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The Reproductive Biology of Female Atlantic Herring in U.S. Waters: Validating Classification Schemes for Assessing the Importance of Spring and Skipped Spawning

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Abstract

Atlantic Herring *Clupea harengus* are iteroparous (repeat spawners) with group-synchronous oocyte development and determinate fecundity, and they are total spawners. However, they also exhibit plasticity in other aspects of their reproductive biology including spawning seasonality and skipped spawning. Previous studies in other regions have reported skipped spawning and errors in macroscopic classifications of maturity, both of which could bias estimates of reproductive potential, but a critical assessment of these in U.S. waters is lacking. In the Gulf of Maine and Georges Bank, herring are assessed as a single stock complex, where females typically mature as 3 to 4 year olds and may live up to 11 years. To evaluate the magnitude of skipped spawning, we collected the ovaries of Atlantic Herring from fishery-dependent and fishery-independent sources over multiple seasons and evaluated them histologically to assess imminent (indicated by vitellogenic or maturing oocytes) or recent spawning (evidenced by the presence of postovulatory follicles). Gonad histology allowed us to determine spawning seasonality and skipped spawning. Macroscopic maturity classification was more accurate in fall (1–4% incorrect maturity) than in spring (7% incorrect maturity). The spatial distributions of immature and mature fish from both fishery-dependent and fishery-independent sources differed, which affected the estimation of maturity at length and age. We estimated 9–14% spring spawners in the region, but we did not find evidence of skipped spawning. The time series of the macroscopic data that were available (1987–2018) showed increases in spring spawning with latitude, but the proportions have not changed much over recent decades. The effects of up to 30% spring or skipped spawning on a stock assessment of Atlantic Herring were evaluated. Spring spawning had little effect relative to assuming 100% fall spawning (the current assumption), and skipped spawning decreased the scale of spawning stock biomass (*SSB*) and related reference points, with the degree of change increasing with skipped spawning rates, but it had few consequences otherwise.

Atlantic Herring *Clupea harengus* are of commercial importance throughout their range across the eastern and western North Atlantic. Over this broad geographic range, reproductive plasticity is evident, indicated by stock-specific size and age at maturity, period of oocyte development, spawning seasonality, egg sizes, spawning areas, and reproductive senescence (Iles 1964; van Damme et al. 2009; dos Santos Schmidt et al. 2017; Benoit et al. 2018). Recently, shared genetic variants that are associated with spawning seasonality were identified in geographically distant populations of Atlantic Herring (Lamichhaney et al. 2017). In addition to this diversity of reproductive

strategies that has a genetic basis, variable reproductive investment that is influenced by environmental conditions over multiple seasons (dos Santos Schmidt et al. 2017) and even skipped spawning (i.e., not all mature fish spawn in every year; Skjaeraasen 2009; Rideout and Tomkiewicz 2011; Skjaeraasen 2012; Rodgveller et al. 2016) have been reported for Atlantic Herring in the eastern Atlantic. For Norwegian spring-spawning herring, Engelhard and Heino (2005) inferred high rates of skipped spawning (that 50% skipped their second spawning opportunity) from an analysis of growth patterns from scales, but a following study by Kennedy et al. (2011) of direct evidence of this phenomena via gonad histology determined that skipped spawning is not a common feature in that stock. In the Baltic, histological studies have reported skipped spawning (12% of developing females; Bucholtz et al. 2013) and ovarian abnormalities that lead to reproductive failure (10–15% with occasional events up to 61%; Ojaveer et al. 2015). However, detailed investigations that use the gonad histology of the spawning strategies of Atlantic Herring in U.S. waters that include multiple spawning seasons and consideration of skipped spawning are currently lacking.

The presence of multiple seasonal spawning components (i.e., contingents) within a stock can complicate the assessment of maturity, which is most accurately estimated close to spawning (and such cases lack a singular season when all of the mature population is close to spawning). Including fish that are outside of their spawning season tends to increase errors in maturity estimation, and this can affect estimates of spawning stock biomass (SSB). Macroscopically assessed maturity data from Atlantic Herring is available from the Gulf of Maine and Georges Bank. However, systematic differences in the maturity-at-age estimates between fishery-dependent and fishery-independent sources were reported in a recent stock assessment (Deroba 2015). The fishery-dependent-based estimates of maturity at age had larger interannual variation (especially at age 3) and lower proportions of mature at length (especially for smaller sizes) than estimates from survey samples did. These differences and the variation in age-3 maturity led to a noteworthy uncertainty during the 2015 assessment because (1) spawning stock biomass at maximum sustainable yield (SSB_{MSY}) varies with age-3 maturity at a constant F_{MSY}; (2) a relatively large year-class was age 3 in 2014, the terminal year of the assessment, which contributed to a 2014 SSB that exceeded the SSB_{MSY} reference point by more than twofold; and (3) the assessment estimates a stock–recruit curve that assumes that maturity is known without error in the estimation of SSB each year. Incorrectly specifying maturity at age could lead to bias in the MSY reference points, bias in annual estimates of stock and recruitment, and ultimately to incorrect conclusions about stock status and inappropriate management advice.

The accuracy of macroscopic-based maturity determinations from fishery-dependent and fishery-independent sources in the Gulf of Maine and Georges Bank has not been formally investigated, but inaccuracy in the maturity staging of Atlantic Herring by using macroscopic criteria has been reported elsewhere (McPherson et al. 2011). Similarly, oocyte development and maturity classification of Atlantic Herring based on microscopic characteristics has been documented in other areas (van Damme et al. 2009; McPherson et al. 2011; Kennedy et al. 2011; Bucholtz et al. 2013) but it is not detailed in the U.S. waters of the northwestern Atlantic. In the Gulf of Maine and Georges Bank, Atlantic Herring are assessed as a single stock and generally assumed to be fall spawners (Melvin et al. 2009, Richardson et al. 2010). Although minor amounts of spring spawning have been reported (Tibbo et al. 1958), it is not quantified or considered in stock assessments. Observations of seemingly "nonparticipatory" mature fish that were collected during the fall spawning season raised concerns that these were skipped spawners (M. Cieri, Maine Department of Marine Resources, personal communication), and the effect that this might have on the stock assessment was unknown. An understanding of oocyte development is necessary to determine skipped spawning, especially for the resting type (Rideout and Tomkiewicz 2011), which is complicated in this case of Atlantic Herring by the possibility of either spring or fall spawning in this region. In this sense, both spring spawning and skipped spawning represent spawning omissions, on a seasonal or annual basis, respectively.

In this study we applied histological (microscopic) methods to document oocyte development throughout the year for both spring- and fall-spawning Atlantic Herring. Using oocyte stages and other histological characters, we developed criteria to assign maturity stages, spawning seasonality, and skipped spawning, and we assessed the accuracy of macroscopic maturity determinations from both fishery-dependent (commercial port samples) and fishery-independent bottom trawl surveys in the Gulf of Maine and Georges Bank. Given the different spatial coverage and intensity of these two data sources, we also investigated spatial heterogeneity in the maturity classes and the resulting interpretation of maturity. Since the stock assessment of Atlantic Herring assumes that all mature fish spawn in fall, we then evaluated the implications of observed reproductive diversity on a stock assessment.

METHODS

Oocyte development and histology-based maturity classification.— We obtained gonad samples from Atlantic Herring from multiple sources that were operating at different times of the year. The samples that were obtained from the Northeast Fisheries Science Center (NEFSC) spring and autumn bottom trawl surveys (SBTS and

ABTS, respectively) were processed at sea. Each was maturity-classified macroscopically following Burnett et al.'s (1989) criteria (Table 1), and fish weight and gonad weight were measured (to the nearest ±0.1 g). The samples that were obtained from the NEFSC Cooperative Research Program (CRP) Study Fleet were held on ice and transported to the laboratory where they were processed less than 24 hours after capture; fish weight and gonad weight were measured to the nearest ±0.001 g. Gonad samples were also obtained from the Maine Department of Marine Resources (DMR) sampling of the commercial catch. The samples from the Maine DMR were usually frozen (but they were fresh in some cases; 39 out of 100). They were processed in the laboratory and maturity-classified macroscopically by using a different scheme than was used for the NEFSC samples (Table 1), and fish weight and gonad weight were measured to the nearest ±1.0 g. In all cases, after weighing the gonad a small portion was preserved in 10% buffered formalin for histology and the otoliths were removed for aging. The preserved tissue samples were processed according to standard protocols; they were dehydrated in ethanol, embedded in paraffin, thin sectioned, and stained with Mallory's trichrome. The histological sections were viewed with a digital microscope (Nikon Coolscope II), and the oocytes were staged following criteria that were modified from Grier et al. (2009), Brown-Peterson et al. (2011), and Press et al. (2014). Additional microscopic characters were recorded including the thickness of

the gonad wall, the presence and stage of postovulatory follicles (POFs), and the presence and stage of atresia (Figure 1). The gonad wall thickens after a reproductive cycle, especially for total spawners (e.g., Winter Flounder, Press et al. 2014), so it is useful for separating immature from resting fish. Gonad wall thickness ranged from 7–350 μm; values less than 25 μm were considered thin, and those that were 25 μm or greater were considered thick. The histology of the frozen samples from the Maine DMR (61 of 100) showed degradation of the intracellular structures, but we were still able to interpret the structures that are necessary for assigning maturity and spawning seasonality (see Supplemental Figure S1 available separately online). The diameters of the oocytes (~60–80 per fish), sectioned through the nucleus, were measured by using an image analysis (ImageJ) of nonoverlapping images (4–23 per fish) from the histological sections of representative individuals from each month that were available. The purpose of the measurements was to track the developing cohort of oocytes and their separation from the reservoir of primary growth oocytes. The absolute numbers of oocytes of different sizes can be biased by this approach (specifically by the underrepresentation of smaller oocytes). However, given our interest in sizes of the developing cohort, we did not consider it necessary to correct for measurement bias (e.g., by using stereological techniques). In addition, such measures from histological sections will be slightly smaller than those from whole months (particularly for the developing oocytes) but we chose the former, which allowed the accurate determination of oocyte stage.

The histological characters and oocyte diameters (Figure 2) from all of the months that were sampled were used to develop classification criteria for assigning maturity stages and spawning seasonality (Table 2). The histology-based classifications were compared with the macroscopic at-sea assessments for ABTS 2014, ABTS 2015, SBTS 2016, and the 2015 commercial port samples (June–October). The sampling protocol for the histological samples that were collected from the NEFSC surveys for verification was as follows: at each station, after determining the maturation stage of the individuals that had been sampled for age and growth, one fish of each macroscopic maturity stage was selected for histology sampling until a total of 100 samples across all maturity stages was reached. This protocol ensured that the histological samples covered all of the stages that were encountered and came from a wide region. Similarly, 100 random histological samples were drawn from the fish that were sampled by the Maine DMR during the third quarter of 2015, the objective being to cover as broad a range in dates, areas, and macroscopic stages as possible, with a higher priority on fresh (not frozen) samples, which produce higher quality histology.

Accuracy analysis (QA/QC) of macroscopic maturity estimation.— The accuracy of the macroscopic maturity

TABLE 1. Macroscopic and histological maturity classification schemes that were used in the NEFSC surveys (Table 11 in Burnett et al. 1989) and Maine DMR sampling of commercial catch (Table 3B in Burnett et al. 1989). The corresponding histological classes are listed (following Brown-Peterson et al. 2011, with potential skip spawning following Rideout et al. 2005). In some cases, multiple stages in one scheme are represented by a single stage in another scheme.

| Macroscopic classes NEFSC	Macroscopic classes Maine DMR	Histological classes
Immature	I (Immature)	Immature
	II (Immature will spawn next season)	Immature first-maturing
Developing	III (Ripening, early stage)	Early developing
	IV (Ripening mid stage)	Late developing
		Spawning capable
		Skipped spawning (reabsorbing)
Ripe	V (Ripe)	Spawning active
Ripe and running	VI (Spawning)	
Spent	VII (Spent)	Regressing
Resting	VIII (Resting)	Regenerating
		Skipped spawning (resting)
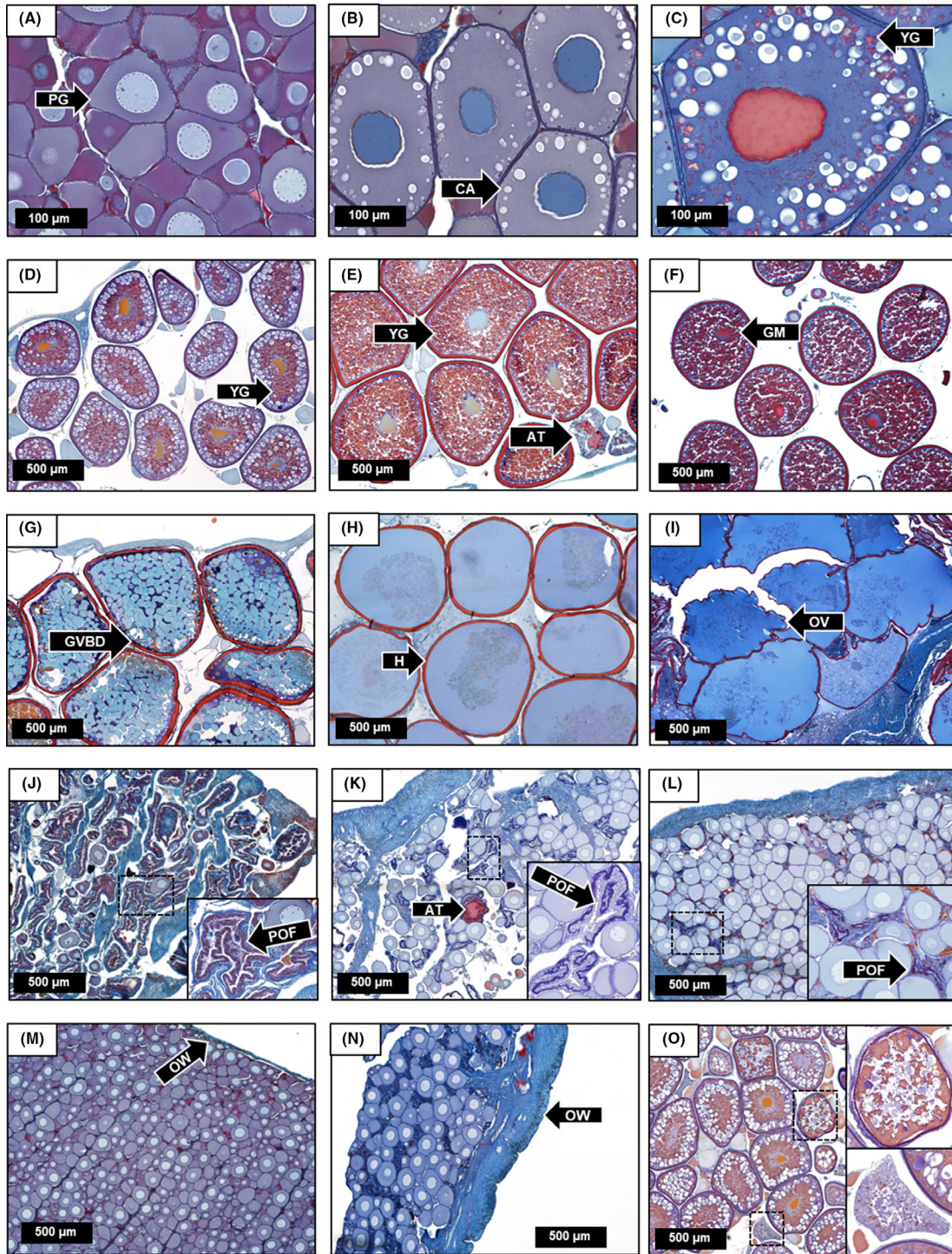
FIGURE 1. Histological criteria that were used to assess maturity for Atlantic Herring. The oocyte stages were (A) primary growth, (B) cortical alveolar, (C) early vitellogenesis, (D) early-mid vitellogenesis, (E) late vitellogenesis, (F) germinal vesicle migration, (G) germinal vesicle breakdown–early hydration, (H) hydration, and (I) ovulated, in this case residual. The postovulatory follicle stages were (J) recent, (K) intermediate, and (L) old. The ovarian wall stages were (M) thin and (N) thick. Atresia stages included (O) early alpha (top inset), late alpha (bottom inset) and beta (not shown). The abbreviations are as follows: PG, primary growth oocyte; CA, cortical alveoli; YG, yolk granules; AT, atresia; GM, germinal vesicle migration; GVBD, germinal vesicle breakdown; H, hydrated; OV, ovulated; POF, postovulatory follicle. All of the sections were stained with periodic acid Schiff–Mallory trichrome.
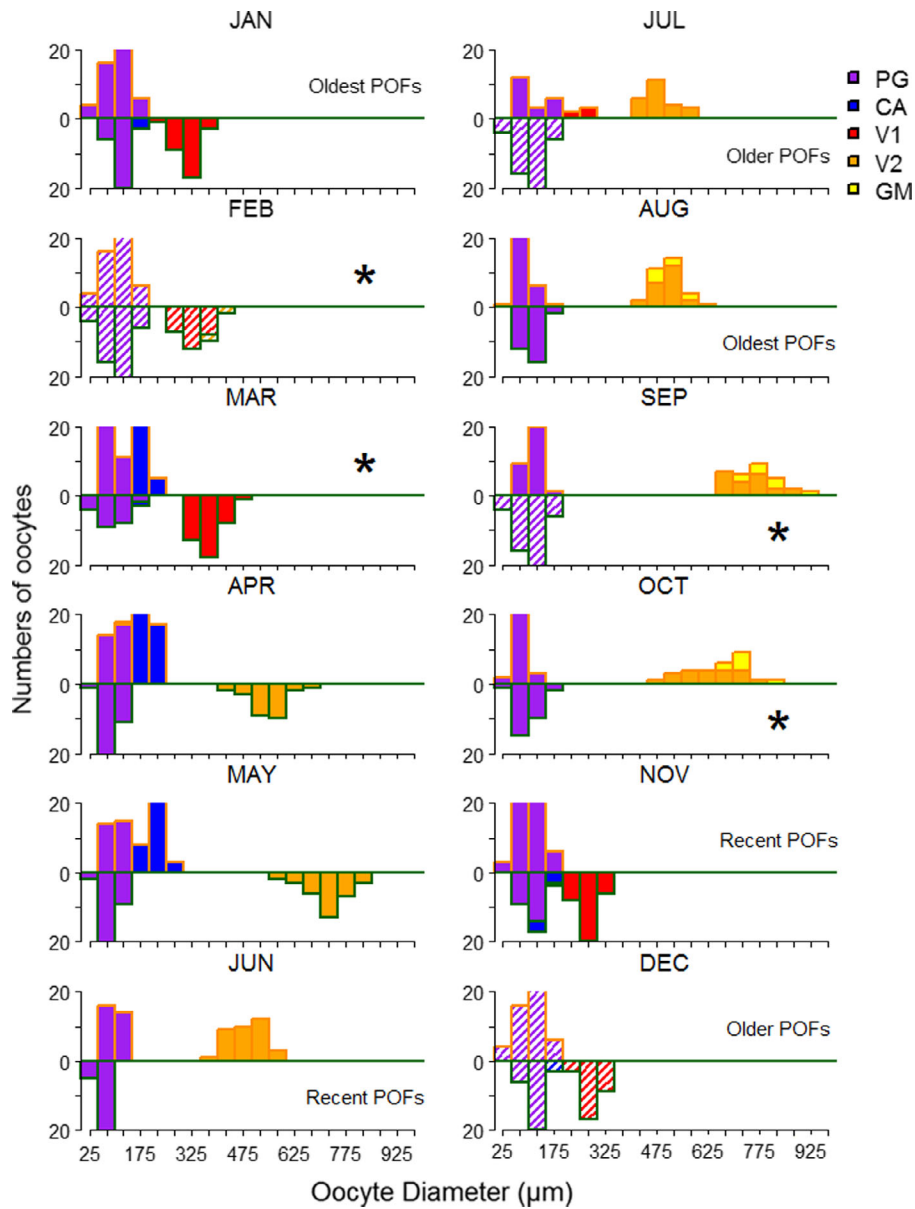
FIGURE 2. Monthly oocyte size distributions for representative mature Atlantic Herring (solid bars) or estimated from adjacent months and observed oocyte growth rates (shaded bars). Within each month, the distribution on the top represents a fall spawner (outlined in orange) and that on the bottom a spring spawner (outlined in green). The types of postovulatory follicles (POFs) present are indicated for each group in the months that they occur. The asterisks (*) indicate the months for each spawning group where skipped spawners and resting fish could not be distinguished. The abbreviations are as follows: PG, primary growth; CA, cortical alveolar; V1, early vitellogenic; V2, late vitellogenic; GM, germinal vesicle migration. The range for the *y*-axis is restricted to highlight the less abundant size-classes.

staging for Atlantic Herring was assessed for the NEFSC surveys (for 2014 ABTS, 2015 ABTS, and 2016 SBTS) and the Maine DMR commercial port samples (June–October 2015). The collections from the NEFSC Northeast CRP Study Fleet were used to inform the histological characters (oocyte stages, POF persistence) and oocyte size distributions in the months that were not sampled from the other sources and were used solely in the development of

classification criteria (meaning that no comparison of macroscopic vs. histologic determinations were performed). Because the histological samples were not random selections of the macroscopic observations, we calculated the proportions of each histological stage within each macroscopic stage. We then used these proportions to estimate the numbers of each histological stage for all of the macroscopic observations within each survey to obtain more

TABLE 2. Microscopic ovarian characteristics for each histological maturity class. Ovarian wall thickness was categorized as thin (<25 μm) or thick (≥25 μm).

Histological classes	Characteristics
Immature	Ovaries small with thin ovarian wall and little space between oocytes; only oogonia and primary growth (PG) oocytes were present.
Immature first-maturing	PG, cortical alveoli (CA), oocytes present with thin ovarian wall.
Early developing (repeat)	Ovaries with PG, CA; thick ovarian wall and/or late stage postovulatory follicles (POFs) indicating prior spawning.
Late developing	Enlarging ovaries with early vitellogenic (V1) and late vitellogenic (V2) oocytes.
Spawning capable	Large ovaries with V2 oocytes present. Atresia of vitellogenic oocytes may be present. Early stages of oocyte maturation (OM) can be present.
Skipped spawning (reabsorbing)	Mass atresia of vitellogenic oocytes.
Spawning active	Oocytes undergoing late germinal vesicle migration (GVM), germinal vesicle breakdown (GVBD), hydration (H), or ovulation (O).
Regressing	Flaccid ovaries with thick ovarian wall; atresia and recent POFs present. Most advanced oocyte stage is primary growth, with some residual secondary (V1, V2) or tertiary growth (GVM, GVBD, H, O) oocytes possible.
Regenerating	Small ovaries with thick ovarian wall. Late stage atresia or POFs may be present. Only oogonia and PG oocytes present.
Skipped spawning (resting)	Small ovaries with thick ovarian wall. Only oogonia or PG oocytes present; no secondary or tertiary growth oocytes, recent POFs, or atresia. No indication of participation in the proximal spawning season (fall or spring) and no indication of advancing a cohort of oocytes for the next spawning season (spring or fall). Definitive diagnosis is restricted to certain months.

realistic estimates of errors in maturity staging. In a few instances, the macroscopic stages were sampled but not histology (e.g., a spent fish in the 2014 ABTS and the 2016 SBTS), so error rates could not be quantified. For these we assumed that the assignments for all of the stages were correct for the expansion to the entire survey.

Estimation of spring and/or skipped spawning.— Based on the histological classification and season of collection, we were able to assign spawning seasonality for mature and maturing fish. Specifically, within each data source or survey (which occurred at different times of the year), the histological classes were assigned to either spring or fall spawning considering the time required for oocyte maturation and the period of data collection with respect to the spawning seasons. For immature fish that have not yet initiated secondary development of oocytes, it was not possible to identify spawning seasonality. The identification of skipped spawners is limited to discrete portions of the year, and in the case of Atlantic Herring this is further complicated by the potential for either spring or fall spawning. Given the concerns that skipped spawning occurring in this stock, we established criteria to identify hypothetical skipped spawners based on the season of collection, oocyte stages, POFs, and atresia (Table 2). These criteria were developed from our observations and other histological studies of Atlantic Herring and other species (e.g., Winter Flounder *Pseudopleuronectes americanus*—

another total spawner with a benthic egg; McBride et al. 2013; Press et al. 2014) and reviews on skipped spawning (Rideout et al. 2005; Rideout and Tomkiewicz 2011). The resorbing type of skipped spawner is distinguished by the presence of mass atresia (>50%) of the vitellogenic oocytes in any season, whereas in certain months histological criteria cannot distinguish the resting-type skipped spawners of one season from resting spawners of the other season.

Spatial heterogeneity in maturity classes.— The spatial distributions of samples from the fishery-independent surveys and fishery-dependent collections were evaluated to investigate heterogeneity in both overall coverage and with respect to maturity classes. Specifically, the spatial distribution of immature and mature individuals at first-maturing ages (2 and 3 years) were plotted. We compared the maturity ogives from the fishery-dependent collections with the ogives from the fishery-independent surveys that were constrained to various spatial coverages (e.g., inshore strata).

Sensitivity of the stock assessment.— The sensitivity of the recent stock assessment model was evaluated by fitting the assessment model for each of three different definitions of *SSB* that corresponded to partial spring spawning, skipped spawning, or 100% fall spawning. With the exception of modifying the *SSB* calculation, all of the inputs and settings were identical to those of the 2015 stock assessment, which included the internal estimation of a Beverton–Holt stock–recruit relationship (Deroba 2015).

For spring spawning, some fraction of the stock was assumed to have spawned in May, while the remainder of the surviving fish spawned in October. The annual *SSB* related to recruitment in the following year was the sum of the spring and fall spawners:

$$SSB_{y,spr} = SSB_{y,Jan1} \times p_s \times \exp\left(\frac{5}{12} \times Z_y\right) + SSB_{y,Jan1} \times p_f$$
$$\times \exp\left(\frac{10}{12} \times Z_y\right),$$

where $SSB_{y,spr}$ was spawning stock biomass in year y and *spr* denoted that the calculation included spring spawners, $SSB_{y,Jan1}$ was spawning stock biomass on January 1, p_s was the fraction of the stock that spawned in spring, $p_f = 1 - p_s$ was the fraction of the stock that spawned in fall, and Z was total instantaneous mortality.

$$Z_y = M + F_y,$$

where M was instantaneous natural mortality, and F was the fully selected instantaneous fishing mortality that was estimated for each year in the 2015 stock assessment (Deroba 2015). Skipped spawning (SSB_{skip}) was approximated by allowing only a portion of the mature fish to spawn in the fall of each year, which is equivalent to excluding the spring spawners from the equation for $SSB_{y,spr}$ above:

$$SSB_{y,skip} = SSB_{y,Jan1} \times p_f \times \exp\left(\frac{10}{12} \times Z_y\right).$$

Fall spawning (SSB_{fall}), as assumed in recent stock assessments, was calculated with $p_f = 1$:

$$SSB_{y,fall} = SSB_{y,Jan1} \times \exp\left(\frac{10}{12} \times Z_y\right).$$

These methods for calculating *SSB* assumed that the same maturity ogive had been applied in both seasons and ignored within-year growth. The models were fit by using a range of values for $p_s(p_f)$, shown in Table 3. The time series plots of the estimates of *SSB*, recruitment, and fully selected fishing mortality were qualitatively examined for differences between the assessment that was modified for spring or skipped spawning and that for 100% fall spawning (i.e., as in the 2015 assessment; Deroba 2015). As 100% fall spawning is the current assumption in the stock assessment, the results are discussed relative to this assumption. The values of estimated steepness (i.e., the fraction of recruitment at its equilibrium, unexploited level that is achieved when *SSB* is reduced to 20% of its equilibrium, unexploited level; Francis 1992) and unexploited *SSB* were also compared.

RESULTS

Oocyte Development, Histology-Based Maturity Classification, and QA/QC of Macroscopic Maturity Estimation

Seasonal oocyte development followed two distinct schedules, culminating in final oocyte maturation (and spawning) in either late spring to early summer or late summer to fall. The monthly size frequencies of the oocytes and oocyte development stages were used to assign individuals to a spawning group (spring, before June 1; or fall, after June 1).

Using microscopic verification, we found the macroscopic method to be reasonably accurate for Atlantic Herring in the fall surveys and the fishery-dependent data (2014 ABTS, Table 4; 2015 ABTS, Table 5; 2015 commercial samples, Table 6). Errors in maturity were highest in the spring survey period (2016 SBTS, Table 7). Overall, direct agreement ranged from 60.0–88.4%, and errors in the determination of sex (2.0–7.0%) and maturity (0–12.6%) were evident in all of the surveys (Table 8). Minor disagreements in developing, ripe, ripe and running, spent, and resting phases (but not affecting maturity assignments) between the histologic and macroscopic methods were also evident in all of the surveys. During spring, many fish that were classified as resting at sea were undergoing early development, which was only visible via histology. For the fall surveys, when they were scaled up to include all of the fish that were evaluated for macroscopic classification, the percentages of incorrect maturity assignment increased slightly (0.6–1.2%) but remained below 5%. In a similar vein, although error rates on the spring survey were higher, the few late-developing and spawning active females were accurately identified, confirming spring spawning in the region. When the results of the spring survey are scaled up, the percentage of direct agreement was unchanged (60% vs. 61.6%); however, the percentage of incorrect maturity declined (from 12.6% to 7.3 %) due to the lower overall frequency of immature fish that were sampled (the stage where these errors occurred).

Spatial Differences in Maturity

The spatial distribution of the samples from the NEFSC surveys differed from those of the commercial

TABLE 3. Range of natural mortality (*M*), proportion of spring or skipped spawners (p_s), and proportion of fall p_f spawners that were evaluated.

M	p_s	p_f
0.20	0.10	0.90
0.35	0.20	0.80
0.50	0.30	0.70

samples that were obtained from the Maine DMR, which were predominately from inshore statistical areas (512, 513, and 514; Figure 3). The distributions of the mature females with macroscopic maturity determinations were compared with that of fish that were ages 2 and 3, which were well sampled and represent the onset of maturity. The fall spatial distributions of younger (age 2 and 3 fish) and immature fish in 2014 and 2015 (Figures 4A–D) were also more restricted to inshore regions than were those of fish at older ages and mature stages. In spring, Atlantic

Herring were more widely distributed, including immature individuals (Figures 4E–F). The evaluation of maturity from bottom trawl surveys separately for inshore and offshore regions revealed differing agreement with the commercial data that varied by age. When the analysis of fall survey data is constrained to inshore regions, the differences in maturity between survey and commercial sources decrease for fish of ages 2 and 3 (Figure 5). The pattern for older age-4 and age-5 fish reversed, with higher proportions mature in the commercial data, but the

TABLE 4. Results for the accuracy analysis (QA/QC) for the 2014 fall bottom trawl survey (2014 ABTS; October 15–November 12). The first two rows indicate the number (and % frequency) of macroscopic and histological observations of each stage for the survey. In fall, immature first-maturing fish are not expected to spawn until the following calendar year, and they are not included in SSB (i.e., they are not mature). The green cells indicate direct agreement between the at-sea macroscopic and histological classifications for those that were sampled. The red and unshaded cells indicate disagreements that did or did not, respectively, affect maturity estimation (in terms of SSB). The subscripts for the histological classes denote the spawning season that was assigned given the period of sampling.

Number and histological class	Immature	Developing	Ripe	Ripe and running	Spent	Resting
N macroscopic	13 (2.6)	26 (5.1)	24 (4.7)	0 (0)	8 (1.6)	436 (86.0)
N histology	8 (8.8)	14 (15.4)	11 (12.1)	0 (0)	0 (0)	58 (64.0)
Immature$_{UNKNOWN}$	8	0	0	0	0	3
Immature first-maturing$_{SPRING}$	0	0	0	0	0	0
Early developing$_{SPRING}$	0	1	0	0	0	2
Late developing$_{FALL}$	0	7	6	0	0	0
Spawning capable$_{FALL}$	0	1	2	0	0	0
Spawning active$_{FALL}$	0	0	0	0	0	0
Regressing$_{FALL}$	0	1	2	0	0	3
Regenerating$_{FALL}$	0	4	1	0	0	46
Regenerating$_{SPRING}$	0	0	0	0	0	5
Skipped spawning	0	0	0	0	0	0

TABLE 5. Results of the accuracy analysis (QA/QC) for the 2015 fall bottom trawl survey (2015 ABTS; September 13–November 5). The first two rows indicate the number (and % frequency) of macroscopic and histological observations of each stage for the survey. In fall, immature first-maturing fish are not expected to spawn until the following calendar year, and they are not included in SSB (i.e., they are not mature). The green cells indicate direct agreement between the at-sea macroscopic and histological classifications for those that were sampled. The red and unshaded cells indicate disagreements that did or did not, respectively, affect maturity estimation (in terms of SSB). The subscripts for the histological classes denote the spawning season that was assigned given the period of sampling.

Number and histological class	Immature	Developing	Ripe	Ripe and running	Spent	Resting
N macroscopic	60 (11.1)	45 (8.3)	13 (2.4)	6 (1.1)	1 (0.2)	417 (77.0)
N histology	11 (12.5)	18 (20.5)	5 (5.7)	1 (1.1)	1 (1.1)	52 (59.1)
Immature$_{UNKNOWN}$	7	0	0	0	0	0
Immature first-maturing$_{SPRING}$	0	0	0	0	0	1
Early developing$_{SPRING}$	1	0	0	0	0	2
Late developing$_{FALL}$	0	15	2	0	0	0
Spawning capable$_{FALL}$	0	1	2	0	0	0
Spawning active$_{FALL}$	0	0	0	0	0	0
Regressing$_{FALL}$	0	2	1	0	0	3
Regenerating$_{FALL}$	3	0	0	1	1	41
Regenerating$_{SPRING}$	0	0	0	0	0	5
Skipped spawning	0	0	0	0	0	0

TABLE 6. Results of the accuracy analysis (QA/QC) for the 2015 commercial samples (June–October). The first two rows indicate the number (and % frequency) of macroscopic and histological observations of each stage for the survey. Immature first-maturing and early developing fish that are sampled in summer are expected to spawn that fall, and they are included in *SSB* (i.e., as being mature). The green cells indicate direct agreement between the at-sea macroscopic and histological classifications for those that were sampled. The red and unshaded cells indicate disagreements that did or did not, respectively, affect maturity estimation (in terms of *SSB*). The subscripts for the histological classes denote the spawning season that was assigned given the period of sampling.

Number and histological class	I	II	III	IV	V	VI	VII	VIII
N macroscopic	255 (12.7)	71 (3.5)	1094 (54.5)	135 (6.7)	44 (2.2)	162 (8.1)	18 (0.9)	229 (11.4)
N histology	2 (2.0)	5 (5.1)	45 (45.9)	12 (12.2)	10 (10.2)	13 (13.3)	4 (4.1)	7 (7.1)
Immature$_{UNKNOWN}$	2	1	0	0	0	0	0	0
Immature first-maturing$_{FALL}$	0	2	0	0	0	0	0	0
Early developing$_{FALL}$	0	2	10	0	0	0	0	0
Late developing$_{FALL}$	0	0	34	10	0	1	0	0
Spawning capable$_{FALL}$	0	0	1	2	10	7	0	0
Spawning active$_{FALL}$	0	0	0	0	0	5	0	0
Regressing$_{FALL}$	0	0	0	0	0	0	4	0
Regenerating$_{FALL}$	0	0	0	0	0	0	0	0
Regenerating$_{SPRING}$	0	0	0	0	0	0	0	7
Skipped spawning	0	0	0	0	0	0	0	0

TABLE 7. Results of the accuracy analysis (QA/QC) for the 2016 spring bottom trawl survey (2016 SBTS; April 8–June 6). The first two rows indicate the number (and % frequency) of the macroscopic and histological observations of each stage for the survey. In the spring, immature first-maturing fish would be expected to spawn in the calendar year (that fall), so they are included in *SSB* (i.e., they are not immature). The green cells indicate direct agreement between the at-sea macroscopic and histological classifications for those that were sampled. The red and unshaded cells indicate disagreements that did or did not, respectively, affect maturity estimation (in terms of *SSB*). The subscripts for the histological classes denote the spawning season that was assigned given the period of sampling.

Number and histological class	Immature	Developing	Ripe	Ripe and running	Spent	Resting
N macroscopic	36 (7.9)	32 (7.1)	4 (0.9)	1 (0.2)	4 (0.9)	376 (83.0)
N histology	13 (13.7)	14 (14.7)	2 (2.1)	1 (1.1)	0 (0.0)	65 (68.4)
Immature$_{UNKNOWN}$	1	0	0	0	0	0
Immature first-maturing$_{FALL}$	2	0	0	0	0	0
Early developing$_{FALL}$	4	4	0	0	0	22
Late developing$_{SPRING}$	0	9	2	0	0	2
Spawning capable$_{SPRING}$	0	0	0	0	0	0
Spawning active$_{SPRING}$	0	0	0	0	0	0
Regressing$_{SPRING}$	0	0	0	1	0	0
Regenerating$_{FALL}$	6	1	0	0	0	41
Regenerating$_{SPRING}$	0	0	0	0	0	0
Skipped Spawning	0	0	0	0	0	0

differences were less pronounced. However, the fall survey data consistently showed small percentages of immature fish at ages 4 and 5 compared with the commercial data.

Rates of Spring and Skipped Spawning

Using the histological criteria (Table 2), we were able to determine the spawning seasonality of mature female Atlantic Herring that had been collected throughout the year (Table 8). Since immature fish had not yet initiated secondary development of oocytes, they could not be attributed to either spawning season. When scaled up to all observations for each survey, the estimated percentage of spring spawners that were determined during the 2014 and 2015 fall bottom trawl surveys (11.4% and 13.8%, respectively) were comparable to the estimate that was obtained during the spring bottom trawl survey (9.1%). No skipped-spawning individuals were observed in any season. The macroscopic differences between spring and fall spawners were obvious in winter and spring (Figure 6). The proportion of spring spawners that were collected during the spring bottom trawl survey increased with latitude and was more prevalent than it was in the 1980s (Figure 7).

TABLE 8. Summary of sex and spawning group determinations for the four data sources. For males, the percentages that are listed in parentheses are the percentages of males that were incorrectly classified as females based on the macroscopic data. For females, the percentages that are listed in parentheses are the percentages of mature females in that spawn group. The direct agreement is the sum of the diagonal green cells for the survey (Tables 4–7), and the incorrect maturity is the sum of the red cells in each table. The percentages that are included for the accuracy assessment (QA/QC) are calculated for females only.

Sex and data source	Spawn group	2014 (ABTS)	2015 (ABTS)	ME2015 (Q3)	2016 (SBTS)
N Macroscopic		507	542	2,008	453
N Histology		99	92	100	101
Males: N (% incorrect sex)		7 (7.0)	4 (4.3)	2 (2.0)	6 (5.9)
Females: N (%)		92 (88.6)	88 (95.7)	98 (98.0)	95 (94.1)
Mature	Spring spawner	8 (9.9)	10 (12.3)	7 (7.4)	14 (14.9)
	Fall spawner	74 (91.3)	71 (87.7)	88 (92.6)	80 (85.1)
	Skipped spawning	0 (0)	0 (0)	0 (0)	0 (0)
N Immature	Unknown spawning season	11	7	3	1
QA/QC: N (%)	Direct agreement	68 (73.1)	69 (77.5)	84 (88.4)	57 (60.0)
	Incorrect maturity	3 (3.2)	3 (3.4)	1 (1.0)	12 (12.6)
Scaled to survey (%)	Direct agreement	81.0	83.0	94.9	61.6
	Incorrect maturity	4.4	4.0	0.7	7.3
	Spring spawner	11.4	13.8	13.2	9.1
	Fall spawner	88.6	86.2	86.8	90.9

Sensitivity of the Stock Assessment

The stock assessment estimates when the stock assessment allowed for spring spawning were insensitive to the value of p_s, so only the results for $p_s = 0.3$ are reported here. The time series plots were generally similar between the assessment model with spring spawning and 100% fall spawning (Figure 8). The estimates of steepness and unfished SSB were also similar (Table 9). While the histological analyses above found no evidence of skipped spawning, anecdotal observations of spawning omission in herring from the Gulf of Maine and Georges Bank in fall in the northwestern Atlantic were the motivation for this study given the skipped spawning that has been reported in other populations (referenced above). Thus, our objectives were to determine the root cause of observed spawning omission (spring and/or skipped spawning) and to evaluate the potential consequences of these on the stock assessment. The evaluations of the sensitivity of the stock assessment to spring and/or skipped spawning are reported for the sake of completeness and generality because they are relevant to other stocks. When the stock assessment allows for skipped spawning, differences in the time series plots from 100% fall spawning were only evident for SSB, with SSB lower with skipped spawning than with 100% fall spawning (Figure 8). The degree of difference in the SSB time series increased with the proportion of skipped spawners, but only the results with 30% skipped spawning were reported for simplicity. The estimated steepness with skipped spawning was similar to that with 100% fall spawning, but unfished SSB was lower (Table 9). Skipped spawning seems to scale SSB and the related reference points, but with few other consequences.

DISCUSSION

Oocyte Development, Histology-Based Maturity Classification, and QA/QC of Macroscopic Maturity Estimation

Spring- and fall-spawning Atlantic Herring in the Gulf of Maine and Georges Bank showed distinct oocyte development cycles, which are similar to the differences between Norwegian spring and summer spawners that initiate oocyte development at different times (dos Santos et al. 2017). In contrast, autumn- and winter-spawning herring in the North Sea initiate oocyte development at the same time, with both development and down-regulation occurring over a longer period in the latter, leading to fewer but larger eggs (van Damme et al. 2009). Maturity misclassifications were minor, arising from poor resolution of detail in fish that were evaluated outside of their spawning season. Because spawning occurs in multiple seasons, errors that were associated with ambiguity during nonspawning were also spread across seasons. Misclassifications of sex occurred in all of the surveys (summarized in Table 8). Most of these misclassifications occurred for small and immature fish, where it is more difficult to differentiate sex macroscopically. Additionally, for most individuals during the spring survey period, the gonads were very small, which made it more difficult to distinguish males from females macroscopically. This likely led to the higher rates of incorrect maturity in the spring (Table 7), and it supports the continued estimation of maturity from samples that are obtained closest to the main spawning season in fall. The results from the spring also indicate that histology was able to identify early developing fish
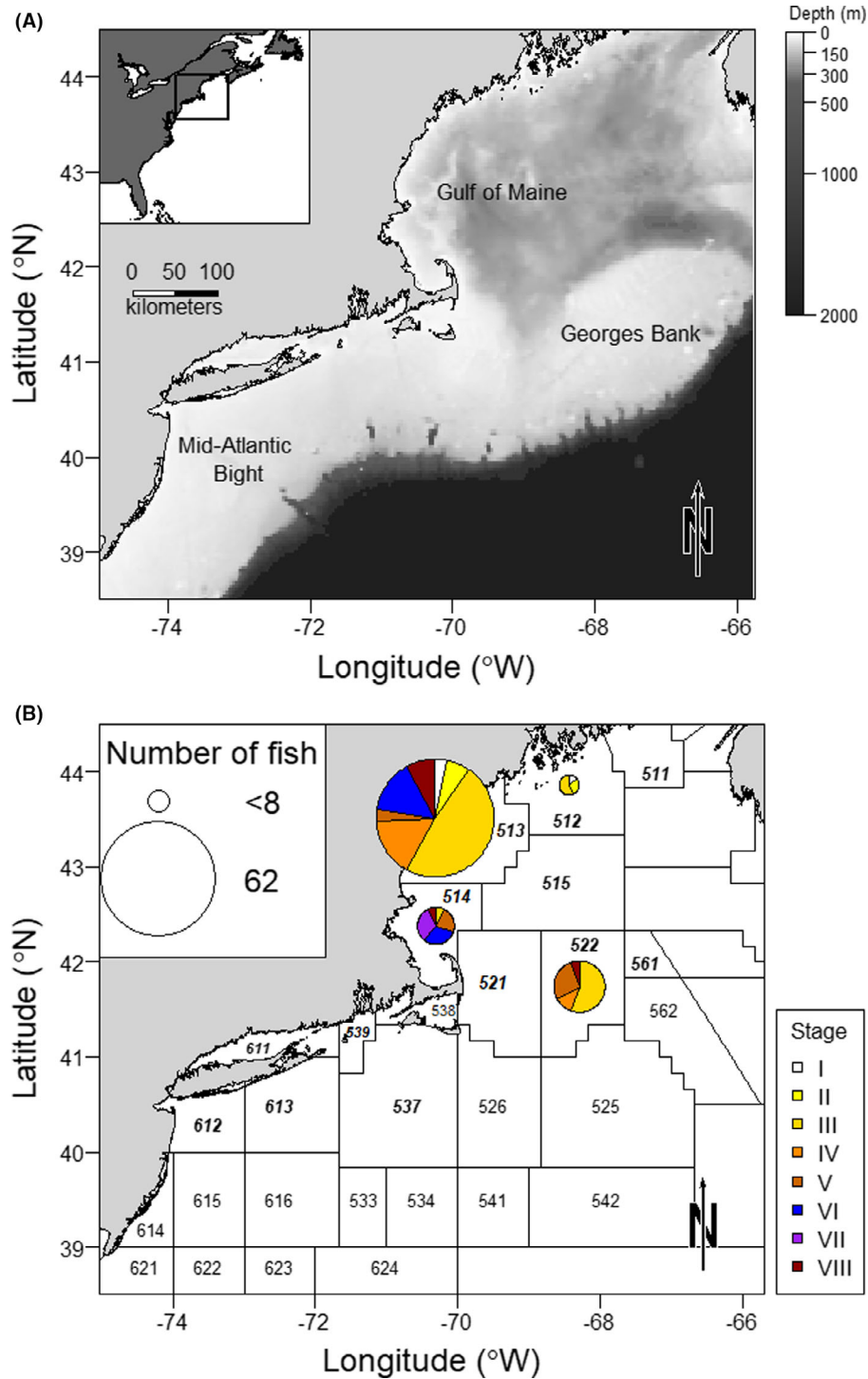
FIGURE 3. Study area on **(A)** the Northeast U.S. continental shelf and **(B)** the distribution and summary of female Atlantic Herring that were analyzed histologically from fishery-dependent collections June–October 2015 by the statistical areas that are used by the NEFSC for commercial fisheries data collection. The statistical areas with an average of > 100 maturity observations per year over the last 10 years are indicated in bold italics.

before this was evident macroscopically (early developing fish that were classified as resting at sea). Similar to a recent study on Sablefish (Rodgveller 2018), the greatest

accuracy of the macroscopic methods was in the period that is closest to spawning. This is not surprising because the microscopic characters that define early developing fish
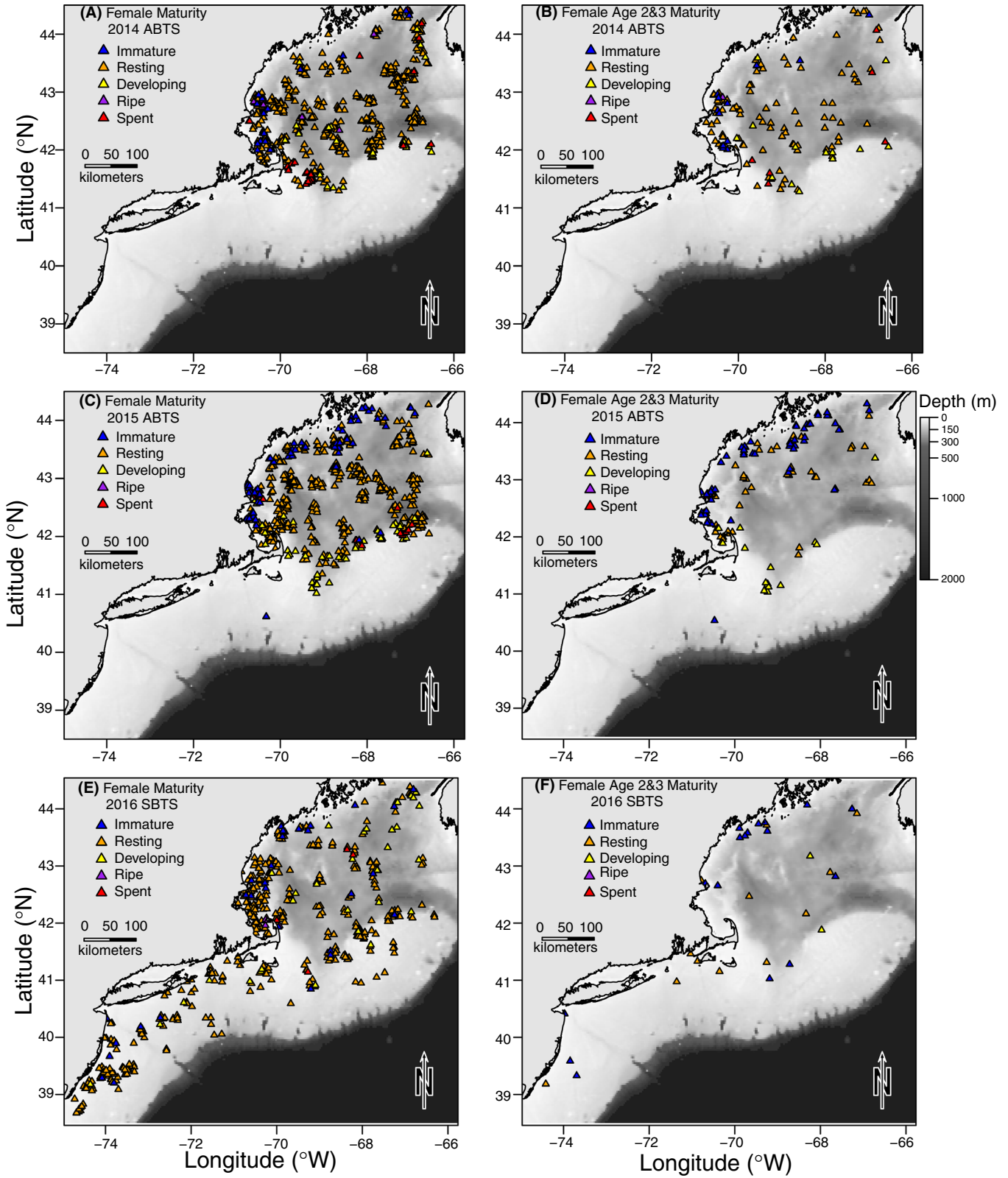
FIGURE 4. Distribution of **(A), (C), (E)** all and **(B), (D), (F)** age-2 and age-3 females that were sampled for age, growth, and maturity on the NEFSC 2014 ABTS (A, B), the 2015 ABTS (C, D), and the 2016 SBTS (E, F). The points are jittered to reduce overplotting.
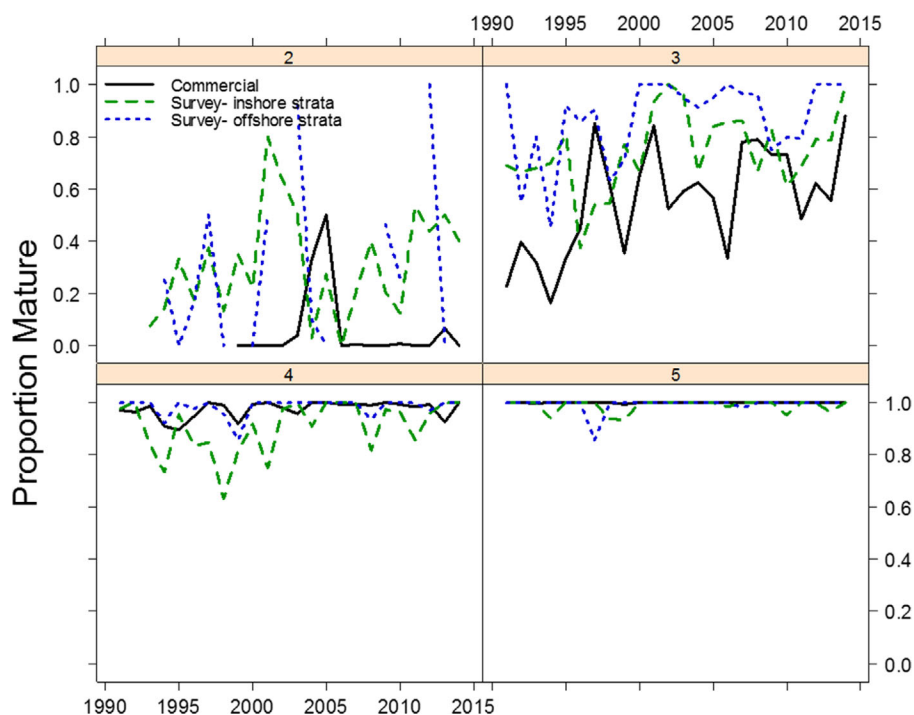
FIGURE 5. Proportion of female Atlantic Herring mature at age (age-specified in the "strip" of each panel) from the third-quarter commercial fishery samples, the inshore strata (strata 26–27, 37–40), and the offshore strata (strata 13–14, 16–23) of the NEFSC fall survey.

are not readily visible with the naked eye, and the macro-scopic characters that define developing include enlarge-ment of the ovary, which is only beginning. Several late developing and one spent fish were collected in the spring, a clear indication of spring–early summer spawning. Inter-estingly, the spent fish was classified as ripe and running at sea. This individual contained advanced and mature oocytes that histology indicated were residual (i.e., left over), but macroscopically they would have appeared as hydrated oocytes and/or ovulated eggs. During winter and spring, the difference in ovary condition between spring and fall spawners is readily obvious macroscopically (Fig-ure 6). Therefore, the estimation of spring spawning from developing and spawning active (ripe, ripe and running) Atlantic Herring in the spring is considered to be reliable (but not without error). Nonetheless, a low percentage (9.1–13.8%, Table 8) of Atlantic Herring were classified histologically as spring spawners.

As the sampling scheme was stratified by maturity, it was necessary to scale up the histological results to match the proportion of each maturity stage within the popula-tion. To determine overall errors in macroscopic classifica-tions in the surveys, we applied stage-specific error rates to all of the fish that were examined macroscopically on the surveys (Table 8). In fall, most Atlantic Herring are developing, which was sometimes confused with resting (regenerating) but was never confused with immature. Therefore, proportionally more developing fish

(determined with a low error rate) in fall diluted the effect of higher error rates in the rarer stages (e.g., resting), increasing the percentages of direct agreement. Although fewer developing fish were observed in spring, which decreased overall agreement, they were accurately identi-fied macroscopically, supporting the use of macroscopic observations to identify spring spawners in that season. The commercial port sample was the most precise (Table 8), possibly due to being performed by a single experi-enced person. In contrast, the NEFSC survey data is col-lected by multiple individuals per survey that have varying levels of experience with respect to Atlantic Herring matu-rity. Annual training workshops on fish maturity are held at the NEFSC to address this potential source of error.

Spatial Differences in Maturity

Heterogeneity in the spatial distribution of Atlantic Herring with respect to maturity stage was identified and shown to affect estimations of maturity at size and age. Most immature fish remain inshore in fall (i.e., they do not undergo spawning migrations offshore), so samples that are obtained inshore will have more immature fish (both overall and at a given age). The proportion that is mature at ages 2 and 3 varies in the time series of fishery-dependent (commercial) samples (Deroba 2015), but the influence of the uneven spatial coverage of the fishery-dependent samples through the time series is unknown. The survey data indicates that immature individuals are
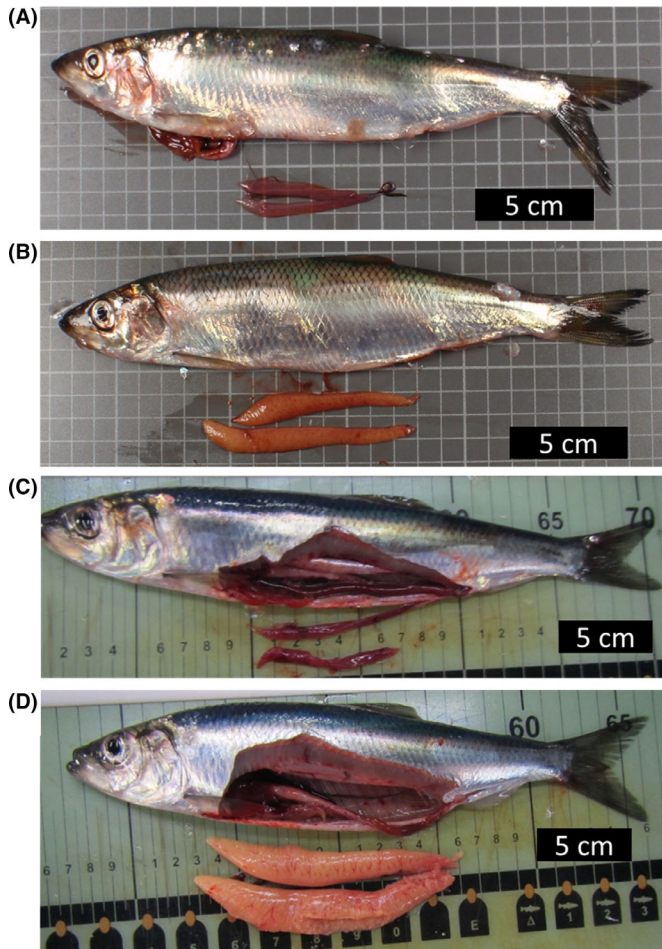
FIGURE 6. Photographs of fall- and spring-spawning Atlantic Herring that were captured in spring: **(A)** a resting female (fall spawner) and **(B)** a developing female (spring spawner), which were sampled on January 22, 2015, from a commercial catch (NEFSC CRP Study Fleet), and **(C)** a resting female (fall spawner) and **(D)** a developing female (spring spawner), which were sampled on April 25, 2017, during the NEFSC spring bottom trawl survey.

found closer to shore in fall and first-time maturing (ages 2 and 3) fish have greater spatial overlap with the bottom trawl survey than immature fish at the same ages do. The spatial difference in maturity likely contributes to the observed differences in the estimated proportions of mature-at-age fish from survey and commercial data sources in fall. The increased agreement for maturity at size between commercial and inshore survey strata compared with offshore strata (Figure 5) strongly suggests that the differences resulted from the underlying spatial distribution of sampling and not in the interpretation of maturity. The minor differences that were observed for older ages (4 and 5) are most likely the result of classification errors of resting fish as immature (e.g., Table 5), and they are also influenced by small sample sizes (particularly when the data is restricted by strata). Other studies have

demonstrated the importance of representative sampling of populations for sex and maturity, especially when there is spatial heterogeneity of the population components (e.g., in species with separate juvenile and adult habitats, Gillanders et al. 2003; Adams 2017; differential habitat use by sex, Langan et al. 2019; or when spawning occurs at specific sites, Lowerre-Barbieri et al. 2016). Given spatial variation in size and age at maturity in fishes, even within a stock (Winton et al. 2014), obtaining samples from a wide geographic range and in proportion to population densities is recommended. As shown here for Atlantic Herring, perceived variation in maturity can arise due to differential distributions of immature and mature individuals (e.g., as is caused by spawning migrations). For Haddock *Melanogrammus aeglefinus* from the northeastern region of the Arctic, migrations of spawning fish outside the sampling region were shown to bias estimates of skipped spawners (Skjeraasen et al. 2015). Accurately estimating functional maturity (and/or stock reproductive potential) requires representative sampling of the population of interest; however, reproductive data and samples are often poorly measured compared with the measurements for other population parameters (Tomkiewicz et al. 2003). Fishery-independent (survey) samples are usually preferred for estimating maturity because they capture a more complete size distribution that includes immature individuals. However, Atlantic Herring are not managed by using size limits and commercial harvest operates in a manner (in terms of area and gear) that includes many immature fish. Notably more macroscopic maturity data is available across statistical areas in the region from the fishery-dependent source than from the fishery-independent surveys each year. The large sample sizes (the sample sizes from the annual bottom trawl surveys were approximately 25% of that from the ME2015 [Q3] data; Table 8), broad spatial coverage (the statistical areas shown in bold italics in Figure 3B), and consistent representation of immature individuals throughout the time series supports the use of commercial data to estimate maturity in this case. The results presented here for the estimation of Atlantic Herring maturity demonstrate potential biases due to incomplete sampling coverage of the heterogeneous distributions of immature and mature fish.

Estimation of Spring and/or Skipped Spawning

Spring spawning Atlantic Herring were evident from the NEFSC spring bottom trawl surveys. The macroscopic classification of development can be unambiguous (Figure 6), but about a third of the fish that were classified macroscopically as developing in spring were not classified histologically as spring spawners (but as either early developing or regenerating fall spawners). Even considering the observed error rates, our results indicate a low percentage of spring spawners in the Gulf of Maine and Georges
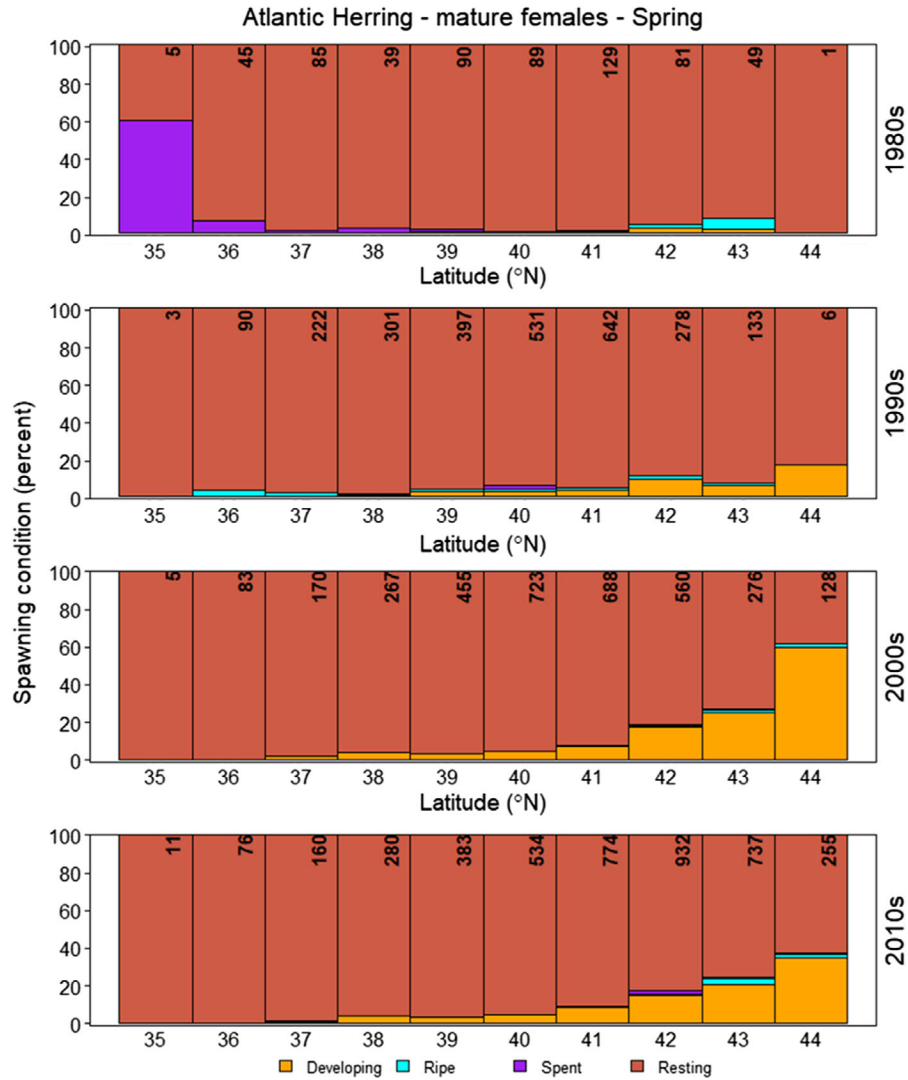
FIGURE 7. Time series of mature female macroscopic maturity, collected on the NEFSC spring bottom trawl survey summarized by decade and degree latitude. For simplification, the maturity classes Ripe and Ripe and Running are aggregated and shown as Ripe. Developing, Ripe, and Spent groups represent spring spawning Atlantic Herring.

Bank. A summary of Atlantic Herring maturity from the SBTS time series (1987–2018) summarized by decade and degree latitude across all strata (Figure 7) indicates a latitudinal trend in the proportion of spring spawning Atlantic Herring (developing, ripe, and spent) that were encountered. Assuming that all of the developing, ripe, and spent fish that were sampled during the spring surveys were spring spawners, the proportions of spring spawning increases with latitude: <5% south of 41°N, 5–15% from 41–42°N, and 15–60% at 43–44°N. Although the rates of spring spawning were higher at the northern extent of the survey (Northern Gulf of Maine and Scotian Shelf), fewer fish were sampled in that region earlier in the time series. Melvin et al. (2009) indicated an increase in the percentage of spring spawning in herring at higher latitudes over a

broader range in the western Atlantic (40–52°N). They proposed a conceptual model in which spawning was limited to autumn in the south and spring in the north, with a mix of both between. Using this conceptual model and inferring environmental temperature as a proxy for spawning type, they predicted an increase in the autumn spawners under warming ocean temperatures. Although our results agree with theirs regarding increased spring spawning with latitude, our results differ with their conceptual model that predicted only fall spawning in the Gulf of Maine and Georges Bank. Further, our decadal analysis does not indicate recent declines in spring spawning, as is predicted by Melvin et al.'s (2009) model given recent increases in water temperature in the Gulf of Maine (Pershing et al. 2015, Saba et al. 2016). Recruitment of spring-
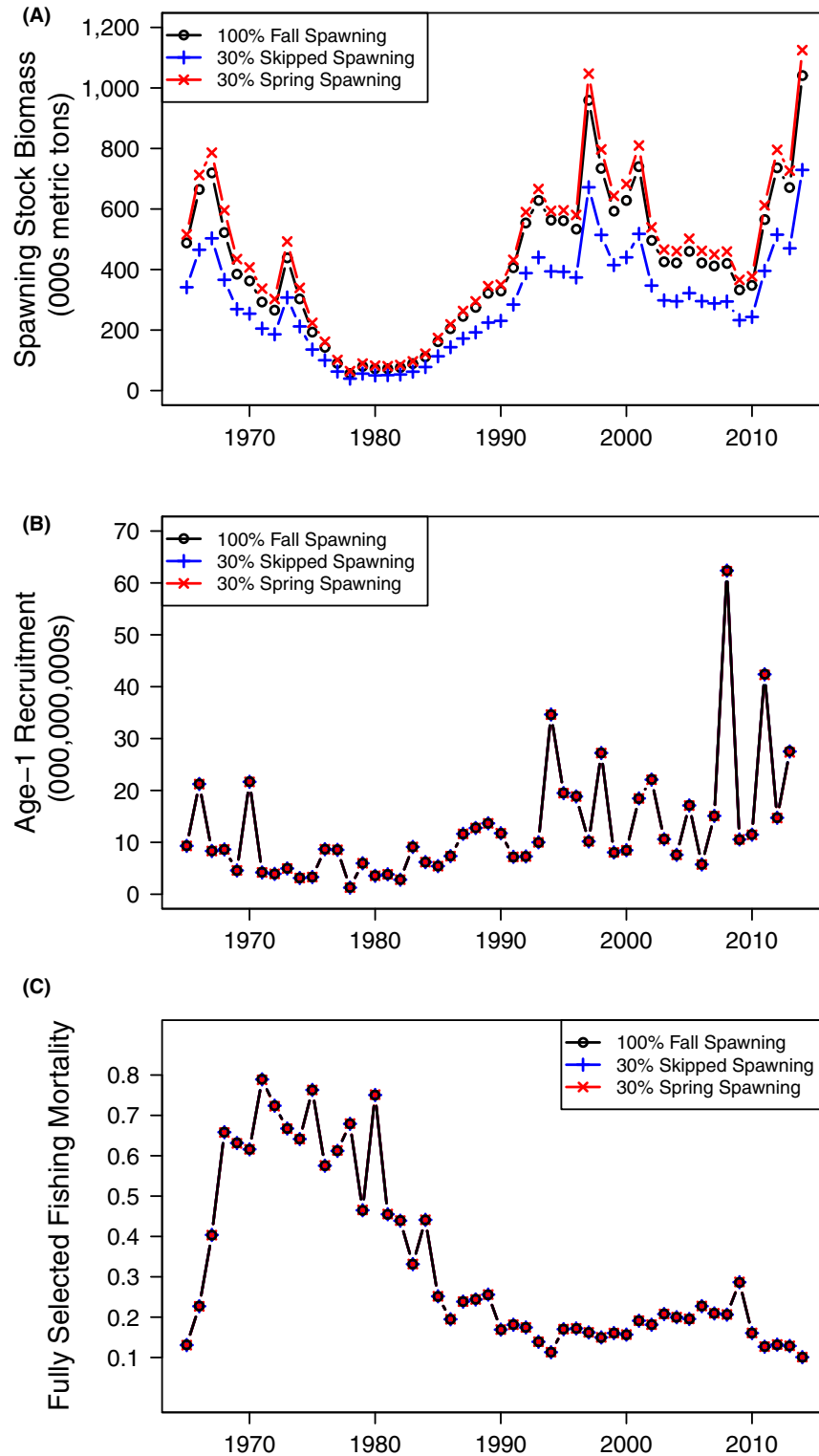
FIGURE 8. Time series estimates from the stock assessment models, assuming all fall spawning and 30% spring or skipped spawning for **(A)** spawning stock biomass, **(B)** age-1 recruitment, and **(C)** fully selected fishing mortality. The differences between the scenarios in (B) and (C) are so minor that they are obscured by overplotting.

TABLE 9. Estimates of unfished spawning stock biomass (*SSB*) and steepness from an assessment with 100% fall spawning and 30% spring or skipped spawning.

Stock assessment estimate	Fall spawn only (2015 assessment)	With 30% spring spawning	With 30% skipped spawning
Unfished *SSB* (metric tons)	845,176	885,784	591,623
Steepness (unitless)	0.44	0.43	0.44

and fall-spawning herring in the Gulf of St. Lawrence has been linked to different environmental drivers, indicating that spring- and fall-spawning herring are adapted to specific conditions for reproduction (Brosset et al. 2019). This contradicts earlier research that indicated that there are not discrete sympatric seasonal-spawning populations (i.e., there is no genetic basis for spawning seasonality) among herring in the western Atlantic (McQuinn 1997a, 1997b), and herring that spawned in one season could "cross over" and spawn as adults in the other season, depending on their juvenile growth characteristics and time at maturation. Also, Lamichhaney et al. (2017) found genetic factors associated with spawning seasonality that were shared between both eastern and western Atlantic Herring stocks. Therefore, recent research provides increasing evidence of adaptations that are related to spring or fall spawning in Atlantic Herring that have a genetic basis. Fisheries management of Atlantic Herring in the United States currently considers substock structure to some extent through spatially explicit annual and seasonal quotas. If seasonal spawning adaptations can be better defined to identify stock components then these could be evaluated in a metapopulation model (Secor et al. 2009) to evaluate the adequacy of existing measures. However, data that provide adequate spatial and temporal scales to inform such management considerations may be elusive. For example, current stock assessments assume a single unit despite spatially explicit quotas, and recent attempts at aligning the stock assessment to the spatial scale of interest to management have failed due to inadequate data on stock migration and mixing (NEFSC 2018).

Due to the different oocyte development cycles and comingling of spring- and fall-spawning Atlantic Herring in the Gulf of Maine and Georges Bank, it is difficult to confirm individuals as being a resting-type skipped spawner; individuals may simply be recovering or preparing to spawn in the off or alternate spawning season. These constraints may have prevented us from identifying skipped spawning that was occurring (i.e., false negative or type II error). However, by comparing the proportions of spring and fall spawners that were determined in both seasons, we were also able to infer skipped spawning that may have been missed histologically. For example, if the estimated proportion of spring-spawning Atlantic Herring obtained in fall were significantly higher than the estimated proportion obtained in the spring, we might suspect substantial skipped spawning. This was not evident in our analysis, so we concluded from both the direct histological observations and the estimates of spring and fall spawning contingents determined at different times of the year that skipped spawning was not prevalent in this region in the years that were examined. Similarly, Kennedy et al. (2011) found that skipped spawning was rare for Norwegian spring-spawning herring, in contrast to the higher rates (10–15%) that have been reported in the Baltic (Bucholtz et al. 2013; Ojaveer et al. 2015).

Sensitivity of the Stock Assessment

The results of the histology-based maturity classifications suggested that skipped spawning was not occurring and that spring spawners were occurring in relatively low proportions to fall spawners. The stock assessment was generally insensitive to the levels of spring spawning that were evaluated, which included proportions that were larger than were suggested by histology. The effects of ignoring spring spawners on stock assessments and subsequent management decisions, such as those for annual quotas, are also likely inconsequential. However, this conclusion should be revisited if seasonal spawning adaptations continue to manifest with increased proportions of spring spawners. To evaluate the effect of spawning seasonality more effectively, the stock assessment model could also be amended to have multiples seasons within a year as opposed to the annual time step that is currently used (NEFSC 2018). However, attempts at seasonally and spatially explicit stock assessment models for Atlantic Herring have failed due to a lack of sufficient data resolution (NEFSC 2018). Despite the insensitivity of the stock assessment model and subsequent management decisions to spring spawning, conservation efforts that are directed at maintaining each spawning component may be worth considering because such biodiversity can increase the resilience of species and ecosystems to human-induced perturbations (e.g., harvest and climate change; Worm et al. 2006; Hiddink et al. 2008). Also, the effects of spring and skipped spawning on the stock assessment were only evaluated assuming that the proportions in each spawning category were time invariant. Given the results of this study, time-varying rates of skipped spawning would be of greater consequence than spring spawning is due its larger

effects on *SSB*. In particular, increasing or decreasing trends in the proportion of skipped spawning would lead to increases or decreases in the perceived productivity of the stock (e.g., increased steepness). In systems where skipped spawning is prevalent, long-term monitoring of the rates of occurrence could be used to advance this research and evaluate the effects of those time-varying dynamics. Such research would require a time series of histological maturity data that is beyond the limited period that is reported here.

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SUPPORTING INFORMATION

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