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Environmental effects on recruitment dynamics and population projections of NAFO Division 4TVn Spring Spawning Atlantic Herring

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Foreword

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

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ABSTRACT

This document represents an application of the Ecosystem Approach to Fisheries Management by linking Herring recruitment dynamics and environmental drivers to better understand the mechanisms and the implications for assessment and management. In a time series of population estimates analysis, Herring spawning stock biomass was mostly driven by recruitment and high spawning stock biomass did not lead to high recruitment values. A regime shift analysis showed that both the sea surface temperature of all regions of the Southern Gulf of St. Lawrence (sGSL) and the spring spawning Herring recruitment abruptly shifted from a cold water/high recruitment regime (1978-1991) to a warmer water/low recruitment regime (1992-2017) in the early 1990s. Stock recruit relationships were successfully fitted to each of the regime periods and the expected recruitment for a given SSB is lower in the recent regime than in the 1978-1991 regime. A model estimating spring spawning Herring recruitment based on zooplankton variables was able to predict recruitment values with a sufficient level of performance that it could be used in the stock assessment process. The effect of using different assumptions about Herring recruitment in populations projections was tested using a simulation study. In this case, showing the two best models output (5 recent years and zooplankton model) would be the most informative to the 4TVn spring spawning Herring assessment.

INTRODUCTION

An ecosystem approach to fisheries management (EAFM) requires that management decisions take into account changes in the ecosystem which may affect the species being fished. This includes the effects of climate, habitat, and the interactions of target fish stocks with predators, competitors, and prey species (DFO 2009). In stock assessments, reference points and stock status are often calculated by assuming stationary population processes (growth, recruitment, natural mortality). Under climate change and associated ecosystem effects, this assumption may be violated. Variability in fish stock size often results from variation in recruitment (Fogarty et al. 1991), and recruitment failures can have dramatic impacts on fisheries (e.g. Ljunggren et al. 2010; Whitmore et al. 2013). Understanding the effects of environmental variation on recruitment and integrating them in stock assessment and management is then an important step towards an EAFM.

Northwest Atlantic Fisheries Organization (NAFO) Division 4TVn spring spawning Atlantic Herring (*Clupea harengus*) has been in the critical zone of the Precautionary Approach since 2002, and requires a rebuilding plan under Canada’s modernized *Fisheries Act*. High natural mortality, declining weight-at-age, fishing mortality and low recruitment are factors impeding the recovery of the stock. A previous study of environmental drivers of 4TVn spring Herring recruitment found that high recruitment was associated with cold surface water, long periods with sea ice and high abundance of cold-water Arctic copepods, whereas downward shifts in recruitment were concordant with changes in the zooplankton community toward species more adapted to warmer waters (more small copepods and less cold-water Arctic copepods; Brosset et al. 2018). However, the analysis was performed using axes from a Principal Component Analysis (PCA) on an ecosystem matrix as variables in Generalized Additive Models (GAM), making the direct links between specific variables and recruitment difficult to operationalize in a stock assessment context. Another reason to revisit the relationship is that Brosset et al. 2018 used the Herring Virtual Population Analysis (VPA) model output for recruitment values, while the 4TVn Herring stock assessment now uses a statistical catch at age (SCA) model estimating time-varying natural mortality, thus generating different recruitment estimates.

This document represents an application of the EAFM by linking Herring recruitment dynamics and environmental drivers to better understand the mechanisms and the implications for assessment and management, in order to operationalize the relationships into the stock assessment process. The main objectives are to 1) describe the stock-recruit data and relationships, 2) assess if regime shifts occurred in Herring recruitment and in the Gulf of St. Lawrence (GSL), 3) develop a predictive model of the number of Herring recruits from the effects of environmental drivers, and 4) compare the effect of various assumptions on Herring recruitment on simulated stock size in population projections.

METHODS

TIME-SERIES OF POPULATION ESTIMATES

Spawning stock biomass (SSB; ages 4+) and recruitment (number of age 2 fish) data for years 1978 to 2019 were obtained from the population model used in the 2020 assessment (Turcotte et al. 2021). The number of age 2 fish was lagged two years (to the cohort year) to assign recruitment to the SSB that produced it. Cross correlation of the two univariate series (recruitment and SSB) was used to identify which variable is leading the other in recruitment dynamics (Szuwalski et al. 2019).

REGIME SHIFT

A commonly used method to detect shifts in marine systems is the Sequential t-test Analysis of Regime Shifts (STARS, Rodionov 2004, 2005; Stirnimann et al. 2019). Briefly, a Regime Shift Index (RSI) is calculated to accept or reject the hypothesis of a regime shift at each observation, determining whether the following values are significantly different from the mean of the previous regime (Stirnimann et al. 2019). To assess if a regime shift in Herring recruitment occurred along a shift in global environmental conditions in the GSL, the regime shift analysis was performed on two time series: (1) on the herring recruitment time series, and (2) on the GSL sea surface temperature (SST) time series.

To assess if and when a regime shift occurred in the Herring recruitment time series, the STARS method was used with a cut-off length of 12 years and a significance level of p = 0.05. The cut-off length is the moving window in which the STARS algorithm calculates the probability of a regime shift and determines the minimum length of the regimes for which its magnitude remains intact (Stirnimann et al. 2019). This cut-off length was used because regimes of a dozen years were identified in a nearby area (the Gulf of Maine; Perretti et al. 2017). Cut-off lengths between 10 and 15 years were tested and provided similar results.

To asses if and when a regime shift occurred in the GSL SST time series, the GSLEA R package (Duplisea et al. 2020) was used to obtain SST data between 1982 and 2021 (data from Galbraith et al. 2021) for each ecosystem approach region (Figure 1). The STARS algorithm was used to identify regime shifts in the GSL SST data using a cut-off length of 12 years.

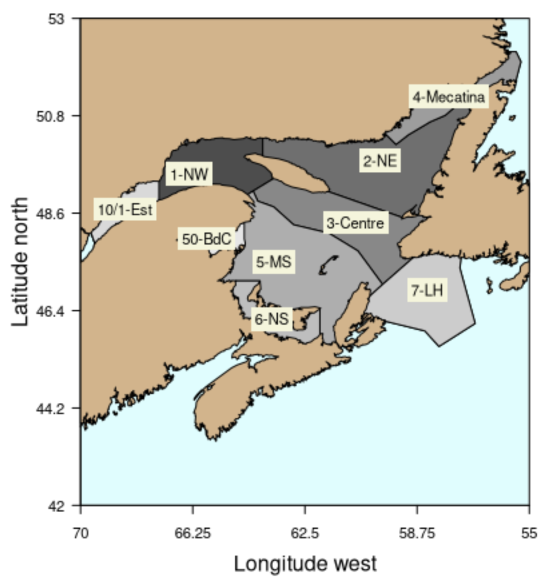

Figure 1: Map of ecosystem approach regions in the Gulf of Saint Lawrence, regions used here include 1 to 6 and 50. NW = Northwest, NE = Northeast, MS = Magdalean Shallows, NS = Northumberland Strait, BdC = Baie des Chaleurs.

STOCK RECRUIT RELATIONSHIPS

Ricker Stock-Recruit Relationship (SRR) models were fit to the data, as a Ricker model offers a better fit than Beverton-Holt or Hockey stick models (results not shown). The Ricker model was of the form:

$$R = \alpha S e^{-\beta S}$$

where R is the number of recruits (age 2 fish) two years after the cohort year (the year they were produced), S is SSB in the cohort year, α is an index of stock-independent mortality and β is an index of stock-dependent mortality (Ricker 1954, 1975). Parameters were estimated using the nls function in the R software (R Core Team 2021). Ricker SRR models were fit to the 1978-2017 data, with models fit independently in different Herring recruitment regimes.

ENVIRONMENTAL EFFECTS ON RECRUITMENT

The GSLEA R package (Duplisea et al. 2020) was used to obtain a matrix of environmental variables for the ecosystem approach region 5 (Magdalean Shallows, Figure 1). A time-series of zooplankton abundance data was available for years 2001 to 2019. Southern Gulf of St. Lawrence (sGSL) data are only available for region 5, as it is where the Shediac Valley sampling station is located.

Based on the findings of Brosset et al. 2018, a hypothesis of 3 main drivers of spring recruitment was established where the drivers would be: 1) the abundance of the main zooplankton prey item for Herring larvae, 2) a phenology variable, i.e. an indicator of the timing of the abundance of prey for Herring larvae, and 3) an indicator of oceanographic conditions (warm or cold years). Data from 43 variables were used to build a correlation matrix along with spring spawning Herring recruitment. The list of variable names and description is provided in Appendix 1. A correlation matrix (including Herring recruitment values) was used to identify variables that had high correlation coefficients with Herring recruitment. Cross-correlation factor analyses were used to assess if the correlation was maximal in the recruitment year.

A negative binomial general linear model (GLM) of Herring recruitment by environmental covariates was built using the MASS library in R. As the model using a Poisson distribution was over-dispersed, a negative-binomial GLM with a log link function was used and dispersion was close to 1. Model assumptions were verified by plotting the residuals against the fitted values and calculating variance inflation factors. Independence was assessed by plotting the Pearson's residuals against the covariates. Models with all combinations of covariates were fit and compared using Akaike information criterion (AIC) and explained deviance.

POPULATION PROJECTIONS

The numbers of age 2 spring spawning Herring in 2018 and 2019 were predicted from the zooplankton GLM using the 2018 and 2019 values of the covariates identified in the correlation matrix (abundance of large calanoid copepods early in the summer, the ratio of *Calanus hyperboreus* copepodites IV/I-IV early in the summer and the abundance of warm water zooplankton).

To project the population forward, the SCA model from the 2020 stock assessment was used (Turcotte et al. 2021). Approximate 95% credible intervals were obtained for quantities estimated by the model based on 210,000 Markov chain Monte Carlo (MCMC) samples with the first 10,000 samples discarded and every 40th of the subsequent samples saved. Population estimates are posterior medians based on the MCMC sampling. The population model was projected forward 50 years to 2069 during the MCMC sampling of the joint posterior distribution of the parameters. This takes into account uncertainties in the parameter estimates. 50 year projections were used to allow for the population state to stabilize, allowing a comparison of the stable states between projection methods. Natural mortality was fixed as the average of the last 5 years and weight-at-age vectors were randomly selected from the last 5 years of the assessment years.

Various recruitment assumptions were modeled for population projections and named as follows:

1. Regime high: average number of recruits estimated by STARS in a high recruitment regime,
2. Regime low: average number of recruits estimated by STARS in a low recruitment regime,
3. Ricker high: Ricker SRR parameters from low recruitment regime,
4. Ricker low: Ricker SRR parameters from high recruitment regime,
5. 5 recent years: random number of recruits from last 5 years (2015-2019) and
6. Plankton model: number of recruits in 2020 and 2021 predicted from zooplankton model, number of recruits for projection years 2022 to 2069 randomly selected from number of recruits predicted by the zooplankton model in years 2017 to 2021 (last 5 years of available zooplankton data).

For assumptions 1 and 2, the number of recruits was entered in the projection function of the population model. These assumptions do not incorporate uncertainty in the recruitment estimates from the population model, as the STARS analysis used median recruitment values from the population model MCMC sampling. For assumptions 3 and 4, the number of recruits for each year was estimated in the projection function of the population model using the Ricker SRR equation as SSB values for projection years were calculated. These assumptions do not incorporate uncertainty in the recruitment estimates used for the SRR. However, the uncertainty in SSB estimates is incorporated in the projections. For assumption 5, recruitment values were randomly selected among the population model estimates of recruitment, incorporating the uncertainty in the recruitment estimates. For assumption 6, a vector of number of recruit values predicted by the zooplankton GLM equation was integrated in the projections function of the SCA population model. This assumption does not incorporate uncertainty in the recruitment estimates, as the plankton model used median recruitment estimates from the population model MCMC sampling.

RESULTS

TIME SERIES OF POPULATION ESTIMATES

Figure 2 shows that the highest recruitment values of the time series all occurred before 1992, and that they occurred both at the lowest SSB values (1979-1982), and the highest values of SSB (1988 and 1991). Figure 2 also shows that the peaks in recruitment always occurred before a peak in SSB, suggesting that high recruitment generates high SSB. On the other hand, high SSB values did not seem to lead to high recruitment values. This was supported by the cross-correlation factor analysis (Figure 2), that showed a positive correlation between SSB and recruitment but with a negative lag, meaning that the big positive changes in SSB always occurred after large positive changes in recruitment. The relationship was significant between negative lags of 4 and 7 years, suggesting that high recruitment produced high SSB for the years 4 to 7 post-recruitment year.

REGIME SHIFT

The STARS analysis of spring spawning Herring recruitment showed a regime shift in the year 1992, where the average recruitment between 1978 and 1991 (476,000 fish) diminished to a lower level for the period 1992-2017 (275,000 fish; Figure 3).

For SST values in all of the GSL ecosystem approach regions, a regime shift occurred in the early 1990s where the initial colder state (1982-early 1990s) shifted to a warmer state (Figure 4). For the regions specific to the sGSL, the shift occurred in 1993 for the Baie des Chaleurs (10.0 °C to 11.2 °C), and in 1994 for the Magdalen Shallows (10.3 °C to 11.3 °C) and

Northumberland Strait (11.7 °C to 12.7 °C). A colder regime was identified by the STARS analysis in the final cut-off window (2018-2020) for all regions except Mecatina. However, Stirnimann et al. 2019 showed that the STARS method may return one or more false regime shifts towards the end of the time series and that they should be disregarded.

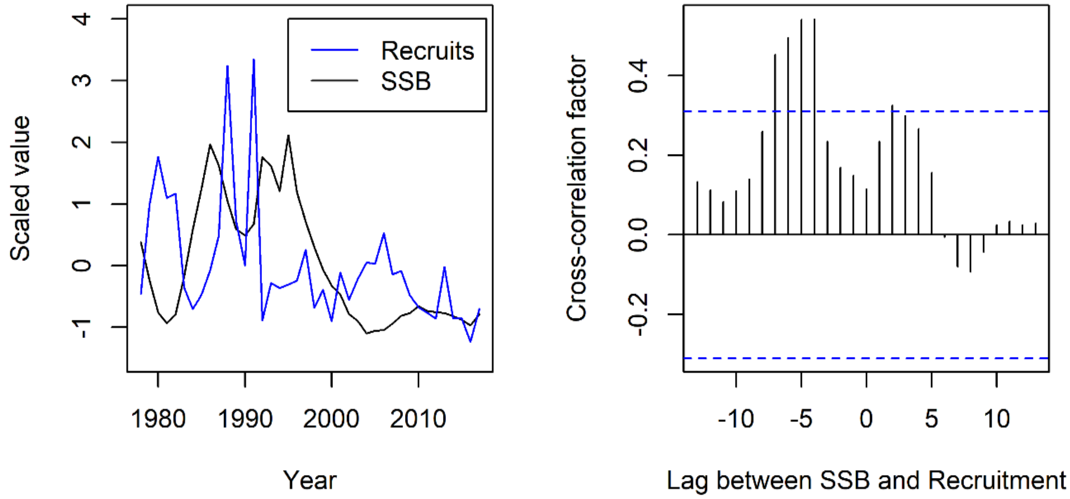

Figure 2: Scaled values of estimated SSB (black line) and recruits (blue line, number of age 2 fish) in the year they were produced (cohort year) of NAFO Division 4TVn spring spawning Atlantic Herring (left panel) and Cross-correlation factor analysis between SSB and recruitment (right panel), vertical black lines indicate correlation coefficient for lag years and blue horizontal dashed lines indicate significance level threshold.

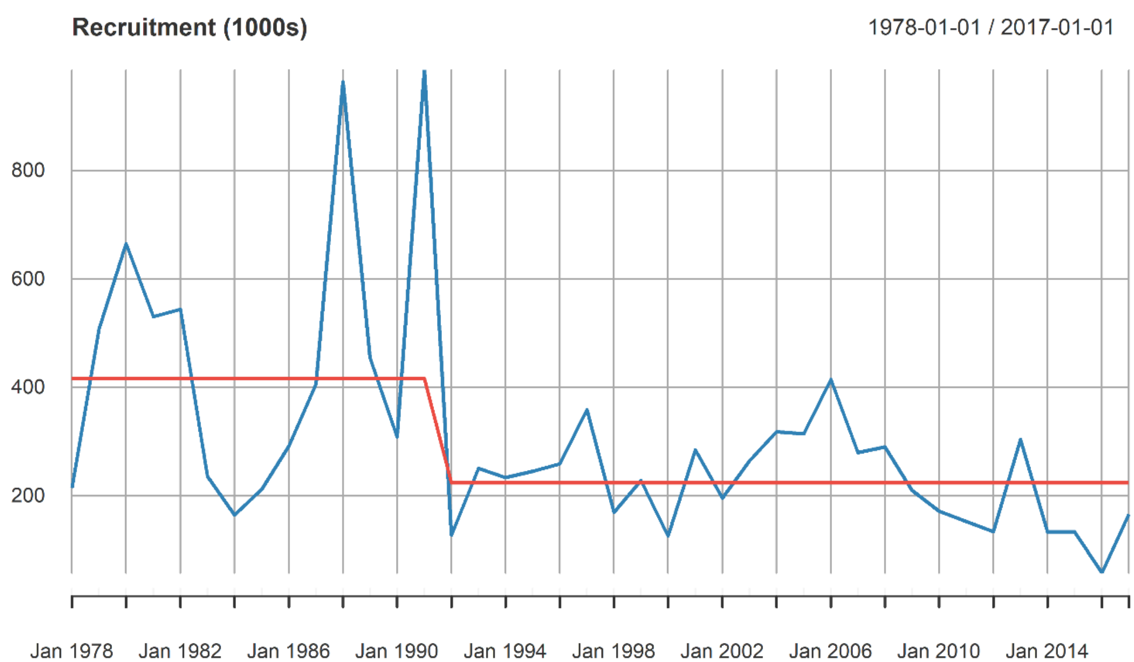

Figure 3: STARS algorithm analysis of regime shift in NAFO Division 4TVn spring spawning Atlantic Herring recruitment between 1978 and 2017. The blue line is the number of recruits in the year they were produced and the red line identifies the regimes and the regime shift (1992).

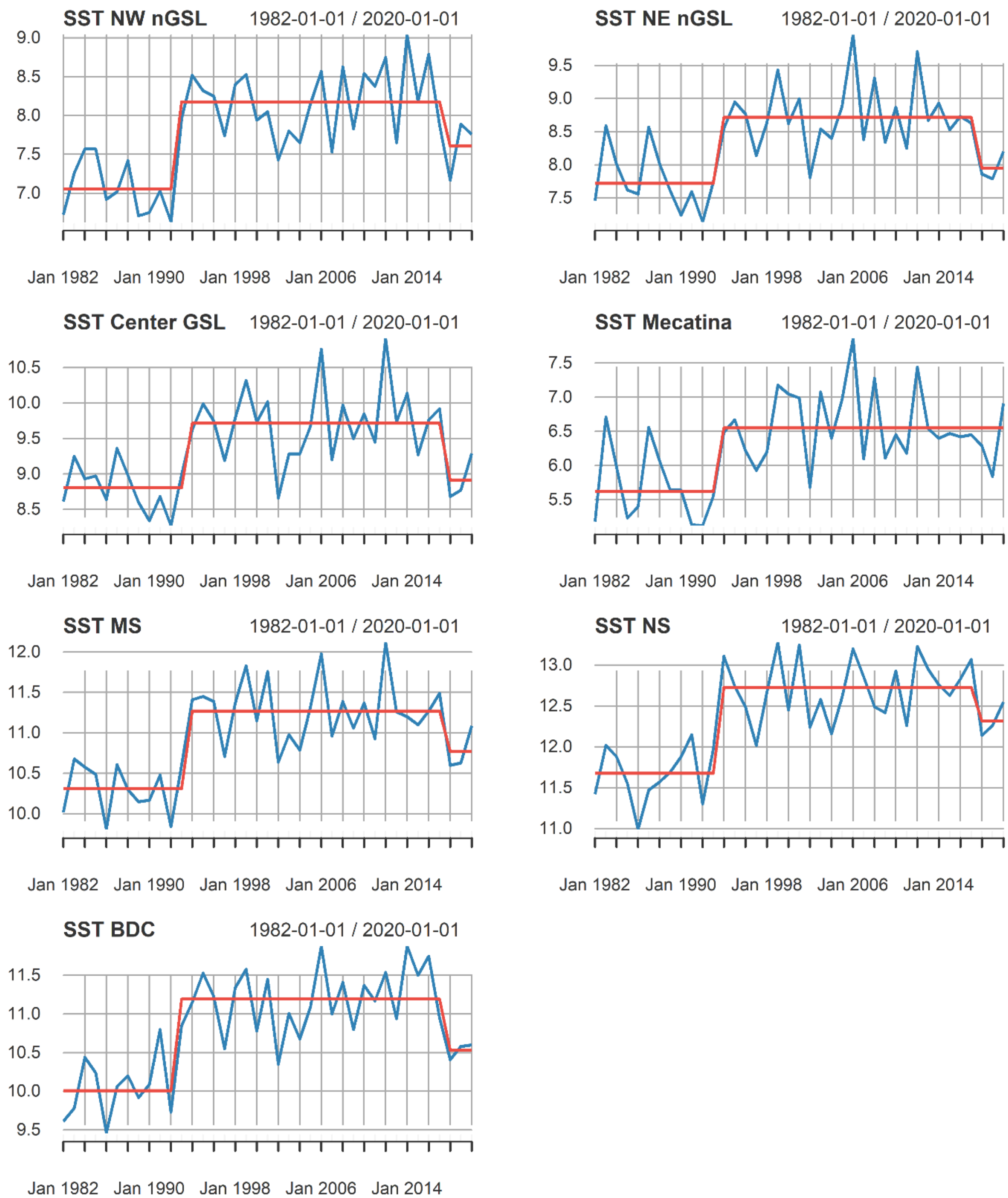

Figure 4: STARS algorithm analysis of sea surface temperature (SST) regime shift in GSL ecosystem approach regions between 1982 and 2020. The blue line is SST (degrees Celsius) and the red line identifies the regimes and the regime shifts. NW = Northwest, NE = Northeast, MS = Magdalen Shallows, NS = Northumberland Strait, BDC = Baie des Chaleurs.

STOCK RECRUIT RELATIONSHIPS

Over the years 1978-2017, the Ricker SRR model parameters were significant (α = 10.2843, p = 0.0000596, β = 0.000010115, p = 0.0000309). The relationship showed high variance around the expected number of recruits for a given SSB (Figure 5). The fit of the Ricker model showed important vertical spread in recruitment values at the lowest observed SSB values (between 30 and 40,000 metric tons of SSB) and around 125,000 metric tons of SSB.

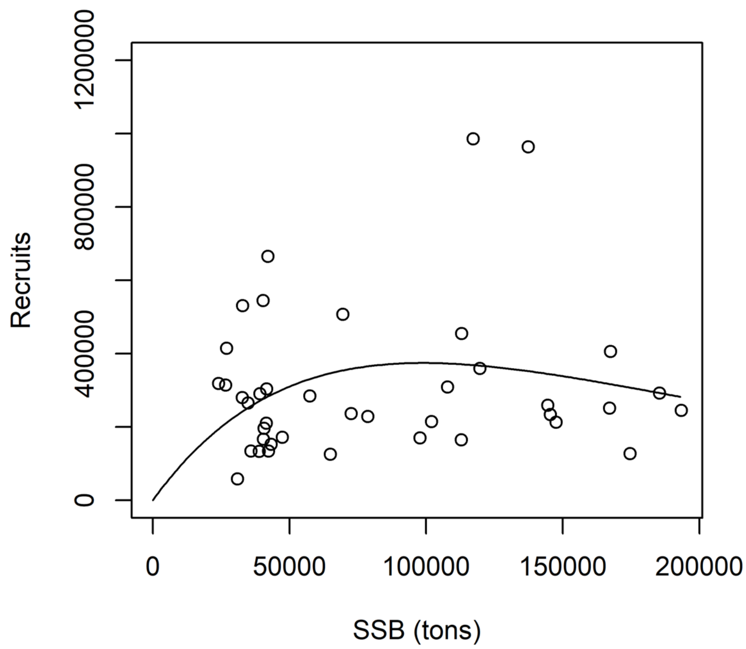

Figure 5: Stock-recruit relationship for NAFO Division 4TVn spring spawning Atlantic Herring for years 1978 to 2017, points are estimated values and lines is Ricker model fit.

Ricker SRR models were fit to each of the time series of SSB and recruits defined by the regime shift analysis. The 1978-1991 Ricker model fit showed a relationship with significant parameters (α = 20.837505549, p = 0.02924, β = 0.000014260, p = 0.00288). The 1992-2017 Ricker model fit also showed a relationship with significant parameters (α = 8.429944506, p = 0.000000355, β = 0.000011088, p = 0.000000794). Model fit was good for both regimes even with considerable variation around the mean expected recruitment (Figure 6). The SRR for the recent regime showed a lower expected recruitment for the spring spawning Herring stock after 1992. For the five most recent years estimates, the 2013 data point was above the expected recruitment value, but years 2014 to 2017 were all under the expected recruitment values (Figure 6).

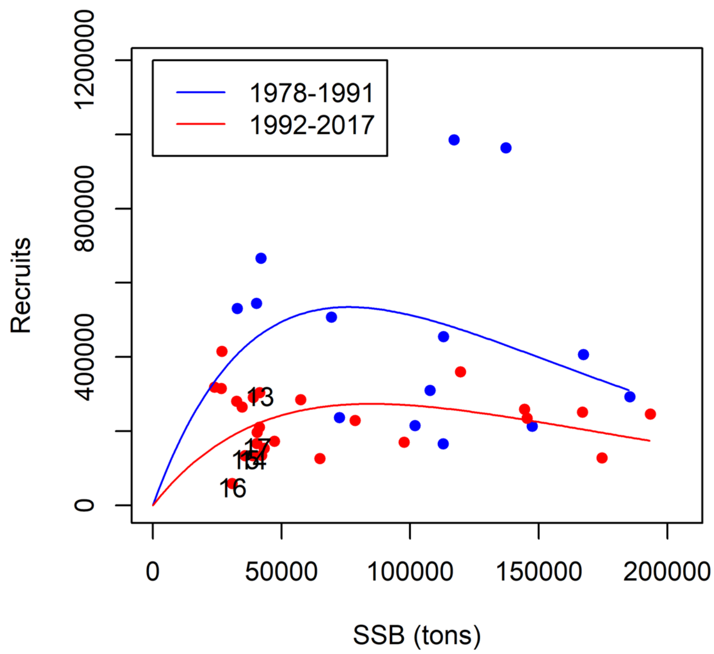

Figure 6: Stock-recruit relationships for two times series of NAFO Division 4TVn spring spawning Atlantic Herring: regime 1978-1991 (blue line and points) and regime 1992-2017 (red line and points), points are estimated spawning stock biomass (SSB) (in metric tons) values and lines are Ricker model fit, years 2013 to 2017 are identified by labels (13 to 17).

ENVIRONMENTAL EFFECTS ON RECRUITMENT

Three variables from the matrix of environmental variables had the highest correlation coefficients with recruitment and corresponded with the stated hypothesis of potential recruitment drivers: 1) large calanoid copepods abundance early in the summer ($r = 0.57$, $p = 0.018$; hereafter *large.cal*) 2) *Calanus hyperboreus* copepodite IV/I-IV ratio early in the summer ($r = 0.57$, $p = 0.016$; hereafter *hyp.ratio*) and 3) warm water zooplankton abundance ($r = -0.73$, $p = 0.001$; hereafter *warm.zoo*). Data for these 3 variables were from Blais et al. 2021. *Large.cal* and *warm.zoo* are functional group variables and their values are the sum of abundances of species as described in Table 1. High values of *hyp.ratio* indicate that the *C. hyperboreus* development occurred early in the spring.

The Pearson correlation coefficient between the covariates were 0.55 for *large.cal* and *hyp.ratio* ($p = 0.02$), -0.26 for *hyp.ratio* and *warm.zoo* ($p = 0.32$), and -0.53 for *large.cal* and *warm.zoo* ($p = 0.03$). A cross correlation factor analysis was used to assess if a lag was present between the zooplankton variables and the recruitment variables. A lag of 0 for all zooplankton variables indicated an effect of the variable in the same year as the recruitment occurred (Figure 7). Maximum correlations all occurred at the 0 lag and correlations were all significant ($p < 0.05$) at the 0 lag.

Table 1: Species composition of group variables (Large calanoid copepods early in the summer and warm water zooplankton).

Large calanoid copepods early in the summer	Warm water zooplankton
Anomalocera spp. *Calanus finmarchicus* *Calanus glacialis* *Calanus hyperboreus* *Euchaeta spp.* *Metridia spp.* *Paraeuchaeta norvegica* *Pleuromamma borealis* *Pleuromamma robusta*	*Centropages spp.* *Clausocalanus spp.* *Metridia lucens* *Nannocalanus minor* *Paracalanus spp.* *Pleuromamma borealis* *Pleuromamma robusta*

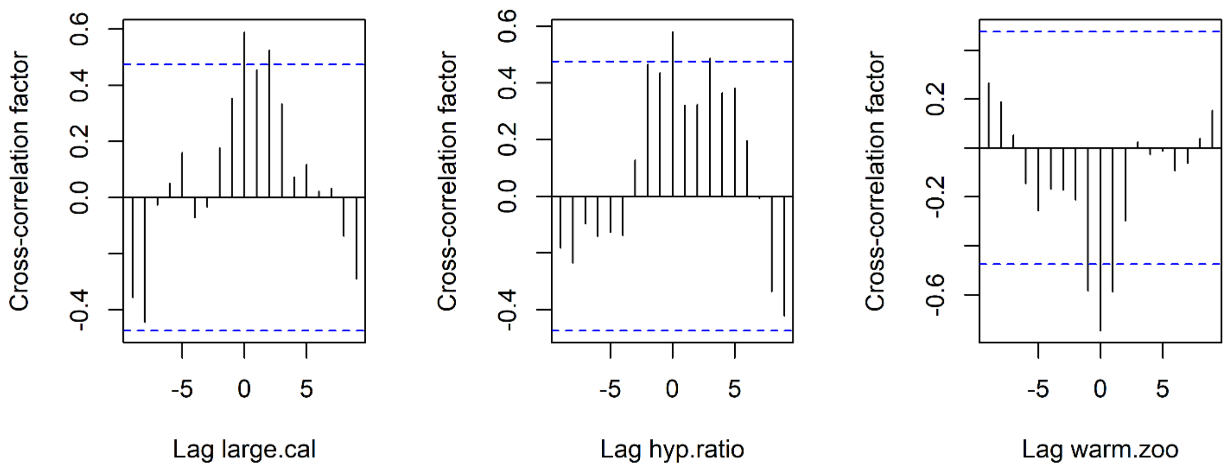

Figure 7: Cross-correlation factor analysis between large Calanoid copepods abundance early in the summer and spring Herring recruitment (left panel), between the ratio of Calanus hyperboreus copepodites IV/I-IV and spring Herring recruitment (middle panel) and between warm water zooplankton abundance and spring Herring recruitment (right panel), vertical black lines indicate correlation coefficient for lag years and blue horizontal dashed lines indicate the significance level threshold.

The abundance of large.cal was near the average between 2001 and 2006, followed by the highest values observed in 2007 and 2008, before declining to generally lower values (except for a peak in 2013) until 2019 (Figure 8). The hyp.ratio was highest between 2001 and 2013, followed by two low values in 2014 and 2015 and intermediate values between 2016 and 2019. The warm.zoo abundance was lowest between 2001 and 2007, increased until 2011 and decreased again to low values in years 2012, 2013 and 2014. Values increased again in 2015 and 2016 before declining until 2019.

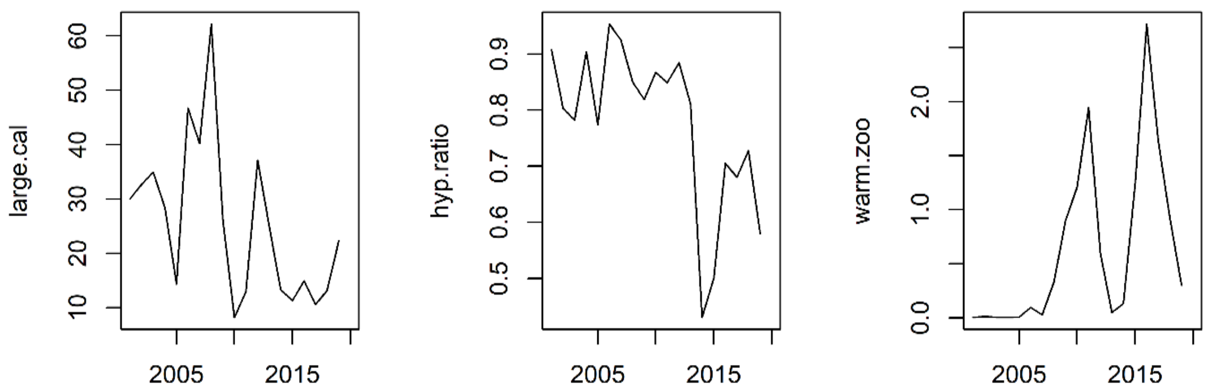

Figure 8: Trends in values of abundance of large calanoid copepods early in the summer (left panel), ratio of Calanus hyperboreus copepodites IV/I-IV (middle panel), and warm water zooplankton abundance (right panel) in the southern Gulf of St Lawrence between 2001 and 2019.

Models 3 and 4 showed the highest AIC values and explained less deviance than models 1 and 2 (Table 2). Models 1 and 2 showed the lowest AIC values and were within 2 AIC values of each other, while both explaining 74% of the deviance. Model 1 included all covariates while model 2 excluded the *large.cal* covariate. In model 1, the *large.cal* covariate was non-significant (p = 0.76406), while *hyp.ratio* (p = 0.00426) and *warm.zoo* (p = 0.000000214) were highly significant. GAMs were also tested but relationships were linear. Other GLMs using other recruitment-correlated variables were also tested. However, this reported set of variables performed best.

As the *large.cal* and *hyp.ratio* variables were highly correlated (Pearson correlation coefficient = 0.55), the model could not separate their effects on recruitment, or identify if there was an effect from each variable. However, as models 1 and 2 performed equally well and the 3 variables selected were supported by the starting hypothesis of spring Herring recruitment drivers, the selected model should include all 3 variables. As models 1 and 2 are within 2 AIC values of each other, including *large.cal* did not reduce the quality of predictions from the model.

Table 2: Model description, AIC, deltAIC (difference in AIC from lowest AIC model) and deviance explained by the model (%). R = Spring spawning Herring recruitment, large.cal = large Calanoid copepods abundance early in the summer, hyp.ratio = Calanus hyperboreus ratio of copepodites IV/I-IV, warm.zoo = Warm water zooplankton abundance.

model	AIC	deltaAIC	Deviance explained (%)
(1) log(R) ~ large.cal + hyp.ratio + warm.zoo	425.9	1.9	74
(2) log(R) ~ hyp.ratio + warm.zoo	424.0	0.0	74
(3) log(R) ~ large.cal + warm.zoo	430.1	4.1	63
(4) log(R) ~ large.cal + hyp.ratio	438.8	14.8	39

The selected model reads as follows:

$$\log(R) = 11.56685 - (0.00001525 \times large.cal) - (0.00409746 \times warm.zoo) + (0.01351475 \times hyp.ratio)$$

Where log(R) is the number of age 2 Herring on the log scale. The model predicted an increase in the number of recruits as the *hyp.ratio* increased, a decrease in the number of recruits as *warm.zoo* increased, and almost no change in recruitment as *large.cal* changed (Figure 9). The model fit the observed values very well (Figure 10). Only two observations were poorly predicted, a high value in 2006 and a low value in 2012. Recruitment was relatively high in 2001-2008 and relatively low in most years from 2009 to 2017.

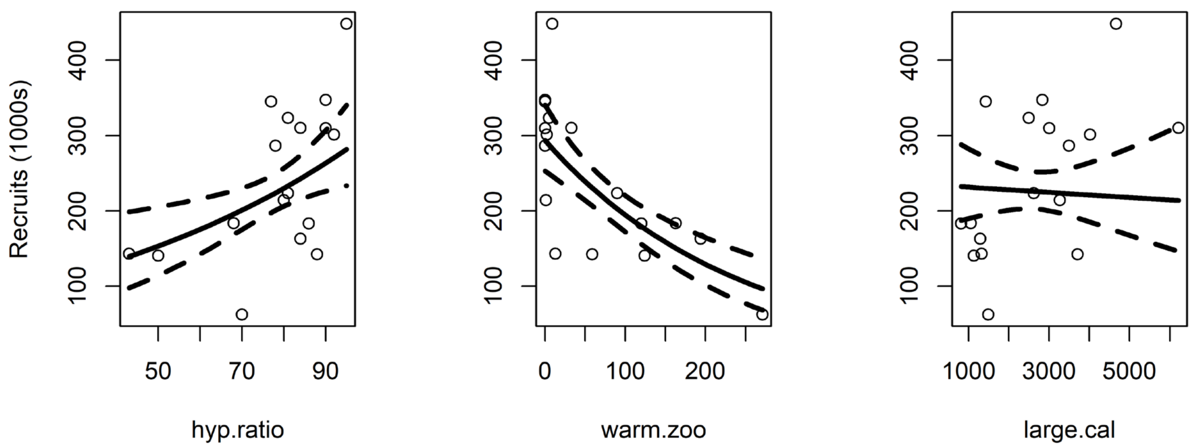

Figure 9: Relationship between the number of spring spawning Herring recruits and ratio of Calanus hyperboreus copepodites IV/I-IV (left panel), warm water zooplankton abundance (middle panel) and abundance of large calanoid copepods early in the summer (right panel) in the southern Gulf of St Lawrence between 2001 and 2017. Points are observed recruits (number of age 2 fish) in function of the covariates, black solid line is the average relationship from a negative binomial model, dashed black lines indicate 95% confidence intervals.

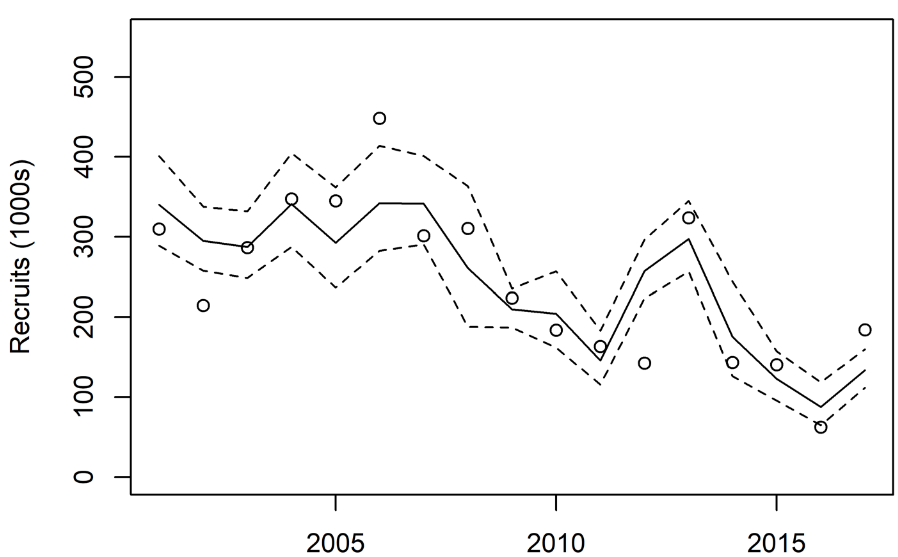

Figure 10: Model fit of the number of recruits predicted from a negative binomial GLM. Points are observed recruits (number of age 2 fish) in function of years, black solid line is the predicted values, dashed black lines indicate 95% confidence intervals.

POPULATION PROJECTIONS

The zooplankton GLM of Herring recruitment predicted 106,157 recruits in 2018 and 106,204 recruits in 2019 (Figure 11). These values are similar to values predicted for years 2015 to 2017, and are among the lowest values of the time series (2001 to 2019).

Figure 11: Trend in predicted number of spring spawning Herring recruits (in thousands) from a negative binomial GLM. Black solid line is the average predicted values, red points indicate values for years 2018 and 2019, red vertical lines are 95% confidence intervals.

The various assumptions about Herring recruitment used in the population projections had a large impact on the SSB trajectory in the projection period of 50 years (Figure 12) and on the 2 year projections (Figure 13) used for the production of advice on the risk associated with catch levels. The *High regime* and *Ricker high* scenarios showed similar trajectories with a rapid increase in SSB above the limit reference point (LRP) by 2022, and an equilibrium near 100,000 metric tons of SSB a few years later. Other projection methods, which are more reflective of current ecosystem trends and Herring dynamics, showed a slower rate of change in SSB for the first years of the projections. The *Low regime* scenario showed an increase in SSB and an equilibrium just above the LRP. The *Ricker low* scenario showed a slower increase in SSB and an equilibrium just below the LRP. The *5 recent years* scenario showed a very small increase in SSB and an equilibrium near the 2019 SSB level. The *Plankton model* scenario showed a decrease in SSB in the first years of the projections and found an equilibrium near the lowest observed SSB of the time series.

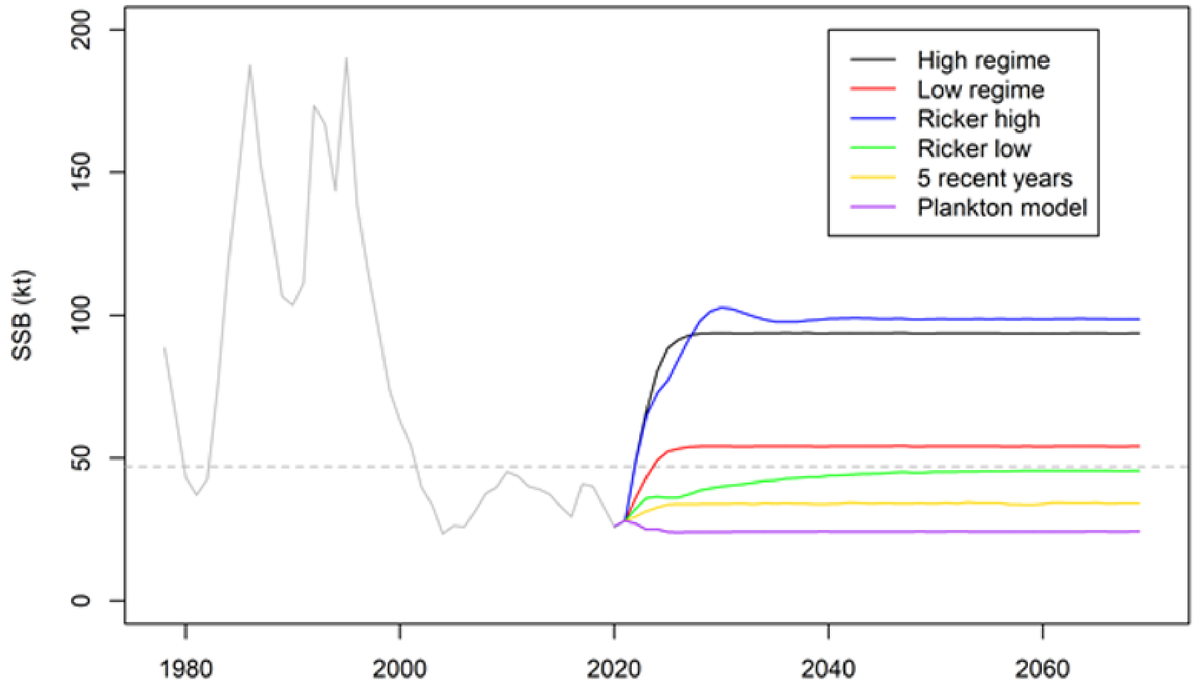

Figure 12: Spring spawning Atlantic Herring population projection in spawning stock biomass (SSB) (measured in units of metric kilotons (kt)) from year 2020 to year 2069. Colored lines show different model assumptions about Herring recruitment used for projections: Black line is number of recruits from high recruitment regime, red line is number of recruits from low recruitment regime, blue line is number of recruits from a Ricker stock recruit model in the high recruitment regime, green line is number of recruits from a Ricker stock recruit model in the low recruitment regime, yellow line is random number of recruits from 5 last assessment years and purple line is number of recruits predicted from a zooplankton model. Grey horizontal dashed line is the limit reference point, solid grey line is model estimated SSB for the assessment period (1978-2019).

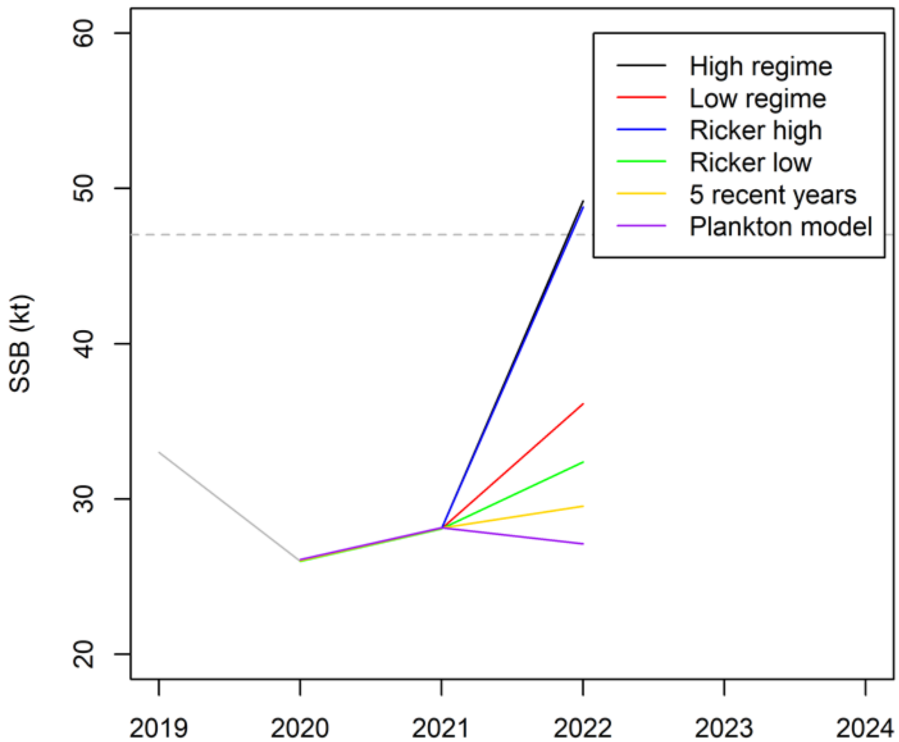

Figure 13: Spring spawning Atlantic Herring population projection in spawning stock biomass (SSB) (measured in units of metric kilotons (kt)) from year 2020 to 2022. Colored lines show different model assumptions about Herring recruitment used for projections: Black line is number of recruits from high recruitment regime, red line is number of recruits from low recruitment regime, blue line is number of recruits from a Ricker stock recruit model in the high recruitment regime, green line is number of recruits from a Ricker stock recruit model in the low recruitment regime, yellow line is random number of recruits from 5 last assessment years and purple line is number of recruits predicted from a zooplankton model. Grey horizontal dashed line is the limit reference point, solid grey line is model estimated SSB for the assessment period (1978-2019).

DISCUSSION

TIME SERIES OF POPULATION ESTIMATES

High recruitment events in spring spawning Herring have occurred at both high and low SSB values, either allowing the stock to quickly rebuild (early 1980s) or to maintain high SSB (late 1980s and early 1990s). The variability in recruitment was very high over the beginning of the time series. Herring are generally more likely to have very large recruitment events than non-forage fish and overall to display greater variability in recruitment (Trochta et al. 2020). Herring biomass also generally declines to lower minima, recovers to higher maxima and shows larger changes in biomass, implying Herring are more prone to booms and busts than non-forage fish species (Trochta et al. 2020). 4TVn spring Herring recruitment has exhibited less variability since 1992, with a long period of recruitment failure and few strong year classes.

Forage fish recruitment dynamics often vary over time and a large fraction of the variation is not driven strongly by spawning biomass (Szuwalski et al. 2019). This seems to be the case for 4TVn spring spawning Herring, as SSB variations were driven by recruitment variations in the cross correlation factor analysis. Contrarily, high SSB did not lead to high recruitment values. As found in a previous study of GSL Herring recruitment drivers, SSB accounted for very little of the variability in Herring recruitment and in contrast, environmental factors accounted for a high proportion of this variability (4R and 4T stocks; Brosset et al. 2018).

REGIME SHIFT

The Gulf of St. Lawrence is seeing a trend towards warmer waters, shorter duration of ice season, lower ice volume (Galbraith et al. 2021), changes in primary and secondary production phenology, a decrease of cold-water copepods abundance and an increase of warm water copepods abundance (Blais et al. 2021). These long-term changes in the sGSL sea surface temperature and composition of the zooplankton community has been shown to correlate with 4TVn spring spawning Herring recruitment (Brosset et al. 2018). From 1992 to 2014, the contribution of cold/arctic water copepod species such as *Calanus glacialis* and *Metridia longa* to the zooplankton community declined (Brosset et al. 2018). During the same time period, the abundance of small copepods typical of warm water, and of *Calanus hyperboreus* (another Arctic species) increased, while *Calanus finmarchicus* abundance did not show any clear long-term trend (Brosset et al. 2018).

Broadly speaking, zooplankton are ectothermic, short-lived, and track environmental variation of water masses, making them good indicators of climate change (Richardson 2008). In cold, mixed and turbulent surface waters, the system is nutrient-rich and the phytoplankton community is dominated by centric diatoms, supporting high production and a zooplankton community dominated by large copepods. In contrast, warm and stratified surface waters are nutrient-poor and the phytoplankton community is dominated by smaller phytoplankton, only supporting gelatinous zooplankton and small crustaceans. This long, inefficient foodweb is of poor nutritional quality, supporting a far smaller biomass of higher trophic levels (Richardson 2008). For example, *Calanus* species dynamics are strongly influenced by water temperature and their global distribution is projected to be modified by climate change effects on water masses in the North West Atlantic (Grieve et al. 2017).

A regime shift is as an abrupt change from one stable state to another. As demonstrated by the STARS analyses in this study, both the sea surface temperature of the sGSL and the spring spawning Herring recruitment abruptly shifted from a cold water/high recruitment regime to a warmer water/low recruitment regime in the early 1990s. It is unclear if the above cited changes in other oceanographic variables and in primary and secondary production indicators are better described by long term trends (drifting changes) or by regime shifts (an abrupt change). Establishing the occurrence of an ecosystem shift requires the demonstration of an abrupt change in productivity in many components of a system and is not the aim of this exercise. Nevertheless, the results shown here support the hypothesis that the low reproductive success of the 4TVn spring spawning Herring stock is occurring in a warm period, which is consistent with a model suggesting that cold environmental conditions favour spring spawners, whereas warm conditions favour fall spawners in Western Atlantic Herring stocks (Melvin et al. 2009). The identified regime shifts in sGSL SST involve a ~1 °C increase in temperature. It is unclear if this scale of change is expected to have a substantial direct biological effect on Herring recruits. The effect of the increase in SST on Herring recruitment is probably through indirect effects on secondary production dynamics and phenology.

Regime shifts in the primary production components of other systems and their impact on fish recruitment has been described in other systems. In the Northeast US Continental Shelf, regimes in recruitment success of many fish species broadly coincided with changes in the copepod community (Perretti et al. 2017). In the North Sea, changes in the zooplankton community have been linked to regime-like dynamics in Atlantic cod recruitment (Beaugrand et al. 2003). Looking at marine fish productivity alone, shifts are very common. Of the 230 fish stocks studied by Vert-pre et al. (2013), 69% were best explained by a model that took shifts in productivity into account.

STOCK RECRUIT RELATIONSHIPS

The pathway leading to recruitment is complex and is composed of many stages (spawning behaviour, egg production and/or early life stages survival). Variability in these processes can result in stock-recruit relationships that display high variance around the mean expected number of recruits per spawner. In the case of 4T spring spawning Herring, the high variance in the SRR modeled over all years (1978 to 2019) results in a SRR that is unsuitable to derive reference points and inform management decisions. When analyzing the stock-recruit dynamics over the whole time series, it is evident that recruitment leads SSB and thus, the likeliness of predicting the number of recruits obtained from a SSB value is low. As observed by Szuwalski et al. 2019, the probability of observing a significant SRR for a stock with purely recruitment driven dynamics is high in the case of forage fish because as recruitment shifts from high to low states (and back), spawning biomass quickly follows.

One way to better reflect the “true” SSB-recruitment dynamics is to assess if a regime shift in recruitment occurred, and fit SRRs for each of the time period for which the regimes are defined (Perälä et al. 2017; Szuwalski et al. 2019). The variance around the SRR modeled over the regime periods was still high, but more reflective of the expected number of recruits per SSB under different conditions.

The fact that SRRs were successfully fitted to each of the time series by regime period supports the finding of a regime shift in Herring recruitment in 1992 and that the expected recruitment for a given SSB is lower in the recent regime than in the historical regime. The spring spawning Herring stock is therefore less likely to rebuild in the current regime than it was in the former regime. Even if the stock did quickly rebuild from low SSB in the early 1980s, the recruitment levels that allowed the stock to rebuild are not expected at a similar SSB status in the current regime. Moreover, the recruitment values in recent years (all but 2013) were lower than the average SRR curve, indicating that even this model of recent recruitment might be too optimistic for contemporary spring Herring recruitment dynamics.

ENVIRONMENTAL DRIVERS OF RECRUITMENT

A previous study used PCA axes on an ecosystem matrix as variables in GAMs and found significant environmental effects on Herring recruitment (Brosset et al. 2018) but direct links between specific variables and recruitment would be difficult to operationalize in a stock assessment context using this method. Here, the GLM predicting spring spawning Herring recruitment based on zooplankton variables was able to predict recruitment values with a sufficient level of performance that it could be used in the stock assessment process. The aim of this study was not to find the drivers of every stage that leads to successful recruitment, but rather to find a good set of indicators that can improve the estimation of the number of recruits used for Herring population projections. As zooplankton data is available at the end of each year, and Herring recruitment is only observed at the minimum 2 years after the cohort year (often needing more sampling years to confirm the population age composition), this tool allows for the predictions of what the recruitment will potentially be for population projections before the abundance of recruits is observed in commercial or survey catch samples.

The variables used in the model were considered as indicators of key processes for Herring recruitment. The variable describing the abundance of large calanoid copepods early in the summer (*large.cal*) is a group variable that is composed of the sum of the abundances of all stages of the large calanoid copepod species in June (Table 1). The main diet items of 4TVn adult Herring are the three large calanoid copepods found in the sGSL (and the main components of that group variable), *Calanus finmarchicus*, *Calanus hyperboreus*, and *Calanus glacialis* (Darbyson et al. 2003). However, no study on the diet of spring spawning Herring larvae in the sGSL is available. In an adjacent area of the GSL, Wilson et al. (2018) found that the critical stage leading to recruitment of Herring larvae was when larvae reached 13 mm and transitioned from a generalist predator feeding on smaller calanoid copepods to a specialist feeding on larger calanoid copepods. The abundance of the prey described by the *large.cal* variable could also enhance adult Herring condition and egg quality, which would be supported by the cross-correlation factor analysis with a significant correlation at year-1 (when the oocytes starts developing in the adult). For this modelling exercise, the assumed mechanism for the effect of the total abundance of large calanoid copepods early in the summer on Herring recruitment was through food availability to Herring larvae.

The second variable in the plankton model is a variable describing the *Calanus hyperboreus* copepodite ratio of stage IV/copepodite stage I-IV abundance in the month of June (*hyp.ratio*). High values of this variable indicate a high ratio, meaning that the *C. hyperboreus* development occurred early in the spring. The match-mismatch hypothesis of recruitment states that availability of adequate prey in the weeks after hatching is considered necessary for a strong year class to emerge (e.g. Cushing 1990). The critical period for this match probably extends through the late-larval/early-juvenile stages and the prey must be of suitable quality (Bollens et al. 1992). *Calanus hyperboreus* reproduces in the winter in deep regions of the GSL. It is active for a short period in the spring in the surface layer, during which it is available to surface transport (Plourde et al. 2003; Plourde et al. 2019). In this study, the assumed mechanism for the effect of the *Calanus hyperboreus* copepodite ratio on Herring recruitment was through a phenology indicator of the timing of availability of food for larval Herring (including all suitable Herring larvae prey item).

The warm water zooplankton variable (*warm.zoo*) is also a group variable composed of the sum of the annual abundances of various zooplankton species that are typical of warmer water (Blais et al. 2021). This group variable is probably a good indicator of the yearly oceanographic conditions (warmer or colder years) in the GSL and showed a negative effect on recruitment. Sea surface temperature and ice conditions variables did not correlate strongly with spring Herring recruitment and their inclusions in predictive models did not perform well. The abundance of warm water zooplankton probably reflects the cascade of effects of warmer environmental conditions in a given year that result in impaired spring Herring recruitment via direct effects (inappropriate food items in terms of species composition and abundance, prey size, behaviour or quality [energetic content]). In this study, the assumed mechanism for the effect of the the warm water zooplankton abundance variable on Herring recruitment was through a quantitative indicator of the quality of the food items available to Herring larvae, as a result of water temperature effects on the zooplankton community.

The model showed a strong effect of *hyp.ratio* but no effect of *large.cal* (Appendix 2). Hence, there seems to be marginal support for including it in the model. However, when interpreting the results, it should be remembered that *large.cal* was correlated with *hyp.ratio*, but also with *warm.zoo* (to a lesser extent) and that the effect on recruitment is potentially coming from all covariates. As the relationship is model dependant, recruitment estimates can change and the effect of each variable can also change in the future as years of data will be added in the future. Hence, the *large.cal* variable should be kept in the model and the correlation between covariates and a potential effect of *large.cal* should be monitored in future assessments. The fact that the model was able to predict a high period, a decline followed by a low period and the 2013 peak is an indication that the zooplankton variables are an accurate choice of variables to predict Herring recruitment. The time series of zooplankton data only covered years in the low recruitment regime identified in the regime shift section above. Hence, recruitment considered high in analyses using the plankton model will actually be low compared to recruitment before 1992 (the cold water/high recruitment regime). This should be kept in mind to avoid a shifting baseline effect (Pauly 1995).

POPULATION PROJECTIONS

The choice of a recruitment forecasting method can have important consequences on projections (Punt et al. 2016; Subbey et al. 2014; Van Beveren et al. 2021). For early maturing stocks with important long-term variability in recruitment, like Herring, the choice of a particular recruitment forecast method over another could be consequential for the evaluation of risks associated with management decisions in medium term projections (5-10 years; Van Beveren et al. 2021). As a single best recruitment forecasting method does not exist over a range of stocks (Van Berveren et al. 2021), comparing multiple hypothesis and methods is suggested (Maunder and Thorson 2019; Punt et al. 2016). Such an evaluation across a range of assumptions can help select the forecast method and identify the potential impact that these assumptions have on the scientific advice.

Of the long-term forecast methods tested here, the regime high and Ricker high scenarios produced future population states that were not reflective of the stock status observed since the 1990s, clearly illustrating the shift in productivity that the stock experienced. Note that all projections are assuming stationary natural mortality, weight-at-age, selectivity and recruitment, while all these processes actually vary through time. Nonetheless, the comparison of projection methods still allows the examination of the impacts of various assumptions about recruitment. The four other forecast methods produced future population states the were more consistent with the recent history of the stock but the Ricker low and regime low scenarios still produced stable states at levels that either have not been observed since the 1990s (Ricker low) or observed only for one year since the 1990s (regime low). The two forecast methods that produced future populations states similar to observed states in the recent past were the 5 recent year and zooplankton model scenarios.

The 5 recent years scenario produced future population states that were similar to observed states since the early 2000s. That scenario is reflective of the number of age 2 recruits estimated by the population model which is subject to an important bias: the last estimated value of recruitment is not informed by age composition data in the population model. The estimate is then mostly driven by the historical average value (which is higher than all recent values in this case). The same applies to the number of age 2 in the year previous to last, where only year of age composition containing some information on ages 3 in the last year is available to inform the model. These age groups are not well sampled by the gears used to produce the age composition in model indices. Consequently for the vector of 5 values of recruitment estimates, the accuracy declines as values get closer to the terminal year. Another negative aspect of this forecast method is that it does not carry information about future recruitment.

Contrarily, the zooplankton model scenario incorporates information about future recruitment as it uses the terminal year state of plankton indicators to predict the number of recruits two years ahead. This is a considerable advantage over the other methods explored here, as it uses field data to estimate future recruitment, versus stock assessment model outputs to model future recruitment. If the predictive power of the model is reliable enough, this is information that should be used in the risk assessment and the provision of scientific advice. In this case, the zooplankton model predicted number of recruits in 2018 and 2019 that are similar to 2015 to 2017 values, indicating no change in expected recruitment. This model could be used directly in the population model to project the population in time and generate the advice, or shown in comparison with the 5 recent years scenario, or be used as a qualitative indicator of future prospects for the stock. In this case, showing the two best models (5 recent years and zooplankton model) would be the most informative for the 4TVn spring spawning Herring assessment. Over the short-term projections, these two forecast methods would most likely produce almost identical harvest risk assessments, especially considering uncertainty in estimates of population status. However, the long-term projections would enable the examination of the inherent effects of recruitment dynamics on the population that are difficult to discern from short-term projections.

CONCLUSION

One uncertainty about this analysis is that the recruitment values are model-dependant. Hence, when the model changes or new years of data are added to the model, the recruitment estimates change and the environment relationship can change. Also, the recent regime has low recruitment along with negatively correlated natural mortality for 2-6 v 7+ age groups. It is possible that these processes are confounded in the estimation process. A way to account for this would be to estimate the recruitment-environment relationship inside of the model in an integrated model.

Another uncertainty lies in the fact that the analysis uses model outputs as recruitment values. The correlation between Herring recruitment and the zooplankton index is quite good, but, there are several steps leading from observable data to this correlation that should be investigated further. Field studies to collect eggs, larvae and zooplankton at spawning sites should be undertaken in order to obtain real data and draw better-informed conclusions.

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APPENDIX 1

Table A1.1: Variable name and description for variables extracted from the environmental matrix in the SGLEA R package and used in the correlation matrix analysis.

Variable	Description
amplitude	Highest concentration reached during the phytoplankton bloom
calanus.finmarchicus.annual	Abundance of *Calanus finmarchicus* annual
calanus.finmarchicus.early_summer	Abundance of *Calanus finmarchicus* in early summer
calanus.hyperboreus.annual	Abundance of *Calanus hyperboreas* annual
calanus.hyperboreus.early_summer	Abundance of *Calanus hyperboreas* in early summer
calanus.hyperboreus.fall	Abundance of *Calanus hyperboreas* fall
ci.civ.cfin.early_summer	Ratio Copepodite Stage I-IV/ Total Copepodite abundance, *C. Finmarchicus* in early summer
ci.civ.cfin.fall	Ratio Copepodite Stage I-IV/ Total Copepodite abundance, *C. Finmarchicus* in fall
civ.glac.fall	Ratio Copepodite Stage IV/ Total Copepodite abundance, *C. Glacialis* (fall only)
civ.hyp.early_summer (hyp.ratio)	**Ratio Copepodite Stage IV/ Copepodite stage I-IV abundance, *C. Hyperboreus* (early summer only)**
cold.annual	Cold/arctic zooplankton species (*Calanus glacialis* and *Metridia longa*) abundance annual
cold.early_summer	Cold/arctic zooplankton species (*Calanus glacialis* and *Metridia longa*) abundance in early summer
cold.fall	Cold/arctic zooplankton species (*Calanus glacialis* and *Metridia longa*) abundance in fall
decrease.10	Timing of when water first cools to 10 C
decrease.12	Timing of when water first cools to 12 C
duration	The duration of the phytoplankton bloom
dw2_t.annual	Total dry weight of zooplankton annual
dw2_t.early_summer	Total dry weight of zooplankton in early summer
dw2_t.fall	Total dry weight of zooplankton in fall
ice.duration	Duration of the ice season
largecal.annual	Abundance of large *Calanus* annual
largecal.early_summer (large.cal)	**Abundance of large *Calanus* in early summer**

Variable	Description
largecal.fall	Abundance of large *Calanus* in fall
last.ice	Timing of the last appearance of ice
magnitude	Area under the curve
non.copepods.early_summer	Abundance of non-copepod zooplankton in early summer
pseudocalanus.annual	Abundance of *pseudocalanus* annual
pseudocalanus.early_summer	Abundance of *pseudocalanus* in early summer
pseudocalanus.fall	Abundance of *pseudocalanus* in fall
sst	Sea surface temperature annual
sst.month10	Sea surface temperature in October
sst.month11	Sea surface temperature in November
sst.month5	Sea surface temperature in May
sst.month6	Sea surface temperature in June
sst.month7	Sea surface temperature in July
sst.month8	Sea surface temperature in August
sst.month9	Sea surface temperature in September
start	Day of the year when the phytoplankton bloom starts
start.10	Timing of when water first warms to 10 C
start.12	Timing of when water first warms to 12 C
warm.annual (warm.zoo)	**Warm-water zooplankton species (*Metridia lucens, Centropages spp.,Paracalanus spp., and Clausocalanus spp.*) Abundance annual**
warm.early_summer	Warm-water zooplankton species (*Metridia lucens, Centropages spp.,Paracalanus spp., and Clausocalanus spp.*) Abundance in early summer
warm.fall	Warm-water zooplankton species (*Metridia lucens, Centropages spp.,Paracalanus spp., and Clausocalanus spp.*) Abundance in fall

APPENDIX 2

This appendix shows the output from the summary R function for the GLM of spring spawning herring recruitment by zooplankton covariates, and the model diagnostic plots for the model generated by the check_model function of the performance R package (Figure A2.1).

```
Call:
glm.nb(formula = rec ~ largecal.early_summer + warm.annual +
    civ.hyp.early_summer, data = spring, init.theta = 20.00777803,
    link = log)

Deviance Residuals:
     Min        1Q     Median       3Q      Max
-2.40681  -0.54778   0.08281   0.62301   1.51224

Coefficients:
                 Estimate    Std. Error   z value        Pr(>|z|)
(Intercept)     11.56685065  0.34266871  33.755   < 0.0000000000000002 ***
large.cal       -0.00001525  0.00005079  -0.300     0.76406
warm.zoo        -0.00409746  0.00079004  -5.186     0.000000214 ***
hyp.ratio        0.01351475  0.00472797   2.858     0.00426 **
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for Negative Binomial(20.0078) family taken to be 1)

    Null deviance: 66.223  on 16  degrees of freedom
Residual deviance: 17.142  on 13  degrees of freedom
AIC: 425.9

Number of Fisher Scoring iterations: 1


              Theta:  20.01
          Std. Err.:  6.81

 2 x log-likelihood:  -415.898
```

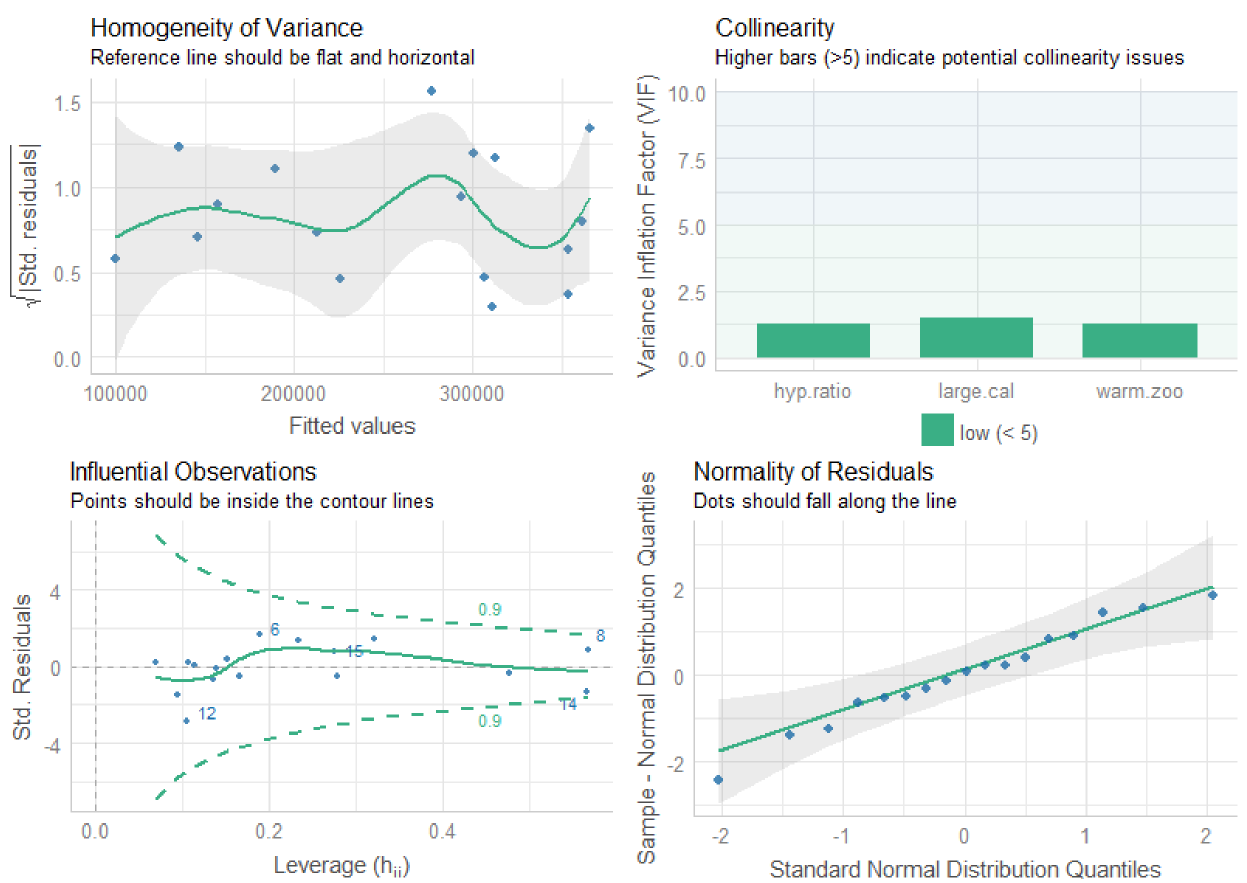

Figure A2.1: Model diagnostics for the GLM of spring spawning herring recruitment by zooplankton covariates.