



Reproductive Ecology of Dragonfishes (Stomiiformes: Stomiidae) in the Gulf of Mexico

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The most abundant fishes on Earth live in the meso- and bathypelagic (deep-pelagic, collectively) zones of the open ocean, where they play a key role in deep-sea food webs by mediating energy flow from surface waters to great depth. Of these fishes, the most speciose taxon is the family Stomiidae (dragonfishes). Despite being the numerically dominant predators of the global mesopelagic zone, stomiid reproductive ecology is poorly known. Research surveys rarely catch larger adults, impeding reproductive ecology studies. Between 2010 and 2011, the Offshore Nekton Sampling and Analysis Program sampled the Gulf of Mexico using a research-sized, opening/closing trawl (10-m² MOCNESS) and a commercial-sized, high-speed rope trawl (HSRT). Size-distribution analysis by gear type revealed: the HSRT caught more specimens per species, and the HSRT caught significantly larger specimens, whereas the MOCNESS sampled more juveniles. Gonads were dissected from 714 individuals representing 47 species, and the 12 dominant species were analyzed in further detail. Gonadal histology assessment indicated that stomiids are gonochoristic and exhibit asynchronous oocyte development and batch spawning. A total of 11 of the 12 species had sex ratios that did not significantly differ from a 1:1 (male:female) ratio ($P < 0.05$). Histological analysis indicated that females mature at larger sizes than males. Given the lack of age and growth data for this family, these data are critical for estimating stomiid production rates, a key element for quantifying the role of stomiids in the transfer of organic matter within the deep-pelagic zone, the planet's largest cumulative ecosystem.

Keywords: Stomiidae, reproduction, mesopelagic, sex ratio, gonad histology, maturity, size distributions

INTRODUCTION

Mesopelagic (200–1,000 m depth) fishes comprise the majority of Earth's fish biomass (Irigoiien et al., 2014; Nelson et al., 2016). A study by Gjøsæter and Kawaguchi (1980) used trawl catch data to estimate the global aggregate biomass of mesopelagic fishes to be 1×10^9 tons. However, the authors also indicated that this number was likely an underestimate due to trawl avoidance (most research-sized nets are relatively small compared to commercial nets) and extrusion (specimens passing through the meshes of larger, commercial-sized trawls) (Kashkin and Parin, 1983). More recent studies based on modeling and acoustic data (Koslow et al., 1997; Kaartvedt et al., 2012) suggest the global biomass to be significantly higher than earlier estimates; for example, the biomass of mesopelagic fishes between 40°N and 40°S alone is estimated to be at least an order of magnitude

higher, between 7 and 10 billion metric tons (Koslow et al., 1997; Kaartvedt et al., 2012; Irigoien et al., 2014). Given their high abundance and biomass, mesopelagic fishes likely play a significant role in global, deep-pelagic food webs.

The most speciose family of mesopelagic fishes (305 valid species; Fricke et al., 2018a) is the Stomiidae (*sensu* Fink, 1985), collectively including the snaggletooths (Astronesthinae), viperfishes (Chauliodontinae), black dragonfishes (Idiacanthinae), loosejaws (Malacosteinae), scaleless black dragonfishes (Melanostomiinae), and scaly dragonfishes (Stomiinae). These predatory fishes inhabit all oceans, including the Southern Ocean (Gibbs, 1969; Fink, 1985; Kenaley, 2007), and while they predominantly occupy the mesopelagic zone, evidence indicates that some species thrive in the deeper waters of the bathypelagic (1,000–4,000 m depth) zone (Gibbs, 1969; Childress et al., 1980). Ecologically, stomiids play an important role in deep-sea ecosystems because they are trophic mediators and link surface waters to those of the deep-pelagic. Most stomiids are vertical migrators and migrate to the epipelagic (0–200 m depth) zone at night to feed on the heightened influx of lanternfishes (Myctophidae), the primary fish zooplanktivores in most oceanic food webs (Clarke, 1974; Hopkins and Gartner, 1992). By bringing carbon fixed in the surface waters to their deeper daytime depth ranges, stomiids regulate deep-sea energy flow and play a vital role in the interzonal transfer of energy between the epipelagic, mesopelagic, and bathypelagic zones (Sutton and Hopkins, 1996a).

Quantifying carbon flow through mesopelagic systems requires an estimate of fish biomass and production, which in turn requires data on reproduction. Although aspects of stomiid feeding ecology have been quantified (Clarke, 1982; Sutton and Hopkins, 1996a; Butler et al., 2001; Kenaley, 2012), the data gap regarding their reproductive ecology remains, a consequence of insufficient sample sizes of adults due to the type of gear commonly used to collect specimens. Larger, sexually mature stomiids are likely more adept at net avoidance than smaller juveniles (Clarke, 1974; Fisher and Pearcy, 1983; Sutton and Hopkins, 1996b), thereby impeding synoptic studies of reproductive biology. However, hermaphroditism is known to occur in Gonostomatidae, a sister taxon in the Stomiiformes. Reproductive information is a key component of bioenergetics modeling, which takes into account the productivity of species and is frequently applied to several areas of study such as predator-prey interactions and ecosystem modeling (Hansen et al., 1993). Each of these areas requires knowledge about the reproduction of its component species. In this paper, we utilize one of the largest sets of deep-pelagic samples, one that utilized two complementary gear types to sample both juveniles and large adults. By using samples obtained with a Multiple Opening/Closing Net and Environmental Sensing System (MOCNESS) midwater trawl, as well as a high-speed rope trawl (HSRT), we had an unprecedented opportunity to investigate stomiid reproductive ecology.

Anthropogenic events may significantly hinder the capacity for mesopelagic fishes to regulate energy flow in the deep sea because such events can create unfavorable conditions for growth

and survival. For example, repercussions of hydrocarbon toxicity on larval fishes due to catastrophes such as oil spills have been widely documented, including declines in productivity at the population level due to decreases in reproductive health (Brown et al., 1996; Short, 2003). The Gulf of Mexico is particularly relevant in this regard given the location, size, and duration of the *Deepwater Horizon* oil spill (DWHOS), which lasted from April–September 2010. In order to understand the impact of the DWHOS on deep-pelagic fishes and expand our knowledge base of important predators, the focus of this study was to quantify reproductive parameters and investigate reproductive life history characteristics of stomiids in the Gulf of Mexico. The following questions relating to stomiid reproductive ecology were investigated: (1) Are stomiids gonochoristic, like most teleosts, or hermaphroditic, like sister taxa in the order Stomiiformes? (2) What type of oocyte development and spawning pattern is exhibited by stomiids? (3) What are the sex ratios of stomiid species? and (4) What are the sizes at maturity for stomiids in the Gulf of Mexico? These results can be used to further investigations of the impact of anthropogenic events to deep-pelagic assemblages, as well as general studies on mesopelagic ecosystems and carbon flow.

MATERIALS AND METHODS

Sample Collection

A series of seven cruises was conducted in the Gulf of Mexico between 2010 and 2011 as part of the DWHOS Offshore Nekton Sampling and Analysis Program. A total of 1,600 trawl samples were collected at stations arranged in a grid pattern across the northern gulf, most of which were seaward of the 1,000-m isobath (**Figure 1**). All sampling occurred both day and night from the surface to 1,500 m depth using two gear types in order to catch a broad assortment of individual sizes and species.

During three cruise series, sampling was conducted with a six-net, 10-m² mouth area MOCNESS midwater trawl (Wiebe et al., 1985), with each net having a uniform mesh size of 3 mm (stretched). Each deployment produced up to five discrete-depth, quantitative samples; the sixth net was an oblique tow from the surface to 1,500 m and catches in this net were not processed quantitatively. Sampling occurred in each month from January–September 2011, and a total of 46 stations were sampled either twice (17 stations) or three times (29 stations) (**Figure 1A**). Additional sampling details can be found in Burdett et al. (2017) and (Sutton et al., 2020). On four additional cruises, specimens were collected using a HSRT (Dotson and Griffith, 1996) with an effective mouth area of 165.47 m² (Sutton & Mercier unpubl. data) and a graded mesh size (stretched) of 3.2 m at the mouth which tapered to 19 mm at the cod end. A total of 17 stations were sampled one to four times (**Figure 1B**), with each cruise lasting 3 weeks, between December 2010 and September 2011. Specimens used in this study were opportunistically selected from both gears to increase the size spectrum from juveniles to spawning-sized adults.

After capture and subsequent identification and data logging, all stomiid specimens were fixed in a 10% (v:v) formalin:seawater solution. Specimens were stored in formalin until sample

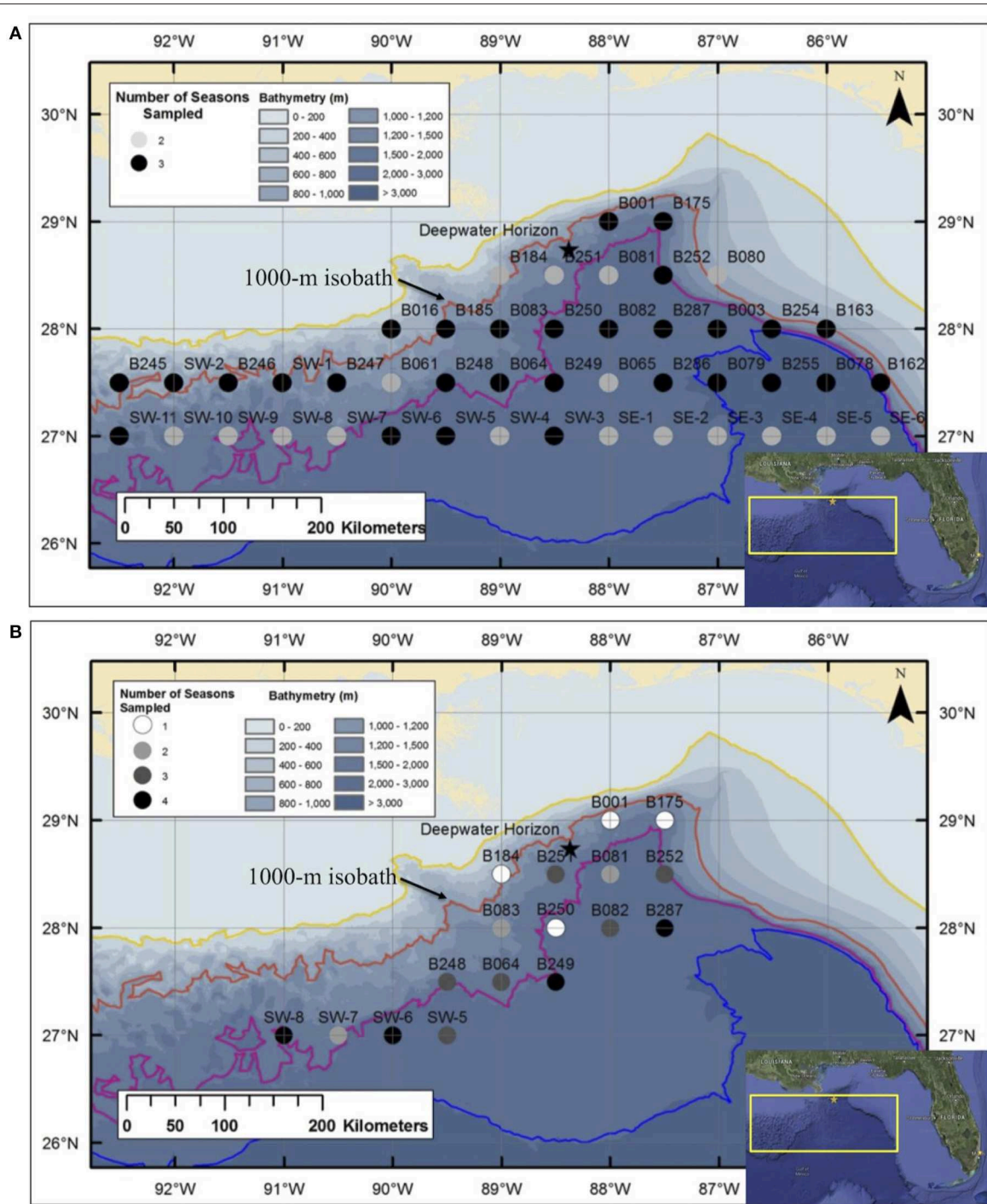


FIGURE 1 | Deepwater stations sampled in the Gulf of Mexico during: **(A)** *Meg Skansi 6*, *Meg Skansi 7*, and *Meg Skansi 8* cruises between January and September 2011; and **(B)** *Pisces 8*, *Pisces 9*, *Pisces 10*, and *Pisces 12* cruises between December 2010 and September 2011. All adjacent sampling stations were equidistant from each other by 30 nautical miles (55.6 km). Isobaths, from top to bottom, indicate depths of 200, 1,000, 2,000, and 3,000 m, respectively. The 1,000-m isobath is individually labeled for reference. The black star marks the site of the *Deepwater Horizon* oil spill that occurred between April and September 2010.

processing began back in the laboratory and were never transferred to alcohol after fixation. Just before they were processed, specimens were transferred to water to de-gas under

a fume hood. Specimens for this study were selected during sequential processing of trawl samples at the Nova Southeastern University Oceanic Ecology Laboratory. When practical, all

TABLE 1 | Cruise details from the 2010 to 2011 expeditions in the Gulf of Mexico and the total number of stomiid specimens from each cruise used in this study (N_{study}).

Cruise	Date	Sampling gear	N_{tows}	N_{samples}	Total stomiids	N_{study}
<i>Pisces</i> 8	1–20 Dec 2010	HSRT	37	37	2,915	75
<i>Meg Skansi</i> 6	27 Jan–31 Mar 2011	MOCNESS	65	270	901	19
<i>Pisces</i> 9	22 Mar–11 Apr 2011	HSRT	36	36	2,093	20
<i>Meg Skansi</i> 7	14 Apr–30 Jun 2011	MOCNESS	92	373	905	7
<i>Pisces</i> 10	21 Jun–14 Jul 2011	HSRT	48	48	4,510	61
<i>Meg Skansi</i> 8	18 Jul–30 Sep 2011	MOCNESS	95	445	765	95
<i>Pisces</i> 12	7–29 Sep 2011	HSRT	50	50	6,103	437
SUMMARY						
7 cruises	Dec 2010–Sep 2011		423	1,259	18,192	714

The total number of samples processed quantitatively (one tow yielded up to five samples on MOCNESS cruises, and one sample on HSRT cruises) is denoted by " N_{samples} ". HSRT, High-Speed Rope Trawl; MOCNESS, Multiple Opening/Closing Net and Environmental Sensing System.

specimens for each species collected on the seven cruises (Table 1) were used in this study. In cases of superfluous specimens, a subsample spanning the available size spectrum was chosen for the species.

Specimen Processing

Stomiid specimens were selected for reproductive analysis as they became available during a large-scale, quantitative taxonomic analysis program. Specimens were identified using the keys of Gibbs (1964a,b, 1969), Morrow (1964a,b,c), Morrow and Gibbs (1964), Barnett and Gibbs (1968), Goodyear and Gibbs (1969), Gibbs et al. (1983), Gomon and Gibbs (1985), Gibbs and McKinney (1988), Sutton and Hartel (2004), Kenaley and Hartel (2005), Kenaley (2007), and Flynn and Klepadlo (2012). Species were measured to the nearest 0.1 mm standard length (SL) and total wet weights were recorded to the nearest 0.01 g. Entire gonads were removed and the wet weight recorded to the nearest 0.001 g. All gonads were stored in 70% ethanol for at least 1 week prior to histological preparation.

Histology

Transverse subsections of 1–2 cm were removed from the middle of one lobe of the preserved gonads and dehydrated using an automated tissue processor before being embedded in paraffin. Gonadal tissue was cross-sectioned twice at 5 μm using a microtome, then mounted on glass microscope slides, rehydrated, stained with Harris's hematoxylin, and counterstained with eosin- γ with phloxine following routine histological procedures (Avwioro, 2011).

Histological sections were examined with a compound microscope as an aid in determining sex, as well as one of five reproductive phases. Without reference to body length or date of capture, tissue sections were classified as "immature," "developing," "spawning capable," "regressing," or "regenerating" following the criteria of Brown-Peterson et al. (2011). Based on key histological markers (type of spermatogenic cells present in males, type and size of oocytes in females), samples were classified as "mature" if they were in one of the four latter reproductive phases. Gonads that were underdeveloped and unable to be identified as male or female with certainty were

classified as "undifferentiated." Photomicrographs were taken of demonstrative samples to show key structures involved in the reproductive development of males (Figure 2) and females (Figure 3). Specimens ($N = 41$) in which the reproductive phase could not be determined unequivocally were not assigned a maturity phase and were excluded from analyses.

Statistical Analysis

All statistical analysis was performed using R 0.98.1062 (R Development Core Team, 2013) for the 12 dominant ($N \geq 19$ individuals) species, and results were considered significant at $P < 0.05$. Sex ratios were calculated using the total number of males to females, both immature and mature. Sex ratios were also calculated for only the mature males and females of each species. A Chi-Square Goodness of Fit Test was performed using the `chisq.test()` function to determine if the sex ratio of each species diverged from the expected ratio of 1:1 (male: female). All specimens identified as "undifferentiated" were incorporated only in size distribution analyses.

The size at 50% maturity (L_{50}) was estimated using the "MASS" package (Venables and Ripley, 2002) `glm()` and `dose.p()` functions for binomial regression to show the percentage of mature specimens as a function of 10-mm size class. In cases where complete model separation occurred (i.e., each size class had *only* immature specimens, or *only* mature specimens), size at maturity was determined to be the smallest mature specimen. Size at maturity, based on histological results, was used in conjunction with size distributions by gear type to extrapolate what portion of all measured specimens of each species caught during the seven cruises was immature or mature. Additionally, a t -test was used to assess gear selectivity by comparing the mean sizes of specimens collected with the MOCNESS and HSRT.

RESULTS

Sampling

In total, 714 specimens representing 47 stomiid species were examined, the majority of which (61%) were collected in the fall of 2011. Of the 714 specimens, 364 females, 318 males, and 32 undifferentiated specimens were identified. For the 12

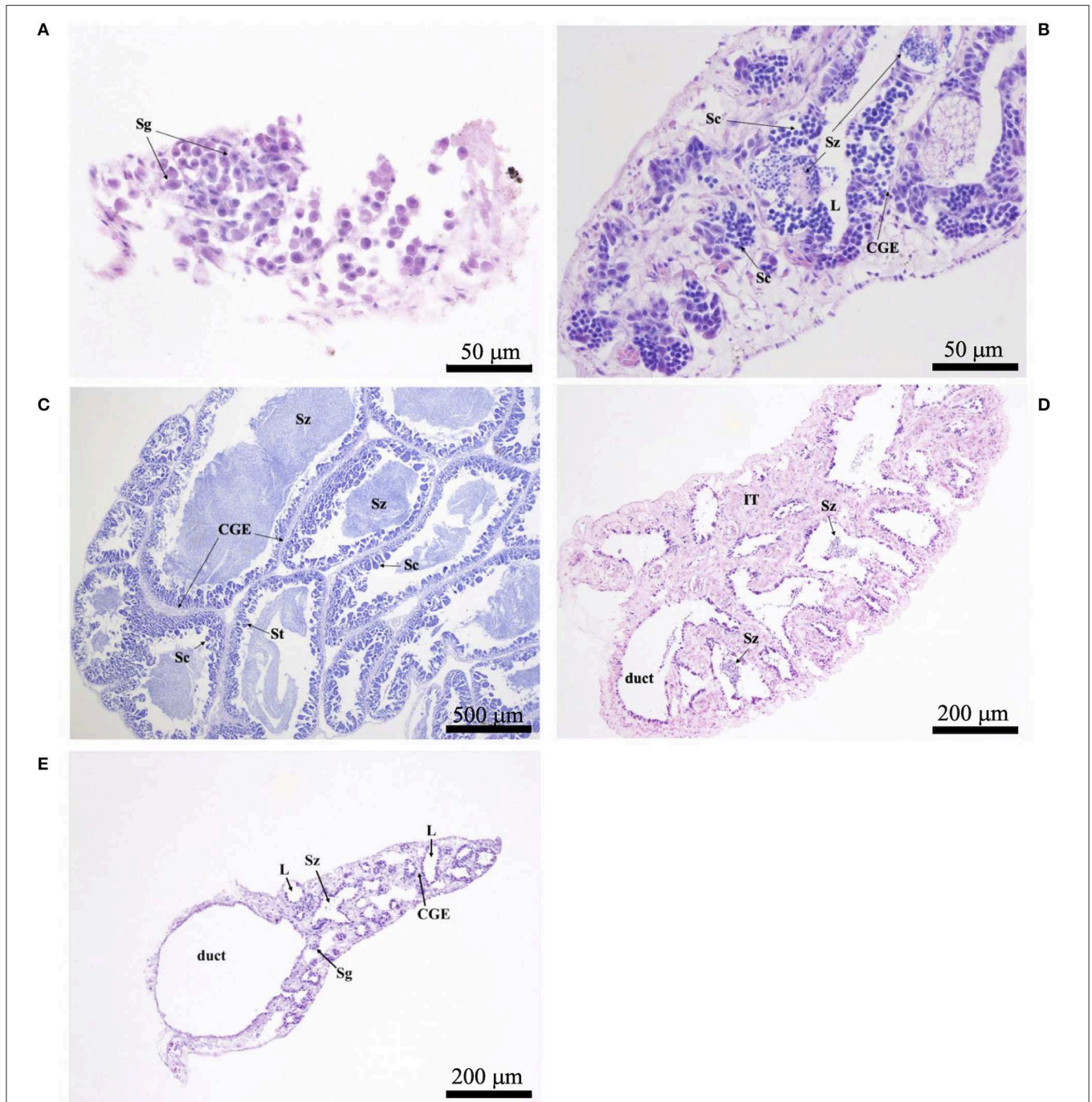
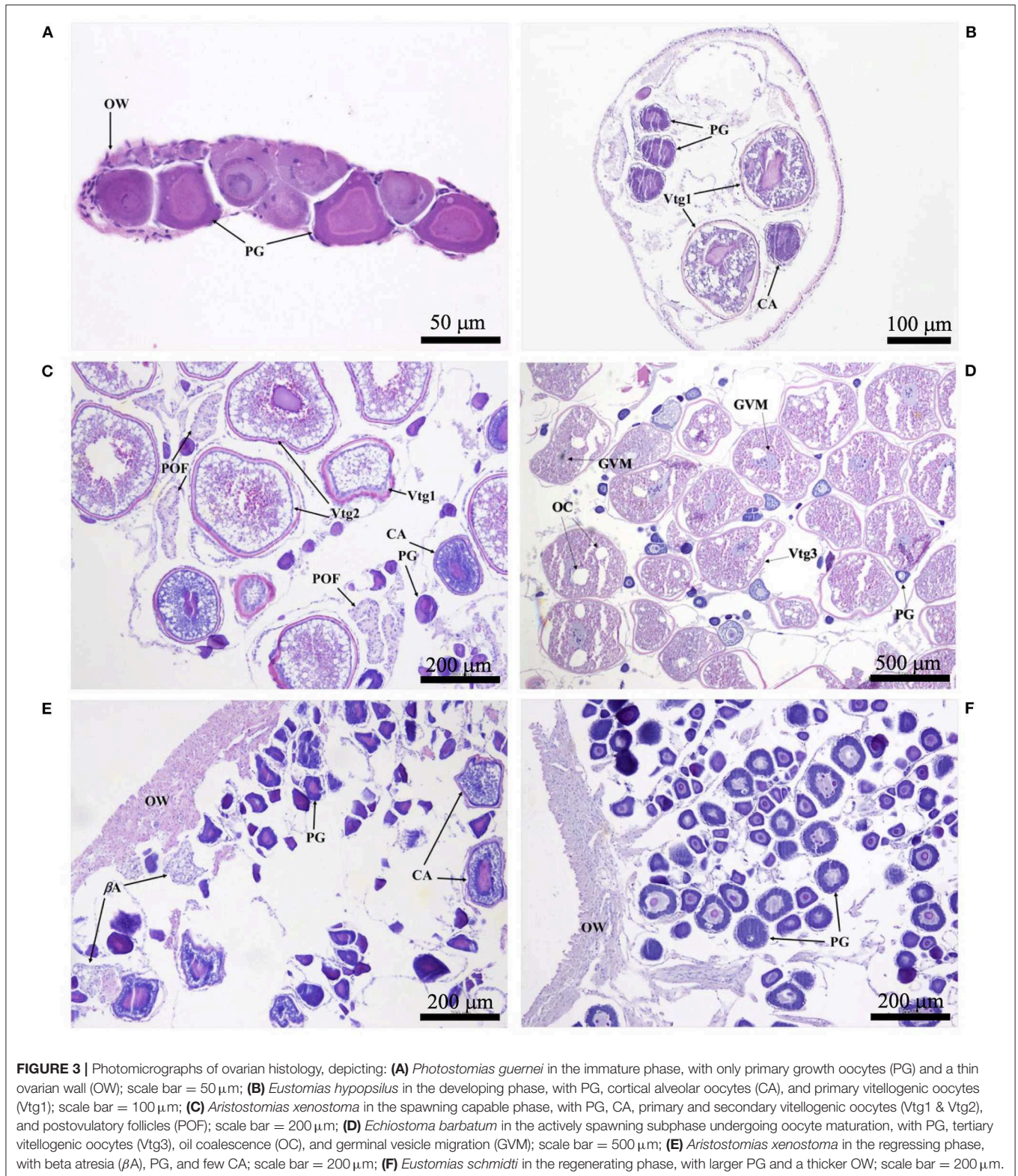


FIGURE 2 | Photomicrographs of testicular histology, depicting: **(A)** *Astronesthes atlanticus* in the immature phase, with only spermatogonia (Sg) in the testes; scale bar = 50 μm ; **(B)** *Melanostomias melanops* in the developing phase, with spermatocysts of spermatocytes (Sc), and cysts of spermatozoa (Sz) that have not yet entered the lobular lumina (L). Continuous germinal epithelium (CGE) present; scale bar = 50 μm ; **(C)** peripheral tissue of *Echiostoma barbatum* in the spawning capable phase, with Sc, spermatids (St), Sz, and CGE; scale bar = 500 μm ; **(D)** *Melanostomias melanops* in the regressing phase, with residual Sz in the lumina and duct; note the expanded interstitial (connective) tissue (IT); scale bar = 200 μm ; **(E)** *Echiostoma barbatum* in the regenerating phase, with residual Sz in some lobules, empty lumina (L), CGE, and Sg proliferation; scale bar = 200 μm .

dominant species, the size and weight compositions of female, male, and undifferentiated specimens sampled are shown in **Table 2**. Morphometric data for the less-abundant 35 species are presented in **Supplementary Table 1**.

Reproductive Strategy

No histological evidence of testicular and ovarian tissue was observed simultaneously in any stomiid gonad, indicating that stomiids are gonochoristic. Following the terminology of Grier



and Uribe (2009), male stomiids possess an unrestricted, lobular testicular structure. Histological assessment of the testes also indicates that males are able to spawn continuously, as evidenced

by the preponderance of spawning capable individuals (83%) and scarcity of individuals in the regressing and regenerating phases. In females, 25% of all specimens were spawning capable. Oocytes

TABLE 2 | Count, size range, mean standard length (SL), and standard deviation, range of wet weight, and mean wet weight and standard deviation of 12 dominant stomiid species collected in the Gulf of Mexico between 2010 and 2011.

Taxon	N	SL Range (mm)	Mean SL (mm)	Weight Range (g)	Mean Weight (g)
ASTRONESTHINAE					
<i>Astronesthes atlanticus</i> (Parin and Borodulina, 1996)	19				
Female	10	55.9–169.7	121.6 ± 31.0	1.31–28.74	15.26 ± 8.40
Male	9	95.3–149.8	122.7 ± 17.9	7.33–26.26	15.92 ± 6.57
<i>Astronesthes richardsoni</i> (Poey, 1852)	24				
Female	13	59.9–181.1	123.8 ± 41.6	1.00–40.09	15.37 ± 12.99
Male	8	72.7–154.5	122.1 ± 33.3	1.00–29.21	14.67 ± 10.30
Undifferentiated	3	63.0–83.5	70.0 ± 11.7	1.07–3.09	1.82 ± 1.11
<i>Astronesthes similis</i> (Parr, 1927)	22				
Female	12	57.6–121.1	79.0 ± 21.9	1.09–13.00	4.34 ± 4.42
Male	8	67.8–121.9	92.3 ± 21.1	2.03–10.68	6.08 ± 3.92
Undifferentiated	2	59.2–68.0	63.6 ± 6.2	1.24–1.78	1.51 ± 0.38
CHAULIODONTINAE					
<i>Chauliodus sloani</i> (Bloch and Schneider, 1801)	75				
Female	50	55.3–250.0	165.9 ± 58.4	0.40–47.24	15.00 ± 11.60
Male	24	68.1–200.0	160.6 ± 39.0	0.82–21.42	10.32 ± 6.11
Undifferentiated	1	69.9	69.9	0.59	0.59
MALACOSTEINAE					
<i>Aristostomias xenostoma</i> (Regan and Trewavas, 1930)	36				
Female	14	44.9–120.5	81.7 ± 19.9	0.50–14.73	4.45 ± 3.78
Male	22	48.5–117.3	85.5 ± 21.7	0.62–13.56	5.75 ± 4.39
<i>Malacosteus niger</i> (Ayres, 1848)	89				
Female	47	46.8–178.9	102.6 ± 34.5	0.45–53.40	9.02 ± 12.24
Male	41	51.8–117.3	87.9 ± 14.6	0.47–12.23	3.49 ± 2.24
Undifferentiated	1	48.8	48.8	0.33	0.33
<i>Photostomias guernei</i> (Collett, 1889)	73				
Female	39	46.0–116.4	85.8 ± 22.8	0.24–6.61	2.65 ± 1.93
Male	33	64.1–116.9	100.6 ± 13.6	0.92–5.87	3.39 ± 1.48
Undifferentiated	1	58.7	58.7	0.49	0.49
MELANOSTOMIINAE					
<i>Echistoma barbatum</i> (Lowe, 1843)	72				
Female	33	86.0–312.3	224.3 ± 74.2	4.01–240.54	95.16 ± 70.67
Male	35	83.2–276.5	224.1 ± 51.1	3.37–126.88	72.50 ± 36.18
Undifferentiated	4	77.6–92.7	84.7 ± 6.2	1.95–3.81	2.66 ± 0.82
<i>Eustomias fissibarbis</i> (Pappenheim, 1914)	21				
Female	11	66.7–170.0	112.7 ± 31.5	0.46–11.09	3.85 ± 3.28
Male	10	80.8–119.8	100.7 ± 10.7	0.88–3.85	1.95 ± 0.90
<i>Eustomias hypopsilus</i> (Gomon and Gibbs, 1985)	30				
Female	20	86.0–140.9	125.4 ± 13.3	0.59–3.50	1.79 ± 0.67
Male	10	109.3–119.6	115.2 ± 3.3	0.78–1.91	1.35 ± 0.37
<i>Eustomias schmidti</i> (Regan and Trewavas, 1930)	75				
Female	41	82.5–281.6	134.9 ± 56.6	0.67–123.33	12.77 ± 23.52
Male	27	77.0–152.4	114.1 ± 21.9	0.62–7.06	2.74 ± 1.86
Undifferentiated	7	77.5–92.0	83.7 ± 4.8	0.78–1.36	0.95 ± 0.20
<i>Melanostomias melanops</i> (Brauer, 1902)	26				
Female	14	92.3–206.9	159.5 ± 37.6	1.14–39.03	16.66 ± 13.45
Male	12	127.0–189.6	163.5 ± 20.3	5.37–22.28	13.66 ± 5.34

Species listed by subfamily and sex. Taxonomic authorities provided by Fricke et al. (2018b).

in all developmental stages, without dominant populations, were observed to be simultaneously present in the ovary, indicative of asynchronous oocyte development and batch spawning.

Through this type of oocyte development, stomiids either spawn more than once during each spawning season, or continuously throughout the year with no discrete spawning season.

TABLE 3 | Overall and mature sex ratios of 12 dominant stomiids in the Gulf of Mexico, listed by subfamily.

Taxon	Overall				Mature			
	<i>N</i>	Sex ratio (M:F)	χ^2	<i>P</i>	<i>N</i>	Sex ratio (M:F)	χ^2	<i>P</i>
ASTRONESTHINAE								
<i>Astronesthes atlanticus</i>		1:1.11	0.05	0.819		1:1	0	1
Female	10				8			
Male	9				8			
<i>Astronesthes richardsoni</i>		1:1.63	1.19	0.275		1:1.17	0.08	0.781
Female	13				7			
Male	8				6			
<i>Astronesthes similis</i>		1:1.5	0.80	0.371		1:0.43	1.60	0.206
Female	12				3			
Male	8				7			
CHAULIODONTINAE								
<i>Chauliodus sloani</i>		1:2.08	9.14	0.003		1:1.35	1.19	0.276
Female	50				31			
Male	24				23			
MALACOSTEINAE								
<i>Aristostomias xenostoma</i>		1:0.64	1.78	0.182		1:0.27	9.14	0.002
Female	14				6			
Male	22				22			
<i>Malacosteus niger</i>		1:1.15	0.41	0.522		1:0.44	8.64	0.003
Female	47				17			
Male	41				39			
<i>Photostomias guernei</i>		1:1.18	0.50	0.480		1:0.82	0.60	0.439
Female	39				27			
Male	33				33			
MELANOSTOMIINAE								
<i>Echiostoma barbatum</i>		1:0.94	0.06	0.808		1:0.67	2.0	0.157
Female	33				20			
Male	35				30			
<i>Eustomias fissibarbis</i>		1:1.1	0.05	0.827		1:0.20	5.33	0.021
Female	11				2			
Male	10				10			
<i>Eustomias hypopsilus</i>		1:2	3.33	0.068		1:1.60	1.38	0.239
Female	20				16			
Male	10				10			
<i>Eustomias schmidtii</i>		1:1.52	2.88	0.090		1:0.42	6.08	0.014
Female	41				11			
Male	27				26			
<i>Melanostomias melanops</i>		1:1.17	0.15	0.695		1:0.58	1.32	0.251
Female	14				7			
Male	12				12			

Calculated chi-square value (χ^2) and *P*-value (*P*) also presented, with degrees of freedom = 1.

Bolded values indicate species with sex ratios of statistical significance.

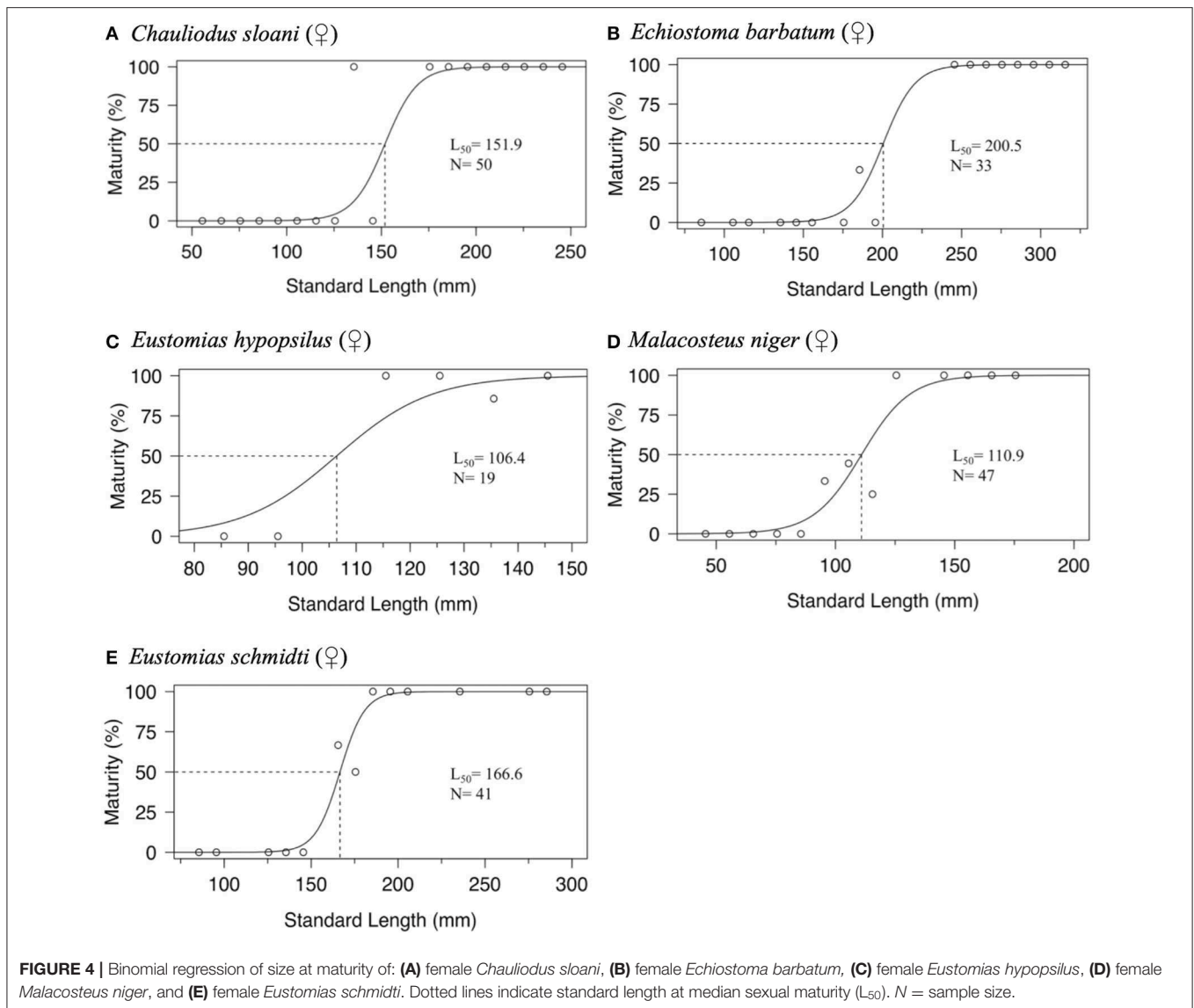
Sex Ratio

Chauliodus sloani was the only species in which the overall sex ratio (juveniles included) significantly differed from the expected 1:1 ratio; this species exhibited a sex ratio of 1:2.08, indicating a significant female bias ($P = 0.003$) (Table 3). When considering mature (adult) fish only, the observed sex ratio significantly favored males in the species *Aristostomias xenostoma*, *Eustomias fissibarbis*, *Eustomias schmidtii*, and

Malacosteus niger, presumably because males mature earlier than females (Table 3).

Size at Maturity

Maturity data were sufficient to estimate size at 50% maturity of five species using binomial regression. In increasing order, female size (SL) at 50% maturity was 106.4 mm in *Eustomias hypopsilus*, 110.9 mm in *Malacosteus niger*, 151.9 mm in *Chauliodus sloani*,



166.6 mm in *Eustomias schmidti*, and 200.5 mm in *Echiostoma barbatum* (Figure 4). In females of *E. hypopsilus*, the smallest mature specimen was larger than the estimated size at 50% maturity (Table 4) due to small sample size, especially in intermediate size classes.

Binomial regression was not appropriate for the remaining species either because there was not enough variation in the ratio of immature to mature specimens per size class, or because size classes were perfect predictors of maturity state (all specimens were either immature or mature in a given size class). No immature males of *Aristostomias xenostoma*, *Eustomias fissibarbis*, *Eustomias hypopsilus*, *Melanostomias melanops*, and *Photostomias guernei* were identified, and less than four specimens were classified as immature for *Astronesthes atlanticus*, *Astronesthes richardsoni*, *Astronesthes similis*, *Chauliodus sloani*, and *Malacosteus niger*. The length of the smallest mature specimen of each sex was considered the size at maturity in

species for which L_{50} could not be estimated. Specimen size at which the smallest mature individual was identified, as well as L_{50} and L_{99} , is presented in Table 4. Males reached maturity at smaller lengths than their female conspecifics in all 12 species.

Size Distributions

Size-frequency distributions are shown in Figure 5 for each of the 12 dominant species. Distributions were separated by gear type to demonstrate the differing size selectivity of the MOCNESS and HSRT. Two patterns emerged, both of which were observed for every species: the MOCNESS captured smaller juveniles more effectively than the HSRT (Figure 6; two sample t -test, $t = 42.3$, $P < <0.001$), and the HSRT caught more specimens per species. Superimposing the size at maturity based on histological data revealed a third pattern: the majority of specimens collected with the HSRT were mature.

TABLE 4 | Smallest size (standard length) at maturity, length at 50% maturity (L_{50}), and length at 99% maturity (L_{99}) of 12 dominant stomiids in the Gulf of Mexico, listed by subfamily, and sex.

Taxon	Sex	Smallest Mature (mm)	L_{50} (mm)	L_{99} (mm)
ASTRONESTHINAE				
<i>Astronesthes atlanticus</i>	Female	109.1	–	–
	Male	106.7	–	–
<i>Astronesthes richardsoni</i>	Female	121.8	–	–
	Male	115.7	–	–
<i>Astronesthes similis</i>	Female	106.9	–	–
	Male	73.4	–	–
CHAULIODONTINAE				
<i>Chauliodus sloani</i>	Female	133.7	151.9	191.1
	Male	95.5	–	–
MALACOSTEINAE				
<i>Aristostomias xenostoma</i>	Female	83.5	–	–
	Male	48.5	–	–
<i>Malacosteus niger</i>	Female	92.4	110.9	157.5
	Male	66.3	–	–
<i>Photostomias guernei</i>	Female	71.4	–	–
	Male	64.1	–	–
MELANOSTOMIINAE				
<i>Echiostoma barbatum</i>	Female	189.9	200.5	246.7
	Male	158.0	–	–
<i>Eustomias fissibarbis</i>	Female	147.8	–	–
	Male	81.0	–	–
<i>Eustomias hypopsilus</i>	Female	119.9	106.4	146.3
	Male	109.3	–	–
<i>Eustomias schmidti</i>	Female	165.1	166.6	199.1
	Male	77.0	–	–
<i>Melanostomias melanops</i>	Female	161.0	–	–
	Male	127.0	–	–

Empty cells indicate L_{50} and L_{99} were not calculated using binomial regression due to the lack of size overlap between immature and mature specimens, or lack of immature males and females for some species.

DISCUSSION

Histology and Reproductive Strategy

This study is the first extensive examination of the reproductive ecology of stomiids, the top predators of the mesopelagic zone, collected using multiple gear types that sample the full known size range of the taxa. No histological evidence of testicular and ovarian tissue was observed simultaneously in the gonad, indicating that stomiids are gonochoristic, unlike other species within the Stomiiformes. For example, protandric hermaphroditism has been documented in species of the family Gonostomatidae, including *Cyclothone atraria* (Gilbert, 1905); *Sigmops bathyphilus* [sensu Miya and Nishida (2000), formerly *Gonostoma bathyphilum* (Vaillant, 1884)]; *S. elongatus* [sensu Miya and Nishida (2000), formerly *Gonostoma elongatum* (Günther, 1878)]; and *S. gracilis* [sensu Miya and Nishida (2000), formerly *Gonostoma gracile* (Günther, 1878)] (Kawaguchi and Marumo, 1967; Fisher, 1983; Miya and Nemoto,

1985; Badcock, 1986). Considering that the deep-pelagic habitat harbors a lower abundance (per volume) of fishes and larger nearest-neighbor distances between conspecifics than coastal seas (Marshall, 1954), the chance of finding a mate is lower, and thus hermaphroditism could confer benefits through population-level “bet-hedging.” Typically, the terminal sex is female, meaning the bulk of the biomass of these species is found within the egg-producing component. However, maintaining separate sexes can increase reproductive fitness relative to hermaphroditism in two ways: energy can be focused on gamete production instead of reconfiguring the reproductive system, and reproductive opportunities will not be forfeited while undergoing the change (Warner, 1975; Helfman et al., 2009).

Gonochorism may benefit longer-lived predators during large-scale disturbances by preserving genetic diversity. If stomiids were protandrous hermaphrodites like other hermaphroditic stomiiform fishes, a sudden decline in smaller fishes due to a large-scale disturbance (DWHOS) could hypothetically cause a large-scale cohort loss of spawning females some length of time after the event. Smaller fishes may be more vulnerable to oil toxicity than larger fishes (Barron et al., 2004), so the loss of this cohort, which would never have been able to spawn, could result in a loss of genetic diversity at the population level. As genetic diversity is a primary attribute of resilience to disturbance, the finding of gonochorism in this keystone predator group (Sutton and Hopkins, 1996a) is significant.

Sex Ratio

Departure from the expected 1:1 sex ratio is not common in most fishes (Conover and Van Voorhees, 1990). For *Chauliodus sloani*, we found there was a significant bias in favor of females among juveniles. One hypothesis that can explain this is that females reach maturity at a larger size than males (Table 4). Overall, we found the higher ratio of females to males to be the exception; in most cases where sex ratio significantly favored one sex over the other, males were favored. This pattern held for *Aristostomias xenostoma*, *Malacosteus niger*, *Eustomias fissibarbis*, and *Eustomias schmidti*. One possible explanation for this pattern is that males mature faster because development of spermatozoa is energetically less costly than development of ova. If the assemblage of these species actually favors males, having a higher ratio of males to females would increase the probability of females finding mates. We believe that female location of a mate may be facilitated by dimorphisms in light organs; many stomiids have males that possess enlarged postorbital photophores in contrast to those of females, which are smaller or absent (Gibbs, 1964a; Morrow and Gibbs, 1964; Krueger and Gibbs, 1966; Borodulina, 1994, 2009). The benefit of larger postorbital photophores in males may be to aid females in finding a mate by increasing male detectability over greater distances in an environment with diminished light levels (Herring, 2000). The larger postorbital photophore in males can be seen as an evolutionary trade-off to small size, and thus restricted mobility, in male stomiids. Alternatively, divergence from a 1:1 sex ratio can be attributed to other factors such as differential growth rates

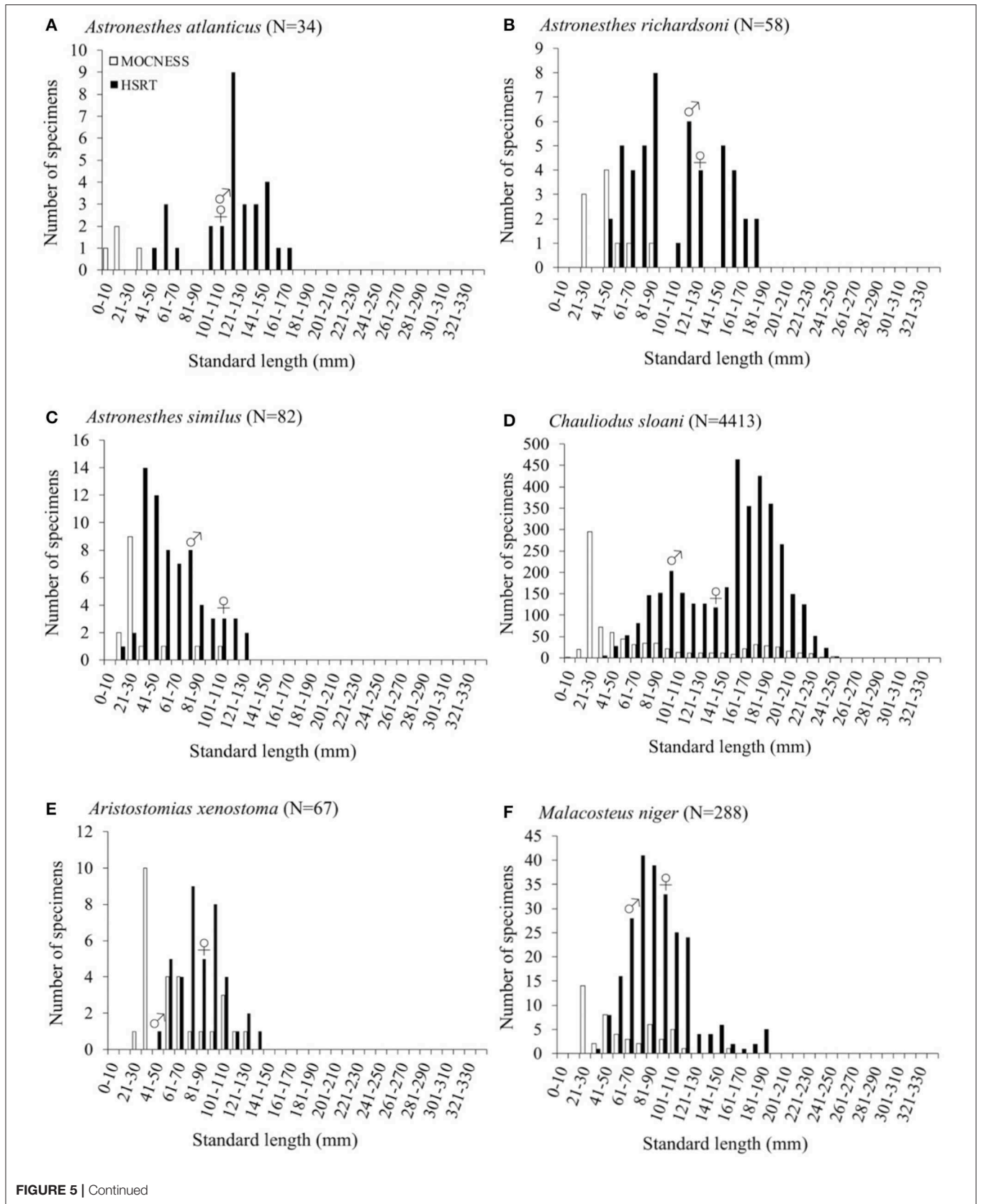
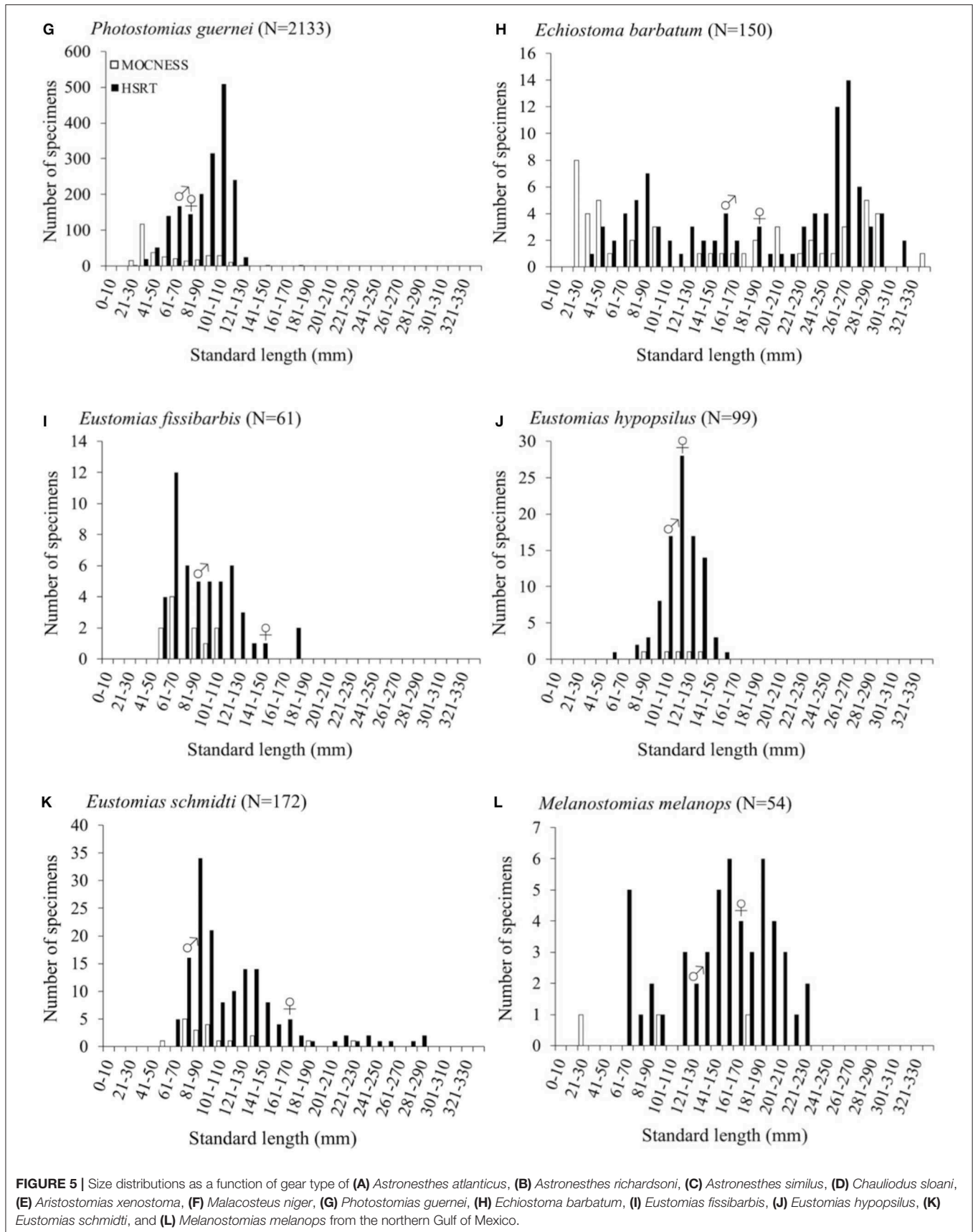
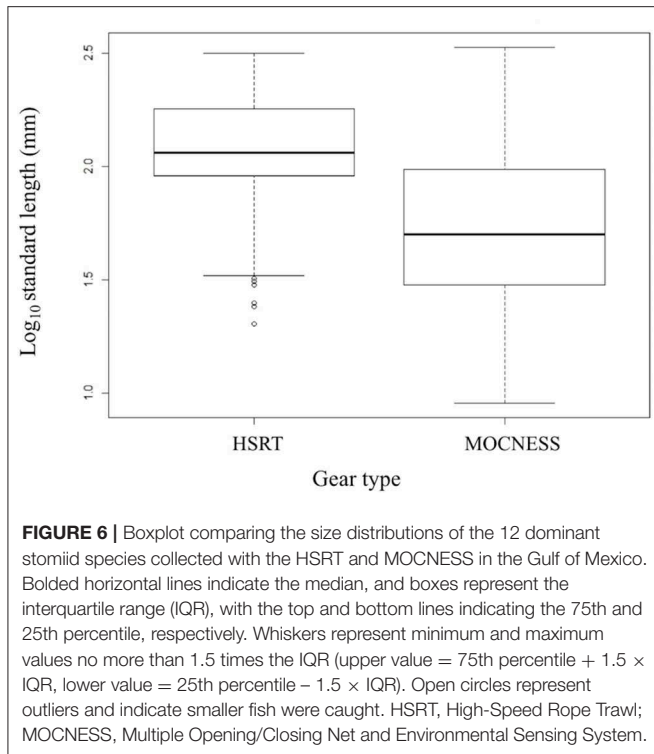


FIGURE 5 | Continued





and differences in spatial distributions between sexes (Trindade-Santos and Freire, 2015), or a genetic basis for sex determination. Little is known about the mechanism of sex determination in stomiids, but Chen (1969) presented evidence of heterogamety in the form of the XO sex type in *Sternoptyx diaphana* (Family Sternoptychidae), a family in the same order as the stomiids.

Previous studies on stomiid sex ratios are limited, so comparisons are not possible for most of the species studied. Based on 100 specimens taken with 40 and 60-ft midwater trawls, Krueger and Gibbs (1966) found the overall sex ratio of *Echiostoma barbatum* from the Mississippi Delta to be significantly female-biased, at 2:1, which differed from this study. Specimens ranged in size from 51.0 to 291.0 mm SL, with the largest male being 252 mm SL and the largest female at 291 mm. Krueger and Gibbs (1966) indicated that *E. barbatum* has dimorphic postorbital photophores and suggested that high male mortality is responsible for a female-biased sex ratio. While larger photophores may increase detection by females, the reasoned drawback is the simultaneous attraction of potential predators due to a more conspicuous display signal. Stomiids have been found in the diets of epipelagic fishes and mammals (Robison and Craddock, 1983; Flynn and Paxton, 2013), but no sex determination was made of those predated-upon individuals. If males experience higher rates of mortality due to increased detection by predators, sex ratios might favor females. However, the data presented in this study do not support this hypothesis.

Size at Maturity

The current data support the conclusion that, in general, female stomiids mature at larger sizes than males, which is a

common life-history pattern in deep-sea fishes (Herring, 2002). In this study, *Echiostoma barbatum* was found to reach 50% maturity at much smaller lengths (158.0 mm SL for males, 189.9 mm SL for females) than those determined by Krueger and Gibbs (1966); they reported that males and females were mature at 220 and 271 mm SL, respectively. Differences in size at maturity of *E. barbatum* may be attributed to contrasting methodologies between studies. While we used histology to classify maturity state, Krueger and Gibbs (1966) relied upon oocyte size and macroscopic observations of gonads. Histology is a more accurate method to classify internal gonadal development and ultimately reveals more information on the reproductive development of fishes (West, 1990).

Size at maturity has also been reported in studies from other waters. For example, two species of *Photostomias* collected near Hawaii are reported to mature at 60 and 120 mm SL (Clarke, 1982), which is similar to the minimum length at maturity found in our study. However, Clarke did not report the species due to taxonomic uncertainty of the genus. Kenaley (2009) clarified the taxonomy of the unidentified *Photostomias* species collected by Clarke (1982). Clarke (2000) mentioned that female *Eustomias fissibarbis* and *Eustomias schmidti* from the North Atlantic Ocean mature at larger sizes than males, but no specific lengths were provided for comparison. The differences in size at maturity of *E. barbatum* and *Photostomias guernei* between this study and previous studies may be a result of the number and size of specimens available for histological analysis, or differences in environmental conditions, or gear types between the studies. For *P. guernei*, this difference may even be attributed to species; Kenaley (2009) described the two unidentified species from Clarke (1982) as new to science.

Binomial regression was not used to estimate minimum size at maturity in males and females of most species due to complete separation of maturity state. Small sample size, especially for male stomiids, likely contributed to complete separation. Only 11 (4%) of 239 male specimens were identified as immature. In males of *Aristostomias xenostoma*, *Eustomias fissibarbis*, *Eustomias hypopsilus*, *Eustomias schmidti*, and *Melanostomias melanops*, the smallest mature individual identified was also the smallest individual overall, suggesting that males of these species may mature at even smaller sizes. Alternatively, it could also suggest that immaturity is a relatively short-lived phase in the reproductive cycle of male stomiids, and reaching maturity is a rapid process. The example of the ribbon sawtail fish *Idiacanthus fasciola* Peters 1877, a species of barbeled stomiid, lends credence to this hypothesis. Males are no more than 10–20% the standard length of mature females, and are mature immediately following transformation from the larval stage (Marshall, 1954; Clarke, 1983). A larger sample of specimens representative of smaller size classes would likely improve the estimate of size of maturity in stomiids.

Size Distributions

While an advantage to using individual gear types for sampling midwater fishes is the targeting of specific sizes (Kashkin and Parin, 1983; Millar, 1992), it is also a potential hindrance, especially when assessing the size distributions of species

assemblages. Using one type of gear can bias results and produce spurious conclusions because of size-specific selectivity (Willis et al., 2000). Gear selectivity in trawls is largely related to mesh size. In this study, the MOCNESS had a 3-mm mesh size and primarily caught smaller specimens. MacLennan (1992) reported that with smaller mesh sizes, the chance of smaller fishes escaping through the net is reduced. Larger nets, such as the rope trawl, effectively collect larger fishes, and yield a larger catch per unit effort (e.g., time) (Kashkin and Parin, 1983). Larger, mature stomiids would have been greatly underrepresented from the sample set and true size distributions would be poorly reflected if the only specimens used in this study were collected with the 10-m² MOCNESS. The reproductive component of the assemblage would have been missed. From a sampling standpoint, the benefits of using a large rope trawl only apply to larger predatory species, not for smaller taxa. Using the larger gear was crucial to effectively sample the reproductive component of stomiid assemblages, and, in conjunction with the MOCNESS, depict a more accurate representation of stomiid size distributions in the Gulf of Mexico.

The Link Between Reproductive Ecology and Oil Contamination in Pelagic Ecosystems

A recent paper by Romero et al. (2018) chronicled the exposure and contamination of mesopelagic fishes by the DWHOS, using polycyclic aromatic hydrocarbon (PAH) signatures as a proxy to identify DWHOS hydrocarbons. These authors presented baseline (pre-spill) PAH levels, along with levels shortly after (2010–2011) and 5–7 years after the DWHOS. The authors reported a dramatic increase in PAH levels in muscle tissues of vertically migrating fishes from the families Gonostomatidae, Sternoptychidae, and Myctophidae (all primary prey of Stomiidae) in 2010–2011, then a reduction in PAH muscle tissue loads in 2015–2017 (but still above pre-spill levels). The primary pathway of incorporation of PAHs was identified as contaminated prey consumption. The findings most relevant to this study, however, were the heightened levels of PAHs in ovaries of fishes collected between 2015 and 2017, with eggs containing 13× more PAHs than other tissues. Furthermore, PAH levels from the eggs of fishes collected during this period were above levels known to cause abnormalities in developing fishes (Sundberg et al., 2006; Sørrhus et al., 2017). An explanation for the differences in PAH concentration between eggs and somatic tissue is the maternal transfer of contaminants to offspring. Lipophilic contaminants such as PAHs are transferred to the egg during vitellogenesis, when maternal resources for embryo development are stored in the yolk (Lubzens et al., 2017). This mechanism of oil contaminant retention is important for future risk assessment and monitoring studies in the deep-pelagic ocean, where biological (e.g., egg production), chemical (e.g., oil composition), physical (e.g., animal and oil dispersion), and behavioral (e.g., vertical migration) factors are key processes with respect to exposure to contaminants, with bioaccumulation of organic chemicals in mesopelagic fishes potentially higher than their shallower counterparts (Romero et al., 2018).

Continued threats of major contamination events in the Gulf of Mexico are likely, given the trajectory of oil extraction going deeper (Sutton et al., 2020) and the increased likelihood of accidents with greater platform depth (8.5% for every 30 m; Muehlenbachs et al., 2013). The average depth of ultra-deep drilling in the Gulf of Mexico is now over 500 m deeper than *Deepwater Horizon* (Murawski et al., 2020). Therefore, given the link between oil contamination, egg production, and bioaccumulation, it is becoming increasingly important to understand the dynamics of deep-pelagic fish reproduction to understand the full effects of oil spills in the deep-pelagic environment.

In conclusion, given the link between increasing petrogenic contamination of the deep ocean and fish reproduction, the key questions for which we have urgent need for information include: (1) how often do fishes spawn (e.g., iteroparous vs. semelparous, total vs. batch spawning); (2) what proportion of the fish population spawns; and (3) when do females produce eggs. In this study, the first extensive study on the reproductive ecology of stomiids in the Atlantic Ocean, as well as the largest study on the reproductive ecology of this family globally, we provide evidence that the 12 stomiids investigated maintain separate sexes, exhibit asynchronous oocyte development and batch spawning, and generally have even sex ratios, with females reaching maturity at larger sizes than males. Further studies of the deep-pelagic domain in other regions will allow comparisons of stomiid reproduction on a global basis, though future investigators must carefully consider gear type due to the inherent avoidance capacity of larger fishes. Our findings provide critical keystone predator data for oceanic ecosystem and bioenergetics modeling and suggest that stomiid reproductive tactics enhance the taxon's resilience to point-source disturbances such as DWHOS, which ideally would serve to maintain carbon flow and the reproductive health of the deep-pelagic Gulf of Mexico.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

ETHICS STATEMENT

Ethical review and approval was not required for the animal study because the vertebrate animals we worked with for this study were all dead before research began.

AUTHOR CONTRIBUTIONS

AM conducted the research, analyzed the data, and wrote the manuscript with input from DK, DW, and TS. DK also provided statistical guidance and DW assisted in reading histology slides and analyzing histological data. TS oversaw all aspects of this research, including the collection, and identification of specimens. All authors have agreed to being listed as such and approve of the submitted version of this manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2020.00101/full#supplementary-material>

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Conflict of Interest: TS, one of the editors for the research topic in which this manuscript will be submitted, is also a coauthor on this manuscript. However, he did not review this paper.

The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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