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Spawning in the deep: reproductive life history of four mesopelagic fishes of the northwestern Atlantic Ocean

Lyndsey S. Lefebvre*, Heidi M. Sosik and Joel K. Llopiz

Biology Department, Woods Hole Oceanographic Institution, Woods Hole, MA, United States

The biomass of mesopelagic fishes is estimated to be on the order of or to exceed that of fishes in the epipelagic. Despite their abundance and importance as an ecological link between surface and deep ocean habitats, there is a dearth of basic life history data for mesopelagic fishes. Reproductive biology data are critical for understanding population dynamics and estimating production of a species, particularly when age and growth data are lacking. Between July 2018 and August 2022, collections were made in the western North Atlantic utilizing multiple net types to capture a broad size-range of mesopelagic fishes. Histological analysis of gonad tissue from four numerically dominant species—*Argyropelecus aculeatus* (Sternoptychidae), *Benthosema glaciale* (Myctophidae), *Scopelogadus beanii* (Melamphaidae), and *Sigmops elongatus* (Gonostomatidae) —were examined to describe aspects of reproduction. We determined that *A. aculeatus* and *B. glaciale* are gonochoristic batch spawners with indeterminate fecundity, and the standard length at which 50% of females were mature (L_{50}) was 39.45 and 33.77 mm, respectively. *S. beanii* were found to be gonochoristic, iteroparous, and likely have multi-year oocyte development with an L_{50} of 90.38 mm. *S. elongatus* was confirmed as a protandrous hermaphrodite, iteroparous, and had an L_{50} of 200.45 mm. This study is the first to present regional maturity ogives for all four species and to describe detailed reproductive patterns in *A. aculeatus, S. beanii*, and *S. elongatus*. These results contribute to the data necessary for quantifying the role of mesopelagic fishes in global biogeochemical cycles and for ensuring responsible use of mesopelagic resources.

1 Introduction

The ocean's mesopelagic zone (comprising pelagic waters of approximately 200–1000 m depth) is a vast habitat occupying roughly 20% of the global ocean volume (ICES, 2021). While the mesopelagic is unfamiliar to many, remote, and extremely difficult to access, it is not safe from anthropogenic impacts. Advancements in technology and depletion of nearshore resources is pushing commercial fisheries into deep sea habitats (Victorero et al., 2018; Watson and Morato, 2013). Increasing temperatures associated with climate change are expected to affect the mesopelagic through shifting oxyclines (Seibel and Wishner, 2019), shoaling of the deep scattering layer (Proud et al., 2017), deoxygenation (Gong et al., 2021), increased ocean acidification (Yang et al., 2022), and shifting vertical and latitudinal species distributions (Iglesias et al., 2024; Liu et al., 2024). Ultimately, the effects of climate change are complicated and not expected to be uniform across taxa, regions, or ocean basins (Koslow et al., 2019). These physical, chemical, biological, and ecological shifts are occurring simultaneously as the high biomass present in the mesopelagic zone is garnering attention in the development of commercial fisheries, either for direct or indirect (as aquaculture feed) consumption (Fjeld et al., 2023; Grimaldo et al., 2020), putting this ecologically important habitat at risk for major degradation.

Fishes of the mesopelagic are among the most numerous vertebrates on the planet and are estimated to comprise 5–15 billion metric tons (Irigoien et al., 2014; Kaartvedt et al., 2012; Proud et al., 2019), or approximately 50% to 94% of the total global fish biomass (Bianchi et al., 2021; Gjosater and Kawaguchi, 1980; Jennings et al., 2008). Due in large part to the prevalence of diel vertical migration in many species, these midwater fishes are an important ecological link between surface production and the deep sea (Isaacs et al., 1974; Sutton, 2013). Mesopelagic fish feeding activity in epipelagic waters and respiration and excretion at depth make mesopelagic fishes a significant component of the biological carbon pump (Boyd et al., 2019; Longhurst et al., 1990), though the precise magnitude of their influence in the global biogeochemical cycle remains unknown (McMonagle et al., 2024). In addition to their role in vertical ecological connectivity, these primarily zooplanktivorous and micronektivorous fishes connect lower and upper trophic levels, serving as prey for larger, deep-dwelling fishes as well as for apex predators such as billfishes, sharks, marine mammals, and seabirds (Choy et al., 2013; Iglesias et al., 2023; Potier et al., 2007; Young et al., 2015).

Despite their numerical abundance, biomass, and critical ecological role, little is known about mesopelagic fishes' biology, ecology, and basic life history compared to their epipelagic and nearshore counterparts (Caiger et al., 2021). Age, growth, and reproductive analyses, which provide data for metrics such as population structure, growth rates, mortality rates, size and age at maturity, spawning seasonality, and productivity, are fundamental to understanding population dynamics of a species (Morgan, 2017). Of the studies to comment on reproductive parameters of mesopelagic fishes, few present detailed histological analysis (Caiger et al., 2021), which is generally considered the most accurate method of assessment (West, 1990). With a few

exceptions (Garcia-Seoane et al, 2014; Knorrn et al., 2024; Marks et al., 2020), maturity ogives (estimates of the proportion of females mature at a given length or age) are lacking, despite that ogives are key metrics in population stock assessment models and are important for management. To fully appreciate how mesopelagic fishes will respond to ocean changes and anthropogenic influences, a more complete understanding of their population sizes and reproductive dynamics is needed.

This study describes aspects of the reproductive life history of four mesopelagic fish species collected in the Slope Sea of the western North Atlantic. The study species were selected based on their numerical dominance in net collections and ecological importance in the region. *Argyropelecus aculeatus* (Sternoptychidae) is broadly distributed in the Atlantic, Pacific, and Indian Oceans (Howell and Krueger, 1987; Schultz, 1964). No formal reproductive studies were found in the literature for any members of the genus, though aspects of reproduction based on visual observation of whole gonads from fish collected in the Bermuda Ocean Acre were described in Howell and Krueger (1987). *Benthosema glaciale* is a member of the species-rich Myctophidae family, a group that is estimated to represent the highest amount of vertebrate biomass on Earth (Catul et al., 2011). *B. glaciale* is found throughout the North Atlantic and in the Mediterranean Sea and is the numerically dominant myctophid north of 35°C (Sutton et al., 2008). Studies in other regions have described the reproductive strategies and estimated maturity parameters for *B. glaciale* (Garcia-Seoane et al, 2014; Halliday, 1970; Mazhirinia, 1988), but substantial variability has been observed, indicating that the full diversity of reproductive parameters has not yet been fully circumscribed. *Scopelogadus beanii* (Melamphaidae) has a broad distribution that overlaps with *A. aculeatus* (Froese and Pauly, 2024) and is associated with the Gulf Stream in the North Atlantic (Kotlyar, 2019). The reproductive biology of *S. beanii* has not been previously described. *Sigmops elongatus*, from the most numerically abundant vertebrate family (Gonostomatidae), is a predatory fish with a worldwide distribution. Limited reproductive data from the tropical Pacific and Gulf of Mexico have been collected for this hermaphroditic species. All these species of interest, except *S. beanii*, are known to participate in diel vertical migration, and due to their numerical abundance in our collections, are likely to play important roles in the regional biological carbon pump.

The primary objectives of this study were to describe the gender systems and patterns of reproduction, as well as to estimate regional female maturity parameters from histological examination of gonad tissue from *A. aculeatus, B. glaciale, S. beanii*, and *S. elongatus*. These results further the knowledge base of some of the mesopelagic region's key players and can be used to further investigate their ecology, behavior, and role in biogeochemical cycles.

2 Materials and methods

2.1 Sample collection

All fish in this study were collected in the "Slope Sea" off the US Atlantic coast (Csanady and Hamilton, 1988; Richardson et al.,

2016) approximately 165 to 275 km south-southwest of Martha's Vineyard over water depths of 1300 m to 2800 m (Figure 1). Collections occurred primarily during four cruises specifically devoted to better understanding the ocean's mesopelagic zone as part of the Woods Hole Oceanographic Institution's Ocean Twilight Zone Project (OTZ) between July 2018 and August 2022 (Figure 1; Table 1). Collections were supplemented from five Northeast U.S. Shelf Long-Term Ecological Research (NES-LTER) cruises between February 2019 and July 2021 (Figure 1; Table 1). Sampling occurred both night and day from the surface to a maximum of 1000 m depth, utilizing multiple gear types, as detailed below, to catch a range of fish species and sizes (Figure 1; Table 1).

A modified Marinovich midwater trawl (MARMWT) was used on OTZ cruises in July and August of 2018 and 2019 (Table 1). The MARMWT had an approximate mouth area of 49 m^2, with graduated mesh sizes from 7 cm at the mouth to 3.8 cm at the cod-end. The MARMWT was towed obliquely, and maximum tow depths ranged from 50 m to 780 m over bottom depths of 2300 to 2800 m. The trawl catch was cursorily examined immediately upon retrieval: an unmeasured subsample of fish, visually selected to approximate the diversity of the catch, was removed, wrapped in foil, and quickly frozen in liquid nitrogen. After a minimum of 24 hours, flash frozen samples were transferred to -80^{0}C freezers where they were stored until processing. The remainder of the catch was sorted to the lowest taxonomic level practical with each taxon weighed en masse; lengths were recorded for up to 150 individuals per taxon and discarded.

A five-net multiple opening-closing net and environmental sensing system (MOCNESS; Wiebe et al., 1985) with a mouth area of 10 m^2 was used on OTZ cruises in March 2020 and August

2022 (Table 1). Each tow produced up to four obliquely towed depth-binned samples from nets with 333 μm mesh and one obliquely towed sample from the surface to the tow's maximum depth (400 m to 1000 m) with a 3 mm mesh net. After net retrieval, large organisms (>20 mm approximately in length) were removed, identified to the lowest taxonomic level practical, photographed, wrapped in foil, and frozen in liquid nitrogen. After a minimum of 24 hours, flash frozen samples were transferred to -80^{0}C freezers where they were stored until processing. On the March 2020 cruise, prior to flash freezing of large organisms 13 specimens of interest (n=8 *S. beanii*; n=5 *S. elongatus*) were placed on ice for at-sea dissection to obtain fresh gonads for comparison to flash frozen samples.

NES-LTER sampling occurred at the farthest offshore station (L11, ~39° 46.4′ N, 70° 53′ W) over bottom depths of approximately 1600 m of water (Figure 1; Table 1). Fish were collected via a midwater, Tucker-style trawl (MWT) that used a 10-m^2 MOCNESS net with 3-mm mesh strung between two MOCNESS net bars (Wiebe et al., 1985); the upper bar was outfitted with a tow bridle and a 36 kg clump weight was attached to each end of the lower bar. The net was deployed to approximately 1000 m and either immediately retrieved (oblique tow; three cruises) or held at depth for two hours before retrieval (two cruises). Once aboard, large fish (approximately >20 mm in length) were removed, identified to the lowest taxonomic level practical, photographed, wrapped in foil, and frozen in liquid nitrogen. The remainder of the catch was discarded. After a minimum of 24 hours, flash frozen samples were transferred to -80^{0}C freezers, where they were stored until processing. On the July 2021 cruise, prior to flash freezing of large organisms, 11 specimens of interest (n=5 *B. glaciale*; n=3 *S. beanii*; n=2 *S. elongatus*) were
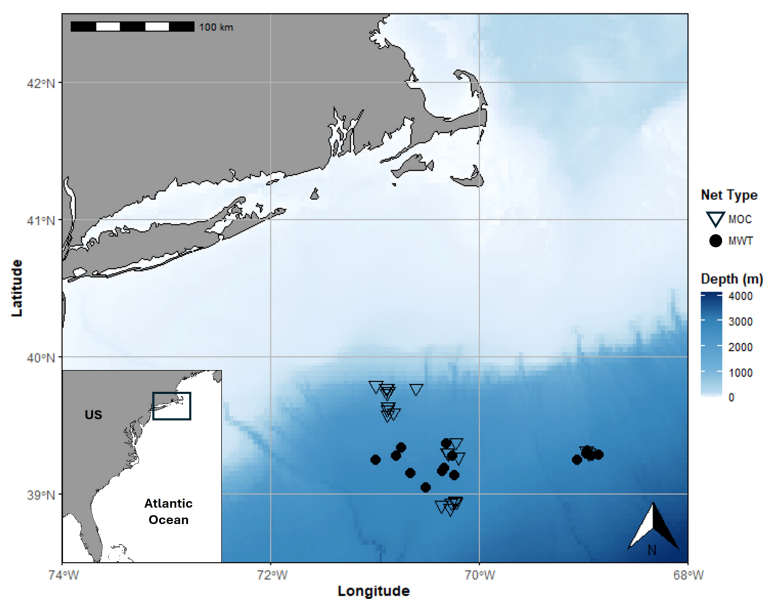

FIGURE 1
Map of tow locations by gear type for the collection of mesopelagic fish species in the Slope Sea of the Northwestern Atlantic Ocean. Net type used for each tow is denoted by the symbol shape. MOC, Multiple Opening/Closing Net and Environmental Sensing System (10 m^2; open triangle); MWT, Marinovich midwater trawl (closed circle).

TABLE 1   Summary of cruises during which mesopelagic fishes were collected for reproductive and associated studies.

Cruise ID	Date	Project	Tow Type	Net used	N_{tow}	N_{net}	N_{soi}	N_{histo}
HB1805	11–21 Aug 2018	OTZ	MWT	MARMWT	5	5	117	72
EN627	4 Feb 2019	NES-LTER	MWT	MOC10	1	1	9	3
HB1907	24 Jul - 8 Aug 2019	OTZ	MWT	MARMWT	9	9	131	79
EN649	3 Feb 2020	NES-LTER	MWT	MOC10	1	1	10	5
AR43	11–16 Mar 2020	OTZ	MOC	MOC10	5	22	116	68
EN657	15 Oct 2020	NES-LTER	MWT	MOC10	1	1	33	30
EN661	5 Feb 2021	NES-LTER	MWT	MOC10	1	1	15	14
EN668	18 Jul 2021	NES-LTER	MWT	MOC10	1	1	10	9
HB2205	4–18 Aug 2022	OTZ	MOC	MOC10	6	23	181	51
			MWT	MOC10	1	1	5	3

Species of interest (SOI) included *Argyropelecus aculeatus, Benthosema glaciale, Scopelogadus beanii*, and *Sigmops elongatus*. MARMWT, Marinovich Midwater Trawl; MOC10, 10m² multiple opening-closing net and environmental sensing system (MOCNESS); MWT, midwater trawl type single net tow; MOC, MOCNESS style tow; NES-LTER Northeast Shelf Longterm Ecological Research; N_{histo}, number of SOI processed for histology; N_{net}, number of nets sampled; N_{soi}=number of SOI collected; N_{tow}, number of tows conducted; OTZ, Ocean Twilight Zone.

placed on ice for at-sea dissection to obtain fresh gonads for comparison to flash frozen samples.

2.2 Sample processing

Fish that were dissected at-sea were identified to species, photographed, and measured for SL. Gonads were excised and fixed in 10% neutral buffered formalin.

In the laboratory, all flash frozen fish from MOCNESS and MARMWT samples were identified morphologically to the lowest taxonomic level possible. Standard length (SL) to the nearest mm and wet weight to the nearest 0.01 g were recorded. The four species of interest in this study were selected based on their numerical abundance in these collections. For flash frozen MWT collections, only individuals of the species of interest were identified and further processed. All following methods and analyses refer only to the four species of interest.

In addition to SL and weight, muscle tissue for genetic identification was removed, a subset of which was genotyped to confirm species identification. When possible, gonads were excised and weighed to the nearest 0.0001 g. The gonadosomatic index (GSI) was calculated as the quotient of gonad weight and somatic weight (total weight minus gonad weight) * 100. Depending on gonad size, a portion of or the entire gonad lobe was placed into a biopsy bag within a tissue cassette and fixed in 10% neutral buffered formalin. Gonads were not available from all collected fish due to the poor condition of thawed specimens, small size of the fish, loss of the tissue in histological processing, or early lab protocols that did not preserve tissue (see Table 1 for number of histology samples per cruise).

2.3 Histology

All available gonad tissue samples for specimen of interest were processed histologically (n=335) with standard techniques, using paraffin as a blocking medium (Humason, 1972). Thin sections (5

μm) were mounted on glass slides and stained with Schiff's-Mallory trichrome. A subset thought to represent a variety of stages of ovarian development were stained and counter-stained with hematoxylin and Eosin Y for comparison (Humason, 1972).

Without reference to size or date of capture, histological sections were examined with a compound microscope (40-400x) to determine sex and comment on reproductive strategy (e.g. described as gonochoristic/hermaphroditic, semelparous/iteroparous, and total/ batch spawner; see Murua and Saborido-Rey, 2003). An exact binomial test was performed to determine if the observed sex ratio in histology samples was significantly different from 1 male to 1 female. For hermaphrodites, the sex was recorded as male or female when a single gonad tissue type was evident or transitional when both male and female tissue were present. Males were not analyzed further as seasonal cycles are less distinct and due to artifacts of freezing that made distinguishing stages of spermatogenesis uncertain. For females, the diameter of the most advanced oocyte stage (where the nucleus was present) and thickness of the ovarian wall (when present in the section) was measured to the nearest μm using an ocular micrometer. For *A. aculeatus, B. glaciale*, and *S. beanii* specimens, each ovary was assigned a reproductive phase based on the most advanced oocyte stage present, incidence and stage of atresia, and the presence of postovulatory follicle complexes (POFs; Table 2). Reproductive phases were not assigned to *S. elongatus* due to low sample sizes and difficulty distinguishing between freezing artifacts and typical oogenesis. Reproductive phases were based on descriptions of oocyte development in Wallace and Selman (1981) and Grier et al. (2009) and utilized standard terminology suggested by Lowerre-Barbieri et al. (2023) with species-specific modifications (Table 2).

Artifacts due to freezing precluded precise descriptions of discrete stages of cortical alveolar, vitellogenic, and maturation-stage oocytes. However, within histological sections, enough oocytes with internal structure were present to confidently identify the most advanced oocyte stage as having cortical alveoli or vitellogenin and to determine when later stages of oocyte maturation were occurring (germinal vesicle breakdown and lipid coalescence). Furthermore,

TABLE 2 Descriptions of reproductive states, phases, and histological criteria for reproductive studies of *Argyropelecus aculeatus* (AA), *Benthosema glaciale* (BG), *Scopelogadus beanii* (SB), and *Sigmops elongatus* collected in the Northwestern Atlantic between 2018 and 2022.

Reproductive State	Phase	General Description/ Histological Indicators	Species-specific modifications	Freezing Artifacts Considerations
Immature	Immature	Oogonia, PG, or CA; tissue appears compact and well organized; OW thin	OW range (µm): <50 (AA); <20 (BG);<30 (SB)	Early stages of CA difficult to detect due to disruption of cytoplasm, but are distinguished from PG based on the marked increase in size; compactness of immature tissue unaffected by freezing
Mature or first time maturing	Early Developing	Early vitellogenesis; small vitellogenin granules evident in periphery of cell and size of these oocytes distinctly larger than PG/ CA. Tissue compact and well organized in first maturing; tissue more dispersed with older atresia in repeat spawners	Vtg range (µm) = 150-260 (AA); 130-270 (BG); 200-350 (SB)	General melted appearance of cytoplasm but individual yolk granules can still be seen; OD may resemble coalescence but occurs in all oocyte stages
	Late Developing	Vitellogenesis pronounced: vitellogenin evident throughout cytoplasm; increase in oil droplets throughout the cell. POFs may be present in repeat spawners	Vtg range (µm) = 220-450 (AA); 245-450 (BG); 340-500 (SB)	General melted appearance of cytoplasm but individual yolk granules can still be seen; OD may resemble coalescence but occurs in all oocyte stages
Mature	Spawning Capable	Oocyte maturation evident as GVM, GVB, or hydration; coalescence of oil droplets and vitellogenin.	OM range (µm) = 440-620 (AA); 410-450 (BG); 450-600 (SB)	General melted appearance of cytoplasm but individual yolk granules can still be seen; OD coalescence distinguished from artifact because not evident in PG/ CA oocytes
Between Spawning	Regressing/Regenerating	PG or CA most advanced-non atretic oocytes; atresia present (alpha, beta, and/or later stages). Tissue not densely packed; POFs may be present; OW thick		General melted appearance of cytoplasm; POFs evident due to SMT staining
Sex change (protandrous, sequential hermaphrodite)	Transitional	Obvious male and female tissue present; male tissue degrading; only oogonia and PG present in female tissue. Sex recorded as dominant tissue	Only applies to *S. elongatus*	Transition may start earlier and evidence may be visible later but freezing artifact precludes

Reproductive phases were based on descriptions of oocyte development in Wallace and Selman (1981) and Grier et al. (2009) and utilized standard terminology suggested by Lowerre-Barbieri et al. (2023) with species specific modifications. The majority of fish were flash frozen in liquid nitrogen prior to the removal of the gonads: histological artifacts resulting from the freezing and thawing process were considered. CA, cortical alveoli/cortical alveolar stage oocytes; GVB, germinal vesicle breakdown; GVM, germinal vesicle migration; OD, oil droplet; OM, oocyte maturation; OW, ovarian wall; PG, primary growth stage oocyte; POF, post-ovulatory follicle complex; Vtg, vitellogenic.

histological sections from gonads fixed at sea were examined to inform interpretation of frozen tissue such as diameter and appearance of different stage oocytes.

Oocyte size frequency distribution diagrams were completed to inform the reproductive strategies. For each species, a single female with ovaries in the closest reproductive phase to spawning (actively spawning for *A. aculeatus* and *B. glaciale*; developing for *S. beanii*; phase not applicable for *S. elongatus*) and which had >100 oocytes with nuclei visible in histological slides was selected for analysis. For each selected individual, multiple non-overlapping photomicrographs were captured with a Leica ICC50 HD camera mounted to Leica DM 1000 LED compound microscope using the 4x objective. All oocytes with a visible nucleus and a diameter >65 µm for *A. aculeatus, B. glaciale*, and *S. beanii* and >30 µm for *S. elongatus* were measured using Fiji (vers. 2.14.0). Small primary growth oocytes and oogonia were not measured as these stages would not be available for use in the forthcoming reproductive events.

Based on histological markers and the assigned ovarian phase, females were classified as immature or mature. Immature females were those with primary growth oocytes or, to be conservative, cortical alveolar oocytes and no evidence of prior reproductive activity (e.g., no POFs, minimal atresia, thin ovarian walls). These individuals were presumed to have never participated in spawning. Mature females were those staged as early developing and later for *A. aculeatus*, *B. glaciale*, and *S. beanii* or with vitellogenic oocytes or POFs for *S. elongatus* (Table 2). The ovaries of mature females had cortical alveolar oocytes with evidence of reproductive activity (thick ovarian walls, POFs, or pronounced alpha or beta atresia) as the most advanced oocyte stage or further advanced oocytes with or without prior evidence of spawning. These individuals were physiologically capable of reproducing and/or had reproduced previously.

Maturity ogives were modeled for each species using generalized linear models with binomial error structure (0=immature; 1=mature) and logit link functions as:

$$P_x = \frac{1}{1+e^{-(\alpha+\beta x)}}$$

where P_x is the proportion of females mature at length x, α is the intercept of the linear predictor, and β is the slope. The length at which 50% and 95% of females were mature (L_{50} and L_{95}, respectively), and model parameters were reported in addition to the minimum observed length at maturity (L_{min}).

All analyses were completed using R version 4.1.2 (R Core Team, 2024) and results were considered significant at $P<0.05$. The "MASS" (Venables and Ripley, 2002) and "ggplot2" (Wickham, 2016) packages were used to plot and estimate parameters of the generalized linear models.

3 Results

In total, 2423 fish were collected, of which 627 were specimens of interest (lengths available for 602; Table 3), with 71% of samples collected in July and August. All species were represented in collections from both MARMWT and MOCNESS nets (Figure 2). The body lengths of fish collected were dependent on net type, with the MOCNESS collecting the broadest range of lengths. In general, more large individuals were collected in the MARMWT compared to MOCNESS nets (Figure 2). Within a species, male and female length ranges were similar, except for *S. elongatus* (Table 3).

Gonad samples were available for histology from 335 fish (Table 1). Freshly fixed gonads were available for *B. glaciale* (n=4); *S. beanii* (n=11), and *S. elongatus* (n=3). Artifacts in frozen tissue included: (1) a "melted" appearance of intracellular and interlamellar areas due to rupturing of cell membranes and cellular components; (2) the formation of vacuoles (reminiscent of oil droplet coalescence that occurs during oocyte maturation);

and (3) the premature disintegration of the nuclear membrane (Figure 3). Artifacts present in frozen tissue precluded detailed descriptions of oogenesis such as descriptions of discrete stages of cortical alveolar, vitellogenic, and maturation stage oocytes. However, general patterns could be discerned due to the presence of structural characteristics of oocyte stages (e.g. cortical alveoli, early vitellogenin accumulation, germinal vesicle migration visible; POFs evident) and general appearance of tissue sections (e.g. compact, well-organized tissue still being distinguishable from the less organized tissue of repeat spawners). Schiff's Mallory trichrome was the preferred stain due to the distinct staining of cortical alveoli and the follicular basement membrane in POFs. The subset of tissues stained with hematoxylin and eosin-Y were useful for confirming the presence of vitellogenin in frozen tissues.
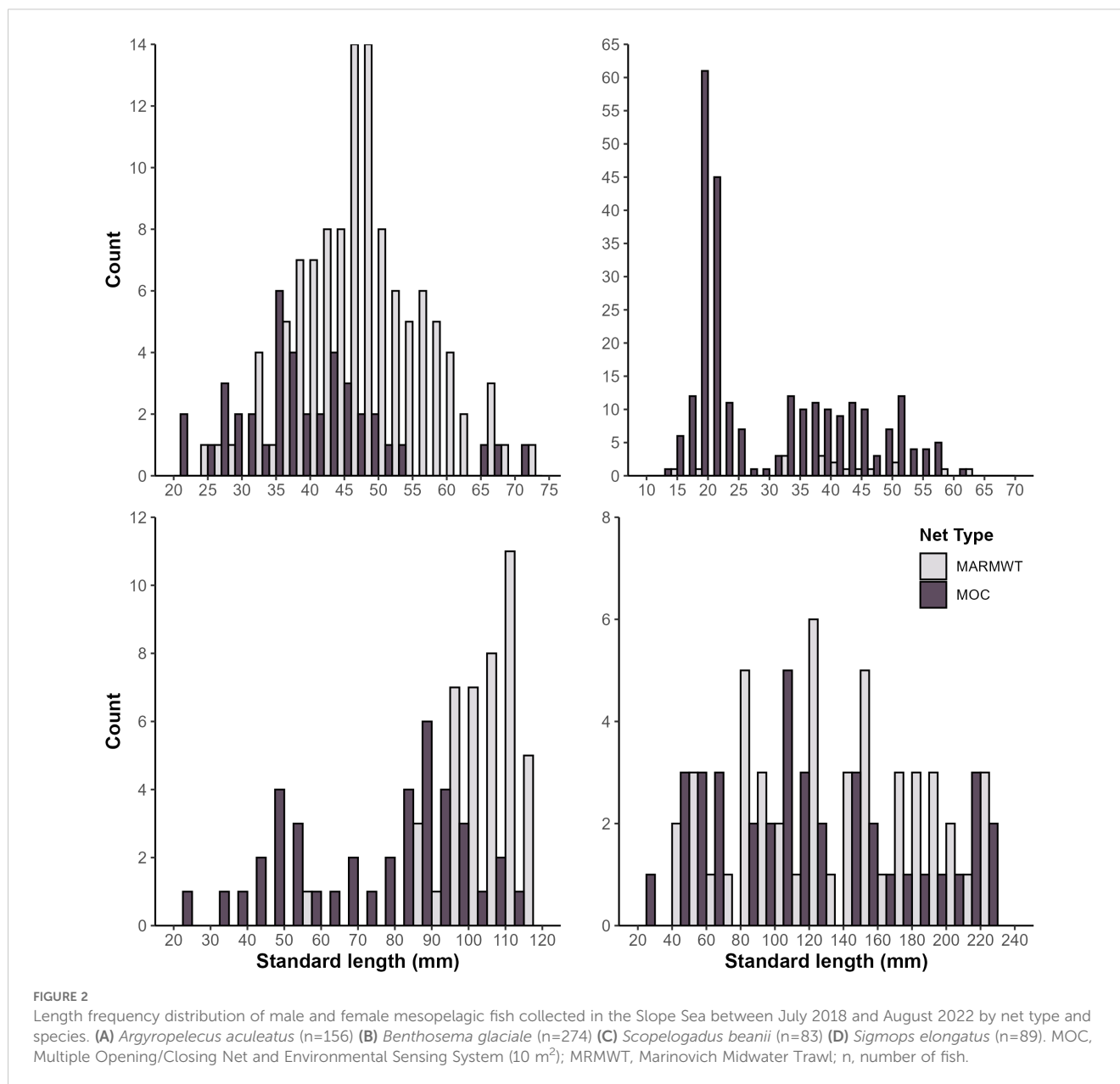
3.1 Gender systems & sex ratios

A. aculeatus, B. glaciale, and *S. beanii* were found to be gonochoristic: male and female lengths overlapped throughout their size ranges, and no simultaneous histological evidence of testicular and ovarian tissue in a sample was observed (Tables 3, 4). *S. elongatus* were found to be protandrous hermaphrodites. All fish ≤102 mm SL were male, and those ≥179 mm SL were female (Tables 3, 4). Five fish 103–147 mm SL were observed to have both testicular and ovarian tissue present; three had predominantly male tissue with primary growth oocytes present while two had predominately female tissue with degrading male tissue still evident.

The observed sex ratio for *A. aculeatus* (1:1.05) was not significantly different from 1:1 male:female (p=0.86). The observed sex ratios for *B. glaciale* and *S. beanii* were 1:2.1 (p<<0.05) and 1:1.8 (p=0.03), respectively. Considering individuals with transitional

TABLE 3 Summary of collections of mesopelagic fish collected in the Slope Sea between 2018 and 2022 for reproductive studies.

Species	Sex	N	SL Range (mm)	Mean SL ± stdev	Weight Range (g)	Mean Weight ± stdev
Argyropelecus aculeatus		156	10 - 73	50 ± 11	0.05 - 14.90	4.58 ± 2.37
	Female	64	25 - 73	42 ± 8	0.75 - 14.19	6.09 ± 3.48
	Male	61	20 - 63	50 ± 11	0.34 - 8.47	3.38 ± 1.57
Benthosema glaciale		274	14 - 63	31 ± 13	0.02 - 3.40	0.62 ± 0.75
	Female	68	19 - 63	41 ± 9	0.08 - 3.40	1.17 ± 0.74
	Male	33	31 - 62	44 ± 9	0.34 - 2.83	1.30 ± 0.67
Scopelogadus beanii		83	25 - 120	89 ± 24	0.37 - 42.22	20.48 ± 11.40
	Female	45	35 - 120	93 ± 23	0.93 - 42.22	22.53 ± 11.65
	Male	25	45 - 119	94 ± 18	2.36 - 34.15	21.99 ± 8.98
Sigmops elongatus		89	29 - 270	132 ± 57	0.14 - 65.16	14.84 ± 16.70
	Female	22	145 - 270	199 ± 30	11.42 - 65.16	36.27 ± 16.33
	Male	11	71 - 151	112 ± 26	1.09 - 15.03	6.79 ± 4.84
	Transitional	5	103 - 161	132 ± 11	4.81 - 19.42	10.28 ± 5.16

The total number (N) of fish collected and the total that were successfully sexed through histological analysis are listed. g, grams; SL, standard length; stdev, standard deviation.

FIGURE 2
Length frequency distribution of male and female mesopelagic fish collected in the Slope Sea between July 2018 and August 2022 by net type and species. **(A)** *Argyropelecus aculeatus* (n=156) **(B)** *Benthosema glaciale* (n=274) **(C)** *Scopelogadus beanii* (n=83) **(D)** *Sigmops elongatus* (n=89). MOC, Multiple Opening/Closing Net and Environmental Sensing System (10 m^2); MRMWT, Marinovich Midwater Trawl; n, number of fish.

gonads the sex of the dominant tissue type, the observed sex ratio was 1:2.2 in *S. elongatus* (p<<0.05).

3.2 Female reproductive strategies & maturity

All phases of ovarian development were observed in *A. aculeatus* (Figure 4A). GSI values ranged from 0.25 to 11.75 (n=112) and were significantly different among ovaries staged as early developing, developing, and spawning (p<0.05; Figure 5A). We classified *A. aculeatus* as iteroparous (capable of participating in multiple spawning events; Murua et al., 2003) based on the observation of POFs in tissues with early secondary growth oocytes (cortical alveolar and early vitellogenic; Figure 6A).

Oocyte development was group synchronous, with up to two distinct clutches of vitellogenic oocytes present (e.g. early and late vitellogenic clutches; Figure 7A). One female (67 mm SL) had primary growth, cortical alveolar, early vitellogenic oocytes, maturing oocytes, and POFs present, indicating the fish had spawned previously, was nearing a spawning event, and had additional oocytes developing and in reserve for future reproduction. Summer (July and August) was a period of reproductive activity for *A. aculeatus* based on the preponderance of females with developing and spawning capable ovaries and POFs. However, spawning frequency and seasonality could not be determined due to lack of sufficient seasonal coverage: all but two females (both immature) were collected in summer. Of females collected at night (n=52), 19% (n=10) had ovaries in the spawning capable phase indicating they were closer to spawning than females
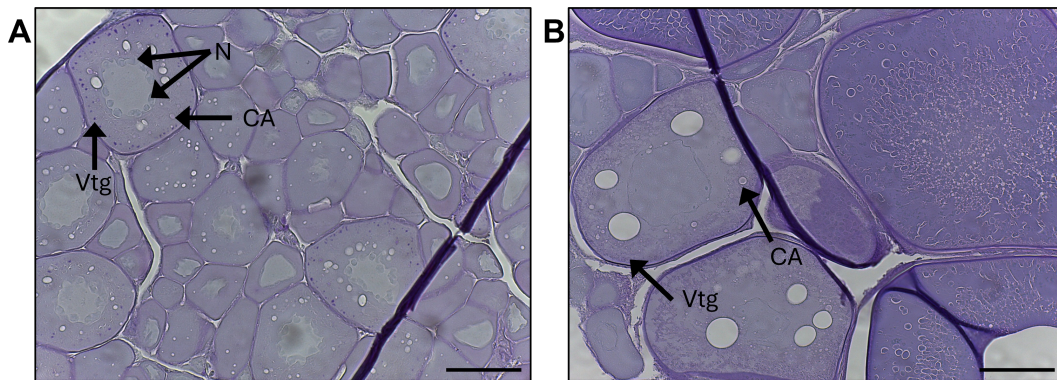
FIGURE 3
Histological micrographs of ovarian tissue from *Benthosema glaciale* stained with Schiff's Mallory Trichrome demonstrating some artifacts of freezing on tissue quality. **(A)** Tissue collected from freshly caught specimen (58 mm standard length [SL]) with ovaries in an early developing stage. Vitellogenin droplets (Vtg), cortical alveoli (CA), and nucleoli (N) are distinct. **(B)** Tissue collected from a specimen (39 mm SL) frozen in liquid nitrogen and stored at -80°C. Vtg are diffuse and less distinct. Nucleoli may be ruptured. Pre-oocyte maturation stage vitellogenic oocytes resemble lipid coalescence due to rupturing of Vtg. Scale bars = 100 µm.

collected during day tows (1 out of 12 with spawning capable ovaries in day tows). One female (58 mm SL) had regressing ovaries with evidence of recent cessation of spawning (POFs and atretic cortical alveolar and vitellogenic oocytes) and a reserve stock of primary growth oocytes, suggesting this fish would be capable of participating in the next spawning season. The smallest mature female *A. aculeatus* was 34 mm SL. Estimates of L_{50} and L_{95} were 39.5 and 45.7 mm SL, respectively (Table 5; Figure 8A).

All phases of ovarian development were observed in *B. glaciale* (Figure 4B). GSI values ranged from 0.67 to 10.34 (n=39) and were significantly different among all phases except between early developing and regenerating (p=0.38; Figure 5B). We classified *B. glaciale* as iteroparous based on the observation of POFs and secondary growth oocytes within the same tissue (Figure 6B). Oocyte development was group synchronous with up to four distinct batches of secondary growth oocytes (Figure 7B): one female (38 mm SL) had primary growth, cortical alveolar, early vitellogenic, late vitellogenic, and hydrating oocytes present. Winter (February and March, n=39) was a period of reproductive activity based on the prevalence of females with ovaries staged as developing and the collection of fish with spawning capable ovaries exclusively in this season. Only three fish with developing ovaries were collected in the summer (Figure 8B). Diel periodicity of spawning was unclear as spawning capable fish were collected in both day

(n=4) and night (n=2) tows. The only fish collected with hydrating oocytes, indicating imminent spawning, was collected around 1030 hrs local time. Estimates of L_{50} and L_{95} were 33.77 mm and 40.55 mm SL, respectively (Table 5; Figure 8B).

All phases of ovarian development except regenerating were observed in *S. beanii* (Figure 4C). GSI values ranged from 0.54 to 3.68 (n=18) and were not significantly different between developing and spawning capable phases (Figure 5C). We classified *S. beanii* as iteroparous due to the presence of POFs and developing oocytes in the same individual and the presence of a reserve stock of primary growth oocytes (Figure 6C). Oocyte development was asynchronous, with a continuum of secondary growth oocytes from the cortical alveolar through vitellogenic stages in developing ovaries and through maturation stage oocytes in spawning capable ovaries (Figure 7C). All fish with spawning capable ovaries (n=10) were collected in the summer at night; reproductive seasonality and diel periodicity was ambiguous, as 67% (n=30) of samples analyzed were collected in July and August. Most of those fish (90%; n=27) were collected at night. *S. beanii* observed in this study began to mature at 85 mm SL (L_{min}) with L_{50} and L_{95} estimated at 90.4 mm and 98.1 mm, respectively (Table 5; Figure 8C).

Ovaries from *S. elongatus* were not assigned reproductive phases due to low sample sizes and difficulty in distinguishing freezing artifacts

TABLE 4 Summary of reproductive traits of *Arygyropelecus aculeatus*, *Benthosema glaciale*, *Scopelogadus beanii*, and *Sigmops elongatus*, as determined through histological analysis of male and female gonad tissue.

| Species	Gender System	Female Lifetime Reproductive Schedule	Spawning Strategy	Female Fecundity Type
Argyropelecus aculeatus	Gonochorisim	Iteroparous	Batch	Indeterminate
Benthosema glaciale	Gonochorisim	Iteroparous	Batch	Indeterminate
Scopelogadus beanii	Gonochorisim	Iteroparous	Unknown	Unknown
Sigmops elongatus	Protandrous hermaphroditism	Iteroparous	Unknown	Unknown
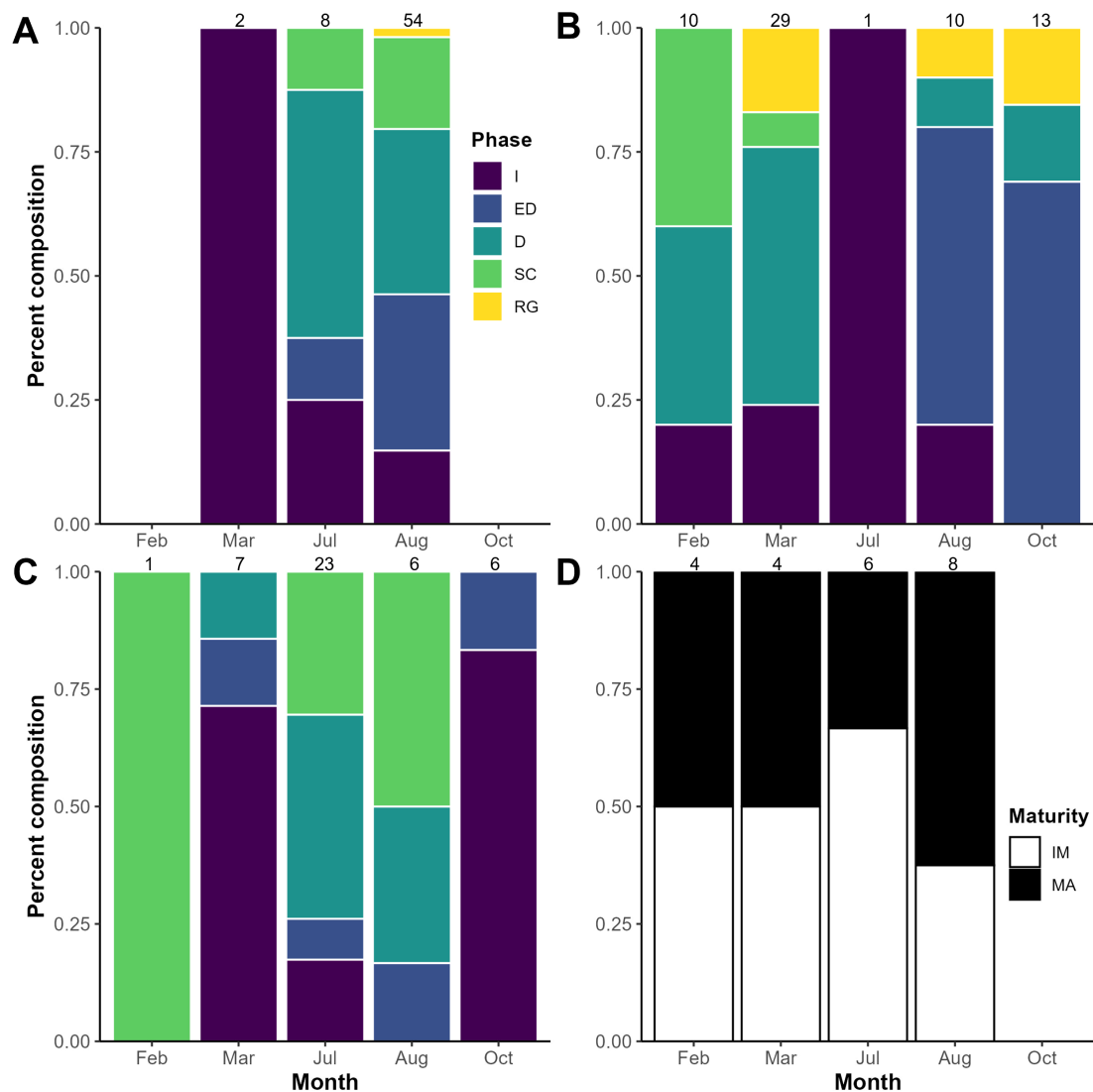
FIGURE 4
Reproductive phases or maturity by month for mesopelagic fishes collected in the Slope Sea between 2018 and 2022. Percent composition of female in each reproductive phase for **(A)** *A. aculeatus*, **(B)** *B. glaciale*, and **(C)** *S. beanii*, respectively. **(D)** Maturity status by month for female *Sigmops elongatus*. Numbers above the bars denote sample size by month. I, immature; ED, Early developing; D, Developing; SC, Spawning Capable; RG, Regressing/regenerating; IM, immature; MA, mature.

from typical oogenesis. With SMT staining, cortical alveoli appeared to be present in oocytes as small as 40 μm, and vitellogenesis appeared to be advanced in relatively small oocytes (200-280 μm; Figure 6D) based on intense eosinophilic staining in comparison stain slides. The average GSI of females with vitellogenic oocytes was 1.76 compared to 0.58 in those with less advanced oocytes. Assignment of female maturity was based on presence of vitellogenic oocytes or POFs. The smallest individual with vitellogenic oocytes (L_{min}) was 179 mm SL. *S. elongatus* appeared to be iteroparous as females based on the observation of primary and secondary growth oocytes, beta atresia, and POFs in the same tissue of two females 213 and 270 mm SL (Figure 4D). POFs were estimated to be old based on their size and appearance and were present in 5 individuals (209–270 mm SL). Oogenesis appeared to be group synchronous with the observation of a single group of vitellogenic oocytes when present (Figure 7D).

Spawning seasonality could not be assessed based on the available samples. Excluding transitional individuals, *S. elongatus* females had an estimated L_{50} of 200.45 and L_{95} of 239.27 mm SL (Table 5; Figure 8D), and the smallest mature female was 179 mm SL.

4 Discussion

To our knowledge, the work described here is the first to detail the reproductive patterns in *A. aculeatus*, *S. beanii*, and *S. elongatus*; presents the first histologically determined maturity ogives for any *Argyropelecus* species, *S. beanii*, and *S. elongatus*; and presents the first maturity ogive in this region of the North Atlantic for *B. glaciale*, to the best of our knowledge. The use of multiple types of sampling gear allowed for collection of a broad size range, up to the
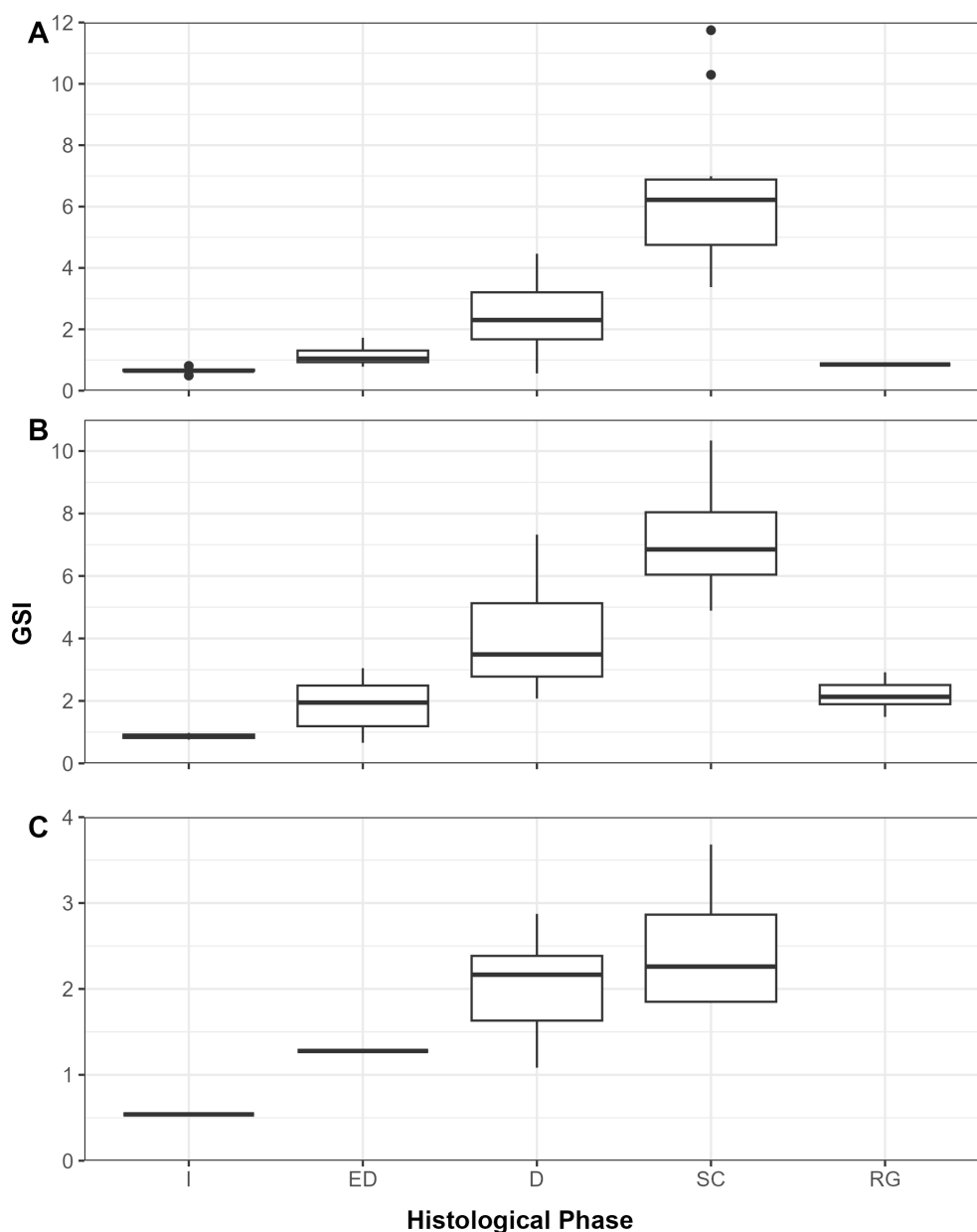
FIGURE 5
Female gonadosomatic index (GSI) by histologically determined reproductive phase in three mesopelagic fishes, **(A)** *Argyropelecus aculeatus* (n=53), **(B)** *Benthosema glaciale* (n=39), and **(C)** *Scopelogadus beanii* (n=18), collected in the Slope Sea between 2018 and 2022. GSI values were significantly different (p<0.05) for females with ED, D, and SC ovaries in all species. For *B. glaciale*, GSI values between ED and RG ovaries were not significantly different (p>0.05) I, immature; D, developing; ED, early developing; N, number of fish; RG, regressing/regenerating; SC, spawning capable.

reported maximum size for each taxon of interest. These novel data were obtained despite the challenges of using fragile frozen tissues, which were mitigated by comparing fresh tissues and using alternate stains.

4.1 Gender systems & sex ratios

Gonochorism was the dominant gender system observed in the taxa in this study, consistent with that of teleosts more generally.

While less than 1% of vertebrates demonstrate hermaphroditism, the majority of those that do are fishes (Kuwamura et al., 2020). Hermaphroditism in general, and protandry (male to female sex-change) specifically, is thought to be favored when mating is random and size-selective increases in reproductive success are more pronounced in females (Sunobe, 2023; Warner, 1988). The high relative abundances of Myctophids, Melamphaids, and Sternoptychids observed in many studies (Olivar et al., 2017; Sutton et al., 2008) suggest that conspecifics aggregate; presumably, aggregations formed due to increased food
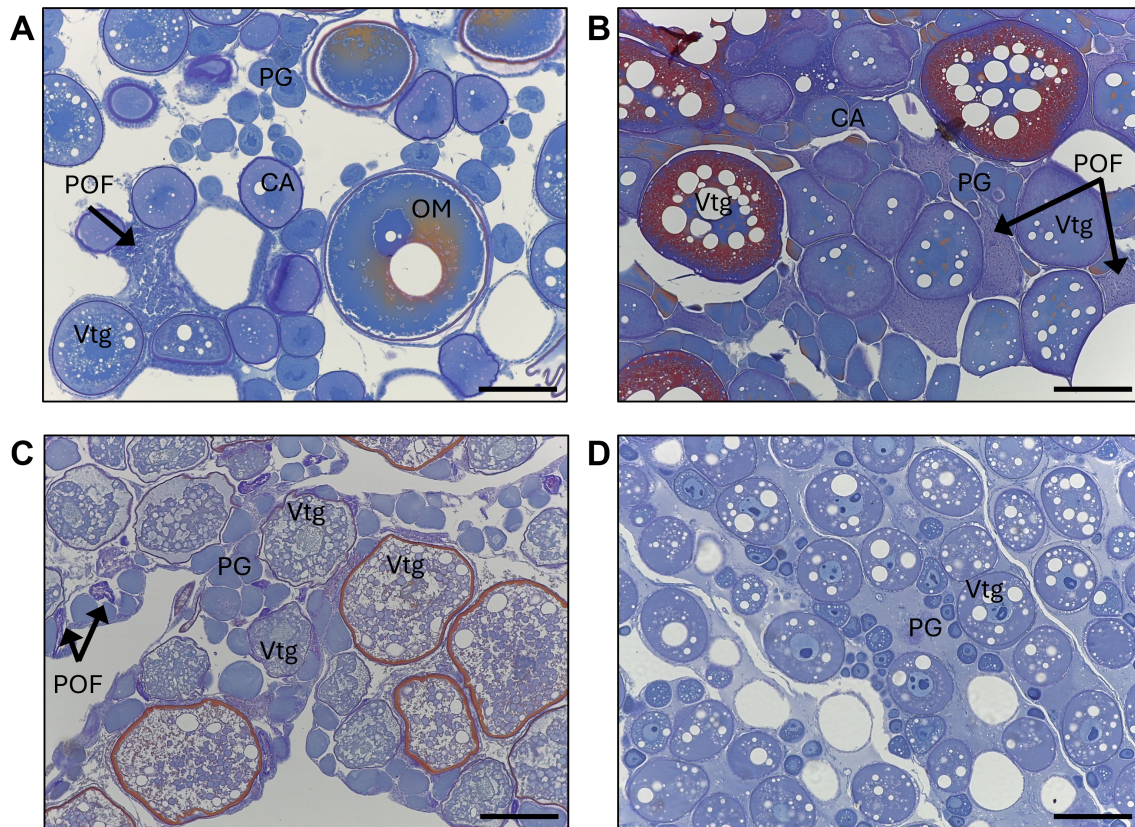
FIGURE 6
Histological micrographs from ovarian tissue stained with Schiff's Mallory Trichrome from mature mesopelagic fishes collected in the Slope Sea between 2018 and 2022. **(A)** *Argyropelecus aculeatus* (standard length [SL]=54 mm) **(B)** *Benthosema glaciale* (SL=38 mm) **(C)** *Scopelogadus beanii* (SL=117 mm **(D)** *Sigmops elongatus* (SL=179mm). CA, cortical alveolar oocyte; OM, oocyte maturation stage oocyte; PG, primary growth oocyte; POF, postovulatory follicle complex; Vtg, vitellogenic oocyte. Scale bars = 200µm.
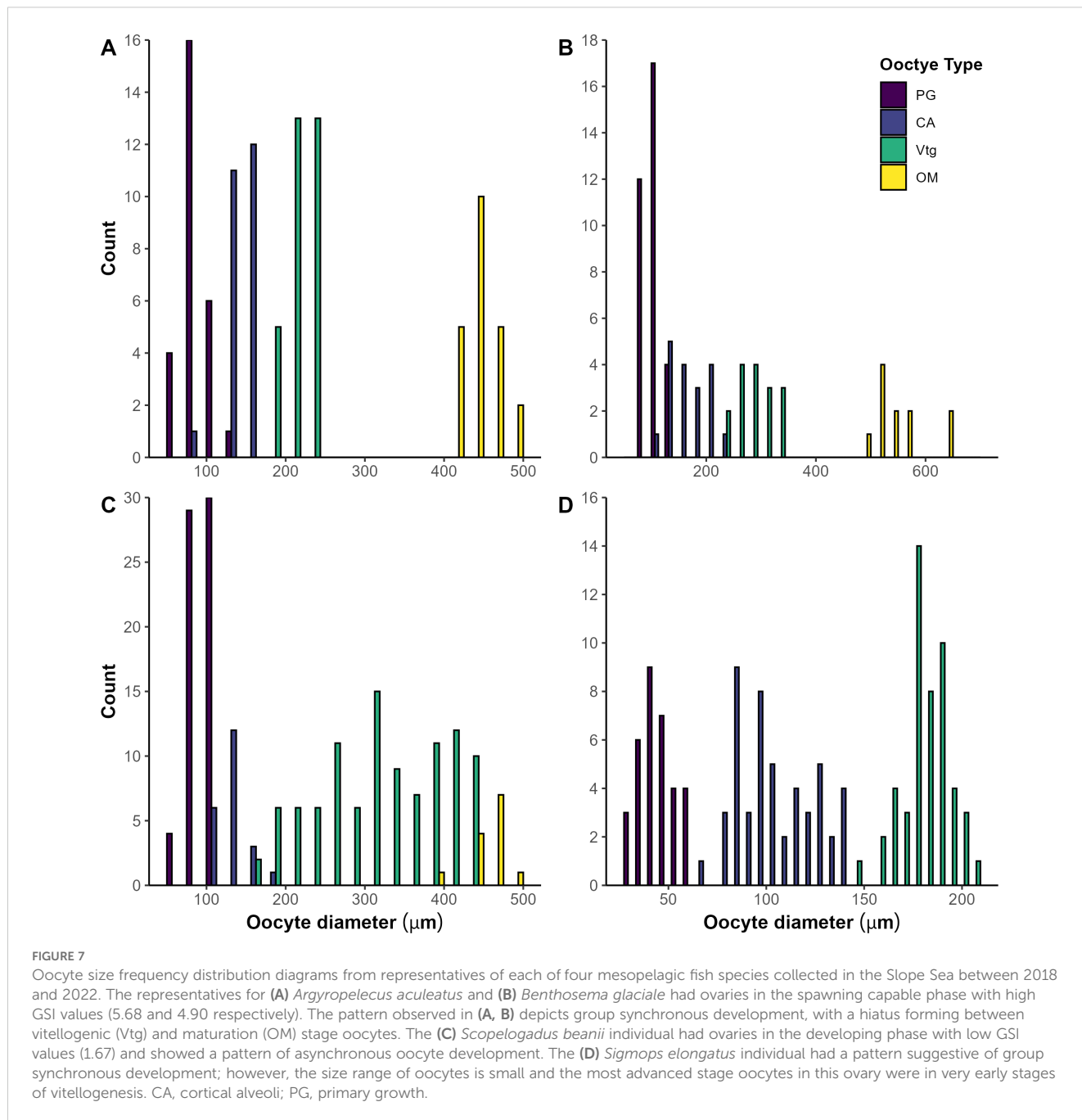
availability associated with oceanographic features that concentrated prey would also provide enhanced spawning opportunities. *S. elongatus* are primed for protandry if they are more solitary than the other species of interest in this study and given that in many fish taxa, female reproductive success increases disproportionately with size (Barneche et al., 2018; Fitzhugh et al., 2012; Hixon et al., 2014).

The sex ratios we observed in this study skewed female when different from parity (*i.e.* in all but *A. aculeatus*). Skewed sex ratios can occur when there are sex-based differential mortality, longevity, or growth rates (Charnov, 1982; Clarke, 1983; Linkowski et al., 1993). Sex ratios that skew female increase the egg producing biomass of a population and have been observed in other mesopelagic species (Andresen et al., 2025; Clarke, 1983). It should be noted, however, that the observed ratios in this or any study may be influenced by accessibility, discernability, and robustness of ovaries compared to testes, and may not be a precise representation of the catch or the overall population. In this study, testes were more difficult to distinguish in the body cavities of these relatively small species, especially in presumably immature fish. Flash freezing made the internal organs, and the testes in particular, difficult to extract as they were more delicate compared to those from freshly dissected individuals and from

females. Furthermore, beyond the differences in accessibility of gonads, there may be diel, seasonal, size and/or depth patterns in distribution by sex seen in other mesopelagic taxa (Almeida and Rossi-Wongtschowski, 2007; Halliday, 1970; Howell and Krueger, 1987; Kawaguchi and Mauchline, 1982) that are not evident in the limited collections of any single study.

4.2 Female reproductive strategies

All species we examined appeared to be iteroparous, capable of participating in multiple reproductive events over the course of their lifetimes (Murua and Saborido-Rey, 2003). Evidence of iteroparity in female specimens included the presence of oogonia and primary growth oocytes in ovaries of all developmental stages, but particularly those staged as developing and spawning-capable: these oocyte stages are not found in reproductively active semelparous fishes (Heins and Brown-Peterson, 2022; Lowerre-Barbieri et al., 2011). Furthermore, POFs, the remnants of ovarian follicles that remain and slowly degrade after mature oocytes are ovulated, were observed in ovaries from all species. Additional evidence we observed in *A. aculeatus* and *B. glaciale* included individuals that appeared to be between spawning seasons (i.e. those with regressing/regenerating ovaries). Iteroparity, which is the

FIGURE 7
Oocyte size frequency distribution diagrams from representatives of each of four mesopelagic fish species collected in the Slope Sea between 2018 and 2022. The representatives for **(A)** *Argyropelecus aculeatus* and **(B)** *Benthosema glaciale* had ovaries in the spawning capable phase with high GSI values (5.68 and 4.90 respectively). The pattern observed in **(A, B)** depicts group synchronous development, with a hiatus forming between vitellogenic (Vtg) and maturation (OM) stage oocytes. The **(C)** *Scopelogadus beanii* individual had ovaries in the developing phase with low GSI values (1.67) and showed a pattern of asynchronous oocyte development. The **(D)** *Sigmops elongatus* individual had a pattern suggestive of group synchronous development; however, the size range of oocytes is small and the most advanced stage oocytes in this ovary were in very early stages of vitellogenesis. CA, cortical alveoli; PG, primary growth.

TABLE 5 Model parameters of binomial linear regression with logit error structures performed to determine the lengths of maturity for female mesopelagic fishes collected in the Slope Sea between 2018 and 2022.

Species	N	α	β	L_{min} (mm)	L_{50} (mm)	SE_{L50}	L_{95} (mm)	SE_{L95}
Argyropelecus aculeatus	64	-18.71	0.47	34	39.45	1.32	45.66	2.13
Benthosema glaciale	63	-14.66	0.43	33	33.77	1.26	40.55	1.98
Scopelogadus beanii	43	-34.53	0.38	85	90.38	2.01	98.09	3.46
Sigmops elongatus	22	-15.20	0.08	179	200.45	7.46	239.27	17.63

α, intercept of the linear predictor; β, slope; L_{min}, standard length at first maturity; L_{50}, standard length at which 50% of females are mature; L_{95}, standard length at which 95% of females are mature; SE, standard error.

FIGURE 8
Logistic regression for the estimated proportion of females mature at a given standard length for female mesopelagic fishes collected in the Slope Sea between 2018 and 2022, **(A)** *Argyropelecus aculeatus*, **(B)** *Benthosema glaciale*, **(C)** *Scopelogadus beanii*, and **(D)** *Sigmops elongatus*. The length at which 50% of the females were mature (L_{50}) is denoted by dashed lines. Shading indicates 95% confidence intervals. N, number of samples; No. Obs, number observed at given length for immature (0) and mature (1) females.

dominant reproductive strategy in teleosts (Wootton and Smith, 2015), is typically viewed as a bet-hedging strategy, acting to increase lifetime reproductive potential by spreading risk over multiple years and environmental conditions. Iteroparity is thus thought to be favored in temporally heterogeneous systems with high variability in reproductive success and is associated with relatively delayed adult maturity (Bell, 1976; Wilbur and Rudolf, 2006). The temperate waters of the Slope Sea from which our fish were collected are characterized by large seasonal fluctuations in productivity. These fluctuations are associated with interannual variability in the timing of the spring bloom (Dutkiewicz et al., 2001), as well as highly stochastic effects of Labrador Sea and Gulf Stream waters and frequent passage of warm and cold core eddies with complex ephemeral impacts on regional chemical and biological conditions (Csanady and Hamilton, 1988). The mesopelagic depths of these regions, with their integral connection to

variations in surface flow and productivity, are likely to exhibit both spatial and temporal patchiness in resource availability. This unpredictability would make semelparity highly risky for mesopelagic fishes in these regions and would favor repeat spawning as an adaptive strategy for maximizing lifetime reproductive output.

Among iteroparous fishes, many species exhibit batch spawning: repeated spawning throughout a reproductive season. The development of multiple stages of secondary growth oocytes that we observed in *A. aculeatus* and *B. glaciale* is consistent with a batch spawning strategy (Murua and Saborido-Rey, 2003). The discrete batches of vitellogenic and maturing oocytes along with primary growth and cortical alveolar oocytes that we found also suggest these species have indeterminate fecundity, with the reproductive potential of the species being a product of batch fecundity and the number of spawning events throughout the

season (Hunter et al., 1992; Murua and Saborido-Rey, 2003). The spawning frequency (duration between spawning events) could not be determined in this study due to small sample sizes and lack of seasonal coverage; however, *A. aculeatus* and *B. glaciale* could produce a minimum of three and four batches, respectively. The indeterminate batch spawning strategy and minimum batch number we report is consistent with those for *B. glaciale* in other regions (Garcia-Seoane et al, 2014; Mazhirinia, 1988) and myctophids more generally (Dalpadado, 1988; Sarmiento-Lezcano et al., 2020; Sassa and Takahashi, 2022). We did not find earlier reports on reproductive strategy for *Argyroplecus* sp., though other Sternoptychid species have an indeterminate batch fecundity strategy (Almeida and Rossi-Wongtschowski, 2007; Goodson et al., 1995; Salvanes and Stockley, 1996; Young et al., 1987).

Diel periodicity of spawning in *B. glaciale* and *A. aculeatus* could not be determined in this study. Given that eggs are positively buoyant (Sundby and Kristiansen, 2015) and larvae are found in epipelagic waters (Daudén-Bengoa et al., 2020; Sassa et al., 2004; Wang et al., 2021), it is possible spawning occurs at night in shallow waters. This strategy is hypothesized to confer a survival advantage and optimize larval growth by releasing eggs in warmer and more productive waters compared to the deeper layers (Gartner, 1993). Conversely, as temperature is positively correlated with rates of oogenesis (Kjesbu et al., 2010; Kurita et al., 2011), it is also possible that exposure to shallower warmer water temperatures at night allows for more rapid development of the forthcoming oocyte batch which is then released at mesopelagic depths during the day. Myctophid species show both strategies (Gartner, 1993; Sassa, 2019), and our data do not clarify the strategy taken by the species of interest in our study. Whether spawning occurs in the epi- or mesopelagic, species that participate in diel vertical migration, such as *A. aculeatus* and *B. glaciale*, likely have more rapid oogenesis compared to deep-dwelling species due to increased metabolic rates associated with an increase in mean ambient temperature.

We observed multiple stages of secondary growth oocytes present in ovaries of *S. beanii*, but these fishes demonstrated asynchronous oocyte development and a lack of distinct batches. *S. beanii* occupy the deeper mesopelagic and shallow bathypelagic and do not participate in diel vertical migration (Cook et al., 2013; Govindarajan et al., 2023; Marohn et al., 2021). The continuum of secondary growth oocytes we observed may reflect prolonged oogenesis due to the low mesopelagic temperatures (2 to 5°C; (Helfman et al., 2009). *S. beanii* may experience multi-year oocyte development, as observed in a variety of cold-water species (Gunnarsson et al., 2006; Junquera et al., 2003; Lefebvre and Field, 2015; McBride et al., 2022). Whether spawning occurs annually or at another interval remains unclear.

4.3 Female reproductive seasonality & maturity

Seasonality of spawning in *A. aculeatus* could not be conclusively determined due to most fish being collected in July and August in the

current study; the spawning activity we observed during this time was consistent with the summer through fall peak suggested for the species in the Sargasso Sea based on the abundance of postlarvae in plankton collections (Howell and Krueger, 1987). Our observation of a regressing/regenerating female of 58 mm SL in August, as well as the late summer collection by Howell and Krueger (1987) of seven fish 57–71 mm SL with resting ovaries, suggests that even if there are not distinct spawning seasons, mature individuals experience interspawning periods.

The L_{50} we estimated for *A. aculeatus* (39.5 mm SL) was similar to the upper end of "subadults" for the species suggested by Howell and Krueger (1987). In the earlier study, ovaries were examined macroscopically and a coarse estimate of L_{min} of 52 mm SL was based on "large ova near the size at spawning" being visible over 90% of the ovary (Howell and Krueger, 1987). However, the authors noted a 35 mm female in "breeding condition", suggesting some individuals mature at a smaller size. Our maturity criteria were conservative, in general, using vitellogenesis as the indicator of maturity: reproductive studies often use presence of first stage of secondary growth oocytes (cortical alveolar) to indicate maturity (Lowerre-Barbieri et al., 2011; Wallace and Selman, 1981). Because there are observed differences between physiological maturity (i.e. when an individual is physiologically capable of reproducing) and functional maturity (i.e. when an individual begins to contribute to production), as well as skipped spawning (i.e. missed reproduction events) in mature adults, documented across a wide variety of taxa (Kennedy et al., 2011; Lefebvre and Field, 2015; McBride et al., 2022; Rideout and Tomkiewicz, 2011), we conducted sensitivity analyses to determine how our L_{50} estimates would change using an even more conservative criteria of intermediate vitellogenesis (Supplementary Figure S1A). This sensitivity analysis resulted in an L_{50} of 48.69 mm SL for *A. aculeatus* and could be considered as the most conservative estimate for population assessment models of the species, given its unknown population dynamics. Additional collections of freshly fixed gonads throughout the year would assist in clarifying the most appropriate assignment of maturity.

We observed *B. glaciale* spawning activity in the Slope Sea during the winter (February and March), and fish were in the early stages of development for the subsequent spawning season in the summer and fall (July, August, and October). The winter and early-spring spawning in the western North Atlantic we documented was supported in other studies of the species based on the condition of ovaries of mature females in the summer and winter (Garcia-Seoane et al, 2014; Halliday, 1970) as well the presence of postlarvae in midwater collections from May and June (Halliday, 1970). Consistent with the current study, Garcia-Seoane et al (2014) presented evidence of a seasonal, batch spawning and indeterminate fecundity pattern for *B. glaciale* in the Flemish Cap off Nova Scotia. The early spring spawning we observed for *B. glaciale* in the Slope Sea would result in larvae residing in the epipelagic during the seasonal zooplankton production maxima (Friedland et al., 2015). The species is estimated to live up to seven years (Garcia-Seoane et al, 2014; Gjosater, 1973; Halliday, 1970; Kristoffersen and Salvanes, 2009), and preliminary aging efforts associated with the current study suggest females are mature by at

least age three (unpublished data). The maximum age, age at maturity, and observation of regressing/regenerating females implies individuals participate in multiple spawning seasons.

The L_{50} for *B. glaciale* reported here (33.46 mm SL) is notably smaller than that reported for the species off Nova Scotia by Garcia-Seoane et al., 2014 (47.6 mm SL) and the L_{min} reported in the same area by Mazhirinia, 1988 (46 mm SL). In both previous studies, regional differences in size at maturity were noted, with a decrease from west to east across the Atlantic (L_{50} = 24.5 mm in the Balearic Sea [Garcia-Seoane et al., 2014]; L_{min} =33 mm in the Hatton Plateau [Mazhirinia, 1988]. The criteria we used to define maturity are different from that of Garcia-Seoane et al (2014), who used the cortical alveolar stage to define maturity (the maturity criteria used by Mazhirinia, 1988 is not well defined). However, more conservative maturity criteria, as we used, would result in an increased L_{50} if all else were equal. Instead, the comparatively low size at maturity reported here is most attributable to regional differences: the collections off Nova Scotia occurred north of the 42nd latitude in the North Atlantic Drift biogeographic zone, while the current collections occurred at 39-40°N in what is considered the Central North Atlantic ecoregion (Sutton et al., 2017). There are generally positive relationships between asymptotic length and latitude (Gertseva et al., 2017) as well as asymptotic length and length at maturity (Froese and Binohlan, 2000) in marine fishes. Furthermore, intraspecific differences in length or age at maturity and other reproductive parameters (i.e. fecundity and spawning frequency) across biogeographical breaks are well documented in other taxa (Head et al., 2014; Lefebvre et al., 2018; McBride et al., 2013). We performed a sensitivity analysis by temporal restricting samples to those from the reproductive season (February and March) and using a more conservative criteria of mid-vitellogenesis, which resulted in a minimal increase in L_{50} to 34.32 mm SL (Supplementary Figure S1B).

Summer was a period of reproduction for *S. beanii* based on our observations, although it remains unknown if spawning occurs in other seasons due to the apparent size selectivity and seasonal usage of collection gears in the current study. The MARMWT collected primarily larger, mature individuals and was only deployed in July and August. To the best of our knowledge, this is the first report of the reproductive biology of *S. beanii*. Their congener *Scopelogadus mizolepis* were reproductively active in March and April in the eastern central Atlantic (Knorrn et al., 2024). No fish with regressing/regenerating ovaries were collected in this study, potentially due to the afore mentioned bias in sampling gear and season or because, upon reaching maturity, this species spawns continuously and dies. The latter "functionally semelparous" strategy has been suggested for other Melamphaids (Keene et al., 1987; Knorrn et al., 2024).

The maturity ogive presented is the first reported for *S. beanii* and the estimated L_{50} (90 mm SL) is notably larger than that reported for its congener *S. mizolepis* (46 mm SL, Knorrn et al., 2024). *S. beanii* reside in higher latitudes than *S. mizolepis* and attain higher maximum lengths (Ebeling and Weed, 1963; Keene et al., 1987; Kotlyar, 2019, Kotlyar, 2020). This stark difference in L_{50} is unsurprising considering the afore discussed trend in latitude and maturity and that metabolic growth rates are likely different between tropical and temperate species. A sensitivity analysis on maturity estimates was not possible for *S.*

beanii due to a lack of model convergence based on our samples (i.e. all fish below 98 mm SL were immature; all above were mature).

The paucity of *S. elongatus* females with spawning capable ovaries in this study precluded interpretation of oogenesis, fecundity, or seasonal patterns. The maximum observed oocyte diameter (280 μm) was much smaller than that observed in other the species examined in this study (400-650 μm). While freezing artifacts made the determination of discrete vitellogenic stages impossible, the largest oocytes observed in *S. elongatus* appeared to be advanced due to the amount of vitellogenin present (as evidenced in comparison slides stained with hematoxylin and eosin-y). Therefore, it is possible that *S. elongatus* may have smaller eggs compared to the other taxa observed, a strategy that would maximize fecundity and spread risk among many gametes in a species with unpredictable spawning opportunities.

The estimated L_{50} for female *S. elongatus* in the current study (200 mm SL) is the first reported based on histological analysis for the species. The L_{min} observed here (179 mm SL) was similar to that reported for females in the central Pacific (182 mm SL; Clarke, 1983). Fisher (1983) reported a L_{min} of 125 mm SL in the Gulf of Mexico based primarily on microscopic viewing of whole mounts and limited histological sections. Similarly, the size range of transitional fish was lower in the Gulf of Mexico (86–117 mm; Fisher, 1983) compared to in the Slope Sea (103–147 mm). Off Hawaii, the largest male observed was 10 mm smaller than the smallest mature female (Clarke, 1983); while the author declared the species to be gonochoristic, transitional tissue is difficult to detect barring histological analysis (Sadovy and Shapiro, 1987).

4.4 Conclusions

As resources of the mesopelagic garner attention for potential extraction and as we aim to understand how climate change will impact the global oceans and biogeochemical cycling, life history data, and reproductive life history in particular, remain a critical data gap necessary to understand the impact mesopelagic fishes have on these systems. The female reproductive strategy of iteroparous batch spawning observed in *A. aculeatus* and *B. glaciale* in this study are consistent with the dominant strategies seen in epipelagic and shallow-water demersal fish species. Iteroparity is theoretically consistent with a life history that relies upon longevity to reach full reproductive potential, highlighting the risk of overharvesting smaller individuals. The probable multi-year oocyte development in *S. beanii* and the confirmed protandrous hermaphroditism in *S. elongatus* make these species vulnerable to mortality prior to contributing to reproduction. Furthermore, the taxa observed here are larger at maturity than congeners and conspecifics in other regions, underscoring the vulnerability of these populations to overexploitation due to directed or incidental fishing of immature individuals. Gaining species-level resolution and a fuller understanding of geographical and taxonomic diversity of reproductive traits within and among taxa is critical for management of some of the world's most abundant vertebrates, many of which are highly vulnerable to the looming threat of deep-water commercial extraction. Careful consideration of these (and similar)

data will be necessary for the development of a sustainable mid-water fishing management plan.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

The animal study was approved by Woods Hole Oceanographic Institution Institutional Animal Care and Use Committee (WHOI IACUC), Project ID numbers 24708.01 and BI26870.01. The study was conducted in accordance with the local legislation and institutional requirements.

Author contributions

LL: Conceptualization, Data curation, Formal Analysis, Investigation, Methodology, Resources, Software, Validation, Visualization, Writing – original draft, Writing – review & editing. HS: Data curation, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Writing – review & editing. JL: Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Writing – review & editing.

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Conflict of interest

The 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.

Generative AI statement

The author(s) declare that no Generative AI was used in the creation 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.2025.1582706/full#supplementary-material

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