Fish population growth in the Gulf of St Lawrence: effects of climate, fishing and predator abundance

Pablo Brosset[1],*, Joël M. Durant[2], Elisabeth Van Beveren[1], Stéphane Plourde[1]

[1]**Fisheries and Oceans Canada, Maurice Lamontagne Institute, Mont-Joli, Quebec G5H 3Z4, Canada**
[2]**Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biosciences, University of Oslo,**
PO Box 1066 Blindern, 0316 Oslo, Norway

ABSTRACT: Climate variability, fishing and predation are the main factors affecting fish population dynamics. In this study, the drivers of population growth variability were investigated for 7 fish stocks (2 cod, 4 herring and 1 mackerel stock) in the Gulf of St. Lawrence (NW Atlantic). The annual population growth sensitivity to both recruitment and survival (i.e. how much population growth depends on recruitment and survival) was estimated through elasticity analyses before being linked to harvesting history as well as environmental conditions (climate and predation). Stock-specific generalized additive models showed that population growth was most sensitive to recruitment variability with decreasing fish generation time, increasing water temperature and, in some cases, with predation. The dependence of population growth on recruitment, however, was generally close to 0, albeit higher for pelagic stocks than for demersal ones. This indicates that adult survival was more important than recruitment in shaping population growth and thus population size. As climate mainly acts on recruitment while fishing affects adult survival, management efforts seem more important than climate variability in regulating population growth, especially for long-lived cod. Nevertheless, population growth may become increasingly dependent on recruitment variability with warming waters; therefore, more flexible management strategies should be developed to cope with these oscillations.

KEY WORDS: Cod · Herring · Mackerel · Recruitment · Matrix model · Leslie matrix · Management

1. INTRODUCTION

Mechanisms affecting productivity and hence biomass of marine fish populations are still widely unknown (Houde 1987, Szuwalski et al. 2015). Population productivity is determined by the strength of biological processes (e.g. recruitment and somatic growth), which are difficult to investigate since these estimates are mainly available for data-rich stocks. The strength and drivers of population productivity are also space-, time- and species-specific, since they depend on varying life-history parameters and harvesting history. For instance, population growth of exploited species exhibits higher sensitivity to productivity variability than that of of unexploited spe-

cies (Hsieh et al. 2006), due to fishery-induced truncation of the age structure (Berkeley et al. 2004, Hutchings & Reynolds 2004, Stige et al. 2017). Thus, recruitment variability has a greater influence on stock size if the mature population consists of a small number of age classes (Stearns 1992, Ottersen et al. 2013), reducing the populations' robustness to environmental variations. Additionally, climate change and predation also affect maturity and survival and consequently the sensitivity of populations to recruitment variability (Leggett & Deblois 1994). Therefore, there is a considerable interest and need in understanding population growth changes in temporally varying environments and fishing pressure, not only for ecology but also for conservation and management.

In the Northwestern Atlantic, fish populations of the Gulf of St. Lawrence (GSL) are mostly threatened by overexploitation, climate change and predation by expanding seal populations (Savenkoff et al. 2017). Among the main fish species, mackerel *Scomber scombrus*, herring *Clupea harengus* and cod *Gadus morhua* have a long history of fisheries (Swain et al. 2015, Swain 2016, DFO 2017a,b). In addition to the effects of fishing, these stocks experience large fluctuations in biomass, related to environmental variability acting through bottom-up and top-down process on recruitment success (cod: Lambert 2011, Swain & Benoît 2015; mackerel: Plourde et al. 2015; herring: Brosset et al. 2019). Moreover, grey seal *Halichoerus grypus* abundance has sharply increased since the mid-1990s in both the northeast and south GSL (Hammill et al. 2014, Swain & Benoît 2015), potentially increasing predation pressure on herring and cod (Hammill & Stenson 2000). Given the growing concern about fisheries management, and how sensitive population dynamics are to different pressures, it is particularly relevant to understand fish stock fluctuations in the GSL. Indeed, recent examples have shown that untangling the effect of habitat dynamics (e.g. climate change and predation) and fishing on vital rates (e.g. recruitment or adult survival) have led to a better understanding of population dynamics, with important implications and improvements for management (Ezard et al. 2010, Thorson et al. 2015, Durant & Hjermann 2017).

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

The aim of this study was to assess the contribution of recruitment to population growth (hereafter 'recruitment elasticity' or 'elasticity') and to identify the main drivers of elasticity variability in the GSL ecosystem. We investigated how age structure, climate, potential predation and fishing pressure affect the importance of recruitment in population growth for 7 stocks (4 herring, 2 cod and 1 mackerel stock). Considering different stocks belonging to different trophic levels and habitats, as well as having different exploitation histories will allow further understanding of GSL commercial stock dynamics. Ultimately, given the importance of recruitment and/or adult survival to the population growth, this will help to identify appropriate management measures for these stocks, which could be helpful to resource managers to anticipate potential responses of species to environmental variability.

2. MATERIALS AND METHODS

The 7 commercial fish stocks considered in this study inhabit one or more Northwest Atlantic Fisheries Organization (NAFO) areas (Fig. 1). Three stocks are located in the northern part of the GSL: 4R spring herring, 4R fall herring and northern cod (4RS + 3Pn). Three stocks are located in the southern part: 4T spring herring, 4T fall herring and the southern
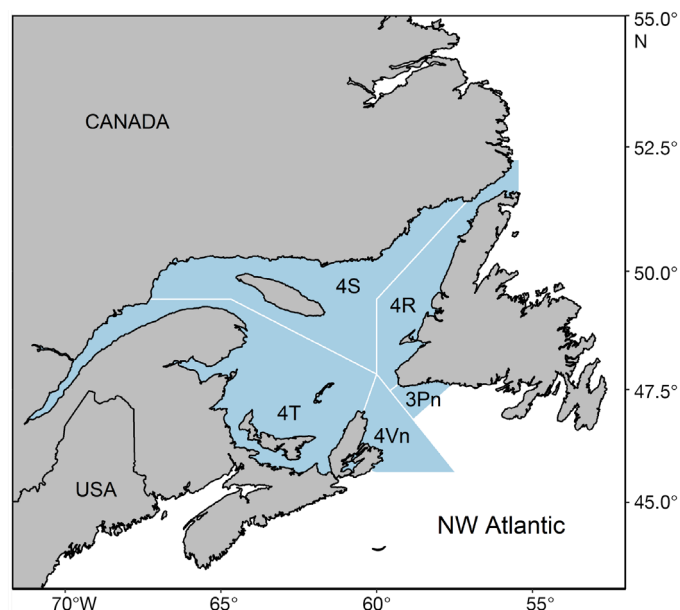

Fig. 1. Management areas for Atlantic herring, cod and mackerel in the Gulf of St. Lawrence. Note that mackerel are managed at the scale of the entire Gulf with no distinction between areas

cod from area 4T. We also analysed a seventh stock, referred to as Canadian contingent mackerel, which migrate between the US and the Canadian east coast (reproducing in the southern GSL around May–July, Moores et al. 1975). These stocks are economically important and their management can be improved, or can benefit from all additional knowledge on population dynamics. Moreover, the 7 stocks include demersal (i.e. cod), and pelagic fish (i.e. mackerel and herring) with different population structures (e.g. longevity) as well as contrasting harvest histories, allowing us to conduct a comparative study on the drivers of population dynamics. These 7 stocks were chosen because of the availability of age-structured biological data (annual maturity- and weight-at-age) and stock assessment model outputs (annual abundance-at-age and fishing mortality).

2.1. Biological data and estimates

Stock specific data (maturity-at-age) and estimates (abundance-at-age and fishing mortality-at-age) were extracted from assessment reports from the Canadian Department of Fisheries and Oceans (DFO) for each year (Table 1). Recruitment estimates are derived from stock assessment models and represent abundance at age 1 (mackerel) or age 2 (herring and cod). Annual fishing mortality estimates (F_y) were calculated by averaging the fully selected age classes of the F-at-age matrix ($F_{a,y}$): F_{4-10} for spring and fall 4R herring and F_{4-8} for mackerel and both cod stocks. The 2 cod stocks (northern and southern) and all the herring stocks were modelled using virtual population analysis (VPA, Swain et al. 2015, DFO 2017b), whereas a newly developed state-space

Table 1. Data and estimate types and sources used, if applicable by stock and with indication of the considered time period. In the time period column, years in parentheses are those used for generalized additive model analyses, as environmental time series only begin in 1971 and transient population growth elasticity to recruitment calculations shorten the length of the time series. GSL: Gulf of St. Lawrence, DFO: Fisheries and Oceans Canada

Stock	Time period	Data	Source
Northern stocks			
4R spring herring	1965–2016 (1971–2008)	Fishing mortality (F_{4-10})	DFO unpublished
		Maturity at age (%)	Grégoire et al. (2015), updated to 2016
		Weight at age (kg)	Grégoire et al. (2015), updated to 2016
		Number at age (10^6)	DFO unpublished
4R fall herring	1965–2016 (1971–2008)	Fishing mortality (F_{4-10})	DFO unpublished
		Maturity at age (%)	Grégoire et al. (2015), updated to 2016
		Weight at age (kg)	Grégoire et al. (2015), updated to 2016
		Number at age (10^6)	DFO unpublished
Northern cod (4RS+3Pn areas)	1974–2015 (1974–2007)	Fishing mortality (F_{5-8})	Brassard et al. (2018)
		Maturity at age (%)	Brassard et al. (2018)
		Weight at age (kg)	Brassard et al. (2018)
		Number at age (10^6)	Brassard et al. (2018)
Southern stocks			
4T spring herring	1978–2015 (1978–2009)	Fishing mortality (F_{4-10})	Swain (2016)
		Maturity at age (%)	DFO unpublished
		Weight at age (kg)	Leblanc et al. (2015)
		Number at age (10^6)	Swain (2016)
4T fall herring	1978–2015 (1978–2008)	Fishing mortality (F_{4-10})	Swain (2016)
		Maturity at age (%)	LeBlanc et al. (2015)
		Weight at age (kg)	LeBlanc et al. (2015)
		Number at age (10^6)	Swain (2016)
Southern cod (4T+4Vn areas)	1971–2014 (1971–2007)	Fishing mortality (F_{5-8})	Swain et al. (2015)
		Maturity at age (%)	Swain et al. (2015)
		Weight at age (kg)	Swain et al. (2015)
		Number at age (10^6)	Swain et al. (2015)
Entire GSL			
Mackerel	1968–2016 (1971–2010)	Fishing mortality (F_{5-8})	Grégoire & Beaudin (2014), updated to 2016
		Maturity at age (%)	Grégoire & Beaudin (2014), updated to 2016
		Weight at age (kg)	Grégoire & Beaudin (2014), updated to 2016
		Number at age (10^6)	Grégoire & Beaudin (2014), updated to 2016

assessment model was used for the mackerel stock (DFO 2017a, Van Beveren et al. 2017). As the use of stock estimates from stock assessment models can introduce some pitfalls (Brooks & Deroba 2015, Legault & Palmer 2016, Palmer et al. 2016), we only selected stocks with models carefully peer-reviewed and robust against natural mortality and selectivity changes.

2.2. Environmental data

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

2.3. Predation strength

Predation has an influence on population growth, so top-down effects (i.e. the main predators' abundances) should also be considered (Table 2). However, most stocks were assessed with VPA models assuming constant natural mortality (M). Because in such cases all residual mortality was assumed to be attributed to fishing, we only tested this link for southern cod and mackerel, which presumed a time-varying M and a constant M with process error (allowing for deviations in M), respectively (Swain et al. 2015, Doniol-Valcroze et al. 2019). Seals have been described as predators of mackerel and cod in the GSL (Hammill et al. 2007, Swain & Benoît 2015). Therefore, grey seal abundances were considered as potential drivers of cod and mackerel population growth. Seal abundance estimates were obtained for the northeastern and the southern region, the southern seal abundance matching with the southern cod stocks and the sum of seal

Table 2. Environmental data description for the Gulf of St Lawrence (GSL) during the period 1971–2014 and the sources used

Data	Description	Source
Surface temperature	Annual anomaly of upper layer temperature in August an averaged between May and November	Galbraith et al. (2018)
Cold intermediate layer (CIL) temperature	Annual anomaly of the 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 salinity in 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 northeastern GSL and southern GSL sealsfor the north part	Hammill et al. (2014)
		Swain & Benoît (2015) for the south part

abundances for both regions matching with mackerel distribution in the GSL.

2.4. Statistical analyses

We aimed to (1) estimate the importance of recruitment on population growth (i.e. elasticity) and (2) determine how this is affected by key parameters such as age structure, longevity, fishing mortality, environmental conditions and natural mortality (potential predators).

2.4.1. Elasticity calculations

To estimate the relative importance of recruitment and survival on population growth for each population, we started by constructing annual Leslie transition matrices $\mathbf{A}_t$ to summarize the dynamics of age-structured populations between time t and time $t+1$ (Leslie 1948, Caswell 2007). Annual population-specific abundance-at-age matrices (stock assessment outputs) were compiled to determine the fecundity (i.e. the contribution of each age class a to the recruitment at year t, R) and the survival (i.e. the survival, 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 calculated R as follows:

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

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

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

$$\mathbf{A}_t = \begin{Bmatrix} R_{1,t} & R_{2,t} & R_{3,t} & \dots & R_{a\max-1,t} & R_{a\max,t} \\ S_{1-0,t} & 0 & 0 & \dots & \dots & 0 \\ 0 & S_{2-1,t} & 0 & \dots & \dots & 0 \\ \dots & \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & 0 & \dots & S_{a\max-(a\max-1),t} & 0 \end{Bmatrix}$$

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

To evaluate the proportional change in the population growth rate resulting from a known proportional change in recruitment, the transient elasticity method (i.e. changes in population size and structure before reaching population stable stage distribution) defined by Caswell (2001), and described by Durant et al. (2013) and Durant & Hjermann (2017) was followed. Transient elasticity uses transient dynamics, which can reveal effects of short-term patterns affecting population dynamics (Caswell 2007). Transient elasticity indicates the relative contribution of recruitment or survival to population growth changes for each year by simulating the population growth from year t to year $t+t_g$ with and without changes in initial recruitment or survival values (Caswell 2001). Thus, for each year, the transient elasticity analysis was performed by increasing the recruitment by 1% for each age class (by manipulating R_i values in the top-row elements of $\mathbf{A}_t$) and simulating population growth for the next t_g years, while holding the other parameters at their original value. The t_g value used was approximately equal to the mean of the year-specific generation time μ_t (the mean age of the parents of the offspring produced by a cohort over its lifetime), according to the recommendations of Caswell (2001) and Durant et al. (2013). The annual generation time μ_t (which changes from year to year, and reflects the hypothetical generation time realized if the rates from a given year are held constant for long enough) is computed from $\mathbf{A}_t$ and defined as follows:

$$\mu_t = \frac{\sum_i i \left(\prod_{j=1}^{i-1} S_{j,t} \right) R_{i,t}}{\sum_i \left(\prod_{j=1}^{i-1} S_{j,t} \right) R_{i,t}} \tag{2}$$

where we defined $\prod_{j=1}^{0} S_{j,t} = 1$ (Caswell 2001).

Thus, changes in recruitment at time t will have time to be reflected in the mature population at time $t+t_g$ and can be compared between species (Durant et al. 2013). To check if the *a priori* chosen 1% level of perturbation did not affect the results of the generalized additive model (GAM) analyses (see Section 2.4.2), a bootstrap procedure (100 replicates) was used to test different perturbation values on the orig-

inal recruitment ranging from −20 to +20% (i.e. sensitivity analysis). Whatever the level of perturbation chosen, no significant difference was observed in the GAM analyses, so the 1% level of perturbation was kept.

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

2.4.2. Linking elasticity to population and external factors

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

$$E[y] = a + s_1(V_1) + s_2(V_2) + \dots + s_n(V_n) + \varepsilon \quad (3)$$

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

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

3. RESULTS

Time series of stock assessment estimates (stock abundance and fishing mortality, Fig. 2) and calculated generation time, population growth and transient elasticity to recruitment (Fig. 3) are displayed for all stocks. Abundance highly fluctuated for all stocks but included long periods of very low abundance for both cod stocks (between 1990 and 2010 for northern cod; since 1992 for southern cod, Fig. 2) and 4T spring herring (since 2003, Fig. 2). Fishing mortality (F) decreased over time for both cod stocks, reaching lower values after 1992 (Fig. 2). In contrast, F mainly increased (sometimes slightly) over time for 4R herring and mackerel, whereas F alternated between periods of low and high values for 4T herring (with low values for both spawning components since
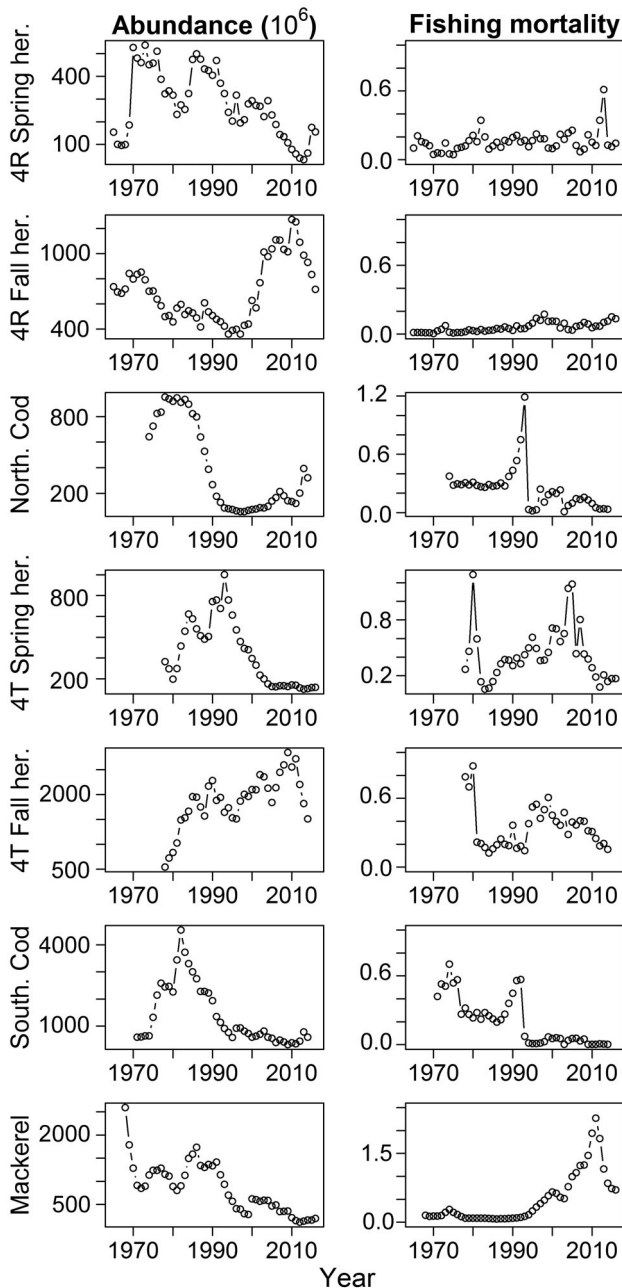
Fig. 2. Stock abundance and fishing mortality time series for the 7 stocks of the Gulf of St. Lawrence (GSL) considered in the study (North: 4R spring and fall herring, northern cod; South: 4T spring and fall herring, southern cod; all GSL: mackerel). Note that ranges on *y*-axes differ among panels

2010, Fig. 2). Generation time alternated between high and low values across time periods, with amplitudes of around 2.5 yr for 4R herring (from 4.55 to 7.34 and from 5.44 to 7.65 for 4R spring and fall herring, respectively) and 3.5 yr for mackerel (from 5.80 in the 1970s to 2.13 in 2011, Fig. 3). Generation time amplitudes for cod (from 5.65 to 6.93 and from 6.21 to 7.95 for northern and southern stocks, respectively)

and 4T herring (from 4.58 to 5.96 and 4.76 to 5.83 for spring and fall stocks, respectively) were less pronounced (Fig. 3). F consistently had a significant and negative effect on generation time (linear model, p always <0.01 for all stocks). Population growth highly fluctuated and never displayed a clear trend for the herring and mackerel stocks (Fig. 3). Changes were rather periodic for cod, with a decrease from the 1980s to the beginning of the 1990s, and an increase to most recent years marked by a short-term decrease during some years at the end of the 2000s. The recruitment elasticity (e_{rec}) was close to 0 (indicating that the survival elasticity, e_{sur}, was close to 1) and highly variable for all stocks but differences appeared between stocks (Fig. 3). On average, the lowest e_{rec} values among the stocks studied were estimated for demersal stocks (both northern and southern cod stocks, 0.10 ± 0.03 and 0.09 ± 0.05 mean ± SD, range 0.05–0.18 and 0.04–0.24, respectively). The highest e_{rec} values among the stocks studied were estimated for Atlantic mackerel (0.24 ± 0.17, 0.034–0.83). Spring (4R: 0.18 ± 0.16, 0.02–0.75; 4T: 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 intermediate e_{rec} values, although with more pronounced variability for 4R herring (Fig. 3). Conversely, the e_{sur} was higher for cod than for herring and mackerel.

Deep-sea salinity, the sea ice volume and the CIL index anomalies were highly unstable, with alternating positive and negative periods with no long-term trends (Fig. 4). The St. Lawrence runoff anomaly mainly decreased from 1971 to 2003 (with a slight increase from 1990 to 1998), then increased from 2003 to 2014 (Fig. 4). The SST in August and between May and November fluctuated with no discernible pattern between 1971 and the 1990s, after which an increase was observed (Fig. 4). Similarly, an increasing trend occurred after 1992 for the deep-water temperature at both 150 and 300 m (Fig. 4). Seal abundance remained steady at low levels during the 1970s in 4R and 4T, followed by an increase up until 2014, where the highest recorded values since 1970 were observed (Fig. 4).

Stock-specific GAMs accounting for the year to year changes in the recruitment elasticity e_{rec} explained between 34% (northern cod) and 62% (southern cod) of the deviance (Table 3). Generation time, water temperature and St. Lawrence runoff were the main variables explaining e_{rec} variability (Table 3). The decrease in the generation time led to an increase in e_{rec} for mackerel, and 3 out of the 4 herring stocks (i.e. 4R spring and both 4T stocks); however, this was not
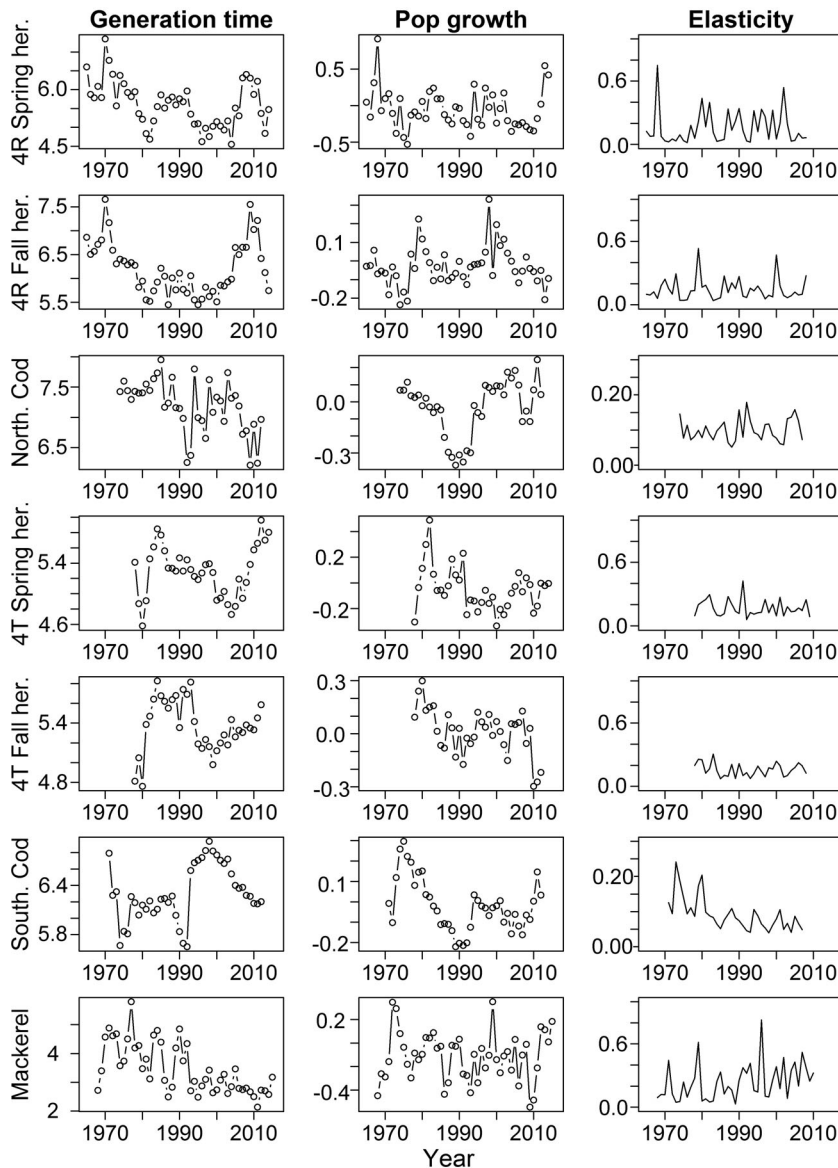
Fig. 3. Generation time, population growth (Pop growth) and transient population growth recruitment elasticity time series for the 7 stocks of the Gulf of St. Lawrence (GSL) considered in the study (North: 4R spring and fall herring, northern cod; South: 4T spring and fall herring, southern cod; all GSL: mackerel). Note that ranges on *y*-axes differ among panels

a positive effect of *F* was also found for southern cod (Fig. 4). No effect of stock or predator abundance was found, regardless of the stock considered. In all stocks, leave-one-out analyses showed that the optimal model was very stable, even when years were removed, and was not influenced by potential points with high leverage (see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m624p167_supp.pdf).

The selected GAMM revealed that generation time and water temperature at 150 m were significant variables explaining e_{rec} variability when considering all stocks together (R^2 = 0.32, Table 3, Fig. 7). The generation time had a negative effect on e_{rec} (Fig. 7), with smaller generation time associated with higher e_{rec} values. Water temperature at 150 m had a positive effect; warmer temperatures were correlated with higher e_{rec} values (Fig. 7). Other environmental variables (SST, sea ice volume, deep-water salinity, St. Lawrence runoff), as well as fish abundance and *F* did not significantly explain variability in e_{rec} when all stocks were considered together (Fig. S2).

4. DISCUSSION

By compiling biological data for 7 of the most important fish stocks in the GSL, this study is the first to report the sensitivity of population growth to recruitment of northwest Atlantic fish stocks. We investigated both the relative importance of changes in recruitment to annual population growth as well as how fisheries, climate and predation could affect the importance of recruitment. Regardless of the stock considered, adult survival rate (and thus fisheries management) was more important than recruitment in determining fish population growth, as e_{rec} values were closer to 0 than 1. The variability of the relative importance of recruitment to population growth was generally explained by age truncation (i.e. shorter generation time) and increased water temperatures, with some stock-specific differences. Specifically, increased water temperatures affected mainly the southern stocks' e_{rec}, indicating the highest sensitivity of

found for cod (Figs. 5 & 6). The effect of environmental conditions and fishing mortality depended on the stock considered (Table 3). For 4R fall herring, both 4T herring stocks, as well as southern cod, the e_{rec} was positively related to warm conditions (i.e. high surface and/or intermediate water temperature and low ice coverage, Figs. 5 & 6). St. Lawrence runoff exhibited a positive relationship with northern cod e_{rec}, a negative relationship with 4R spring herring e_{rec} (Fig. 5) and a dome-shape relationship with mackerel (Fig. 6). Higher deep-water salinity was significantly linked to higher e_{rec} for 4R spring herring (Fig. 5). Additionally,
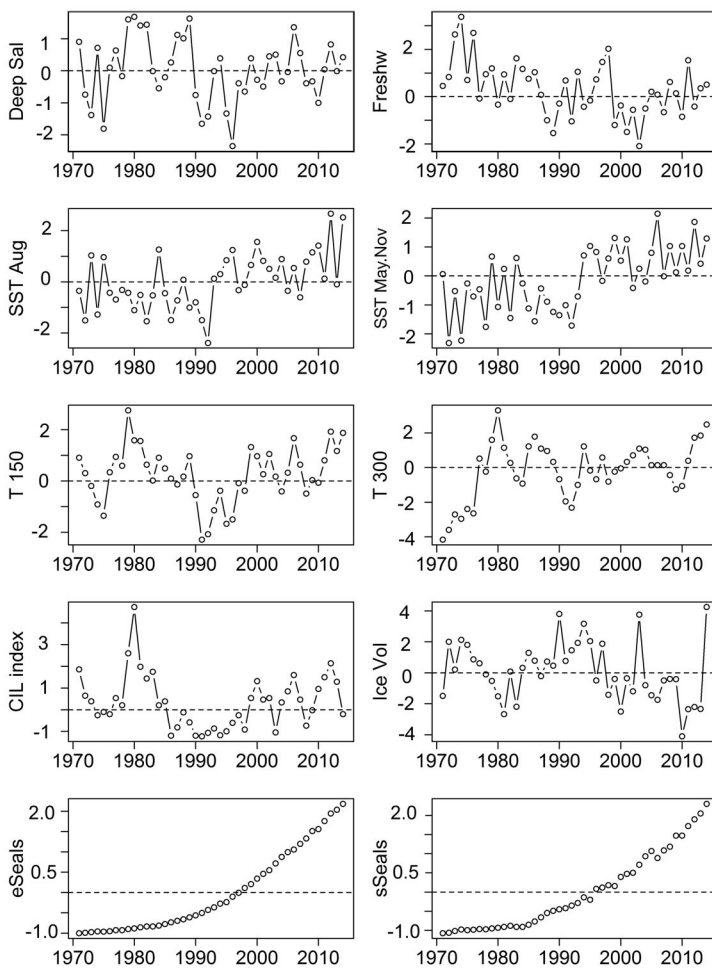
Fig. 4. Time series of the environmental parameter anomalies from the Gulf of St. Lawrence (GSL). Deep Sal: deep-water salinity; Freshw: St Lawrence runoffs; SST Aug: sea surface temperature in August; SST May.Nov: SST mean between May and November; T 150: intermediate water layer temperature (150 m); T 300: deep-water layer temperature (300 m); CIL index: cold intermediate layer temperature index; Ice Vol: ice volume; eSeals (sSeals): seal population abundance in the northeastern (southern) GSL

southern population growth to ongoing and future climate change through recruitment variability.

4.1. Effects of generation time, fishing and predation

Reduced generation time increased the dependence of population growth rate on recruitment in most stocks, especially for the shorter-lived species (i.e. mackerel and herring in the GSL). This finding emphasizes how e_{rec} can be affected by the long-term deterioration of the population age structure (Rouyer et al. 2011, Hidalgo et al. 2012). Additionally, this corroborates the fact that species with the shortest gen-

eration time are more sensitive to changes in recruitment when the older age classes are less represented or quasi-absent in the stock (Berkeley et al. 2004). However, 4R fall herring and both cod stocks were not significantly affected by generation time. This indicates that the relationship is not general, as it has already been suggested in a similar study on 11 stocks (Durant & Hjermann 2017). Climate and fisheries harvesting can both influence age structure and thus generation time at different time scales (Conover & Munch 2002). In this study, we observed a significant negative correlation of generation time with fishing mortality, corroborating previous studies on population age truncation due to fishing (Ottersen et al. 2006, Rouyer et al. 2011). However, due to the relatively small R^2 of 0.35, factors other than fishing mortality act on generation time variability. For example, environmental variability strongly affects age structure (Ottersen et al. 2006). However, environmental long-term changes in the GSL until the beginning of the 2010s was relatively low compared to other regions (Galbraith et al. 2018). Thus, high fishing pressure on larger individuals, through its effect on stock demographic structure, seems to be a very important factor for stock dynamics and sensitivity to recruitment variability in the GSL. This stresses the need to balance harvesting and alternative fisheries to attenuate the pressure on old individuals in order to reduce population growth rate sensitivity to recruitment and climate variability. This is also consistent with the observation that the 4R fall herring, as well as both cod stocks, have recently experienced low fishing pressure in the GSL and display lower e_{rec} values than other stocks. Stocks exposed to lower fishing pressure may experience weaker generation time variations, and thus be less sensitive and more resilient to changes in recruitment (Planque et al. 2010).

For the considered stocks, the direct effect of fishing pressure on elasticity to recruitment was weak and only significant for the southern cod model. This may be because of the lack of variability and pattern in estimated fishing mortality over time, with the exception of 4T spring herring, southern cod and mackerel. In contrast, the generation time better captured short-term elasticity variations and was selected by the model. For southern cod, this suggests that fishing mortality may have a quicker effect on e_{rec} than for other stocks. With lower fishing mortality and therefore lower population growth sensitivity to recruit-

Table 3. Details of the best generalized additive models (GAMs) testing the effects of age structure, environmental variability and fishing pressure on transient population growth recruitment elasticity. The generalized additive mixed model (GAMM) included stock as a random variable. Generation time (μ): yearly mean age of spawners producing offspring; F: fishing mortality for the age ranges indicated by subscripts in Table 1; Deep Sal: deep-water salinity; Freshw: St Lawrence runoffs; SST Aug: sea surface temperature in August; SST May.Nov: mean SST between May and November; T 150: intermediate water layer temperature (150 m); CIL: cold intermediate layer temperature; Ice Vol: ice volume; Dev: % of deviance explained; GSL: Gulf of St. Lawrence. Significance of each term is noted as *p < 0.05, **p < 0.01, ***p < 0.001

| Stock	Time series	Best GAM selected	Dev
Northern stocks			
4R spring herring	1971–2008	Elasticity ~ μ** + Freshw* + Deep Sal*	58
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*	
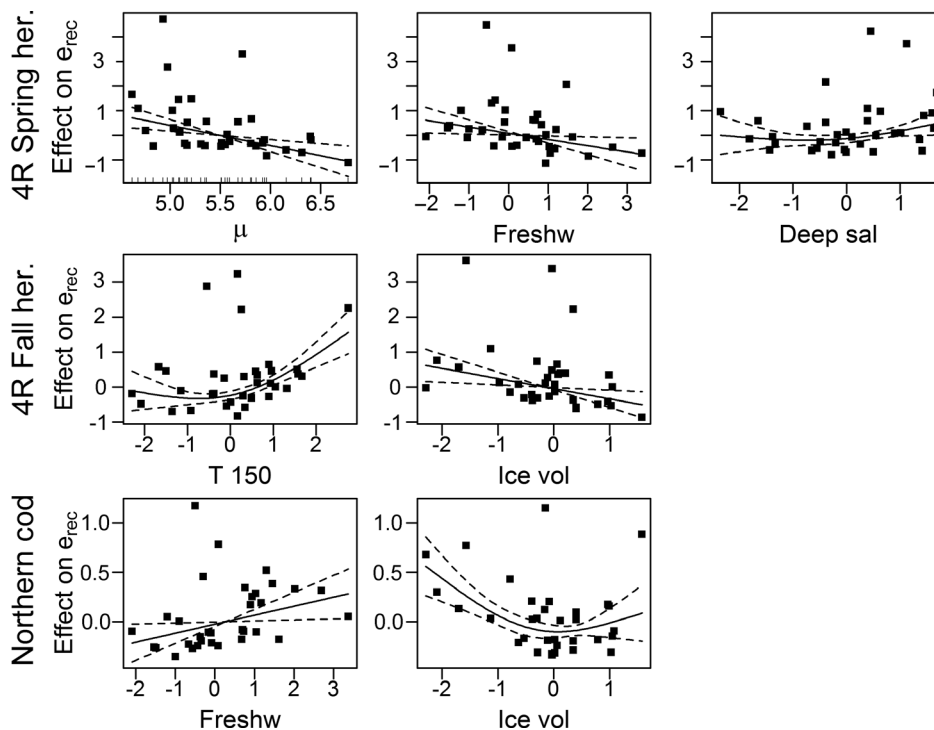
Fig. 5. Partial generalized additive model (GAM) plots for the 3 northern stocks showing the population growth recruitment elasticity (e_{rec}) in response to: generation time (μ); water temperature at 150 m (T 150); deep-water salinity (Deep sal); Ice vol: ice volume; Freshw: St. Lawrence runoffs. Other environmental variables and fish abundance were never significant. Black dots represent the partial residuals, and the solid line represents the estimated mean effect of the independent variables and its 95% confidence interval (dashed lines)

ment, cod adult survival (and thus fisheries management and/or predation) would have a stronger effect on southern cod stock population growth. When considered (i.e. for southern cod and mackerel), predation did not display any significant effect on elasticity to recruitment. For mackerel, grey seal predation pressure might be too small to trigger significant effects relative to fishing and environmental changes. This is more surprising for southern cod, as predators (e.g. seals) were shown to strongly affect cod population dynamics (i.e. recovery) since its collapse in the 1990s (Swain & Benoît 2015). This sudden increasing predator importance in the mid-1990s could have not been detected due to the 1971–2007 time series used in this study. Moreover, the limited number of predators available with reliable abundance indices, as well as the examination of only predator abundance to represent the complex dynamics of the trophic links (e.g. cod is both predator and prey) may also prevent finding significant links with recruitment elasticity in the GSL.

4.2. Effects of climate variability

This study considered a large range of environmental variables. Water temperature in particular had an important effect on fish population growth elasticity to recruitment, especially in the southern GSL. For 4R fall herring, 4T herring stocks and southern cod, warmer environmental conditions (through either high surface or intermediate water temperature and/or less ice) were linked to an increase in the dependence of population growth on recruitment. Consequently, these 4 stocks may be more productive in warmer
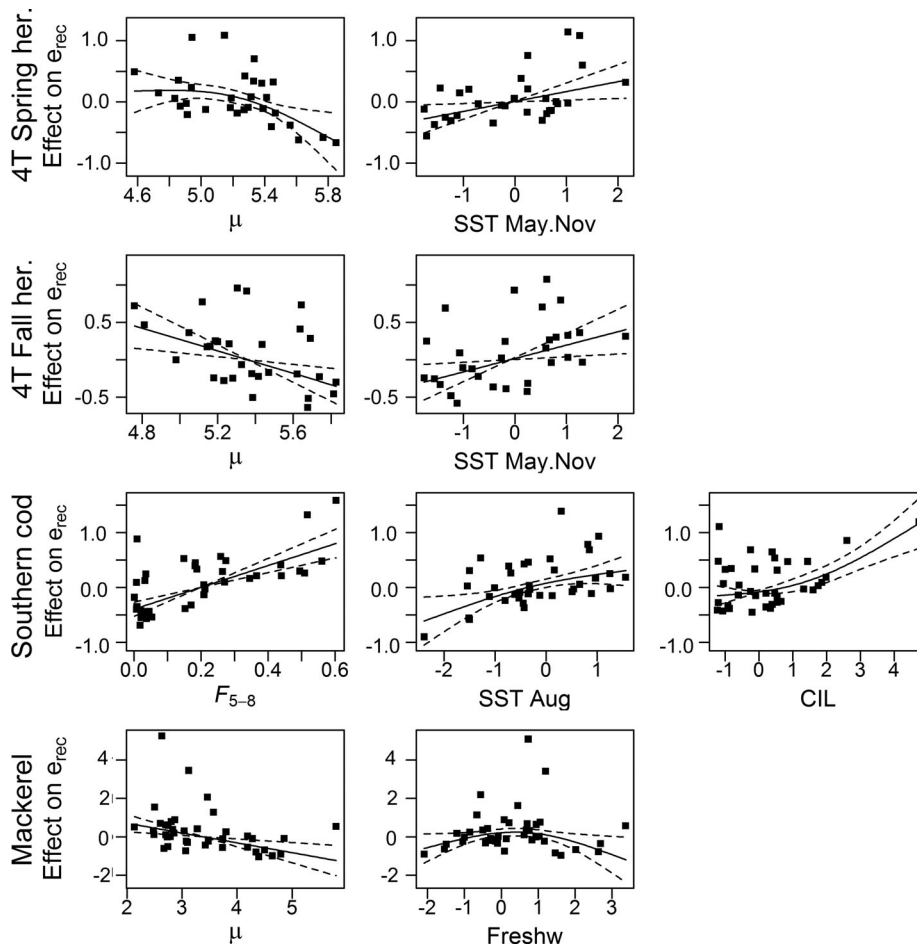
Fig. 6. Partial generalized additive model (GAM) plots showing the population growth recruitment elasticity (e_{rec}) for the 3 southern stocks and the mackerel in response to: generation time (μ); sea surface temperature in August (SST Aug); mean SST between May and November (SST May.Nov); cold intermediate layer temperature (CIL); St Lawrence runoffs (Freshw); and fishing mortality (F). Other environmental variables and fish abundance were never significant. Black dots represent the partial residuals and the solid line represents the estimated mean effect of the independent variables and its 95% confidence interval (dashed lines)

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

While warming waters seem to always have a positive effect on e_{rec}, the effects of the other environmental variables (salinity, freshwater runoff) were stock-specific, and might be specific to the biology of each species. For example, freshwater runoff had the inverse effect on e_{rec} for northern spring herring (negative) and cod (positive), while both species are late spring spawners. Since cod and herring larvae prey on distinct plankton species (Fortier & Gagné 1990, Robert et al. 2011), different levels of freshwater runoff favouring different plankton species may therefore indirectly act on their recruitment (Ouellet et al. 1997, Légaré et al. 2014). Moreover, higher deep-water salinity values, an indicator 0of nutrient-rich deep water entering into the GSL (Galbraith et al. 2018), were shown to only increase 4R spring herring e_{rec}. This suggests that the variability in growth rate dependency on recruitment can result from climate-induced changes affecting both the development and the
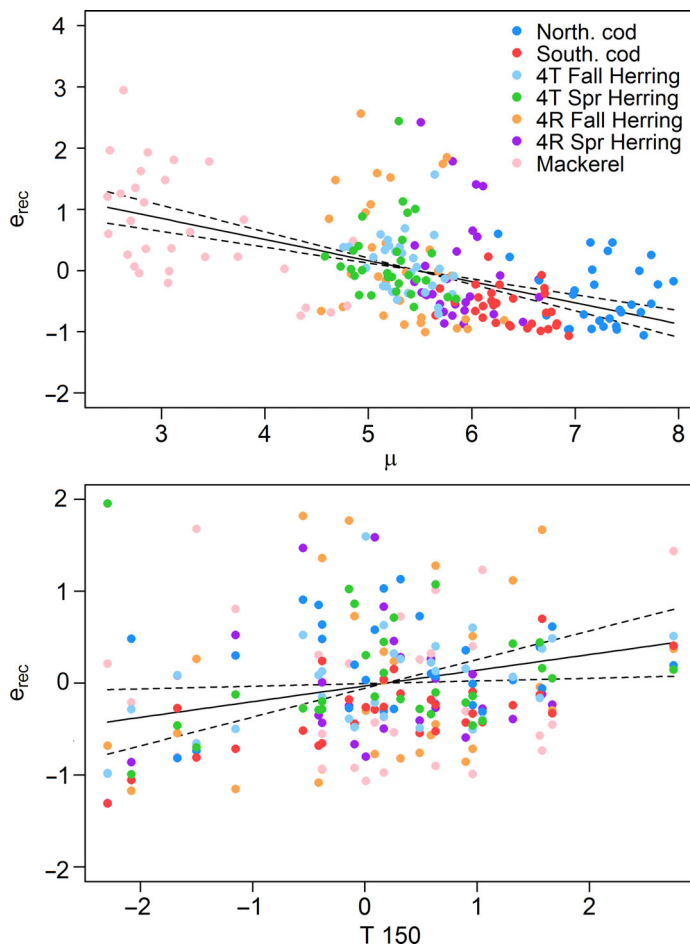
waters, and their population growth is likely to be more sensitive to climate fluctuations. Indeed, warmer environmental conditions were shown to enhance recruitment for fall herring by favouring the temporal match between food resources and fall herring larvae production (Brosset et al. 2019) but also induced larger larval size in cod (Pepin et al. 1997). The temperature effect might have been occurring more clearly in the southern GSL because this area experienced relatively more warming than the northern GSL (Galbraith et al. 2018). Therefore, stocks inhabiting this zone, such as 4T herring and southern cod, are expected to experience more pronounced environmental changes and thus to be more susceptible to physical and biological changes related to temperature change. Interestingly, spring herring recruitment

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

survival of early life stages, as well as shaping recruitment dynamics through bottom-up changes.

4.3. Management implications and possible consequences for the future

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

Short-lived pelagic species are more dependent on recruitment peaks and optimal environmental condi-

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

Firstly, there was a clear increase in e_{rec} for mackerel after 2000, when its exploitation rate reached maximum levels and its generation time decreased (DFO 2017a, Van Beveren et al. 2017). For this currently overexploited stock, population growth consequently became increasingly dependent on strong recruitment events and hence environmental changes. Such knowledge is noteworthy for management, as stock recovery will be highly dependent on environmental conditions. Furthermore, over the long term, unfavourable environmental conditions will probably impact recruitment. Secondly, in the future, stock-specific growth of all stocks considered may become more dependent on recruitment rather than adult survival, making them potentially more challenging to manage. Waters, particularly in the south (Galbraith et al. 2018), are likely to become warmer (Srokosz et al. 2012), which would result in higher importance of recruitment to population growth. Hence, future stocks of longer-lived species like cod might behave more similarly to the dynamics of short-lived populations (Durant & Hjermann 2017). However, predictions were not conducted, as the extrapolation of drivers (e.g. temperature) would potentially result in estimates lying outside of the scope of observations. However, Lee (2017) proposed a novel approach including the possibility for drivers to attain previously unrecorded

values, which could be used in further work to determine the potential population growth rate for the next decade.

4.4. Additional remarks

Stock assessment estimates of population abundance are subject to multiple sources of uncertainty (Brooks & Deroba 2015, Palmer et al. 2016), and results using these estimates should be considered cautiously. Except for mackerel, abundance and fishing mortality estimates come from the same assessment model (i.e. a VPA), keeping the assessment framework uniform among 6 out of 7 stocks. Even if mackerel stock estimates were calculated with a state-space assessment, which differs from the VPA (e.g. it simultaneously estimates observation and process errors), the same care was conducted by checking model assumptions that could strongly influence the stock assessment outputs. Indeed, whichever the assessment model used, we carefully checked for the potential effect of natural mortality misspecification, as it can have an important effect on stock estimates through the interplay between mortality and recruitment. Whenever strong empirical indications to include time-varying mortality existed (i.e. for seal predation on cod, Swain & Benoît 2015), it was considered in the model to avoid increasing recruitment variability. Likewise, the high degree of confidence in stock assessment model inputs made us confident about potential weak and constant observation errors across stocks. Combined with the sensitivity analyses carried out during the stock assessment process, elasticity and leave-one-out analyses, we are confident in the robustness of our results and conclusions against the potential uncertainty from the use of stock estimates for post hoc analyses. Furthermore, this is strengthened by the consistency of our results with previous studies (Durant & Hjermann 2017, Wang et al. 2017), as well as the corroboration with species-specific differences found in our study and ecological knowledge in the current literature (Plourde et al. 2015, Swain & Benoît 2015, Brosset et al. 2019).

4.5. Conclusions

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

LITERATURE CITED

Benton TG, Grant A (2000) Evolutionary fitness in ecology: comparing measures of fitness in stochastic, density-dependent environments. Evol Ecol Res 2:769–789

Berkeley SA, Hixon MA, Larson RJ, Love MS (2004) Fisheries sustainability via protection of age structure and spatial distribution of fish populations. Fisheries 29:23–32

Bourgault D, Koutitonsky VG (1999) Real-time monitoring of the freshwater discharge at the head of the St. Lawrence estuary. Atmos-Ocean 37:203–220

Brassard C, Gauthier J, Lussier JF, Way M, Collier F (2018) The status of the Northern Gulf of St. Lawrence (3Pn, 4RS) cod stock (*Gadus morhua*) in 2016. Res Doc 2018/039. DFO, Canadian Science Advisory Secretariat, Ottawa

Brooks EN, Deroba JJ (2015) When 'data' are not data: the pitfalls of post hoc analyses that use stock assessment model output. Can J Fish Aquat Sci 72:634–641

Brosset P, Doniol-Valcroze T, Swain DP, Lehoux C and others (2019) Environmental variability controls recruitment but with different drivers among spawning components in Gulf of St. Lawrence herring stocks. Fish Oceanogr 28: 1–17

Burnham K, Anderson D (2002) Model selection and multi-model inference: a practical information-theoretic approach, 2nd edn. Springer-Verlag, New York, NY

Caswell H (2001) Matrix population models: construction, analysis, and interpretation, 2nd edn. Sinauer Associates, Sunderland, MA

Caswell H (2007) Sensitivity analysis of transient population dynamics. Ecol Lett 10:1–15

Conover DO, Munch SB (2002) Sustaining fisheries yields over evolutionary time scales. Science 297:94–96

Crawford BA, Maerz JC, Nibbelink NP, Buhlmann KA, Norton TM (2014) Estimating the consequences of multiple threats and management strategies for semi-aquatic turtles. J Appl Ecol 51:359–366

de Kroon H, Plaisier A, van Groenendael J, Caswell H (1986) Elasticity: the relative contribution of demographic parameters to population growth rate. Ecology 67:1427–1431

DFO (Fisheries and Oceans Canada) (2017a) Assessment of the Atlantic mackerel stock for the northwest Atlantic (Subareas 3 and 4) in 2016. Science Advisory Rep 2017/034. DFO, Canadian Science Advisory Secretariat, Ottawa

DFO (2017b) Assessment of the northern Gulf of St. Lawrence (3Pn, 4RS) cod stock in 2016. Science Advisory Rep 2017/042. DFO, Canadian Science Advisory Secretariat, Ottawa

Doniol-Valcroze T, Van Beveren E, Légaré B, Girard L, Castonguay M (2019) Atlantic mackerel (*Scomber scombrus* L.) in NAFO Subareas 3 and 4 in 2016. Res Doc 2018/062. DFO, Canadian Science Advisory Secretariat, Ottawa

Durant JM, Hjermann DØ (2017) Age-structure, harvesting and climate effects on population growth of Arcto-boreal fish stocks. Mar Ecol Prog Ser 577:177–188

Durant JM, Hidalgo M, Rouyer T, Hjermann DØ and others (2013) Population growth across heterogeneous environments: effects of harvesting and age structure. Mar Ecol Prog Ser 480:277–287

Ezard THG, Bullock JM, Dalgleish HJ, Millon A, Pelletier F, Ozgul A, Koons DN (2010) Matrix models for a changeable world: the importance of transient dynamics in population management. J Appl Ecol 47:515–523

Flockhart DTT, Pichancourt JB, Norris DR, Martin TG (2015) Unravelling the annual cycle in a migratory animal: Breeding-season habitat loss drives population declines of monarch butterflies. J Anim Ecol 84:155–165

Fortier L, Gagné JA (1990) Larval herring (*Clupea harengus*) dispersion, growth, and survival in the St. Lawrence estuary: match/mismatch or membership/vagrancy? Can J Fish Aquat Sci 47:1898–1912

Galbraith PS, Chassé J, Caverhill C, Nicot P, Gilbert D, Lefaivre D, Lafleur C (2018) Physical oceanographic conditions in the Gulf of St. Lawrence during 2017. Res Doc 2018/050. DFO, Canadian Science Advisory Secretariat, Ottawa

Gerber LR, Heppell SS (2004) The use of demographic sensitivity analysis in marine species conservation planning. Biol Conserv 120:121–128

Glaser SMS, Ye H, Sugihara G (2014) A nonlinear, low data requirement model for producing spatially explicit fishery forecasts. Fish Oceanogr 23:45–53

Grégoire F, Beaudin L (2014) Évaluation analytique du maquereau bleu (*Scomber scombrus* L.) des sous-régions 3 et 4 de l'OPANO en 2013. Doc rech 2014/079. Pêches et Océans Canada, Secrétariat canadien de consultation scientifique, Ottawa

Grégoire F, Girard L, Beaulieu JL, Légaré B (2015) Analyse exploratoire du modèle ADAPT NFT pour les stocks de hareng (*Clupea harengus harengus* L.) de la côte ouest de Terre-Neuve, 2000–2013. Secr can de consult sci du MPO. Doc de rech 2014/106

Hammill MO, Stenson GB (2000) Estimated prey consumption by harp seals (*Phoca groenlandica*), hooded seals (*Cystophora cristata*), grey seals (*Halichoerus grypus*) and harbour seals (*Phoca vitulina*) in Atlantic Canada. J Northwest Atl Fish Sci 26:1–23

Hammill MO, Stenson GB, Proust F, Carter P, McKinnon D (2007) Feeding by grey seals in the Gulf of St. Lawrence and around Newfoundland. NAMMCO Sci Publ 6:135–152

Hammill MO, den Heyer CE, Bowen WD (2014) Grey seal population trends in Canadian waters, 1960-2014. Res Doc 2014/037. DFO, Canadian Science Advisory Secretariat, Ottawa

Hayes DB (2000) A biological reference point based on the Leslie matrix. Fish Bull 98:75–85

Hidalgo M, Rouyer T, Bartolino V, Cerviño S and others (2012) Context-dependent interplays between truncated demographies and climate variation shape the population growth rate of a harvested species. Ecography 35: 637–649

Hidalgo M, Olsen EM, Ohlberger J, Saborido-Rey F, Murua H, Piñeiro C, Stenseth NC (2014) Contrasting evolutionary demography induced by fishing: the role of adaptive phenotypic plasticity. Ecol Appl 24:1101–1114

Houde E (1987) Fish early life dynamics and recruitment variability. Am Fish Soc Symp 2:17–29

Hsieh C, Reiss CS, Hunter JR, Beddington JR, May RM, Sugihara G (2006) Fishing elevates variability in the abundance of exploited species. Nature 443:859–862

Hutchings JA, Reynolds JD (2004) Marine fish population collapses: consequences for recovery and extinction risk. Bioscience 54:297–309

Lambert Y (2011) Environmental and fishing limitations to the rebuilding of the northern Gulf of St. Lawrence cod stock (*Gadus morhua*). Can J Fish Aquat Sci 68:618–631

LeBlanc CH, Mallet A, Surette T, Swain D (2015) Assessment of the NAFO Division 4T southern Gulf of St. Lawrence Atlantic herring (*Clupea harengus*) stocks in 2013. Res Doc 2015/025. DFO, Canadian Science Advisory Secretariat, Ottawa

Lee CT (2017) Elasticity of population growth with respect to the intensity of biotic or abiotic driving factors. Ecology 98:1016–1025

Légaré B, Beaulieu J, Girard L, Grégoire F (2014) Les stocks de hareng (*Clupea harengus harengus* L.) de la côte ouest de Terre-Neuve (Division 4R de l'OPANO) en 2013. Doc rech 2014/091. Pêches et Océans Canada, Secrétariat canadien de consultation scientifique, Ottawa

Legault CM, Palmer MC (2016) In what direction should the fishing mortality target change when natural mortality increases within an assessment? Can J Fish Aquat Sci 73: 349–357

Leggett WC, Deblois E (1994) Recruitment in marine fishes: Is it regulated by starvation and predation in the egg and larval stages? Neth J Sea Res 32:119–134

Leslie PH (1948) Some further notes on the use of matrices in population mathematics. Biometrika 35:213–245

Megrey BA, Lee Y, Macklin SA (2005) Comparative analysis of statistical tools to identify recruitment-environment relationships and forecast recruitment strength. ICES J Mar Sci 62:1256–1269

Moores JA, Winters GH, Parsons LS (1975) Migrations and biological characteristics of Atlantic mackerel (*Scomber scombrus*) occurring in Newfoundland waters. J Fish Res Board Can 32:1347–1357

Ottersen G, Hjermann DO, Stenseth NC (2006) Changes in spawning stock structure strengthen the link between climate and recruitment in a heavily fished cod (*Gadus morhua*) stock. Fish Oceanogr 15:230–243

Ottersen G, Stige LC, Durant JM, Chan KS, Rouyer TA, Drinkwater KF, Stenseth NC (2013) Temporal shifts in recruitment dynamics of North Atlantic fish stocks: effects of spawning stock and temperature. Mar Ecol Prog Ser 480:205–225

Ouellet P, Lambert Y, Castonguay M (1997) Spawning of Atlantic cod (*Gadus morhua*) in the northern Gulf of St. Lawrence: a study of adult and egg distribution and characteristics. Can J Fish Aquat Sci 54:198–210

Palmer MC, Deroba JJ, Legault CM, Brooks EN (2016) Comment on 'Slow adaptation in the face of rapid warming leads to collapse of the Gulf of Maine cod fishery'. Science 352:423

Pepin P, Orr DC, Anderson JT (1997) Time to hatch and larval size in relation to temperature and egg size in Atlantic cod (*Gadus morhua*). Can J Fish Aquat Sci 54:2−10

Planque B, Fromentin JM, Cury P, Drinkwater KF, Jennings S, Perry RI, Kifani S (2010) How does fishing alter marine populations and ecosystems sensitivity to climate? J Mar Syst 79:403−417

Plourde S, Grégoire F, Lehoux C, Galbraith PS, Castonguay M, Ringuette M (2015) Effect of environmental variability on body condition and recruitment success of Atlantic mackerel (*Scomber scombrus* L.) in the Gulf of St. Lawrence. Fish Oceanogr 24:347−363

R Core Team (2016) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Robert D, Levesque K, Gagné JA, Fortier L (2011) Change in prey selectivity during the larval life of Atlantic cod in the southern Gulf of St Lawrence. J Plankton Res 33:195−200

Rouyer T, Ottersen G, Durant JM, Hidalgo M and others (2011) Shifting dynamic forces in fish stock fluctuations triggered by age truncation? Glob Change Biol 17: 3046−3057

Savenkoff C, Gagné JA, Gilbert M, Castonguay M and others (2017) Le concept d'approche écosystémique appliqué à l'estuaire maritime du Saint-Laurent (Canada). Environ Rev 25:26−96

Srokosz M, Baringer M, Bryden H, Cunningham S and others (2012) Past, present, and future changes in the Atlantic meridional overturning circulation. Bull Am Meteorol Soc 93:1663−1676

Stearns SC (1992) The evolution of life histories. Oxford University Press Oxford

Stige LC, Yaragina NA, Langangen Ø, Bogstad B, Stenseth NC, Ottersen G (2017) Effect of a fish stock's demographic structure on offspring survival and sensitivity to climate. Proc Natl Acad Sci USA 114:1347−1352

Swain DP (2016) Population modelling results for the assessment of Atlantic herring (*Clupea harengus*) stocks in the southern Gulf of St. Lawrence (NAFO Division 4T) to 2015. Res Doc 2016/061. DFO, Canadian Science Advisory Secretariat, Ottawa

Swain DP, Benoît HP (2015) Extreme increases in natural mortality prevent recovery of collapsed fish populations in a Northwest Atlantic ecosystem. Mar Ecol Prog Ser 519:165−182

Swain D, Savoie L, Cox SP, Aubry E (2015) Assessment of the Southern Gulf of St. Lawrence Atlantic cod (*Gadus morhua*) stock of NFO Div. 4T and 4Vn (November to April), March 2015. Res Doc 2015/080. DFO, Canadian Science Advisory Secretariat, Ottawa

Szuwalski CS, Vert-Pre KA, Punt AE, Branch TA, Hilborn R (2015) Examining common assumptions about recruitment: a meta-analysis of recruitment dynamics for worldwide marine fisheries. Fish Fish 16:633−648

Thorson JT, Monnahan CC, Cope JM (2015) The potential impact of time-variation in vital rates on fisheries management targets for marine fishes. Fish Res 169:8−17

Van Beveren E, Duplisea D, Castonguay M, Doniol-Valcroze T, Plourde S, Cadigan N (2017) How catch underreporting can bias stock assessment of and advice for northwest Atlantic mackerel and a possible resolution using censored catch. Fish Res 194:146−154

Vélez-Espino LA, Fox MG, McLaughlin RL (2006) Characterization of elasticity patterns of North American freshwater fishes. Can J Fish Aquat Sci 63:2050−2066

Wang T, Gao X, Jakovli I, Liu HZ (2017) Life tables and elasticity analyses of Yangtze River fish species with implications for conservation and management. Rev Fish Biol Fish 27:255−266

Wood S, Wood MS (2015) Package 'mgcv.' R Package version:1−7. https://cran.r-project.org/web/packages/mgcv/index.html

Zuur AF, Ieno EN, Smith GM (2007) Analysing ecological data. Springer, New York, NY