

Evidence for reproductive senescence in a broadly distributed harvested marine fish

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Supplement 1. Accounting for the sampling design in the analyses

Data for individual herring were obtained using a length-stratified sampling scheme for stocks south of the Laurentian channel and from random sampling for the remaining stocks (see Methods in the main text). To evaluate whether the main analyses required modification to account for the sampling scheme, we compared stratified and unstratified estimates of the proportion of herring that were immature as a function of years following maturity onset and standardized length (in 10 mm blocks) for the five stocks in question. There was a strong correspondence between the two types of estimates across all five stocks (Fig. S1), suggesting that no bias is expected for analyses that do not account for the stratification.

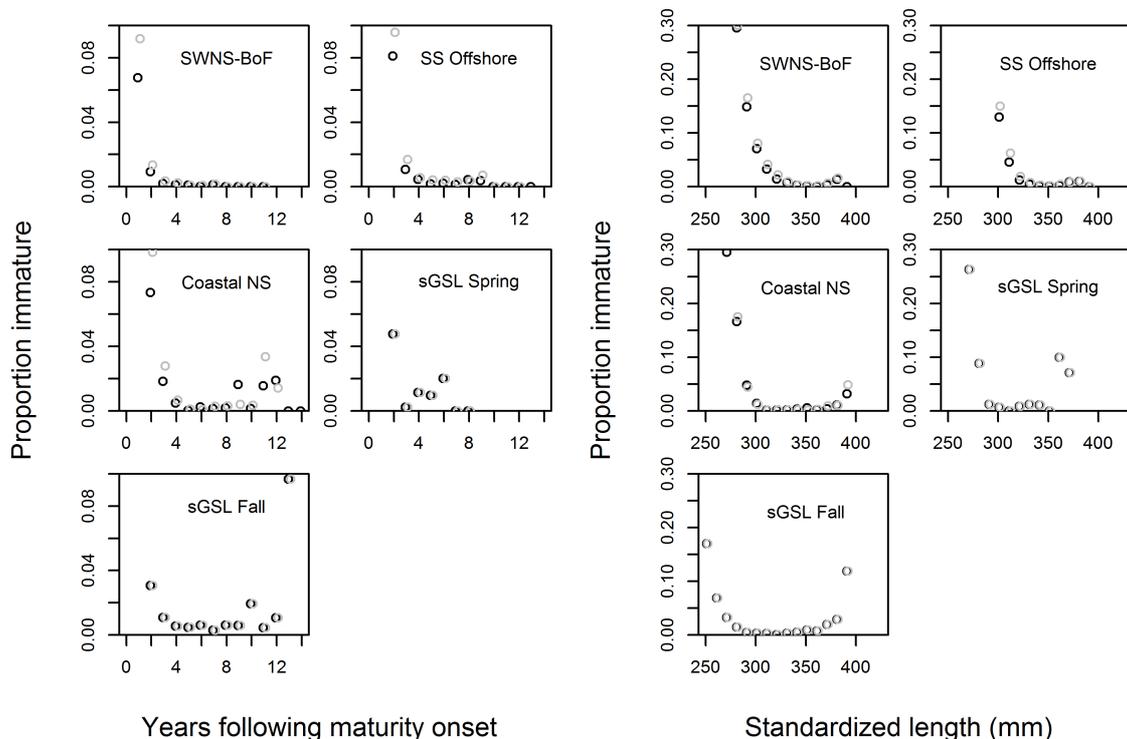


Fig. S1. The proportion of herring that were immature as function of standardized age (left panels) and standardized length (right panels) based on unstratified (grey circles) and stratified (black circles) estimates for the five stocks south of the Laurentian channel.

Supplement 2.

Sensitivity of the analysis to the choice of minimum standardized age and length values

The analysis of the increasing incidence of macroscopically immature herring with standardized age and length in older and larger fish using the Firth logistic regression models required selecting data that represented only the ascending portion of the relationship. This was accomplished by setting minimum values of standardized age and length for the analysis such as to exclude the initial decrease in incidence of immature fish with age and length that typifies the normal maturation process. A range of minimum values appeared appropriate based on patterns in the data and the exact choice was somewhat arbitrary. The analysis was therefore repeated for a range of values for standardized age (5-8 years) and standardized length (between 320 and 380 mm in 15 mm increments) that excluded the initial decrease in incidence in all stocks to evaluate the sensitivity of the analysis to the choice of minimum values.

Models with additive standardized age and stock effects were judged to be most suitable for the analyses for all minimum standardized age values given non-significant interaction terms in all cases (Table S1; Fig. S2). Predictions for the proportion of immature herring as a function of standardized age from the suitable models were largely insensitive to the choice of minimum value for the SWNS-BoF, SS Offshore, Coastal NS and sGSL Fall stocks (Fig. S2). In contrast, predictions varied considerably for the sGSL Spring stock, particularly for minimum ages of seven and eight years compared to five and six years. This result appeared to be driven in large part by a lack of data at older standardized ages for this stock. Based on these results and to include the most data possible, a minimum standardized age of 5 yrs was chosen for the analysis presented in the main text.

For minimum standardized length values of 320 and 335 mm, the interaction between length and stock was statistically significant and models with this interaction term were judged to be suitable for the data (Table S1; Fig. S3). For the minimum values of 350 to 380 mm, the interaction was not statistically significant and models with only the additive effects of length and stock were considered more suitable. Predictions for the proportion of immature herring as a function of standardized length from the suitable models included the initial declining phase of relative incidence with increasing length for the SWNS-BoF, SS Offshore and 4R Fall stocks when minimum standardized length was 320 mm (Fig. S3). Predictions were largely consistent for all stocks at minimum values of 350 and 365 mm, but diverged for the sGSL Spring stock at a minimum value of 380 mm because the vast majority of the data for that stock were not retained. Based on these results, a minimum standardized length values of 350 mm was chosen for the analysis presented in the main text.

Table S1. Summary of results for the Firth logistic regressions for different minimum values of standardized age or standardized length included in the analyses. Shown are the Chi-square statistic values and associated p-values from the likelihood ratio tests for the factor 'stock' in a model with a single slope coefficient and for the interaction between stock and either standardized length or age.

Minimum	Effect: stock		interaction	
	χ^2	P-value	χ^2	P-value
sAge (df=4)				
5 yrs	38.29	9.75e-08	3.42	0.4891
6 yrs	27.65	1.47e-05	2.07	0.7222
7 yrs	12.23	0.0157	2.22	0.6942
8 yrs	14.92	0.0049	2.18	0.7036
sLength (df=14)				
320 mm	490.5	<1.0e-16	371.94	<1.0e-16
	3			
335 mm	183.1	<1.0e-16	32.63	3.26e-03
	6			
350 mm	124.6	<1.0e-16	15.51	0.3440
	4			
365 mm	86.15	2.02e-12	12.85	0.5382
380 mm	49.45	7.54e-06	7.59	0.9095

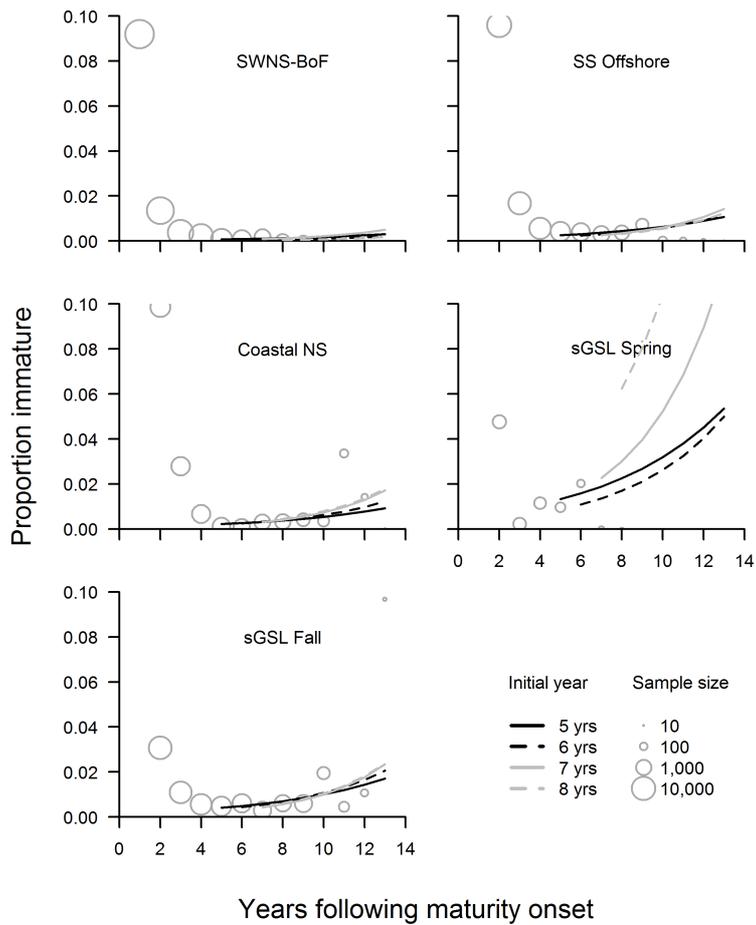


Fig. S2. The observed proportion of macroscopically immature herring as a function of standardized age (years following maturity onset in the cohorts; circles) for each of the five stocks from south of the Laurentian Channel (panels). The predictions are based on the most suitable for model for each of the four minimum standardized age values. Standardized ages were rounded to the nearest 10 mm prior to calculating the observed proportions. Circle diameter reflects the number of fish used to calculate the proportions.

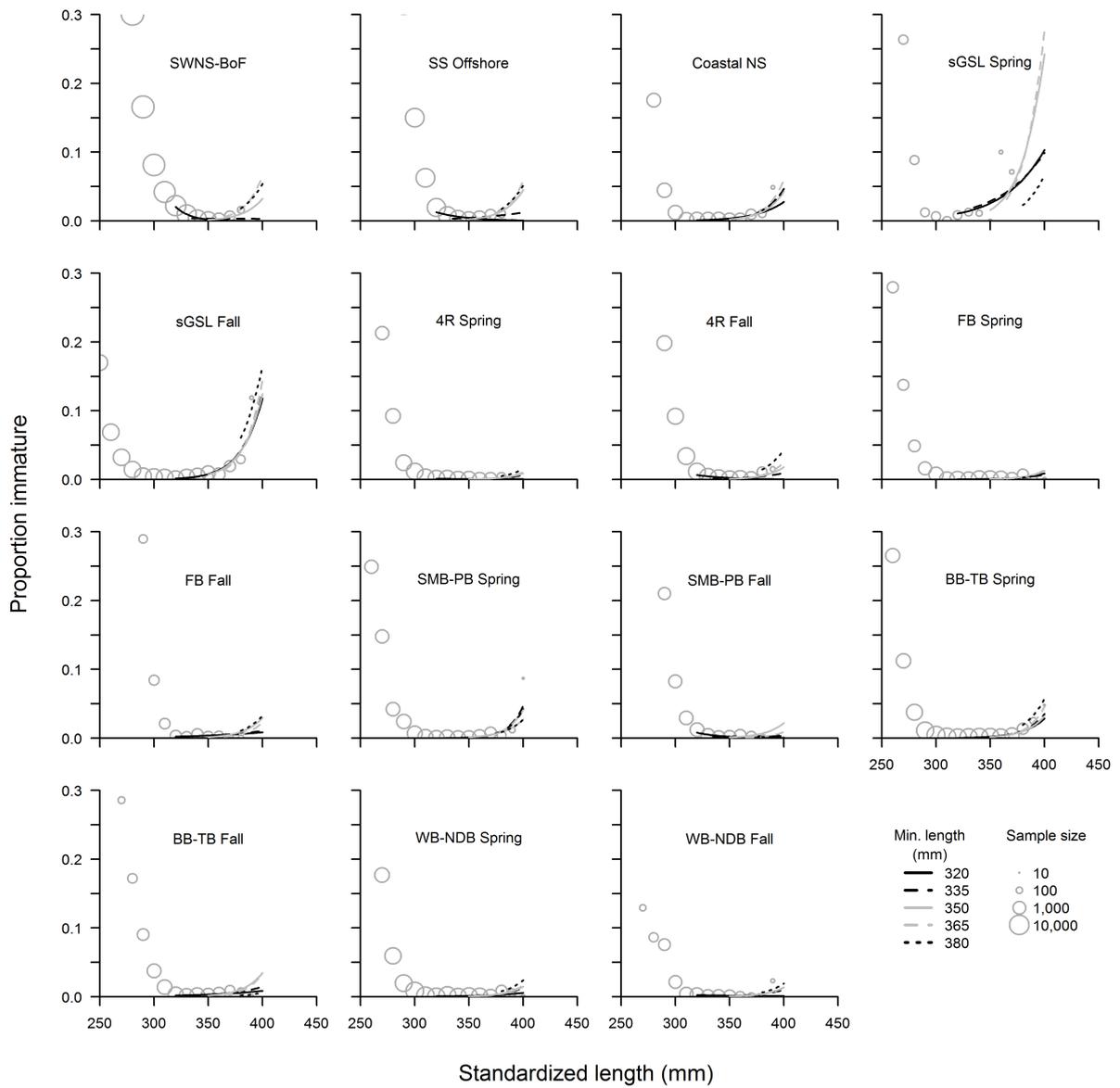


Fig. S3. The observed (circles) and predicted (lines) proportion of macroscopically immature herring as a function of standardized length for each stock (panels). The predictions are based on the most suitable model for each of the five minimum standardized length values. Standardized lengths were rounded to the nearest 10 mm prior to calculating the observed proportions. Circle diameter reflects the number of fish used to calculate the proportions.

Supplement 3. Estimation of reproductive value

Lifetime reproductive value (*LRV*; eq 7 in the main text) was calculated for typical and theoretical unusually late maturing herring to evaluate the plausibility that increases in the proportion of immature fish with age reflects a late maturing strategy associated with higher survival for a subset of herring, rather than reproductive senescence.

For typical herring, inputs for that calculation include the mean weight at age and the maturity ogive for typical herring from cohorts born in 1990-1994 in the southern Gulf of St. Lawrence fall spawning stock. Mean weight at age was estimated by fitting a von Bertalanffy model to the data for individual herring using nonlinear least squares:

$$W_a = W_\infty(1 - \exp(-k \cdot (a - t_0)))$$

where W_a is the weight at age a , W_∞ is the asymptotic weight, k is the rate parameter, and t_0 is the theoretical weight at age zero (Fig. S4b). The maturity ogive was estimated using logistic regression of the individual data for ages zero to 9 (Fig. S4c). The inputs were truncated to age 9 to exclude the older ages at which increasing proportions of immature fish were observed (see main text).

Older immature herring were found to be on average 2.3 percent larger than same age mature herring (see Results in main text). Under the hypothesis of unusual maturation delay, this difference would reflect a growth premium for delaying maturation or perhaps size-dependency in the enhanced survival of late maturing fish. The lengths and subsequently the weights for late maturing fish were therefore adjusted for this difference, which in turn affected the calculation of fecundity at age using eq 8 in the main text (Table S2).

The relative survival premium for an unusually late maturing fish was estimated using the regression in eq 6 (main text). The model fit the data very well, resulting in an estimated survival premium of 0.618 (0.003 SE) (Fig. S5). This survival premium was assumed to apply to all ages up to the assumed age of maturation (Table S2).

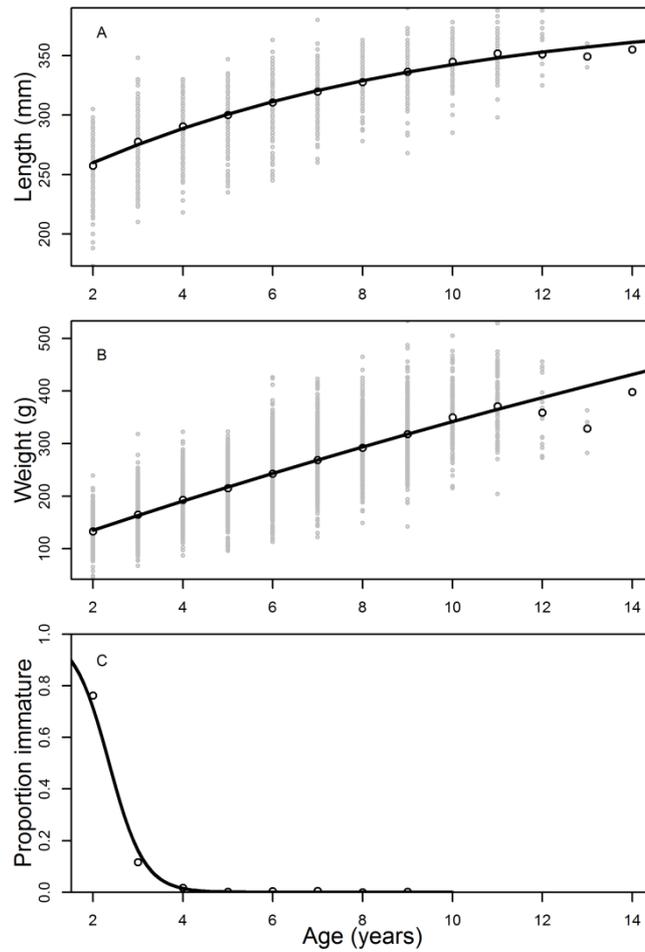


Fig. S4. Individual (grey circles), average (white circles) and modelled (line) length (A), weight (B) and proportion immature (C) as a function of age for herring from cohorts born in 1990-1994 in the southern Gulf of St. Lawrence fall spawning stock. The model used for length and weight at age is a von Bertalanffy model fit to individual observations, while the model for the proportion immature is a logistic regression fit to individual observations.

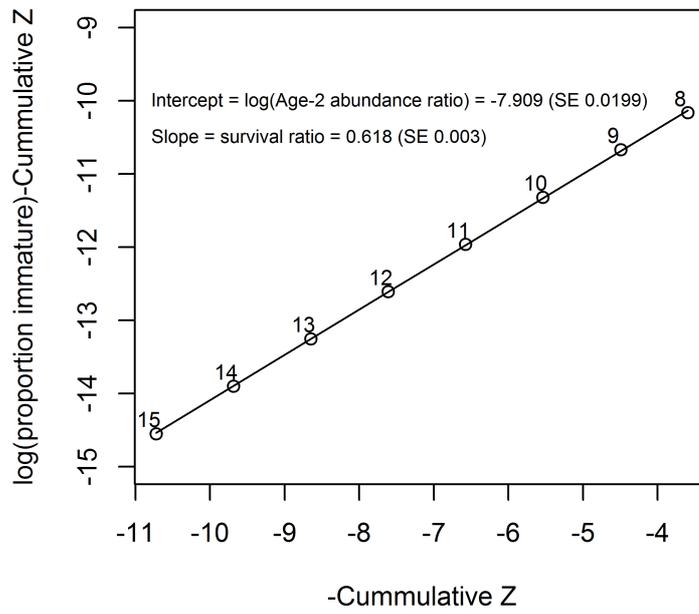


Fig. S5. Regression used to derive an estimate of the survival premium (or ratio) for theoretical unusually late maturing herring (eq 6 in main text). The circles are the age-specific input observations, labelled with the age, and the line is the fit of the linear regression.

Table S2. Age-specific average annual reproductive value (RV_a ; thousands of eggs) for typical and unusually late maturing herring. The expected lifetime reproductive value (LRV), is the sum of RV_a values across ages. The age-dependent inputs used in calculating RV are the weight (g), fecundity (thousands of eggs), probability of being mature and the total mortality. The sources for the inputs are indicated in the text.

Age	Typical herring					Late maturing herring				
	W_a	Fec_a	Mat_a	Z_a	RV_a	W_a	Fec_a	Mat_a	Z_a	RV_a
2	128.1	46.3	0.26	0.20	9.844	141.6	-	0.00	0.12	0.000
3	159.7	61.1	0.83	0.21	33.636	176.5	-	0.00	0.13	0.000
4	189.7	75.9	0.98	0.30	36.709	209.7	-	0.00	0.18	0.000
5	218.1	90.5	1.00	0.57	25.331	241.1	-	0.00	0.35	0.000
6	245.1	104.8	1.00	0.75	13.808	270.9	-	0.00	0.47	0.000
7	270.7	118.8	1.00	0.78	7.167	299.2	-	0.00	0.48	0.000
8	295.0	132.4	1.00	0.86	3.372	326.1	-	0.00	0.53	0.000
9	318.0	145.5	1.00	1.01	1.348	351.5	-	0.00	0.63	0.000
10	339.8	158.2	1.00	1.09	0.495	375.6	-	0.00	0.67	0.000
11	360.5	170.4	1.00	1.10	0.178	398.5	-	0.00	0.68	0.000
12	380.2	182.2	1.00	1.10	0.064	420.3	-	0.00	0.68	0.000
13	398.8	193.5	1.00	1.10	0.023	440.8	-	0.00	0.68	0.000
14	416.5	204.4	1.00	1.10	0.008	460.4	-	0.00	0.68	0.000
15	433.2	214.8	1.00	1.10	0.003	478.8	243.7	1.0	1.10	0.153
16	449.2	224.8	1.00	1.10	0.001	496.5	255.1	1.0	1.10	0.054
17	464.2	234.3	1.00	1.10	0.001	513.1	265.9	1.0	1.10	0.019
18	478.5	243.5	1.00	1.10	0.000	528.9	276.2	1.0	1.10	0.006
19	492.1	252.2	1.00	1.10	0.000	543.9	286.1	1.0	1.10	0.002
20	505.0	260.6	1.00	1.10	0.000	558.2	295.6	1.0	1.10	0.001
					LRV 131.988					LRV 0.235

Supplement 4. Supplementary figures referenced in the main text

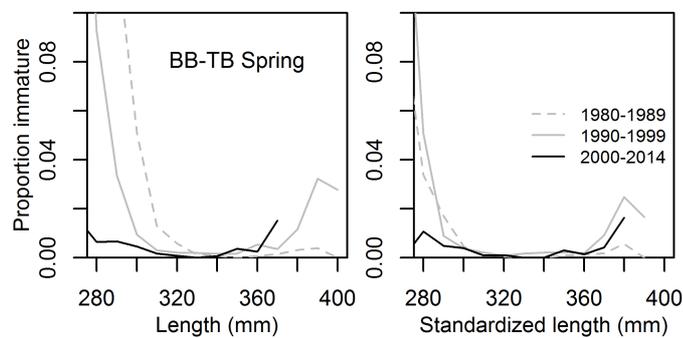


Fig. S6. Example of the effect of length standardization on the relationship between the proportion of immature herring and total length in the Bonavista Bay and Trinity Bay spring spawning stock. The observed proportion of immature herring, summarized in 10 mm bins, is plotted as a function of total length (left panel) and standardized length (right panel) for three time blocks (lines).

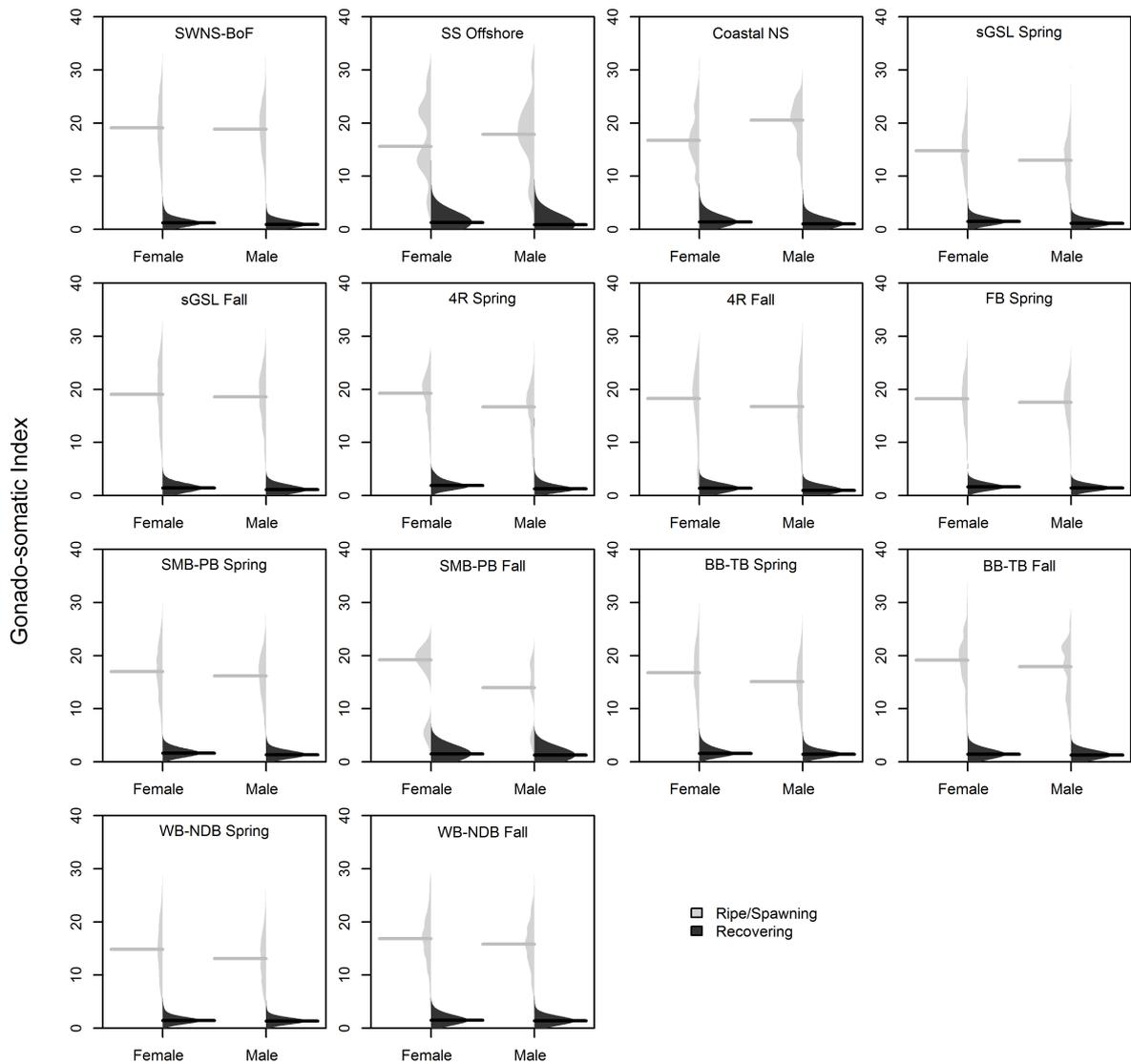


Fig. S7. Density traces of gonadosomatic index values for ripe/spawning (maturity code 6) and recovering (maturity code 8) herring, by sex and by stock (panels). The horizontal lines indicate the median values for each group. Results for the FB-Fall stock are not presented due to low sample sizes.