

## REGULAR ARTICLE

# Reduction in size-at-maturity in unprecedentedly strong cohorts of redbfish (*Sebastes mentella* and *S. fasciatus*) in the Gulf of St. Lawrence and Laurentian Channel

Caroline Brûlé<sup>1</sup>  | Kadra Benhalima<sup>2</sup> | Marie-Julie Roux<sup>1</sup> |  
Geneviève J. Parent<sup>1</sup> | Caroline Chavarria<sup>1</sup> | Caroline Senay<sup>1</sup> 

<sup>1</sup>Maurice-Lamontagne Institute, Fisheries and Oceans Canada, Mont-Joli, Quebec, Canada

<sup>2</sup>Gulf Fisheries Centre, Fisheries and Oceans Canada, Moncton, New Brunswick, Canada

## Correspondence

Caroline Senay, Maurice-Lamontagne Institute,  
Fisheries and Oceans Canada, 850 Rte de la  
Mer, Mont-Joli, QC, G5H 3Z4, Canada.

Email: [caroline.senay@dfo-mpo.gc.ca](mailto:caroline.senay@dfo-mpo.gc.ca)

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## Abstract

Life-history traits, such as size-at-maturity, are key parameters to model population dynamics used to inform fisheries management. Fishery-induced evolution, density-dependent effects, and global warming have been shown to affect size- and age-at-maturity, and resulting spawning stock biomass (SSB) in a wide range of commercial fish stocks. Marked changes in redbfish biomass and environmental conditions in the Gulf of St. Lawrence and Laurentian Channel over the past decade called for a review and update of size-at-maturity for commercially important deepwater redbfish *Sebastes mentella* and Acadian redbfish *Sebastes fasciatus* stocks. Following a 25-year moratorium, local redbfish biomass has recently reached unprecedented levels, co-occurring with an overall warming of bottom water temperatures. Our objectives were (1) to perform a histological assessment of redbfish reproduction stages, including the validation and fine-tuning of a robust visual chart to facilitate monitoring of size-at-maturity and SSB in a transforming environment, and (2) to evaluate changes in size-at-maturity in unprecedentedly strong cohorts of redbfish, and consequences for stock status assessment and fisheries management. Each specimen was genetically identified to species, and gonad reproduction stages were determined by histology and macroscopic appearances. The present study enabled a robust visual chart for continued and cost-effective monitoring of redbfish reproduction stages to be refined and validated, and has shown a large decrease in redbfish length when 50% of the individuals are considered mature that led to an increase in estimates of SSB during the 2011–2021 period for *S. mentella* and *S. fasciatus*. These changes modified the perception of stock status, thus having significant implications for fisheries management. Given that fishery-induced evolution and community structure changes along with global warming are affecting numerous stocks worldwide, the present

Brûlé Caroline and Senay Caroline these authors contributed equally to this work and share first authorship.

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study outlines a major and global challenge for scientists and resources managers. As shown by our results, the monitoring and frequent updates of life-history traits in transforming environments are needed to provide reliable science advice for sustainable fisheries.

#### KEYWORDS

density dependence, fishery-induced evolution, global warming, life-history traits, maturity ogive, population dynamics

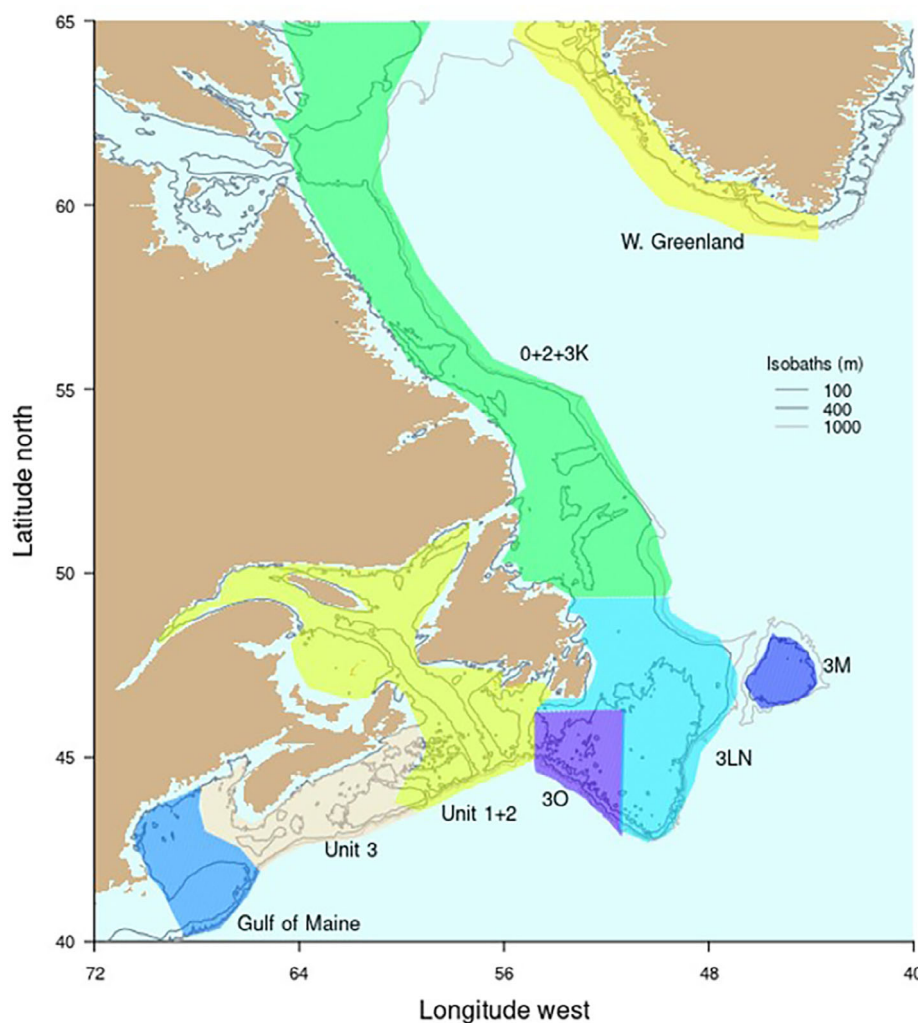
## 1 | INTRODUCTION

Fish life-history traits can vary spatially and temporally due to changes in environmental conditions or human-induced pressures. Life-history traits, such as recruitment success, mortality rate, growth curves, and size-at-maturity ogives, are all key parameters to model population dynamics (Forrest et al., 2008; Licandeo et al., 2020; Rudd & Thorson, 2018; Thorson, 2020). Specifically, maturity ogives are used to determine the spawning stock biomass (SSB), which is an important indicator used to assess stock status and reference points, and to inform the elaboration of appropriate fisheries management measures. Changes in size- or age-at-maturity have been reported for several species (see Sánchez Lizaso et al. [2000] for a review), such as salmon *Oncorhynchus* spp. (Ricker, 1981), whitefish *Coregonus* spp. (Handford et al., 1977), Atlantic mackerel *Scomber scombrus* L. (Overholtz et al., 1991), and many Atlantic groundfish, including Atlantic cod *Gadus morhua* L., haddock *Melanogrammus aeglefinus* L. (Beacham, 1983a; Beacham, 1983b; Beacham, 1983c), and silver hake *Merluccius bilinearis* (Mitchill 1814; Helser & Almeida, 1997). Such maturation changes can be triggered by both environmental and anthropomorphic impacts. For instance, fishery-induced evolution, through size selectivity, may remove particular genes from a stock, which has been shown to favor earlier maturation (Beaudry-Sylvestre et al., 2022; Heino et al., 2015; Moore et al., 2017). Biomass decrease may result in reduced competition, providing more resources per individual, enabling fish to grow and mature faster (Alm, 1959; Jørgensen, 1990; Sánchez Lizaso et al., 2000). In addition, shifts in maturation rates can be affected by changes in environmental conditions, for example changes in water temperature controlling fish metabolism (Jobling, 1981) and changes in habitat preference or species distribution patterns can all interact with maturation (Alm, 1959; Diana, 1983). Given the importance and propensity to vary across time and space of size-at-maturity, monitoring and frequent updates are needed to adjust to stocks' dynamics.

The present study focuses on the two main redfish species present in the Northwest Atlantic (NWA), the deepwater redfish *Sebastes mentella* (Travin, 1951) and the Acadian redfish *S. fasciatus* (Storer, 1854). Both species are combined and simply referred to as "redfish" in fishery statistics due to their morphological similarities. In the NWA, redfish catches peaked at 400,000 metric tonnes (t) in 1959 and ranged between 135,000 and 286,000 t during the 1960–1993 period (Lear, 1998). Since 1993, catches have decreased

substantially. For instance, 40,308 t were landed in 2018 for all NWA redfish stocks (Cadigan et al., 2022). Various stocks are present in the NWA (Figure 1), here we investigated Units 1 and 2 redfish, which correspond to the Northwest Atlantic Fisheries Organization (NAFO) Divisions 4RST and from January to May Subdivisions 3Pn4Vn, and Subdivisions 3Ps4V4Wfgj and from June to December Subdivisions 3Pn4Vn, respectively. In the Gulf of St. Lawrence (GSL) and the Laurentian Channel, fisheries in the 1980s and 1990s relied on one or few important cohorts, which were mostly depleted before the Unit 1 moratorium in 1995 and an important reduction in total allowable catch (TAC) in Unit 2 in 2001. After 25 years of low redfish biomass and fishery harvests, cohorts from 2011, 2012, and 2013 caused a large increase in biomass in Units 1 and 2. A stock assessment (DFO, 2018a) and a management strategy evaluation (DFO, 2018b) suggested that *S. mentella* and *S. fasciatus* stocks could sustainably support a fishery of 40,000 to 60,000 t in both Units 1 and 2 by 2026. This was further supported by the 2021 stock assessment (DFO, 2022; Senay et al., 2023) indicating that redfish biomass was among the highest values of the time series starting in 1984. This unprecedented redfish recruitment co-occurred with an overall warming of bottom water temperatures above historical averages in the Laurentian and other deep channels of the GSL from 2011 onwards (Galbraith et al., 2022). Temperatures at 250 and 300 m have reached the highest values observed in the series which began in 1915. Warmer temperatures (>5°C at 200 and 300 m) were also observed in 1980 when the previous strong recruitment, albeit less abundant than the 2011–2013 cohorts, was observed in the GSL. Given that redfish biomass now dominates the demersal and benthic fish community of the GSL (Senay et al., 2023), there was a need to update recent cohorts' life-history traits to ensure representative and reliable stock assessment and management decisions.

Redfish are ovoviparous and produce sporadic recruitment events. Previous studies have estimated  $L_{50}$  (length when 50% of the individuals are considered mature) for different stocks (Table 1). Redfish size-at-maturity tends to be larger in the northern stocks (Mayo et al., 1990; Ni & Sandeman, 1984). However, all studies presented at least one potential bias or inadequacy. They all relied completely or partially on the number of anal fin soft rays for species identification (Gascon, 2003; St.-Pierre & de Lafontaine, 1995). These species distinction techniques have been proved to be unreliable to identify redfish accurately at the individual level, which can only be achieved by genetic methods (Benestan et al., 2021; Senay et al., 2021). In



**FIGURE 1** Northwest Atlantic redfish (*Sebastes* spp.) approximate stock areas. Some stock designations correspond to Northwest Atlantic Fishery Organization Divisions but only the portions where redfish are expected to be found are shaded. *S. mentella* and *S. fasciatus* are divided into separate stocks such as Units 1 (Divisions 4RST and from January to May Subdivisions 3Pn4Vn) and 2 (Subdivisions 3Ps4Vs, Subdivisions 4Wfgj, and from June to December Subdivisions 3Pn4Vn), while they are combined in the other areas (Divisions 0, 2, 3K; Cadigan et al., 2022).

addition, if maturity description was provided, it was based on macroscopic examination without prior histologic validation (St.-Pierre & de Lafontaine, 1995) or partially inspired from the reproduction stages of Echeverria (1987), who generalized the external morphology of gonads based on the cellular morphology across 34 *Sebastes* species. Histology provides robust information to classify individuals in the different stages of their reproductive cycle by an objective method (Brown-Peterson et al., 2011). The maturity ogives used in Units 1 and 2 redfish stock assessments until recently are derived from Gascon (2003), with  $L_{50}$  values between 19.6 and 25.4 cm (Figure A1).

Important changes in redfish biomass and environmental conditions in the GSL and Laurentian Channel in the last decades called for a review and update of size-at-maturity for commercially important redfish stocks. The objectives of this study were (1) to perform an histological assessment of redfish reproduction stages, including the validation and fine-tuning of a robust visual chart to facilitate monitoring of size-at-maturity and SSB in a transforming environment, and (2) to evaluate changes in size-at-maturity in unprecedentedly strong cohorts of redfish, and consequences for stock status assessment and fisheries management.

## 2 | MATERIALS AND METHODS

### 2.1 | Redfish sampling

From 1995 to 2009, reproduction stages based on gonad macroscopic appearance were routinely evaluated and recorded for redfish caught in Unit 1 by the Department of Fisheries and Oceans Canada (DFO) annual survey. The visual chart used during this period is presented in Figure A2 (unpublished data). For the purpose of this study, redfish were collected with bottom otter trawl (Figure 2 and Table A1) in August and September 2018 and 2019 in Unit 1, and by an industry survey conducted in August and September 2018 in Unit 2. *S. mentella* and *S. fasciatus* were collected in 79 and 77 stations, respectively, giving a total of 113 samples (41 stations with both species). A maximum of 37 redfish were selected from each station for a total of 757 fish biopsied immediately in situ. Fish sampling was stratified based on length, sex, and NAFO Division. Absolute species identification was not possible until subsequent genetic analyses, nevertheless a combination of anal fin ray counts and depth was used as the best available proxies of species identity to ensure a fair distribution of sample sizes across fish size, sex, space, and species.

TABLE 1 Parameters  $a$  and  $b$ , and standard errors ( $\pm$ SE, when available) of the logistic regressions fitted to determine the size-at-maturity ( $L_{50}$ ) of redfish in the Northwest Atlantic.

Species	Year	Location	Sex	a (±SE)	b (±SE)	L <sub>50</sub> (cm)	N	Source	Comments		
Mixed <i>S. fasciatus</i> / <i>S. mentella</i>	1957–1969	NAFO Div. 3P	F	–	0.804	29.61 (±0.090)	4948	Ni and Sandeman (1984); Ni and Templeman (1985)	Stages at maturity only based on macroscopic examination without prior histology validation		
			M	–	0.809	18.56 (±0.095)	4643				
		NAFO Div. 4R	F	–	0.773	26.60 (±0.134)	2711	Ni and Sandeman (1984)	Immature female: ovary tiny; ovarian wall transparent and delicate; eggs, if present usually less than 0.2–0.3 mm diameter; no evidence of old eye pigment or darker peritoneum		
			M	–	0.726	18.71 (±0.152)	2711		Immature male: testes translucent, string-like; width usually <1 mm		
		NAFO Div. 4S	F	–	0.810	26.89 (±0.250)	1002		Fish that did not meet these criteria were considered as mature		
			M	–	0.615	19.23 (±0.239)	1170		Fork length ranged from 5 to 50 cm		
		NAFO Div. 4T	F	–	0.925	28.12 (±0.178)	816				
			M	–	0.776	18.77 (±0.263)	857				
		NAFO Div. 4V	F	–	0.958	26.36 (±0.259)	594				
			M	–	1.460	17.40 (±0.307)	486				
<i>S. fasciatus</i> <i>S. mentella</i> Mixed <i>S. fasciatus</i> / <i>S. mentella</i>	1989–1990	NAFO Div. 4W	F	–	0.599	24.44 (±0.189)	1427				
			M	–	1.010	17.37 (±0.180)	1283				
		NAFO Div. 3L	F	–	0.302	34.65 (±0.315)	999				
			M	–	0.330	21.80 (±0.667)	1128				
		NAFO Div. 3N	F	–	0.303	29.58 (±0.271)	1263				
			M	–	0.362	16.32 (±0.709)	1307				
		Gulf of St. Lawrence (NAFO Div. 4RS)	F	–0.8261 (±0.099)	21.10 (±2.54)	25.54	–	St.-Pierre and de Lafontaine (1995)	Stages at maturity only based on macroscopic examination adapted from Ni and Templeman (1985) and Echeverria (1987)		
			F	–0.5461 (±0.036)	14.170 (±0.941)	25.95	–		Proportion of matures is stage 2 and above		
					F	–0.5621 (±0.0349)	14.57 (±0.910)	25.92	2649		Species identification based on the number of fin soft rays instead of genetics
<i>S. fasciatus</i> <i>S. mentella</i>	1996–1998	Gulf of St. Lawrence	F	–10.605	0.441	24.1	1837	Gascon (2003)	Bias caused by commercial samples (fish are mostly >26 cm)		
			M	–10.687	0.545	19.6			Equation used: proportion mature = $\frac{1}{1+e^{-(a+by)}}$		
			F	–9555	0.377	25.4			Relied on the number of soft rays in the anal fin, the gas bladder musculature or the MDH-A* allele composition for species identification instead of genetics		
			M	–7521	0.33	22.8					

(Continues)



TABLE 1 (Continued)

Species	Year	Location	Sex	a (±SE)	b (±SE)	L <sub>50</sub> (cm)	N	Source	Comments
Mixed <i>S. fasciatus</i> / <i>S. mentella</i>	1996–2000	NAFO Div. 3L	F	-	-	34.71 (±0.62)	12,437	Ávila de Melo et al. (2005); Power (2001)	Detailed description of the maturity state technique unavailable Fish were classified as immature or mature based on a visual examination of gonads using a reduced categorization of maturity stages of Ni and Templeman (1985) Ovarian sections were examined using a compound microscope and classified as immature or mature Fish were categorized as immature if they were in either ovarian development stage 1 immature or stage 2 maturing
			M	-	-	23.94 (±0.21)	11,768		
	NAFO Div. 3N		F	-	-	30.40 (±0.35)	16,547		
			M	-	-	20.00 (±0.17)	17,005		
<i>S. fasciatus</i>	2011–2012	Gulf of Maine	F	-	0.97	21.66	658	Sullivan et al. (2017)	

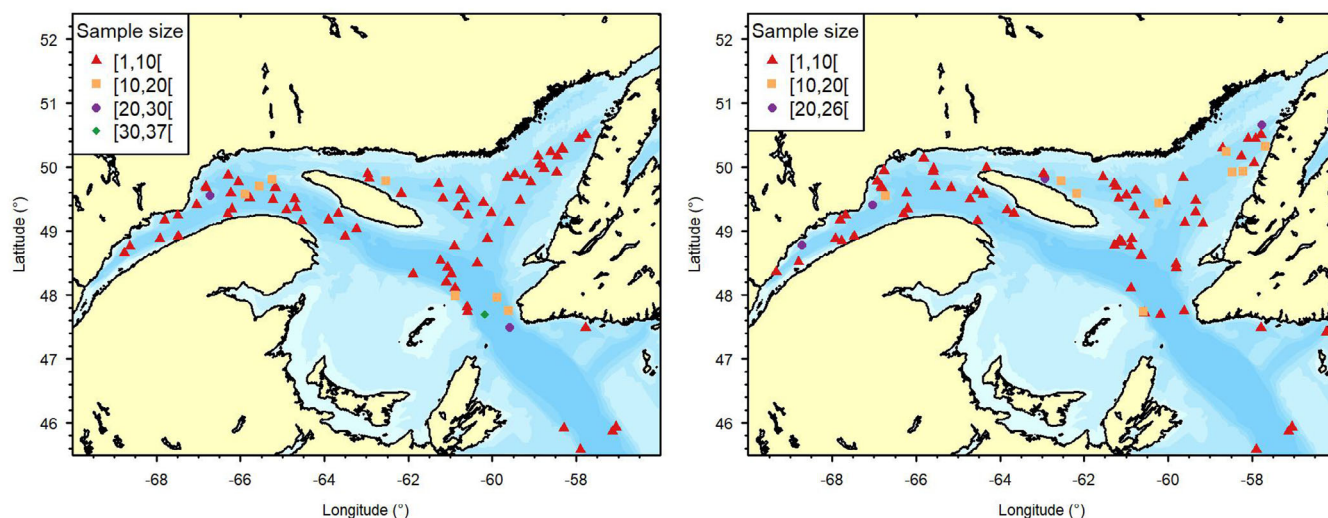
Abbreviations: Div, Division; F, female; M, male; NAFO, Northwest Atlantic Fisheries Organization; *S. fasciatus*, *Sebastes fasciatus*; *S. mentella*, *Sebastes mentella*.

Generally, *S. fasciatus* has a lower anal fin ray count and is located in shallower habitats than *S. mentella* (Senay et al., 2022). For each sampled redfish, fork length was measured to the nearest millimeter (mm) and total mass was determined (g). A fin clip was collected and preserved in ethanol for subsequent genetic analyses. Gonads were extracted, subsampled, and fixed in a Bouin's solution for at least 3 weeks before preparation for further histologic analyses. A general picture of the reproductive organs was taken with a standard camera (Tough TG-5<sup>®</sup>; Olympus).

## 2.2 | Genetic species identification

We designed a new quantitative polymerase chain reaction (qPCR) assay to discriminate *S. mentella* and *S. fasciatus*. We first aligned sequences from the second intron of the nuclear 7S ribosomal protein gene from multiple specimens to characterize intra- and interspecific diversity. We used the two sequences available at the National Center for Biotechnology Information (NCBI, <https://www.ncbi.nlm.nih.gov>; accession numbers JX887158 [*S. mentella*] and JX887156 [*S. fasciatus*]) and generated new sequences from specimens of both species (*S. mentella*, *N* = 21, accession numbers OR425372-OR425392; *S. fasciatus*, *N* = 20, accession numbers OR425393-OR425412). DNA was extracted from tissues with the Qiagen DNeasy blood and tissue kit. We amplified the second intron of the 7S gene using primers 5'-AGCGCCAAAATAGTGAAGCC-3' and 5'-GCCTTCAGGTCAGAGTTCAT-3' (Chow & Hazama, 1998). Each 20 µL PCR reaction contained 1 µL of template DNA, 100 nM of each primer and 10 µL of Qiagen Multiplex PCR master mix 2X from the Qiagen Multiplex PCR Kit. Cycling conditions consisted of an initial 15 min at 95°C, followed by 30 cycles of 30 s at 95°C, 60 s at 55°C, and 2 min at 72°C, with an elongation step of 10 min at 72°C. PCR amplicons were then Sanger sequenced using a Big Dye™ Terminator v3.1 reagent kit and Applied Biosystems 3130 genetic analyzer. Each 20 µL reaction contained 0.5 µL BigDye™ Terminator v3.1 Ready Reaction Mix (Applied Biosystems), 500 nM of forward or reverse primer (sequences were produced in both directions), 10 µL trehalose 10%, and 3.75 µL of 5X sequencing buffer. Cycling conditions consisted of 96°C for 1 min, followed by 25 cycles of 96°C for 10 s, 50°C for 5 s, and 60°C for 4 min. The alignment of a total of 22 *S. mentella* and 21 *S. fasciatus* sequences was performed using Geneious 9.1.4 (<https://www.geneious.com>).

We then designed in silico new qPCR primers targeting a sequence of 68 nucleotides within the second intron of the 7S gene with an insertion of 11 nucleotides specific to *S. mentella*. We validated in vitro the new primers 5'-GTTGGAAGTTGATTGCTGG-3' and 5'-CAMTGACAGTCAGTGGATTTATTT-3' (Sigma-Aldrich) for their capacity to discriminate species. Each 20 µL qPCR reaction contained 1 µL of template DNA, 400 nM of each primer, and 10 µL SYBR® Select Master Mix 2X (Applied Biosystems). Cycling conditions consisted of an initial 2 min at 50°C, followed by 2 min at 95°C, then 40 cycles of 95°C for 15 s, 60 s at 56°C, and finally 30 s at 95°C, 30 s at 65°C, and 30 s at 95°C using an AriaMx Real-Time PCR System (G8830A; Agilent Technologies).



**FIGURE 2** Sampling locations of (a) deepwater redfish *Sebastes mentella* (79 stations) and (b) Acadian redfish *Sebastes fasciatus* (77 stations) in 2018 and 2019. Sample size classes are indicated by different colors and symbols.

We then identified the species of 247 fish sampled across the NWA with the qPCR assay. Species identification was already accessible for the 247 fish which were previously genotyped using 24,603 single nucleotide polymorphisms and classified as *S. mentella* or *S. fasciatus* using Admixture (Benestan et al., 2021). We estimated the accuracy of species identification with the qPCR assay based on single nucleotide polymorphisms species identification. DNA extraction and qPCR-based species identification were processed as indicated in this section. Species identification using the qPCR assay was accurate for 237 of the 247 specimens tested. Although hybrids are rare, most *S. mentella* in the study area and some *S. fasciatus* in the GSL have introgressed genomes (Benestan et al., 2021). However, the qPCR assay cannot characterize introgression present between *Sebastes* species.

### 2.3 | Reproduction stages based on histology

Gonad samples were removed from the Bouin's solution, rinsed with 70% ethanol, dehydrated in a series of aqueous ethanol solutions, cleared in xylene, and then embedded in paraffin wax in a vacuum chamber. Blocks were sectioned serially at 5–6  $\mu\text{m}$  intervals on a rotary microtome. Two slides per tissue comprising five serial sections were prepared. Serial sections were mounted on glass slides and stained with modified Masson's trichrome technique (Gabe, 1968) using ethanol and xylene as dehydration and clearing agents, respectively. Final mounts were made with cover glass slips using Paramount as a mounting resin. Light microscopic examinations were performed under an Olympus BX51<sup>®</sup>. The histologic sections were viewed and photographed under a light compound microscope equipped with a color digital camera using bright field optic Olympus SC50<sup>®</sup>.

Redfish species exhibit an ovoviparous reproductive strategy. Fertilization and development of the embryos occur within the ovary, where the fully developed larvae are extruded, leaving behind the post-ovulatory follicles and residual larvae (Aranzábal et al., 2009). The reproduction stage terminology used in this work follows

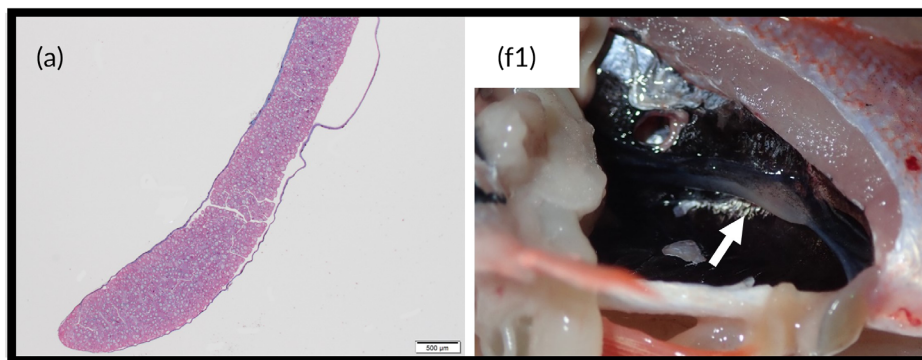
Echeverría (1987), Filina et al. (2017), Ni and Sandeman (1984), Ni and Templeman (1985), and St-Pierre and de Lafontaine (1995). For female redfish, reproduction stages were determined based on the examination of the oocyte characteristics such as the formation of cortical alveoli, the degree of yolk accumulation, and oocyte size, as well as the thickness of the ovarian wall and signs of larvae extrusion (Benoît et al., 2020; Echeverría, 1987; Filina et al., 2017). For male redfish, the microscopic criteria of fullness of the seminiferous tubules and presence of spermatogonia (i.e., gamete development) were used to discriminate reproduction stages (Echeverría, 1987).

On the basis of the histologic characteristics of gonads, six reproduction stages were distinguished for females ("immature", "developing", "maturing", "mature", "post-ovulatory/recovering", and "resting", Figure 3) and four for male redfish ("immature", "maturing", "mature", "recovering", Figure 4). Given that only three females were classified as "resting", they were included in the post-ovulatory/recovering category for further analyses. The distribution of lengths within each category is illustrated in Figure 5 for each combination of species and sex.

### 2.4 | Reproduction stages based on macroscopic gonad appearance

The visual chart used during the DFO Unit 1 survey from 1995 to 2009 for redfish was mainly based on gonad size, shape, and color (Figure A2, unpublished data), but was never validated by histology. Macroscopic appearance categories from these older charts were refined. Six macroscopic stages were distinguished for females (categories "F1" to "F6"; Figure 3) and four for male redfish (categories "M1" to "M4"; Figure 4). The main characteristics to distinguish categories were the size, form, opacity, and color of ovaries and their oocytes and testes. The updated chart has one more category than the previous version for females because it considers a stage after the extrusion of larvae ("F6"; Table 2). For males, both stages named

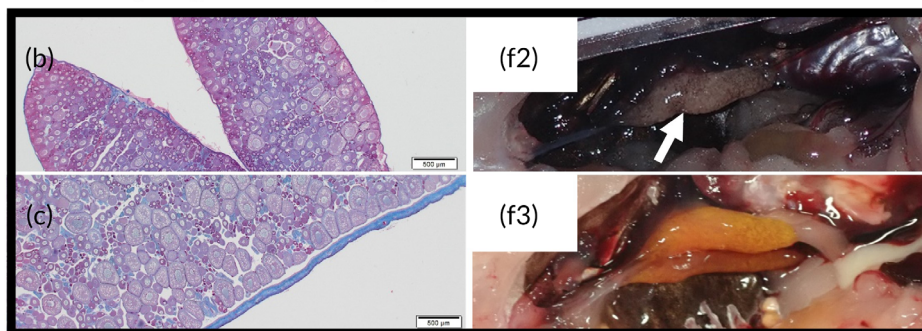
## Immature



(a) **Immature ovaries**, ovary wall is thin, transparent, and very small oögonia are found.

(f1) Transparent, ribbonlike, flaccid ovary.

## Developing/maturing



(b) **Developing ovaries**, primary oocytes with large nuclei and many nucleoli showing cortical alveoli initially aligned in the peripheral cytoplasm.

(c) **Maturing ovaries**, first sign of vitellogenesis with yolk granule deposition in oocytes, increasing cortical alveoli with presence of yolk granules.

(f2) Small firm gonads, from beige to dark pink.

(f3) Gonads light orange or yellow in colour, oocytes easily detected, presence of small oil drops.

**FIGURE 3** Female redfish (*Sebastes* spp.) reproduction stages based on light micrograph cross-sections (left) and their associated gonad appearance based on the macrograph general view (right). Four categories are considered: “immature”, “developing/maturing”, “mature”, “post-ovulatory/recovering/resting”. This classification approach was adapted from Ni and Sandeman (1984), Ni and Templeman (1985), Echeverria (1987), St.-Pierre and de Lafontaine (1995), and Filina et al. (2017).

post-copulation of the year and post-copulation of last year (Figure A2) were merged into one category (“M4”; Table 3) considering the untested assumption of the time since the last copulation and their similar descriptions.

### 2.5 | Comparison of visual and histological methods

Ground-truthing of the older visual chart was undertaken using recent data (2018–2019) by pairing histology and macroscopic gonad appearance methods. Mosaic plots were used to compare redfish reproduction stages based on histology and macroscopic gonad appearances using the *mosaic plot* function from the *graphics* package (Murrell, 2019). This was done to summarize the relationships (if any)

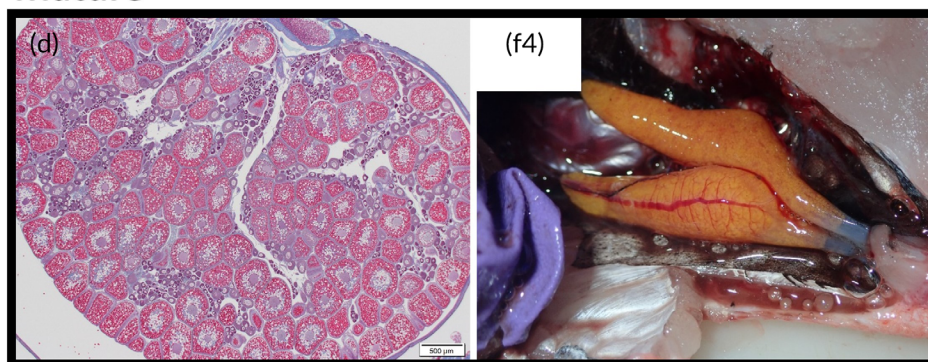
between the more convenient and easy-to-use visual chart method (i.e., macroscopic stages), and the more precise histological method for determining redfish reproduction stages. For each sex, a  $\chi^2$  test assessed whether the two methods were significantly (at  $p < 0.05$ ) associated using the *chisq.test* function from the *stats* package (R Core Team, 2013). Some histological stages and macroscopic categories were combined to obtain significant  $\chi^2$  tests.

### 2.6 | Revised maturity ogives based on histological data

Redfish maturity ogives were updated based on reproduction stage information determined from gonad histology. Size-at-maturity was estimated by a logistic regression using a Bernoulli distribution



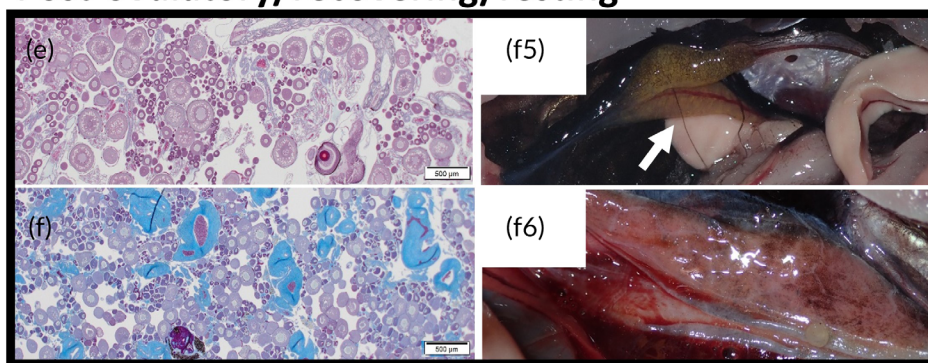
## Mature



(d) **Mature ovaries**, cytoplasm of oocytes filled with fused yolk granules (red dot), stretched ovary.

(f4) Gonads are soft and swollen orange or yellow in color, rich vascularization on the ovary wall.

## Post-ovulatory/recovering/resting



(e) **Post-ovulatory/recovering ovaries**, numerous extruded larvae and black pigments remaining in ovaries, unextruded larvae.

(f5) Black pigmentation through the wall of ovaries caused by the eyes of embryos. Rich vascularization on the ovary wall.

(f) **Resting ovaries**, the oocytes returned to the stage of total inactivity, presence of residual follicles which remained in the ovaries after larvae extrusion, the follicles are empty and presence of cell pigment clusters purplish.

(f6) Flaccid ovaries, which seems partially deflated.

**FIGURE 3** (Continued)

(family = binomial [link = "logit"]) with the *glm* function in the *stats* package (R Core Team, 2013), in accordance with the following general equation:

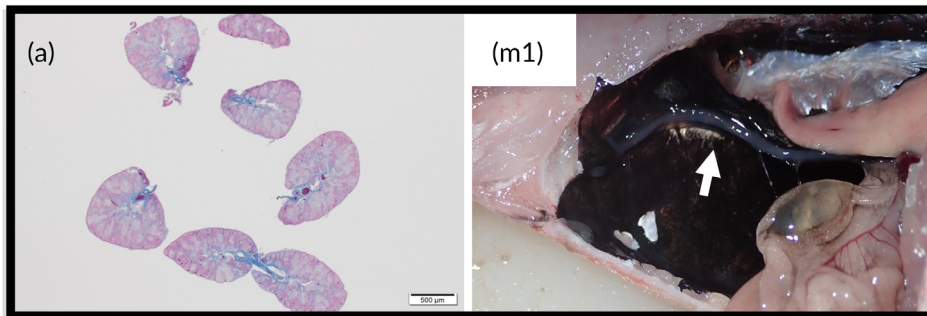
$$\text{proportion mature} = \frac{e^{(\beta_0 + \beta_1 L)}}{1 + e^{(\beta_0 + \beta_1 L)}}$$

where the proportion mature is predicted based on individual reproduction stage (i.e., "immature" or "mature", a factor having two levels) and length (*L*), and where  $\beta_0$  and  $\beta_1$  correspond to the intercept and the slope of the logistic equation. Species (given that redfish species are often not distinguished) and sex were also included as additional predictors, both separately and as interactions. Model equations are presented in Table 4.

The distinction between "immature" and "mature" fish was made by applying an approach similar to Lubzens et al. (2010) and Filina

et al. (2017) for *Sebastes* species, Farley et al. (2014) for albacore tuna (*Thunnus alalunga*), and Pacicco et al. (2023) for yellowfin tuna (*Thunnus albacares*), whereby all reproduction stages except immature individuals were considered to be "mature". Multiple models were compared based on Akaike Information Criterion (AIC), Nagelkerke's adjusted  $R^2$  (Barton, 2020), and likelihood ratio test using the *anova* (test = "Chisq") function from the *stats* package (R Core Team, 2013) to identify the most parsimonious one. AIC is a relative measure of a statistical model based on a trade-off between the goodness of fit and complexity (Fergus et al., 2011). The results from the most parsimonious model were further investigated. The  $L_{50}$  was computed with standard errors (SE) using the function *dose.p* from the *MASS* package (Venables et al., 2002). The confidence intervals at 95% were computed using the *ggpredict* function from the *ggeffects* package (Lüdtke et al., 2023) and results were plotted using the *ggplot* function from the *ggplot2* package (Chang et al., 2021).

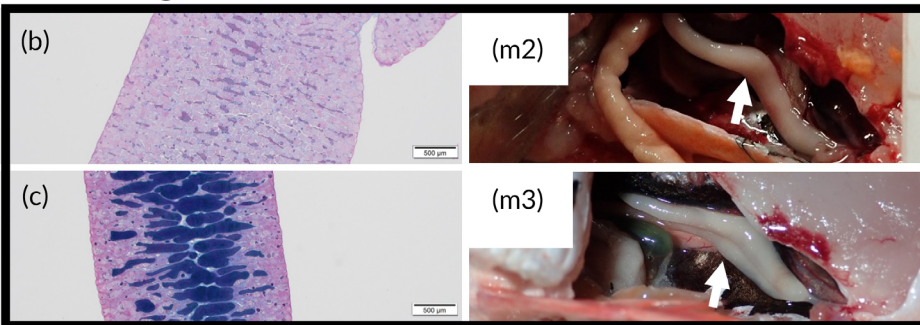
## Immature



(a) **Immature testes**, small clusters of a spermatogonia.

(m1) Small, thin, clear testes.

## Maturing/mature



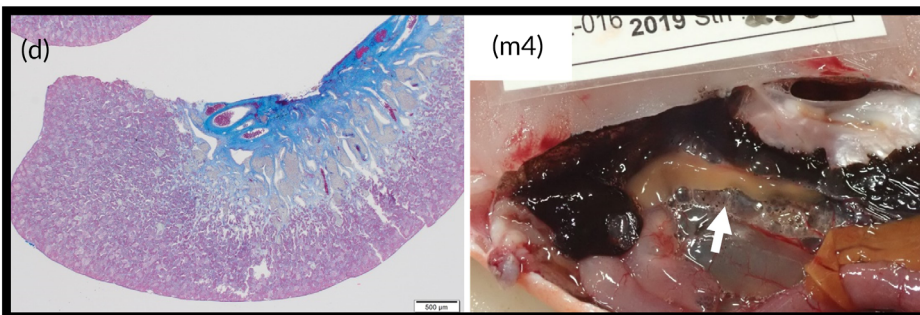
(b) **Maturing testes**, seminiferous tubules almost filled with spermatids and spermatozoa.

(m2) Firm filamentary testes, white in color.

**Mature testes**, seminiferous tubules completely filled with spermatozoa.

(m3) Firm ribbonlike testes, creamy and milky white, full of milt. Spermatozoa released when pressure applied to abdomen or when the testes is cut.

## Recovering



(d) **Recovering testes**, empty seminiferous tubules, spermatogonia present.

(m4) Filamentary/ribbonlike testes, beige in colour, which seems partially deflated.

**FIGURE 4** Male redfish (*Sebastes* spp.) reproduction stages based on light micrograph cross-sections (left) and their associated gonad appearance based on the macrograph general view (right). Three categories were considered: “immature”, “maturing/mature” and “recovering”. This classification approach was adapted from Echeverria (1987).

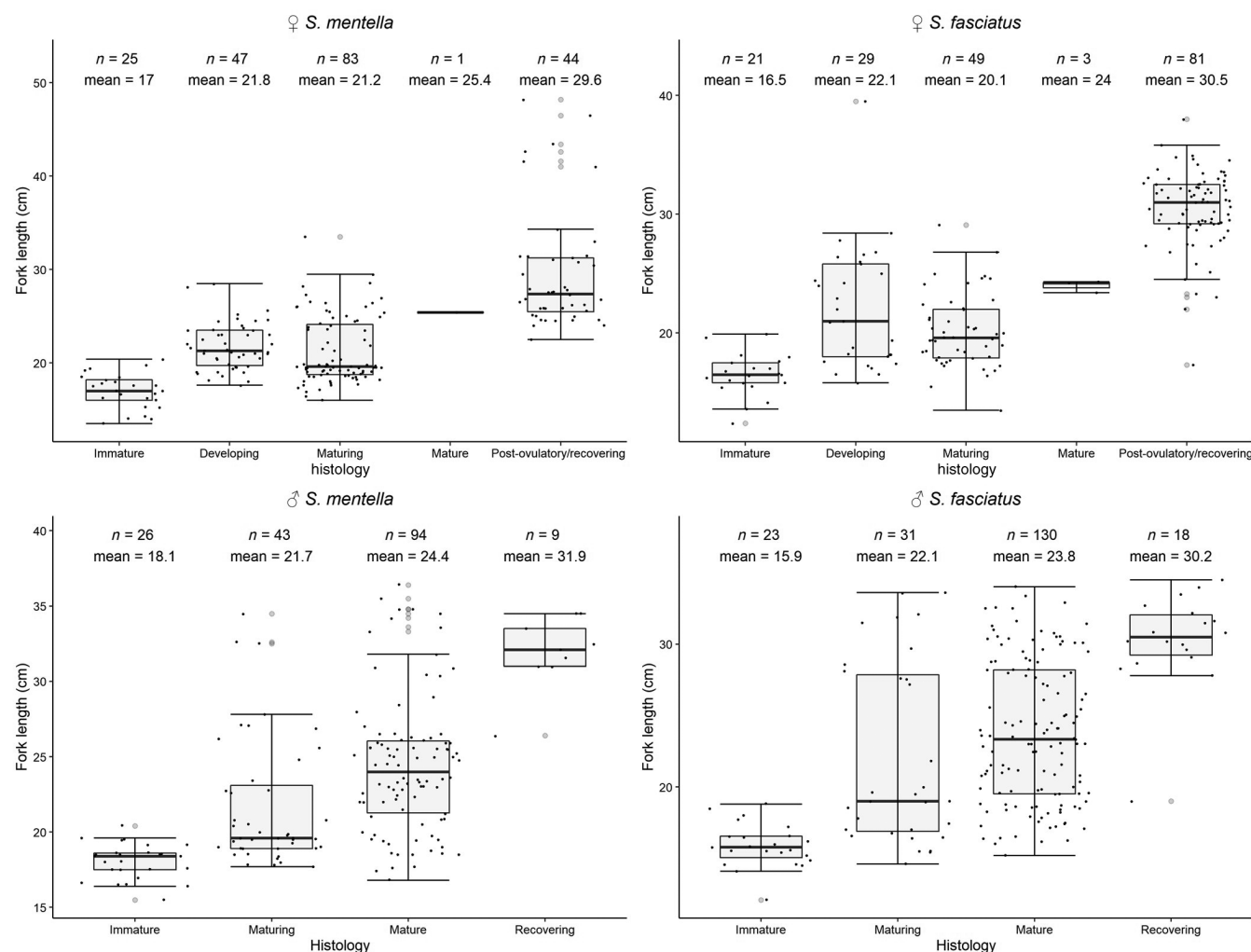
### 2.7 | Investigation of changes in size-at-maturity based on macroscopic gonad appearance

Unfortunately, the raw data collected between 1996 and 1998 (e.g., fish length, sex, anal fin ray count, maturity, location, and depth) used in Gascon (2003) could not be retrieved, but reproduction stages from the DFO Unit 1 survey were available to inform comparisons of  $L_{50}$  between the two periods and ascertain that changes were not caused by methodological differences (i.e., gonad histology versus macroscopic appearance). The 1996–1998 period was chosen because it corresponded to the one used to compute the maturity ogives implemented in stock assessments until recently (Gascon, 2003; Senay et al., 2021).

Changes in size-at-maturity were therefore investigated using reproduction stages from macroscopic gonad appearance from 1996 to 1998 and the current study (2018–2019). The length range of the 1996–1998 specimens was truncated to 12–50 cm, corresponding to 98% (17,603 out of 17,802) of specimens, to ensure reliable comparisons with the current period. Considering the lack of quality of some pictures, a subset of 706 out of the 757 specimens from 2018 to 2019 sampling was retained for robust evaluation of redfish reproduction stage based on gonad macroscopic appearances.

In 1996–1998, fish classified as stages 901 (for females) or 401 (for males) were taken to be immature, and all other classifications were assumed to represent “mature” redfish (Figure A2). In 2018–2019, fish classified as “F1” and “F2” (female without visible





**FIGURE 5** Boxplot of length distribution within reproduction stages based on histology for each combination of species and sex. In each boxplot, the black dots are the observations, the rectangles show the lower quantile, the median, and the upper quantile, the whiskers correspond to 1.5 multiplied by the interquartile range, and the gray dots are considered as outliers. The number of observations ( $n$ ) and the average length for each categories are indicated.

eggs) and “M1” (for male) were taken to be immature to correspond to the 1990s classification. All other categories were assumed to represent mature fish (Tables 2 and 3). By doing this, similar criteria were used to define immature and mature fish in both periods. A logistic regression was fitted to observations for females and males in each period to assess maturity ogives and  $L_{50}$  using the same  $glm$  procedure as described above.

## 2.8 | Consequences for stocks status assessment and fisheries management

Species- and sex-specific ogives (Figure A1; Gascon, 2003) have been used since 2009 to estimate the SSB in the GSL (DFO, 2010). The stock assessment used time series beginning in 1984 to evaluate stock status based on the Canadian precautionary approach (PA) framework (Bourdages et al., 2022; DFO, 2006; Senay et al., 2021). The earlier redfish maturity ogives from Gascon (2003) were applied to the whole time series by multiplying the number-at-

length by proportion mature-at-length, and then converting numbers to biomass with length-at-weight relationships to obtain SSB estimates. Starting in 2011, which corresponds to the arrival of the new cohorts in Units 1 and 2, and to an important increase in water temperature, the ogives based on gonad histology in the current study were applied and distinguished from Gascon (2003) ogives to compare the SSB. Stock trends and stock status relative to reference points were contrasted prior to and after applying the new maturity ogives for each species separately.

All statistical analyses were performed in the R statistical software version 2021.09.0-351 (R Core Team, 2023).

## 2.9 | Ethics statement

The care and use of experimental animals complied with the Canadian Council on Animal Care animal welfare laws, guidelines, and policies as approved by the Maurice Lamontagne Institute Council on animal care (IML-2018-041 and IML-2019-036).

**TABLE 2** Comparison of histology reproduction stages as well as present study and 1990s macroscopic gonad appearance categories for female *Sebastes* spp.

Histology reproduction stage	Present macroscopic category	1990s macroscopic category
<b>Immature:</b> Ovary wall is thin, transparent, and very small oogonia are found.	<b>F1:</b> Transparent, ribbonlike, flaccid ovary.	<b>(901) Immature (no reproduction this year):</b> Ovaries are small, generally <1 cubic centimeter (cc) and almost always <2 cc. Ovarian wall is clear, transparent and fragile. Egg diameter is usually $\leq 0.2 - 0.3$ mm. No sign of old ocular pigment nor of peritoneum pigmentation.
<b>Developing:</b> Primary oocytes with large nuclei and many nucleoli showing cortical alveoli initially aligned in the peripheral cytoplasm.	<b>F2:</b> Small and firm, from beige to dark pink.	
<b>Maturing:</b> First sign of vitellogenesis with yolk granule deposition in oocytes, increasing cortical alveoli with presence of yolk granules.	<b>F3:</b> Gonads light orange or yellow in color, oocytes easily detected, presence of small oil drops.	<b>(902) Mature (eggs not clear yet):</b> Augmentation of eggs and ovaries size. We can hypothesize that larvae will be produced this year. No sign of old ocular pigment nor of peritoneum pigmentation. Egg diameter is usually 1.0–1.2 mm. They become clearer and split inside the ovary. Eggs are clear, no sign of cellular division yet nor of larvae formation.
<b>Mature:</b> Cytoplasm of oocytes filled with fused yolk granules (red dot), stretched ovary.	<b>F4:</b> Soft and swollen, orange or yellow, rich vascularization on the ovary wall. Black pigmentation through the ovary wall (caused by the eyes of embryos).	<b>(903) Mature (sign of larvae formation):</b> Signs of cellular divisions and larvae development. Some larvae may present visible ocular pigment. Eggs and larvae may have been pushed out of the oviduct by pressure changes or brutal manipulation.
<b>Post-ovulatory/recovering:</b> Numerous extruded larvae and black pigments remaining in ovaries, unextruded larvae.	<b>F5:</b> Black pigmentation through the wall of ovaries caused by the eyes of embryos. Rich vascularization on the ovary wall.	<b>(904) Spawning (larvae are ready to be extruded):</b> Larvae have hatched, yolk sac is resorbed and larvae are ready to be expelled. Some hundreds or thousands may be left.
<b>Resting:</b> Oocytes returned to the stage of total inactivity, presence of residual follicles which remained in the ovaries after larvae extrusion, the follicles are empty and presence of cell pigment clusters purplish.	<b>F6:</b> Flaccid ovaries, which seem partially deflated.	<b>(905) Post-spawning (ovary is shriveled and sagging):</b> Peritoneum may be stained with blood or show dark pigmentation. Possible presence of old eye pigments or residual larvae. New eggs may be forming.

### 3 | RESULTS

#### 3.1 | Redfish sample and species identification

Redfish genetic analyses resulted in 372 individuals identified as *S. mentella* and 385 as *S. fasciatus* (Figure 2). Redfish length and mass varied between 13.5 and 48.2 cm, and 26 and 1523 g, respectively, in *S. mentella*, and between 12.1 and 39.5 cm, and 24 and 746 g, respectively, in *S. fasciatus*. Females of both species reached larger sizes and weights than males (Table 5). The sex ratio of the samples (female: male) was 200♀:172♂ for *S. mentella* and 183♀:202♂ for *S. fasciatus*.

#### 3.2 | Maturity ogives based on gonad histology

The majority of *S. mentella* females in our sample were classified as “maturing” based on histological analyses, while the majority of

*S. fasciatus* females were classified as “post-ovulatory/recovering” (Figure 5). Most males from both species were classified as “mature” during summer months (Figure 5).

The comparison of logistic regression models indicated that based on  $R^2$  all models explained similar fraction of the variation, and that only Model 1 and Model 5 were significantly different based on likelihood ratio tests. In regard to AIC, the most parsimonious model (difference in AIC of 1880) included length and a significant interaction between species and sex (Model 5), and explained 56.18% of the variation (Table 4), therefore maturity ogives were developed for each combination of species and sex. When maturity ogives were developed for each combination of species and sex independently,  $L_{50}$  ranged from 15.91 cm for males *S. fasciatus*, to 17.95 cm for male *S. mentella* (Figure 6). Intermediate values were observed for female *S. mentella* (17.17 cm) and *S. fasciatus* (16.26 cm). The species and sex-specific ogives explained between 53.27% and 59.09% of the variation in maturity.

### 3.3 | Comparison of maturity assessment based on histological and macroscopic gonad examination

Prior to conducting  $\chi^2$  tests illustrated by mosaic plots, reproduction stages were merged. For females, the “developing” and “maturing” intermediate histological stages were combined, and the final histological stages were grouped in a “post-ovulatory/recovering/resting” stage. For

**TABLE 3** Comparison of histology reproduction stages as well as present study and 1990s macroscopic gonad appearance categories for male *Sebastes* spp.

Histology reproduction stage	Present macroscopic category	1990s macroscopic category
<b>Immature:</b> Small clusters of a spermatogonia.	<b>M1:</b> Small, thin, clear testes.	<b>(401) Immature (no reproduction this year):</b> Testes are clear and translucent and filiform, width less than 1 mm.
<b>Maturing:</b> Seminiferous tubules almost filled with spermatids and spermatozoa.	<b>M2:</b> Firm filamentary testes, white in color.	<b>(402) Mature (will copulate this year):</b> Testes are translucent to whitish and increase in diameter. Sign of milt formation.
<b>Mature:</b> Seminiferous tubules completely filled with spermatozoa.	<b>M3:</b> Firm ribbonlike testes, creamy and milky white, full of milt. Spermatozoa released when pressure applied to abdomen or when the testes is cut.	<b>(403) Ready to copulate or half empty:</b> Testes are white, highly developed, irregular in shape. Milt in the vas deferens.
<b>Recovering:</b> Empty seminiferous tubules, spermatogonia present.	<b>M4:</b> Filamentary/ribbonlike testes, beige in color, which seems partially deflated.	<b>(404) Post copulation of the year:</b> Testes are sagging and whitish in color. Some milt may remain in the vas deferens.

males, “maturing” and “mature” intermediate histological stages were combined, both describing fish from the spawning stock. Macroscopic categories F2 and F3, F5 and F6, and M2 and M3 were also merged.

Following the grouping of categories, there was a significant association between histological stages and macroscopical appearances as determined for both female ( $\chi^2 = 334.25$ ,  $df = 9$ ,  $p$  value  $< 2.2 \times 10^{-16}$ ) and male ( $\chi^2 = 360.95$ ,  $df = 4$ ,  $p$  value  $< 2.2 \times 10^{-16}$ ) redfish collected in 2018–2019. For females, the histological stages “immature”, “developing/maturing”, “mature”, and “post-ovulatory/recovering/resting” were significantly positively associated with macroscopical appearances F1, F2/F3, F4, and F5/F6, respectively (Figure 7). For males, histological stages “immature”, “maturing/mature”, and “recovering” were significantly positively associated with macroscopical appearances M1, M2/M3, and M4, respectively (Figure 7). The association was only marginally significant in the case of “maturing/mature” and M2/M3.

When using the visual chart (Figures A3 and A4), the resulting  $L_{50}$  values were similar to the ones obtained by using histologic reproduction stages for females, but slightly higher for males (Figure A5), suggesting that this could be an appropriate monitoring tool, especially for females. Moreover, a significant decrease in  $L_{50}$  was observed between the 1996–1998 and 2018–2019 periods (Figure 8).

### 3.4 | Consequences of updated maturity ogives on SSB and perception of stock status

The observed reduction in size-at-maturity in recent years caused the SSB for both species to inflate (Figure 9) relative to the SSB derived

**TABLE 5** Mean ( $\pm$  standard deviation) and range [minimum, maximum] of length and mass by species and sex.

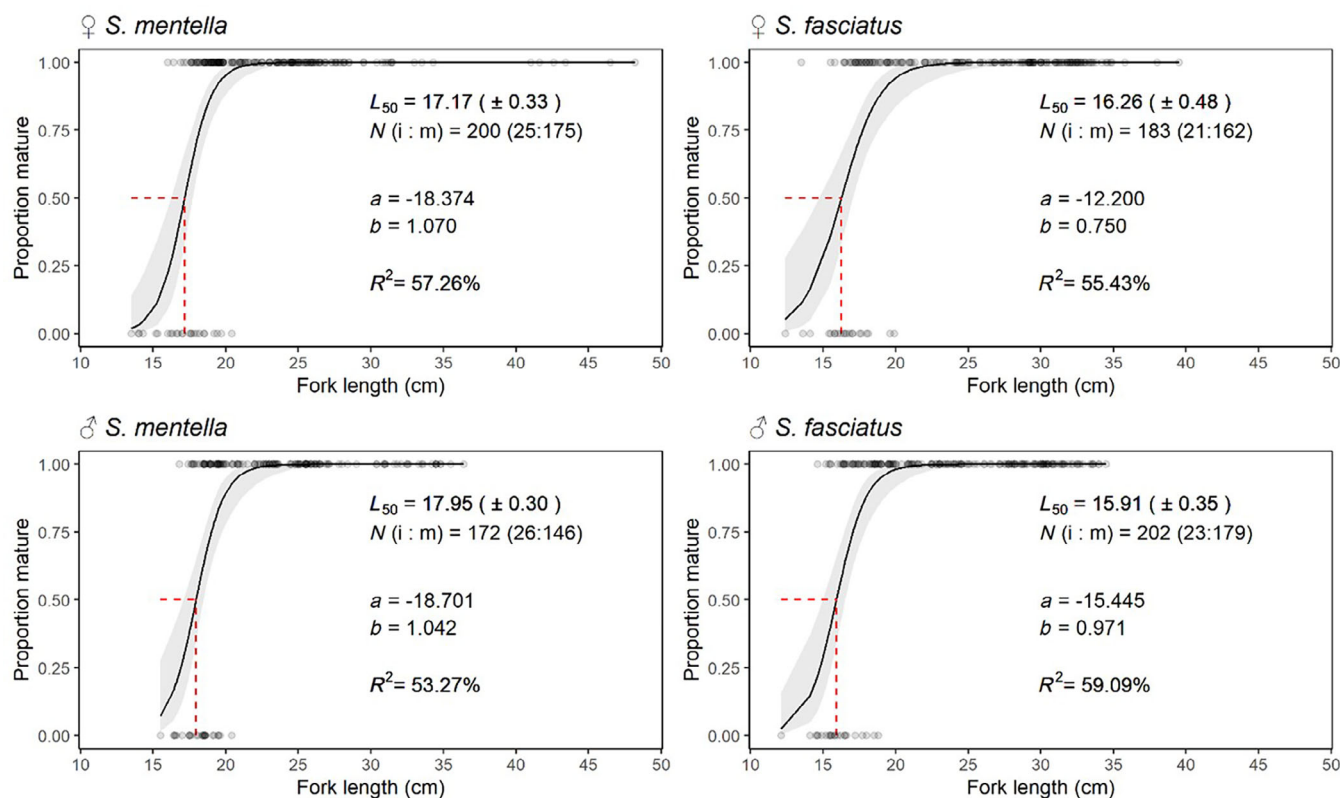
Species	Sex	Length (cm)	Mass (g)
<i>S. mentella</i>	♀	22.7 $\pm$ 5.6 [13.5, 48.2]	189 $\pm$ 212 [26, 1523]
<i>S. mentella</i>	♂	23.2 $\pm$ 5.1 [15.5, 36.4]	188 $\pm$ 145 [41, 657]
<i>S. fasciatus</i>	♀	24.7 $\pm$ 6.4 [12.4, 39.5]	249 $\pm$ 171 [24, 746]
<i>S. fasciatus</i>	♂	23.2 $\pm$ 5.8 [12.1, 34.5]	209 $\pm$ 147 [24, 629]

Abbreviations: *S. fasciatus*, *Sebastes fasciatus*; *S. mentella*, *Sebastes mentella*.

**TABLE 4** Comparison of models including different explanatory variables, length, and species and sex, as well as their potential interaction for predicting the proportion mature-at-length.

Model	Explanatory variable	Equation	AIC	$R^2$	$p$ value
Model 5	length + species * sex	$\text{logit } P(Y = 1) = \beta_0 + \beta_1 L + \beta_2 (\text{species} * \text{sex})$	<b>314,204</b>	56.18	
Model 2	length + species	$\text{logit } P(Y = 1) = \beta_0 + \beta_1 L + \beta_2 \text{species}$	316,084	55.14	0.053
Model 4	length + species + sex	$\text{logit } P(Y = 1) = \beta_0 + \beta_1 L + \beta_2 \text{species} + \beta_3 \text{sex}$	317,524	55.24	0.454
Model 6	length * species * sex	$\text{logit } P(Y = 1) = \beta_0 + \beta_1 (L * \text{species} * \text{sex})$	318,854	56.41	0.154
Model 1	length	$\text{logit } P(Y = 1) = \beta_0 + \beta_1 L$	328,807	52.52	0.001
Model 3	length + sex	$\text{logit } P(Y = 1) = \beta_0 + \beta_1 L + \beta_2 \text{sex}$	330,700	52.54	0.743

Note: Equation, AIC,  $R^2$ , and the likelihood ratio test  $p$  value are presented for each model. Lowest AIC is in bold.



**FIGURE 6** Maturity ogives based on histology as a function of fork length (cm) for each combination of species and sex.  $L_{50}$  (± standard error), sample size ( $N$ ) of immature (i) and mature (m) individuals,  $a$  and  $b$  parameters, as well as  $R^2$  are indicated in each panel. The red dotted lines correspond to  $L_{50}$  and the shaded areas to 95% confidence intervals.

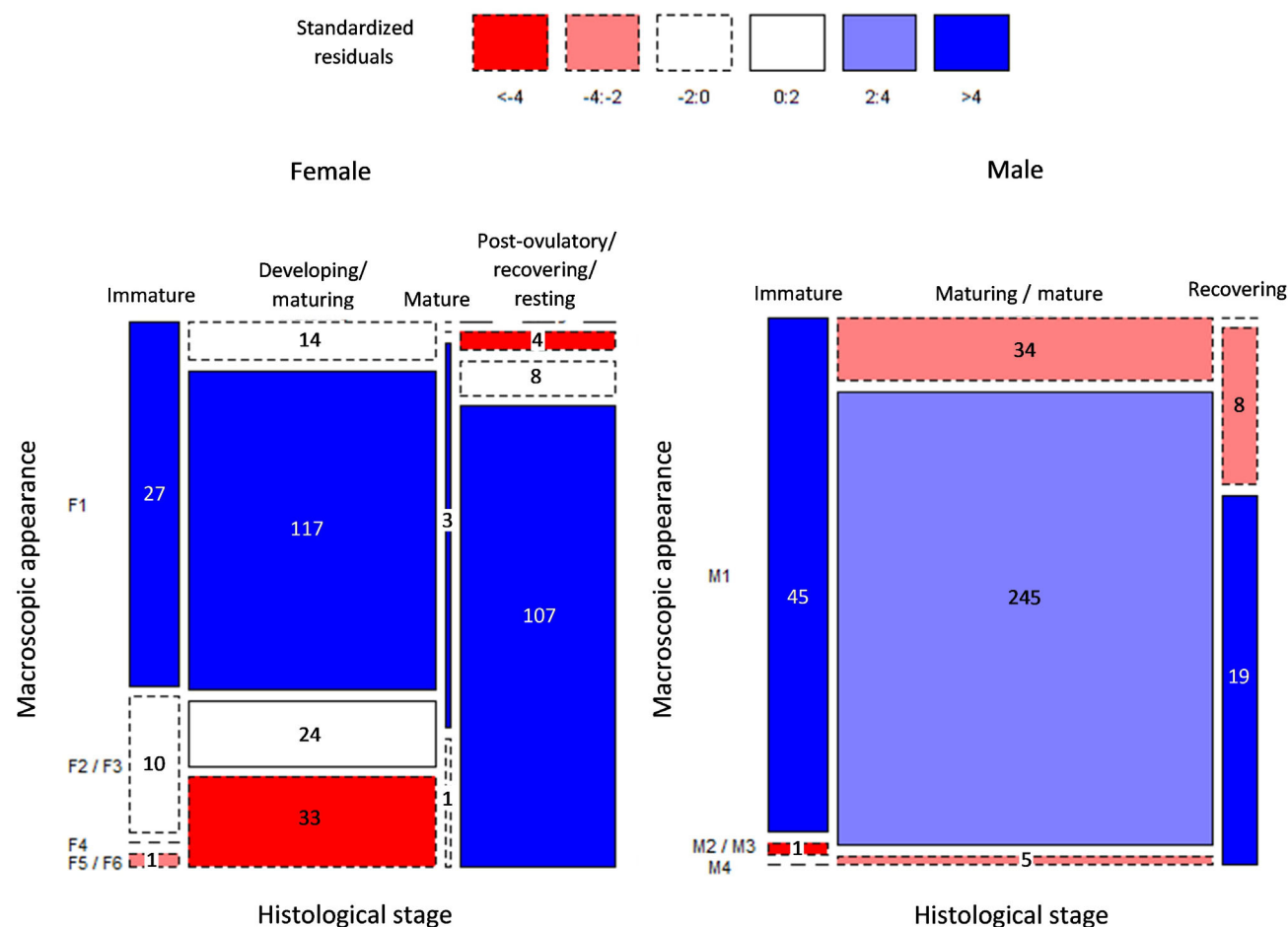
using the maturity ogives from the late 1990s (Gascon, 2003). In both cases, large confidence intervals are present because of the important variability in redfish biomass within the survey, which has a random stratified sampling design. The recent increase in SSB for *S. mentella* was more rapid when the trend was depicted based on the new maturity ogives. The stock was above the proposed Upper Stock Reference (USR; 265 kt) and considered in the healthy zone of the PA since 2017 based on Gascon (2003) maturity ogives and since 2016 based on the new ones. Updated maturity ogives also changed the perception of stock status for *S. fasciatus*, which reached the healthy zone (above the proposed USR of 168 kt) only in 2021 based on Gascon (2003) ogives, while it would have been considered in the healthy zone in 2017, 2018, and 2021 based on the new ones at SSB values similar to those observed prior to the moratorium on commercial fisheries. Given that no important recruitment event happened between 1980 and 2011, there were very low numbers of juvenile redfish during this period, therefore the selection of one set of ogives or the other had no significant impact until circa 2015, when the 2011–2013 cohorts started maturing. The choice of 2011 as a starting point for using the new ogives is a subjective decision. By using 2011, only a small proportion of redfish that briefly experienced warmer temperatures is maturing at smaller size. However, choosing a later year would imply that a small proportion of the 2011–2013 cohorts would mature all at once, creating a discontinuity in the SSB timeseries.

## 4 | DISCUSSION

The present study enabled a robust visual chart for continued and cost-effective monitoring of redfish reproduction stages to be refined and validated, and has shown an important decrease in redfish  $L_{50}$  that led to an increase in estimates of SSB during the 2011–2021 period for *S. mentella* and *S. fasciatus*. These changes modified the perception of stock status as evaluated based on the Canadian PA framework, thus having important implications for fisheries management. Given that fishery-induced evolution and community structure changes along with global warming are affecting numerous stocks worldwide, the present study outlines a major and global challenge for scientists and resources managers. As shown by our results, the monitoring and frequent updates of life-history traits in transforming environments are needed to provide reliable science advice for sustainable fisheries.

### 4.1 | Redfish reproduction and size-at-maturity

Redfish from all reproduction stages were observed in our sample, despite specimens having been collected solely in August and September, suggesting some level of reproductive asynchrony among individuals. This is surprising given that it was previously thought that copulation took place during the fall through early winter (September



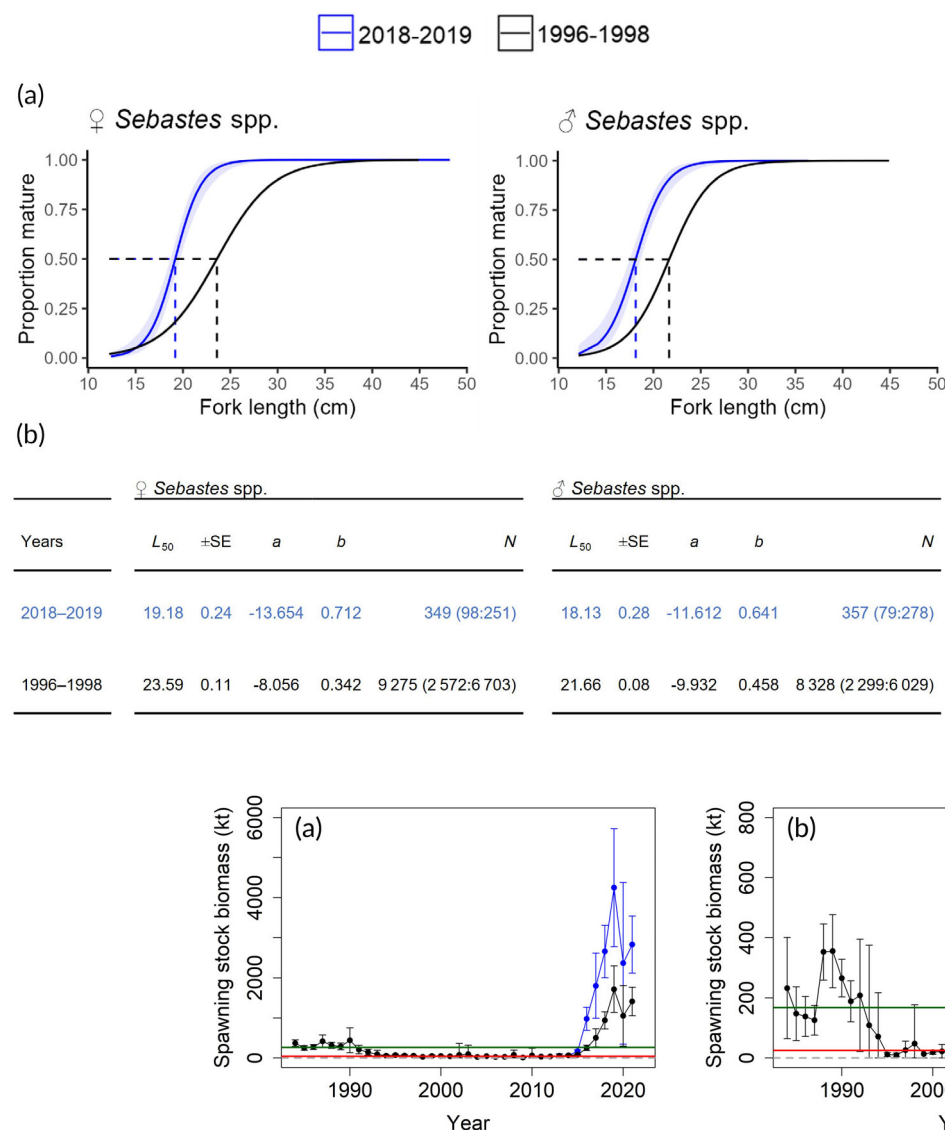
**FIGURE 7** Mosaic plot comparing reproduction stages based on histology and the macroscopic gonad appearances of female and male *Sebastes* spp. Cell height represents the contribution (%) of each reproduction stage based on histology to each macroscopic appearance. Cell width is proportional to each histological stage contribution to the total sample. The numbers indicated in the boxes correspond to the number of individuals. Pearson standardized residuals  $>2$  indicate a significant positive association (blue), between  $-2$  and  $2$  no association (white), and  $<-2$  significant negative association (red).

to December), that spermatozoa were maintained in a state of physiological dormancy inside females until their ovaries mature during winter (January to March), and that larval extrusion occurred in spring (April to June), with *S. mentella* releasing larvae approximately 3–4 weeks earlier than *S. fasciatus* (Ni & Templeman, 1985). Starting as early as November, redfish have been thought to migrate to the Cabot strait (NAFO Subdivisions 3Pn4Vn) and to return in the GSL in spring (Atkinson & Power, 1991; Morin et al., 1994; Power, 2003). Histological analyses of gonads collected during other seasons are required to improve knowledge of redfish reproduction timing in the GSL and Laurentian Channel, as done in other studies (Filina et al., 2017; Klubansky & Scharf, 2015).

In addition to maturity ogives, fecundity allometric relationships should be investigated to better quantify larvae production based on the actual spawning capacity (Beyer et al., 2021; Brown-Peterson et al., 2011; Ganas & Lowerre-Barbieri, 2017; Lefebvre et al., 2018; Lowerre-Barbieri et al., 2011). Smaller-sized mature individuals may produce a lower number of larvae compared to larger individuals, resulting in an overall reduction in the strength of recruitment events.

*Sebastes* species tend to have slow growth rates and high longevity. Individuals may therefore present unusual patterns of ovarian development, such as abortive maturation events during an extensive adolescent period (Lefebvre & Field, 2015). In this case, physiologically mature females may be functionally immature as they are not yet contributing to recruitment. Instead, mass atresia, which is the arresting of development and subsequent resorption of the leading cohort of vitellogenic oocytes, may be assessed (Ramsay & Witthames, 1996). Skipped spawning events may also modulate larvae production, as observed in other marine fishes (Jørgensen et al., 2006; Rideout et al., 2005; Rideout & Tomkiewicz, 2011; Skjæraasen et al., 2012; Skjæraasen et al., 2015). This phenomenon is often related to lower condition factors (Haraldstad et al., 2018; Jørgensen et al., 2006), probably as a way to increase individual lifetime fitness and lifetime fecundity/recruit production (Bull & Shine, 1979; Rideout et al., 2005). Ultimately, spawning ogives would be more appropriate than maturity ogives to inform stock status evaluation based on SSB, as they would consider functionally mature individuals rather than all physiologically mature ones (Lefebvre et al., 2018). In all cases, routine





**FIGURE 8** Comparison of maturity ogives based on macroscopic gonad appearance categories following the visual chart used in the 1990s (F1 + F2 as immature for females and M1 as immature for males) to contrast  $L_{50}$  between the 1996–1998 (black) and 2018–2019 (blue) periods. (a) Overlap among resulting ogives where shading represents 95% confidence intervals. (b)  $L_{50}$ , standard error (SE),  $a$  and  $b$  parameters, and number of individuals (immature:mature).

**FIGURE 9** Spawning stock biomass in the GSL DFO survey from 1984 to 2021 based on Gascon (2003) ogives (black) and with the new ogives starting in 2011 (blue) with 95% confidence intervals. The proposed upper stock reference (green line) and limit reference point (red line) for deepwater redfish *Sebastes mentella* (a) and Acadian redfish *Sebastes fasciatus* (b) are shown. The 0 y-axis value is indicated by a gray dashed line. Note the different scales on the y axis. kt, kilotonne.

monitoring of the reproductive traits of commercial redfish species is essential to reliably inform stock assessment and the formulation of science advice for fisheries management in a changing environment. This can be done most effectively and reliably by applying a visual chart for reproduction stage determination based on macroscopic gonad examination that has been corroborated and validated against histological information. Visual charts based on standardized terminology have been shown to make comparisons easier between species and even populations (Brown-Peterson et al., 2011; Flores et al., 2019; Ganas & Lowerre-Barbieri, 2017; Lowerre-Barbieri et al., 2011). The revised visual chart for redfish species proposed herein can be used to investigate changes in size at maturation across seasons or locations, and to better understand the redfish reproductive cycle in time and space.

## 4.2 | Potential causes of $L_{50}$ decrease in recent years

An important decrease in male and female redfish  $L_{50}$  in Units 1 and 2 was observed. This occurred following the emergence of strong cohorts more than 25 years after the collapse of the redfish fishery, which led to the 1995 moratorium in Unit 1 allowing only a summer index fishery of 2000 t and imposing an important reduction of quotas in Unit 2, from 28,000 t in 1993 to 8500 t since 2006. Fisheries targeting larger fish and systematically removing particular genes from a population have been shown to modify life-history traits by increasing reproductive investments and inducing a shift towards earlier maturation at smaller sizes and reducing post-maturation growth (Beaudry-Sylvestre et al., 2022; Chuwen et al., 2011). There is no such evidence

for the redfish fishery given that it is mostly conducted by bottom trawlers with nets that provide a low level of selectivity (Cheng et al., 2020). Before the moratorium, landings were mainly composed of 25–35 cm individuals, following stock size composition (Senay et al., 2023), while discards at sea of fish smaller than the minimum regulatory size of 22 cm were common. Duplisea (2018) indicated that the proportion of small fish landed may have been underestimated by a factor of 150–200 in the 1980s and 1990s.

Density-dependent mechanisms have also been evidenced to affect maturation in natural populations, even if the direction of the effect may vary among species. A common response of marine populations to increasing density is a reduction in individual growth rate, given the lower resources availability per capita. This can result in an increase in age-at-maturity, while diverging impacts on size-at-maturity have been reported (Sánchez Lizaso et al., 2000). In some fish populations, size-at-maturity is insensitive to variation in density, while the corresponding age-at-maturity can change substantially as a result of density dependence in growth (Beverton, 2002; Rochet, 1998). In other cases, growth lowered by food restriction leads to late maturation at smaller size (Atkinson & Sibly, 1997; Berri-gan & Charnov, 1994). Unfortunately, growth was not quantified in the present study given the challenges in aging long-lived species. Campana et al. (2016) have developed a promising method for aging redfish by image-enhanced burnt otoliths that could be used to better understand how growth may contribute to the substantial decrease of  $L_{50}$  (Catalán et al., 2018; Morales-Nin & Geffen, 2015; Newman et al., 2017) and clarify the mechanisms affecting maturation.

Temperature warming may be an important driver of the observed reduction in redfish  $L_{50}$ . Specimens from the strong cohorts of 2011–2013 emerged during a period of warming bottom water temperature increasing from 5.3°C in the 1990s to 5.7°C in 2011–2013, and reaching up to 7°C in recent years at 300 m (Galbraith et al., 2022). Temperature can affect individual metabolic rate and multiple life-history traits in fish, including growth, developmental time, and maturation (Angilletta, 2009). Fish tend to mature at smaller sizes in warmer waters (Atkinson, 1994; Atkinson & Sibly, 1997), yet the specific mechanisms by which temperature influences size at maturation remain uncertain (Shapiro Goldberg et al., 2019). There is evidence suggesting that temperature can affect maturation directly (Kuparinen et al., 2011) and/or indirectly through temperature-induced changes in individual growth rate (Berner & Blanckenhorn, 2007; Sibly & Atkinson, 1994). In redfish, earlier maturation with temperature warming is supported by observed latitudinal variations, with southern populations having generally lower  $L_{50}$  (e.g., 21.66 cm for females in the Gulf of Maine) than northern populations (e.g., 34.71 cm for females in 3 L), with some variability possibly associated with differences in redfish species distinction and sampling periods (Table 1, Mayo et al., 1990; Ni & Sandeman, 1984). Similar to our results and since 2014, a decrease in  $L_{50}$  was observed in the warming waters of the GSL for Greenland halibut *Reinhardtius hippoglossoides* (Gill 1861, Gauthier et al., 2021; Yan et al., 2023). Disentangling the relative contributions of a changing environment, long-term fishing effects, and density-dependent mechanisms on redfish maturation will require experimental data and knowledge of the species local

temperature preferendum, of the metabolic consequences of moving away from that preferendum, and of local trophodynamic processes affecting individual growth. While the exact causes of  $L_{50}$  decrease cannot be explicitly identified at this time, the available evidence suggests that temperature may play an important role. Earlier maturation often comes with the price of leaving less energy for growth and reaching smaller maximum size across a wide range of species (Thorson, 2020). Hordyk et al. (2015) suggested that in general  $L_{50}$  are around two-thirds of maximum size. Such a trade-off between maturation and maximum size may impact redfish productivity and longer-term fishery perspectives.

#### 4.3 | Implication of SSB increase for science and management

The decrease in  $L_{50}$  led to an increase in estimates of SSB during the 2011–2021 period for *S. mentella* and *S. fasciatus*, which changed stock status relative to reference points. Both species would have been considered in the healthy zone of their respective PAs earlier based on the updated ogives. This could have important implications in terms of both science and management. For instance, Units 1 and 2 redfish management strategy evaluation (DFO, 2018b; Licandeo et al., 2020; McAllister et al., 2021) had a list of special circumstances under which an update of operating model(s) would be required. One of them was an important change in life-history traits, for instance size-at-maturity, growth, or recruitment, and the resulting SSB. The present findings add to a growing body of evidence stressing that models should be revised to reflect changes in productivity based on the most recent life-history information (Audzijonyte et al., 2016; Beaudry-Sylvestre et al., 2022; King & McFarlane, 2003). The development of a redfish aging monitoring program would be useful to better understand the mechanisms underlying changes in life-history traits. Cadigan and Campana (2017) concluded that complementary age-based models should be prioritized to address the drivers of the life-history traits of redfish in more detail. In terms of management implications, having both species in the healthy zone could lead to a quicker removal of the moratorium, higher quotas, or different management measures to ensure sustainable exploitation rates based on current stock status and dynamics. Based on the Canadian PA, exploitation rates should be maximal when stocks are in the healthy zone, above their USR. In the cautious zone, between the USR and the limit reference point (LRP), exploitation rates should vary with stock status and diminish towards the critical zone, below the LRP, where exploitation rates should be reduced as much as possible and a rebuilding plan should be developed to promote recovery (DFO, 2009).

The GSL and Laurentian Channel redfish stocks illustrate how rapid changes in environmental conditions and marine community structure can affect productivity assumptions in stock assessment models, and lead to potential bias in science advice for sustainable fisheries. Our results highlight the importance of continuous monitoring and confronting model assumptions with up-to-date empirical observations to ensure robust assessment results and advice in a changing environment.

## AUTHOR CONTRIBUTIONS

C.B. contributed with ideas, data analyses, and manuscript preparation. K.B. contributed with histological analyses and manuscript preparation. M.-J.R. contributed with ideas, data analyses, and manuscript preparation. G.J.P. contributed with ideas, genetic analyses, and manuscript preparation. C.C. contributed with genetic analyses and manuscript preparation. C.S. contributed with project conception, ideas, data generation, data analyses, and manuscript preparation.

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## DATA AVAILABILITY STATEMENT

Data and R codes for the qPCR assay validation will be available from Github upon acceptance of the manuscript.

## ORCID

Caroline Brûlé  <https://orcid.org/0009-0006-3828-1882>

Caroline Senay  <https://orcid.org/0009-0005-4365-4164>

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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