Evaluating growth dimorphism, maturation, and skip spawning of Atlantic halibut in the Gulf of Maine using a collaborative research approach

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Abstract

The data-limited nature of Atlantic halibut (*Hippoglossus hippoglossus*) in U.S. waters hampers evaluation of what may be a slow but steady rebuilding pattern. Here, we collaborate with the commercial fishery to design and implement a multi-gear sampling program that collected 100s of biological samples from throughout the Gulf of Maine in a five-year period, 2014–2018. Examination of sectioned otoliths revealed a maximum age of 12 years (females) and 13 years (males); in comparison, Atlantic halibut as old as 40–50 years have been collected elsewhere in the western North Atlantic. Growth modeling confirmed sexual dimorphism, with a larger asymptotic length (L_∞) for females (214 cm fork length [FL]) than males (195 cm FL). Estimates of median female length at maturity, L_{50}, of 128 cm FL (124–132 cm, 95% confidence limits), and median female age at maturity, A_{50}, of 9.6 years old (9.0–10.8 years), were longer and older than previous reports for the Gulf of Maine, likely resulting from our use of histological instead of macroscopic methods to classify maturity. Histology demonstrated that vitellogenesis initiated in individuals in spring, nearly a year prior to spawning, which allowed us to identify first-time (primiparous) spawners and provided the first potential evidence of skip spawning for this species. Finally, an index was developed to track the proportion of potentially mature females in the fishery, which showed an increasing trend; this qualitative tool may prove useful in a data-limited environment for evaluating the relative stock status of Atlantic halibut.

Keywords: age, cooperative research, life history, reproduction, *Hippoglossus hippoglossus*

Introduction

The current stock status of Atlantic halibut, *Hippoglossus hippoglossus*, in U.S. waters is unknown but is considered well below target levels based on qualitative evaluation of the stock and historical evidence of much higher abundance (Blaylock and Legault, 2012; Hennen, 2020). Bottom trawls exhibit relatively poor catchability for Atlantic halibut, and persistently low catches in standardized fishery-independent bottom trawl surveys in U.S. waters confounds the detection of abundance trends (Hovgård and Riget, 1992; Zwanenburg *et al*., 2003; Rago, 2018; DFO, 2020). Evidence of rebuilding is limited but includes: 1) managed fishery catches that have steadily increased from about 40 metric tons (mt) annually during the fishing years 2002–2004 to about 140 mt during 2017–2019, and 2) a time series of commercial catch standardized to fishing effort that shows a stable or

slightly increasing trend (Hansell *et al*., 2020). In contrast to the U.S. situation, Atlantic halibut in Canadian waters are certified by the Marine Stewardship Council. Much higher landings are reported, between 2500 and 4100 mt each year since 2010 (DFO, 2020), and the value of this fishery in Canada has increased seven-fold since the early 2000s (Shackell *et al*., 2021).

Atlantic halibut are managed and assessed independently by the United States and Canada with conflicting evidence these stocks may (Kersula and Seitz, 2019; Liu *et al*., 2019) or may not (Seitz *et al*., 2016; Shackell *et al*., 2016) be connected. Recent genomic evidence suggests two genotypic stocks in the western North Atlantic: one across the North American continental shelf region and another in the semi-enclosed Gulf of St. Lawrence (Kess *et al*., 2021). Such genetic structure is overlaid by additional spatial structure in life history traits and migratory contingents (Shackell *et al*., 2021).

U.S. Atlantic halibut is likely to remain data limited, for some time, regarding assessment and management. Life history traits typically provide useful context for such data-limited situations. For example, heavily overfished stocks are characterized by size and age truncation, with corresponding loss in reproductive potential (Hixon *et al*., 2014; Barnett *et al*., 2017). In the case of Atlantic halibut, females can live to 38 and males to 50 years (Armsworthy and Campana, 2010), but in U.S. waters, Sigourney *et al*., (2006) observed few fish older than 13 years.

Confounding a direct interpretation of age truncation as a result of fishing pressure, Atlantic halibut exhibit broad geographic variability in life history traits. Growth rates are faster and sizes at maturity are smaller in warmer, southern waters (Armsworthy and Campana, 2010; Shackell *et al*., 2019; Shackell *et al*., 2021). Atlantic halibut in the Gulf of Maine may experience faster growth rates because of higher temperatures than in most Canadian waters, and they appear to exhibit sexual dimorphism as evident in most flatfish species, but growth modeling of fish captured in the Gulf of Maine has not been reported in the literature (Sigourney *et al*., 2006; Shackell *et al*., 2019).

Some aspects of Atlantic halibut reproduction are not well understood in U.S. waters but general reproductive principles are known based on halibut from other areas. Atlantic halibut is an iteroparous, batch spawner with group-synchronous oocyte development with respect to vitellogenesis (Norberg *et al*., 1991; Neilson *et al*., 1993). The final stages of oocyte maturation appear to begin in January – indicating the initiation of winter spawning – becoming transparent and reaching sizes of 2.3–3.4 mm (Haug and Gulliksen, 1988). Haug and Gulliksen (1988)

estimated annual fecundity of Atlantic halibut to range from 0.5 to 7.0 million eggs for females from 132 to 195 cm total length. Elevated temperatures have been demonstrated to delay spawning and reduce quantity and quality of eggs for Atlantic halibut (Brown *et al*., 2006).

In this study, we provide new life history parameters for Atlantic halibut at the southern range of its geographic distribution in the western North Atlantic. We overcame a chronic issue of low sample sizes by partnering with fishermen, and used a variety of fishing gears, which resulted in large numbers of fish of all sizes, both sexes, and year round throughout the Gulf of Maine (Read and Hartley, 2006; Fairclough *et al*., 2014; Thiel *et al*., 2014). We used best practices for ageing fish, including a direct comparison of thin-sectioned otoliths to whole otoliths (Karlson *et al*., 2013). We also applied gonad histology as a best practice to evaluate reproductive maturity and to reveal evidence of primiparity and skip spawning (Rideout and Tomkiewicz, 2011; McBride *et al*., 2013). Finally, to aid in future evaluation of the population, we propose the use of an index that approximates the proportion of mature females in the fishery, as a qualitative tool for evaluating the relative stock status.

Materials and methods

Collaborative sampling

A collaborative research approach between federal, state, and industry partners sampled Atlantic halibut throughout the Gulf of Maine. The largest single so urce of biological samples came from a novel, collaborative fishery-dependent sampling program lead by the Cape Cod Commercial Fishermen's Alliance (CCCFA) and The Nature Conservancy (TNC), who used multiple bottom-tending gear types (trawl, longline, and gillnet), fishing predominantly east of Cape Cod (Fig. 1; sample sizes tabulated in Supplemental Materials). Fishermen were compensated for each complete halibut sample, under conditions set forth in an Exempted Fishing Permit (EFP) by NOAA fisheries, and issued to 23 collaborating fishing businesses. Researchers trained collaborating fishermen through in-person training sessions, written protocols, and with a 'how-to' video https://www.youtube.com/watch?v=XhMV9e3UA14 (CCCFA, 2018) recorded by participating fishermen. Fishermen were provided sampling kits including tools, datasheets, a spring scale, and various sampling containers. Northeast multispecies regulations limit fishermen to landing one legal sized (> 41 inches, 104 cm) halibut per trip; under the EFP, the number of samples per day was increased to five in order to maximize sample collection, although it was extremely rare to receive five samples from a single trip.
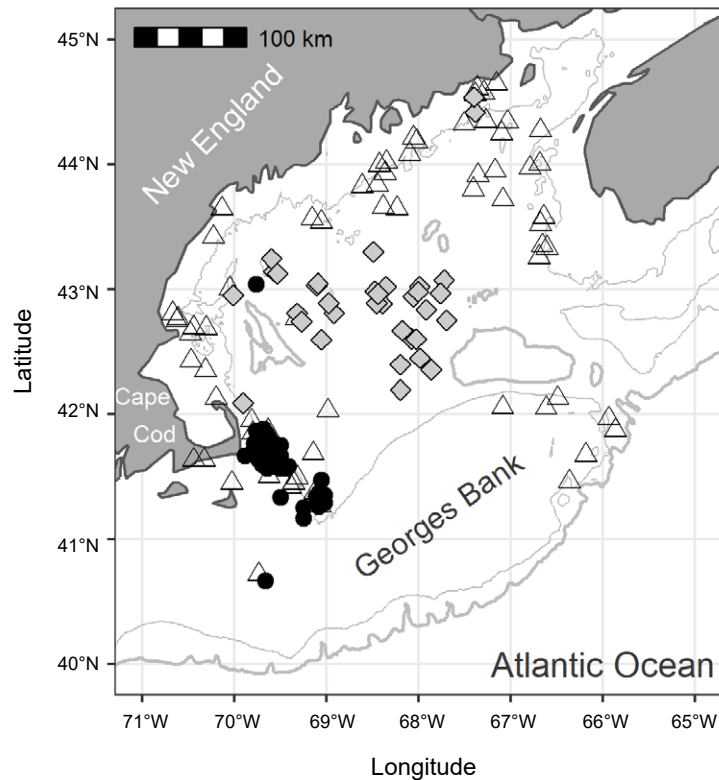
Fig. 1. Atlantic halibut (*Hippoglossus hippoglossus*) were collected throughout the Gulf of Maine, as depicted here for females used in the reproductive analyses. This plot of individuals collected identifies the multiple fishing gears used: bottom trawls (open triangles), gillnets (solid circles), and longlines (gray diamonds). A single fish collected by rod and reel is not shown. The North American continent is in dark gray, and the 100 m and 250 m isobaths are outlined in the thin and thick gray profiles, respectively. The entire scale bar is 100 km. See Supplemental Materials for sample sizes by source, gear, month, and year.

Additional halibut were obtained from several other sources: Maine's commercial fishery; the Maine and New Hampshire inshore bottom trawl survey; the Northeast Fisheries Science Center's (NEFSC) Ecosystem Survey Branch bottom trawl survey (Politis *et al*. 2014); the NEFSC's Cooperative Research Branch (CRB) bottom longline survey (McElroy *et al*. 2019); an industry-based bottom trawl survey in partnership with the Massachusetts Division of Marine Fisheries; and lastly, the NEFSC CRB Study Fleet Program.

Fish were collected as early as 2014–16, and sampling rates increased markedly in 2017–18 as a result of the partnership with CCCFA and TNC. Fish were collected in all months of the year except March during the 5-year period 2014–2018 (Supplemental Materials).

Fish were initially processed at sea and samples were stored on ice to be processed and preserved in the laboratory within 48 hours. Fork length (FL) was measured and reported to the nearest 1 cm. Total mass (TM) was measured to the nearest 1 g by fishery-independent sources or 500 g by fishery-dependent sources, and reported in kg. Ovary mass (OM) was recorded to the nearest g, and the gonadosomatic index was calculated as GSI = OM/(TM-OM) × 100. Sagittal otoliths were excised and stored dry in envelopes for ageing. Approximately 1 cm3 piece of tissue was excised from the middle of the ovary and fixed in 10% neutral-buffered formalin for gonad histology.

Otolith ageing

Age determinations were made on whole sagittal otoliths prior to sectioning for subsequent determinations. Halibut

sagittal otoliths differ slightly in shape between the eyed side of the fish and the blind side. When possible, both otoliths from each fish were examined side by side. The asymmetrical (eyed side) otolith tends to be thinner and wider which yields clearer annuli during whole otolith ageing. Whole otoliths were immersed in mineral oil and the distal surface was examined with reflected light. Oil was wiped off after ageing to prevent clearing of the otoliths.

After each sample had been aged whole, the otoliths were embedded in epoxy and thin sectioned through the core with a low-speed diamond wafering saw. These sections were then affixed to glass microscope slides and examined either with reflected (Fig. 2) or transmitted light. The age readers preferred the use of reflected light, except in the oldest fish where increased magnification was needed. The symmetrical otolith was preferred for age determination of thin sections as they are thicker, yielding to better separation of annuli in the primary reading plane along the edge of the sulcal groove.

All structures (n = 421) were assigned an age by two independent readers, with no knowledge of fish size, sex, or previously assigned ages. For structures in which there was disagreement in age between readers, a third joint reading was conducted to reach a consensus age. If a consensus could not be reached, the sample was discarded.

Although otolith ageing with a thin section method has been validated by Armsworthy and Campana (2010), we had not aged this species previously, so we compared ages from surface reads of whole otoliths to sectioned otoliths, and a subsample (n = 92) of the otoliths (whole and sectioned) was aged twice by each reader to assess within reader precision. Estimates of age precision included coefficient of variation (Chang, 1982), percent agreement, and percent agreement + 1 year. Precision estimates were generated between readers (n = 327) and within readers (n = 92) for a subset of the structures. Tests
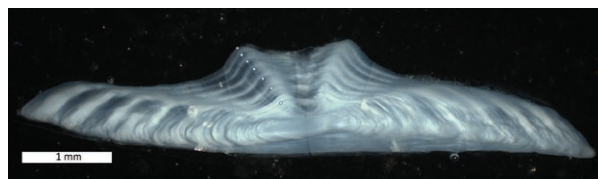

Fig. 2:   Cross section of an Atlantic halibut (*Hippoglossus hippoglossus*) otolith viewed with reflected light. This individual was captured in May with the translucent zone nearly complete at the edge. Counting the edge, this fish was determined to be age 7 (annuli and edge marked with white dots on left side of the sulcus).

of symmetry (Bowker's, Evans and Hoenig's, McNemar's, as described by McBride [2015]) were performed using the FSA package in R (Ogle *et al*., Version 0.8.30, 2020). Due to difficulty reading whole otoliths and very low reader confidence, consensus ages were only reached for the subset of whole otoliths.

Final age assignments were based on the number of annuli counted on the sectioned otoliths, the capture date, and the amount of otolith growth after the final completed annulus. This grouped all fish spawned in a given calendar year into the same age group. A birthdate of December 1st was used, based on the literature and evidence presented herein, to calculate biological ages for use in growth modeling.

The von Bertalanffy and Gompertz growth models were evaluated for sex-specific growth of Atlantic halibut. Models were varied to allow each combination of model parameters to be fixed or variable between sexes. Size and age data of 93 males and 297 females were fit to both models and evaluated using Akaike's Information Criterion (AIC) within R software (version 3.6.3) (Supplemental materials).

Our ability to evaluate gear bias was limited by small sample sizes for long line and rod and reel. However, length at age for ages 4–8 were compared between gillnet-captured fish and bottom-trawl-captured fish using Student's t tests.

Chapman-Robson mortality estimates were calculated using the FSA package in R (Ogle *et al*., Version 0.8.30, 2020). Mortality was calculated with all data combined, by sex, and by gear, including 95% confidence intervals.

Ovarian Histology and Oocyte Staging

Subsamples of fixed ovarian tissue were trimmed to < 4 mm thickness, placed in a cassette, and returned to formalin until histology processing. These subsamples were prepared using standard paraffin embedding techniques (McBride *et al*., 2013), including sectioning the tissue using a rotary microtome set to 5 µm, mounting on microscope slides, and staining with Schiffs-Mallory trichrome. Histology slides were viewed (20–400x) on a monitor using a microscope and digital camera.

Descriptions for oocyte stages, including post-ovulatory follicles (POFs) and oocyte atresia, were modified from Neilson *et al*. (1993) for Atlantic halibut; Kennedy *et al*. (2011) for Greenland halibut, *Reinhardtius hippoglossoides*; Press *et al*. (2014) for winter flounder, *Pseudopleuronectes americanus*; and Fish (2020) for Pacific halibut, *Hippoglossus stenolepis* (See also Supplemental Materials). At their most advanced, primary growth (PG) germ cells were small (< 200 µm) with nucleoli scattered

along the periphery of the nucleus (Fig. 3). Development of early cortical alveoli (EC) in the germ cell were the first cytoplasmic inclusions noted, appearing initially as scattered, unstained vacuoles on the periphery of the cell. A late cortical alveoli (LC) germ cell stage was recognized once a biphasic dark-light ring of inclusions developed around the periphery of the cytoplasm. An early vitellogenesis (V1) stage emerged as orange inclusions appeared proximal to the outer ring of cortical alveoli. Vitellogenic inclusions spread until the cytoplasm was 'fully yolked' (V2). Histology plate images were scanned using the Grundium Ocus slide scanner and images were taken using Aperio ImageScope software (Figs. 3, 4).

Evidence of oocyte maturation — either migration or breakdown of the nucleus or hydration of the cell — was not observed. Evidence of ovulation was rare, with only the oldest stages of post-ovulatory follicles observed. Follicular atresia was identified as early (alpha) or late (beta), and ranked by extent, but offered little additional information to classify maturity. Tunica (gonad wall) thickness was measured to the nearest micron, as an index of maturity, when present in the histology section. Measurement of the tunica occurred at an intact section of the tissue, away from edges caused by excision of the tissue (see Fig. 4 and Supplemental Materials).

Later, we refer to oocyte stage-specific maximum oocyte diameters. These were measured from images of approximately 300 oocytes per female suspended in water, as captured using a microscope and camera (Leica M26 scope
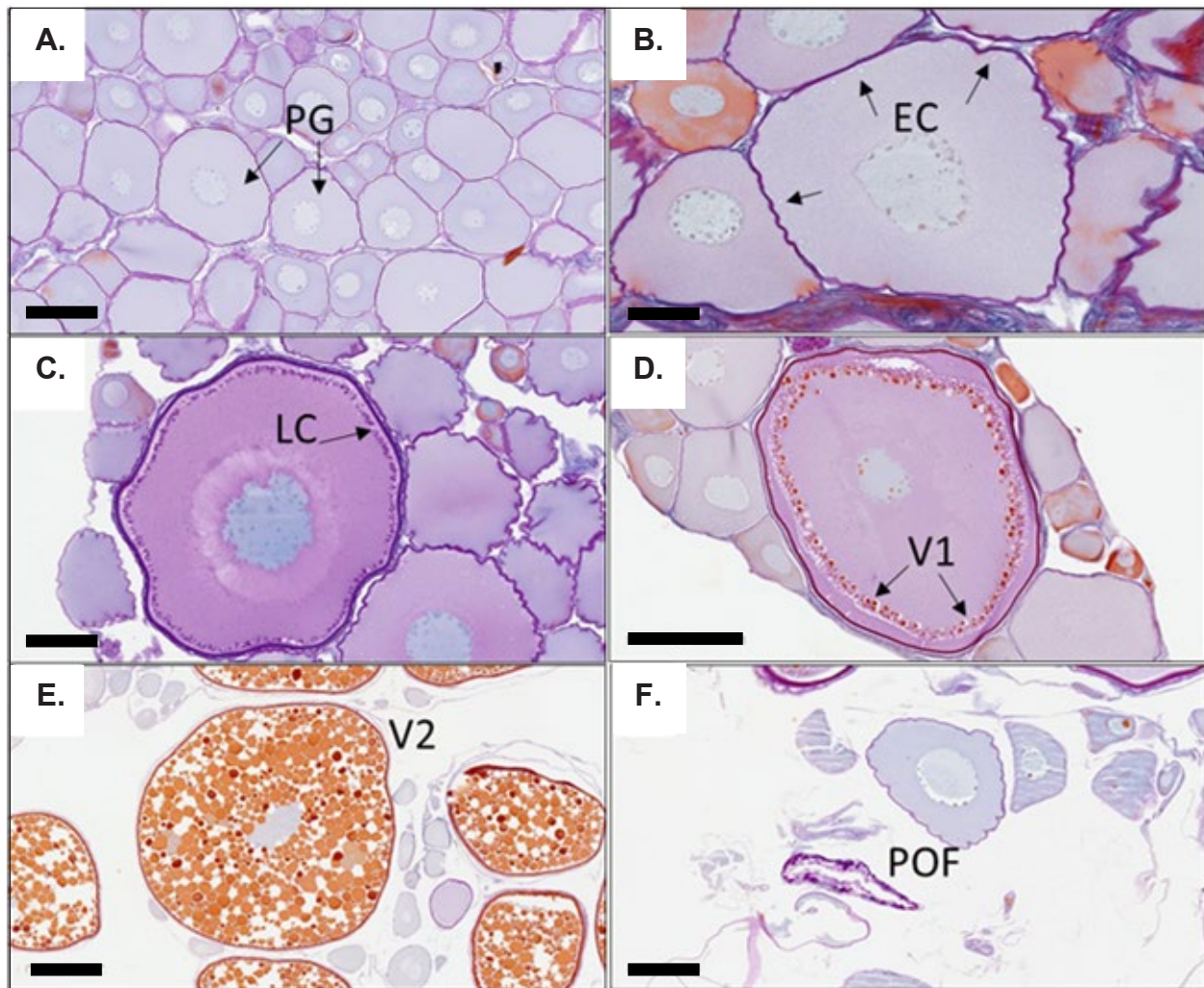

Fig. 3.   Images of primary and secondary oocyte development of Atlantic halibut (*Hippoglossus hippoglossus*). **A**) An immature fish with primary growth (PG) oocytes, **B**) early development of cortical alveoli (EC) in the cytoplasm, **C**) late development of cortical alveoli (LC) in the cytoplasm, **D**) early development of yolk (V1), **E**) full development of yolk (V2), and **F**) an older post-ovulatory follicle (POF). Scale bars are 100 microns (A, C, F), 70 microns (B); 200 microns (D), or 400 microns (E).
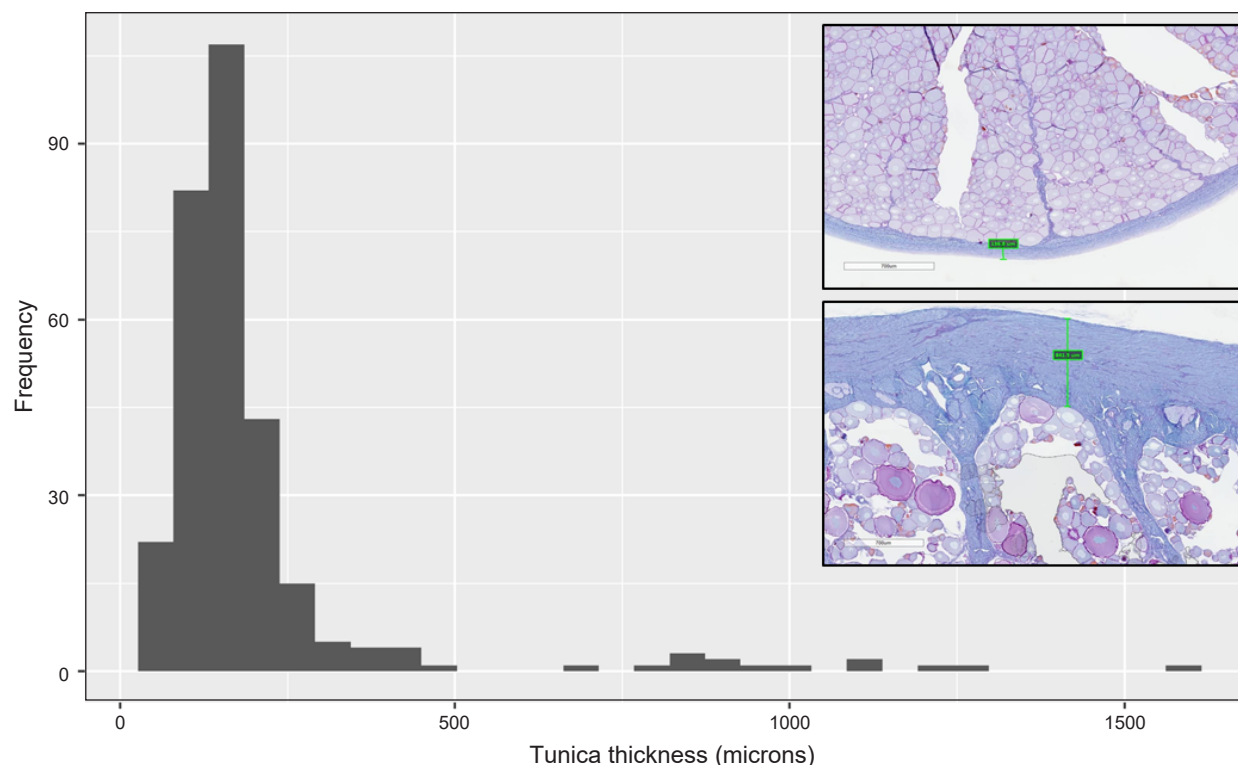
Fig. 4.   Frequency of female Atlantic halibut (*Hippoglossus hippoglossus*) tunica (gonad wall) thickness, measured from histology slides of ovarian tissue. The threshold for maturity based on tunica thickness was ≥ 500μ. Specific images are inset of (top) an immature fish showing thin tunica (137μ), and (bottom) a mature fish with thick tunica (842μ). The scale bar in both photomicrographs is 700μ.

and Leica DFC295 camera). Image analysis software (ImageJ with the plugin ObjectJ) was used to manually measure the oocyte diameters. The most advanced oocyte stage (MAOS) of these whole oocytes was identified from a paired sample of ovarian histology.

Maturity classification, ageing, and modelling

Maturity was classified following criteria initially developed for Greenland halibut (Kennedy *et al*., 2011) and winter flounder (Press *et al*., 2014). In the former, vitellogenesis required more than a year to complete, whereas in the latter, vitellogenesis started 10–12 months prior to spawning. Atlantic halibut were classified as immature if they did not have vitellogenic oocytes, any POFs, or a thin tunica (< 500 μ). They were classified as mature if they had vitellogenic oocytes (MAOS V1 or V2), POFs of any age, or a thick tunica. The use of a thick or thin tunica is directed at distinguishing all immature classes from resting fish, the latter of which is a mature class and often confused with immature fish macroscopically (*e.g.*, McBride *et al*., 2013). Support of the specific threshold of 500 μm is presented elsewhere in this paper (Fig. 4).

The binomial, logistic model — logit (mature) = $e^{a+bX}/(1 + e^{a+bX})$ — was used to estimate maturity parameters, where a and b are estimated and X is length or age. Confidence limits (95%) were estimated by bootstrapping the data using the sizeMat package in R (Torrejon-Magallanes, 2020).

Changes in Proportion Mature Over Time

In the absence of an effective fishery-independent survey for Atlantic halibut in U.S. waters, fishery-dependent data have been used for stock assessment (Hennen, 2020). In particular, commercial discard rates have been used as an index of abundance. As discarded fish are typically small, a new index was developed to track the proportion of fish landed larger than the L_{50}, determined herein as 128 cm, as measured by port samplers.

Atlantic halibut regulations in the United States have restricted fishermen to one landed fish per trip since 1999, and the minimum size of retention was adjusted from 36 to 41 inches (91.4, 104 cm) in 2009, which starts our time series. In practice, this results in some unknown degree of highgrading where the largest fish encountered is the

most likely to be landed. Therefore, the size composition of landed fish may be reasonably indicative of trends in the average maximum size of fish encountered. The annual proportions were estimated as the proportion of fish larger than the L_{50} estimate, using U.S. catches since 2009, and the time series was fit with a generalized linear model (GLM). The data are binomially distributed, where fish > L_{50} were given a 1 and fish < L_{50} were given a 0. The model used year to predict the proportion mature.

Comparing the proportion mature in the Canadian Scotian shelf (4WXZ) stock of Atlantic halibut to the U.S. stock was of interest as the CA stock is relatively data rich and has increased over recent years (DFO, 2020). Fixed station longline survey data from area 4WXZ was also fit to a GLM using year to predict proportion > L_{50}. Survey data in this case were preferred as there is reason to believe that the selectivity of fishers in area 4WXZ has changed, in order to better target larger Atlantic halibut (den Heyer pers. com).

Results

Collaborative, multigear sampling

Atlantic halibut were collected throughout the Gulf of Maine (Fig. 1). Bottom trawls collected Atlantic halibut in all years, 2014–2018, all around the Gulf of Maine, in both U.S. and Canadian waters, with some samples on the northeast peak of Georges Bank and offshore of southern New England (Supplemental Materials). Gillnets operated by the CCCFA focused their fishing offshore of Cape

Cod, sampling in 2017–18. Longline sampling collected Atlantic halibut in all years, primarily in the deeper portions of the Gulf of Maine.

A wide size range of fish was collected, and the size ranges differed between gears. Fish caught by bottom trawl had the smallest median size (84 cm fork length), but the widest range of sizes (30–171 cm; n = 118; Fig. 5). Fish caught by gillnet had the narrowest inter-quartile range, and the longline gear had the highest median. Although, longline gear is typically used to target larger Atlantic halibut in commercial fisheries of the Gulf of Maine and Scotian Shelf, the longlines used here were rigged for groundfish (cod, haddock, pollock) with small (12/0 size) hooks and squid bait, as compared to the larger 16/0 hooks, and half herring bait preferred by commercial halibut fishermen. The sex composition from the CCCFA catch east of Cape Cod were overwhelmingly female: only 27 of the 234 halibut with confirmed sex identification were male (88% female).

Age and growth

Atlantic halibut was a difficult-to-age species, even for Reader 1, who had more experience with otoliths than Reader 2. With whole otoliths, both readers agreed that they had very low confidence, and the results presented a mix of low precision and bias (Table 1). Whole otoliths yielded younger ages than sectioned otoliths across most age classes (Table 2). The opacity of the whole otoliths reduced the visibility of the annuli laid down in the first few years of life.

Table 1.   Precision estimates for Atlantic halibut (*Hippoglossus hippoglossus*) ages. Sample size (n), Chang's coefficient of variation (CV), percent agreement, percent agreement within 1 year (% within 1), and symmetry test (Evans Hoenig) significance are reported. The results between all tests of symmetry were largely the same, so only the results from Evans and Hoenig's test is shown (ns denotes no significance and * denotes $P < 0.05$), as recommended by McBride (2015).

|	Method and read	n	%CV	% agreement	% within 1	Evans Hoenig
Within Reader	Whole, Reader 1	92	16.52	39.1	82.6	*
	Whole, Reader 2	92	15.73	39.1	84.8	*
	Sectioned, Reader 1	92	7.97	53.8	95.7	ns
	Sectioned, Reader 2	92	16.87	18.3	75.0	*
Between Reader	Whole, first reading	327	11.85	44.2	85.3	ns
	Whole, second reading	92	8.25	63.0	97.9	*
	Sectioned, first reading	92	11.41	40.9	97.2	*
	Sectioned, second reading	327	10.64	47.4	88.1	ns
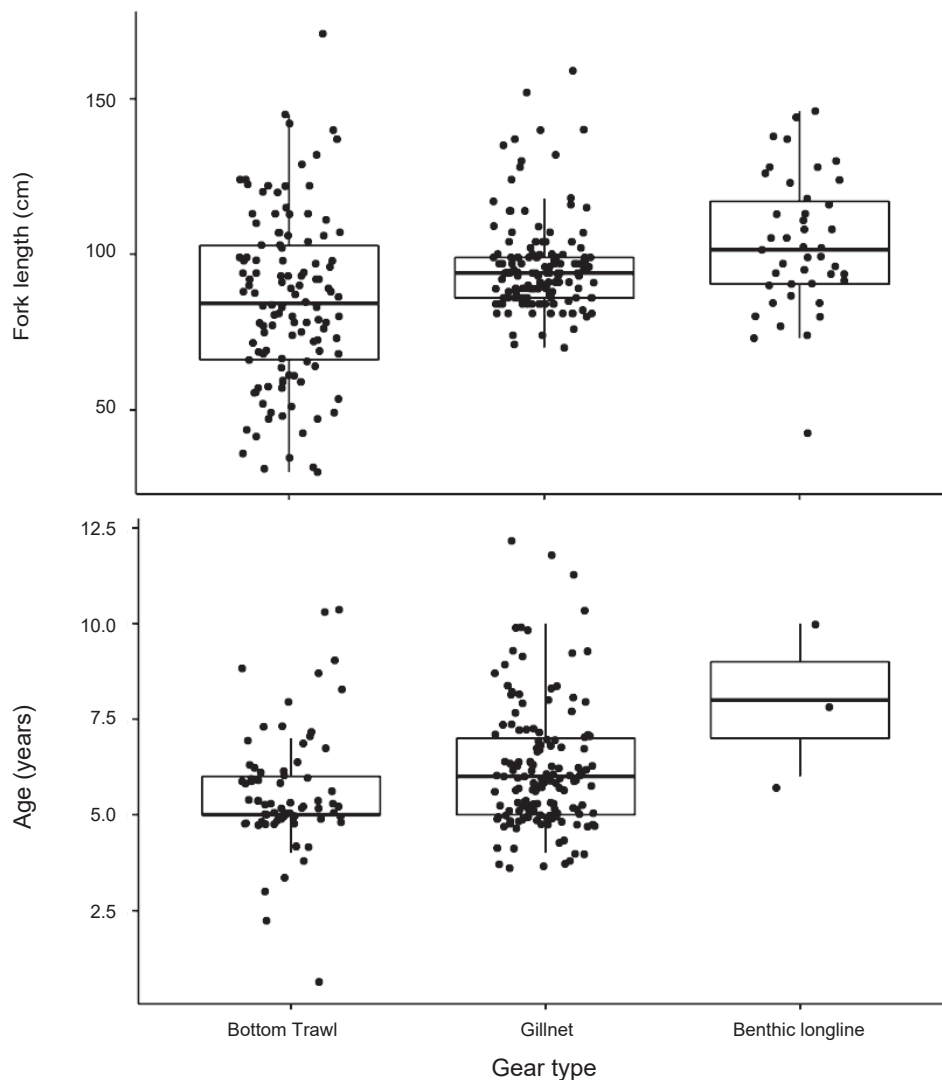
Fig. 5.   Sizes (top) and ages (bottom) of female Atlantic halibut (*Hippoglossus hippoglossus*)
used for reproductive analyses. Both size and age differed significantly by gear type
(Kruskal-Wallis test, $P < 0.001$). Data are plotted as jittered points overlaid on a
box-whisker plot, where the median is surrounded by a box of the inter-quartile range
(IQR), and the whiskers are an additional 1.5 times the interquartile range. A single fish
(130 cm fork length) collected by rod and reel is not shown.

Neither reader had specific experience ageing this species
before, and precision and bias improved from the first to
second reads, particularly with sectioned otoliths (Table 1;
%CV, Evans Hoenig test). With sectioned otoliths, Reader
2 exhibited bias between reads where Reader 1 did not
(Table 1; Evans Hoenig test). This was likely due to the
experience level of the readers.

Atlantic halibut were assigned ages from 0 to 13 years.
Average age of females was slightly older (5.8 years;

5.6–6.0 years) [mean; 95% confidence limits] than males
(4.5; 4.0–5.0). Despite this, the maximum recorded age
of males (13 years, $n = 52$) was slightly older than that of
females (12 years, $n = 247$) (Fig. 6).

By gear, bottom trawls captured the largest age range
(0–10 years; Fig. 6). Gillnets captured older fish but ages
were truncated at the low range (4–13 years). The other
gears had smaller sample sizes and the ages were within
2–11 years.

Table 2.   Age frequency table of Atlantic halibut (*Hippoglossus hippoglossus*) ages from sectioned and whole otoliths. Grey boxes represent agreement between structures.

Whole otolith age	\ Sectioned otolith age									
	0	1	2	3	4	5	6	7	8	9
9									1	
8									1	1
7								1	3	
6							5	4	3	
5						19	10	3		
4					4	18	3			
3					10	1				
2										
1		4	2							
0		3								

Atlantic halibut demonstrated dimorphic growth between sexes. In terms of model selection, the von Bertalanffy model allowing only L_∞ to vary by sex had the lowest AIC value (Table 3). Although minimal differences were seen in AIC values between the von Bertalanffy model and the Gompertz model allowing for sexual dimorphic growth, the von Bertalanffy estimated a more realistic t_0 value. The final selected model for length (*L*, cm) at age (*t*, yr) was $L_t = 195(1 - e^{-0.093(t-0.217)})$ for males and $L_t = 214(1 - e^{-0.093(t-0.217)})$ for females (Model vB5, Table 4, Fig. 7). Females were predicted with this model to be 1.3 cm larger at age one, 6.8 cm larger at age five, 11.3 cm larger at age 10, and 14.2 cm larger at age 15 ($\Delta L_\infty = 19$ cm between sexes).

The Chapman-Robson estimate of total mortality (Z) for all data combined was 0.60 (95% confidence limit = 0.52–0.69) for ages five and older (Table 5). Estimates of Z varied by gear and sex from a low of 0.60 (0.51–0.69) for females to a high of 0.66 (0.54–0.79) for males.

Student's t-tests revealed significant differences in length at age between gillnet captured fish and bottom trawl captured fish. Halibut aged 4 and 5 captured with a gillnet were larger than fish captured with a bottom trawl. The inverse relationship was true for ages 7 and 8.

Oogenesis

Oocyte development required several years. Primary growth (PG) oocytes were observed, as the most advanced oocyte stage, in females as young as one year old and as small as 30 cm (sample sizes, $n_{aged} = 197$, $n_{total} = 261$). Further steps in oocyte development took at least four more years. Early development of cortical alveoli (EC) first appeared in females as young as five yr. and as small as 64 cm ($n_{aged} = 7$, $n_{total} = 14$), and late development of cortical alveoli (LC) first appeared in females as young as six yr. and as small as 102 cm ($n_{aged} = 7$, $n_{total} = 15$). First development of secondary, vitellogenic (V1) oocytes appeared in females as young as nine yr. and as small as 117 cm ($n_{aged} = 1$, $n_{total} = 6$), and full development of vitellogenesis (V2) first appeared in females as young as nine yr. and as small as 81 cm ($n_{aged} = 9$, $n_{total} = 17$).

An advancing cohort of vitellogenic oocytes emerged in spring and grew rapidly in the following months, creating a bimodal distribution of oocyte sizes that is characteristic of group synchronous development of vitellogenic oocytes (Table 6; Supplemental Materials). Maximum sizes of different oocyte stages were: 671 μm (LC), 828 μm (V1), 1873 μm (V2), as measured from whole oocytes (see also Supplemental Materials for oocyte diameters measured from gonad histology of individual females). The emergence and advance of a vitellogenic cohort of oocytes was also evident in monthly plots of the GSI, when the ovarian weight relative to the ovary-free female weight maximized in October at 8.5% (Fig. 8).

Indications of spawning were rare and indirect. The reset of GSI values after November, suggested a likely winter spawning season (Fig. 8). No females were observed to be actively spawning, either with oocytes advanced to nucleus migration or hydration of the oocyte (Fig. 9). No females appeared in a spent condition, either with ovaries containing relatively fresh POFs, extensive atretic yolked oocytes, residual eggs in the lumen, or a mix of these traits. Only two females had any POFs at all, and while these were unambiguously recognizable as a two-layered structure with a collapsed lumen, they were well degraded and not new (Fig. 3).

Maturity and Skipping

The median length at maturity, L_{50}, was 128 cm, with 95% confidence limits between 124 and 132 cm FL (Fig. 10). The median age at maturity, A_{50}, was 9.6 years old, with 95% confidence limits between 9.0 and 10.8 years (Fig. 10).
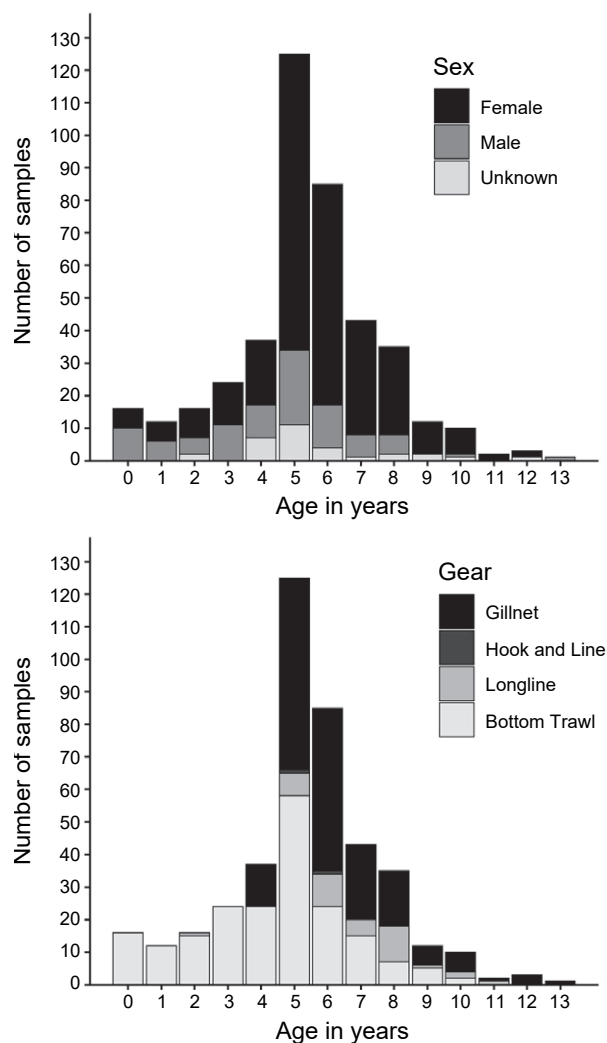
Fig. 6.   Atlantic halibut (*Hippoglossus hippoglossus*) age
frequency by sex (top) and gear (bottom).

Not all mature fish (*i.e.*, with evidence that they had spawned in the past) had traits to indicate they were preparing to spawn in the next spawning season (*i.e.*, skip spawners). One of 24 females identified as mature was large (135 cm FL), with a thick ovarian wall (1230 μ), but its most advanced oocyte stage was previtellogenic (LC). At the time it was caught, in late July, this resting fish was likely skipping that year's spawning cycle. This sample indicates the skipping rate among mature females was 4.2%. This estimate may be biased (low) because we did not exclude any females collected in November–December, when Atlantic halibut migrate to the continental slope (see Discussion).

A second skip spawner was detected using a different selection method. Again, skipping implies that a fish has spawned in the past, so first we selected females with a

thick tunica (> 500 μm). And skipping implies the spawning frequency is mis-specified (in this case every year). Finally, to check for spawning capable ovaries among fish prior to the spawning migration to continental slope waters undertaken by this species, we selected females in the month of October, which precedes the spawning period. These criteria resulted in four females, 117–145 cm FL, each with thick tunicas (685–1000 μm). Three had spawning capable ovaries: an advanced cohort of fully yolked oocytes (MAOS: V2, GSI = 5.0 – 8.5), which would predict that they would ovulate in the approaching winter spawning period. However, the smallest mature female (117 cm FL, 900 μm tunica thickness) was not prepared to spawn within a few months (MAOS: V1, GSI =0.95). This very small sample indicated the skipping rate among mature females was 25%. This estimate may be biased (high) because it assumes that the individual diagnosed as a skipper could not advance in vitellogenesis sufficiently from fall to winter to spawn, which is likely based on other northern flatfishes, but an assumption based on limited sample sizes in our study.

The two skippers observed here, both aged as nine years old, were classified as mature females that are not part of the spawning stock in that reproductive cycle. One of them appeared as resting, with no evidence advancing a vitellogenic cohort of oocytes at time of capture in July, while the other female was developing, but it showed only early signs of vitellogenesis in October, with no evidence it was prepared to ovulate eggs in the winter spawning period that was imminent.

We also considered that we could identify first-time spawners, or primiparous females, based on evidence that the advance of a vitellogenic cohort of oocytes may proceed most of the year in advance of the spawning season, when in combination with immature fish having a thin tunica. One fish could be identified as a first-time spawner by these combined criteria: A female with both a thin tunica (374 μm) and a MAOS of V1 was 122 cm FL, unknown age, caught in April, with a modest gonad to body ratio (GSI = 0.96). Five of the six females with a MAOS of V1 were caught in April–May (Table 6), suggesting a pronounced seasonality initiating vitellogenesis (except for the skip spawner that initiated vitellogenesis in October, as mentioned in the preceding paragraph). This isolated example of a primiparous female was among the group of 24 mature females, representing 4.2% of the mature fish.

Changes in Proportion Mature Over Time

The proportion of fish larger than the L_{50} = 128 cm has increased since 2009 in both the U.S. and Canadian Scotian shelf stocks (Fig. 11). For the U.S. stock, this proportion

Table 3. Multiple growth models were fit to the length and age data of Atlantic halibut (*Hippoglossus hippoglossus*). Model parameters were allowed to vary between sexes in different combinations. Degrees of freedom and AIC values are shown AIC.1 denotes the difference in AIC values from the best fit model.

model type	sex variable parameters	df	AIC	AIC.1	model.seq
Gompertz	L_∞, G, X	7	3936	1.60	Go1
	G, X	6	3937	3.17	Go2
	L_∞, X	6	3935	1.21	Go3
	L_∞, G	6	3936	1.96	Go4
	L_∞	5	3935	0.75	Go5
	G	5	3936	1.50	Go6
	X	5	3937	2.46	Go7
	none	4	3937	2.82	Go8
von Bertalanffy	L_∞, K, T_0	7	3937	2.98	vB1
	K, T_0	6	3937	2.79	vB2
	L_∞, T_0	6	3936	2.11	vB3
	L_∞, K	6	3935	1.00	vB4
	L_∞	5	3934	0.00	vB5
	K	5	3936	1.39	vB6
	T_0	5	3938	3.76	vB7
	none	4	3939	4.29	vB8

has been increasing at a rate of approximately 18% per year (where year is a significant predictor of the odds of proportion mature, with a coefficient of 0.173 [$P < 0.001$], and $e^{0.173} = 1.18$ or 19%). The trend in the Canadian data is less dramatic, but based on more data ($n = 6\,091$ lengths vs. 1 244 for the US). In the Canadian data, year predicts proportion mature with a coefficient of 0.0825 [$P < 0.001$], representing an annual increase in the odds of proportion mature of about 9%.

Discussion

Collaborating with commercial harvesters during their operational fishing trips increased sample sizes, numbers of large fish, and spatiotemporal coverage. In terms of life history, this allowed updated, reasonably precise estimates of dimorphic growth and patterns of reproduction and maturity by Atlantic halibut in the Gulf of Maine. This study also showed an increase in the proportion of mature fish in both the U.S. and Canadian Scotian Shelf stocks, providing some hope for rebuilding the U.S. stock.
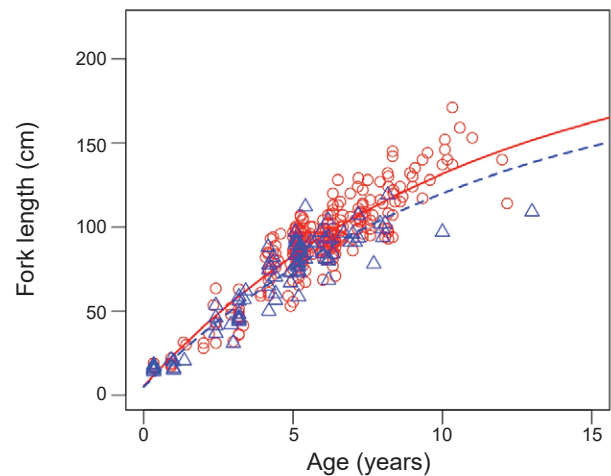

Fig. 7.   Atlantic halibut (*Hippoglossus hippoglossus*) growth. Red circles represent females, blue triangles males. Red solid line (female) and blue dashed line (male) are the growth curves as plotted by model vB5 (see Tables 3, 4).

Table 4. Model parameters for the von Bertalanffy model with separate asymptotic maximum lengths for each sex (*i.e.,* L$_\infty$F, the female asymptotic maximum length), accounting for sexual dimorphism of Atlantic halibut (*Hippoglossus hippoglossus*). These parameters are for model vB5 from Table 3.

	Estimate	Std. Error	t value	Pr(>|t|)	95% LCI	95%UCI
L$_\infty$F	214.0	44.02	4.860	0.000	127.5	300.5
K	0.093	0.030	3.079	0.002	0.034	0.152
t$_0$	0.217	0.342	0.636	0.525	-0.454	0.889
L$_\infty$M	195.2	41.04	4.760	0.000	114.5	275.8

Collaborative Research

We characterize our partnership with commercial fishermen as 'collaborative,' rather than merely 'cooperative,' in that the fishermen were involved in all aspects of the project from forming the research question, to developing sampling methods, to collecting biological samples and reviewing results (Yochum *et al*., 2011). During the project design phase fishermen accurately projected the number of samples they as a group could deliver over two years, which increased the annual sample number from 18 per year in 2014–2016, to over 100 per year in 2017–2018. This resulted in an overall yield of 197 females, 63% of all female Atlantic halibut samples collected for the study. Our study was not designed to address the issue of highly skewed sex ratios in the commercial catch, but we note our results were very similar to the 4F:1M ratio reported in retained catches of Pacific halibut, so this does not appear to be unexpected (Loher *et al*., 2022). In a separate study, Hansell *et al*. (2020) also collaborated with Maine fishermen to develop a time series of standardized catch of Atlantic halibut, which serves as an index of abundance to track trends in population abundance of this data-limited fishery.

Working with commercial fishermen was a highly cost-effective approach to collect biological samples for a relatively rare species like Atlantic halibut, where fishermen landed 0–5 fish per day under an exempted fishing permit. The cost of chartering fishing vessels to target Atlantic halibut would have been prohibitively expensive considering the low daily catch and absence of a targeted fishery. Through the collaborative development of the project, fishermen agreed to financial reimbursement per complete sample, which was designed to compensate fishermen for the cost of carefully completing the biological sampling and sample delivery, while at the same time not bei ng so high that fishermen would be tempted to target Atlantic halibut for the funds.

Age and growth

Atlantic halibut collected for ageing in this study were of size (14–171 cm) and age ranges (0–13 years) similar to those seen by Sigourney *et al*. (2006), whose samples came from a similar geographic region; in fact, many of Sigourney *et al*.'s samples came from the same federal bottom trawl survey which has been ongoing since the 1960s. We report ageing error rates transparently but find no comparable reports of ageing error in the literature
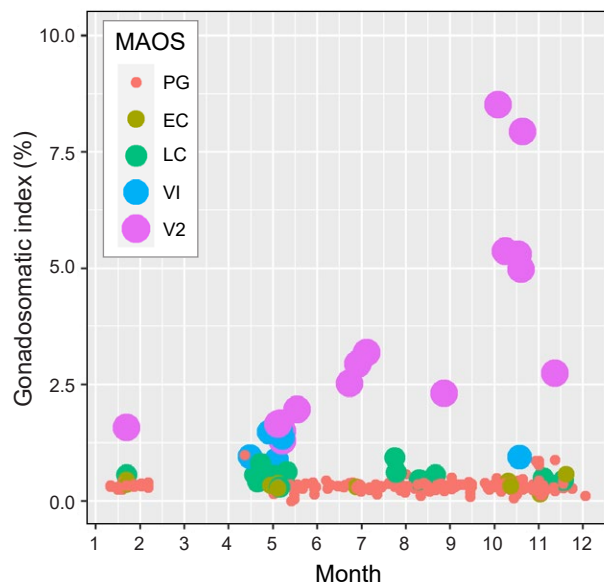

Fig. 8. Seasonal patterns of the gonadosomatic index of female Atlantic halibut (*Hippoglossus hippoglossus*) individuals. The most advanced oocyte stage (MAOS) of each female is indicated by color and increasing symbol size denotes more advanced oogenesis (see Fig. 3 for oocyte stages). Monthly tick marks indicate the first of each month (1 = January 1, all years of data pooled).

Table 5. Chapman-Robson total mortality estimates and confidence intervals for Atlantic halibut (*Hippoglossus hippoglossus*) captured in this study. Ages five and older were used for mortality estimates. Samples of all fish were also subset by sex and the dominant fishing gears.

Sample	Z	95% LCI	95% UCI
All fish	0.60	0.52	0.69
Female	0.60	0.51	0.69
Male	0.66	0.54	0.79
gillnet	0.61	0.51	0.70
trawl	0.62	0.46	0.77

to evaluate the relative precision in ageing this species among studies. Moreso, there are other factors that affect maximum sizes and ages in growth studies of Atlantic halibut. In particular, Armsworthy and Campana (2010) reported larger (232 cm) and older (50 years) Atlantic halibut from Canadian waters. But their larger maximum size and age may be at least partly an artifact of much larger sample size, because they examined 2 000 thin-sectioned otoliths, selected from an archive of about 65 000 fish. When sample sizes are larger, often, so is the size and age range. Also, their methods describe a post-stratification procedure of this archive (*e.g.*, five fish per 3-cm length bin), which over represents larger and older fish relative to sampling the entire catch as we did here. Finally, the majority of their samples were from longline gear (83%), whereas the majority of our samples were from bottom trawl and gillnet gear (86%; Supplemental Materials). Longline gear catch more faster growing fish than bottom trawls (Armsworthy and Campana, 2010; Sigourney *et al.*, 2006), whereas gillnets exhibit dome selectivity (*e.g.*, in this study gillnets did not capture any fish younger than age four, and age four and age five fish were larger at age than those captured by bottom trawl). Other specific gear

configurations (*e.g.*, hook size on longlines) confound simple comparisons of different samples, as well. These factors, together with the rebuilt condition of Atlantic halibut in Canadian waters, all contribute to much larger and older fish in the Armsworthy and Campana (2010) report. As a historical benchmark, a halibut larger than 300 kg was caught in the Gulf of Maine in 1917 (Klein-MacPhee, 2002), whereas our largest fish, 171 cm FL, was 10 years old and weighed 44.5 kg.

Consistent with previously published work (Armsworthy and Campana, 2010; Sigourney *et al.*, 2006; Bowering, 1986; Shackell *et al.*, 2019), female Atlantic halibut in this study grew larger than males. The asymptotic length (L_∞) parameter fit better when modeled separately by sex, with reasonable precision considering the relatively small sample size of the largest fish. Such sexual dimorphism in growth of Atlantic halibut increases the variance of size at age in unsexed samples. Our estimations of asymptotic lengths (214 cm for females and 195 cm for males) were smaller than those produced by Armsworthy and Campana (2010) (232 cm F, 175 cm M). This is not surprising given the differences in sampling design, gear configurations, and Atlantic halibut longevity in U.S. versus Canadian waters.

Given the opportunistic sampling nature of this study in both the gear used and the area sampled, mortality estimates are preliminary. The migratory nature of Atlantic halibut, coupled with the lack of very large, reproductively active individuals in our samples, suggests that our sampling efforts were not inclusive of the whole stock. The absence of those largest individuals likely biased our mortality estimates high. Two tagging studies on the Scotian Shelf and Grand Banks of the western North Atlantic Ocean showed lower total mortality estimates of Atlantic halibut: 0.37–0.46 (years: 2007–2009), or 0.24 (males, year 2009) and 0.41 (females, year 2009) (den Heyer *et al.*, 2013; Trzcinski and Bowen, 2016). However, lower total mortality is expected in Canada, where the fishery is certified by the Marine Stewardship Council.

Table 6. Seasonality of reproductive development among female Atlantic halibut (*Hippoglossus hippoglossus*), indicated as the number of fish by most advanced oocyte stage (MAOS) captured each month. See text for characterization of oocyte stages.

MAOS	Month												Sum
	1	2	3	4	5	6	7	8	9	10	11	12	
PG	16	10	0	4	34	22	26	31	24	53	42	1	263
EC	2	0	0	1	6	1	0	0	0	2	2	0	14
LC	1	0	0	3	4	1	2	2	0	0	2	0	15
V1	0	0	0	2	3	0	0	0	0	1	0	0	6
V2	1	0	0	0	5	2	2	1	0	5	1	0	17
Sum	20	10	0	10	52	26	30	34	24	61	47	1	315

Reproduction and maturity

The results from gonad histology were consistent with previous characterizations of Atlantic halibut as iteroparous with group-synchronous oocyte development with respect to vitellogenesis (Haug and Gulliksen, 1988, Neilson *et al*., 1993). In particular, we document a prolonged period of vitellogenesis (months), first-time maturing females (primiparity), repeat spawners (iteroparity), and

new evidence of mature females skipping spawning. Fig. 9 integrates the published maturity scheme used by the Northeast Fisheries Science Center (NEFSC; Burnett *et al*, 1988), which is based entirely on macroscopic characters, with the processes of oogenesis and ovarian microstructure informed by gonad histology. In our region, the relative rarity of Atlantic halibut in the NEFSC bottom trawl survey is a challenge for quality assurance of training staff on at-sea maturity determinations of this
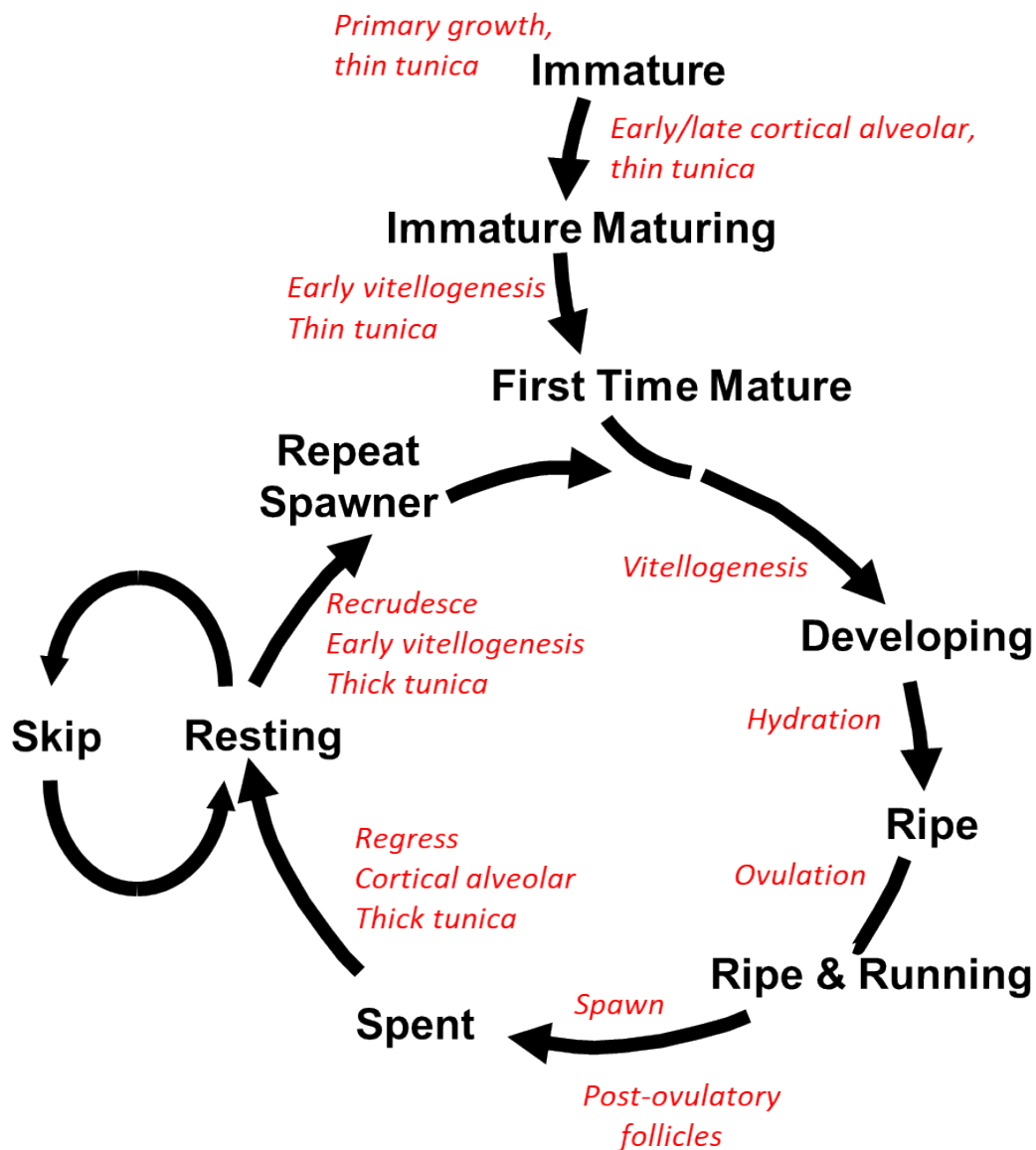
Fig. 9.   Proposed maturity classification scheme for female Atlantic halibut (*Hippoglossus hippoglossus*), with major maturity classes in bold and histological features in *italics*. Both the immature and immature maturing classes showed no prospect of spawning within a year or any past spawning. Spawning capable (ripe), actively spawning (ripe and running), or immediately post-spawn (spent) were not observed in this study.
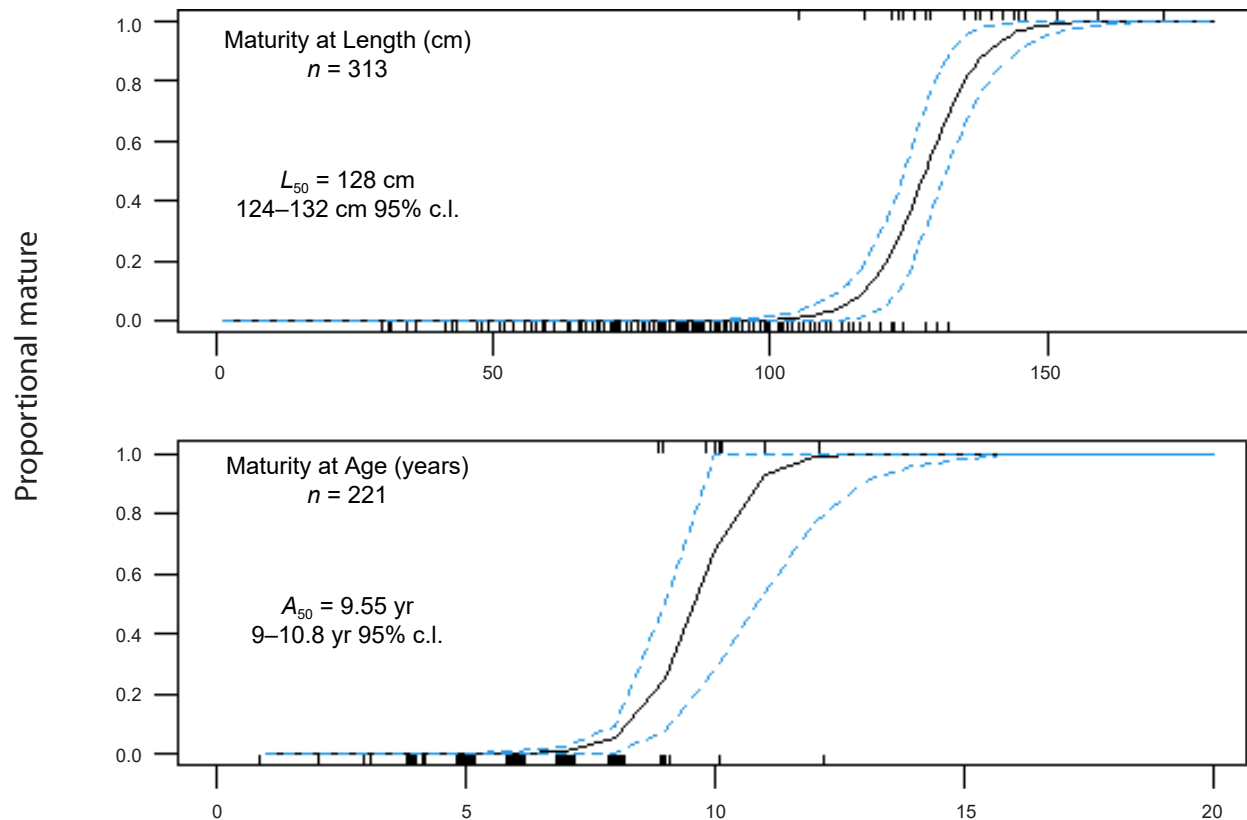
Fig. 10.   Proportion mature as a function of length (top) and age (bottom) for female Atlantic halibut (*Hippoglossus hippoglossus*).
The solid line is the predicted ogive, dashed (blue) line are the 95% confidence limits (c.l.). The tick marks on each x-axis
indicate the individual sizes or ages (jittered) of mature (upper axis) and immature (lower axis) and n = the total number
of individuals.

species. This updated scheme (Fig. 9) will be used together
with a photographic catalog of whole gonad images (see
Supplemental Materials) as part of this training.

The median length at female maturity, L_{50} = 128 cm FL,
was longer than previous reports for Atlantic halibut in
the Gulf of Maine, and the median age at maturity, A_{50} =
9.5 years old, was older, too (Shackell *et al*. 2021; their
Fig. 7). The most direct geographic comparison of size or
age at maturity would be that of Sigourney *et al*. (2006),
who reported female L_{50} = 103 (4.8 SE) cm and A_{50} = 7.3
(0.41 SE) yr. for Atlantic halibut from the Gulf of Maine
collected during 1977–2001. A changing, in this case in-
creasing, median size or age at maturity between Signour-
ney *et al*.'s and our results could well be representative of
this population as maturation schedules can change with
changes in fishing pressure (Rørvik *et al*., 2021) and indi-
ces indicate a level or increasing population size (Hansell
et al., 2020). However, as the Gulf of Maine Atlantic
halibut population is data-limited, we are not able to ad-
dress this directly. Older collections from fishing grounds

offshore of Nova Scotia demonstrate smaller maturity: L_{50}
= 116 (2.2 SE) cm during 1947 (McCracken, 1958) and
L_{50} = 107 (5.2 SE) cm during 1959–1963 (Kohler, 1967).
McCracken (1958) estimated a similar age at maturity,
at roughly 10–12 years. The several decade differences
between some of these studies, and an expectation that
maturation is not time-invariant, confounds simple geo-
graphic comparisons (but see Shackell *et al*. 2021 who
assemble such a comparison).

The differences in maturity schedules are also likely the
result of our use of ovarian histology, whereas previous
reports used macroscopic methods. Our ability to be
more precise about the presence of vitellogenesis, likely
increases the estimate of age at maturity by one year.
Oogenesis proceeded slowly in Atlantic halibut, with only
pre-vitellogenic growth stages observed among females <
9 years old in our samples. Vitellogenesis unfolded over
most of the year preceding spawning, much like shown
for Pacific halibut by Fish *et al*. (2022). We postulate this
creates a situation, when the ovary is viewed macroscopi-

cally, that some fish with MAOS = LC are confused as resting and erroneously classified as mature, as the case for other regional flatfish such as winter flounder (McBride *et al*., 2013). Using gonad histology, where the tunica thickness can be accurately determined, can distinguish immature and mature individuals. Given the potential for

measurement bias between histological and macroscopic studies, a conservative conclusion is that the mean age and size at maturity of female Atlantic halibut in the Gulf of Maine and around Nova Scotia has been fairly stable at 7–12 years and 100–130 cm.
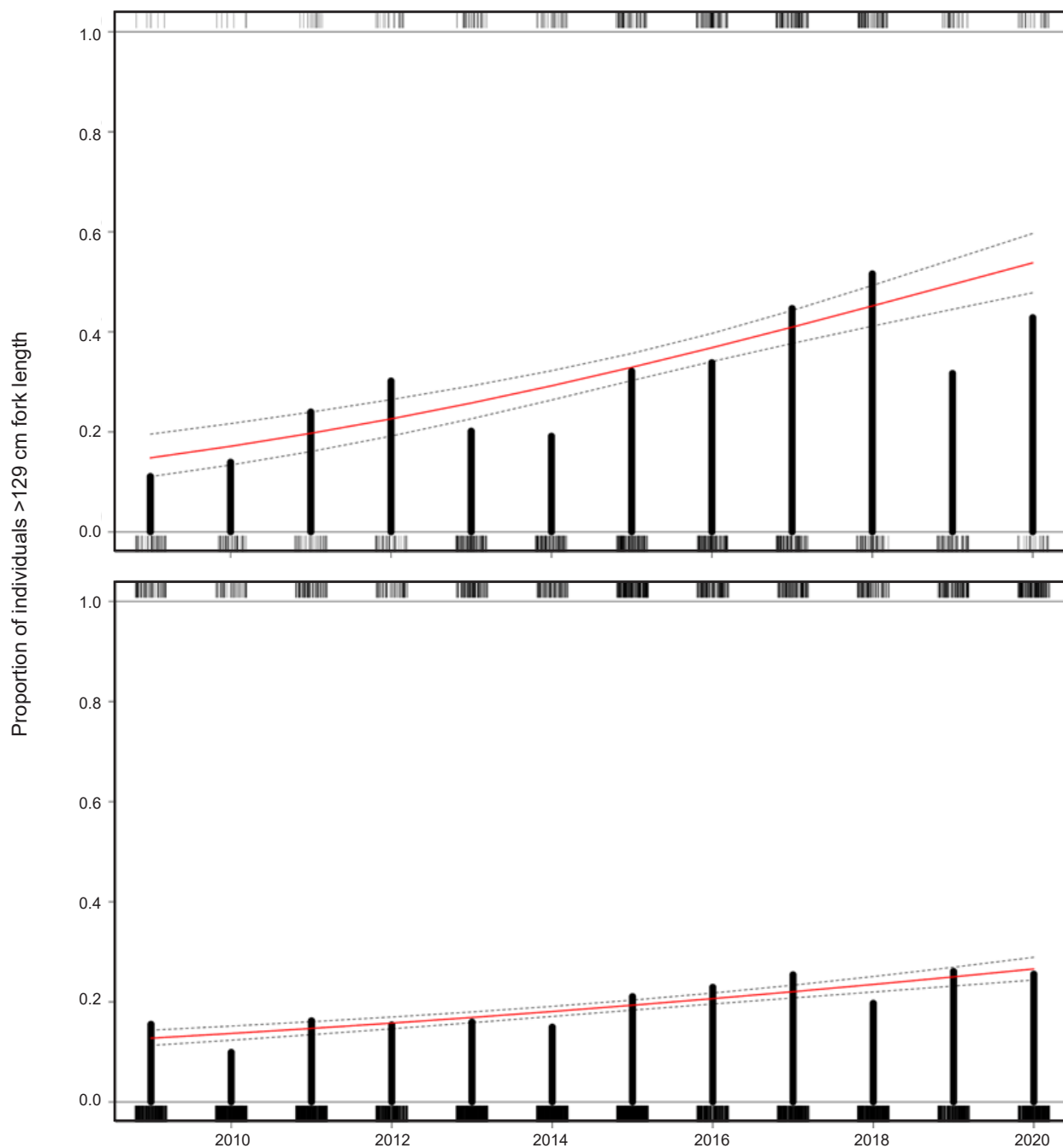
Fig. 11. Proportion mature of Atlantic halibut (*Hippoglossus hippoglossus*) in U.S. landed commercial catch (above) and Canadian longline fixed station survey (below). The bars are the proportion of fish with (length > 129 cm), the rug plots represent sample size and the red line is the fit from a binomial family GLM to the binary (0 ≤ 129 cm and 1 > 129 cm) dataset for each group. The dotted lines are the 95% confidence intervals.

Details of oocyte maturation and ovulation were not observed directly, presumably because Atlantic halibut migrate to the continental slope, outside of our sampling range, to spawn. Liu *et al*. (2019) observed tagged halibut in the Gulf of Maine making long-distance movements suggesting a spawning migration. These fish move to the Northeast Channel off Georges Bank, where neither fishing nor fishery-independent surveys takes place, explaining why we did not collect spawning halibut. Liu *et al*. did not observe abrupt ascents, which could be interpreted as spawning activity, but halibut were in these deep, presumptive spawning habitats during winter, from January to May.

Further east, in the Gulf of St. Lawrence, spawning occurred at depths of 200 m or deeper during winter, from mid-December to late-April with a peak in mid-February (Le Bris *et al*., 2018; Gatti *et al*., 2020). Still further east, in deep (800–1000 m) waters south of the Grand Banks, Armsworthy *et al*. (2014) report abrupt ascents, interpreted as spawning rises, during later autumn – early winter, from October to January. In the eastern Atlantic, the spawning season is so predictable (December–March) that the halibut gillnet fishery in Norway has been prohibited during parts of January–February since the 1950s (Godø and Haug, 1988; Haug and Gulliksen, 1988).

On the other American coast, Pacific halibut have been collected on their spawning grounds, with multiple lines of evidence of winter spawning seasonality (January–February). Evidence of spawning includes the appearance of POFs, and a more complete characterization of oogenesis and gonad maturation (*e.g.*, maximum oocyte size = 2.0 –2.5 mm, a maximum reported GSI of 15% for females; Fish *et al*., 2020, 2022).

Presumably, mature U.S. Atlantic halibut females that remain in our sampling range during the spawning season are skip spawners, but this requires additional, precise information about their spawning migration and an ability to capture them across these habitats (Rodgveller *et al*. 2016). Instead, we interrogated two samples for which we considered immature and mature females should be well mixed. Both skip spawners detected were, not surprisingly, young (9-year-old fish). Skip spawning is more likely among smaller and younger fish that may be energetically challenged compared to larger and more experienced females (Burton, 1994; Rideout and Tomkiewicz, 2011; Tronbøl *et al*., 2022). The calculations presented herein assume a prolonged period of vitellogenesis, which appears supported by our data, and a winter spawning period, which is consistently demonstrated by a number of studies reviewed in the previous paragraphs. Both samples used

for these calculations were small, and therefore preliminary, but of interest as the first estimates for this species.

Accuracy in skip spawning rates is important for correctly specifying the spawning stock biomass in stock assessments, when not all mature fish spawn as expected. Electronic tagging data is a complementary tool that could contribute to evaluating skip spawning rates for halibut. Tagging data for Pacific halibut suggest that approximately 10% of mature fish are skip spawning (Loher and Seitz, 2008). The number of fish tagged and released in our region is increasing, which should soon reveal more about Atlantic halibut spawning times, frequencies (*e.g.*, skipping), and the behaviors of spawning contingents in U.S. and neighboring waters (W. DeVoe, State of Maine, pers. comm.). Multiple lines of evidence about skip spawning are needed for robust estimates of skipping rates in different populations of halibut species.

Management Implications

The U.S. Atlantic halibut stock has been depleted for at least a century (Grasso, 2008). Recent U.S. stock assessments have shown evidence of modest population increases over the last decade, and as evident herein, the proportion of mature fish in both U.S. and Canada waters has increased over the same period. These coupled trends are an indicator of an increase in reproductive potential. Now that an estimate of size at maturity exists, it is reasonably cost effective to continue to track the proportion of fish above this size as a proxy for mature females, which could be a useful qualitative assessment tool for this data-limited stock. However, it is important to understand the fishery context for using such an approach because alternative interpretations exist. For example, an increase of proportion mature in an increasing stock is contra-indicative of high fishing pressure, whereas an increase of proportion mature in a stable or decreasing stock may be indicative of recent recruitment failure.

Comparing the proportion mature between spatially adjacent stocks may be of some interest as well. In this case, we compared the proportion mature in U.S. waters to the Canadian Scotian Shelf population, within the Gulf of Maine (Fig. 1). Proportion mature is increasing in both areas, although the trend is less defined in the Canadian data. Several factors may drive the differences in magnitude of trend between the areas. The Canadian data are survey based, while the U.S. data are from commercially landed fish. Current U.S. regulations stipulate that only one Atlantic halibut per trip can be landed, which equates to a tendency for the largest fish encountered to be landed and all others discarded. The Canadian data are measure-

ments of all fish encountered on the survey. The selectivities associated with the two data sets are therefore quite different and may influence results. The Canadian stock has been stable or increasing for many years and supports a large and valuable fishery. The U.S. stock has been depleted for a century and has not supported a directed fishery for most of that period. Therefore, the scope for stock increase (*i.e.* the distance from theoretical carrying capacity) in the U.S. is probably much greater. Finally, the extent of movement between the two areas is unknown and it is possible that some mature fish from Canada have relocated to U.S. waters, which might potentially affect the proportion mature in each area.

Alternatively, size composition of discarded fish from U.S. fishery observer data could be used to compare the U.S. and Canadian stocks. Unfortunately, Atlantic halibut encounter rates in the United States remain low, observer coverage of longline gear (the gear most likely to capture large Atlantic halibut) is low (generally < 10%; Hogan *et al.*, 2019), and there are very few mature fish among the discarded Atlantic halibut length data over the time period concerned ($n = 6$ fish). There is some possibility of using the kept fish from U.S. observer data, but there are far more Atlantic halibut observations in the landings data and combining the two introduces the possibility of double counting. Ideally, the U.S. data would come from a fishery independent survey, as the Canadian data does –which removes the possibility of spatial bias commonly associated with fishery dependent data (Paloheimo and Dickie, 1964) – but U.S. surveys do not sample Atlantic halibut well (Hennen, 2015).

A truncated age distribution is a common symptom of a stock in poor condition (Hilborn and Peterman, 1996). This describes a situation in which a disproportionate amount of the mature fish have been removed, leaving mostly young and immature fish in the population. This situation is dire for any stock, as mature fish supply the reproductive material for future recruitment. In this sense, a high proportion of mature fish might indicate a healthy stock. When a fishery targets immature fish, they can be removed before reproducing, which can reduce reproductive potential, as for example, when a large year class of fish is fished down before reaching maturity. When a fishery targets mature fish, the effect depends on the contribution of each age class to reproductive value (Kindvater *et al.*, 2016; Marshall *et al.*, 2021). Overall, we are cautious about simple interpretations of proportion mature as an indicator of stock health. Nonetheless, an increasing trend of proportion mature together with an increasing trend of stock size is generally an indicator of a healthy stock and relatively low mortality. As there is evidence that both the U.S. and Scotian shelf Atlantic halibut stocks are increas-

ing (Rago, 2018; DFO, 2020), our new observations of an increase of proportions mature indicates an increase in the reproductive potential of each stock.

Acknowledgements

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