1 and 2 were removed for DNA extraction. Genomic DNA was extracted using Qiagen DNAeasy Tissue Kit (Qiagen, Inc., Valencia, CA, USA) following the instructions provided. DNA fragments about 940 base pairs (bp) long comprising the 3′ end of the 28S gene nuclear rDNA gene were amplified by PCR using forward primer 1274: (5′-GAC CCG TCT TGA AAC ACG GA-3′) [18] and reverse primer 1276 (5′-CTA GTT GCT TCG GCA GGT GAG-3′) [19]. The PCR reactions were performed under the protocols described in [19]. The resulting PCR products were gel purified using QIAquick Gel Extraction Kit (Qiagen, Inc.) following kit instructions and sent to Eurofins Genomics (Louisville, KY, USA) for sequencing. Sequencing reactions used the same primers. Contiguous sequences were assembled using Sequencher™ (Version 4.10.1, GeneCodes Corp., Ann Arbor, MI USA) and submitted to GenBank.

Sequences of other species of *Argulus* obtained from GenBank were used for comparison are *A. foliaceus* EU370442 [20], *Argulus* sp. AY210804 [21], and *Argulus* sp. AF363322 [22]. Sequences were aligned using MAFFT version 6.611b [23] with 1,000 cycles of iterative refinement and the genafpair algorithm. All pairwise comparisons of sequence data exclude gaps and were trimmed to the shortest sequence.

2.3. Ecological Data and Analyses

Ecological terms for parasites follow that of [24]: prevalence of infection (as percentage ± 95% confidence interval), and abundance (number per fish whether infested or not). All fish were released alive; therefore, reported abundances should be viewed as conservative as some individual specimens of *Argulus* could have been missed. For Gulf sturgeon, size classes follow that of [25] with individuals <89 cm FL considered to be juveniles, those 89–125 cm FL as subadults; and those >125 cm FL as adults. Prevalence of *Argulus* was compared by size class, host capture location, and year using a chi-square analysis. We used a negative binomial general linear model (GLM.nb) and log-link function in the MASS library of R (Version 3.6.0) to analyze abundance. Our model included FL, location, host condition (Fulton's condition factor—*K*), and year of capture. We followed the formula for K in [26]

$$K = 100 \times \frac{\text{W}}{\text{FL}^3}. \tag{1}$$

We used a Kruskal–Wallis H test to determine if there were differences in abundance among all up-river locations including the Census site and Gulf sturgeon holding areas (DL, PMC, and CB). For all statistical analyses α < 0.05.

3. Results

3.1. Argulus flavescens Wilson, 1916

Type host: *Amia calva*.
Type locality: Sunfish Lake, Fairport, IA, USA.
Other hosts and locations: *Pylodictis olivaris* (as *Leptops olivaris*), Sunfish Lake, IA [27]; *Micropterus salmoides* (as *Aplites salmoides*), Myakka River, FL, USA [28]; *A. calva*, Lake Okeechobee, FL, USA [28,29]; *Erimyzon sucetta*, *Ameiurus natalis*, *A. nebulosus*, *Ictalurus punctatus*, and *Floridichthys carpio*, Lake Okeechobee [29]; *Cyprinus carpio* Lake Texoma, OK, USA [30]; *Hypanus* sp. (as *Dasyatis* sp.), *Amia calva*, *Paralichthys* sp., *Mugil* sp., *Micropogonias* sp. (as *Micropogon* sp.), and *Micropterus* sp., coastal Gulf of Mexico and Mississippi River system, USA [31]; *I. punctatus* Wills Creek, OH, USA [32]; *M. salmoides*, Lake Creek, IL, USA [33]; *Notropis wickliffi*, Mississippi River, IL [33]; *Acipenser oxyrinchus desotoi*, *Pylodictis olivaris*, Pascagoula River, MS, USA (this study).
Measurements: Based on 13 males and 13 gravid females from Gulf sturgeon and 1 male and 1 female from flathead catfish (Figure 2). Total length (mm) 3.58 (2.68–4.50) in males, 4.58 (2.55–6.67) in females. Carapace length (CL; mm) 2.55 (2.10–3.23) in males, 3.37 (2.07–4.74) in females; maximum carapace width (mm) 2.33 (1.81–3.07) in males, 3.22 (1.92–4.28) in females. Carapace posterior sinus length 515 (308–645) in males representing 20% (12–28%) CL, 896 (442–1379) in females representing 25% (21–29%) CL; width at midpoint of sinus 401 (241–498) in males, 693 (342–1053) in females. Cephalothorax length (mm) 1.60 (1.33–2.00) in males, 2.13 (1.57–2.79) in females; anterior width (mm) 1.31 (1.02–1.58) in males, 1.60 (1.07–2.00) in females. Abdomen length (AL) 926 (613–1130) in males, 996 (510–1226) in females; maximum width 645 (448–845) in males, 798 (472–1057) in females. Abdomen posterior sinus length 201 (162–249) in males representing 22% (19–29%) of AL, 331 (132–451) in females representing 33% (26–38%) of AL; width at midpoint of sinus 71 (38–104) in males, 83 (44–112) in females. Eye diameter 161 (138–188) sinistral and 169 (142–193) dextral in males, 175 (157–189) sinistral and 182 (160–201) dextral in females; transverse distance 460 (364–544) in males, 594 (485–787) in females. Maxillules outer diameter 525 (436–660) in males, 757 (468–934) in females; inner diameter 361 (300–446) in males, 519 (304–629) in females; number of support rods 48–52 in males, 50–56 in females. Number of sclerites per support rod 4–5 in both sexes.
Sequences deposited: GenBank accession number MN688125 based on 10 identical sequences from Gulf sturgeon and 1 from flathead catfish; MN688126 and MN688127 both from Gulf sturgeon.
Material deposited: Specimens were deposited in the Gulf Coast Research Laboratory Museum, Ocean Springs, MS, USA (GCRLM). The hologenophore for MN688125 (GCRLM 06605); the voucher

for MN688126 (GCRLM 06608) and MN688127 (GCRLM 06609); and 29 additional vouchers (GCRLM 06605-06606, 06608-06609) from *A. oxyrinchus desotoi*; and 1 voucher used for sequencing from *P. olivaris* (GCRLM 06607).

Remarks: Our specimens are morphologically consistent with the descriptions provided by Wilson [27], Mueller [28], and Meehean [7], but with some minor differences. Wilson [27] described *A. flavescens* as having an abdomen that is equally long as wide (at least in females) whereas our specimens of both sexes and from both host species had abdomens that were narrower (abdomen width 60–75% and 70–90% of abdomen length for males and females, respectively). Wilson [27] did not provide a description for the male, but the illustrations of the fourth thoracopod provided by Mueller [28] and Meehean [7] are nearly identical to those observed in our specimens (Figure 2G,H). Neither author described the second thoracopod of males very well. In our specimens, the coxa of the second thoracopod has one broad, semi-bimodal pad along the posteroventral margin with many short, digitate spines. The precoxa of the second thoracopod has a small, posteroventral lobe that also bears spines. The pegs of our specimens have scales along the dorsal lobe and fine sensilla associated with the distal end of the ventral lobe. Coloration of our specimens was consistent with previous authors', with the female having more melanophores concentrated on the thorax and the carapace (particularly above the ovary and lateral extension in the carapace) whereas males have a more "peppered" appearance (Figure 2B) and more melanophores concentrated dorsal to the testes (Figure 2B,E). Most of our female specimens also had some slight pigmentation on the abdomen dorsal to the spermatheca.

Meehean [7] considered *Argulus piperatus* Wilson, 1920 a junior subjective synonym of *A. flavescens*, but this suggestion does not seem to have been followed [4]. Wilson [34] described *A. piperatus* from free-living specimens collected in a tidal portion of the Shubenacadie River, Nova Scotia, Canada. His description included no mention of eggs in the lateral lobes of the carapace (called ramifications of the stomach by Wilson [27]) as is present in nearly all mature female *A. flavescens* (Figure 2C), and it stated that there were only four sclerites in the supporting rods of the maxillules and that the sclerites diminished regularly in size distally whereas the sclerites of *A. flavescens* number four to five and are relatively similar in size. Wilson [34] described the carapace of both sexes of *A. piperatus* as being more elongate than that of *A. flavescens* ($\frac{1}{4}$ longer than wide rather than about equal in size); described both sexes of *A. piperatus* with a larger carapace posterior sinus ($^1/_3$ the carapace length rather than $\frac{1}{4}$ the carapace length as in *A. flavescens*); and described the third thoracopod of males as with a rounded knob with setae on the anterior margin, which, based on the illustration, is about half the length of the socket (a feature not observed in males of *A. flavescens*). Furthermore, *A. piperatus* was described from a river drainage that empties into the Bay of Fundy rather than one of the tributaries of the Mississippi River or a coastal drainage in the southeastern USA. The combined morphological and geographical evidence strongly suggests that *A. piperatus* is not a synonym of *A. flavescens*.

Suárez-Morales et al. [35] reported *A. flavescens* from *Ariopsis assimilis* off Chetumal, Mexico. However, the illustrations they provided of the second, third, and fourth thoracopods of their male specimens clearly shows that their specimens are not *A. flavescens*. In particular, they have illustrated the precoxa of the fourth thoracopod with an anteriorly directed spine approximately equal in length to the peg (no such spine is present in *A. flavescens*). Their illustration of the socket on the third thoracopod is also much smaller (in both length and width) when compared to the broad socket of *A. flavescens* (Figure 2G). They also illustrated the dorsal surface of the coxa of the third thoracopod as having several knobs that are lacking in *A. flavescens*. Finally, the coxa of the second thoracopod has a large, posteriorly directed projection that is lacking in *A. flavescens*. We suggest these combined morphological and geographical differences point to their specimens representing a species that is not *A. flavescens*.

The primary site of infestation for nearly all hosts examined has been the mouth and branchial cavity, at least when the site was reported or when a specimen was recovered directly from a host (i.e., not found in a jar with a fish as in the record of *Notropis wickliffi* [33]). We found *A. flavescens*

primarily in the mouth (both Gulf sturgeon and flathead catfish) and the area surrounding the mouth tube (Figure 2A) of Gulf sturgeon. Only 4 of the 148 parasitized Gulf sturgeon had *A. flavescens* on either the body or at the base of the pelvic fins. Wilson [27] suggested in the remarks section of the original description that the probable host for *A. flavescens* was the flathead catfish and that the specimens on the external surface of the bowfin were only "seeking temporary lodgment." The host list for *A. flavescens* spans several families (particularly with the inclusion of the estuarine hosts), but Ictaluridae is the most represented host group consistent with Wilson's [27] suggestion.
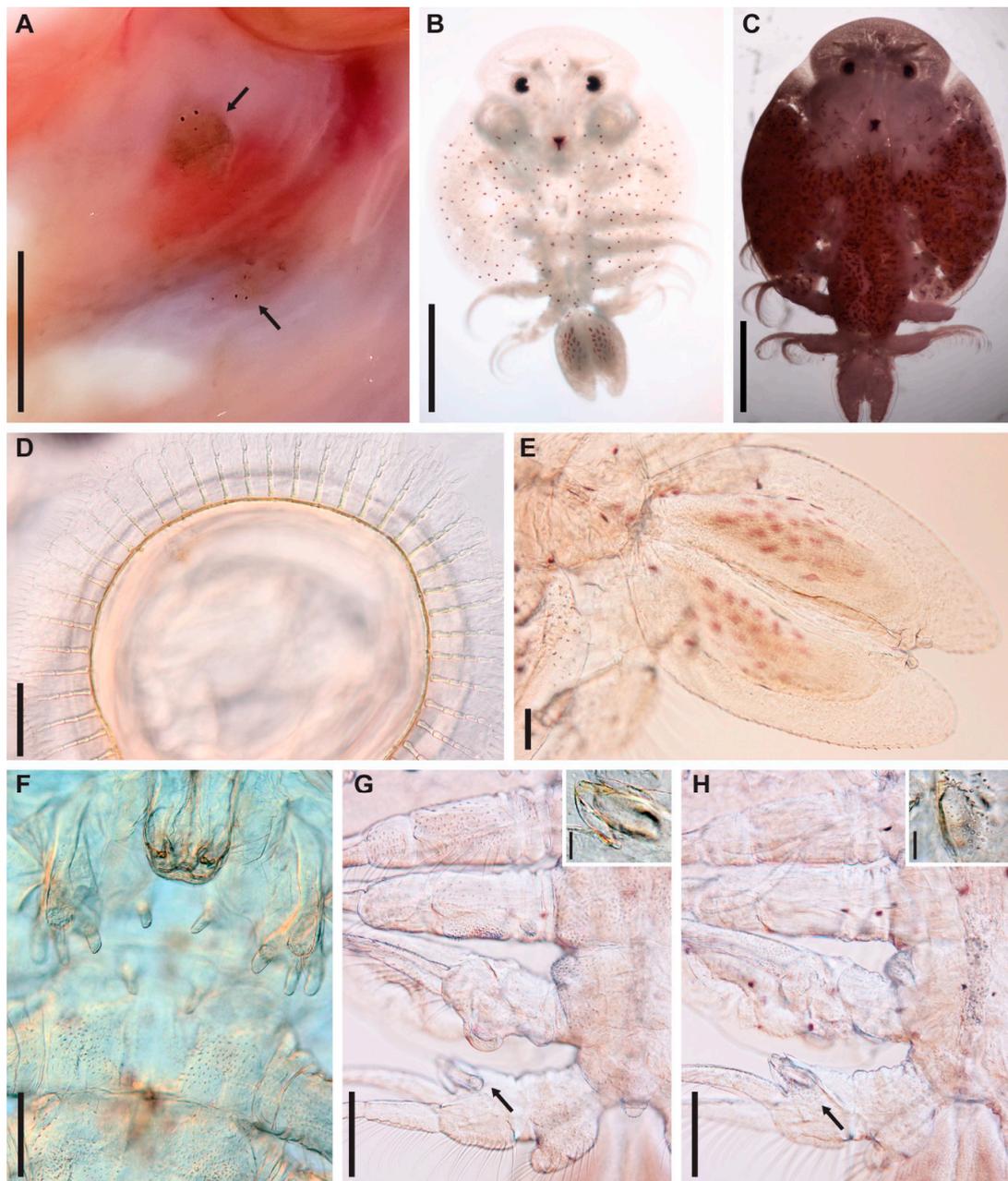
Figure 2. Photograph and photomicrographs of *Argulus flavescens* Wilson, 1916. (**A**) Two individuals (arrows) outside of the mouth of Gulf sturgeon; note inflamed area surrounding their location (Photograph: C. Lapniewski). (**B**) Male, dorsal view, not cleared. (**C**) Female, dorsal view, not cleared. (**D**) Sclerites of support rods in maxillule. (**E**) Abdomen of male. (**F**) Mouth and basal plates of maxillae. (**G**) Ventral plain of male thoracopods; insert shows ventral lobe of peg. Note rounded, boot-like lobe on posterior margin of fourth thoracopod. (**H**) Dorsal plain of male thoracopods; insert shows dorsal lobe of peg. Scale bar = 1 cm (**A**), 1 mm (**B,C**), 100 μm (**D,E**), 250 μm (**F–H**), 50 μm (inserts).

3.2. Argulus americanus Wilson, 1902

  Type host: *Amia calva*.

  Type locality: Huron River, MI, USA.

  Other hosts and locations: *Amia calva*, Lake Maxinkuckee, IN, USA [27]; *A. calva* and *Umbra limi*, Mississippi River, Fairport, IA, USA [27]; *A. calva*, *A. nebulosus*, *Lepomis miniatus* (as *Sclerotis miniatus*), and *Lepomis macrochirus* (as *Helioperca macrochira*) Reelfoot Lake, TN, USA [36]; *Pseudobranchus axanthus*, Gainesville, FL, USA [37]; *Lithobates heckscheri* (as *Rana heckscheri*) Newnans Lake, FL, USA [37]; *A. calva*, Kankaee River, ID, USA (originally collected by Wilson but reported in [38]); *A. calva*, Wisconsin, USA [39]; host not recorded, Lake Erie, OH, USA [32]; *A. calva*, Lake Creek, Little Grassy Creek, and LaRue Marsh, all IL, USA [33]; *A. calva*, Dorcheat Bayou, AR, USA [40]; *A. calva*, Cumbest Bluff, Pascagoula River, MS, USA (this study).

  Measurements: Based on 2 males and 3 gravid females (Figure 3). Total length (mm) 6.06 (5.89–6.23) in males, 6.63 (5.23–8.94) in females. Carapace length (CL; mm) 4.20 (3.73–4.66) in males, 5.40 (4.20–7.40) in females; maximum carapace width (mm) 3.80 (3.28–4.32) in males, 4.89 (3.76–6.93) in females. Carapace posterior sinus length (mm) 1.17 (1.04–1.28) in males representing 28% (27–28%) CL, 1.75 (1.11–2.92) in females representing 31% (27–39%) CL; width at midpoint of sinus 429 (n = 1) in male, 598 (315–823) in females. Cephalothorax length (mm) 2.37 (2.10–2.64) in males, 2.93 (2.28–3.98) in females; anterior width (mm) 1.78 (1.51–2.05) in males, 2.34 (1.74–3.18) in females. Abdomen length (AL; mm) 1.49 (1.26–1.72) in males, 1.63 (1.27–2.26) in females; maximum width 1.90 (1.66–2.13) in males, 2.13 (1.87–2.61) in females. Abdomen posterior sinus length 390 (319–460) in males representing 26% (25–27%) of AL, 435 (376–493) in females representing 33% (28–39%) of AL; width at midpoint of sinus 100 (98–102) in males, 104 (96–112) in females. Eye diameter 166 (155–176) sinistral and 156 (148–164) dextral in males, 193 (164–247) sinistral and 179 (151–228) dextral in females; transverse distance 731 (625–836) in males, 942 (720–1297) in females. Maxillules outer diameter 513 (458–568) in males, 807 (569–1187) in females; inner diameter 376 (328–424) in males, 584 (380–884) in females; number of support rods 45 in males, 43–45 in females. Number of sclerites per support rod 2 in both sexes.

  Sequences deposited: GenBank accession number MN688128 based on one individual.

  Material deposited: 1 hologenophore (GCRLM 06603) and 4 additional vouchers (GCRLM 06603) from *Amia calva*.

  Remarks. Our specimens correspond well with the descriptions by Wilson [41] and Meehean [7]. The hooks, spines, and teeth of the antenna, antennule, and maxillae all have darkened distal tips (more prominent in non-cleared individuals), likely indicating thicker or hardened chitin (Figure 3C,E). Wilson [41] described a small, round knob on the ventral side of the basis of the third thoracopod and a knob ventral to the peg on the fourth thoracopod. In our specimens, we observed fine scales circumventing each of these knobs. Our male specimens have a series of 5 dark blotches around the periphery of each side of the carapace (Figure 3A). Bowfin are by far the most commonly reported host for *A. americanus* based on host records and likely represents the natural host for this species.
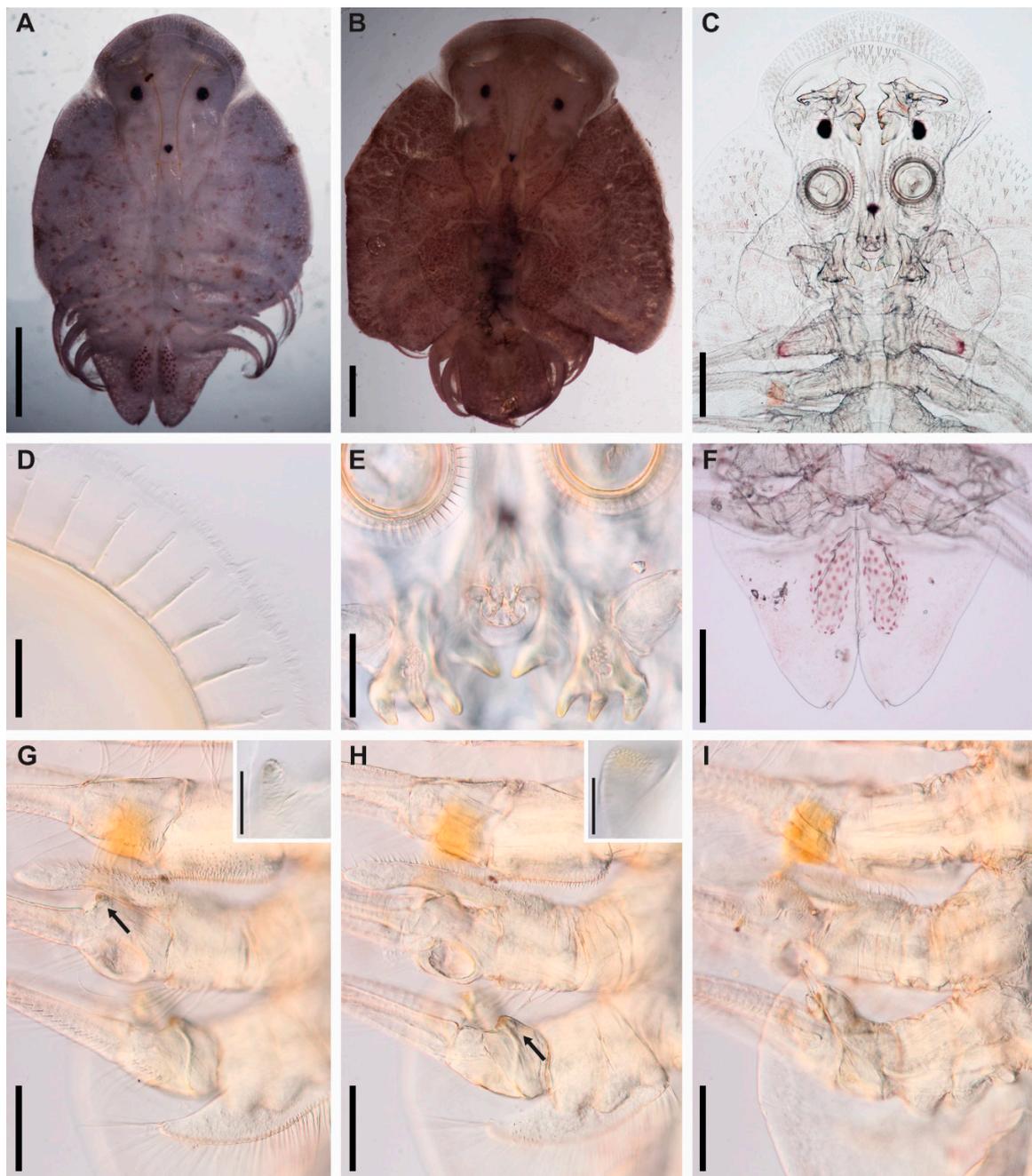
Figure 3. Photomicrographs of *Argulus americanus* Wilson, 1902. (**A**) Male, dorsal view, not cleared. (**B**) Female, dorsal view, not cleared. (**C**) Anterior of male, ventral view, cleared. (**D**) Sclerites of support rods in maxillule. (**E**) Mouth and basal plates of maxillae. (**F**) Abdomen of male. (**G**) Ventral plain of male thoracopods 2–4; insert shows knob on the ventral side of the third leg. (**H**). Middle plain of male thoracopods 2–4; insert shows knob ventral to peg on the fourth leg. (**I**) Dorsal plain of male thoracopods 2–4. Scale bar = 1 mm (**A,B**), 500 µm (**C,F**), 250 µm (**E,G–I**), 50 µm (**D**, inserts).

3.3. Argulus bicolor Bere, 1936

Type host: Strongylura notata.
Type locality: Lemon Bay, FL, USA.
Other hosts and locations: *Archosargus rhomboidalis* (as *Archosargus unimaculatus*), Lemon Bay, FL [42]; *Rhinoptera* sp., *Dorosoma* sp., *Scomberomorus* sp. (as *Scomboromorus* sp.), *Gobionellus* sp., *Strongylura* sp., *Morone* sp., and *Micropogonias* sp. (as *Micropogon* sp.) southeast coast of USA from

North Carolina to Louisiana [31]; *Morone saxatilis*, Chesapeake Bay, USA [43]; *Trachinotus carolinus*, Gulf of Mexico, Texas coast, USA; *Hypanus sabinus*, Pascagoula River Estuary, Mississippi, USA (this study).

Measurements: Based 1 gravid female (Figure 4). Total length (mm) 5.35. Carapace length (CL; mm) 3.19; maximum carapace width (mm) 2.19. Carapace posterior sinus length 909 representing 29%; width at midpoint of sinus 552. Cephalothorax length (mm) 1.63; anterior width (mm) 1.18. Abdomen length (AL; mm) 1.68; maximum width 1.12. Abdomen posterior sinus length 877 representing 52% of AL; width at midpoint of sinus 229. Eye diameter 271 sinistral and 272 dextral; transverse distance 450. Maxillules outer diameter 642; inner diameter 419; number of support rods 60. Number of sclerites per support rod 9.

Sequences deposited: GenBank accession number MN688129 based on one individual.

Material deposited: 1 hologenophore (GCRLM 06603) from Atlantic stingray.

Remarks. Our single specimen matched the description of the female for this species, but is slightly longer and the color of the carapace is cream yellow rather than greyish green. This species has been reported from numerous hosts, including some that are diadromous, estuarine residents, estuarine transients, and somewhat strict marine species. Our report of a single female on Atlantic stingray is the second host record of *A. bicolor* for a myliobatiform.
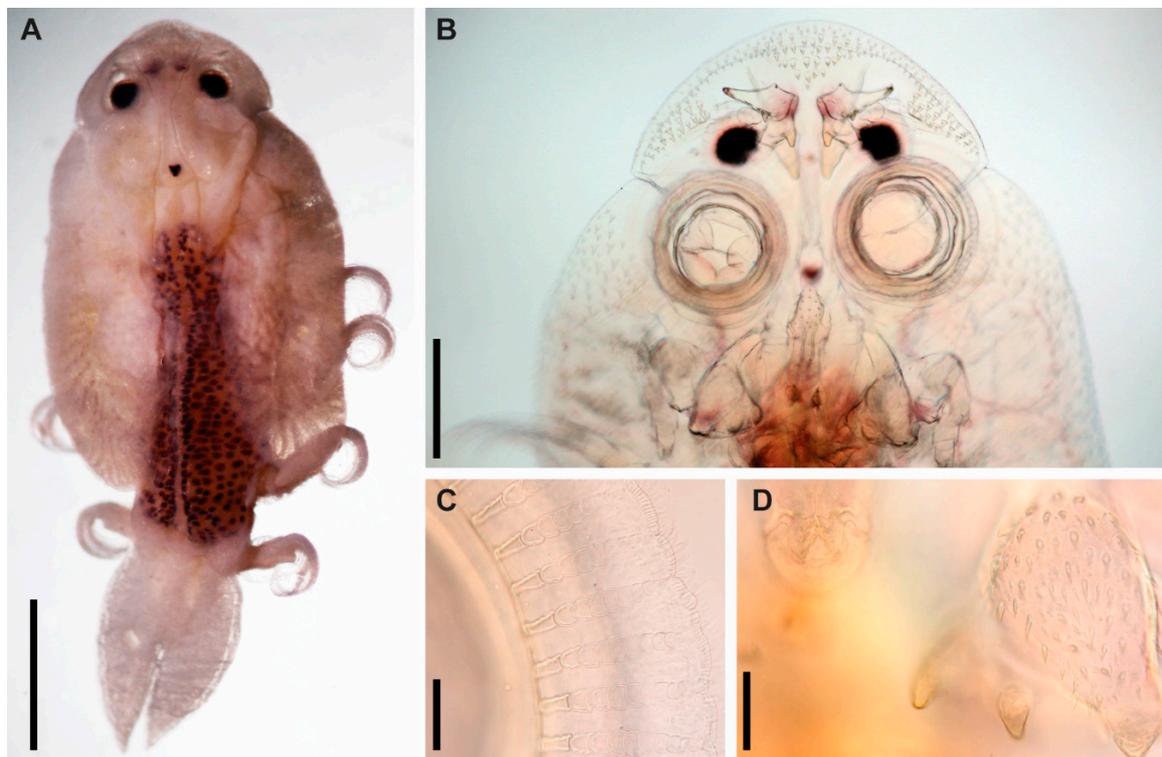

Figure 4. Photomicrographs of female *Argulus bicolor* Bere, 1936. (**A**) Dorsal view, not cleared. (**B**) Anterior, ventral view; note spines at base of mouth tube. (**C**) Sclerites of support rods in maxillule. (**D**) Mouth and basal plate of maxilla. Scale bar = 1 cm (**A**), 500 μm (**B**), 100 μm (**D**), 50 μm (**C**).

3.4. Molecular Results

The 790 bp 28S sequence data for *A. flavescens* had low intraspecific variation (Table 3) and were nearly identical to two sequences deposited for *Argulus* sp. in GenBank (AY210804 and AF363322). The 650 bp 28S sequence for *A. americanus* was slightly more similar to that of *A. foliaceus* (EU370442) than *A. flavescens*. The 651 bp 28S sequence of *A. bicolor* (the only marine species with sequence data) was the most dissimilar compared with the other sequences from freshwater species.

Table 3. Pairwise comparisons (excluding gaps) of percent nucleotide difference and number of base pair differences (in parentheses) for the 28S of species of *Argulus*. n = number sequenced for this study.

Species	n	*Argulus* sp. AY210804	*Argulus* sp. AF363322	*A. americanus*	*A. bicolor*	*A. foliaceus* EU370442
A. flavescens	13	0.0–0.3 (0–2)	0.0–0.4 (0–3)	4.4 (26–28)	7.4–7.6 (43–48)	5.2–5.6 (45–38)
A. americanus	1	4.3 (28)	4.5 (29)	–	7.8 (50)	3.4 (22)
A. bicolor	1	7.4 (47)	7.6 (48)	–	–	7.1 (45)
A. foliaceus EU370442	–	5.0 (36)	5.2 (39)	–	–	–

3.5. Ecology of Argulus flavescens

Of the 209 total Gulf sturgeon captured, 148 (70.8%) were parasitized by *A. flavescens*. Gulf sturgeon were infested with between 1 and 64 individual *A. flavescens* (Figure 5). Prevalence increased with host length (χ^2 = 36.52; $p < 0.001$) with adults having the highest prevalence and juveniles having the lowest (Figure 6A). Prevalence differed by location (χ^2 = 29.19; $p < 0.001$) with the lowest value in the PRE and all upstream locations being relatively similar (Figure 6B). Prevalence also differed among years (χ^2 = 11.12; $p < 0.011$), with 2017 being the lowest (51.2%) and 2018 being the highest (Figure 6C).
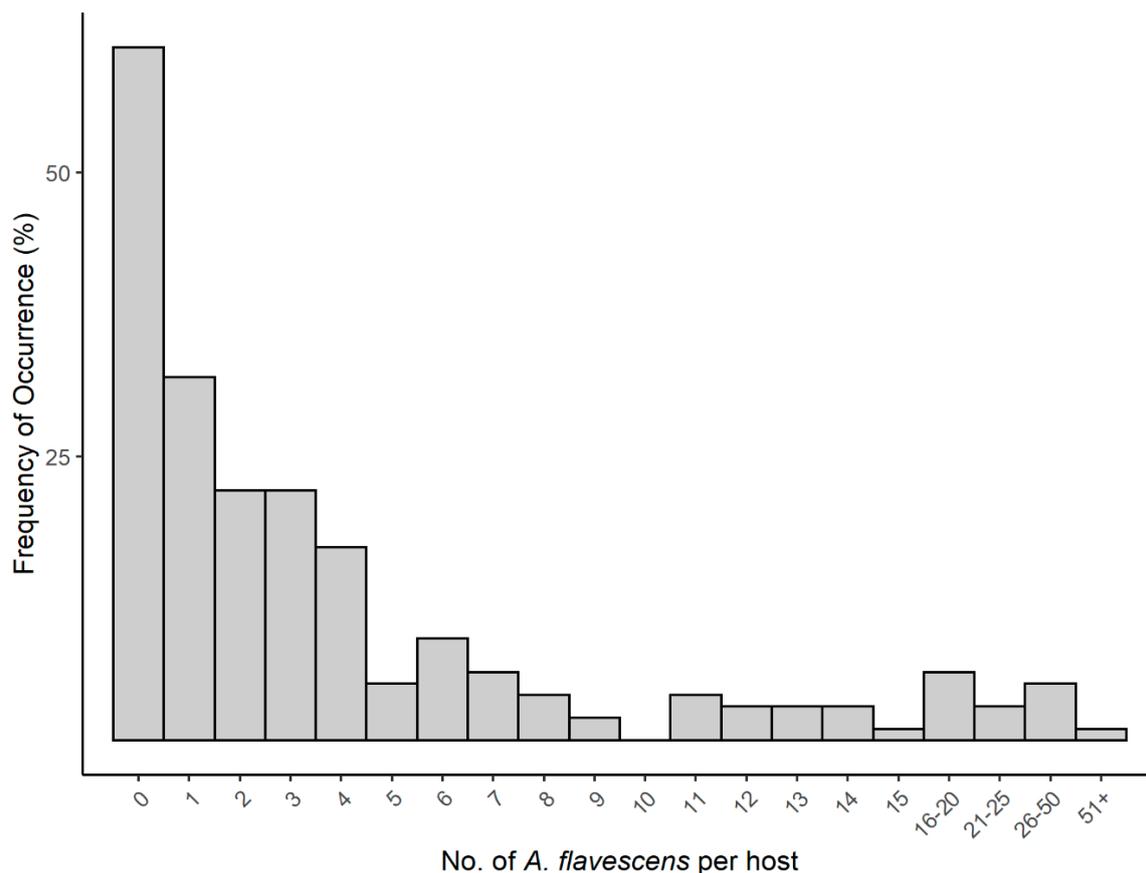

Figure 5. Frequency distribution of *Argulus flavescens* from individual Gulf sturgeon from the Pascagoula River from 2016–2019.
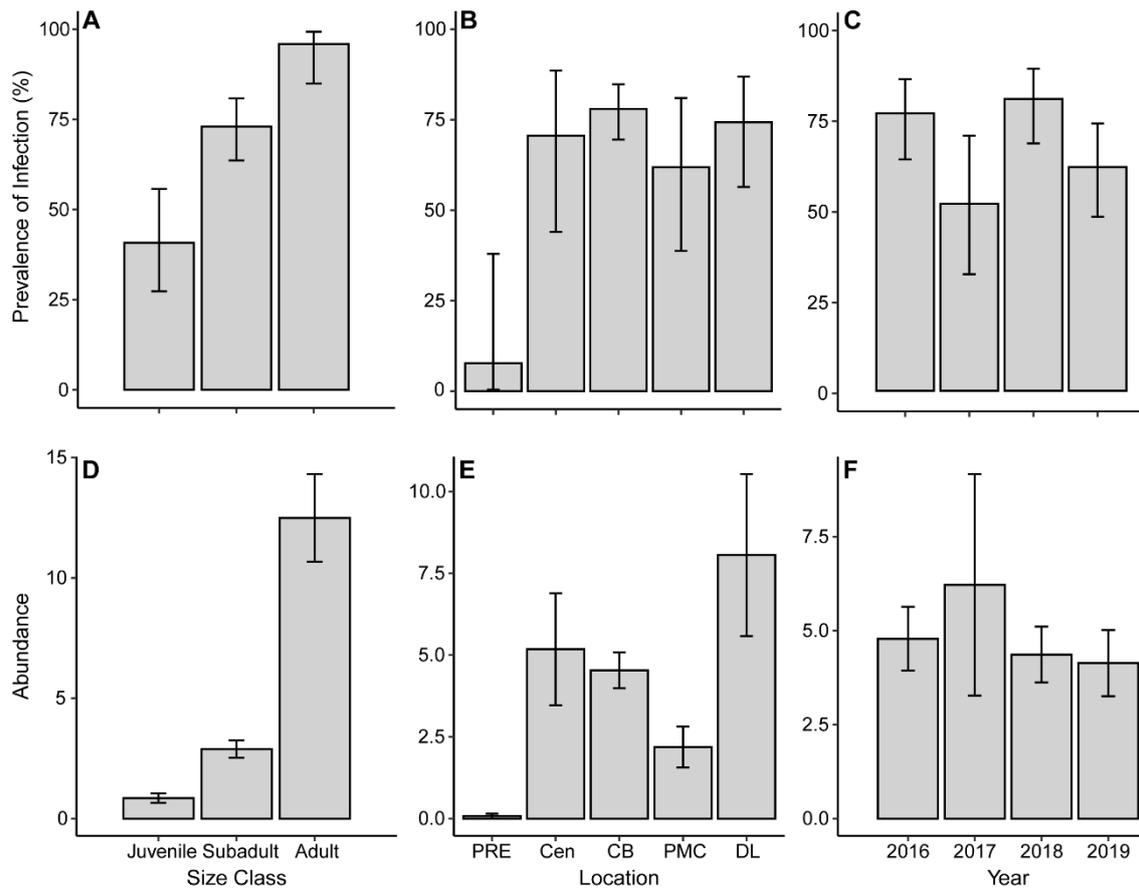
Figure 6. Prevalence (± 95%CI; top row) and abundance (mean ± SE; bottom row) of *Argulus flavescens* on Gulf sturgeon from the Pascagoula River among host size classes (**A,D**), sampling location ((**B,E**); furthest downstream on the left and furthest upstream on the right), and sampling year (**C,F**). Abbreviations PRE: Pascagoula River Estuary; Cen: Census site; CB: Cumbest Bluff; PMC: Paper Mill Camp; DL: Dead Lake.

Our negative binomial GLM used to test if FL, rkm, condition, and year of collection influenced the abundance of *A. flavescens* on Gulf sturgeon indicated that both FL and rkm significantly influenced abundance (Table 4). *Argulus flavescens* was more abundant (Figure 6D) on adult Gulf sturgeon rather than subadults and juveniles. Abundance increased with increasing rkm (from the estuary to the northern most holding area; Figure 6E). Neither year (Figure 6F) nor condition influenced the abundance of *A. flavescens*. The abundance of *A. flavescens* infesting Gulf sturgeon from the three holding areas and the census site did not differ ($\chi^2 = 3.46$; $p = 0.33$).

Table 4. Results of the negative binomial generalized linear model to test the effects of fork length (FL), river kilometer (rkm), condition (Fulton's K), and year of collection on the abundance for *Argulus flavescens* of Gulf sturgeon in the Pascagoula River. Values in bold indicate statistically significant effects at $\alpha < 0.05$.

Variable	Estimate	SE	Z	Pr (>|Z|)
Intercept	276.524	143.135	1.932	0.053
FL (cm)	0.027	0.004	6.702	**<0.001**
rkm	0.020	0.007	2.875	**0.004**
Condition	1.755	1.103	1.591	0.112
Year	−0.139	0.071	−1.956	0.051

4. Discussion

Our study represents the first attempt to describe the argulid fauna of some fishes from the Pascagoula River; however, this attempt still has only occurred within the light of host species incidentally caught while targeting Gulf sturgeon. Beginning in 2018 (as time permitted) we began inspecting additional fish species (see Table 2) for argulids; however, none were found on any hosts other than Atlantic stingray, bowfin, and flathead catfish. In other systems argulids have been reported from longnose gar (five species of *Argulus* see [4]), southern flounder [9], and gizzard shad (at least two species of *Argulus* [27,44]), so it is somewhat surprising that we did not detect any individuals on these hosts. Therefore, a more thorough and systematic approach to documenting the diversity of argulids in the Pascagoula River is needed to determine other host associations. The Pascagoula River is the largest river in the conterminous USA with no dams or other major impediments on the main stem of the river [45]; therefore, this system further provides a great opportunity to study argulid-host interactions in a minimally altered river.

Few argulid species have representative sequence data [2,4,46], which is remarkable given how common argulids occur in both wild and aquaculture settings and as specious as the family is. Our attempts to sequence the COI using the primers in [46] were unsuccessful, but our 28S sequence data resolved two unidentified species of *Argulus* with sequence data (Table 4) as *A. flavescens*. Additionally, our results may hint at the potential of two argulid clades; a freshwater clade and a marine one. The 28S sequence of *A. bicolor* was more dissimilar to the three freshwater species than any of the freshwater species were to one another. This potential relationship is interesting for three reasons. First, the distribution of *A. bicolor* (coastal southeastern USA [7,9,31]) overlaps with that of *A. flavescens* (Mississippi River system and southeastern USA, including coastal waters [7,31]). Second, the host list for *A. bicolor* includes estuarine and anadromous species similar to the host list for *A. flavescens*. Finally, *A. foliaceus* is a Palearctic species whereas all others are Nearctic species [4]. As more sequence data become available for additional argulids, others will be able to more fully test the hypothesis of distinct marine and freshwater clades in a phylogenetic context.

We clearly demonstrated differences in host use patterns for *A. flavescens* on Gulf sturgeon with adult sturgeon having both a more prevalent and more intense infestation relative to subadults and juveniles. Previous studies have documented an increase in parasite abundance (and biomass) with an increase in host size (and biomass) for fishes and mammals (especially those that are ectoparasites) [47–50]. For *A. flavescens* and Gulf sturgeon this could simply be related to an increase in available space in and around the mouth of adult fish relative to subadults and juveniles [50]. However, there are potentially several other explanations that help explain this relationship. Argulids are free swimming ectoparasites that must swim to attach to a host; therefore, a bigger fish presumably offers a larger target for attachment. Additionally, bigger fish produce larger wakes than small fish [51] that may decrease water flow around them thereby reducing the risk of the parasite being distributed downstream [52]. The water of the Pascagoula River is also very turbid and a bigger fish would also cast a larger shadow than a smaller fish that may help *A. flavescens* ambush it during daylight hours [53]. Finally, a strict trophic trade off may occur. Adult Gulf sturgeon make migrations further offshore and to the barrier islands [10] along the north-central Gulf of Mexico whereas juveniles and subadults make shorter migrations and stay nearer estuarine waters [54]. Therefore, adult Gulf sturgeon may represent higher quality hosts relative to that of the other size classes (or other freshwater hosts such as flathead catfish) in that adult Gulf sturgeon potentially have more energy reserves and marine derived fatty acids that may help promote reproductive success for *A. flavescens* (as has been shown for other maxillopodans [55]).

We found an overall decrease in prevalence and abundance of *A. flavescens* on Gulf sturgeon in the PRE relative to four riverine habitats, but we did not see any differences in abundance between upstream locations, including the Census site (CS) and the Gulf sturgeon holding areas (areas where sturgeon congregate from Spring through Fall months). The flathead catfish, which like Gulf sturgeon is another demersal species, is the only other host for *A. flavescens* we found. Based on catch data,

Cumbest Bluff appears to be the Gulf sturgeon holding area with the most use (Table 1) and is also the sampling location where we caught the most flathead catfish (Table 2). Flathead catfish have small home ranges (<5 rkm) in winter months and during the Summer–Fall months [56,57] when Gulf sturgeon are occupying holding areas; therefore, we postulate that flathead catfish may help maintain year round infestations of *A. flavescens* in the Pascagoula River.

Our observations show that Gulf sturgeon lose their *A. flavescens* infestation once they migrate to estuarine and marine waters, which indicates that this species may not tolerate salinity. We suggest the argulid reported by Suárez-Morales et al. [35] from *Ariopsis assimilis* off Chetumal, Mexico represents a different species. The host list provided by Cressey [31] included the estuarine genera *Hypanus* sp., *Paralichthyes* sp., and *Mugil* sp. Presumably the species representing those genera are the Atlantic stingray, *H. sabinus*, the southern flounder, *P. lethostigma*, and the flathead grey mullet, *M. cephalus*, because they are the most common species in those genera found in the nearshore waters of the Gulf of Mexico. All three of those species are euryhaline with some populations being functionally diadromous [58,59]. Since 2016 we have caught one Atlantic stingray and three southern flounder north of the CS (rkm 26) and have seen many mullets jumping north of the CS. Therefore, it is possible that these species acquire an infestation in the river and retain it as they migrate back to estuarine waters, or perhaps the argulids reported by Cressey [31] on these estuarine hosts represent a different species.

Prevalence differed by year with the lowest prevalence in 2017, but abundance did not differ among years. For much of the Fall of 2017 the Pascagoula River experienced increased flow relative to 2016, 2018, and 2019. This resulted in fewer Gulf sturgeon captured, but could have also prevented *A. flavescens* from finding and attaching to Gulf sturgeon since the increased flow may have dispersed the parasites downstream or made swimming more difficult [52].

The parasites of Atlantic sturgeon, *Acipenser oxyrinchus oxyrinchus*, have been better studied [60–62] than those of the Gulf sturgeon, including one report of *Argulus coregoni* Thorell, 1865 from the St. Johns River, Canada [62] although with a much lower prevalence. Atlantic sturgeon follow a more traditional anadromous pattern, with only spawning adults returning to freshwater habitats after they migrate to estuarine and marine waters [63], thereby reducing the window for acquiring an argulid infestation in freshwater. Three other species of *Argulus* have been reported from sturgeon in North America; *Argulus alosae* Gould, 1841 a marine species from the diadromous, shortnose sturgeon, *Acipenser brevirostrum*, *Argulus canadensis* Wilson, 1916 from the lake sturgeon, *Acipenser fulvescens* (as *A. rubicundus*) [27], and *Argulus stizostethii* Kellicott, 1880 also from the lake sturgeon [44]. This study represented the first account of an argulid from Gulf sturgeon and the first to describe the ecology of any argulid from the Pascagoula River system. One behavior of Gulf sturgeon that is well documented is their tendency to jump out of the water (particularly when in holding areas) [10,64], one suggested reason for this jumping behavior is to help shed parasites. Based on the site of infestation of *A. flavescens* being the mouth and mouth folds of Gulf sturgeon, we find it highly unlikely that jumping would help with parasite shedding.

Appendix A

Number of Gulf sturgeon collected at each location by month per year. Not all locations were fished in each month (denoted by a dash). All sampling in the estuary occurred when Gulf sturgeon were expected to be in the estuary (Nov.–early Jun.) and all sampling occurred in the holding areas (Cumbest Bluff, Paper Mill Camp, and Dead Lake) from late June–October. Sampling at the census site

	Estuary	Census Site	Cumbest Bluff	Paper Mill Camp	Dead Lake
2016					
June	-	-	1	-	-
July	-	-	-	-	-
August	-	-	-	-	-
September	-	-	15	1	8
October	-	16	20	-	-
November	-	-	-	-	-
2017					
June	-	-	-	-	-
July	-	-	-	-	-
August	-	-	-	-	-
September	-	-	1	7	13
October	-	0	4	0	-
November	2	-	-	-	-
2018					
June	-	-	4	-	-
July	-	-	-	-	5
August	-	-	10	-	3
September	-	-	-	-	-
October	-	0	33	6	0
November	1	1	-	-	-
2019					
April	1	-	-	-	-
May	5	-	-	-	-
June	4	-	5	-	-
July	-	-	-	-	6
August	-	-	14	-	-
September	-	-	16	7	-

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