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Revisiting Maturity Data: Using Oocyte Diameter and Gonadosomatic Index to Retroactively Apply a New Maturity Scale to Greenland Halibut (*Reinhardtius hippoglossoides*)

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ABSTRACT

Greenland halibut (*Reinhardtius hippoglossoides*) is a deep-water flatfish which lives at temperatures of 1°C–4°C and produces large eggs (> 3 mm). The combination of low temperatures and large eggs has resulted in an unusual ovary development cycle, with vitellogenesis taking more than 1 year. This means that fish with early vitellogenic oocytes (termed functionally immature) will not spawn during the next spawning season and should not be included in the Spawning Stock Biomass (SSB). During the Icelandic autumn groundfish survey, the ovary development of Greenland halibut has been evaluated using a 4-stage maturity scale. The 4-stage scale, unlike the 6-stage scale developed specifically for Greenland halibut, does not separate fish in the first year and second year of vitellogenesis which can lead to inaccuracies in the estimation of SSB. The current study investigates whether the weight of the gonad, expressed as a percentage of total body weight, commonly known as gonadosomatic index (GSI), can be used to evaluate maturity for Greenland halibut. We show, from measurements of oocytes, for Greenland halibut collected in Iceland and East Greenland, 93% of Greenland halibut with a gonadosomatic index (GSI) > 1.5% are in their second year of vitellogenesis and should be considered sexually mature. In addition, 97% of fish with a GSI < 1.5% were considered sexually immature/functionally immature. Application of this GSI-based approach to data collected during the Icelandic autumn groundfish survey demonstrates that it is a practical alternative to visually assessing maturity and can be retroactively applied to past data if gonad weight has been measured. Using GSI to discriminate sexually mature from sexually immature/functionally immature individuals resulted in a length at 50% maturity (L_{50}) 2.4–8.8 cm higher in comparison to visually assessing maturity with the 4-point scale. The GSI-based approach indicated that fish visually classified as 'spent' were misidentified and are a mix of other maturity stages, this is supported by the spawning season being 7–9 months prior to the survey. Our data indicates that L_{50} of Greenland halibut in Iceland increased in 2012, with L_{50} in the period 1996–2010 approximately 73–77 cm whereas in the period 2012–2023 it was approximately 78–81 cm. While, for years 2014–2023, when age was estimated, age at 50% maturity (A_{50}) was 18.2 years.

1 | Introduction

Spawning stock biomass (SSB) of a fish population is estimated from the abundance of each age/length group in the population multiplied by the average weight at age/length as well as the proportion which are considered sexually mature and will spawn at the next spawning opportunity. Female fish are considered sexually mature if vitellogenesis has begun or if they have previously spawned. For practicality, time, and economic considerations, the assessment of maturity is usually done by visually examining the gonads in situ and classifying them to a particular development stage. This has the advantage that it requires no specialised equipment. Knowledge on the gonad development cycle is essential to determine if a fish at a particular development stage will be capable of spawning at the next spawning opportunity and thus whether they should or should not be included in the estimation of SSB.

Greenland halibut (*Reinhardtius hippoglossoides*) is a deep-water flatfish found at depths of ~200–1500 m with a circumpolar distribution (Vihtakari et al. 2021). The adults will rise up into the water column during spawning to release their eggs, with the main spawning season thought to occur around January to March, though some spawning outside of this time is known to occur (Albert et al. 2001; Gundersen et al. 2013; Sigurdsson 1977; Siwicke et al. 2022). It has an unusual ovary development cycle in that when vitellogenesis begins for the first time, it is more than 1 year before the fish will spawn (Kennedy et al. 2011; Rideout et al. 2012). Precise timing for the beginning of vitellogenesis is unknown, but adults have oocytes around 800–1000 μm during January, which then develop towards spawning approximately 1 year later (Kennedy et al. 2011). This extended period for vitellogenesis is likely due to having large eggs (> 3 mm in diameter) and inhabiting low temperatures (1°C–4°C) (Domínguez-Petit et al. 2012; Kennedy et al. 2011; Vihtakari et al. 2021). With vitellogenesis taking more than 1 year to complete, the assessment of maturity becomes more complex as it is not necessarily the case that females with vitellogenic oocytes in their ovary will spawn within the next year. While fish in their first year of vitellogenesis should be considered biologically mature and counted as part of the mature component of the stock, they should not be considered as part of the SSB. Including fish which will not spawn at the next spawning opportunity in the SSB will lead to an overestimation of the total egg production, an important component of the reproductive potential of a stock (Trippel 1999; Kennedy et al. 2014; Núñez et al. 2015). Thus, from a management perspective, fish in their first year of development should be considered functionally immature (Rideout et al. 2012). The current understanding is that only females with oocytes > 1000 μm should be considered as capable of spawning within the next year (Kennedy et al. 2011; Rideout et al. 2012).

Before the realisation of an extended vitellogenic period in Greenland halibut, the developmental stage of their ovaries was assessed against a 4-stage scale similar to that utilised for gadoids (Albert et al. 2001; Junquera and Zamarro 1992; Templeman et al. 1978). A scale specifically designed for Greenland halibut has been developed (Riget and Boje 1989), which has six stages (hereafter referred to as the 6-stage scale). The 6-stage scale considers oocyte size in addition to the general appearance of the ovaries and has been validated with histology (Nielsen and Boje 1995). This scale has been adopted in several countries (ICES 2012) and allows the separation of fish in their first and second year of vitellogenesis, a criterion which is not included in the 4-stage scale.

As ovaries develop towards spawning, they increase in weight due to the deposition of proteins and lipids during vitellogenesis (Tyler and Sumpter 1996). As the weight of the ovary increases, the gonadosomatic index (GSI) (gonad weight expressed as a percentage of body weight) increases, which makes a useful, and easily measurable, metric for evaluating the progression of ovary development. There is a long history of using GSI to understand the reproductive cycle in fishes (Htun-Han 1978; Huang et al. 1974; Wootton et al. 1978). Several studies, in a wide range of species, have proposed using a $GSI_{cut\text{-}off}$ value at which individuals with a GSI value below or above this $GSI_{cut\text{-}off}$ are classified as sexually immature and sexually mature. The $GSI_{cut\text{-}off}$ is estimated using individuals where the maturity stage has been evaluated with accurate methods such as histology (Cao et al. 2021; Flores et al. 2015, 2019; Marisaldi et al. 2019; McPherson et al. 2011; Skjæraasen et al. 2012). The potential for utilising GSI to infer maturity stage for Greenland halibut has previously been investigated and showed promising results (Albert et al. 2001). A GSI-based approach to assessing maturity has the advantage in that it is unbiased and objective. Once the $GSI_{cut\text{-}off}$ value has been established, the collection of the needed data requires minimal training in comparison to classifying ovaries to developmental stages by visual examination.

Surveys targeting Greenland halibut have been ongoing for decades, however any maturity data collected against the 4-stage scale should be treated with caution. Throughout the history of the Icelandic autumn groundfish survey, gonad weight has been routinely measured alongside the assessment of gonad development stage, using the 4-stage scale. If GSI-based methods prove to be beneficial in distinguishing ovary developmental stages of Greenland halibut, then this method can be retroactively applied to past data, giving an opportunity to investigate whether the size-at-maturity of Greenland halibut has varied over time. The aim of this study was to assess the accuracy of using GSI in determining reproductive status and its impact on the estimation of size-at-maturity in female Greenland halibut.

2 | Materials and Methods

2.1 | Ovary Samples

Greenland halibut ovaries were collected during a trawl survey in east Greenland ($n = 126$, fish total length (nearest cm below) 32–111 cm) during August 2010 and around Iceland during October 2022 ($n = 43$, fish total length 41–92 cm) (Figure 1). Samples from both surveys were length stratified with the aim to obtain samples from fish which are sexually immature, in the first year of ovary development, and are in their second year of vitellogenesis. In the current study, fish which are in their second year of vitellogenesis are referred to as sexually mature, while fish in their first year of ovary development are referred to as 'functionally immature'. The total length, total weight, and gonad weight (to the nearest 1 g) were measured for each fish. The ovary developmental stage of each fish was visually assigned using either a four stage (Iceland, Table 1) or six stage (Greenland, Table 2) scale. Gonadosomatic index was calculated for each fish based upon

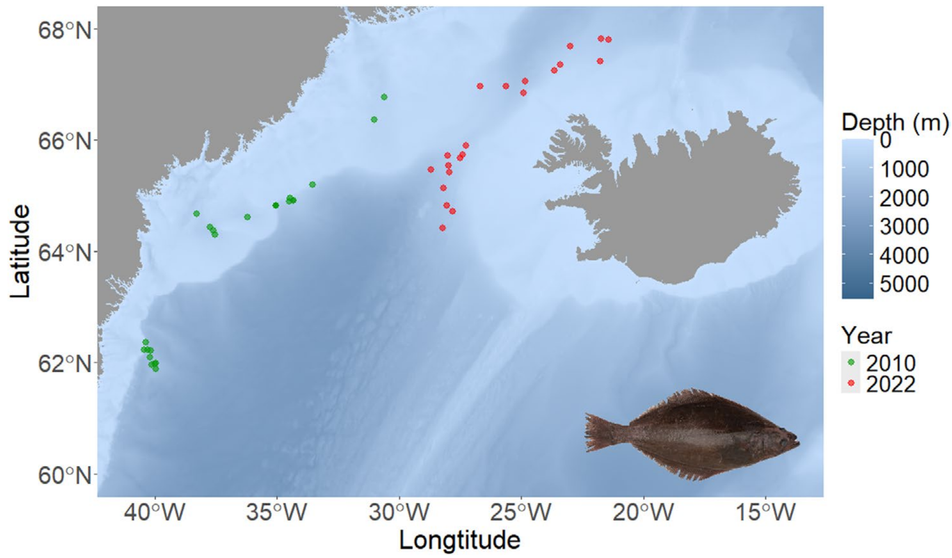

FIGURE 1 | Map of sampling locations for Greenland halibut caught during the Greenland annual trawl survey of east Greenland in 2010 and the Icelandic autumn groundfish survey in 2022. Depth information is from NOAA National Centers for Environmental Information (https://doi.org/10.25921/fd45-gt74) using R package marmap (Pante and Simon-Bouhet 2013). Photograph of Greenland halibut by Svanhildur Egilsdóttir.

TABLE 1 | The 4-stage ovary development scale applied to Greenland halibut during the Icelandic autumn groundfish survey 1996–2023 with the visual description of each stage as well as the maturity designation of each stage.

Code	Ovary stage	Visual description	Maturity classification
A	Immature	Ovaries small and translucent. Eggs not visible with the naked eye	Sexually immature
B	Developing	Ovaries increased considerably in size. Colour red to orange and opaque. Individual eggs visible to the naked eye	Sexually mature
C	Spawning	Ovaries occupy most of the body cavity. Very distended and soft. Hydrated eggs can be extruded on slight pressure	Sexually mature
D	Spent	In recently spent females ovaries are reduced in size, flaccid and bloodshot. Some opaque eggs may occur. Sometimes greyish in colour. Ovary wall thicker than within sexually immature fish	Sexually mature

TABLE 2 | The 6-stage ovary development scale, developed for Greenland halibut, with the visual description of the ovary and the equivalent microscopic criteria as well as the maturity designation of each stage.

Code	Ovary stage	Visual description	Microscopic description	Maturity classification
1	Immature	Ovaries are small. No oocytes are visible to the naked eye	No vitellogenic oocytes present	Sexually immature
2	Developing 1	Oocytes visible to the naked eye, but less than 1 mm in diameter	Single cohort of cortical alveoli or vitellogenic oocytes	Functionally immature
3	Developing 2	Oocytes are 1–2 mm in diameter	There are two cohorts of vitellogenic oocytes. Average oocyte diameter of the larger (in diameter) cohort is between 1000 and 2000 μm	Sexually mature
4	Developing 3	Oocytes are 2–4 mm in diameter	There are two cohorts of vitellogenic oocytes. Average oocyte diameter of the larger (in diameter) cohort is > 2000 μm	Sexually mature
5	Spawning	Ovary is full of hydrated oocytes	Ovary is full of hydrated oocytes	Sexually mature
6	Spent	A small number of hydrated oocytes are present. Ovary may be red	A small number of hydrated oocytes are present	Sexually mature

the equation GSI = 100 × gonad weight/total weight. Depending on ovary size, the ovary, or a section of the ovary was preserved in 10% buffered formalin for later analysis. The preservation of only a section of larger ovaries is considered to have no impact on the results as Greenland halibut ovaries are homogeneous in respect to development stage and oocyte diameter (Nielsen and Boje 1995; Rideout et al. 1999).

In the laboratory, a sample of oocytes from each fish was photographed using a binocular microscope connected to a camera displaying a live image. The photographed oocytes were measured in Image-J (Schneider et al. 2012) either using computer aided particle analysis (Greenland samples) or manually on-screen (Iceland samples). Oocyte size frequency distributions with 25 μm bins (Figure 2) were examined to re-assess the ovary development stage against the 6-stage scale (Table 2). It is currently not possible to separate pre-vitellogenic oocytes from those that have entered the cortical alveoli stage solely based upon diameter measurements of whole oocytes. Thus, the ovaries from the Icelandic samples, which had an oocyte diameter < 350 μm, were examined histologically (in a manner similar to McPherson et al. (2011)) to determine whether oocytes at the cortical alveoli stage were present and the development stage was assigned based upon this information (Table 2). The samples from Greenland were no longer available and could not be analysed histologically, thus, if no vitellogenic oocytes were present, no oocytes were measured, and the fish was classified as sexually immature.

To apply the GSI-based method for Greenland halibut, the conditional probability of the maturity of an individual for a given GSI value was estimated using a generalised linear model (GLM) with a logit link function and binomial error structure in R version 4.4.1 (R Core Team 2023). Fish assigned an ovary development stage of 1 or 2 were classed as sexually immature, while those at stages 3–6 were considered sexually mature. The value

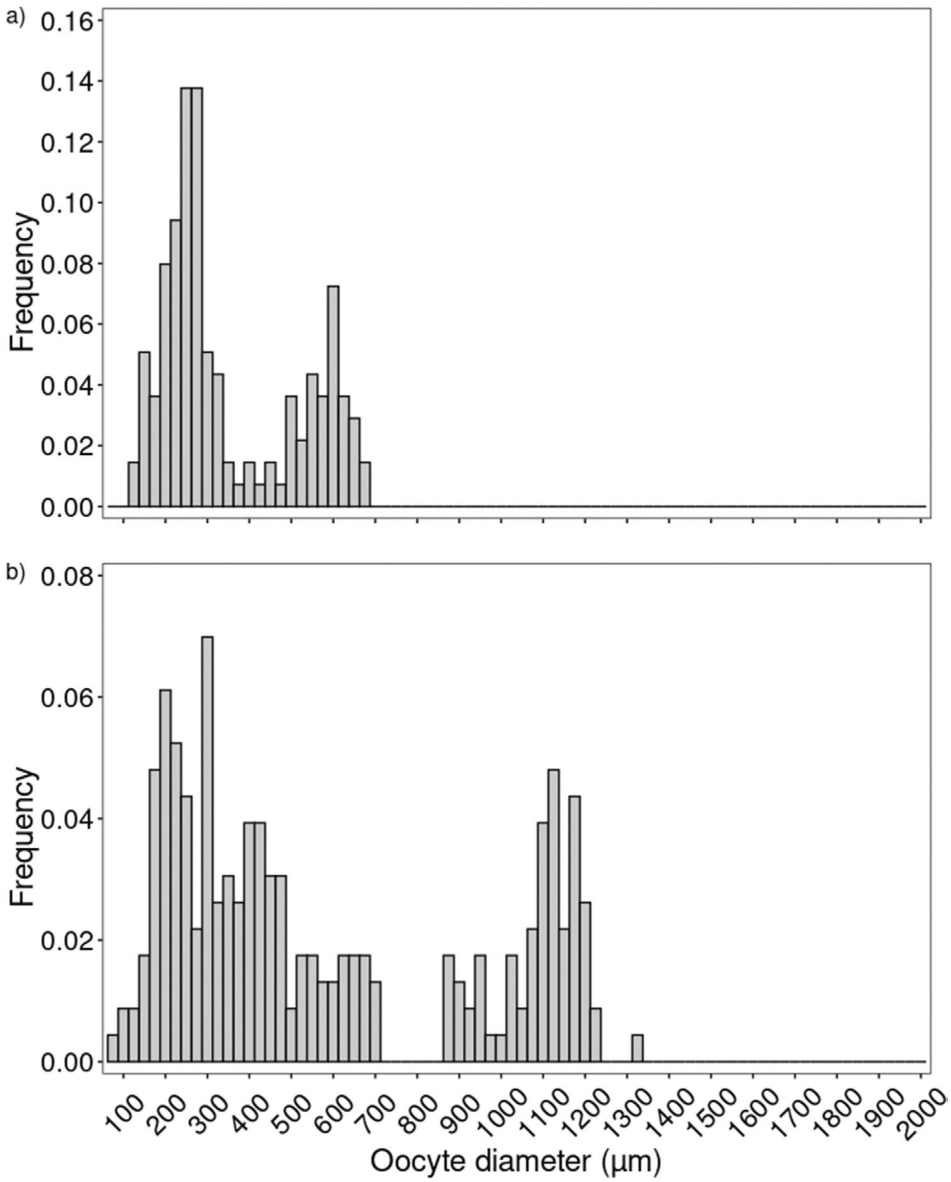

FIGURE 2 | Typical oocyte size distributions for Greenland halibut maturity stages 2 (functionally immature) (a) and 3 (sexually mature) (b), based upon Table 2.

at which an individual is as likely to be sexually mature as sexually immature (probability equal to 0.5) was set as the $GSI_{cut\text{-}off}$ value. The $GSI_{cut\text{-}off}$ value can then be used to assign a maturity status based upon the GSI. The process of assigning a maturity status based upon GSI has previously relied upon a logistic multinomial model with three maturity stages (immature, mature and spent) (Flores et al. 2015, 2019; McPherson et al. 2011). However, as our samples contained very few spent individuals (see results), the GLM approach with two stages was considered more appropriate.

To measure the reliability of the assignment of maturity based upon microscopy and using a $GSI_{cut\text{-}off}$, Cohen's kappa coefficient (k) (Cohen 1960), using the vcd package in R (Meyer et al. 2024) was utilised. A value of k from 0.00 to 0.20 is considered poor while values of 0.21 to 0.40 is low, 0.41 to 0.60 is moderate, 0.61 to 0.80 is considerable and 0.81 to 0.99 is optimum (Landis and Koch 1977).

TABLE 3 | Comparison of the ovary development stages of the Icelandic samples, initially assigned visually against the 4-stage scale (Table 1) and reassessed based upon oocyte size distribution against the 6-stage scale (Table 2).

	6-stage	
4-stage	**2**	**3**
A	27	1
B	3	10
D	2	0

2.2 | Maturity Data

The maturity of Greenland halibut was reassessed for fish captured during the annual Icelandic autumn groundfish survey from 1996 to 2023 using the GSI-based approach that was validated for Greenland halibut during the current study. The Icelandic autumn groundfish survey takes place annually in October all around the Island with 350–400 stations per year at 50–1300 m depth with Greenland halibut being one of the species that is specifically targeted. A sample of Greenland halibut captured at each station is measured for total length and total weight. The ovary development stage is assessed visually based upon the 4-stage development scale (Table 1) and if the fish is at stage B, C, or D, the gonad weight is measured. From 2014 to 2023, otoliths were removed from each fish and analysed to estimate age.

Gonadosomatic index was calculated for each fish in the same manner as above and maturity stage was assigned based upon GSI. Fish with a $GSI < GSI_{cut\text{-}off}$ and $GSI > GSI_{cut\text{-}off}$ were classified as sexually immature and sexually mature respectively. To increase sample sizes for maturity ogives, the samples from a period of 4 years were combined (i.e., 1996–1999, 2000–2003 etc.). Greenland halibut is a slow–growing long–lived species with a 2-year ovary development period which suggest that significant changes in L_{50} between years is unlikely (Albert et al. 2009; Kennedy et al. 2011; Treble et al. 2008). There was no survey in 2011 so the period 2008–2011 included only 3 years i.e., 2008–2010. L_{50}, for each 4-year period, and A_{50} for period (2014–2023), was estimated using the above mentioned GLM routine. To investigate if changes in the size composition of the sampled fish may be influencing the estimation of L_{50} (Kjesbu

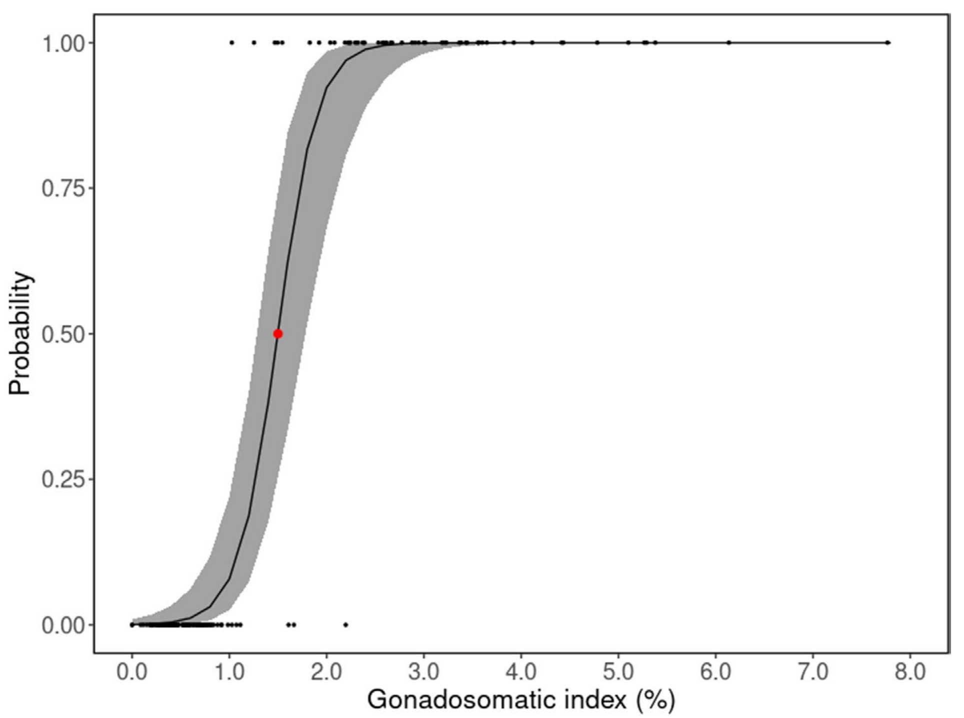

FIGURE 3 | Conditional probability estimated using general linear modelling to classify the probability of individual female Greenland halibut being sexually mature based upon the gonadosomatic index. Red dot indicates the point at which there is equal probability of being sexually immature and sexually mature.

et al. 2025), the Shannon (Diversity) Index (H), in respect to length, was utilised:

$$H = -\sum_{i=1}^{N} p_i \ln p_i$$

where N is the total number of length classes and p_i is the proportion of individuals belonging to the ith length class. For each period, H was calculated using both 1 and 10 (< 50, 50–59, 60–69, 70–79, 80–89, ≥ 90) cm length bins. The presence of a correlation between L_{50} and H was tested using linear regression.

More than 50% of the samples analysed in Greenland which were visually evaluated as stage 1, which are equivalent to stage A in Iceland, were found to be a mix of stage 1 and 2, but none were found to be at stage 3 (Kennedy et al. 2014). The gonad weight of a sample of fish, which had been visually assessed as Stage A (Table 1) was available. Less than 1% of these fish had a GSI > $GSI_{cut\text{-}off}$ (see results) indicating that visually identifying fish at stage A would not impact the results.

TABLE 4 | The number of sexually immature and sexually mature Greenland halibut from both the Icelandic and Greenlandic samples, assessed from oocyte size distributions, which were classified as sexually immature and sexually mature based upon their Gonadosomatic index (GSI).

	GSI	
Maturity	**Immature**	**Mature**
Immature	109	3
Mature	4	53

To avoid confusion, ovary development stages from the 4-stage (Table 1) and 6-stage (Table 2) ovary development scale will be consistently referred to using the code, A–D and 1–6 respectively. The terms sexually immature, functionally immature and sexually mature will be used in the text and refer to the classification of sexual maturity based upon the ovary development stage it has been assigned from the ovary development scale.

3 | Results

3.1 | Calibration of GSI-Based Approach

Greenland halibut for which ovary samples were taken ranged in total length from 32 to 111 cm. All Icelandic samples which were analysed histologically had cortical alveoli oocytes present and were thus classified as functionally immature. Fish classified as functionally immature and sexually mature, based upon measurement of the oocytes or histological examination of the ovaries, ranged from 41 to 90 and 53 to 111 cm respectively.

Regarding the Icelandic samples, of the 28 fish which were initially classified as stage A (sexually immature) on the 4-stage scale, 27 were classified as stage 2 (functionally immature) and one being classified as stage 3 (sexually mature) based upon oocyte measurements and histological examination (Table 3). Two fish classified as stage D (spent) did not exhibit any characteristics

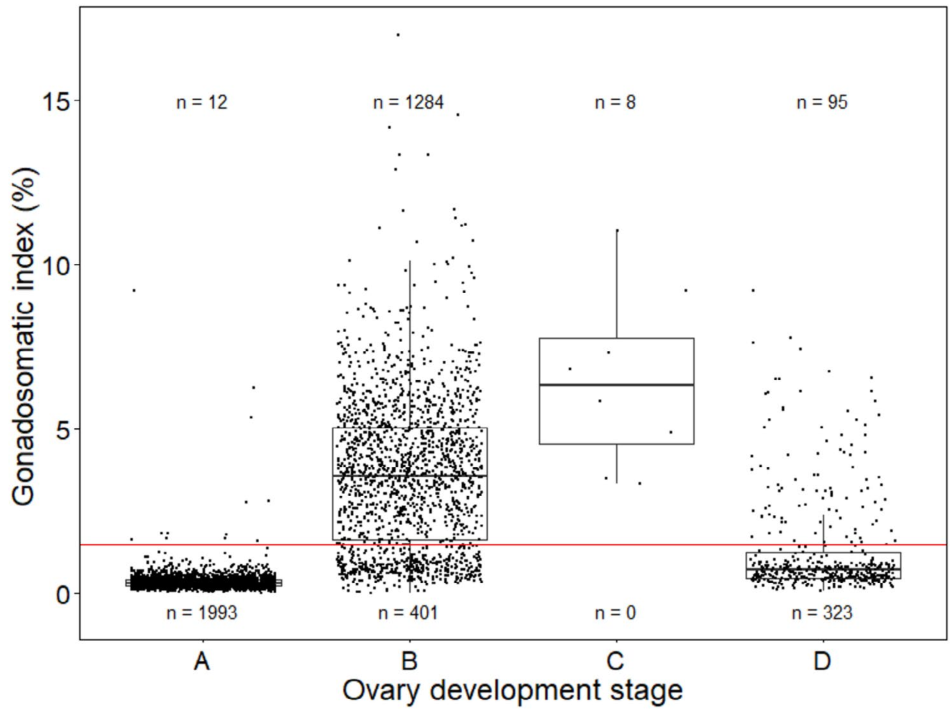

FIGURE 4 | The gonadosomatic index of Greenland halibut caught during the Icelandic autumn groundfish survey at different ovary development stages (A = immature, B = developing, C = spawning, D = spent) visually assessed against the 4-stage scale. Red line represents the $GSI_{cut\text{-}off}$ value of 1.5%. Values are the number of fish for each stage which were assessed as sexually immature (bottom) and sexually mature (top) based upon their GSI being less than or greater than the $GSI_{cut\text{-}off}$ value respectively.

that were consistent with the assignment of stage D and thus assigned to stage 2. For the Greenlandic samples, based upon oocyte measurements, 82 of the fish were classified as sexually immature/functionally immature, 46 were classified as sexually mature which consisted of 44 with ovaries at developing stage 2. Two fish in the Greenlandic samples were classified as spent due to the presence of residual eggs, if the hydrated eggs were not present, they would have fit the description of developing 2.

The GSI value at which there was an equal probability of an individual being sexually immature or sexually mature was 1.5% (Figure 3), with this value being set as the $GSI_{cut\text{-}off}$ value. There was considerable agreement between the assessment of maturity from microscopy and from using GSI (Table 4), with a *k* value of 0.91 (95% CI = 0.84–0.97).

3.2 | Maturity Classification

The GSI of Greenland halibut caught in the Icelandic autumn survey varied from 0.01% to 16.96% and varied between ovary development stages (Figure 4). When reassessing maturity that was initially based upon the visually assigned ovary development stage on the 4-stage scale, for fish classified as stage A, only 0.6% were reclassified as sexually mature based upon the GSI-based method. For fish assessed at stage B (developing), 23.8% were classified as sexually immature/functionally immature when based upon the GSI-based method. Of the fish which were initially classified as stage B, the mean length of fish reclassified as sexually immature based upon the GSI-based method (70.7 cm) was significantly lower (*t*-test, $p < 0.0001$) than those reclassified as sexually mature (80.4 cm). Of the fish originally classified as stage D (spent), 77.3% were classified using the GSI-based method as sexually immature/functionally immature and had a mean length of 70.0 cm (Figure 5). Fish classified as stage D which were classified as sexually mature based upon the GSI-based method had a mean length of 81.4 cm which was significantly greater than those originally classified as stage D and reclassified as functionally immature (*t*-test, $p < 0.0001$) (Figure 5).

3.3 | Estimation of L_{50} and A_{50}

For the GLM, both when estimating L_{50} using maturity assigned upon visual assessment and assigned using the GSI-based method (Figure 6), time period (year span) was a significant factor

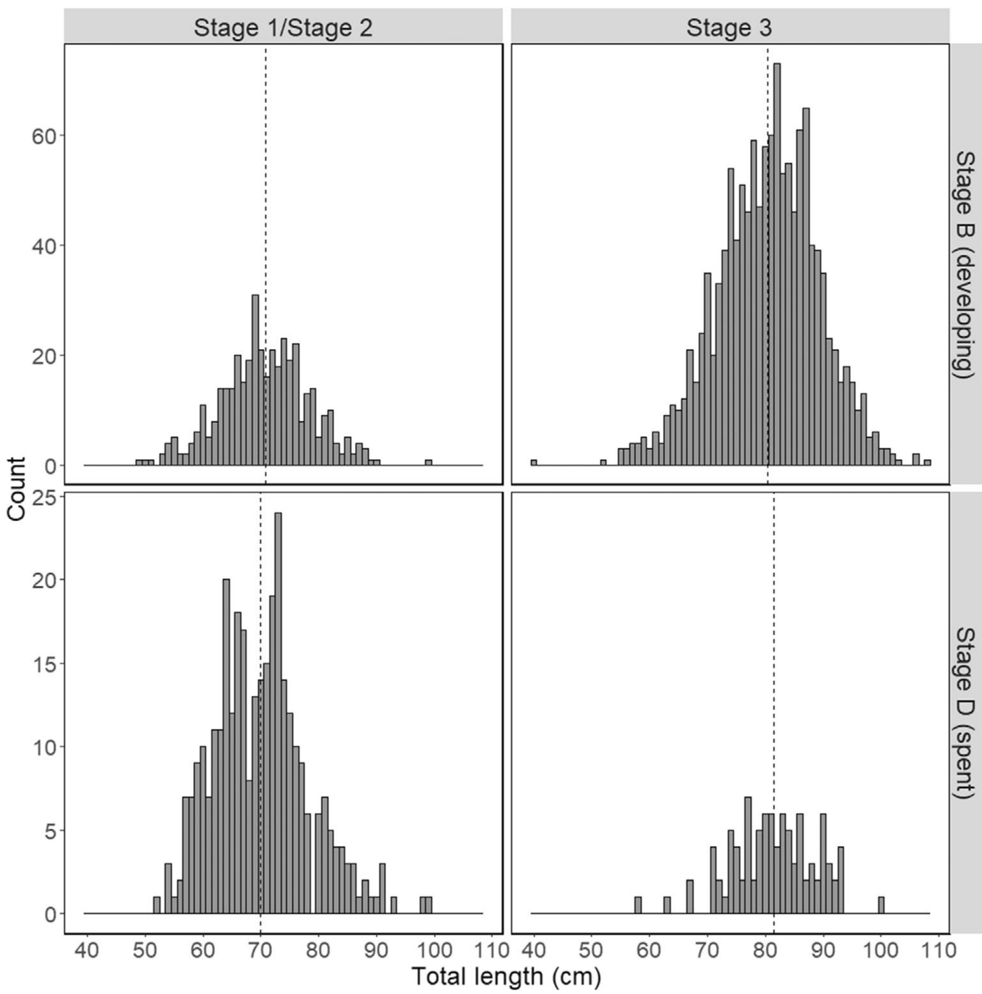

FIGURE 5 | Length distribution of Greenland halibut caught during the Icelandic groundfish survey which were classified as sexually immature (stage 1) or functionally immature (stage 2) and sexually mature (stage 3), based upon the GSI-based method, where their ovary development stage was initially assessed visually as stage B (developing) and stage D (spent) on the 4-stage ovary development scale. Mean value of each distribution is shown by dashed line.

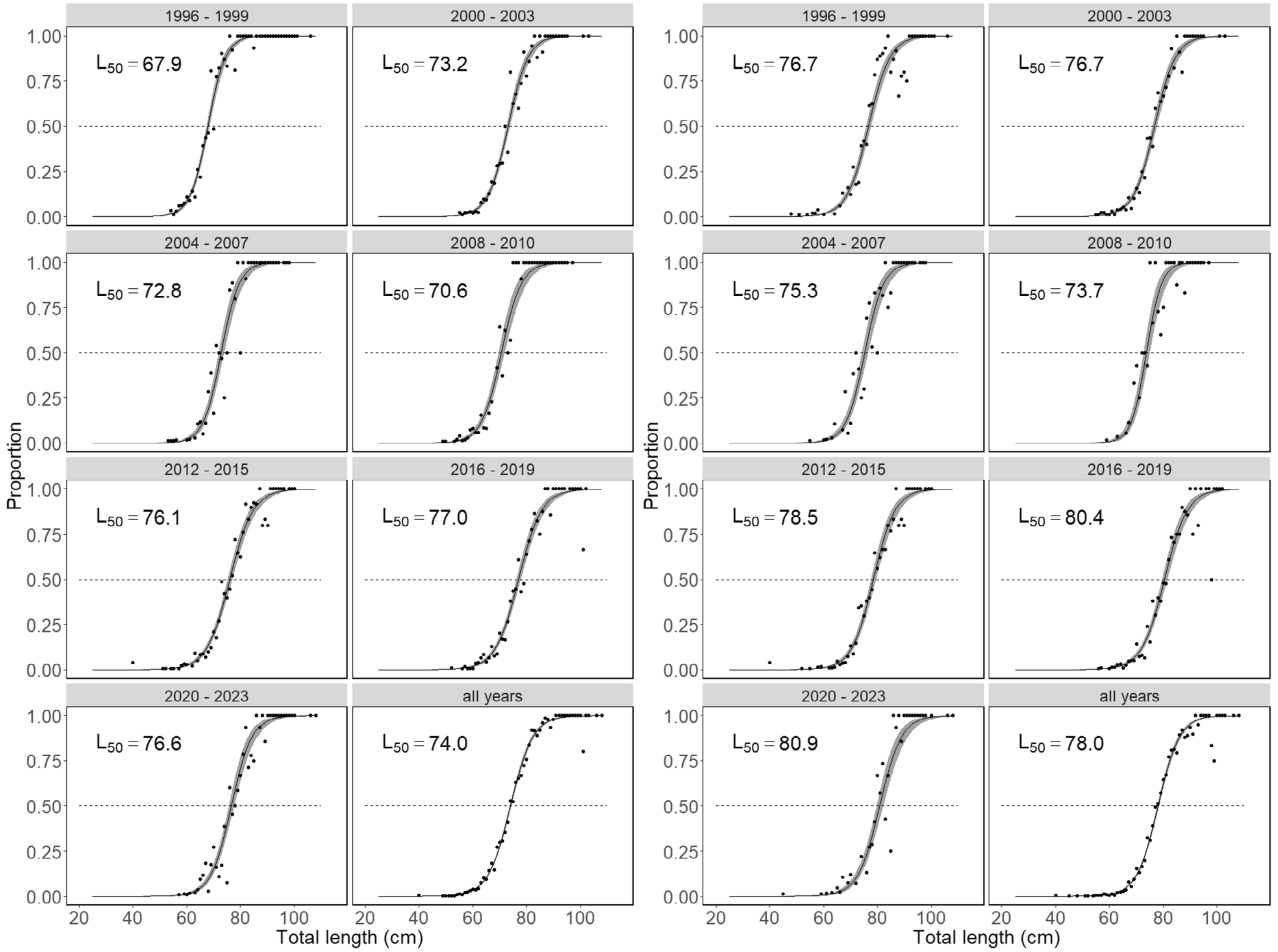

FIGURE 6 | Proportion of Greenland halibut caught during the Icelandic autumn groundfish survey which were considered sexually mature over 4-year periods, and the entire time period, based upon visual assessment of maturity using the 4-stage ovary development scale (left) and the GSI-based method (right). Lines depict the fitted logistic regression models with 95% confidence intervals.

($p<0.001$), and the models with and without time period were significantly different (ANOVA, $p<0.001$). When maturity was assessed based upon the visual assessment of the ovary development stage using the 4-stage scale, L_{50} ranged from 67.9 to 73.2 cm between 1996 and 2010 and from 76.1 to 77.0 cm between 2012 and 2023 (Figure 6). When estimated using the GSI-based method, L_{50} ranged from 73.7 to 76.7 cm between 1996 and 2010 and from 78.5 to 80.9 cm between 2012 and 2023 (Figure 6). When combining data from all years in the periods 1996–2010, 2012–2023 and 1996–2023 for maturity assessed using the GSI-based method, L_{50} is estimated at 76.1, 79.9 and 78.0 cm respectively. There was no significant correlation between L_{50} estimated using the GSI-based method and H when using either 1 or 10 cm length bins (linear regression; $p>0.05$). Greenland halibut, caught between 2014 and 2023, ranged in age from 3 to 22 years, with an A_{50} of 18.2 years when estimated using the GSI-based method (Figure 7).

Consequently, assessing maturity based upon the GSI-based method rather than visually assessing the development stage of the ovary against the 4-stage scale resulted in a higher L_{50} for all time periods with the difference ranging from 2.4 to 8.8 cm and for all years combined, there was a difference of 4.0 cm (Figure 6). A_{50} estimated using maturity assessed by visual examination of the ovaries on the 4-stage scale was 16.7 years, while 18.2 years when using maturity data assigned using the GSI-based method (Figure 7).

4 | Discussion

Based upon the samples analysed in the laboratory, there was good agreement between the GSI-based method and assessment of maturity based upon oocyte size distributions in distinguishing sexually immature and functionally immature Greenland halibut from those that will spawn within the next year. Using the GSI-based method, we were able to retroactively determine the maturity of Greenland halibut caught in the Icelandic autumn groundfish survey back to 1996, which highlights the advantage of routinely collecting gonad weight when visually determining the developmental stage of the ovary. The validation of the GSI-based method for Greenland halibut adds to the broad range of different species, from small pelagic (sardine) to tuna, swordfish and demersal species with different reproductive strategies, for which the method has proved beneficial (Cao et al. 2021; Flores et al. 2015, 2019, 2020; Marisaldi et al. 2019; McPherson et al. 2011). The advantage of the GSI-based method is that it only requires the measurement of body and gonad weight, which is non-subjective and accurate, and

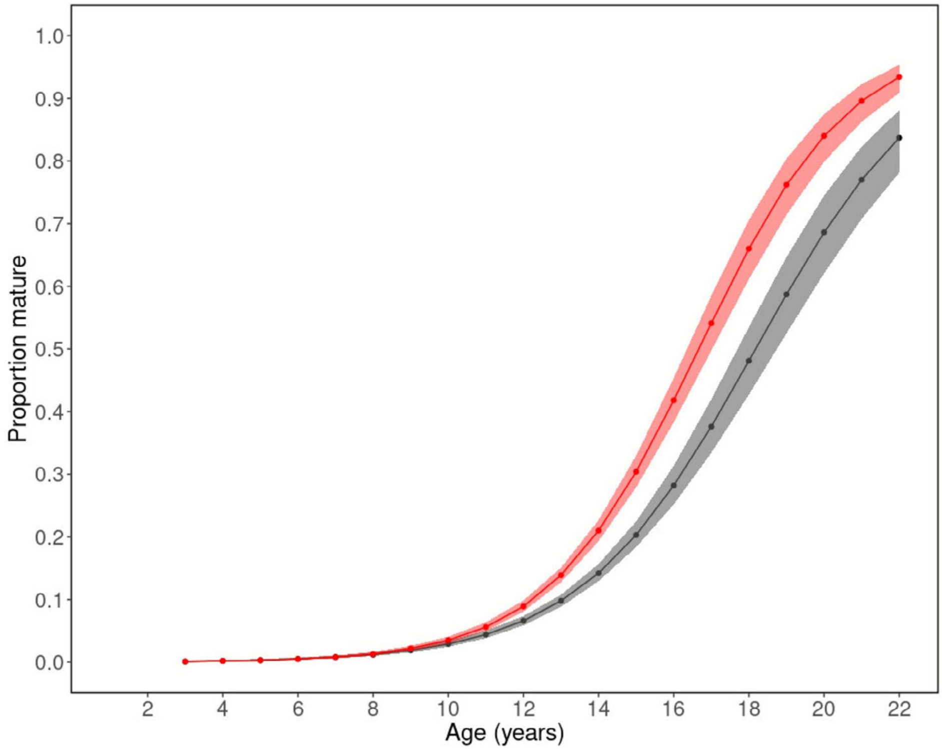

FIGURE 7 | Proportion of each age group of Greenland halibut caught during the Icelandic autumn groundfish survey caught between 2014 and 2023 which were considered sexually mature when ovary stage was assessed visually using the 4-stage scale (red) and when using the GSI-based method (black). Lines depict the fitted logistic regression models with 95% confidence intervals.

requires minimal training in comparison to visually assessing the developmental stage of the ovary. Assuming gonad weight is available, this method could be applied to other populations of Greenland halibut to investigate size/age of maturation in historical data and to aid in the assessment of maturity in ongoing surveys. However, as the relationship between oocyte size and packing density may differ between populations (Dominguez-Petit et al. 2018), the threshold should be validated for each population.

The use of the GSI-based method to evaluate maturity, as opposed to comparison to visual examination of the ovary using the 4-stage scale, led to an increase in L_{50} of 2.0–7.9 cm. This change results from fish which were visually classed as stage B or D, thus developing or spent, which are both considered as being sexually mature, being reclassified as sexually immature/functionally immature when applying the GSI-based method. Reclassifying them in this manner shifts the maturity ogive to the right, resulting in a higher L_{50}. This highlights the importance of not only understanding the gonad development cycle, but also to validate the accuracy of the methods used to assess the ovary development stage of the species in question.

From our sampling of ovaries, two fish caught in Greenland had residual hydrated eggs, and following our terminology, these were classified as spent. However, these fish were also in the process of vitellogenesis and would have been classified as developing 2 had they not contained hydrated oocytes. The GSI of both fish was above 1.5%, which indicates that the GSI-based method is not hindered by the presence of spent fish in its ability to identify sexually mature individuals from those that were sexually immature/functionally immature. However, this conclusion is based upon a small sample size, but given that residual eggs would inflate the resultant GSI, it is likely that spent fish would have a GSI above 1.5% and the conclusion would hold with a higher sample size.

A substantial number of fish caught during the Icelandic autumn groundfish survey were initially classified as spent following visual assessment. Following the GSI-based method, these fish were divided into sexually immature/functionally immature and sexually mature. The length distributions of these two groups were remarkably similar to the length distribution of functionally immature and sexually mature fish respectively which were initially assessed visually as developing (stage B) and then reassessed using the GSI-based method. This indicates that fish identified as spent are likely to have had their ovary stage misidentified which is known to be a common problem when visually assessing ovary developmental stage (Albert et al. 2001). While knowledge on the timing of spawning in Iceland is limited, it is generally considered to take place around January–March (Sigurdsson 1977), 7 to 9 months before our survey so it seems unlikely that fish caught in the survey are at this spent stage.

The L_{50} of Greenland halibut in Iceland does not show large variations over time, but there is an increase around 2010–2012. While previous studies have examined the size-at-maturity of Greenland halibut in different regions over time (Morgan et al. 2003), differing maturity scales between regions and updated knowledge on the gonad development cycle of Greenland halibut warrants renewed investigations into this topic. The reason for the increase in L_{50} is unclear as it does not correlate with the length diversity of the samples (which would indicate an artefact due to the sampling strategy, Kjesbu et al. 2025) nor does it coincide with any marked change in recruitment or SSB in the stock (ICES 2024), in contrast to the decrease in L_{50} in the Gulf of St. Lawrence which coincided with a year of strong recruitment (Chamberland and Benoît 2024). While the population in east Greenland, Iceland and Faroe Islands are assessed together as one stock, there is still some uncertainty surrounding the population structure in these areas and their relationship with neighbouring populations (ICES 2024). This makes it difficult to ascertain whether the change in maturity is a result of changes in the environment around Iceland or linked to the movements of individuals or cohorts immigrating to, or emigrating from, Icelandic waters (Vihtakari et al. 2022). It is worth noting that the L_{50} of Greenland halibut in Iceland is similar to that found for two areas in east Greenland where, during 1997–2012 (all years combined), it was 74.1 and 80.2 cm (Kennedy et al. 2014).

In conclusion, the GSI-based method proved beneficial for distinguishing sexually immature/functionally immature fish from sexually mature individuals and allows the new maturity scale to be applied retroactively. The application of the new maturity scale to the Icelandic Greenland halibut population led to an increase in the estimate of L_{50}. The difference in A_{50} of functionally immature and sexually mature individuals supports the hypothesis that the immature phase lasts at least 1 year, but may be longer. Based upon GSI, it appears that a significant proportion of Greenland halibut identified as spent were misclassified, demonstrating the difficulties in identifying this maturity stage.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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