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ARTICLE

A Life History Study of Atlantic Wolffish Resolves Bias and Imprecision in Length- and Age-at-Maturity Schedules by Recognizing Abortive Maturation

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Abstract

Stock assessments of U.S. Atlantic Wolffish *Anarhichas lupus* are hampered by a landings moratorium and low catches in fishery-independent surveys. Working with the commercial fishing industry, we collected hundreds of fish to overcome a lack of regionally specific life history information. Based on ages from sectioned otoliths, Atlantic Wolffish are long lived (maximum observed age: males = 31 years, females = 29 years). A Gompertz growth model showed that Atlantic Wolffish exhibit dimorphic growth—with larger males across all ages on average. Preliminary estimates of total mortality ranged from 0.15 to 0.21 and were lower than an estimate measured at the beginning of the moratorium. Based on gonad histology, a cohort of vitellogenic oocytes emerged in mature females by April and developed group synchronously to ovulate primarily in October. Skip spawning, which accounts for nonannual spawning, was

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observed in 5.6% of the mature females. Accounting for abortive maturation, a physiological event that delays functional maturation, improved precision and reduced bias of maturity estimates. The resulting median length at functional maturity was 53 cm total length (95% confidence interval = 49–56 cm), and the median age was 6.7 years old (6.2–7.2 years). These estimates are smaller and younger than elsewhere in the western North Atlantic Ocean, confirming that regionally specific maturity parameters are relevant when assessing reference points of the U.S. Atlantic Wolffish fishery.

The Atlantic Wolffish *Anarhichas lupus* is a boreal, marine species distributed on both sides of the North Atlantic Ocean. In the eastern Atlantic Ocean, Atlantic Wolffish is an important fishery species and has potential for aquaculture (e.g., von Beese and Kändler 1969; Jónsson 1982; Moksness and Pavlov 1996; Le François et al. 2010, 2021). Recent assessments in the North Sea suggest declines in abundance and contractions in geographic distribution consistent with effects of fishing pressure and climate change (Bluemel et al. 2022), similar to that reported for other fishery species in the deep sea (e.g., Lloret et al. 2021).

In the western Atlantic Ocean, Atlantic Wolffish ranges from Greenland and Labrador to the Gulf of Maine, where it has historically been part of groundfish fisheries (Bigelow and Schroeder 1953; Albikovskaya 1982; Riget and Messtorff 1988). In our study area, the Gulf of Maine, Atlantic Wolffish are distributed from 20 to 300 m, along the northern flank of Georges Bank, and in both U.S. and Canadian waters, representing the southern extent of this species' range (Figure 1; Nelson and Ross 1992; Briggs and Waldman 2002; Rountree 2002).

The population status in the Gulf of Maine has not been good for some time. In the United States, Atlantic Wolffish was designated a species of concern under the U.S. Endangered Species Act in 2010 (AWBRT 2009), with a similar designation in Canada since the early 2000s (DFO 2013). Although the species of concern status has been lifted, a moratorium on U.S. Atlantic Wolffish landings remains.

The most recent assessment of U.S. Atlantic Wolffish concludes that the population is overfished but that overfishing is not occurring (NEFSC 2020). However, low catches in fishery-independent surveys precludes a reliable abundance index (Helser and Hayes 1995). In addition, the landings moratorium precludes analysis of commercial landings data and places greater emphasis on discard mortality. Another issue, the focus here, is a lack of regionally specific information on age, growth, and reproduction (NDPSWG 2009; Fairchild et al. 2015). In particular, the Atlantic Wolffish maturity schedule, which defines the spawning stock in an assessment, had been deemed imprecise and inaccurate. Median length at maturity, $L50$, varied widely, from 25 to 40 cm TL (by season [spring, fall]

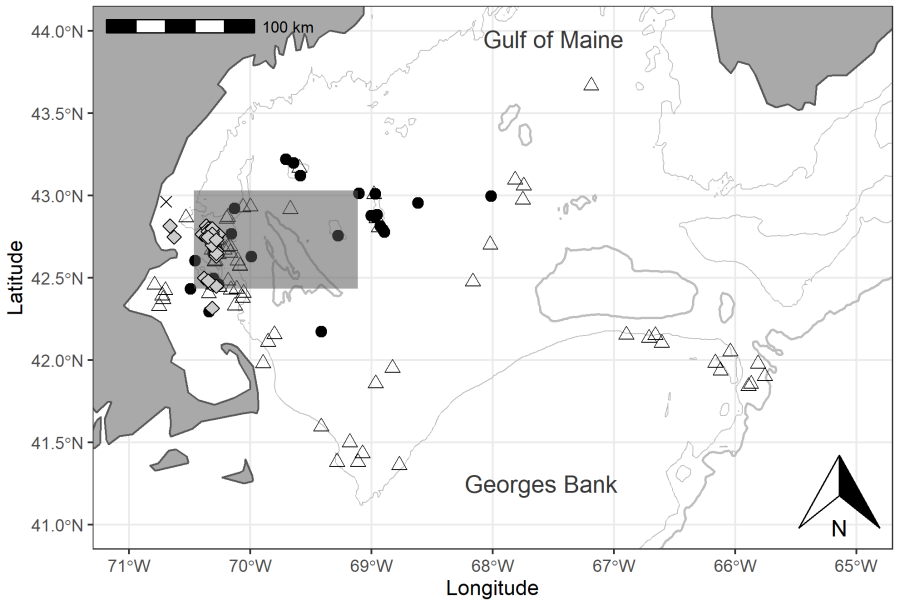

FIGURE 1. Capture locations for female Atlantic Wolffish by sampling program: National Marine Fisheries Service–Northeast Fisheries Science Center (NMFS–NEFSC) bottom longline survey (filled circles), NMFS–NEFSC bottom trawl survey (open triangles), University of New Hampshire cooperative commercial trawl fishing (gray diamonds) and lobster pot (×), and Northeast Cooperative Research Study Fleet program (fish caught within the boundaries of the shaded rectangle). These sampling locations depict the full scope of sampling for females used to examine reproduction. Age samples also included males and the geographic coverage was similar. The 100- and 250-m isobaths are depicted as a thin and thick line, respectively.

and decade [1990s, 2000s]; NDPSWG 2009; NEFSC 2012, 2015; NEFSC, unpublished data [see Supplemental Materials 1]). Some imprecision was likely caused by low sample sizes used to fit a logistic estimator (<60 females per season and decade); small samples sizes and a prolonged period of vitellogenesis (spring–fall) also stymie an effective training program to identify maturity classes during at-sea operations. Moreover, these *L*50s were much smaller than reported elsewhere, in both Canada (range = 51–68 cm TL by region; Templeman 1986) and Iceland (55–73 cm TL by region and year; Gunnarsson et al. 2006; Gunnarsson 2014), which suggests, at best, regionally specific maturity schedules. The lack of confidence in a validated, locally derived maturity schedule was a concern in determining reference points in earlier assessments (e.g., NDPSWG 2009; NEFSC 2012, 2015).

Our goal was to improve the life history information relevant to stock assessment of Atlantic Wolffish. To overcome a persistent challenge (i.e., to achieve sufficient numbers and sizes of Atlantic Wolffish) we engaged in partnership with the commercial fishing industry. This cooperative sampling, in combination with other fishery-independent sampling throughout the Gulf of Maine, collected hundreds of Atlantic Wolffish, using complementary fishing gears to sample the full size and age range of both sexes. Our samples are pooled over a 10-year period, which confounds the ability to track effects of cohort strength or of specific environmental events, such as the warming this region is experiencing (McBride et al. 2018; Friedland et al. 2020). Nonetheless, our enhanced sample sizes made the difference.

Using otolith ages, we are the first to report on sex-specific growth rates for our region, and we evaluate how mortality rates have changed during a moratorium on fishery landings. Using gonad histology, we describe both abortive maturation and skip spawning (Rideout and Tomkiewicz 2011), noting that abortive maturation in our region had previously led to biased underestimates of maturity that are now corrected. We discuss how this information has been used to provide management advice.

METHODS

In the field.— Atlantic Wolffish were obtained from five sources: (1) the Northeast Cooperative Research Study Fleet program, a bottom trawl fishery, (2) the Northeast Fisheries Science Center (NEFSC) bottom trawl survey, (3) the NEFSC bottom longline survey, (4) bycatch from the inshore New Hampshire lobster pot fishery, and (5) a commercial bottom trawling vessel working with scientists from the University of New Hampshire (UNH) on board. Most samples were collected by source 5, trawling in the Stellwagen Bank National Marine Sanctuary, part of Massachusetts Bay, during May–September 2017. Fairchild et al. (2015) concluded that the Stellwagen Bank National Marine Sanctuary was an Atlantic Wolffish foraging area during the summer season. And all together, these sources applied three different gears (bottom trawl, long line, and lobster pot), with overlapping geographic ranges that covered the Gulf of Maine, including Georges Bank (Figure 1).

Fish sampled for further laboratory analysis were collected 9 months of the year and from 2009 to 2018 (Supplemental Materials 2). Total length was measured to the nearest centimeter, whole body weight was measured to the nearest gram, and gonad weight was measured to the nearest 1 g (at sea) or 0.1 g (in the lab). Samples of otolith and gonads were taken for determination of age and reproduction, respectively.

Otolith aging.— Sagittal otoliths were typically removed in the laboratory rather than at sea because of their small size. Upon removal, they were stored dry in envelopes. A total of 474 otoliths were readable as both whole and sectioned preparations, and two readers assigned ages for each otolith, both pre- and postsectioning. For otoliths in which age assignment did not agree between readers, both readers examined the structure together and agreed on a consensus age.

Fairchild et al. (2015) reported ages using otolith sections from an independent sampling in 2011, and here, we evaluate both whole and sectioned otolith methods explicitly following the criteria of McBride (2015): age tables, percent agreement, Chang's (1982) coefficient of variation, and tests of symmetry (Table 1; see also Supplemental Materials 1: Age, Growth & Mortality). Generally, precision declined with older age-groups; specifically, percent agreement declined and Chang's (1982) CV increased, except for sectioned otoliths, for which the CV ranged narrowly from 7.1 to 3.2. Qualitatively, whole-otolith precision decreased as age-group increased and the otoliths thickened. Identifying the first annuli and annuli near the edge was more difficult in whole than in sectioned otoliths. Between-reader disagreements were mostly within 1 year (>70%) and were resolved with subsequent consensus agreement of the first annulus location. Tests of symmetry showed that whole-otolith ages were biased low across all ages compared with sectioned otolith ages. Given the results outlined here, with proper training, sectioning the otoliths of Atlantic Wolffish led to more precise, more accurate ages than aging whole otoliths. Final ages reported in the results were based on consensus ages from two readers using the sectioned-otolith method.

Growth and mortality.— Growth modeling evaluated two different models (i.e., von Bertalanffy and Gompertz growth models) and sex-specific differences (see Supplemental Materials 1: Age, Growth & Mortality, for specific models and all results). Size and age data of 205 males and 241 females were fit to both models and

TABLE 1. Evaluation of precision and bias of Atlantic Wolffish ages, when comparing two methods (whole versus sectioned otoliths) and two readers. Sectioned-otolith consensus ages were used to create age-groupings (e.g., 0–5, 6–10,… 21 years and older). Sample size is indicated as *n*. Percent agreement (PA) is presented to the exact year and within 1 year; CV was calculated by the formula of Chang (1982). For bias, Evans–Hoenig and Bowker's tests of symmetry were performed and evaluated against an alpha value of 0.05 (one asterisk), 0.01 (two asterisks), and 0.001 (three asterisks), where "ns" signifies nonsignificance for both tests, except for "†" which indicates a Evans–Hoenig test <0.05 and a Bowker's test that is not significant.

Structure: reader 1	Structure: reader 2	Age-group	*n*	PA	PA, within 1 year	CV	Bias
Whole: R1	Whole: R2	All	474	50.0	85.0	7.1	ns
	Whole: R2	0–5	147	74.2	98.0	7.1	ns
	Whole: R2	6–10	192	46.4	88.5	6.5	ns
	Whole: R2	11–15	90	32.2	74.4	6.5	ns
	Whole: R2	16–20	21	19.1	57.1	8.5	ns
	Whole: R2	21+	24	25.0	41.7	13.1	ns
Sectioned: R1	Sectioned: R2	All	474	47.7	90.7	6.4	***
	Sectioned: R2	0–5	147	76.2	100.0	6.9	ns
	Sectioned: R2	6–10	192	35.9	92.2	7.1	***
	Sectioned: R2	11–15	90	33.3	81.1	5.3	***
	Sectioned: R2	16–20	21	33.3	71.4	4.5	†
	Sectioned: R2	21+	24	33.3	75.0	3.2	ns
Whole (consensus)	Sectioned (consensus)	All	474	48.1	85.4	6.9	***
	Sectioned (consensus)	0–5	147	78.2	99.3	4.7	ns
	Sectioned (consensus)	6–10	192	41.7	89.6	6.8	***
	Sectioned (consensus)	11–15	90	33.3	86.7	5.0	***
	Sectioned (consensus)	16–20	21	14.3	33.3	10.3	ns
	Sectioned (consensus)	21+	24	0.0	8.3	25.6	***

evaluated using Akaike information criterion (AIC) within R software (The R project for statistical computing; http://www.R-project.org; version 3.6.3). Integer ages were estimated using July 1 as a biological birthday, based on a spawning peak in October and an egg incubation time of 9–10 months (Keats et al. 1985; Moksness and Pavlov 1996).

Chapman–Robson (Chapman and Robson 1960) mortality estimates were calculated using the FSA package in R (FSA version 0.8.30; https://github.com/droglenc/FSA). Mortality was calculated with all data combined by sex, by gear, and for each sex by gear, including 95% confidence intervals. Sample sizes, by gear, were sufficient only for the NMFS–NEFSC bottom trawl survey and the UNH trawl sampling.

Gonad histology.— A total of 255 females were examined for reproductive traits (Supplemental Materials 2). Ovary mass (±1 g) was recorded, and approximately 1 cm^3 of tissue was taken from the middle of either lobe and fixed in 10% buffered formalin. This tissue subsample was trimmed later to <4 mm thickness, placed in a histology cassette, and transferred to 70% ethyl alcohol. These subsamples were dehydrated in a series of increasing ethyl alcohol concentrations before embedding in wax, and thin sections (5 µm) were stained with Schiffs–Mallory trichrome and mounted on microscope slides. In the lab, histology slides were viewed (70–700×) on a large monitor using a microscope and digital camera system.

Identification of oocyte stages, including postovulatory follicles (POFs) and atresia, was modified from Grier et al. (2009), Witthames et al. (2010), and Press et al. (2014). The most advanced oocyte stage (MAOS) was assigned as 1 of 10 stages: one stage of primary growth, four cortical alveolar stages, four vitellogenic stages, and one stage of hydration (full descriptions in Table 2). Postovulatory follicles were classified into three stages: (1) recent, (2) older, and (3) oldest. Two stages of follicular atresia were identified: (1) alpha and (2) beta. Lots of atresia was noted when 50% or greater of the MAOS was in either stage of follicular atresia. These cellular stages were evaluated to assign a maturity class to individual fish (see below). Tunica thickness measurements less than or greater than 300 µm were considered thin and thick, respectively (see bimodal distribution of tunica thickness in Supplemental Materials).

Oocyte diameter frequencies were plotted to document group synchronous oocyte development with respect to vitellogenesis. Images obtained from histology slides were used to capture stage-specific oocyte diameters from April to November. Mature fish were selected for these measurements if their relative gonad weight or gonadosomatic

TABLE 2. Histological criteria for Atlantic Wolffish. Definitions for 10 oocyte stages, postovulatory follicles, and follicular atresia are described. Ranges of fish total length (cm) and ages (years) and sample size (n) are indicated for the total sample as aggregated by the most advanced oocyte stage per fish.

Histology stage	Criteria
	Oocyte stages
Primary growth (PG) 12.5–22 cm, 1–5 years, $n = 13$	Chromatin nucleolus and perinucleolar oocytes were typically observed together and classified as primary growth. These are highly basophilic with a single or few prominent centered nucleoli (chromatin nucleolus) or many peripheral nucleoli (perinucleolar).
Cortical alveolar 1 (C1) 21–25.5 cm, 2–3 years, $n = 4$	Cortical alveoli first appear in the cytoplasm along the periphery of the oocyte as small white, circular inclusions.
Cortical alveolar 2 (C2) 23–64 cm, 2–4 years, $n = 11$	Cortical alveoli fill with dark dots and increase in number, exhibiting a dark ring around the periphery of the oocyte.
Cortical alveolar 3 (C3) 22–88 cm, 3–20 years, $n = 42$	The cortical alveoli continue to grow in number and fill the cytoplasm, progressing towards the germinal vesicle.
Cortical alveolar 4 (C4) 33–95 cm, 3–29 years, $n = 38$	The cytoplasm of the oocyte is completely filled with cortical alveoli, and oil droplets begin to form around the germinal vesicle as small white dots.
Vitellogenesis 1 (V1) 52–99 cm, 6–19 years, $n = 17$	Lipoprotein yolk globules begin to appear as small red dots in the cytoplasm, while the oil droplets increase in number and size. Cortical alveoli are still present around the zona pellucida. The germinal vesicle may be offset, towards the periphery of the oocyte.
Vitellogenesis 2 (V2) 52–109 cm, 7–22 years, $n = 32$	Lipoprotein yolk globules increase in number and size around the germinal epithelium as the cortical alveoli get pushed out towards the zona pellucida, giving the oocyte a halo-like look. The germinal vesicle may be offset, towards the periphery of the oocyte.
Vitellogenesis 3 (V3) 48–90 cm, 6–27 years, $n = 64$	Lipoprotein yolk globules continue to fill the whole cytoplasm and grow in size. The germinal vesicle is likely offset, towards the periphery of the oocyte. A small ring of cortical alveoli can be seen proximal to the zona pellucida.
Vitellogenesis 4 (V4) 55–82 cm, 7–25 years, $n = 31$	Remaining in the follicle, lipoprotein yolk globules completely fill the cytoplasm and begin fusing together. The germinal vesicle is sometimes still present along the periphery but is breaking down.
Hydration (H) 58–69 cm, 6–13 years, $n = 3$	While remaining within the follicle, yolk globules are completely fused and water content is absorbed, increasing the oocyte in size significantly.
	Postovulatory follicle
Recent	A complex structure consisting of granulosa cells (inner layer) and theca cells (outer layer). The columnar granulosa cells are typically separated from the theca, forming an inner ring, and both layers stain light purple. The follicle is large, loosely arranged, and irregular in shape.
Older	The granulosa and theca cell layers remain distinguishable. The granulosa cell layer, which is no longer columnar, stains a deep purple color and the theca cell layer a light purple. The follicle is more compact, approximately the size of a perinucleolar oocyte. The lumen is still visible, but much reduced in size compared to Recent postovulatory follicles.
Oldest	The two-layer structure may be identifiable in some instances, but cell integrity is greatly deteriorated and stains dark purple. The follicle is almost entirely collapsed without a distinguishable lumen and smaller in size than a perinucleolar oocyte.
	Follicular atresia
Alpha	The germinal vesicle disintegrates, the zona pellucida breaks down, and lipoprotein yolk globules are present in early and late vitellogenic oocytes.

TABLE 2. Continued.

Histology stage	Criteria
Beta	Internal oocyte components (lipoprotein yolk globules, cortical alveoli) are digested through phagocytosis. Oocyte appears to have a bubble-like appearance.
Extensive	The presence of 50% or more of alpha and/or beta atresia. Fish exhibiting lots of atresia during certain times of the year (late summer or fall) can be determined to be skipping (mature) or aborting maturation (immature).

index (GSI) > 1.0 (i.e., GSI = ovary weight/ovary-free body weight × 100). Primary growth and cortical alveolar oocytes were measured only if the nucleus was present to reduce bias associated with sectioning. As the oocyte advanced through the stages of vitellogenesis, the nucleus was not always visible due to its large size in these stages and the eventual migration of the nucleus (V2 and V3) and its ultimate breakdown (V4). In these cases, oocytes were measured that represented the average size of oocytes available on the slide.

Reproductive interpretation.—Our female maturity scheme was adapted from Burnett et al. (1989) as informed by order of germ cell development, other gonad histology markers, and time of year. The MAOS, tunica thickness, signs of spawning (POFs), and time of year were all considered when determining 1 of 10 maturity classes (Supplemental Materials 2). Time of year was broken up into four seasons: winter (December–February), spring (March–May), summer (June–August), and fall (September–November).

Three classes for immature fish were determined: (1) immature, (2) immature maturing, and (3) abortive maturation (Figure 2). Immature fish had a MAOS of primary growth (PG) or early cortical alveoli (C1–C2) and a thin tunica wall at any time during the year. Immature maturing fish were identified in the summer and fall by an MAOS of late cortical alveolar (C3–C4), a thin tunica wall, and no signs of previous spawning. Abortive maturation was identified in the summer and fall, characterized by extensive atresia (>50% of the leading cohort in an atretic stage), a thin tunica wall, no evidence of past spawning (i.e., no POFs), and the viable MAOS was a late cortical alveolar stage (C3–C4).

Eight classes of mature fish were determined: (1) first time mature, (2) developing, (3, 4) two classes of spawning active (ripe, ripe and running), (5) spent, (6) resting, and (7) skip spawning, and (8) repeat mature (Figure 2). First-time-mature fish were identified in the winter and spring by a MAOS of late cortical alveolar or early vitellogenesis (V1) and a thin tunica wall. Repeat mature had an MAOS of early vitellogenesis (V1) and exhibited signs of prior spawning (thick tunica wall or POFs). Developing fish had an MAOS of more advanced vitellogenesis (V2–V4). Spawning active fish had an MAOS of hydration and, as Atlantic Wolffish is a total spawner, we did not expect a range of new–old POFs mixed with vitellogenic oocytes. Spent fish had an MAOS of cortical alveolar and signs of recent spawning (recent POFs, encysted oocytes or eggs). Resting fish had an MAOS of any cortical alveolar stage, a thick tunica, and older or oldest POFs. Skip-spawning fish had an extensive amount of atretic yolked cells but did not have a viable MAOS past late cortical alveolar during the prespawning season (July–September). Skip spawners showed no signs of recent spawning (POFs, encysted oocytes or eggs) but had thick tunica (indicative of a mature fish that spawned previously).

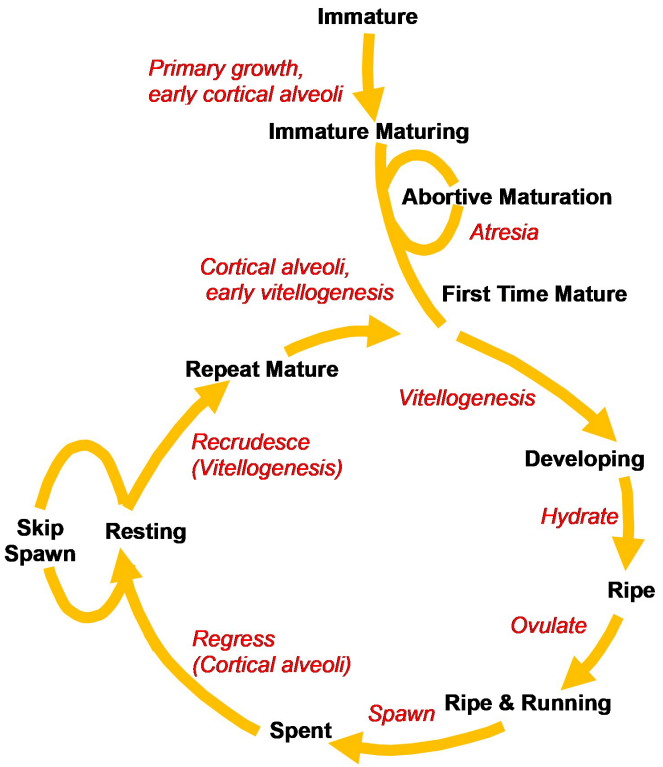

FIGURE 2. The reproductive cycle of a female Atlantic Wolffish, showing 11 maturity classes composed of 3 immature classes: (1) immature, (2) immature maturing, and (3) abortive maturation, and 8 mature classes: (1) first time mature, (2) developing, (3) ripe, (4) ripe and running, (5) spent, (6) resting, (7) skip spawner, and (8) repeat mature. Cellular criteria (in red italics) are included to help identify transition processes from one class to the next.

The binomial, logistic model was used to estimate maturity parameters:

$$\text{logit}(\text{mature}) = e^{a+bX}/\left(1+e^{a+bX}\right),$$

where a and b are estimated, $|a/b|$ is the inflection point, and X is length or age. Confidence limits (95%) were estimated by bootstrapping the data using the sizeMat package in R (https://github.com/ejosymart/sizeMat).

RESULTS

Age and Growth

Atlantic Wolffish were assigned ages from 0 to 31 years (Figure 3A). The average age of both sexes was the same: males = 8.9 years (95% confidence interval = 8.0–9.7) and females = 8.9 years (8.3–9.5). The maximum age of males was slightly older (age 31; $n = 205$) than that of females (age 29; $n = 241$).

By gear, the NMFS–NEFSC trawl survey captured the full age range (0–31 years; Figure 3B). The UNH trawl, with a larger mesh, had a narrower age range (6–31 years). The other gears had smaller sample sizes and the ages were within 4–16 years.

Atlantic Wolffish demonstrated sexually dimorphic growth. In terms of model selection, the Gompertz model had the least uncertainty as the von Bertalanffy models scored ΔAIC values (difference in Akaike information criterion values) consistently higher than the Gompertz models (Table 3). When asymptotic size was allowed to vary in either model, males reached a larger size than females by several centimeters, and the von Bertalanffy model estimated high asymptotic sizes by several centimeters for both sexes (Supplemental Materials 1). The final selected model for length (cm) at age t (years) was $84.7e^{-e^{(-0.249[t-3.31])}}$ for males and $79.8e^{-e^{(-0.249[t-3.31])}}$ for females (model Go5; Tables 3, 4; Figure 4). Although males were only 0.5 cm larger at age 0, they were 4.1 cm larger at age 10, 4.8 cm larger at age 20, and 4.9 cm larger at age 30, as estimated with the Go5 Gompertz model.

The Chapman–Robson estimate of total mortality (Z) for all data combined was 0.20 (95% confidence interval = 0.16–0.23) for ages 8 and older. Estimates of Z varied by combinations of gear and sex from a low of 0.15 (0.09–0.21) for males captured in the UNH trawl to a high of 0.21 (0.11–0.31) for males captured in the NMFS–NEFSC trawl or 0.21 (0.15–0.27) for all females (Supplemental Materials, total mortality estimates).

Reproduction

Oogenesis required at least 6 years to complete. Females with only primary growth oocytes were young (1–5 years) and small (12.5–22 cm TL) (Figure 5A). Early development

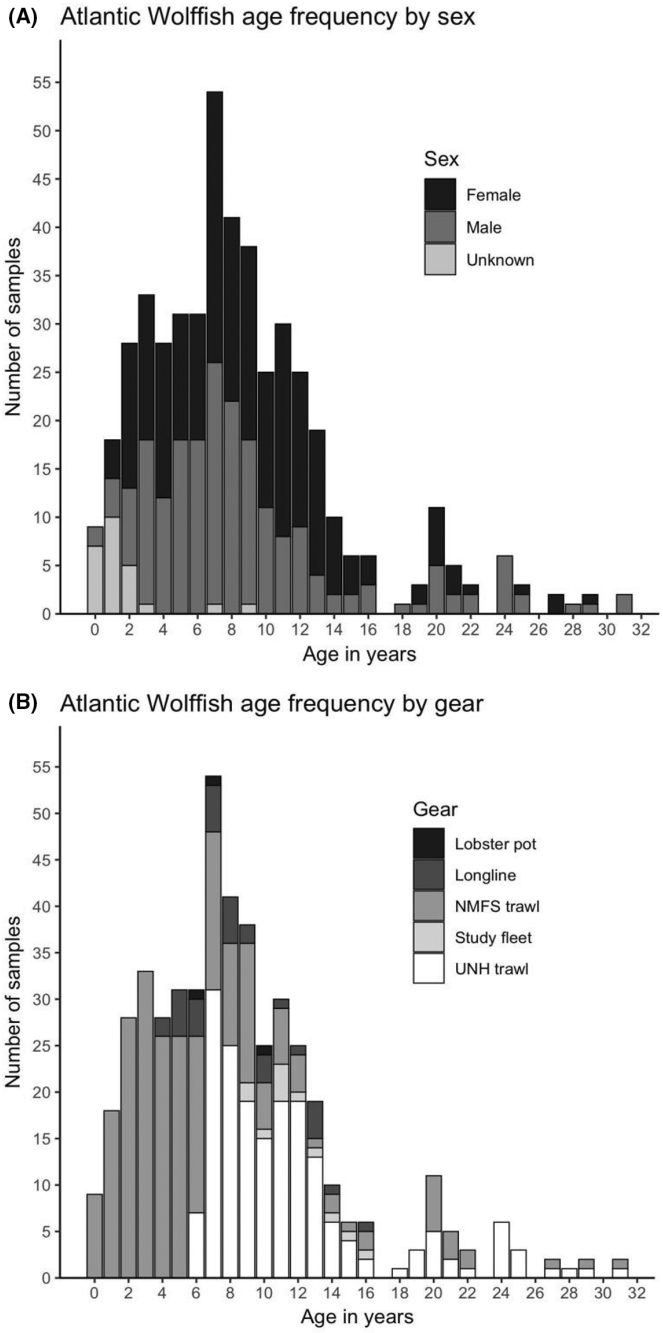

FIGURE 3. Age structure of Atlantic Wolffish by **(A)** sex and **(B)** gear. Sampling gears are the same as in Figure 1.

of cortical alveoli (i.e., stages C1, C2; Table 2; Figure 5B, C), as the MAOS, was not observed in fish younger than age 2 (maximum, age 4) or smaller than 21 cm (maximum, 64 cm). Complete development of cortical alveoli (i.e., C3, C4; Table 1; Figure 5C, D) was not observed in fish younger than age 3 (maximum, age 29) or smaller than 22 cm (maximum, 95 cm). Evidence of vitellogenesis required additional years as yolked stages (Figure 5E–G) or hydrated oocytes

TABLE 3. Atlantic Wolffish growth models. Tabulation of the difference in AIC values (ΔAIC) among various configurations of the von Bertalanffy growth model and the Gompertz growth model. The final model selected was model Go5. Models are listed in descending order of the error terms estimated, from the full model that all three parameters are allowed to vary between sexes (plus overall model error; df = 7) to a fully reduced model, for which no parameter varied (df = 4). See Supplemental Materials 1: Age, Growth & Mortality for complete presentation of the models and the parameter estimates.

Model	Fixed parameters	df	ΔAIC
von Bertalanffy growth model			
vB1	None	7	16.5
vB2	Fix L_∞	6	15.9
vB3	Fix K	6	14.6
vB4	Fix t_0	6	14.7
vB5	Fix K, t_0	5	12.8
vB6	Fix L_∞, t_0	5	13.9
vB7	Fix L_∞, K	5	17.8
vB8	Fix all	4	22.8
Gompertz model			
Go1	None	7	3.9
Go2	Fix L_∞	6	5.9
Go3	Fix G	6	1.9
Go4	Fix X_0	6	1.9
Go5	Fix G, X_0	5	0.0
Go6	Fix L_∞, X_0	5	4.5
Go7	Fix L_∞, G	5	9.0
Go8	Fix all	4	14.3

TABLE 4. The final model selected (model Go5) from the Atlantic Wolffish growth models examined in Table 3.

Parameters	Estimate	SE	t-value	Pr(>|t|)
$L_\infty F$	79.76	1.418	56.25	<0.0001
G	0.2489	0.0131	18.94	<0.0001
X_0	3.311	0.1215	27.26	<0.0001
$L_\infty M$	84.67	1.526	55.48	<0.0001

(Figure 5H, I) were not observed in fish younger than 6 years (maximum, age 27) or smaller than 48 cm (maximum, 105 cm). Indication of oocyte maturation included migration and breakdown of the nucleus and hydration of the oocyte (Figure 5). A single female with an ovulated egg, possibly encysted, together with sperm, was observed in October (not pictured).

Group synchrony of oocytes with respect to vitellogenesis required most of the year as a group of oocyte advances synchronously from 0.5–1.0 mm in April to 3–4 mm in October (Figure 6). Vitellogenesis likely started earlier than April, but we did not have winter collections to document this.

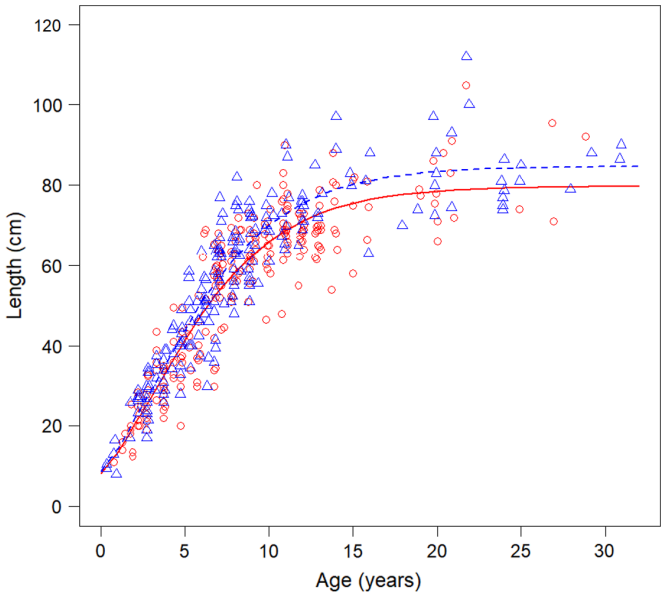

FIGURE 4. Size at age of Atlantic Wolffish was dimorphic by sex. Males (blue triangles) were consistently larger than females (red circles), on average. The predicted curves use model Go5, selected by AIC (Tables 3, 4), and plot males (dashed line) and females (solid line) separately.

A range of POFs was observed, from fresh and relatively uncollapsed to older, compact stages of degradation (Figure 5J–L). Again, as no mature females were collected from December to March, our observation of early POF degradation was limited, but older POFs were recognizable nearly a year later.

Both stages of atresia were observed in approximately half of the fish collected (Figure 7). Alpha or beta atresia, or a combination of the two, were seen in ovaries with quantities ranging from just a few atretic oocytes to extensive amounts in some individuals. Fish exhibiting extensive atresia of the leading cohort during summer and fall months were either classified as abortive maturation or skip spawners.

Peak spawning was observed in October based on changes in the relative gonad weight (GSI) and gonad histology. The GSI indicated a slow but steady recrudescence of the gonad as it increased over 10-fold from spring to fall (Figure 8), resulting from a cohort of yolked oocytes growing from 1 to 4 mm in diameter (Figure 6). Actively spawning females, defined by gonad histology as ripe, were observed on three different dates in August and October (Figure 9); these females were 59–69 cm and geographically widespread (41.4–42.7°N, 68.0–70.3°W). The GSI dropped in October and spent fish appeared in October and November. The ovary weight of mature females returned to 0.1 g by November, signaling a starting point for rebuilding a cohort of oocytes for the next spawning season.

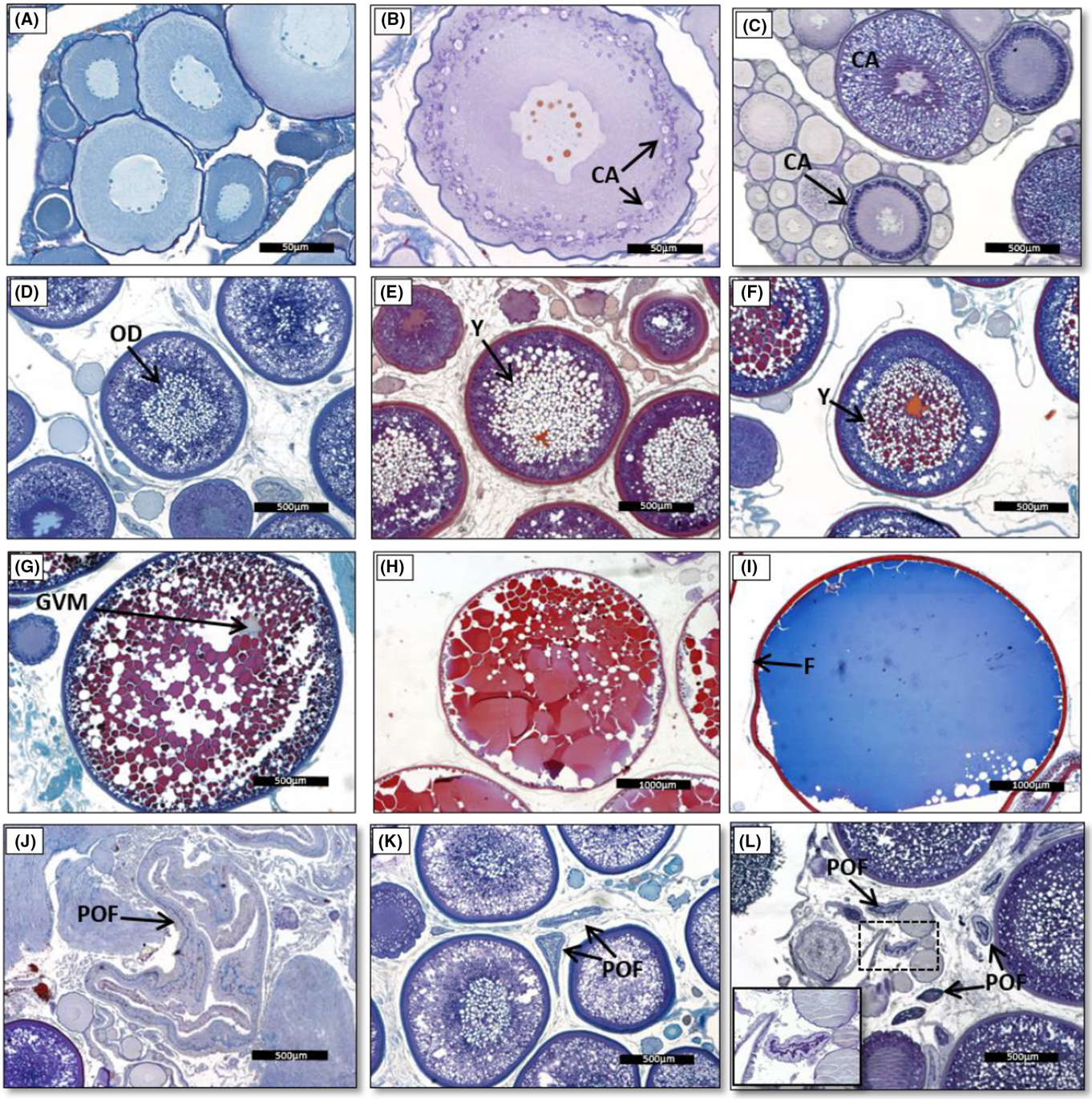

FIGURE 5. This study captured all major oocyte stages of Atlantic Wolffish oogenesis: **(A)** primary growth oocyte, **(B)** oocytes in early-stage cortical alveoli, **(C)** oocytes in midstage cortical alveoli, **(D)** oocytes in late-stage cortical alveoli, **(E)** early-stage vitellogenesis, **(F)** midstage vitellogenesis, **(G)** the migration of the germinal vesicle, **(H)** late-stage vitellogenesis exhibiting the coalescence of yolk, **(I)** hydration of the oocyte still in the follicle, **(J)** recent postovulatory follicles (POFs), **(K)** older POFs, and **(L)** oldest POFs. Abbreviations are as follows: CA = cortical alveoli, F = follicle, GVM = germinal vesicle migration, OD = oil droplets, Y = yolk, and POF = postovulatory follicle. Scale bars are marked as 50, 500, or 1,000 microns.

Deviations from regular maturation and spawning were noted. Skip spawning was observed in September (Figure 9) for a single female (67 cm TL, 9 years old). This individual had a thick tunica wall, an indication of prior spawning, but no current signs of spawning, in addition to an extensive amount of atretic oocytes being

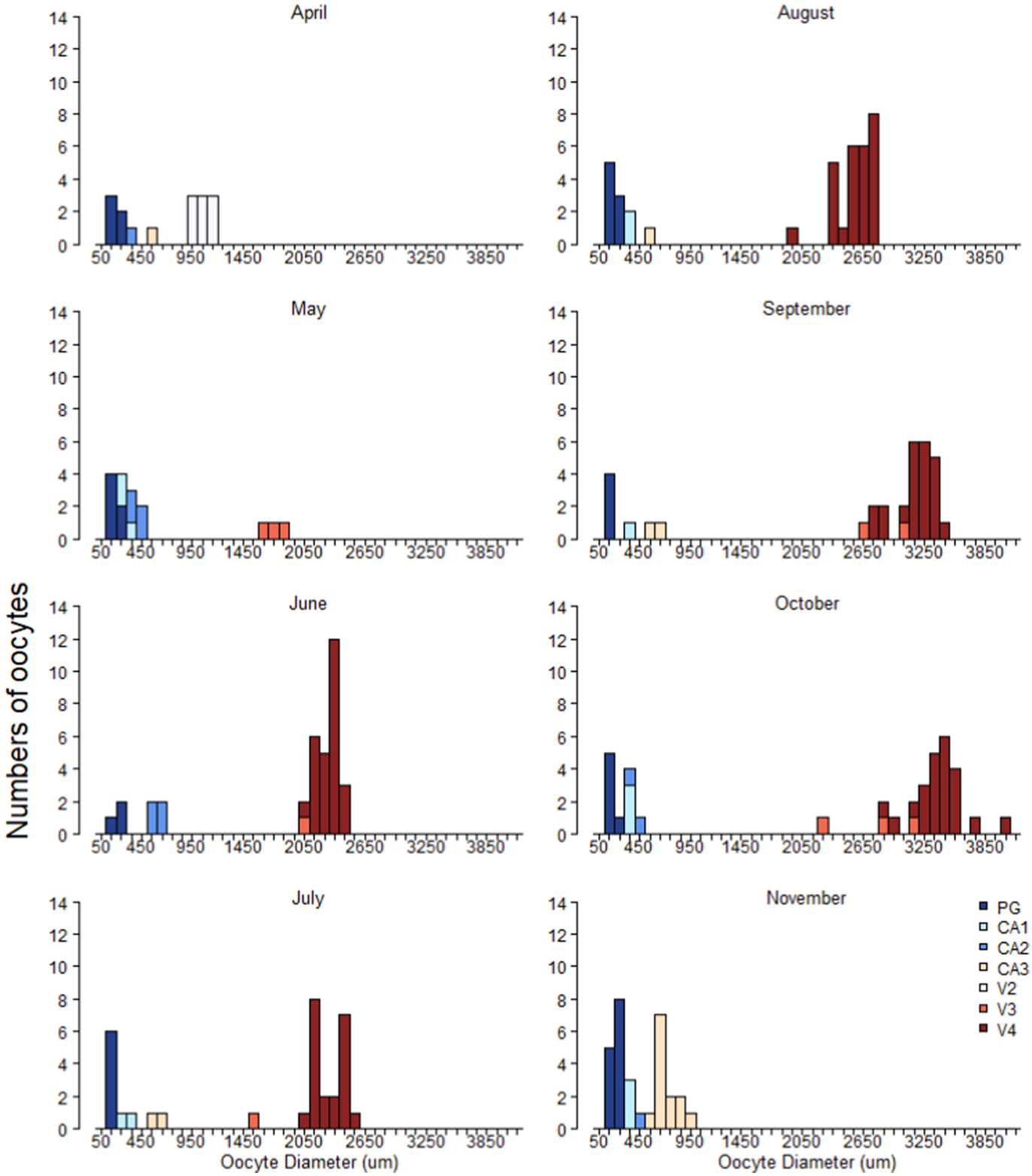

FIGURE 6. Mature female Atlantic Wolffish exhibit group synchronous oocyte development with respect to vitellogenesis. This was evident from oocyte-diameter frequencies measured from histology slides. Every month is represented by one fish that had a gonad–somatic index (ovary weight/ovary-free body weight × 100) greater than 1.0. Oocyte stage codes (PG–V4) are specified, as in Table 2.

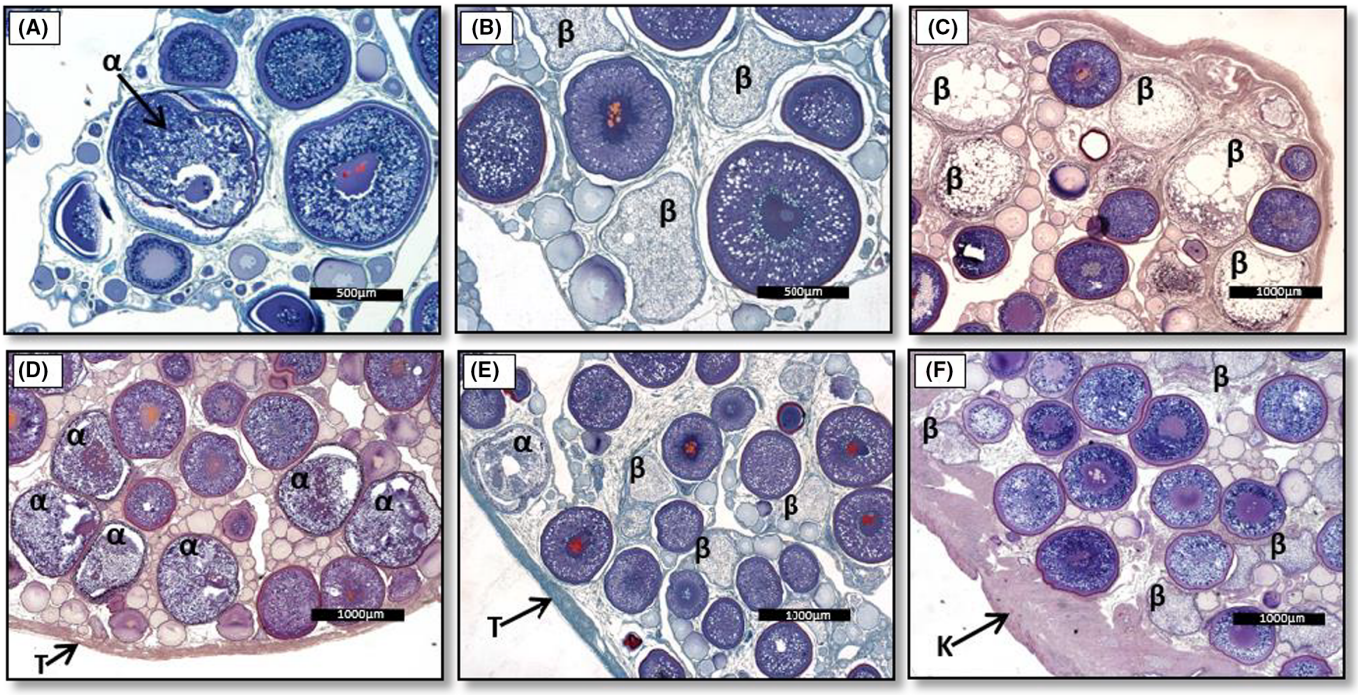

FIGURE 7. Follicular atresia in oocytes was important to identify maturity classes of Atlantic Wolffish: **(A)** alpha atresia, **(B)** beta atresia, **(C)** an extensive amount of beta atresia in advanced stage oocytes, **(D)–(E)** two fall fish exhibiting signs of aborting maturation with lots of alpha and beta atresia and a thin tunica wall, and **(F)** a fall fish skip spawning with large amounts of beta atresia, a thick tunica wall, and no signs of spawning. Abbreviations are as follows: α = alpha atresia, β = beta atresia, T = thin tunica wall, and K = thick tunica wall.

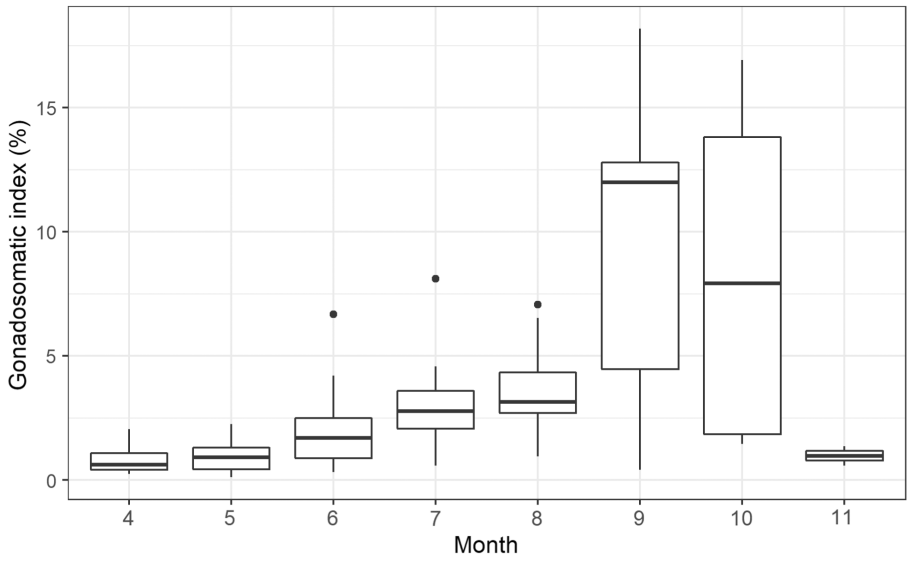

FIGURE 8. Mature female Atlantic Wolffish have a pronounced reproductive seasonality as depicted by monthly relative gonad indices (GSI = ovary weight/ovary-free body weight × 100). The sharp drop in GSI suggests most spawning occurred in or around October. The dark horizontal line is the median, the box contains the interquartile range, the whiskers indicate the nonoutlier range, and dots are outliers. The number of fish representing each month from April to November was 30, 47, 28, 36, 25, 7, 5, and 2, respectively (total $n = 180$).

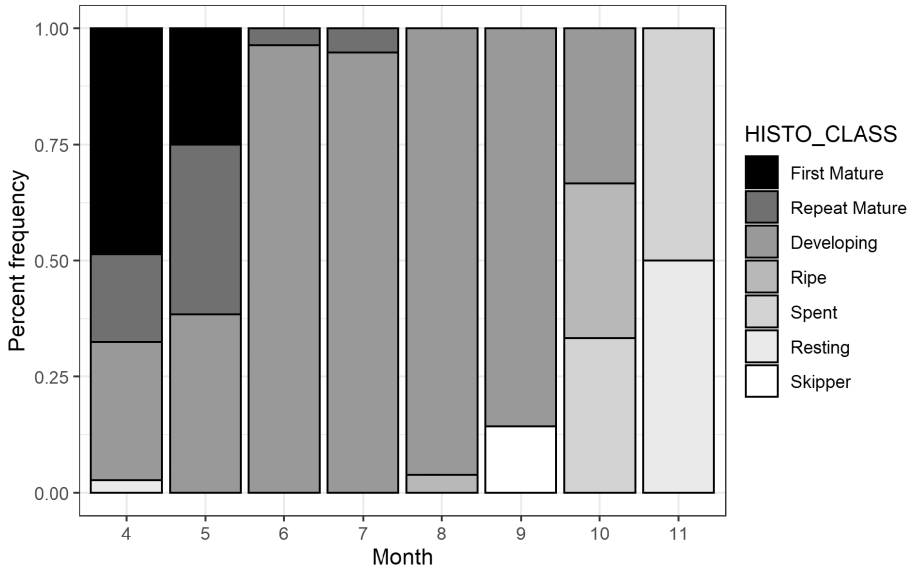

FIGURE 9. Reproductive seasonality, as depicted by percent frequency of maturity classes among mature female Atlantic Wolffish, depicts a several-months-long period of vitellogenesis. Actively spawning fish were observed in August and October. Maturity classes were determined by gonad histology (Figure 2). The number of fish representing each month from April to November was 37, 52, 28, 38, 26, 7, 6, and 2, respectively (total $n = 196$).

resorbed (Figure 7). As calculated during the prespawning period of July–September, 1 of 18 (5.6%) females with histological biomarkers of previous spawning were skip spawning.

Abortive maturation was not observed in the spring but was observed in 14 fish during the summer and fall months (Figures 7, 10). The fish ranged in size from 39.7 to 69 cm TL and were 3–9 years old. During summer and fall, fish revealing abortive maturation were smaller and younger than other mature fish (i.e., length: 51 ± 10 cm [mean $\pm$ SD; $n = 11$] versus 65 ± 11 cm [$n = 15$], $P = 0.010$; age: 6.0 ± 1.8 years [$n = 10$] versus 8.7 ± 3.7 years [$n = 12$], $P = 0.016$, respectively).

Even with the aid of histology, spring collections were misleading with respect to recognizing abortive maturation (i.e., small and young fish collected in spring looked mature but were susceptible to aborting their clutch of yolked oocytes by summer). Then, this requires a distinction between a physiological maturity (suggesting hormones initiating vitellogenesis for the first time) and a functional maturity (where the initiation of vitellogenesis leads to successful spawning), the latter of which is more relevant to estimate spawning stock biomass. Based on summer and fall samples, the median functional length at maturity, $L50$, was 53 cm total length, with 95% confidence that this point lay between 49 and 56 cm, and the median functional age at maturity, $A50$, was 6.7 years old, with 95% confidence that this point lay between 6.2 and 7.2 years (Figure 11).

DISCUSSION

Age and Growth

This study collected the widest age range (0–31 years) of Atlantic Wolffish to date. Fairchild et al. (2015) collected slightly older fish (33 years) but due to gear selectivity captured no fish younger than age 7. In other reports, Atlantic Wolffish were not aged older than 22 years (von Beese and Kändler 1969 [eastern North Atlantic]; Jónsson 1982 [Iceland]; Nelson and Ross 1992 [Gulf of Maine]; Liao and Lucas 2000 [North Sea]; and Gunnarsson et al. 2006 [Iceland]). We postulate that the lower maximum age reported by these other investigations is due to an aging bias introduced by using whole otoliths rather than sectioned otoliths. Our study observed a significant bias between aging methods for the older fish, where whole otoliths yielded younger ages than sectioned otoliths. We cannot, however, account for possible age truncation due to high fishing mortality rates in some of these areas.

The sample size, sex distribution, and age distribution of Atlantic Wolffish in this study allowed us to model growth by sex. Using the Gompertz model, which was found to be a better fit than the Von Bertalanffy model, we describe sexually dimorphic growth, with males reaching a larger size than females ($L_\infty = 84.7$ and 79.8 cm, respectively). Liao and Lucas (2000) reported a larger L_∞ for females than males (115 versus 111 cm); however, their results are not comparable to our results because they used a von Bertalanffy model only, they did not test for sexual dimorphism, and their maximum observed age was

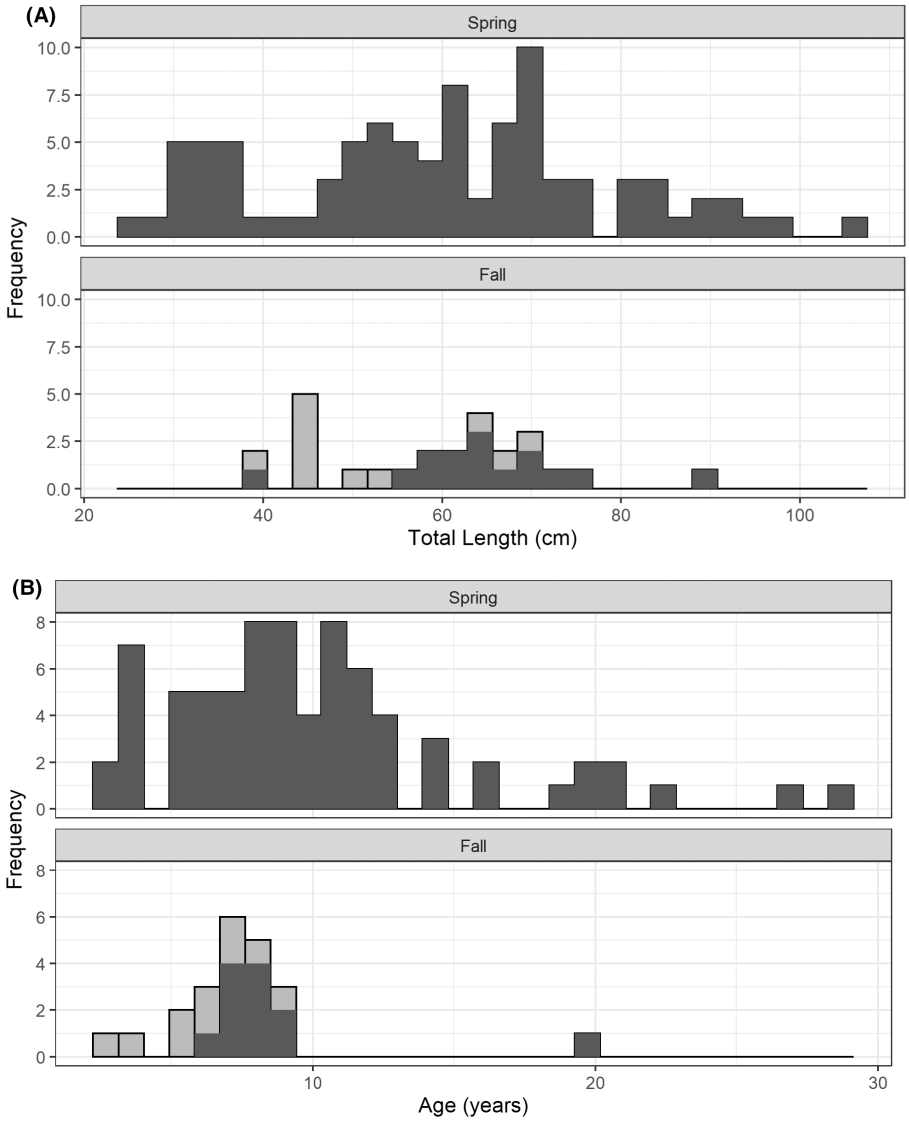

FIGURE 10. **(A)** Length and **(B)** age of mature female Atlantic Wolffish comparing spring and fall collections. Females are either a mature class in spring or fall (black bars) or experiencing abortive maturation in the fall ([stacked] gray bars).

15 years. Jónsson (1982) did not apply a growth model to data for several regions but noted that males grew to larger sizes and older ages than females. The sexual dimorphism observed in our study is of interest, both as a basic and applied research question, but has not been confirmed for this species elsewhere.

Nelson and Ross (1992) also found the Gompertz model to fit Atlantic Wolffish size-at-age data better than the von Bertalanffy model. A limited sample size prevented Nelson and Ross (1992) from sex-specific growth modeling, and their sex-combined model estimated an L_∞ of 98.89 cm. Von Beese and Kändler (1969) used the von Bertalanffy model to estimate a sex-combined L_∞ of 192.5 cm. Both this study and Nelson and Ross (1992) found that the von Bertalanffy model estimated higher asymptotic lengths than the Gompertz model.

We compared model parameters generated from our sectioned otolith ages to the parameters generated from our whole otolith ages (unpublished) and found minimal difference in the asymptotic lengths. We therefore conclude that the difference in aging method (whole otolith versus sectioned otolith) does not explain the differences in observed L_∞ between this study and Nelson and Ross (1992). Nelson and Ross (1992) stated that in their study "The imprecise estimates of the L_∞ indicated that older fish were probably sampled inadequately, and there were probably too few data to successfully model growth; therefore, the growth analyses presented are preliminary at

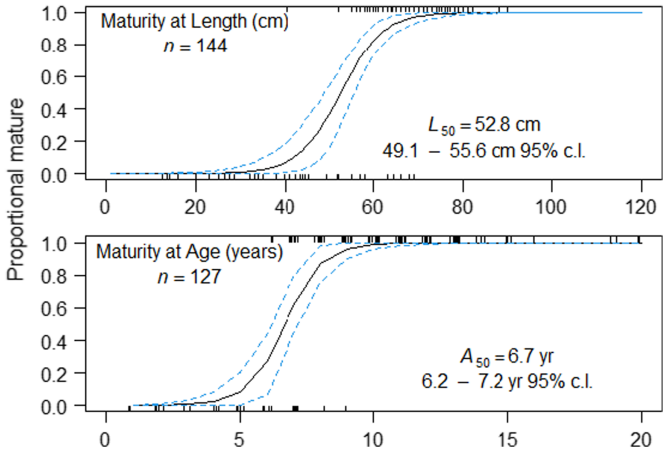

FIGURE 11. Maturity at length (top panel) and age (bottom panel) as calculated from female Atlantic Wolffish collected in the summer and fall. Data for immature and mature females are indicated on the bottom and top axes, respectively, by tick marks; tick marks are jiggered for the age plot to indicate sample size. Females experiencing abortive maturation are considered immature (i.e., these are functional maturity ogives). The one skipper (67 cm, 9 years [yr] old) is mature by definition (i.e., it has spawned in the past). The predicted curve is plotted as a solid black line and the 95% bootstrapped confidence limits are plotted as dashed blue lines. Point estimates are the median values, and 95% confidence limits (c.l.) are estimated by bootstrapping.

best." Given the uncertainty of Nelson and Ross (1992) and our extensive age sampling, we assert that the growth model presented in this paper is the most accurate to date.

Estimates of total mortality for Atlantic Wolffish were calculated in this study ($Z = 0.20$) as well as by Fairchild et al. (2015) ($Z = 0.35$). Fairchild et al. (2015) did their sampling in 2011, only 1 year after a moratorium on the retention of Atlantic Wolffish went into effect (NEFMC 2009), whereas most of the current age samples were collected in 2017. With six additional years of no fishing mortality between the studies, total mortality should decrease as observed, but there remains some uncertainty. Specifically, although sampling locations were similar between studies, sampling gear was different. Mesh size was the same between Fairchild et al. (2015) and the UNH trawl net used in this study, but Fairchild et al. (2015) used a square mesh while the current study used a diamond mesh. The size selectivity difference between the nets makes comparing mortality estimates inconclusive, and while the current stock assessment model is length based, not age based, our efforts to document the age structure and longevity of Atlantic Wolffish in different periods serves as baselines for future comparisons.

Reproduction

Previous evidence that Atlantic Wolffish are capital breeders (i.e., they store energy and draw on it later for reproduction; McBride et al. 2015) matches our observation that females are storing multiple annual cohorts of oocytes in a number of cortial alveoli stages. All this in addition to a unimodal clutch of vitellogenic oocytes produced in spring, which develops for months for a fall spawning event (i.e., group synchronous, determinate fecundity). This type of multiyear process for oogenesis has also been noted by von Beese and Kändler (1969), Pavlov and Novikov (1993), and Gunnarsson et al. (2006). Atlantic Wolffish have internal fertilization, and females release all their eggs (i.e., a total spawner) before the beginning of cleavage (Johannessen et al. 1993; Pavlov and Moksness 1996).

Energy acquisition and allocation in Atlantic Wolffish is also distinctly seasonal, again conforming to a capital breeding pattern. Feeding, condition, and liver indexes are highest in the spring and summer, indicating energy storage primarily in the nonspawning season (Templeman 1986; Falk-Petersen and Hansen 1991). Moreover, Atlantic Wolffish are known to fast around the spawning period, when they replace all of their teeth at once (Jónsson 1982; Templeman 1986).

Although we did not have winter collections, there were multiple lines of evidence about the seasonality of oogenesis and spawning. The most advanced cohort of germ cells transitioned to vitellogenesis in spring. From spring to fall, the relative gonad weight increased over 10-fold as a single, unimodal group of vitellogenic (yolked) oocytes increased in synchrony from 1 to 4 mm in diameter. Our observations of three ripe females in August and October coincide with observations in the Canadian Maritimes of ripe and spent females during September–December (Templeman 1986) and nesting or brooding adults from August to October (Keats et al. 1985). Ovaries returned to a new cycle by November, as noted by Gunnarsson et al. (2006) around Iceland. Because of a long incubation period, eggs and early larvae can be observed until March in the Northwest Atlantic Ocean (Rountree 2002).

Our maturity classification scheme was more complex than those used by others who have employed a more operational approach to classifying maturity. Templeman (1986) classified female maturity macroscopically, based on color and size of the oocytes, and noted differences in GSI between immature (0.1–1.6%) and mature (0.7–28.3%) females. Gunnarsson et al. (2006) adapted a historic scheme of seven classes into four classes—immature 1, immature 2 (MAOS = cortical alveolus), mature 3 (vitellogenesis, will spawn in current year), and mature 4 (spent or recovering from past spawning). Their scheme relied on macroscopic characters, such as oocyte size and stage, which was verified with subsamples of gonad histology and documented with comparative macro- and microscopic images (see also our documentation of our macroscopic images in Supplemental Materials 1); subsequently, the Gunnarsson et al. (2006) scheme has been used by

Gunnarsson (2014) and Gunnarsson et al. (2016). Fairchild et al. (2015) referred to both schemes to separate out immature and mature female Atlantic Wolffish collected on a summer feeding ground in Massachusetts Bay. Based on observations of frozen gonads, they reported that all female Atlantic Wolffish were mature. Here, we sampled this same area in 2017, referred to in Figure 1 as "University of New Hampshire cooperative trawl fishing," with the same gear (bottom trawl) and observed more diversity of maturity classes: 3 immature–maturing, 5 abortive immature, 5 repeat mature, 90 developing, 1 ripe, and 1 skip spawner. All these maturity schemes are compatible with each other, as well as to our scheme, but each offering different levels of resolution for different operational purposes.

Our open-ended approach to investigate maturity revealed abortive maturation and skip spawning, neither of which have been previously described for Atlantic Wolffish. Abortive maturation has been noted in a range of fish taxa: Atlantic Herring *Clupea harengus* (Kennedy et al. 2011), Atlantic Cod *Gadus morhua* (Rideout and Rose 2006), and rockfishes *Sebastes* spp. (Lefebvre and Field 2015; Conrath 2017). Recognizing abortive maturation now, in particular, explains why our historical database assembled from macroscopic observations of Atlantic Wolffish maturity was both imprecise and biased (see Introduction and Supplemental Materials 1). Earlier, stock assessments had responded to this by using multiple knife-edge maturity cutoffs, ranging from 40 to 75 cm TL (NEFSC 2012), which demonstrated considerable variability in calculations of spawning stock biomasses, leading to uncertainty in management advice. Informed by our evolving results, the most recent assessment used 50 and 52 cm (NEFSC 2020) as maturity cutoffs, and going forward, a single value of 52 cm will be used.

Not to say that a fixed value of maturity will persist into the future. As a process, abortive maturation may be energy based and affected by food availability, temperature, and possibly other factors (Tveiten and Johnsen 1999; Tveiten et al. 2001). If food and temperature vary over time, so could $L50$ and $A50$ values, particularly in the Gulf of Maine, which is experiencing very high rates of ocean warming affecting spawning by marine fishes (McBride et al. 2018; Friedland et al. 2020).

Continued monitoring of skip spawning rates appears warranted as well because they too may vary from year to year and have an effect of disassociating mature biomass from spawning biomass. Although we find no detailed examination of skip spawning by Atlantic Wolffish, Falk-Petersen and Hansen (1991) noted that "some individuals were suspected of omitting spawning every year, based on a lack of oocyte differentiation during late summer and early autumn." Skip spawning was not associated with Atlantic Wolffish when reviewed by others (Rideout et al. 2005; Rideout and Tomkiewicz 2011). Our estimate should be considered preliminary as it is based on only a modest sample size (i.e., only 1 skip spawner among 18 mature females). It should be of interest to estimate skipping in other populations. For example, Gunnarsson et al. (2006, 2016) reported variable median maturity points and spawning peaks for different Atlantic Wolffish populations around Iceland. Gunnarsson et al. (2006) advanced the hypothesis that warmer temperatures on the west coast promoted fast growth and early maturation, whereas colder temperatures on the east coast led to slower growth and delayed maturation. Gunnarsson (2014) revisited Atlantic Wolffish maturity in five different years around Iceland, reporting both year-specific $L50$ (55–63 cm) and $A50$ (9.1–10.6 years). Noting a negative relationship between temperature and growth, Gunnarsson (2014) hypothesized that temperatures along the west coast had become too warm for this species and may be limiting its reproductive potential. As ocean temperatures are projected to continue rising, skip spawning rates may also increase as skipping is largely considered an energetic response driven by poor feeding conditions (Burton 1994; Rideout and Tomkiewicz 2011). Much focus on the effects of climate change has centered on changing species distribution; less attention has been paid to changing vital rates (i.e., growth and reproduction). Further research of how marine populations adjust vital rates in response to a changing climate—as part of conditional life history strategies (McBride et al. 2015)—will improve predictions of future fishery productivity in the oceans.

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scientific collecting permit was obtained from the New Hampshire Fish and Game Department that allowed lobstermen to land incidentally caught Atlantic Wolffish in New Hampshire state waters. The UNH Institutional Animal Care and Use Committee reviewed and approved this study (IACUC protocol number 170201). This project was funded by the National Oceanic and Atmospheric Administration Fisheries Saltonstall–Kennedy Grant Program (grant 16GAR023). The data underlying this article will be shared on reasonable request to the corresponding author. There is no conflict of interest declared in this article.

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SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.