

1 **Fish population growth in the Gulf of St Lawrence: the effect of climate, fishing and predator**
2 **abundance**

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4 **Running head page:**

5 Harvesting and climate mediate population growth

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21 **Abstract**

22 Climate variability, fishing and predation are the main factors affecting fish population dynamics. In this
23 study, the drivers of population growth variability were investigated for seven fish stocks (2 cod, 4 herring
24 and 1 mackerel stock) in the Gulf of St. Lawrence (NW Atlantic). The annual population growth sensitivity
25 to both recruitment and survival (how much population growth depends on recruitment and survival) was
26 estimated through elasticity analyses before being linked to harvesting history as well as environmental
27 conditions (climate and predation). Stock-specific generalized additive models showed that population
28 growth was most sensitive to recruitment variability with decreasing fish generation time, increasing
29 water temperature and, in some cases, with predation. The dependence of population growth on
30 recruitment, however, was generally close to 0, albeit being higher for pelagic stocks than for demersal
31 ones. This indicates that adult survival was more important than recruitment in shaping population
32 growth and thus population size. As climate mainly acts on recruitment while fishing affects adult survival,
33 management efforts seemed more important than climate variability in regulating population growth,
34 especially for long-lived cod. Nevertheless, population growth may become increasingly dependent on
35 recruitment variability with warming waters, hence, why more flexible management strategies should be
36 developed to cope with these oscillations.

37

38 **Keywords:** cod, herring, mackerel, recruitment, matrix model, Leslie matrix, management.

39

40 **1. Introduction**

41 Mechanisms affecting productivity and hence biomass of marine fish populations are still widely unknown
42 (Houde 1987, Szuwalski et al. 2015). Population productivity is determined by the strength of biological
43 processes (e.g. recruitment and somatic growth) which are difficult to investigate since these estimates
44 are mainly available for data-rich stocks. The strength and drivers of population productivity are also
45 space-, time- and species-specific, since they depend on varying life-history parameters and harvesting
46 history. For instance, population growth of exploited species exhibits higher sensitivity to productivity
47 variability than of unexploited species (Hsieh et al. 2006), due to fishery-induced truncation of the age
48 structure (Berkeley et al. 2004, Hutchings & Reynolds 2004, Stige et al. 2017). Hence, recruitment
49 variability has a greater influence on stock size if the mature population consists of a small number of age
50 classes (Stearns 1992, Ottersen et al. 2013), reducing the populations' robustness to environmental
51 variations. Additionally, climate change and predation also affect maturity and survival and consequently
52 the sensitivity of population to recruitment variability (Leggett & DeBlois 1994). Therefore, there is a
53 considerable interest and need in understanding population growth changes in temporally varying
54 environments and fishing pressure, not only for ecology but also for conservation and management.

55 In the Northwestern Atlantic, fish populations of the Gulf of St Lawrence (hereafter GSL) are mostly
56 threatened by overexploitation, climate change, and predation by expanding seal populations (Savenkoff
57 et al. 2017). Among the main fish species, mackerel (*Scomber scombrus*), herring (*Clupea harengus*) and
58 cod (*Gadus morhua*) have a long history of fisheries (Swain et al. 2015, DFO 2016, 2017a, b). In addition
59 to the effects of fishing, these stocks experience large fluctuations in biomass, related to environmental
60 variability acting through bottom-up and top-down process on recruitment success (cod: Lambert 2011,
61 Swain & Benoît 2015, mackerel: Plourde et al. 2015, herring: Brosset et al. 2019). Moreover, grey seal
62 (*Halichoerus grypus*) abundance has sharply increased since the mid-90s in both the northeast and south

63 GSL (Hammill et al. 2014, Swain & Benoît 2015), potentially increasing predator pressure on herring and
64 cod (Hammill & Stenson 2000). Given the growing concern about fisheries management, and how
65 sensitive population dynamics are to different pressures, it is particularly relevant to understand fish stock
66 fluctuations in the GSL. Indeed, recent examples have shown that untangling the effect of habitat
67 dynamics (e.g. climate-change and predation) and fishing on vital rates (e.g. recruitment or adult survival)
68 led to a better understanding of population dynamics with important implications and improvements for
69 management (Ezard et al. 2010, Thorson et al. 2015, Durant & Hjermann 2017).

70 The effects of varying vital rates are often integrated into population transition matrix frameworks
71 (Caswell 2001). Based on this, elasticity analyses are commonly applied through transition matrices to
72 investigate the changes in population growth as a function of any specified change in vital rate (i.e.
73 reproduction or survival, Caswell 2007). The elasticity values measure which vital rate generates the
74 greatest change in population growth (de Kroon et al. 1986, Benton & Grant 2000), and thus indicate
75 which is the main driver of population growth variations. Elasticity analysis can therefore be a simple first
76 step in answering important questions in population ecology, as already shown for other diverse taxa (e.g.
77 fish, Gerber & Heppell 2004; turtle, Crawford et al. 2014; butterfly, Flockhart et al. 2015). Such values can
78 be used to pinpoint key life history traits for fisheries management (Rouyer et al. 2011, Hidalgo et al.
79 2014). Moreover, temporal changes in sensitivity to recruitment and survival can be analyzed to
80 investigate which drivers are essential for modulating importance of recruitment or survival on population
81 growth (Ezard et al. 2010, Durant & Hjermann 2017).

82 The aim of this study was to assess the contribution of recruitment to population growth (hereafter
83 recruitment elasticity or elasticity) and to identify the main drivers of elasticity variability in the GSL
84 ecosystem. We investigated how age structure, climate, potential predation and fishing pressure affect
85 the importance of recruitment in population growth for seven stocks (4 herring, 2 cod and one mackerel

86 stock). By considering different stocks belonging to different trophic levels and habitats, as well as having
87 different exploitation histories will allow further understanding of GSL commercial stocks dynamics.
88 Ultimately, given the importance of recruitment and/or adult survival to the population growth found,
89 this will help to identify appropriate management measures on these stocks, which could be helpful to
90 resource managers to anticipate the potential species' response to environmental variability.

91

92

93 2. Materials and methods

94 The seven commercial fish stocks considered in this study inhabit one or more NAFO areas (Northwest
95 Atlantic Fisheries Organization, Fig 1.). Three stocks are located in the northern part of the GSL: 4R spring
96 herring, 4R fall herring and northern cod (4RS + 3Pn). Three stocks are located in the southern part: 4T
97 spring herring, 4T fall herring and the southern cod from area 4T. We also analysed a seventh stock,
98 referred to as Canadian contingent mackerel, which migrate between the US and the Canadian east coast
99 (reproducing in the southern GSL around May-July, Moores et al. 1975). These stocks are economically
100 important and their management can be improved, or can benefit from all additional knowledge on
101 population dynamics. Moreover, the seven stocks include demersal (i.e. cod), and pelagic fish (i.e.
102 mackerel and herring) with different population structures (e.g. longevity) as well as contrasting harvest
103 histories, allowing us to conduct a comparative study of population dynamics drivers. These seven stocks
104 were chosen because of the availability of age-structured biological data (annual maturity- and weight-at-
105 age) and stock assessment model outputs (annual abundance-at-age and fishing mortality).

106

107 2.1 Biological data and estimates

108 Stock specific data (maturity-at-age) and estimates (abundance-at-age and fishing mortality-at-age) were
109 extracted from assessment reports from the Canadian Department of Fisheries and Oceans for each year
110 (DFO, see Table 1). Recruitment estimates are derived from stock assessment models, and represent
111 abundance at age 1 (mackerel) or age 2 (herring and cod). Annual fishing mortality estimates (F_y) were
112 calculated by averaging the fully selected age classes of the F -at-age matrix ($F_{a,y}$): F_{4-10} for spring and fall
113 4R herring and F_{4-8} for mackerel and both cod stocks. The two cod stocks (northern and southern), and all
114 the herring stocks were modelled using Virtual Population Analysis (VPA, Swain et al. 2015, DFO 2017b),
115 whereas a newly developed state-space assessment model was used for the mackerel stock (DFO 2017a,
116 Van Beveren et al. 2017). As the use of stock estimates from stock assessment models can introduce some

117 pitfalls (Brooks & Deroba 2015, Legault & Palmer 2016, Palmer et al. 2016), we only selected stocks with
118 models carefully peer-reviewed and robust against natural mortality and selectivity changes.

119

120 *2.2 Environmental data*

121 Annual anomalies were used to describe the temporal environmental variability in the GSL between 1971
122 and 2014. The selected hydrographic variables from the GSL are, sea ice coverage, sea surface
123 temperature, intermediate and deep-water temperature, St. Lawrence runoffs and deep water salinity
124 (Table 2). Temperature data were obtained from regular monitoring in the GSL (see Galbraith et al. 2018),
125 specifically monthly sea surface temperature in August, and the average between May and November
126 were utilised. Surface temperature may affects the growth and survival of early life stages and juveniles
127 (depending on their spawning season), as already shown for the recruitment process for mackerel
128 (Plourde et al. 2015) and herring (Brosset et al. 2019). Cold intermediate layer (CIL), and deep layer
129 temperature data at 150, 200, 250 and 300m, were used as indicators of habitat and spawning ground
130 suitability for demersal species adult and juvenile stages. Sea ice volume, an index of the temperature,
131 and of the timing of primary producer development, was measured by the Canadian Ice Service by means
132 of aerial surveys and satellite pictures defining ice coverage and thickness (Galbraith et al. 2018). The St.
133 Lawrence runoff (measured using the water level method from Bourgault & Koutitonsky 1999) is a proxy
134 for precipitation and nutrient input in the GSL. Deep-water salinity represents an indicator for the
135 exchange of water masses (i.e., water entry through the Laurentian channel), related to the strength of
136 cold and high level dissolved oxygen Labrador Current water (Galbraith et al. 2018). The selected variables
137 have previously been reported to explain the recruitment dynamics of herring (e.g. water temperature,
138 Brosset et al. 2019), mackerel (e.g. St. Lawrence runoffs and sea surface temperature, Plourde et al. 2015)
139 and cod (water temperature Ouellet et al. 1997), and thus will be important to further understand
140 population growth variability.

141

142 *2.3 Predation strength*

143 Predation has an influence on population growth, so top-down effects (i.e. the main predators'
144 abundances) should also be considered (Table 2). Most stocks were however assessed with VPA-models
145 assuming constant natural mortality. Because in such cases all residual mortality was assumed to be
146 attributed to fishing, we only test this link for southern cod and mackerel, which presumed a time varying
147 M and a constant M with process error (allowing for deviations in M), respectively (Swain et al. 2015,
148 Doniol-Valcroze et al. 2019). Seals have been described as predators of mackerel and cod in the GSL
149 (Hammill et al. 2013, Swain & Benoît 2015). Therefore, grey seal abundances were considered as potential
150 drivers of cod and mackerel population growth. Seal abundance estimates were obtained for the
151 northeastern and the southern region, the southern seal abundance matching with the southern cod
152 stocks and the sum of seal abundances for both regions matching with mackerel distribution in the GSL.

153

154 *2.3 Statistical analyses*

155 We aimed to (I) estimate the importance of recruitment on population growth (i.e. elasticity) and (II)
156 determine how this is affected by key parameters such as age structure, longevity, fishing mortality,
157 environmental conditions and natural mortality (potential predators).

158

159 *2.3.1 Elasticity calculations*

160 To estimate the relative importance of recruitment and survival on population growth for each
161 population, we started by constructing annual Leslie transition matrices A_t to summarize the dynamics of
162 age-structured populations between time t and time t_{+1} (Leslie 1948, Caswell 2007). Annual population-
163 specific abundance-at-age matrices (stock assessment outputs) were compiled to determine the fecundity
164 (i.e. the contribution of each age class a to the recruitment at year t , R) and the survival (i.e. the survival

165 (S_i) between age-class i at year t and age-class $i - 1$ at year $t-1$) of each age-class for each stock. We
 166 calculated R as follows:

167
$$R_{a,t} = \frac{Rec_t MAT_{a,t-1}}{\sum_{a=1}^{a=max} N_{a,t-1} MAT_{a,t-1}}$$

168 where Rec_t is the recruitment at the year t , $MAT_{a,t-1}$ the proportion of mature at age a and time $t-1$
 169 (derived from annual scientific sampling programmes) and $N_{a,t-1}$ the abundance for age a at time $t-1$. The
 170 age index a varies between 1 and $a max$, the older age-class in the population.

171 Thus, the matrices were used to make future predictions of age-class abundance following the
 172 relationship $n_{t+1}=A_t.n_t$ where n_t is the age-class abundance vector at time t . Note that A_t is compiled for
 173 the age structure in year t (hence valid only for the time frame year t to year $t + 1$). For each year, survival
 174 probability and fecundity of each age-class are included in the transition matrix as follows:

175
$$A_t = \left[\begin{array}{cccccc} R_{1,t} & R_{2,t} & R_{3,t} & \dots & R_{a max - 1,t} & R_{a max,t} \\ S_{1-0,t} & 0 & 0 & \dots & \dots & 0 \\ 0 & S_{2-1,t} & 0 & \dots & \dots & 0 \\ \dots & \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & 0 & \dots & S_{a max - (a max-1),t} & 0 \end{array} \right]$$

176 In the Leslie Matrix, the fecundity is always in the first row, representing the contributions of newborns
 177 from the reproduction of each age class. The survival probabilities are always in the subdiagonal. They
 178 represent transitions from one age class to the next. All other entries are 0, because no other transitions
 179 are possible. The realized annual population growth rate (r_t) between t and $t + 1$ is given by the logarithm
 180 of the dominant eigenvalue of the projection matrices A_t (Caswell 2007).

181 To evaluate the proportional change in the population growth rate resulting from a known proportional
 182 change in recruitment, the transient elasticity method (i.e. changes in population size and structure before
 183 reaching population stable stage distribution) defined by Caswell (2001), and described in Durant et al.

184 (2013) and Durant & Hjermann (2017) was followed. Transient elasticity utilises transient dynamic, which
 185 can reveal effects of short-term patterns affecting population dynamics (Caswell 2007). Transient
 186 elasticity indicates the relative contribution of recruitment or survival to population growth changes for
 187 each year by simulating the population growth from year t to year $t + t_g$ with and without changes in initial
 188 recruitment or survival values (Caswell 2001). Thus, for each year, the transient elasticity analysis was
 189 performed by increasing the recruitment by 1% for each age class (by manipulating B_i values in the top-
 190 row elements of A_t) and simulating population growth for the next t_g years, while holding the other
 191 parameters at their original value. The t_g value used was approximately equal to the mean of the year-
 192 specific generation time μ_t (the mean age of the parents of the offspring produced by a cohort over its
 193 lifetime), according to the recommendations of Caswell (2001) and Durant et al. (2013). The annual
 194 generation time μ_t (which changes from year to year, and reflects the hypothetical generation time
 195 realized if the rates from a given year are held constant for long enough) is computed from A_t and defined
 196 as follows:

$$197 \quad \mu_t = \frac{\sum_i i (\prod_{j=1}^{i-1} P_{j,t}) B_{i,t}}{\sum_i (\prod_{j=1}^{i-1} P_{j,t}) B_{i,t}}$$

198 Where we defined $\prod_{j=1}^0 P_{j,t} = 1$ (Caswell 2001).

199 Thus, changes in recruitment at time t will have time to be reflected in the mature population at time $t +$
 200 t_g and can be compared between species (Durant et al. 2013). To check if the *a priori* chosen 1% level of
 201 perturbation did not affect the results of the generalized additive model (GAM) analyses (see the next
 202 section), a bootstrap procedure (100 replicates) was used to test different perturbation values on the
 203 original recruitment ranging from -20 to +20% (i.e. sensitivity analysis). Whatever the level of perturbation
 204 chosen, no significant difference was observed in the GAM analyses, so the 1% level of perturbation was
 205 kept.

206 Annual transient elasticity was then calculated as $e_{rec} = N^{incr}_{(t+t_g)} / N_{(t+t_g)} - 1$ where $N_{(t+t_g)}$ is the number of fish
207 in year $t + t_g$ and $N^{incr}_{(t+t_g)}$ is the same variable but for the simulated case with 1% increased recruitment in
208 year t . The same approach was implemented for every year of the time series (except those that are less
209 than t_g years from the end of the time series where no elasticity values were determined). Note that
210 following the methods used (Durant & Hjermann 2017), the recruitment (e_{rec}) and survival (e_{sur}) elasticity
211 components were sum to 1 (i.e. $e_{sur} = 1 - e_{rec}$), thereby allowing for the relative contribution of each model
212 parameter to population growth to be easily determined. For example, an e_{rec} close to 1 means that the
213 recruitment has a stronger impact on population growth in comparison to adult survival (and the contrary
214 when e_{rec} is close to 0). This is interesting from a management point of view because when e_{rec} is closer to
215 0 than to 1, management efforts (modulating adult survival through fisheries) can have a large impact on
216 stock size fluctuations.

217

218 *2.3.2 Linking elasticity to population and external factors*

219 Generalized additive models (GAMs) are useful to detect ecological interactions (Glaser et al. 2014) and
220 are used as non-parametric approaches (considering both linear and non-linear effects) that generally
221 outperform parametric methods (Megrey et al. 2005). GAMs were applied to relate the fluctuations of
222 elasticity to recruitment to variability of demographic (i.e. generation time, population abundance, fishing
223 mortality and predation), and environmental variables. Analyses were conducted both at a stock-specific
224 level and across all stocks. Stock-specific analyses were performed with GAM, whereas a generalized
225 additive mixed model (GAMM) was used to perform a joint-analysis of all stocks, with stock as a random
226 variable, in order to detect potential general drivers. The models were formulated as follows:

$$227 \quad E[y] = a + s_1(V_1) + s_2(V_2) + \dots + s_n(V_n) + \varepsilon$$

228 Where $E[y]$ is the expected value of the response variable y (i.e. recruitment elasticity), a , is the model
229 intercept, $s_i(V_i)$, is a smooth function of the explanatory variable i , and ϵ , is the error term. Residuals were
230 assumed to follow a beta-distribution as elasticity values are bounded over the interval 0 to 1.

231 Before performing model selection, variance inflation factors (VIFs) were calculated between all
232 explanatory variables to detect collinearity. Covariates with the highest VIFs were subsequently removed
233 from the model until the highest VIF value was inferior to 3 (Zuur et al. 2007). Therefore, water
234 temperature at 200 and 250m were not considered in the models tested in this study. To limit potential
235 overfitting, a forward selection approach was used to limit the number of variables that can be present in
236 the most parsimonious models. After every step, each variable that was not already in the model was
237 tested individually for inclusion in the model. The most significant variable was added to the model, as
238 long as its p -value was below a pre-set level (here 0.05). We performed a model selection procedure
239 choosing the model with the lowest Akaike's information criterion (AICc, Burnham & Anderson 2002),
240 corrected for small sample sizes, that also showed $p \leq 0.05$ for all variables. Assumptions were examined
241 graphically for selected models (i.e. temporal linear trend and autocorrelation in residuals). To test for
242 optimal model stability and for potential points with high leverage, we then performed a leave-one-out
243 analyses as recommended by Brooks & Deroba (2015). Each data point from the recruitment elasticity
244 time series was omitted systematically and then all possible models were refit to the remaining dataset,
245 to determine the rank of the optimal model found with all data. GAMs were fitted in R using the 'mgcv'
246 package (Wood & Wood 2015). All statistical analyses were performed with R 3.3.2 (R Core Team 2016).

247

248 3. Results

249 Time series of stock assessment estimates (stock abundance and fishing mortality, Fig. 2), and calculated
250 generation time, population growth and transient elasticity to recruitment (Fig. 3) are displayed for all
251 stocks. Abundance highly fluctuated for all stocks but included long periods of very low abundance for
252 both cod stocks (between 1990 and 2010 for northern cod; since 1992 for southern cod, Fig. 2) and 4T
253 spring herring (since 2003, Fig. 2). Fishing mortality decreased over time for both cod stocks, to reach
254 lower values after 1992 (Fig. 2). In contrast, F mainly increased (sometimes slightly) over time for 4R
255 herring and mackerel, whereas F alternated between periods of low and high values for 4T herring (with
256 low values for both spawning components since 2010, Fig. 2). Generation time alternated between high
257 and low values across time periods with amplitude of around 2.5 years for 4R herring (from 4.55 to 7.34
258 and from 5.44 to 7.65 for 4R spring and fall herring, respectively) and 3.5 years for mackerel (from 5.80 in
259 the 1970s to 2.13 in 2011, Fig. 3). Generation time amplitudes for cod (from 5.65 to 6.93 and from 6.21
260 to 7.95 for northern and southern stocks, respectively) and 4T herring (from 4.58 to 5.96 and 4.76 to 5.83
261 for spring and fall stocks, respectively) were less pronounced (Fig. 3). F consistently had a significant and
262 negative effect on generation time (linear model, p always <0.01 for all stocks). Population growth highly
263 fluctuated and never displayed a clear trend for the herring and mackerel stocks (Fig. 3). Changes were
264 rather periodic for cod with a decrease from the 1980s to the beginning of the 1990s, and an increase to
265 most recent years marked by a short-term decrease during some years at the end of the 2000s. The e_{rec}
266 was close to 0 (indicating that the e_{sur} was close to 1) and highly variable for all stocks but differences
267 appeared between stocks (Fig. 3). On average, the lowest e_{rec} values among the stocks studied were
268 estimated for demersal stocks (both northern and southern cod stocks, 0.10 ± 0.03 and 0.09 ± 0.05
269 $\text{mean} \pm \text{SD}$, range 0.05-0.18 and 0.04-0.24, respectively). The highest e_{rec} values among the stocks studied
270 were estimated for Atlantic mackerel (0.24 ± 0.17 , 0.034-0.83). Spring (4R: 0.18 ± 0.16 , 0.02-0.75; 4T:
271 0.17 ± 0.07 , 0.06-0.42) and fall herring (4R: 0.14 ± 0.10 , 0.04-0.50; 4T: 0.16 ± 0.06 , 0.07-0.31) showed

272 intermediate e_{rec} values, although with more pronounced variability for 4R herring (Fig. 3). Conversely,
273 the e_{sur} is higher for cod than for herring and mackerel.

274 Deep-sea salinity, the sea ice volume and the CIL index anomalies were highly unstable with alternating
275 positive and negative periods without any long-term trend (Fig. 4). The St. Lawrence runoff anomaly
276 mainly decreased from 1971 to 2003 (with a slight increase from 1990 to 1998), then increased from 2003
277 to 2014 (Fig. 4). The SST in August and between May and November fluctuated without pattern between
278 1971 and the 1990's, after which an increase was observed (Fig. 4). Similarly, an increasing trend occurred
279 after 1992 for the deep-water temperature at both 150 m and 300 m (Fig. 4). Seal abundance remained
280 steady at low levels during the 1970s in 4R and 4T, followed by an increase up until 2014, where the
281 highest recorded values since 1970 were observed (Fig. 4).

282 Stock specific GAM models accounting for the year to year changes in the recruitment elasticity explained
283 between 34% (northern cod) and 62% (southern cod) of the deviance (Table 3). Generation time, water
284 temperature and St. Lawrence runoff were the main variables explaining e_{rec} variability (Table 3). The
285 decrease in the generation time led to an increase in e_{rec} for mackerel, and 3 out of the 4 herring stocks
286 (i.e. 4R spring and both 4T stocks), however, this was not found for cod (Figs. 5&6). The effect of
287 environmental conditions and fishing mortality depended on the stock considered (Table 3). For 4R fall
288 herring, both 4T herring stocks, as well as southern cod, the e_{rec} was positively related to warm conditions
289 (i.e. high surface and/or intermediate water temperature and low ice coverage, Fig. 5&6). St. Lawrence
290 runoff exhibited a positive relationship with northern cod e_{rec} , a negative relationship with 4R spring
291 herring e_{rec} (Fig. 5), and a dome-shape relationship with mackerel (Fig. 6). Higher deep-water salinity was
292 significantly linked to higher e_{rec} for 4R spring herring (Fig. 5). Additionally, a positive effect of F was also
293 found for southern cod (Fig. 4). No effect of stock or predator abundance was found, regardless of the
294 stock considered. In all stocks, leave-one-out analyses showed that the optimal model was very stable

295 even when years were removed and was not influenced by potential points with high leverage (see Fig.
296 S1).

297 The selected GAMM model revealed that generation time and water temperature at 150 m were
298 significant variables for explaining recruitment elasticity variability when considering all stocks together
299 ($R^2 = 0.32$, Table 3 and Fig. 7). The generation time had a negative effect on the recruitment elasticity (Fig.
300 7), smaller generation time being associated with higher e_{rec} values. Water temperature at 150 m had a
301 positive effect, the warmer the temperature, the higher the e_{rec} (Fig. 7). Other environmental variables
302 (surface water temperature, sea ice volume, deep-water salinity, St. Lawrence runoff), as well as fish
303 abundance and F did not significantly explain recruitment elasticity variability when all stocks were
304 considered together (see Fig. S2).

305

306 4. Discussion

307 By compiling biological data for seven of the most important fish stocks in the GSL, this study is the first
308 to report the sensitivity of population growth to recruitment of northwest Atlantic fish stocks. We
309 investigated both the relative importance of changes in recruitment to the annual population growth as
310 well as how fisheries, climate and predation could affect the importance of recruitment. Regardless of the
311 stock considered, adult survival rate (and thus fisheries management) was more important than
312 recruitment to determine fish population growth, as e_{rec} values were closer to 0 than 1. The variability of
313 the relative importance of recruitment to population growth was generally explained by age-truncation
314 (i.e shorter generation time) and increased water temperatures, with some stock-specific differences.
315 Specifically, increased waters temperature affected mainly the southern stocks e_{rec} , indicating the highest
316 sensitivity of southern population growth to ongoing and future climate change through recruitment
317 variability.

318

319 4.1 *Effects of generation time, fishing and predation*

320 Reduced generation time increased the dependence of population growth rate upon the recruitment in
321 most stocks, especially for the shorter-lived species considered (i.e. mackerel and herring in the GSL). This
322 finding emphasizes how e_{rec} can be affected by the long-term deterioration of the population age structure
323 (Rouyer et al. 2011, Hidalgo et al. 2012). Additionally, this corroborates the fact that species with the
324 shortest generation time are more sensitive to changes in recruitment when the older age classes are less
325 represented or quasi-absent in the stock (Berkeley et al. 2004). However, 4R fall herring and both cod
326 stocks were not significantly affected by generation time. This indicates that the relationship is not general
327 as it has already been suggested in a similar study on 11 stocks (Durant & Hjermann 2017). Climate and
328 fisheries harvesting can both influence age-structure and thus generation time at different time scales

329 (Conover & Munch 2002). In this study, we observed a significant negative correlation of generation time
330 with fishing mortality, corroborating with previous studies on population age truncation due to fishing
331 (Ottersen et al. 2006, Rouyer et al. 2011). However, due to the relatively small R^2 of 0.35, factors other
332 than fishing mortality act on generation time variability. For example, environmental variability has been
333 shown to strongly affect age structure (Ottersen et al. 2006). However, environmental long-term changes
334 in the GSL until the beginning of the 2010's was relatively low compared to other regions (Galbraith et al.
335 2018). Thus, high fishing pressure on larger individuals, through its effect on stock demographic structure,
336 seems to be a very important factor for stock dynamics and sensitivity to recruitment variability in the
337 GSL. This stresses the need for balance harvesting and alternative fisheries attenuating the pressure on
338 old individuals in order to reduce population growth rate sensitivity to recruitment and climate variability.
339 This is also consistent with the observation that the 4R fall herring, as well as both cod stocks have recently
340 experienced low fishing pressure in the GSL and display lower e_{rec} values than other stocks. Stocks exposed
341 to lower fishing pressure may experience weaker generation time variations, thus be less sensitive and
342 more resilient to changes in recruitment (Planque et al. 2010).

343
344 For the considered stocks, the direct effect of fishing pressure on elasticity to recruitment was weak and
345 only significant for the southern cod model. This may be because of the lack of variability and pattern in
346 estimated fishing mortality over time, with the exception for 4T Spring herring, southern cod and
347 mackerel. In contrast, the generation time better captured short term elasticity variations and was
348 selected by the model. For southern cod, this suggests that fishing mortality may have a quicker effect on
349 e_{rec} than for other stocks. With lower fishing mortality and therefore lower population growth sensitivity
350 to recruitment, cod adult survival (and thus fishing management and/or predation) would have a stronger
351 effect on southern cod stock population growth. When considered (i.e. for southern cod and mackerel),
352 the predation did not displayed any significant effect on elasticity to recruitment. For mackerel, grey seal

353 predation pressure might be too small to trigger significant effects relative to fishing and environmental
354 changes. This is more surprising for southern cod as predators (e.g. seals) were shown to strongly affect
355 cod population dynamics (i.e. recovery) since its collapse in the 1990's (Swain & Benoît 2015). This sudden
356 increasing predator importance in the mid 1990's could have not been detected due to the 1971-2007
357 time series used in this study. Moreover, the limited number of predators available with reliable
358 abundance indices, as well as the examination of only the predator abundance to represent the complex
359 dynamics of the trophic links (e.g. cod both is a predator and a prey) may also prevent finding significant
360 link with recruitment elasticity in the GSL.

361

362 *4.3 Effects of the climate variability*

363 This study considered a large range of environmental variables. Water temperature in particular had an
364 important effect on fish population growth elasticity to recruitment, especially in the southern GSL. For
365 4R fall herring, 4T herring stocks and southern cod, warmer environmental conditions (through either high
366 surface or intermediate water temperature and/or less ice) were linked to an increase in the dependence
367 of population growth to recruitment. Consequently, these four stocks may be more productive in warmer
368 waters, and their population growth is likely to be more sensitive to climate fluctuations. Indeed, warmer
369 environmental conditions were shown to enhance recruitment for fall herring by favoring the temporal
370 match between food resources and fall herring larvae production (Brosset et al. 2019) but also to induce
371 larger larvae size for cod (Pepin et al. 1997). The temperature effect might have been occurring more
372 clearly in the southern GSL because this area experienced relatively more warming than the northern gulf
373 (Galbraith et al. 2018). Therefore stocks inhabiting this zone, such as 4T herring and southern cod, are
374 expected to experience more pronounced environmental changes and thus to be more susceptible to
375 physical and biological changes related to temperature change. Interestingly, spring herring recruitment
376 is known to be favoured by colder environmental conditions (Brosset et al. 2019), thus an inverse

377 relationship between e_{rec} and temperature was expected for 4T spring herring. This may be explained
378 because Brosset et al. (2019) used large scale indices which did not only reflect the effect of temperature.
379 Thus, while a direct temperature effect might be positive, it may be counterbalanced by indirect negative
380 temperature effects that are included in the large scale indices. The significant effect of water
381 temperature corroborates those obtained for the northeast Atlantic (Rouyer et al. 2011; Durant et al.
382 2013, Durant & Hjermann 2017), where population growth became increasingly dependent on
383 recruitment under warmer environmental conditions. This may reflect the large impact of bottom-up
384 processes, known to influence zooplankton communities in the GSL (Plourde et al. 2015), and thus fish
385 recruitment, beneficial for some stocks (i.e. both 4T herring stocks, 4R fall herring and southern cod).

386
387 While warming waters seem to always have a positive effect on e_{rec} , the effects of the other environmental
388 variables (salinity, freshwater runoff) were stock-specific, and might be specific to each species biology.
389 For example, freshwater runoff had the inverse effect on e_{rec} for northern spring herring (negative) and
390 cod (positive), while both species are late spring spawners. Since cod and herring larvae prey on distinct
391 plankton species (Fortier & Gagné 1990, Robert et al. 2011), different levels of freshwater runoffs favoring
392 different plankton species may therefore indirectly act on their recruitment (Ouellet et al. 1997, Légaré et
393 al. 2014). Moreover, higher deep-water salinity values, an indicator of nutrient rich deep water entering
394 into the GSL (Galbraith et al. 2018), were shown to only increase 4R spring herring e_{rec} . This suggests that
395 the variability in growth rate dependency to recruitment can result from climate-induced changes
396 affecting both the development and the survival of early life stages, as well as shaping recruitment
397 dynamic through bottom-up changes.

398

399 *4.4 Management implications and possible consequences for the future*

400 No fish stocks were equally affected by changes in generation time and environmental conditions,
401 corroborating findings of Durant & Hjermann (2017). We considered different stocks for some of the same
402 species, which underlined the specificity of each in terms of their sensitivity to climate change and fishing
403 pressure, as well as the importance of stock- and species- specific management procedures.

404 Short-lived pelagic species are known to be more dependent on recruitment peaks and optimal
405 environmental conditions in comparison to longer-lived species such as cod (Rouyer et al. 2011). This was
406 shown in the GSL, where pelagic stocks had a relatively higher and more variable e_{rec} compared with a
407 lower e_{rec} exhibited by cod, confirming that long lived species are usually less dependent on recruitment
408 for population growth (Gerber & Heppell 2004, Vélez-Espino et al. 2006). However, regardless of the stock,
409 population growth was consistently determined by adult survival rather than recruitment. This implies
410 that when elasticity is generally inferior to 0.5, as observed, management rather than climate might be
411 responsible for stock size fluctuations. The idea that the population dynamic of the 7 stocks studied is
412 mainly driven by adult survival is encouraging as managers may have larger control over stock size and
413 growth (by modulating fishing mortality), even if current short generation time may also make
414 management measures more uncertain. Moreover, management measures should remain efficient even
415 with climate change, which should help to efficiently maximize adult survival (see Hayes 2000).
416 Nevertheless, some trends need to be recognized and discussed.

417 Firstly, there was a clear increase in e_{rec} for mackerel after 2000, when its exploitation rate reached
418 maximum levels and its generation time decreased (DFO 2017a, Van Beveren et al. 2017). For this
419 currently overexploited stock, population growth became by consequence increasingly dependent on
420 strong recruitment events and hence environmental changes. Such knowledge is noteworthy for
421 management, as stock recovery will be highly dependent on environmental conditions. Furthermore, in
422 the long-term, unfavourable environmental conditions will probably impact recruitment. Secondly, in the

423 future, stock-specific growth of all stocks considered may become more dependent on recruitment rather
424 than adult survival, making them potentially more challenging to manage. Waters, particularly in the
425 South (Galbraith et al. 2018), are likely to become warmer (Srokosz et al. 2012), which would result in
426 higher importance of recruitment to population growth. Hence, stocks of longer-lived species like cod
427 might in the future behave more similarly to the dynamics of short-lived populations (Durant & Hjermann
428 2017). However, predictions were not conducted, as the extrapolation of drivers (e.g. temperature) would
429 potentially result in estimates lying outside of the scope of observations. However, Lee (2017) proposed
430 a novel approach including the possibility for drivers to attain previously unrecorded values, which could
431 be used in further work to determine the potential population growth rate for the next decade.

432

433 *4.5 Remarks*

434 Stock assessment estimates of population abundance are subject to multiple sources of uncertainty
435 (Brooks & Deroba 2015, Palmer et al. 2016), and results using these estimates should be considered
436 cautiously. Except for mackerel, abundance and fishing mortality estimates come from the same
437 assessment model (i.e. a VPA), keeping the assessment framework uniform among 6 out of 7 stocks. Even
438 if mackerel stock estimates were calculated with a state-space assessment, which differs from the VPA
439 (e.g. it estimates simultaneously observation and process errors), the same care was conducted through
440 checking model assumptions that could strongly influence the stock assessment outputs. Indeed,
441 whichever the assessment model used, we carefully checked for the potential effect of natural mortality
442 misspecification, as it can have an important effect on stock estimates through the interplay between
443 mortality and recruitment. Whenever strong empirical indications to include time-varying mortality
444 existed (i.e. for seal predation on cod, Swain & Benoît 2015), it was considered in the model to avoid
445 increasing recruitment variability. Likewise, the high degree of confidence about stock assessment model

446 inputs made us confident about potential weak and constant observation error across stocks. Combined
447 with the sensitivity analyses carried out during the stock assessment process, elasticity and leave-one-out
448 analyses, we are confident in the robustness of our results and conclusions against the potential
449 uncertainty from the use of stock estimates for post-hoc analyses. Furthermore, this is strengthened by
450 the consistency of our results with previous studies (Wang et al. 2017, Durant & Hjermann 2017), as well
451 as the corroboration with species-specific differences found in our study and ecological knowledge in the
452 current literature (Plourde et al. 2015, Swain & Benoît 2015, Brosset et al. 2019).

453

454 **5. Conclusion**

455 The elasticity approach was used to determine population growth sensitivity to recruitment for different
456 fish stocks of the GSL, supporting previous results obtained in the NE Atlantic and Pacific (Durant et al.
457 2013, Durant & Hjermann 2017). Our results highlight that adult survival is the key factor to restore the
458 considered fish stocks, and that even if low generation time and warming conditions increase, the
459 importance of recruitment to population growth makes these stocks more difficult to manage. This
460 reinforces the ongoing management efforts focussing on the development of methods and management
461 strategies that would result in a more accurate control of fishing effort.

462

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471

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630

631

632 Table 1. Data and estimates type and sources used, if applicable by stock and with indication of the
 633 considered time period. In the period column, years between parentheses are those used for GAM
 634 analyses, as environmental time-series only begin in 1971 and transient population growth elasticity to
 635 recruitment calculations shorten the length of the time series.

Stock	Time period	Data	Source
Northeast stocks	4R spring Herring 1965-2016 (1971-2008)	Fishing mortality (F_{4-10})	Unpublished
		Maturity at age (%)	Grégoire et al. (2015), p18, updated to 2016
		Weight at age (kg)	Grégoire et al. (2015), p12, updated to 2016
		Number at age (10^6)	Unpublished
	4R fall Herring 1965-2016 (1971-2008)	Fishing mortality (F_{4-10})	Unpublished
		Maturity at age (%)	Grégoire et al. (2015), p31, updated to 2016
Weight at age (kg)		Grégoire et al. (2015), p25, updated to 2016	
Number at age (10^6)		Unpublished	
North Cod (4RS+3Pn areas) 1974-2015 (1974-2007)	Fishing mortality (F_{5-8})	Brassard et al. (2018), p63	
	Maturity at age (%)	Brassard et al. (2018), p54	
	Weight at age (kg)	Brassard et al. (2018), p32	
	Number at age (10^6)	Brassard et al. (2018), p58	
South stocks	4T spring Herring 1978-2015 (1978-2009)	Fishing mortality (F_{4-10})	Swain (2016), p14
		Maturity at age (%)	Unpublished
		Weight at age (kg)	Leblanc et al. (2015), p39
		Number at age (10^6)	Swain (2016), p13
	4T fall Herring 1978-2015 (1978-2008)	Fishing mortality (F_{4-10})	Swain (2016), p23
		Maturity at age (%)	LeBlanc et al. (2015), p73
Weight at age (kg)		Leblanc et al. (2015), p56	
Number at age (10^6)		Swain (2016), p19	
South Cod (4T+4Vn areas) 1971-2014 (1971-2007)	Fishing mortality (F_{5-8})	Swain et al. (2015), p58	
	Maturity at age (%)	Swain et al. (2015), p50	
	Weight at age (kg)	Swain et al. (2015), p28	
	Number at age (10^6)	Swain et al. (2015), p63	
Entire GSL	Mackerel 1968-2016 (1971-2010)	Fishing mortality (F_{5-8}) Maturity at age (%) Weight at age (kg) Number at age (10^6)	Grégoire & Beaudin (2014), p19, updated to 2016 Gregoire & Beaudin (2014), p15, updated to 2016 Gregoire & Beaudin (2014), p12, updated to 2016 Gregoire & Beaudin (2014), p18, updated to 2016

636

637

638 Table 2. Environmental data description for the Gulf of St Lawrence and the sources used.

Time period	Data	Description	Source
1971-2016	Surface temperature	Annual anomaly of upper layer temperature in August averaged between May and November	Galbraith et al. (2018)
	Cold intermediate layer (CIL) temperature	Annual anomaly of the Cold Intermediate layer (CIL) minimum temperature	Galbraith et al. (2018)
	Deep Temperature	Annual anomaly of temperature at 150, 200, 250 and 300 m	Galbraith et al. (2018)
	Annual Ice volume index	Annual anomaly of ice volume and timing of ice melting	Galbraith et al. (2018)
	Deep Salinity	Annual anomaly of the salinity in the water layers >150 m	Galbraith et al. (2018)
	St Lawrence runoff (m ³)	Seasonal (Jan–June) freshwater discharge at Québec City	Galbraith et al. (2018)
	Seal abundance	Annual estimation of the number of individuals of both the northeastern GSL and the southern GSL seal	Hammil et al. (2014) for the north part Swain & Benoit (2015) for the south part

639

640

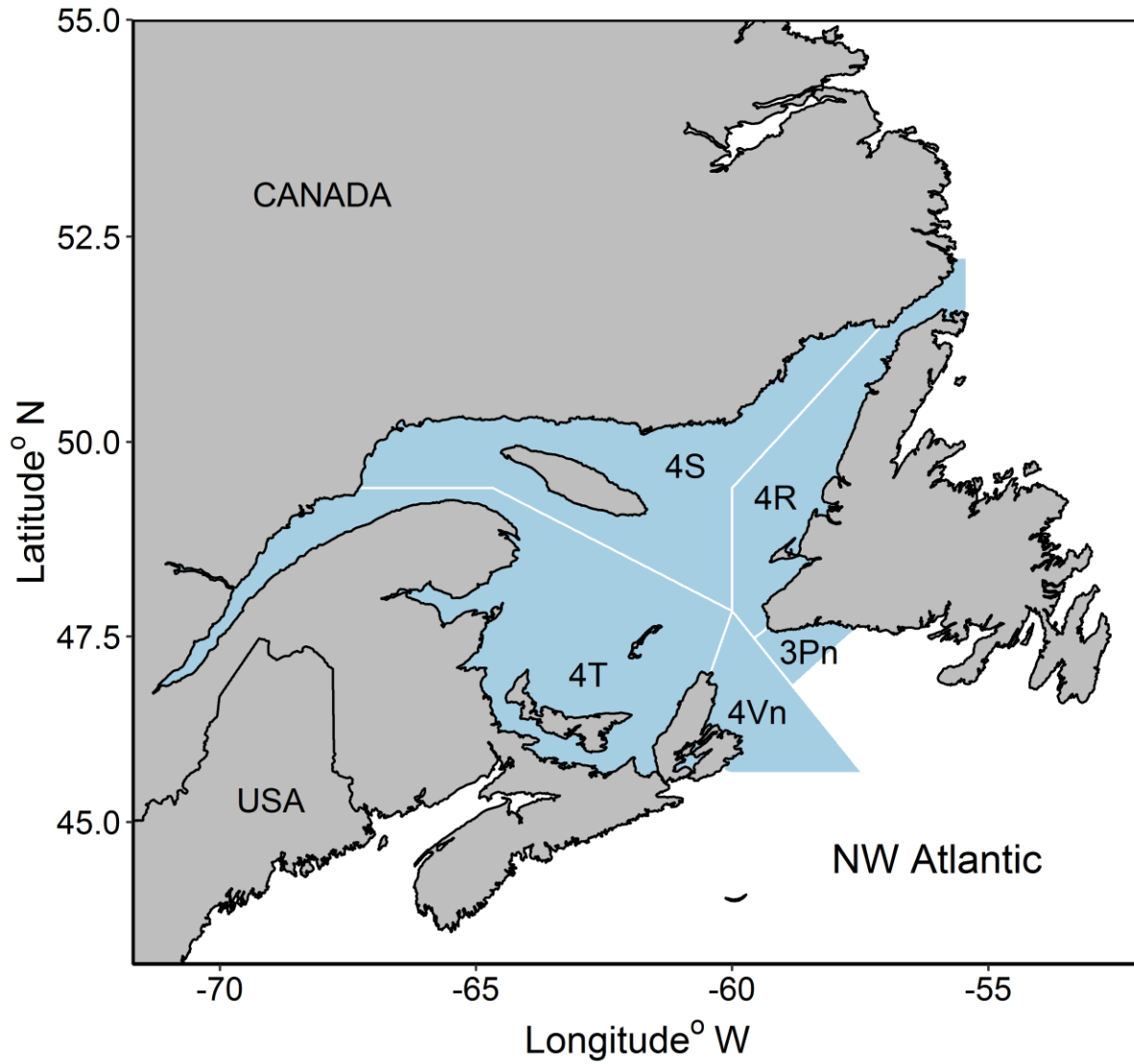
641 Table 3. Details of the best Generalized Additive Models (GAMs) testing the effects of age structure,
 642 environmental variability and fishing pressure on transient population growth recruitment elasticity. The
 643 GAMM model included the stock as a random variable. Generation time (μ): yearly mean age of spawners
 644 producing offspring; F: Fishing mortality for the age range indicated by subscript in Table 1; Deep Sal: Deep
 645 water salinity; Freshw: St Lawrence runoffs; SST Aug: sea surface temperature in August; SST May.Nov:
 646 sea surface temperature mean between May and November; T 150: intermediate water layer
 647 temperature (150 m); CIL: cold intermediate layer temperature; Ice Vol: Ice volume. DEV is the % of
 648 deviance explained. The significance of each term is noted as * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

649

650	Stock	Time series	Best GAM Model selected	DEV
651	Northeastern stocks	4R spring herring	1971-2008 Elasticity ~ μ^{***} + Freshw* + Deep Sal*	58
652		4R fall herring	1971-2008 Elasticity ~ T 150*** + Ice Vol*	42
		Northern cod	1974-2007 Elasticity ~ Ice Vol*** + Freshw**	34
	Southern stocks	4T spring herring	1978-2009 Elasticity ~ μ^{***} + SST May.Nov*	43
		4T fall herring	1978-2008 Elasticity ~ μ^{***} + SST May.Nov*	38
		Southern cod	1971-2007 Elasticity ~ F*** + CIL*** + SST Aug**	62
	Entire GSL	Mackerel	1971-2010 Elasticity ~ μ^{****} + Freshw*	46
		All stocks (GAMM)	1978-2007 Elasticity ~ μ^{****} + T 150*	

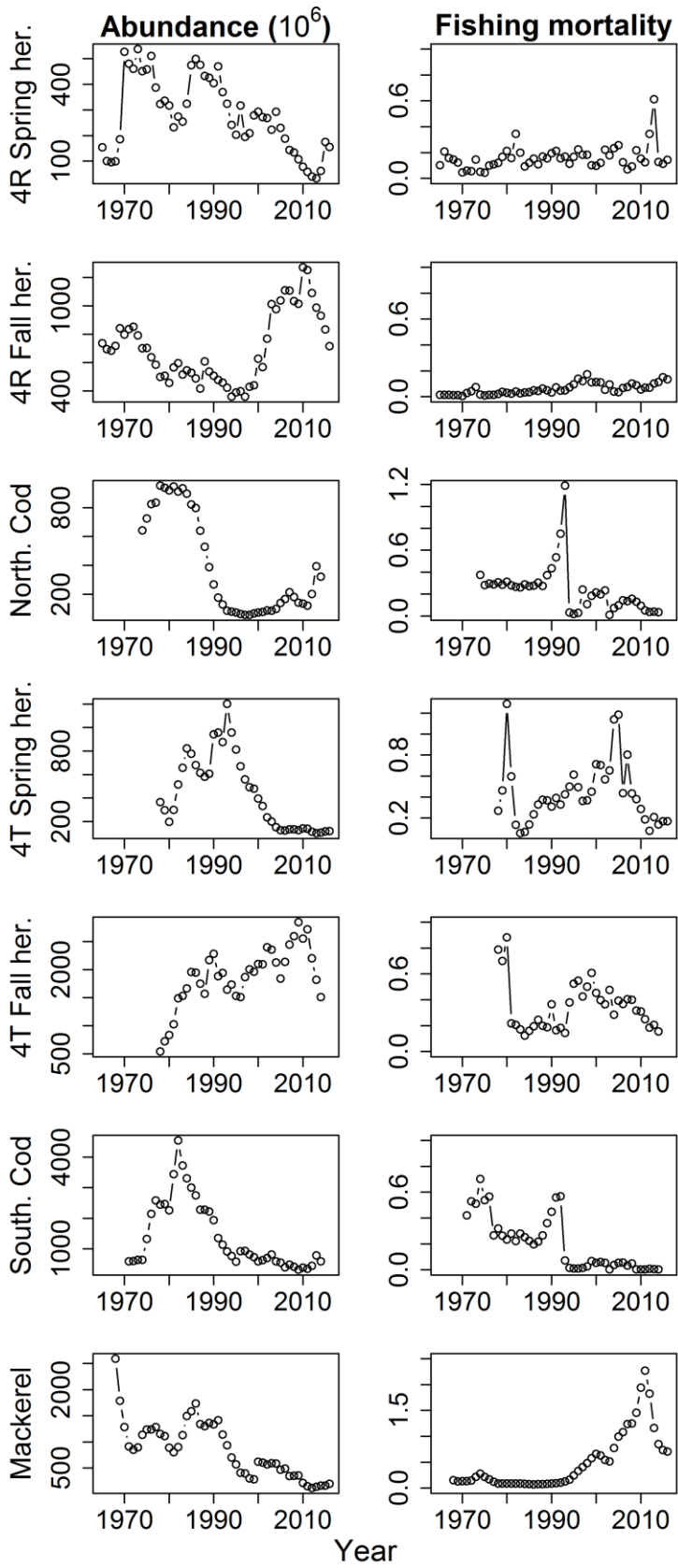
653 Figure captions:

654 Figure 1. Management areas for Atlantic herring, cod and mackerel in the Gulf of Saint Lawrence. Note
655 that the mackerel is managed at the scale of the entire Gulf without distinction between areas.



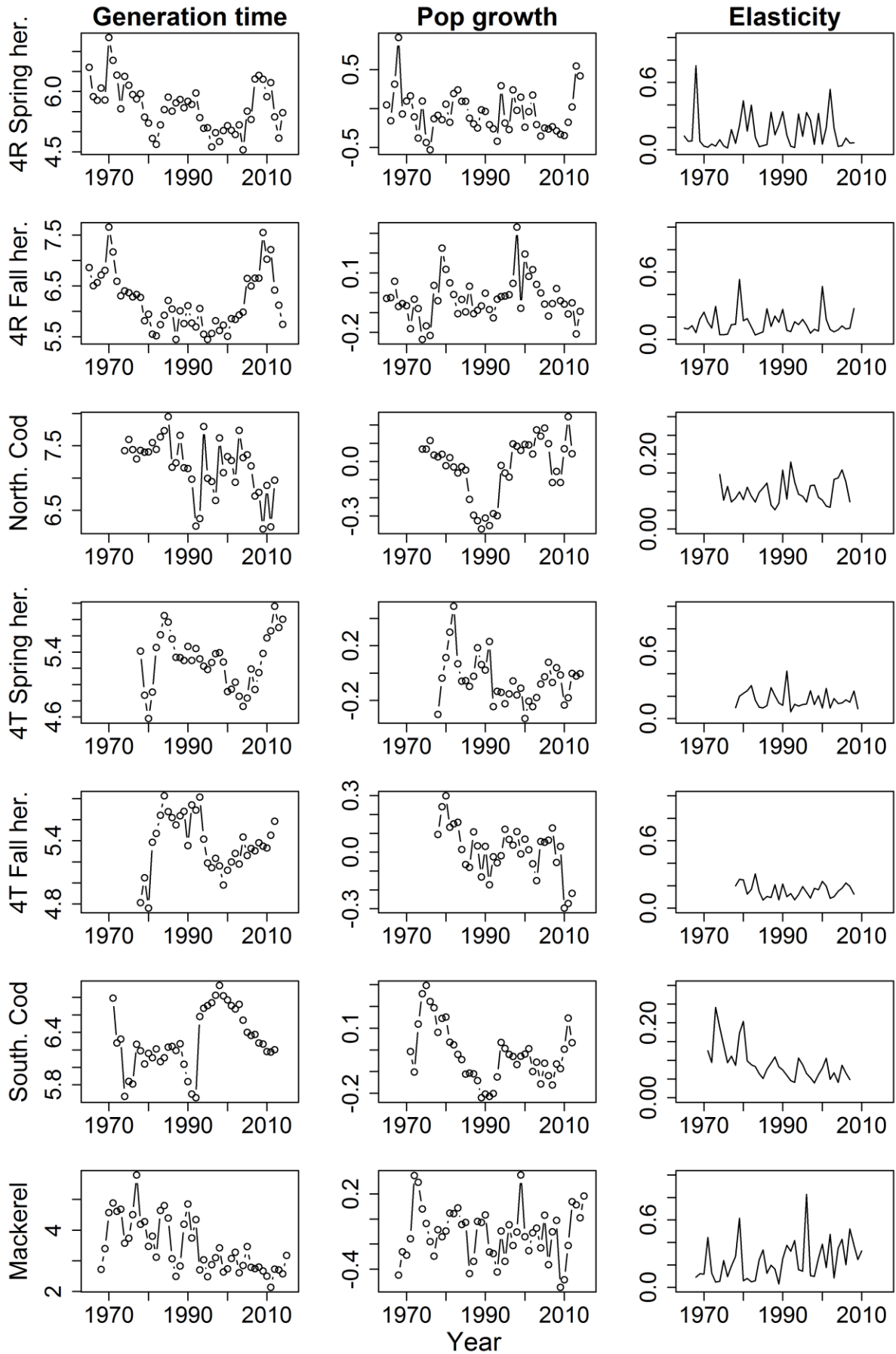
656

657 Figure 2. Stock abundance and fishing mortality time series for the 7 stocks of the Gulf of St Lawrence
658 considered in the study (North: 4R spring and fall herring, northern cod; South: 4T spring and fall herring,
659 southern cod; all GSL: Mackerel). Note that ranges on y axes may differ among panels.

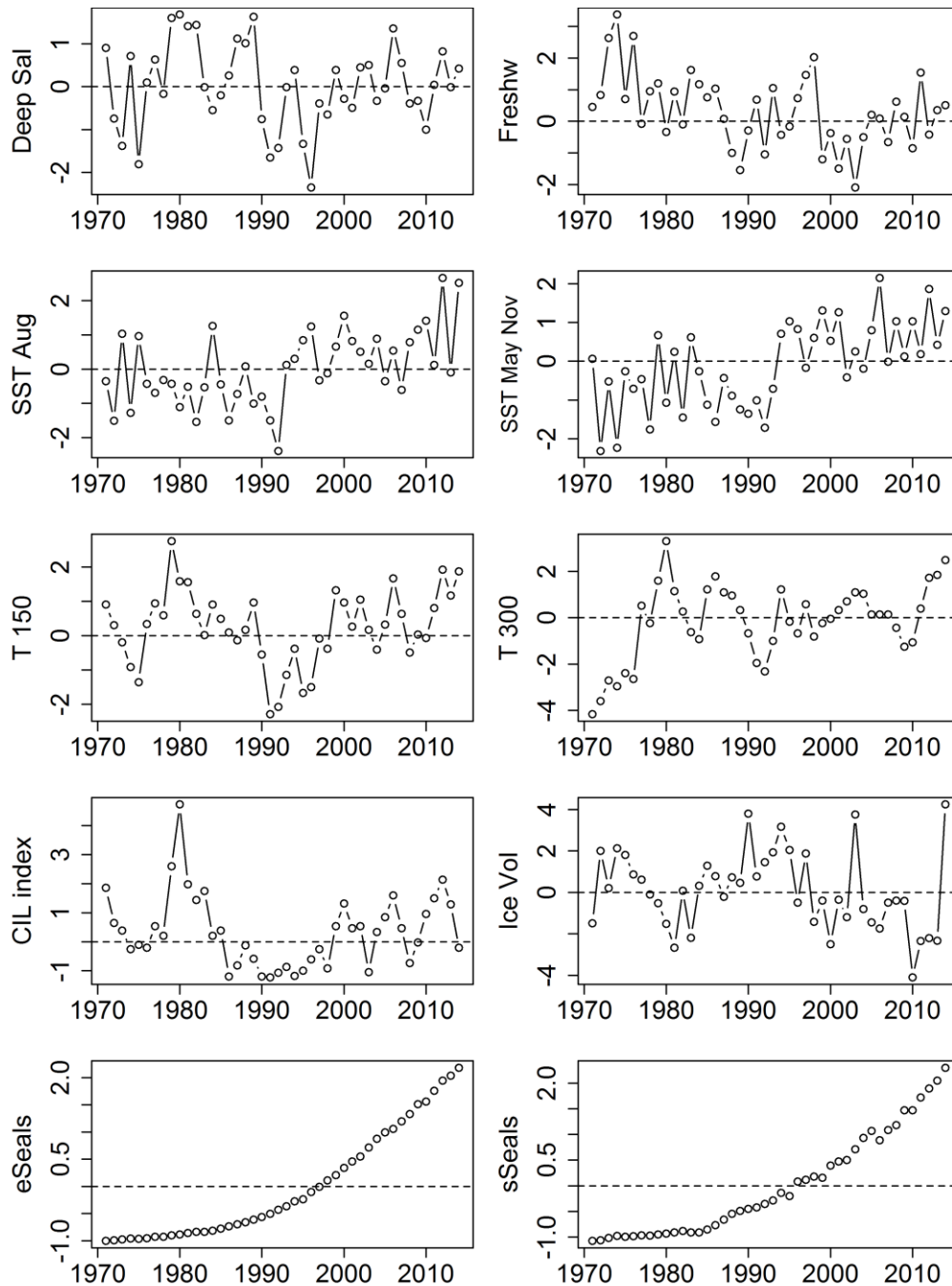


661 Figure 3. Generation time, population growth (Pop growth) and transient population growth recruitment
662 elasticity time series for the 7 stocks of the Gulf of St Lawrence considered in the study (North: 4R spring
663 and fall herring, northern cod; South: 4T spring and fall herring, southern cod; all GSL: Mackerel). Note
664 that ranges on y axes may differ among panels.

665



667 Figure 4. Time series of the environmental parameters anomalies from the Gulf of St. Lawrence (GSL).
 668 Deep Sal: deep water salinity; Freshw: St Lawrence runoffs; SST Aug: sea surface temperature in August;
 669 SST May Nov: sea surface temperature mean between May and November; T 150: intermediate water
 670 layer temperature (150 m); CIL index: cold intermediate layer temperature index; T 300: deep water layer
 671 temperature (300 m); Ice Vol: ice volume; eSeals: seal population abundance in the northeast GSL; sSeals:
 672 seal population abundance in the south GSL.

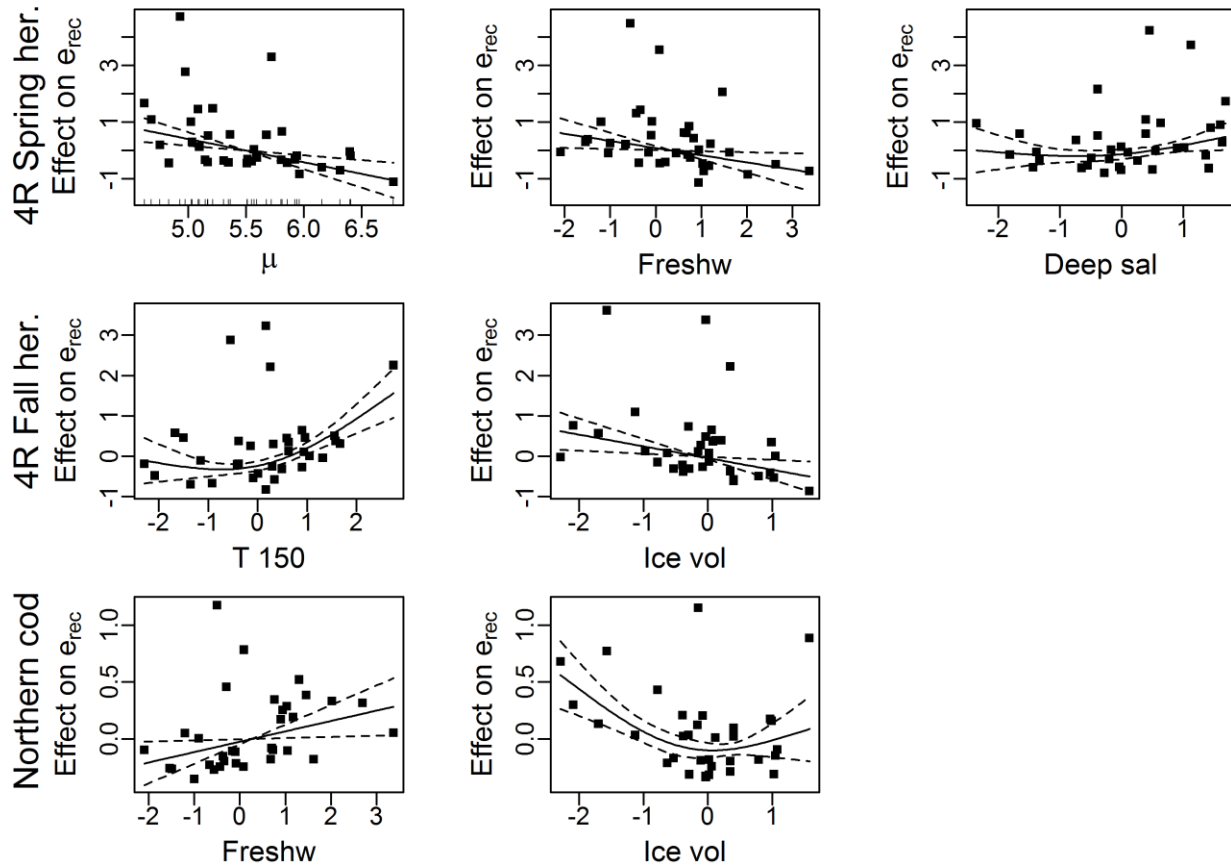


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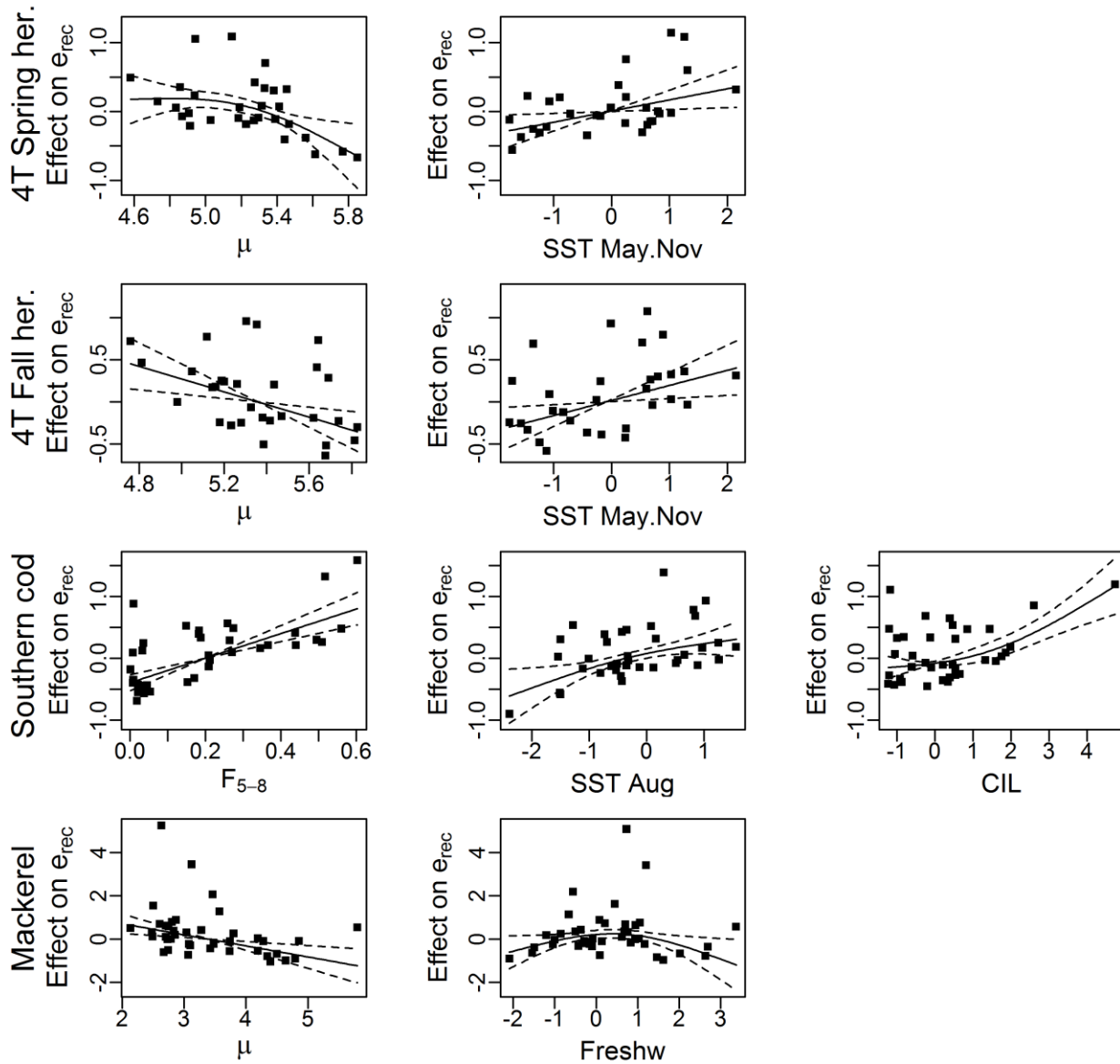
675 Figure 5. Partial GAM plots for the 3 northern stocks showing the population growth recruitment elasticity
 676 (e_{rec}) in response to: generation time (μ); water temperature at 150 m (T 150); deep water salinity (Deep
 677 sal); Ice vol: ice volume; Freshw: St Lawrence runoffs. Others environmental variables as well as the fish
 678 abundance were never significant. Black dots represent the partial residuals and the solid line represents
 679 the estimated mean effect of the independent variables and its 95% confidence interval (dashed lines).

680



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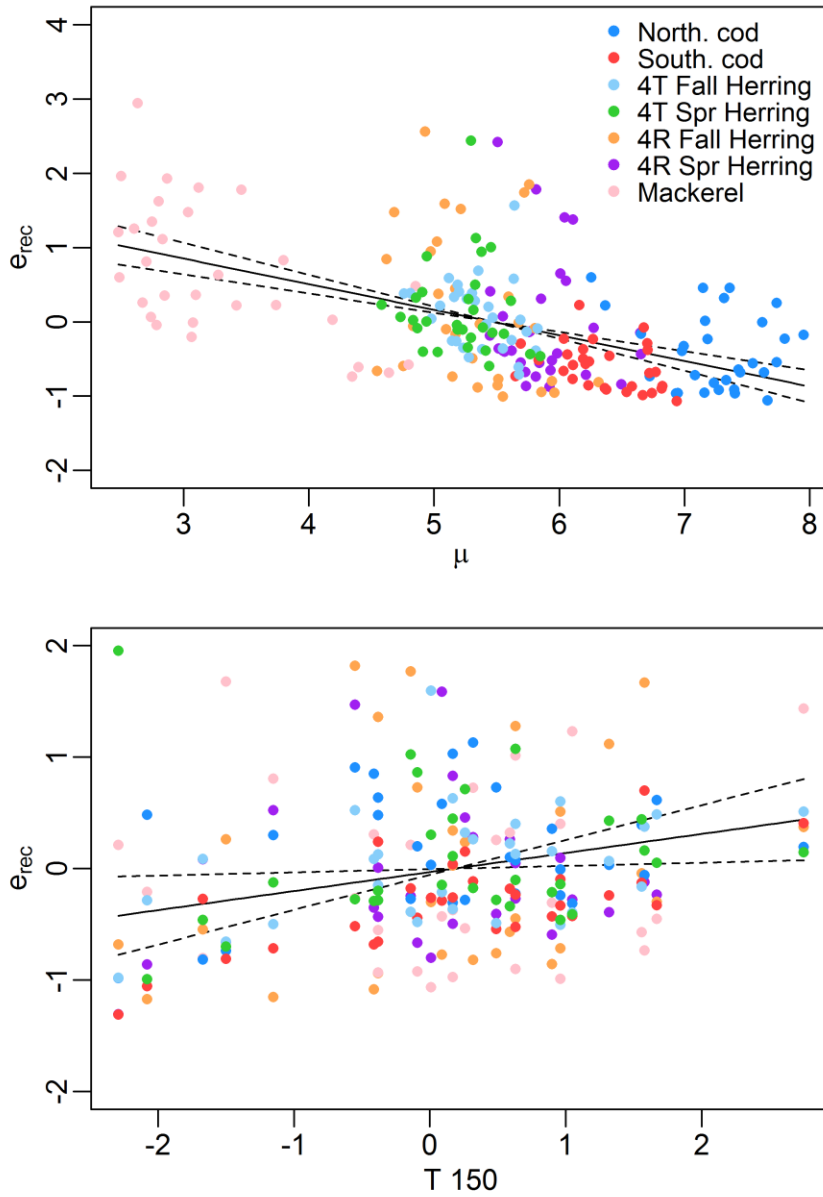
682 Figure 6. Partial GAM plots showing the population growth recruitment elasticity (e_{rec}) for the 3 southern
 683 stocks and the mackerel in response to: generation time (μ); sea surface temperature in August (SST Aug);
 684 sea surface temperature mean between May and November (SST May.Nov); cold intermediate layer
 685 temperature (CIL); St Lawrence runoffs (Freshw); and fishing mortality (F). Others environmental variables
 686 as well as the fish abundance were never significant. Black dots represent the partial residuals and the
 687 solid line represents the estimated mean effect of the independent variables and its 95% confidence
 688 interval (dashed lines).



689

690

691 Figure 7. Partial effects of generation time (μ) and water temperature at 150 m (T 150) on the population
692 growth recruitment elasticity (e_{rec}) found with GAMM analysis. Dots represent the partial residuals and
693 the solid line represents the estimated mean effect of the independent variables and its 95% confidence
694 interval (dashed lines).



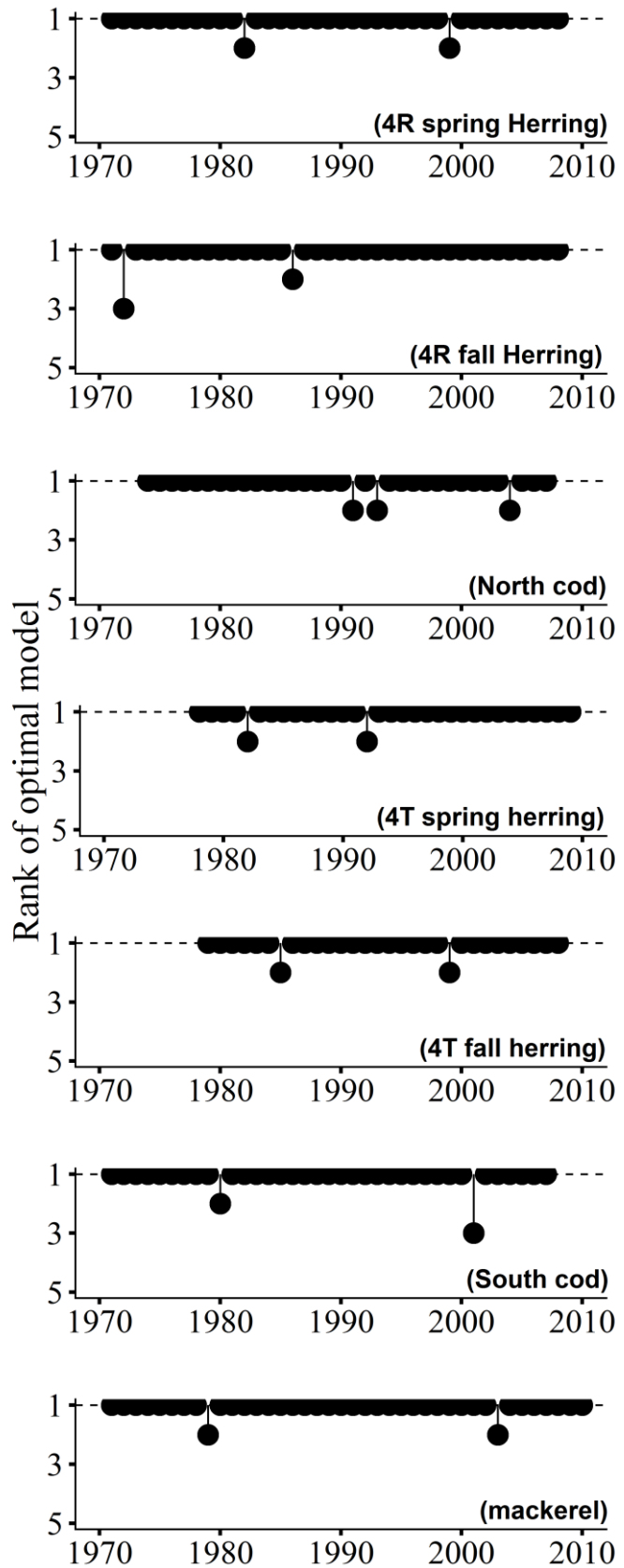
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696 **Supplementary material:**

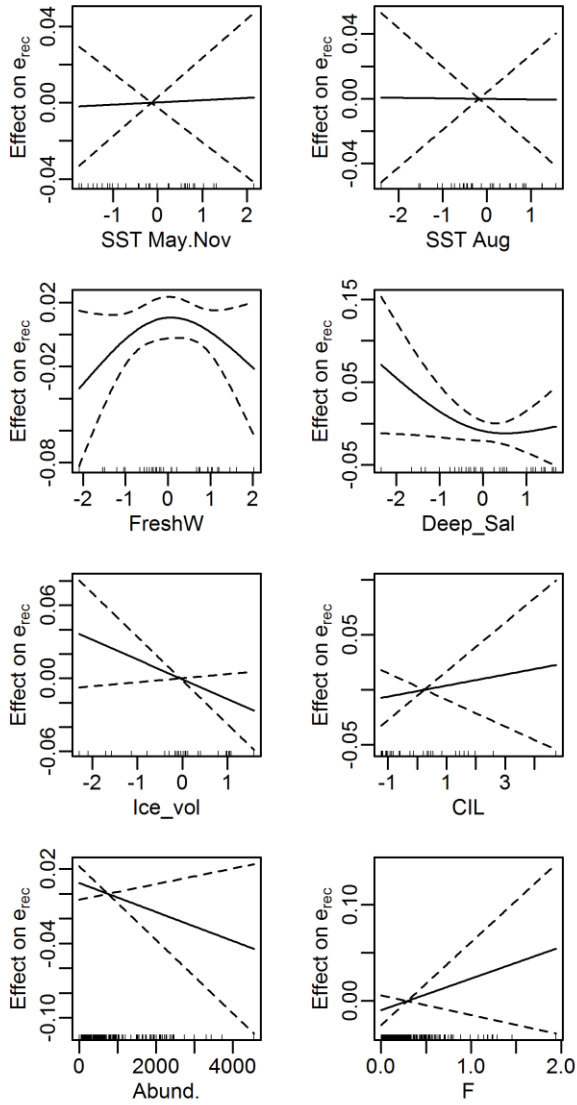
697 Fig S1. Ranking of the optimal elasticity
698 model when the different years are omitted
699 from the analysis (Leave-One Out analysis)
700 for the seven stocks investigated.

701

702



703 Fig S2. Non significant explanatory variables of the population growth recruitment elasticity variability
704 tested by the generalized mixed effect model (GAMM) considering all stocks merged (with stock as a
705 random variable).



706