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Predicting Mortality Reference Points for American Eel (*Anguilla rostrata*)

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Foreword

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

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ABSTRACT

American Eel (*Anguilla rostrata*) is a panmictic, semelparous species with subpopulations all along the eastern coast of North America. Due to significant abundance declines and continuing threats from habitat degradation, they have been assessed as Threatened by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC), though they have not been listed under Schedule 1 of the *Species at Risk Act*. Commercial fisheries remain active in eastern Canada, targeting all continental life-stages. Fisheries and Oceans Canada has adopted a precautionary approach to fisheries management where mortality reference points are identified to maintain healthy populations. Because American Eel life history varies across its range, it is important that mortality reference limits are specific to local populations. Reference points were determined through estimates of silver eel escapement (ESC), a metric which compares the ratio of ESC between an unfished and fished population. Reference limits were identified at 50% ESC, F_{50} ; and 30% ESC, F_{30} . A density-dependent stage-structured matrix model was used to determine mortality reference points for both eel (yellow and silver life stages) and elver fisheries in four geographic zones in Canada. Multiple linear regressions were used to determine whether mortality reference points could be estimated directly from life history data. The most precautionary F_{50} (mortality reference point for upper stock reference limit) estimate for Canada was 0.091 for eels and 0.67 for elvers across Canadian locations assuming a minimum fishing size of 350 mm. However, eel mortality reference points depended on the minimum fishing size, with larger and more varied mortality reference points associated with larger minimum fishing sizes. Results were highly dependent on the density-dependent mechanisms included in the model. When density-dependence acted on many life-history traits, the mortality reference points were larger and more variable. If large turbine mortality was included, the corresponding mortality reference limits decreased, sometimes to the point where no fishing mortality could support the ESC objectives under the model scenarios explored. Sensitivity analysis indicated that silver length and yellow eel survival were influential parameters on model outputs.

INTRODUCTION

American Eel (*Anguilla rostrata*) is a freshwater eel with a broad distribution encompassing the east coast of North America and locations south through the Caribbean and northern South America, and as far north as Greenland (Ulmo Diaz et al. 2023; Cairns et al. 2014). The population is panmictic with no significant genetic differences between eel in the north and south, and no evidence that the offspring of eel from a particular location will return there (Ulmo Diaz et al. 2023). They are catadromous and semelparous, spawning in the Sargasso Sea before their young, called leptocephalus (plural leptocephali), migrate through ocean currents until they reach continent waters and develop into small transparent eel called glass eel (Cairns et al. 2014). These glass eel then develop into elvers; small, pigmented eel, which in turn become yellow eel, the stage American Eel spends most of its life (Cairns et al. 2014). American Eel mature as silver eel, migrate back to the Sargasso Sea to spawn, and die (Cairns et al. 2014). American Eel can also inhabit brackish or saline environments as yellow eel (Cairns et al. 2014). Their wide geographical range and ability to live in both freshwater and saline environments result in wide ranges of life history characteristics (e.g., growth rate, length at maturity, etc.) (Cairns et al. 2014; Vélez-Espino & Koops 2010).

HISTORY OF AMERICAN EEL STATUS IN CANADA

In 2012, the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) assessed American Eel as Threatened (COSEWIC 2012), though it is not currently listed under Schedule 1 of the *Species at Risk Act* and is still fished in some locations. The COSEWIC assessment was based on abundance declines, especially notable in the St. Lawrence basin, and ongoing threats to the species, such as habitat loss through damming, turbine mortality, fishing, and climate change (COSEWIC 2012). Ontario listed American Eel as Endangered provincially in 2007, and American Eel is considered Vulnerable by Quebec and Newfoundland and Labrador (COSEWIC 2012). A Maritimes-specific American Eel assessment could not be fully completed due to a lack of data but noted that elver landings have increased since 1996 (Bradford et al. 2022); an updated analysis reached similar conclusions (DFO 2024). Recent analysis from van der Lee & Koops (2024) indicated that the Canada-wide freshwater abundance of American Eel in Canada has declined since the 1980s.

PRECAUTIONARY APPROACH

Fisheries and Oceans Canada (DFO) uses a Precautionary Approach to managing fisheries (DFO 2006). This framework incorporates uncertainties into harvest levels, identifying mortality reference points to keep a population healthy, or, if the population is not healthy, manage it in such a way as to promote a return of good stock status (DFO 2006). This approach uses metrics of stock size to categorize it as one of: Healthy (population can be fished at a sustainable removal rate), Cautious (population may be fished, but fishing rates should decrease to allow the stock to recover towards the Healthy zone), and Critical (anthropogenic mortality to the stock should be minimized to allow for recovery) (Figure 1; Kronlund et al. 2014; DFO 2006). The upper stock reference point is the stock size that delineates the transition between the Healthy and Cautious zones, while the limit reference point is the transition between Cautious and Critical zones (DFO 2006). Typically, either a maximum sustainable yield (MSY) or a spawner per recruit (SPR) approach is used to determine mortality reference points (Kronlund et al. 2014; DFO 2012; Mace and Sissenwine 1993), though silver eel escapement has been used when managing European Eel (*Anguilla anguilla*) (van der Hammen et al. 2021). Mortality reference points are the instantaneous fishing mortality rates (F) expected to result in the upper stock reference point or the limit reference point (DFO 2006). For example, if the

upper stock reference was 50% SPR, the F_{50} mortality reference point would be the fishing mortality rate that maintained the stock at or above this upper stock reference.

Previous analyses have estimated the mortality reference points of American Eel using SPR analysis, with 50% SPR as an upper stock reference and 30% SPR as a lower reference point. ICES (2001) conducted SPR analysis to estimate mortality reference points for “northern” and “southern” areas of American Eel habitat, finding that southern areas generally were predicted to have higher mortality reference points (minimum estimated F_{50} of 0.11 in southern areas compared to a minimum estimated F_{50} of 0.06 in northern areas). Chaput & Cairns (2011) found similar ranges doing SPR analysis, with a mortality reference point of 0.12 for 50% escapement, and a value of 0.18 for 30% escapement for a yellow eel fishery. Most recently, Bradford et al. (2022) conducted SPR analysis for eel and elver fisheries in the Maritimes, reporting F_{50} values of 0.09 for eels and 0.69 for elvers; and F_{30} values of 0.17 for eels and 1.2 for elvers.

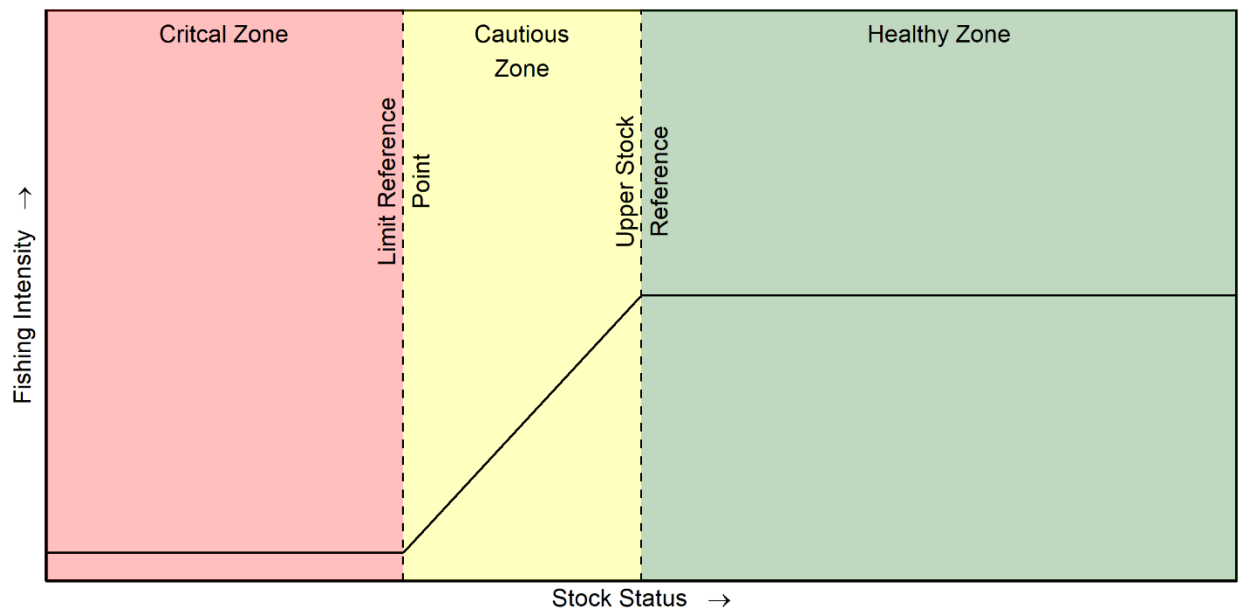


Figure 1. Conceptual diagram showing DFO's precautionary approach (from DFO 2006). The solid line shows the fishing removal rate, while the dotted lines show the transition between the Healthy zone, Cautious zone, and the Critical zone.

OBJECTIVES

The objectives of the presented analyses were to

1. identify fishing mortality reference points for the diversity of life histories observed in American Eel across the Canadian range,
2. identify how fishing mortality reference points need to be adjusted to account for turbine mortality, and
3. determine if simple relationships based on a limited set of measurable life history traits could be used to predict the identified fishing mortality reference points.

A matrix population modelling approach was used to calculate fishing mortality reference points for American Eel across its Canadian range. Matrix models allow for the incorporation of density-dependence in multiple, different life history parameters, allowing for testing a variety of assumptions. Multiple linear regressions were used to determine if life history traits could be used to predict mortality reference points, and how turbine mortality at the silver stage affects

these reference points. A risk map was generated, including inter-annual stochasticity, to examine the probability of meeting the target stock status under different initial population sizes and fishing regimes. Sensitivity analysis was also conducted to determine which life history parameters and life stages have the largest proportional effect on both the population growth rate, and the ratio of recruits to mature silver eel. These analyses were conducted with stochasticity added to the life history parameters to account for uncertainty in their values.

METHODS

LIFE HISTORY

The Canadian range of American Eel was divided into four geographical zones based on differences in life history patterns (Figure 2; Cairns et al. 2014; DFO 2014). These zones include the St Lawrence basin (SL), encompassing the St Lawrence River and Lake Ontario; the Northern Gulf basin (NG) including the Gulf of St Lawrence drainages of Quebec and Newfoundland; the Southern Gulf basin (SG) which includes PEI and the Gulf of St Lawrence drainages of Nova Scotia and New Brunswick; and the Scotia Fundy basin (SF) which includes the Bay of Fundy drainages and Nova Scotian Atlantic drainages.

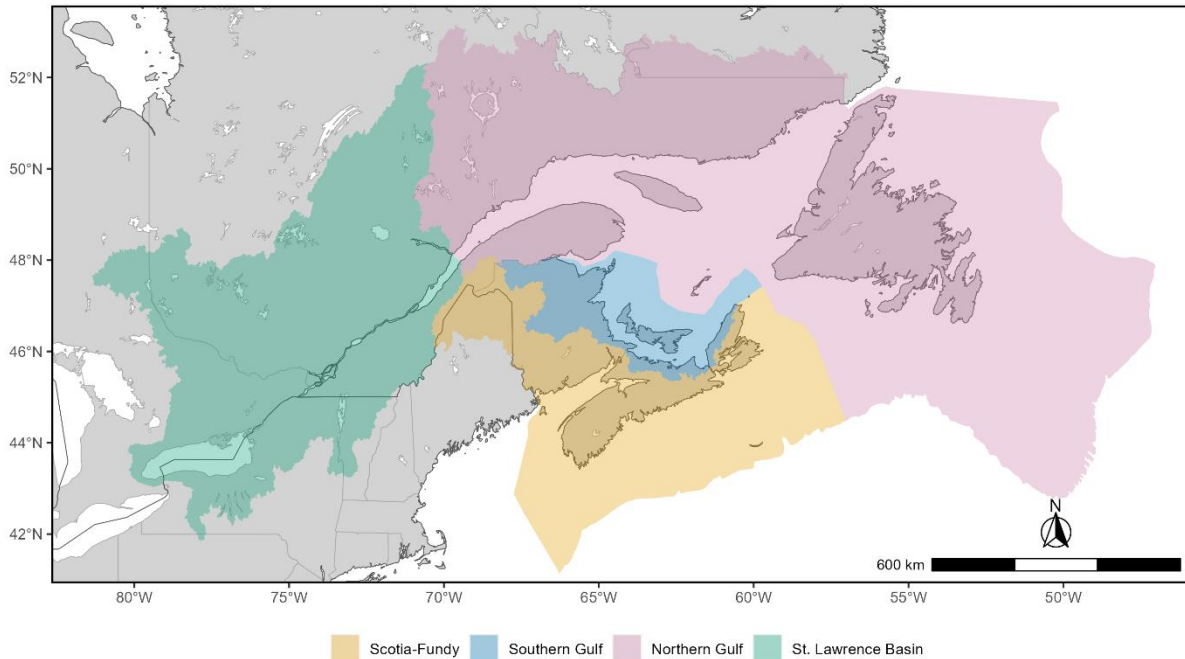


Figure 2. Boundaries of American Eel zones (data from Cairns et al. 2014).

Growth rates and silver lengths

Data from Cairns (2020) and unpublished Canadian data (Thomas Pratt, DFO, pers. comm.) were used to model growth of American Eel. When data were available, the data were filtered to include only known females from freshwater locations. American Eel living in saline environments tends to grow faster and mature younger than eel in freshwater environments (Cairns et al. 2014), but there were insufficient data to analyze saline eel growth separately. Similarly, males tend to grow faster and mature younger and at smaller lengths than females (Cairns et al. 2014), but there were limited data available for a sex-specific analysis.

Both the von Bertalanffy equation and a biphasic growth model were investigated for use as a growth equation. Biphasic growth models differentiate between somatic and reproductive growth, unlike the von Bertalanffy equation, which assumes monophasic growth (Carbonara et al. 2023; Quince et al. 2008). While both equations generate similar ranges of prediction intervals to the data (Appendix 1), the biphasic model parameters (growth rate in mm/year and a direct measure of average population silver length) were preferable to the von Bertalanffy's k growth coefficient and theoretical maximum size. Due to this utility, the biphasic growth curve was chosen as the growth equation in the model.

The biphasic growth model describes length as:

$$length_a = \begin{cases} gr \times a + el & a < a_b \\ gr \times a_b + el & a \geq a_b \end{cases}, \quad (1)$$

where a is age in years, gr is the annual growth rate in mm/year, el is the elver length in mm, and a_b is an inflection point of the piecewise function (hereafter also referred to as the agebreak). When a is smaller than a_b , annual growth is based on gr . At the agebreak, growth effectively stops, and the average silver length (s) is equal to the length at age a_b (Figure 3A). A mean elver length of 63 mm was used based on Canadian data across all locations (Jessop 2010), as there were insufficient data to test the effect of location on elver length.

Most literature reports of growth rate assume constant life-time growth (Cairns et al. 2014), whereas, with the biphasic growth model, growth is constant only to the agebreak. Simulations were used to develop a relationship to allow for a conversion between literature growth rates and the biphasic model (Appendix 1). All future references to somatic growth rate refer to the biphasic growth rate.

Length-Weight

A Canada-wide length-weight relationship was developed for the model. Cairns (2020) reported length-weight data for all four geographic zones in Canada, although the sample size among zones was very unbalanced: $n=187$ in NG; $n=348$ in SL; $n=1954$ in SF; and $n=7348$ in SG. Furthermore, SG had the largest range of lengths: 45 mm to 1,098 mm.

To test for a difference among zones, an analysis of covariance test (ANCOVA) was used. When all the data were included, the results indicated that the SL length-weight relationship had a significantly different slope than the other three groups, and that SF and SG were also significantly different from each other (One way ANCOVA, $F(7, 9829) = 1.16 \times 10^5$, $p < 0.05$). However, the difference was likely due to the unbalanced sample size and data ranges among zones. The model was refit with a random subset of 100 values per zone with a minimum length of 175 mm. This was repeated 10,000 times. In $> 90\%$ of trials there was no significant differences between the zones. When comparing the mean coefficients of the subsampled trials to the coefficients of the grouped data, the subsampled regression visually fit the data better (Appendix 1). Therefore, a single length-weight relationship was fit for the entire Canadian range with length in mm and weight in g:

$$weight = 2.0 \times 10^{-7} (length^{3.35}). \quad (2)$$

Probability of silvering

The probability of silvering, γ_a , is the likelihood that a yellow eel matures into a silver eel at age a . The probability of staying yellow in a given year is therefore equal to $1 - \gamma_a$. The probability of silvering for American Eel is generally thought to be connected to length (Cairns et al. 2014). Multiple mechanisms for determining the probability of silvering were evaluated: maturing as soon as silver length is reached, a constant annual 10% probability of maturing after reaching

silver length, and starting with an annual 10% probability of maturing at some minimum silver age, which increases 1% every year thereafter. Simulations were run to generate the expected silver age and length distribution resulting from each of the three mechanisms, which were compared to distributions from observed data (from Cairns et al., (2020) and Thomas Pratt, DFO, pers. comm.). The mechanism most consistent with the sample data was the silvering probability starting with an 10% probability and increasing by 1% in subsequent years (Appendix 1).

The silvering probability mechanism above describes an individual's likelihood of become a silver eel. The matrix model, however, requires the population-level probability of becoming a silver eel at age a . To calculate this, simulations were run that followed an eel through its life, with each eel having its own unique silver length (based on the mean sl and the Canada-wide standard deviation, Table 1), with growth rates varying year-to-year (based on the mean gr and the Canada-wide standard deviation). Maturity status for individuals were tracked and fit with a logistic regression to give the probability of maturing at age a :

$$\gamma_a = \frac{1}{(1+e^{-0.5(a-int)})}, \quad (3)$$

where int describes the age when 50% of individuals mature. Maturity relationships were generated for a variety of growth rates and silver lengths. The slope of the logistic function was held constant at -0.5 as there was little variability among zones (mean -0.50, standard deviation 0.028) (Figure 3B). With this model, older individuals have a larger cumulative probability of silvering, similar to other models used to describe the silvering probability of European Eel (*Anguilla anguilla*), where larger (and therefore older) eel had a higher probability of being silvers (Briand et al. 2018; van der Hammen et al. 2021). A minimum age of silvering was set at 5 years (γ_1 to $\gamma_4 = 0$) for all locations in Canada to prevent the possibility of unrealistic early maturation.

Fecundity

A Canada-wide fecundity-length relationship was calculated using data from Tremblay (2009). Fecundity is the number of eggs each female produces, and tends to increase exponentially with length in fishes. Upon observation of the grouped data, the separate zones appeared to form a continuous relationship (Figure 3C), with differences between zones largely caused by the different ranges of length values. The fecundity, f , of the population is based on the predicted fecundity at the average silver length, such that:

$$\log_{10}(f) = 3.35 + 1.89(\log_{10}(length)). \quad (4)$$

Survival

Natural mortality of American Eel is difficult to measure empirically. When individuals mature, they leave the population and do not return, which confounds many traditional methods used to estimate mortality (Cairns et al., 2014). In lieu of direct measurements, both the Bevacqua et al., (2011) and the Lorenzen (1996) equations (Equations 5 and 6, respectively) have been used to estimate size-dependent mortality in previous modelling work for American Eel (Bradford et al. 2022; Young & Koops 2014; ASMFC 2012). The Bevacqua equation uses zone, sex and density-specific parameters such that:

$$M_a = e^q \times e^{-E/k \times Temp_K} \times W_a^{-0.46}, \quad (5)$$

where M_a is the instantaneous mortality at age a , W_a is the weight at age a in grams, q is a sex and density-specific coefficient (the value for medium female density was used), E is the

sex-specific activation energy, $Temp_K$ is the average water temperature of the zone in Kelvin, and k is the Boltzmann coefficient (Cairns et al. 2014; Bevacqua et al. 2011).

The Lorenzen equation has fewer parameters:

$$M_a = -\eta \times 3.00 \times W_a^{-0.288}, \quad (6)$$

where η is an adjustment factor that affects the shape and maximum survival output of the curve (ASMFC, 2012). Both curves followed similar shapes (Figure 3D), though the Bevacqua et al. (2011) estimate consistently produced higher survival values than the Lorenzen equation. For the growth rate and silver length combinations found in Canada, the two equations predicted a range of maximum annual survival between 86% - 99%. The lower limit of this range is similar to the estimate of survival of adult European Eel from Dekker (2000) of 87%. By varying the constant, η , in the Lorenzen (1996) equation (Equation 6) between 0.063 and 0.21, the annual survival ranged between approximately 91 - 97% for the average life history in Canada (minimum of 83% with the smallest possible silver length and maximum of 98% for the largest silver length), allowing the curve to mimic the range of both the Lorenzen (1996) equation and the Bevacqua et al. (2011) equation (Figure 3D). To get an estimate of weight, the length was converted using Equation 2. The model assumed that yellow eel and silver eel of the same size had the same natural mortality.

A mean value of 0.0055 annual survival was used to represent elver survival (σ_E ; Jessop 2000). There are relatively little data on the survival of the leptocephali and oceanic stage of American Eel. Therefore the leptocephali survival (σ_L) was solved for to return a stable population growth rate (Young & Koops 2014). With this method, the resulting leptocephali survival is highly dependent on the other life history characteristics for a given simulation.

Density-dependence

Density-dependence was incorporated into the model in three ways; elver survival, probability of silvering, and eel mortality. Density-dependence in elver survival was incorporated using the Beverton-Holt recruitment equation where the density effect at time t (d_t) is equal to:

$$d_t = \frac{\sigma_{E, \lambda=\max} / \sigma_{E, \lambda=1}}{1 + b_{dd} / K_E \times N_{E,t}}, \quad (7)$$

where $N_{E,t}$ is the number of elvers at time t , K_E is the number of elvers at carrying capacity, and b_{dd} is the density-dependent factor that is solved so that when $N_{E,t}$ is equal to K_E and d_t is equal to 1. λ is the discrete-time population growth rate: when it is equal to 1, the population size does not change. σ_E is the annual elver survival, either when $\lambda = 1$, or $\lambda = \lambda_{\max}$. The λ_{\max} , the theoretical maximum population growth rate, was estimated using the allometric size equation from Randall & Minns (2000), which ranged approximately between 1.2 and 1.5 for Canadian life history values. At a density of 0, the elver survival would be equal to its maximum value ($\sigma_{E, \lambda=\max}$), which decreases exponentially as density increases.

Both elver fishing and elver survival density-dependent effects happen in the elver stage, which means an assumption about the relative timing of those events must be made. Two possible options were examined: one where the density-dependent effects happen before the elver fishery, and one where the density-dependent effects happen after the elver fishery. Because the elver fishery removes elvers from the population (therefore reducing $N_{E,t}$), the assumption of density-dependence happening after fishing will likely cause a larger compensation effect d_t , even though the fishing mortality is the same. When the density-dependent effects happen after the elver fishery, fishing mortality (F_{elver}) is applied to $N_{E,t}$ in Equation 7 to represent the number of elvers reduced by the fishing:

$$d_t = \frac{\sigma_E \lambda = \max / \sigma_E \lambda = 1}{1 + b_{dd} / K_E \times (N_{E,t} \times e^{-F_{elver}})}, \quad (8)$$

Density-dependence was also incorporated into the probability of silvering through a density effect on somatic growth rates. Recent eel data from Ontario shows faster growth and younger silvering ages with little change in the size of silvering compared to historical values (EPRI 2018). This may be caused by release of density-dependent growth suppression due to decreased eel density in the St Lawrence (EPRI, 2018). Furthermore, in New York, eel in locations with lower densities had higher average sizes (Camhi et al. 2021). To create density-dependence in growth rate, a maximum growth rate (gr_{max}) was set equal to twice the growth rate at K (gr_K) when yellow eel density is equal to 0, and a minimum growth rate (gr_{min}) was set to half the growth rate at K , where:

$$gr_{a,t} = \left\{ \begin{array}{ll} gr_{max} - gr_K \times \frac{N_{y,a,t}}{K_y} & \frac{N_{y,a,t}}{K_y} < K_{factor} \\ gr_{min} & \frac{N_{y,a,t}}{K_y} \geq K_{factor} \end{array} \right\}, \quad (9)$$

$gr_{a,t}$ is the growth rate at age a , $N_{y,a,t}$ is the mean density each yellow age class a experienced in their life, gr_K is the growth rate when yellow eel density is at its carrying capacity, K_y . K_{factor} is the density breakpoint where the first piecewise equation intersects with gr_{min} where:

$$K_{factor} = \frac{gr_{min} - gr_{max}}{-gr_K}. \quad (10)$$

The probability of silvering equation parameter int (Equation 3) varies depending on the growth rate. Therefore, when the probability of silvering at age was density-dependent, the int parameter changed for each age (int_a), and was determined by:

$$int_{a,t} = e^{(\alpha \times \frac{N_{y,a,t}}{K_y})} + \beta, \quad (11)$$

where α and β are life history-dependent parameters that are solved for so that when $N_{y,a,t}$ is equal to K_y , the int_a is equal to its value at gr_K .

Similarly, the possibility of density-dependent growth rates affecting mortality was also incorporated because mortality is size dependent (Equation 6). Cohort-specific mortality rates were calculate using Equation 5 based on density-dependent growth effects. With relatively little empirical data on density-dependence in American Eel populations, a selection of reasonable combinations were investigated. All analyses were conducted with one of three density-dependent model options. The ‘‘Elver DD’’ option only incorporated density-dependence in elver survival, σ_E . The ‘‘Elver DD + Silv.’’ option refers to models with density-dependence in σ_E and the probability of silvering, γ_a . Finally, the ‘‘Elver DD + Silv. + Mort.’’ included density-dependence in σ_E , γ_a , and eel mortality rate.

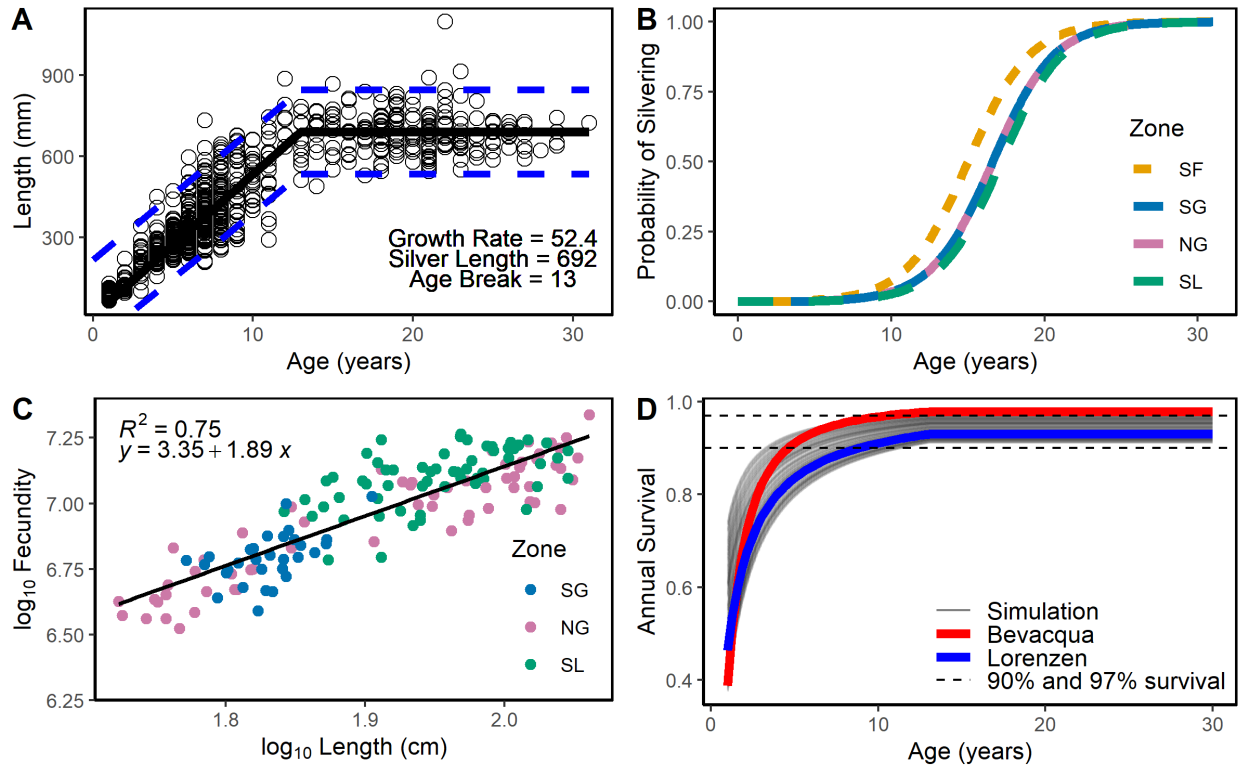


Figure 3. Life history relationships. A) shows an example of biphasic growth for the SG zone (solid black line), including the prediction interval lines (blue lines). B) shows examples of the logistic curve representing the probability of silvering at age for the Canadian geographic zones. C) shows the fecundity length relationship based on data from Tremblay (2009). D) Shows an example of the mortality equation, also showing the Bevacqua et al., (2011) and Lorenzen (1996) equations.

POPULATION MODEL STRUCTURE

The model was a pre-breeding, age-structured matrix population model with an annual time step (Figure 4). The exception was the silver stage (S), which consists of multiple ages. In the model, the leptocephali/glass eel phase (L), the elver phase (E), and the silver stage where the eel migrates from their watershed to the Sargasso Sea all take one year (COSEWIC 2012), with eel spending most of their life as a yellow eel (Y). Because the yellow stage is the majority of the lifespan, for some analyses yellow eel ages were combined into three general stages. The three stages were defined based on the agebreak from the biphasic equation (Equation 1): young yellows were post-elver eel to half of the agebreak; moderate yellows were eel from half of the agebreak until the agebreak; and old yellows were eel that were greater in age than the agebreak (i.e., old enough to silver). All analyses of the model were conducted in R 4.3.1 (R Core Team 2023).

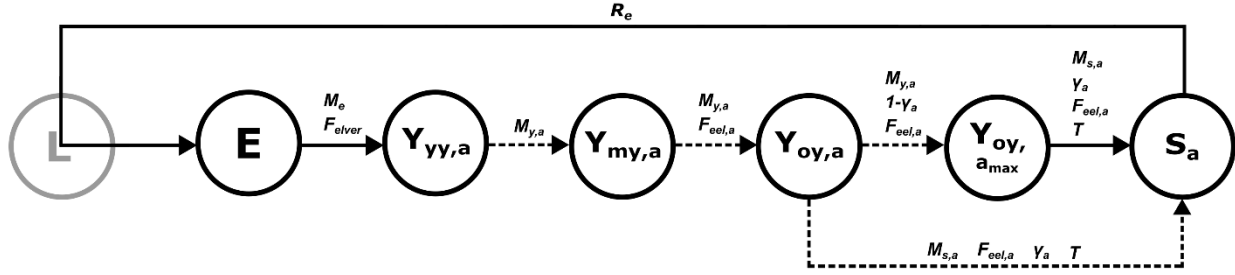


Figure 4. Schematic representation of the matrix population model. The main stages L, E, Y and S describe leptocephali, elvers, yellows and silvers, respectively. Solid lines represent a transition from one age to the next; dashed lines represent transitions among ages within a stage. The leptocephali stage L is in grey because as a pre-breeding model, and the number of leptocephali is not tracked in the population vector. a is age and a_{max} is maximum longevity. The subscript yy denotes young yellow eel; my are moderately aged yellows that are not large enough to silver; and oy are yellow eel large enough to silver. M_e is the elver mortality, and M_a is the mortality at given age. F is the fishing mortality, T is the turbine mortality, R_e is the recruitment of elvers to freshwater, and y_a is the probability of silvering at age a .

The transition matrix M is given by:

$$M = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & R_e \\ E & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & Y_{yy,a} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & \ddots & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & Y_{my,a} & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & \ddots & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & Y_{oy,a} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & \ddots & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & Y_{oy,a_{max-1}} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & S_a & \dots & S_{a_{max-1}} & S_{a_{max}} & 0 \end{bmatrix} \quad (12)$$

Stage-specific abundance, n , each year, t , is calculated from:

$$n_{t+1} = M n_t \quad (13)$$

The dimensions of the matrix were determined by the maximum yellow eel age (set to 25 for all zones) plus 1. Every year the transition matrix values changed depending on the density of the population, which can affect leptocephali survival, probability of silvering and/or mortality depending on the density-dependent model used. The dominant eigenvalue of the matrix represents population growth rate (λ) and indicates the long term status of the population. A $\lambda > 1$ indicates the population is growing exponentially, a $\lambda = 1$ indicates the population is stable, and a $\lambda < 1$ indicates the population is declining towards 0. The dominant right eigenvector of the matrix represents the stable stage distribution (ssd) of the population and indicates the proportional distribution of individuals among stages/ages. This can be used to estimate the number of individuals in all other stages/ages if one is known, assuming equilibrium.

In the pre-breeding model, the recruitment parameter R_e is determined by the mean individual fecundity, f , and the leptocephali survival σ_L :

$$R_e = f \times \sigma_L \quad (14)$$

The elver stage, E , includes annual elver survival, σ_E , the instantaneous fishing mortality, F_{elver} , and the proportion of females in the population ($prop_f$); equal to the Canada-wide average of 95% female (Cairns et al. 2014):

$$E = (e^{-F_{elver}}) \times \sigma_E \times prop_f \times d_t \quad (15)$$

Yellow and silver eel have age-specific mortalities M_a , probabilities of silvering (γ_a) and anthropogenic mortality parameters. $F_{eel,a}$ is the instantaneous fishing mortality, which affects all eel larger than the minimum fishing size (see Anthropogenic harm section below). Silver eel can also be impacted by turbine mortality, T , which can affect all out-migrating silver eel. The yellow transition for an age of a is:

$$Y_a = (1 - \gamma_a) \times e^{-(M_{y,a} + F_{eel,a})} \quad (16)$$

And the silver transition for an age of a is:

$$S_a = \gamma_a \times e^{-(M_{s,a} + F_{eel,a} + T)} \quad (17)$$

Stochasticity

To account for uncertainty in the life history characteristics, stochasticity was included in model parameters across simulation replicates. Life history variables (e.g. growth rate, silver length, fecundity, etc.) were randomly generated from defined distributions to represent the possible variation in characteristics across the Canadian range.

Not all randomly drawn life history combinations are biologically reasonable. Therefore, unrealistic combinations of life history draws (e.g. very large silver length combined with very small growth rate) were discarded. The prediction interval around the observed correlation between silver length and growth rates (from Cairns 2014; growth rates converted to biphasic growth rates) was used to define the reasonable range of combinations for Canada (Figure 5). Only simulations with an agebreak that fell between 7 – 17 years were used for analysis.

Ranges for the Canadian zones were set using the mean growth rates and silver lengths from Cairns et al. (2014), and the Canadian average standard deviations for growth rate and silver length (derived from prediction intervals fitting the biphasic model, see Appendix 1). The range was set to the mean literature value converted growth rate or silver length ± 1.96 multiplied by the Canada-wide standard deviation for growth rate (7.95 mm/year) and silver lengths (89 mm). For most of the zones, this method encapsulated the range found in the literature, except for the NG zone. This zone's range boundaries were therefore expanded to fully capture the wide range of life history found in that location (Table 1). These ranges create subgroups within the Canada wide sampling where certain life histories are likely to be found within Canada.

Table 1. Ranges of growth rate and silver length combinations for each zone, including the overall Canadian range.

| Zone | Growth Rate Range (mm/year) | Silver Length Range (mm) |
|-------------------------|--|---------------------------------|
| Canada-wide (Canada) | 25 – 85 | 350 – 1100 |
| Scotia Fundy (SF) | 25 – 55 | 350 – 725 |
| Southern Gulf (SG) | 30 – 60 | 500 – 850 |
| Northern Gulf (NG) | 45 – 85 | 500 – 1025 |
| St. Lawrence Basin (SL) | 50 – 85 | 750 – 1100 |

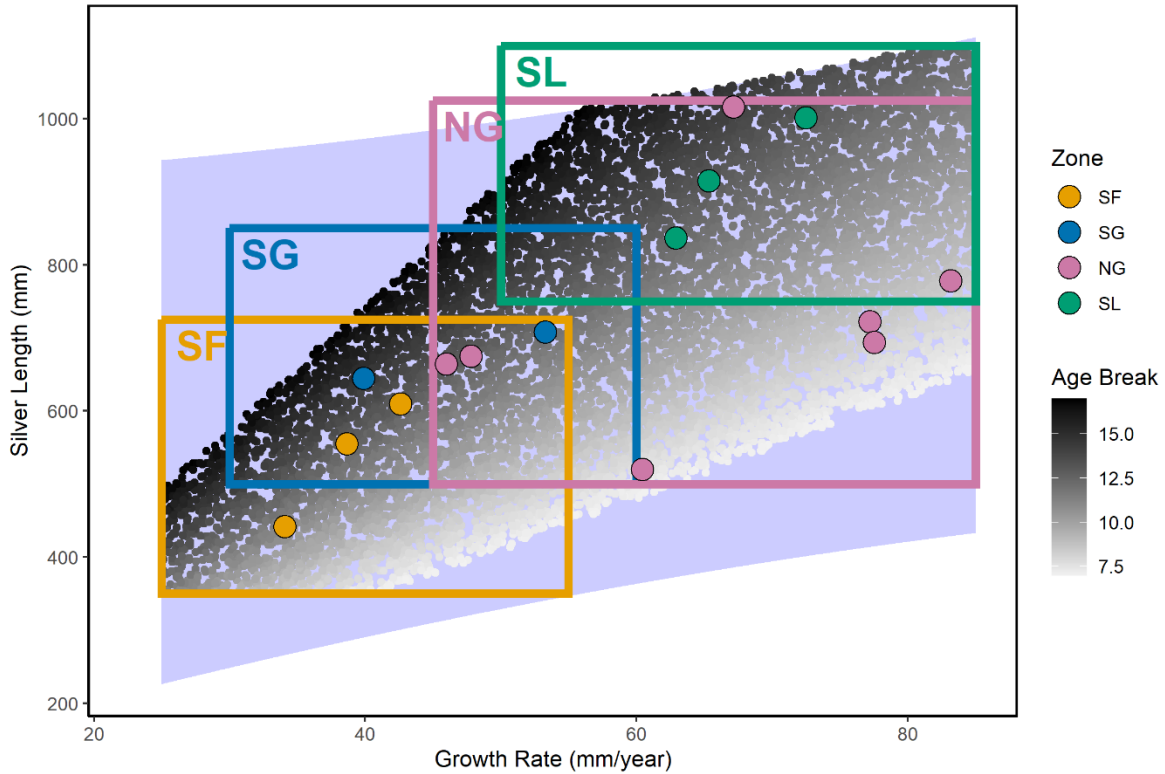


Figure 5. Distribution of biphasic growth rates and silver lengths selected during stochastic simulations. The correlation prediction interval band (the shaded blue area) shows the relationship between growth rate and silver length. The boxes represent zone-specific variation in growth, based on two standard deviation of the mean, except for NG ranges that were expanded to better reflect the range found in literature data. The coloured dots represent the literature values, with the smaller greyscale dots showing possible combinations, shaded based on the agebreak.

Stochasticity was also included in the elver length, fecundity, mortality values, and the λ_{max} . Elver length varied uniformly with minimum and maximum values the standard deviation of 3.26 mm (Jessop 2010) multiplied by 1.96. For the fecundity value, while the fecundity-length equation (Equation 4) was used, the output was varied using a coefficient of variation (CV) of 10%, to allow for some additional variation while still maintaining the overall shape of the relationship (as opposed to a larger coefficient of variation). Mortality was varied by allowing the adjustment parameter η (Equation 5) to vary uniformly between 0.063 and 0.21. Elver survival varied using a uniform distribution ranging from 0.0052 to 0.0057 (Jessop 2000). The λ_{max} value varied uniformly between 1.2 and 1.5, the estimated maximum population growth rate values based on the life history parameters (Randall & Minns 2000)).

Table 2. Summary of main life history parameters used in model.

| Parameter | Definition | Range | Generation |
|------------|--|--|--------------------------|
| sl | Silver length (mm) | 350 – 1100 | Simulated (Figure 5) |
| gr | Biphasic growth rate (mm/year) | 25 – 85 | Simulated (Figure 5) |
| el | Elver length (mm) | 57 – 69 | Simulated (Figure 5) |
| γ_a | Probability of silvering at age a | NA | Calculated (Eqn 3) |
| σ_L | Leptocephali annual survival | 2.0×10^{-5} – 7.2×10^{-3} | Solved for stable output |
| σ_E | Elver annual survival | 0.0052 – 0.0057 | Jessop (2000) |
| $M_{y,a}$ | Yellow eel instantaneous mortality at age a | NA | Calculated (Eqn 6) |
| $M_{s,a}$ | Silver eel instantaneous mortality at age a | NA | Calculated (Eqn 6) |
| f | Number of eggs produced by silver eel; fecundity | 1.3×10^6 – 2.2×10^7 | Calculated (Eqn 4) |
| F | Instantaneous fishing mortality (for eel: F_{eel} or elvers: F_{elver}) | F_{eel} : 0 – 1 F_{elver} : 0 – 6 | Randomly generated |
| T | Instantaneous turbine mortality | 0 – 0.69 | Randomly generated |

Anthropogenic harm

Fishing mortality was represented using the instantaneous fishing rate (F). Fishing mortality could be applied to eel (yellow and silver, F_{eel}) or the elver stage (F_{elver}) or both. Multiple minimum fishing sizes were tested, including a minimum fishing size of 350 mm (Bradford et al. 2022). In Atlantic states in the United States of America, the minimum fishing size is 9 inches (which was rounded to 200 mm) (ASMFC 2024). A larger minimum size limit of 530 mm was also considered (Pers comm. J.F. Dumont MELCCFP).

Age-specific length distributions were generated to find the proportion greater than the minimum fishing size ($p.min$) that were susceptible to the fishery. The maximum and minimum expected size at age was found by calculating the slope between the elver length and the maximum and minimum silver length (based on an average prediction interval of ± 175 mm) (Appendix 1). It was assumed that eel had a uniform distribution between the minimum and maximum length expected at that given age ($length_{a,min}$ and $length_{a,max}$), to attempt to encompass the range possible variation.

The $F_{eel,a}$ is therefore:

$$F_{eel,a} = -\log(1 - (1 - e^{F_{eel}}) \times p.min_a) \quad (18)$$

Turbine mortality, T , impacts out-migrating silver eel. In the SL zone, silver eel migrating from Lake Ontario must successfully pass through multiple dams to return to the Sargasso Sea (the Moses-Saunders dam and Beauharnois dam), resulting in an estimated cumulative mortality rate of 40% (Cairns et al. 2014; COSEWIC 2012). Some locations in other zones may only have one turbine to pass through to reach the Atlantic ocean (e.g. in New Brunswick and Nova Scotia, Cairns et al. 2014). Therefore, the impact of turbine mortality on fisheries reference limits was assessed with mortality ranging from 0% (no turbines in the path of silver migration) to 50% ($T = 0$ to $T = 0.693$).

Population model analysis

The primary purpose of the population model was to estimate both limit and upper mortality reference points for American Eel for the different geographic zones in Canada (Figure 1;

Cairns et al., 2014; DFO, 2014); however these estimates depend on the metric used to evaluate stock status. Various metrics for evaluating stock status exist. Here three metrics, maximum sustainable yield (MSY), spawner per recruit (SPR), and silver escapement (ESC) were considered.

Following a preliminary analysis (Appendix 2) ESC was selected as the preferred metric for stock status. ESC provided mortality reference limits that were generally more consistent and robust than MSY under most model scenarios. ESC and SPR based estimates were similar and highly correlated. Under the model scenario where density-dependence acts following elver fishing mortality however, SPR was insensitive to fishing mortality despite dramatic declines in population abundance. Therefore, it was decided that SPR was not an appropriate metric for evaluating stock status in this analysis. ESC was expressed as a percentage that compares the number of spawners (silver eel) of a fished population to the number of spawners when there is no fishing mortality. For the ESC analysis, 50% ESC (ESC_{50}) was used as the upper stock reference, and 30% ESC (ESC_{30}) as the limit reference point, which allowed comparison to other mortality reference point estimates based on SPR for American Eel (Bradford et al. 2022; Chaput & Cairns 2011; ICES 2001). The mortality reference points are therefore F_{50} , and F_{30} . $F_{extinct}$, the smallest fishing value that will lead to extinction was calculated, allowing examination of how precautionary were the upper stock and limit reference points.

Determining Mortality Reference Points

ESC was calculated as the ratio of silver eel before and after fishing mortality was applied. The ESC is therefore equal to:

$$ESC = \frac{prop_{silver,after}}{prop_{silver,before}}. \quad (19)$$

10,000 stochastic trials were executed to produced ESC values across a range of life history characteristics, fishing mortality rates for both elver and eel fisheries, and density-dependence scenarios. F_{50} and F_{30} were estimated by taking the median of F values with ESC estimates within 0.01 of the target (e.g. 0.49 – 0.51 to get estimates of F_{50}). Additional simulations were conducted to ensure a sample size > 50 for each F_{50} or F_{30} estimate. It is important to note that for this analysis the F_{50} and F_{30} were calculated assuming the underlying population was in a healthy state (i.e. starting from carrying capacity), and are reflective of the fishing mortality values that are likely to result in an ESC of 50% or 30%, respectively. The F_{30} therefore is not the equivalent fishing pressure found in Figure 1, which rather than being larger than F_{50} , should instead decrease to promote the stock to return to the healthy status. The F_{30} calculated in this analysis could be thought of as a maximum F value the stock could be expected to withstand before dropping into the critical zone.

1,000 stochastic trials were run to calculate $F_{extinct}$. $F_{extinct}$ was solved for by setting the density of the population to 0 (i.e. such that the population experiences λ_{max}), and solving for the fishing mortality where $\lambda = 1$. For some simulations it was not possible to calculate $F_{extinct}$; this happened occasionally when the minimum fishing size was large enough to always allow for sufficient escapement of the population to continually persist (and happened more as the minimum fishing size increased). These trials with a very high $F_{extinct}$ were discarded, and therefore not all assumptions have a sample size equal to 1,000.

In addition, simulations were run which included random turbine mortality on silver eel as well as fishing mortality. The turbine mortality (T) value varied between 0 – 50% annual mortality rates (0 – 0.693 instantaneous mortality rate). These trials were used to calculate multiple linear regressions to determine the potential relationship between ESC, fishing mortality and turbine mortality, as well as a key life history trait of silver length. For these simulations, the minimum fishing size was allowed to vary between 200 mm and the integer of 80% of that trial's silver

length, rounded to the nearest centimetre (e.g. the minimum fishing size could be 410 mm, but not 405 mm). This allowed minimum fishing size to be included as a covariate in the multiple linear regressions for eel fisheries.

The regressions related the life history and anthropogenic mortality variables, and the escapement goal to the instantaneous fishing mortality, F . Each regression had up to four covariates: silver escapement, ESC; instantaneous turbine mortality, T ; silver length, SiL ; and minimum fishing size, MS (for eel fisheries). If a covariate did not increase the R^2 of a model by at least 1%, it was deemed to not have an important effect on the predictive power of the model, and was not included. Model assumptions (e.g. no collinearity between variables, and normality of standardized residuals) were checked for each model. These regression results could then be used to predict F_{50} and F_{30} values for given life histories and turbine mortality. The regressions were also used to visualize how the addition of turbine mortality affects the mortality reference points, by calculating the expected mortality reference points, given random life history and random turbine mortality. Similarly, for eel fisheries, the effect of the minimum fishing size on mortality reference points was also explored. Approximate variance around predicted mortality reference points were generated by calculating the mortality reference points for an average Canadian life history ± 0.01 of the target ESC.

Risk matrix

While deterministically derived mortality reference points are useful as a guideline, they do not reflect any possible risk of failing to meet the target ESC in a stochastic environment (i.e. when fished at F_{50} , what is the probability of being above ESC_{50} after a given period of time?). Furthermore, deterministic mortality reference points do not account for how the initial population size may factor into setting reference points. For example, if a population size is well below its carrying capacity K , the mortality reference point will likely need to be reduced, compared to a population in a healthier state. Simulations with stochasticity both in life history and inter-annual stochasticity in survival rate were conducted as part of this risk analysis.

Each individual simulation for the risk maps had an initial ESC that ranged from 0.1 – 1, which was generated by adding a random fishing mortality to a random life history draw. The initial ESC values were binned in increments of 0.1. This initial value assumes that the population had been perturbed, but had reached its stable state. The simulation then tested a range of different test F values (range of 0 - 0.5 for eel fishing; range of 0 - 2.5 for elver fishing when density-dependence happens before fishing; range of 0 - 6 for elver fishing when density-dependence happens after fishing, all binned so that there were 10 bins total), and measured the resulting ESC after a given period of time. For each year of the simulation, inter-annual stochasticity was included (see below). This process was repeated so each combination of binned starting ESC and binned F value had approximately 500 replicates of independent life history draws.

The risk analysis was visualized using a probability-based risk map. The probability of being above a given ESC threshold is the number of trials that finished equal to or above the threshold, divided by the number of trials for that bin combination. For example, if 65 out of 500 trials finished with an ESC equal to or greater than 0.5, then the probability of being above ESC_{50} for that combination of initial ESC and F would be 0.13. This probability was calculated for all bin combinations, for both eel and elver fisheries and density-dependent mechanism combinations. Eel and elver fishing trials had different time horizons for their simulations. Because elver fishing only occurs on one age-class each year, early in the eel life cycle, it takes time for the affects of that fishing to transition through the population, which creates an inherent time delay. Eel fishing on the other hand affects multiple life stages every year, so the population responds with almost no delay. Therefore, eel simulations lasted 10 years; a

common unit of time for fisheries management, while elver simulations lasted for 25 years, to give time for the population to be affected by the fishing mortality.

Inter-annual variation in survival was incorporated into the risk analyses to simulate environmental variation. Variation was added to instantaneous mortality using a stretched beta distribution (which was rescaled to allow values greater than 1). The stretched beta distribution approximates a normal distribution, but removes the extreme values of the distribution to prevent the occasional large deviation from the mean (Morris and Doak 2002). Survival values for yellow and silver eel were varied with a coefficient of variation of 0.2, while leptocephali and elver coefficient of variations were 0.05. Because leptocephali and elver instantaneous mortality were so large, even small perturbations can cause unrealistically large increases in survival. Leptocephali, elver and silver eel survival and variation were independent from all other life stages. Yellow eel were divided into three groups that covered broad categories of ages which were correlated with a factor of 0.5. These stages were based on where the age fell in the biphasic age curve (Equation 1) as described above. For example, if young yellow eel were having a poor year for survival, moderately aged eel were more likely to also have a poor year, while leptocephali, elver and silver eel varied independently.

Sensitivity analysis

Deterministic elasticity analysis (Caswell 2001) was conducted on the model to determine which life history characteristics had the largest effect on the population growth rate. Given a life history value v , (e.g. fecundity, elver survival, yellow fishing mortality, etc.), the elasticity (ϵ_v) is calculated by (Caswell 2001):

$$\epsilon_v = \frac{v}{\lambda} \sum_{i,j} \frac{\partial \lambda}{\partial a_{i,j}} \frac{\partial a_{i,j}}{\lambda v}. \quad (20)$$

Where $a_{i,j}$ is the matrix element in row i and column j , λ is the discrete-time population growth rate. The larger the magnitude of the elasticity, the larger the proportional effect on the population growth rate when that vital rate changes. These elasticities were calculated using 1,000 stochastic life history simulations. Due to the length of time spent as yellow eel, and the large differences of fishing mortalities and probabilities of silvering across yellow ages, the yellow stage was investigated both as an entire class, as well as subsets based on ages: young yellow, moderate yellow, and old yellows (described above). Deterministic elasticity analysis of λ does not allow for density-dependence to be included.

An additional sensitivity analysis was conducted using simulations to examine how influential uncertain life history parameters (elver length, growth rate, silver length, fecundity, and survival values) were on number of silver eel estimates. An initial number of silver eel estimate was calculated for a suite of life history characteristics, one life history parameter was perturbed (a uniform range of a $\pm 10\%$ percent change), and number of silver eel was recalculated. For the survival values, the instantaneous survival was perturbed, due to extreme values (very close to 0 or 1). When variables that affect other life history traits were perturbed, the variables affected were updated to reflect the new value. For example, if silver length was perturbed, the fecundity was recalculated using the new silver length. With the new life history, the new silver eel number is generated, and the percent change between the number of silvers was determined. This simulation was conducted using 1,000 simulations for each life history variable. If the percent change of number of silvers was greater than 10%, then the model was sensitive to changes in that variable; if the percent change of silver eel was less than 10%, the model was not sensitive to that life history variable. The correlation between the percent change in the life history variables and the percent change in silver eel is examined in Appendix 4.

RESULTS

MORTALITY REFERENCE POINTS

For elver fisheries, the assumption of when the density-dependence in elver survival happens relative to the fishing mortality has strong effects on the ESC of the model (Figure 6; Table 3). When density-dependence occurs after the fishing mortality, the population is more resilient to elver fishing mortality while the escapement stays relatively high; however, as the fishing mortality continues to increase, the ESC quickly decreases towards 0. When density-dependence occurs before the fishery, there is a fast decline in ESC at smaller fishing values, which then slowly tapers off as the fishing mortality increases and the ESC approaches 0. This difference in pattern causes the F_{50} and F_{30} values to be larger if the density-dependence occurs after the fishery, but also much more variable. The more density-dependent mechanisms included in the simulation, the more variable the mortality reference points (and, in the case of density-dependence occurring after the fishery, the larger they were as well). However, there was relatively little difference in mortality reference points among zones (Table 3).

The relationship between F and ESC for eel fisheries resembles the elver fishery relationship when density-dependence occurs before the fishery: a rapid decline at small fishing values, which then decelerates as the fishing rate increase (Figure 7). The minimum fishing size affected this relationship, where smaller minimum fishing sizes were associated with smaller F_{50} and F_{30} values, and less overall variability (Figure 7; Table 4). Consistent with elver fishery results, when more density-dependent mechanisms were included in model simulations, the estimates of F_{50} and F_{30} were larger and more variable. The stock status of the eel fishery was greatly affected by the silver length in a given simulation, where larger silver lengths were associated with smaller ESC values for the same F value. Unlike with elver fisheries, there was a notable difference in mortality reference points among zones (Table 4). The Scotia-Fundy zone (SF) consistently had the largest mortality reference points, while the St. Lawrence zone (SL) was consistently the smallest estimate (Table 4).

The question of whether 50% and 30% ESC as reference limits was precautionary was investigated by comparing estimates of F_{50} and F_{30} to $F_{extinct}$ (Table 5). Estimates of $F_{extinct}$ were generally similar among zones and was larger when density-dependence acted only on the elver stage. Under most simulation scenarios, the mortality reference limits were not close to $F_{extinct}$ values: F_{30} was generally $< 50\%$ of $F_{extinct}$. The exception was when density-dependence on the elver stage acted after fishing; in this scenario, F_{30} was approximately 86 – 100% of $F_{extinct}$, indicating that 30% ESC is not a precautionary reference limit. Further simulations were conducted to compare ESC and $F_{extinct}$ for an elver fishery with density-dependence acting before or after fishing for single life history simulations across λ_{max} values (Figure 8). $F_{extinct}$ increased with λ_{max} but was the same regardless of when density-dependence acted. The escapement curves, however, differed when density-dependence acted before fishing followed a more convex shape and curves when density-dependence acted after fishing followed a more concave shape. As a result, escapement was higher at fishing levels closer to $F_{extinct}$ when density-dependence acted after fishing.

In order to monitor the stock to determine its status according to the precautionary approach, ESC could be used directly. However, it may be more feasible in some locations to use yellow eel biomass as a proxy for silver eel escapement. When eel are fished, the proportional yellow eel biomass is larger than its corresponding silver eel escapement (Table 6). For example, if the target escapement for the population is to have a 50% silver escapement, this would correspond to approximately 65% yellow biomass proportionally, depending on the minimum

fishing size (Table 6). The larger the minimum fishing size, the larger this difference between ESC and yellow eel biomass.

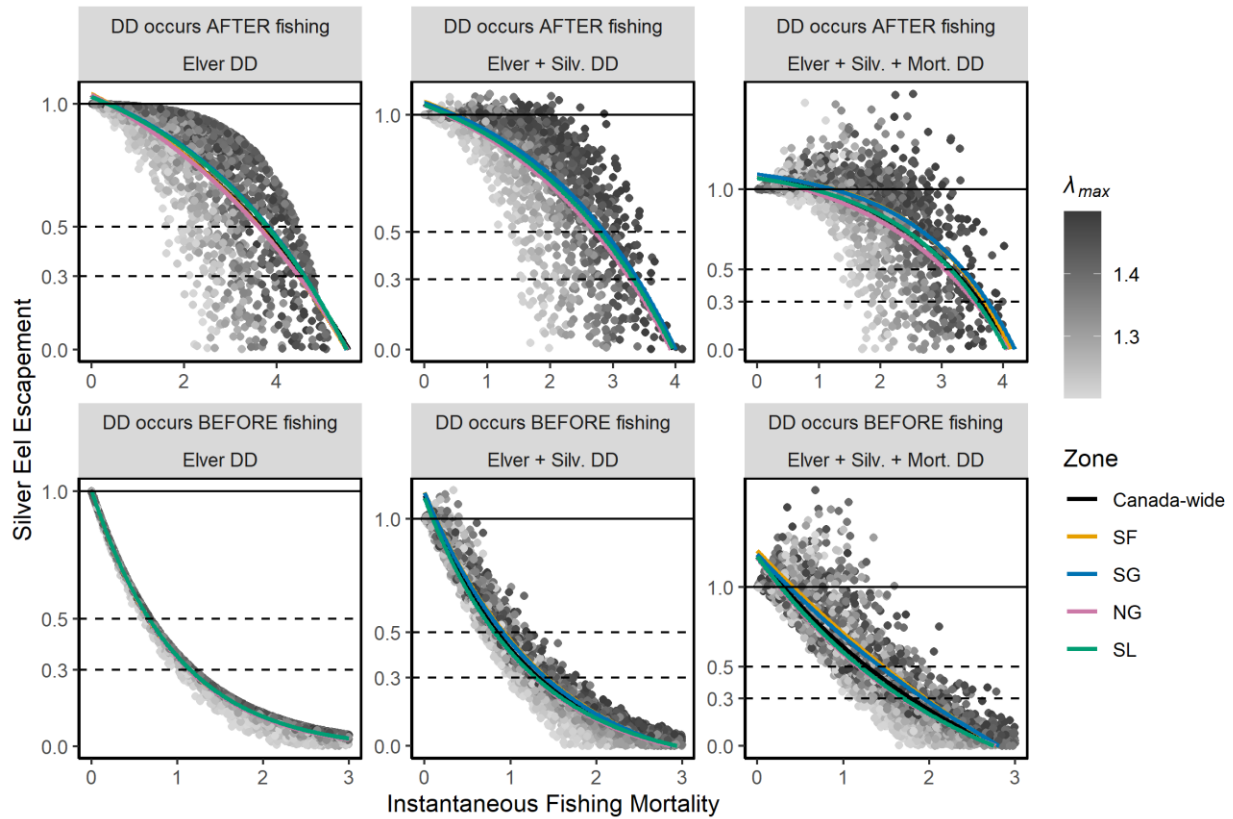


Figure 6. Relationship between instantaneous fishing mortality (F) and silver eel escapement (ESC) for elver fisheries. Lines show zone-specific fits of an exponential decay function (Table 1). Individual points are coloured based on their λ_{max} . ESC_{50} and ESC_{30} are shown as dashed lines, with ESC of 1 as a solid line. Different assumptions about the timing of density-dependence are displayed in rows.

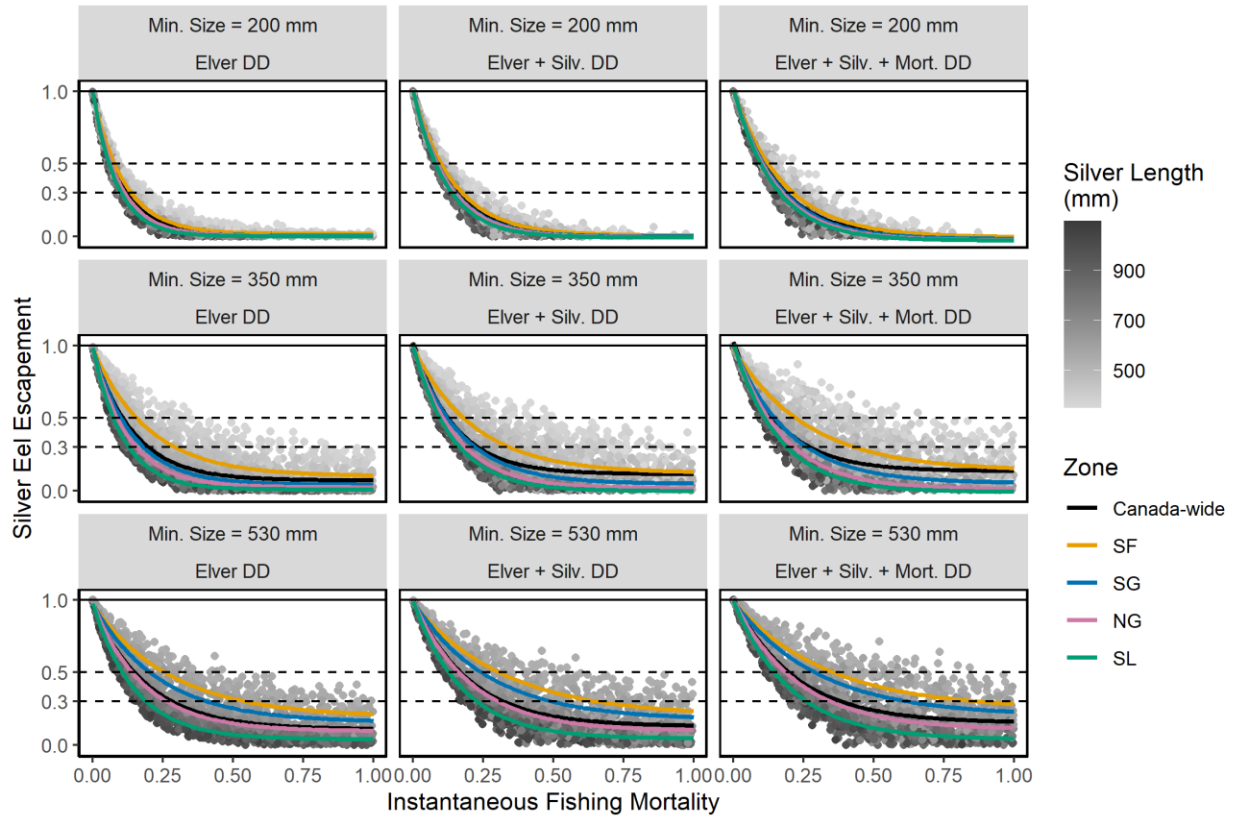


Figure 7. Relationship between instantaneous fishing mortality (F) and silver eel escapement (ESC) for eel fisheries. Lines show zone-specific fits of an exponential decay function (Table 1). Individual points are coloured based on their silver length. ESC_{50} and ESC_{30} are shown as dashed lines, with ESC of 1 as a solid line. Different minimum sizes are displayed in rows.

Table 3. Mortality-based reference points elver fisheries in various zones in Canada under different density-dependent models and timing scenarios. Reference points are expressed as instantaneous fishing mortalities, and are shown as median values (10 – 90% quantiles in brackets) due to skewed distributions. All zones had a sample size of 50.

| ESC Goal | DD timing | Zone | Elver only DD | Elver + Silv. DD | Elver + Silv. + Mort. DD |
|----------|--------------------------|--------|------------------------------|------------------------------|------------------------------|
| | | | Median F (10 – 90% quantile) | Median F (10 – 90% quantile) | Median F (10 – 90% quantile) |
| 50% | DD occurs before fishing | Canada | 0.67 (0.64 – 0.69) | 0.84 (0.76 – 1.0) | 1.2 (1.0 – 1.6) |
| | | SF | 0.67 (0.64 – 0.70) | 0.89 (0.77 – 1.1) | 1.3 (1.0 – 1.7) |
| | | SG | 0.67 (0.64 – 0.69) | 0.89 (0.80 – 1.1) | 1.3 (1.0 – 1.6) |
| | | NG | 0.67 (0.63 – 0.69) | 0.80 (0.73 – 1.0) | 1.1 (0.97 – 1.5) |
| | | SL | 0.67 (0.63 – 0.70) | 0.83 (0.77 – 0.95) | 1.2 (0.92 – 1.4) |
| | DD occurs after fishing | Canada | 3.5 (2.5 – 4.4) | 2.5 (1.9 – 3.1) | 2.4 (1.6 – 3.4) |
| | | SF | 3.5 (2.6 – 4.4) | 2.6 (1.9 – 3.5) | 2.7 (2.1 – 3.4) |
| | | SG | 3.1 (2.5 – 4.4) | 2.4 (1.8 – 3.1) | 2.3 (1.8 – 3.2) |
| | | NG | 3.0 (2.1 – 4.4) | 2.4 (1.6 – 3.1) | 2.4 (1.6 – 3.4) |
| | | SL | 3.5 (2.6 – 4.4) | 2.4 (1.6 – 2.9) | 2.6 (1.8 – 3.3) |
| 30% | DD occurs before fishing | Canada | 1.2 (1.1 – 1.2) | 1.3 (1.2 – 1.5) | 1.7 (1.3 – 2.1) |
| | | SF | 1.2 (1.1 – 1.2) | 1.4 (1.1 – 1.6) | 1.8 (1.5 – 2.1) |
| | | SG | 1.2 (1.1 – 1.2) | 1.3 (1.1 – 1.6) | 1.8 (1.4 – 2.1) |
| | | NG | 1.2 (1.1 – 1.2) | 1.2 (1.1 – 1.4) | 1.6 (1.3 – 1.9) |
| | | SL | 1.2 (1.1 – 1.2) | 1.3 (1.2 – 1.4) | 1.6 (1.3 – 1.9) |
| | DD occurs after fishing | Canada | 3.9 (2.6 – 4.7) | 2.7 (2.1 – 3.3) | 2.7 (2.2 – 3.1) |
| | | SF | 3.5 (2.7 – 4.6) | 2.5 (1.8 – 3.5) | 2.6 (2.3 – 3.2) |
| | | SG | 4.1 (2.7 – 4.7) | 2.6 (1.9 – 3.4) | 2.8 (2.2 – 3.1) |
| | | NG | 3.8 (2.6 – 4.7) | 2.6 (1.9 – 3.3) | 2.6 (2.0 – 3.1) |
| | | SL | 3.7 (2.8 – 4.7) | 2.7 (1.9 – 3.3) | 2.5 (2.2 – 3.2) |

Table 4. Mortality-based reference points eel fisheries in various zones in Canada under different density-dependent models and minimum fishing size scenarios. Reference points are expressed as instantaneous fishing mortalities, and are shown as median values (10 – 90% quantiles in brackets) due to skewed distributions. All zones had a sample size of 50.

| ESC Goal | Min. Fishing Size | Zone | Elver only DD | Elver + Silv. DD | Elver + Silv. + Mort. DD |
|----------|-------------------|--------|------------------------------|------------------------------|------------------------------|
| | | | Median F (10 – 90% quantile) | Median F (10 – 90% quantile) | Median F (10 – 90% quantile) |
| 50% | 200 mm | Canada | 0.064 (0.055 – 0.087) | 0.085 (0.075 – 0.11) | 0.11 (0.095 – 0.14) |
| | | SF | 0.076 (0.057 – 0.10) | 0.10 (0.082 – 0.12) | 0.13 (0.10 – 0.17) |
| | | SG | 0.065 (0.054 – 0.079) | 0.086 (0.078 – 0.10) | 0.11 (0.093 – 0.12) |
| | | NG | 0.067 (0.056 – 0.082) | 0.089 (0.078 – 0.10) | 0.11 (0.092 – 0.12) |
| | | SL | 0.057 (0.053 – 0.065) | 0.081 (0.074 – 0.089) | 0.10 (0.089 – 0.11) |
| | 350 mm | Canada | 0.091 (0.067 – 0.23) | 0.11 (0.087 – 0.24) | 0.14 (0.11 – 0.21) |
| | | SF | 0.21 (0.095 – 0.34) | 0.23 (0.13 – 0.45) | 0.20 (0.13 – 0.42) |
| | | SG | 0.10 (0.074 – 0.13) | 0.12 (0.10 – 0.16) | 0.15 (0.12 – 0.19) |
| | | NG | 0.092 (0.069 – 0.12) | 0.11 (0.085 – 0.14) | 0.13 (0.11 – 0.17) |
| | | SL | 0.073 (0.064 – 0.086) | 0.093 (0.086 – 0.11) | 0.12 (0.10 – 0.13) |
| | 530 mm | Canada | 0.18 (0.099 – 0.45) | 0.20 (0.12 – 0.53) | 0.22 (0.14 – 0.66) |
| | | SF | 0.35 (0.20 – 0.48) | 0.35 (0.21 – 0.59) | 0.42 (0.28 – 0.66) |
| | | SG | 0.34 (0.14 – 0.46) | 0.35 (0.17 – 0.54) | 0.44 (0.21 – 0.77) |
| | | NG | 0.17 (0.10 – 0.35) | 0.20 (0.13 – 0.39) | 0.21 (0.14 – 0.52) |
| | | SL | 0.11 (0.087 – 0.13) | 0.13 (0.11 – 0.16) | 0.16 (0.13 – 0.18) |
| 30% | 200 mm | Canada | 0.12 (0.095 – 0.15) | 0.15 (0.13 – 0.18) | 0.19 (0.16 – 0.23) |
| | | SF | 0.14 (0.10 – 0.18) | 0.18 (0.14 – 0.24) | 0.21 (0.18 – 0.25) |
| | | SG | 0.12 (0.10 – 0.14) | 0.16 (0.14 – 0.18) | 0.19 (0.16 – 0.22) |
| | | NG | 0.11 (0.094 – 0.14) | 0.16 (0.14 – 0.18) | 0.18 (0.16 – 0.20) |
| | | SL | 0.10 (0.092 – 0.12) | 0.14 (0.12 – 0.15) | 0.17 (0.15 – 0.19) |
| | 350 mm | Canada | 0.18 (0.12 – 0.47) | 0.21 (0.16 – 0.38) | 0.25 (0.18 – 0.65) |
| | | SF | 0.36 (0.17 – 0.74) | 0.41 (0.28 – 0.81) | 0.48 (0.27 – 0.82) |
| | | SG | 0.20 (0.14 – 0.26) | 0.23 (0.18 – 0.29) | 0.26 (0.20 – 0.40) |
| | | NG | 0.17 (0.12 – 0.23) | 0.18 (0.16 – 0.23) | 0.22 (0.17 – 0.28) |
| | | SL | 0.13 (0.12 – 0.15) | 0.17 (0.15 – 0.19) | 0.20 (0.18 – 0.23) |
| | 530 mm | Canada | 0.43 (0.19 – 0.87) | 0.36 (0.22 – 0.92) | 0.40 (0.26 – 0.85) |
| | | SF | 0.59 (0.37 – 0.95) | 0.72 (0.41 – 0.94) | 0.71 (0.49 – 0.93) |
| | | SG | 0.57 (0.31 – 0.94) | 0.55 (0.28 – 0.93) | 0.61 (0.34 – 0.93) |
| | | NG | 0.36 (0.21 – 0.69) | 0.33 (0.22 – 0.76) | 0.37 (0.24 – 0.85) |
| | | SL | 0.19 (0.17 – 0.24) | 0.23 (0.20 – 0.30) | 0.29 (0.23 – 0.34) |

Table 5. Comparison of fishing mortality reference values across zones, fisheries and density dependent options. F_{50} and F_{30} values taken from Tables 3 and 4. $F_{extinct}$ represent the median values across life history for each zone. Eel mortality reference points based on a minimum fishing size of 350 mm.

| Density Model | Fish Type | Zone | $F_{extinct}$ | F_{30} | F_{50} |
|--------------------------|-------------------------|--------|---------------|----------|----------|
| Elver DD | Elver DD After Fishing | Canada | 3.9 | 3.9 | 3.5 |
| | | SF | 3.9 | 3.5 | 3.5 |
| | | SG | 4.1 | 4.1 | 3.1 |
| | | NG | 3.8 | 3.8 | 3.0 |
| | | SL | 4.1 | 3.7 | 3.5 |
| | Elver DD Before Fishing | Canada | 3.9 | 1.2 | 0.67 |
| | | SF | 3.9 | 1.2 | 0.67 |
| | | SG | 4.1 | 1.2 | 0.67 |
| | | NG | 3.8 | 1.2 | 0.67 |
| | | SL | 4.1 | 1.2 | 0.67 |
| | Eel | Canada | 0.78 | 0.18 | 0.091 |
| | | SF | 1.0 | 0.36 | 0.21 |
| | | SG | 0.83 | 0.20 | 0.10 |
| | | NG | 0.75 | 0.17 | 0.092 |
| | | SL | 0.68 | 0.13 | 0.073 |
| Elver + Silv. DD | Elver DD After Fishing | Canada | 2.9 | 2.7 | 2.5 |
| | | SF | 2.9 | 2.5 | 2.6 |
| | | SG | 2.9 | 2.6 | 2.4 |
| | | NG | 2.8 | 2.6 | 2.4 |
| | | SL | 3.0 | 2.7 | 2.4 |
| | Elver DD Before Fishing | Canada | 2.9 | 1.3 | 0.84 |
| | | SF | 2.9 | 1.4 | 0.89 |
| | | SG | 2.9 | 1.3 | 0.89 |
| | | NG | 2.8 | 1.2 | 0.80 |
| | | SL | 3.0 | 1.3 | 0.83 |
| | Eel | Canada | 0.62 | 0.21 | 0.11 |
| | | SF | 0.93 | 0.41 | 0.23 |
| | | SG | 0.68 | 0.23 | 0.12 |
| | | NG | 0.59 | 0.18 | 0.11 |
| | | SL | 0.51 | 0.17 | 0.093 |
| Elver + Silv. + Mort. DD | Elver DD After Fishing | Canada | 2.9 | 2.7 | 2.4 |
| | | SF | 2.8 | 2.6 | 2.7 |
| | | SG | 2.9 | 2.8 | 2.3 |
| | | NG | 2.8 | 2.6 | 2.4 |
| | | SL | 3.1 | 2.5 | 2.6 |
| | Elver DD Before Fishing | Canada | 2.9 | 1.7 | 1.2 |
| | | SF | 2.8 | 1.8 | 1.3 |
| | | SG | 2.9 | 1.8 | 1.3 |
| | | NG | 2.8 | 1.6 | 1.1 |
| | | SL | 3.1 | 1.6 | 1.2 |
| | Eel | Canada | 0.64 | 0.25 | 0.14 |
| | | SF | 0.97 | 0.48 | 0.20 |
| | | SG | 0.71 | 0.26 | 0.15 |
| | | NG | 0.57 | 0.22 | 0.13 |
| | | SL | 0.51 | 0.20 | 0.12 |

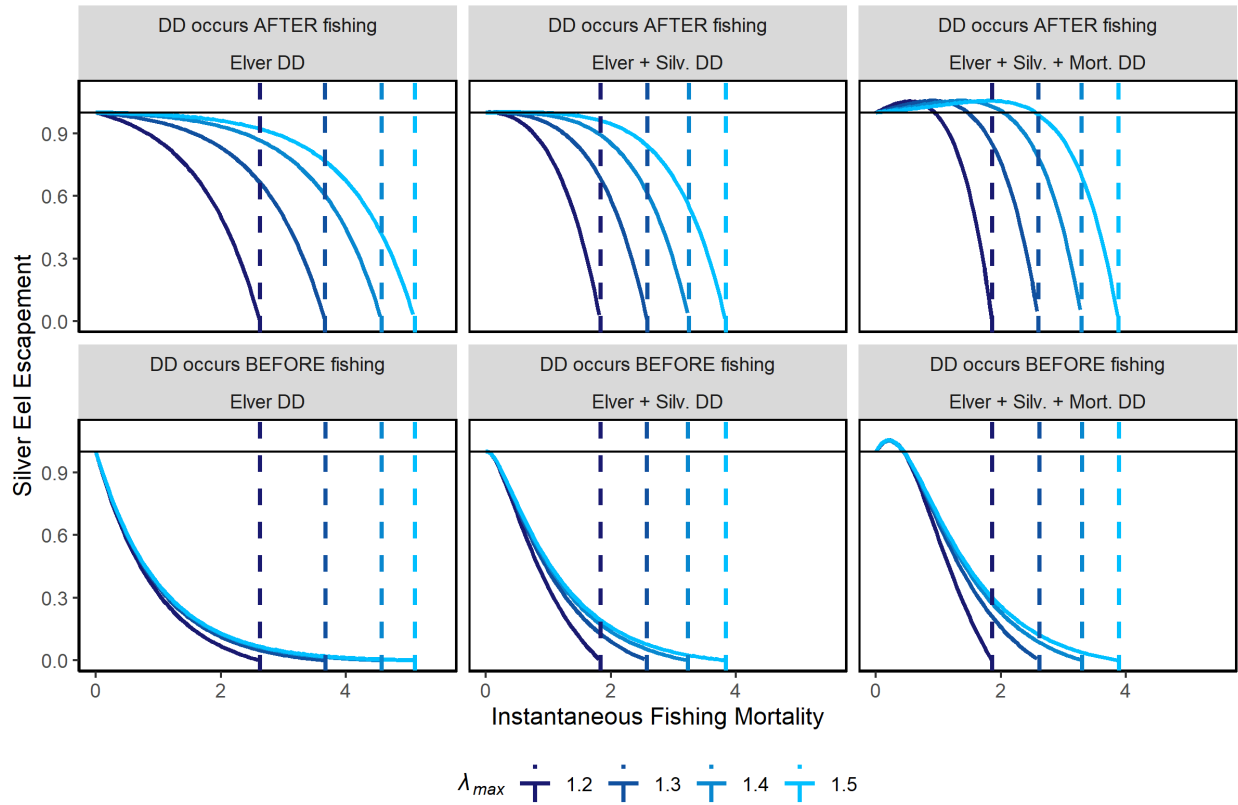


Figure 8. Relationships from a single life history simulations across λ_{max} values. The dashed vertical lines represent the $F_{extinct}$ for each λ_{max} , where larger λ_{max} values are associated with larger $F_{extinct}$. Depending on when density-dependence is assumed to happen in the elver stage, the silver eel escapement follows different trajectories as fishing mortality increases.

Table 6. Comparing escapement goals to corresponding proportional eel biomass values at various minimum fishing sizes (sample size of 150 for each row, assuming Canada-wide data). Results were similar between density-dependent assumptions, and were therefore grouped.

| Minimum Fishing Size | Escapement Goal | Proportional Yellow Eel Biomass |
|----------------------|-----------------|---------------------------------|
| 200 mm | 50% | 61% |
| | 30% | 43% |
| 350 mm | 50% | 66% |
| | 30% | 50% |
| 530 mm | 50% | 72% |
| | 30% | 56% |

TURBINE MORTALITY

As turbine mortality increased, the mortality reference points decreased (Figure 9 and Figure 10). With increasing density-dependence mechanisms, the more variable the relationship between turbine mortality and the mortality reference points. For eel fisheries, as the minimum fishing size increased, the mortality reference points increased in general, regardless of the turbine mortality (Figure 10). When considering the effect on turbine mortality on F_{50} values for eel, at high turbine mortalities (e.g. starting around 25% annual mortality, depending on the minimum fishing size (Figure 10)), the F_{50} values become very small as they approach 0 with the “Elver DD” density-dependent model. Under these scenarios, the combination of life history

and anthropogenic mortality was only predicted to successfully support the silver eel escapement goal of 50% if there was effectively no eel fishing.

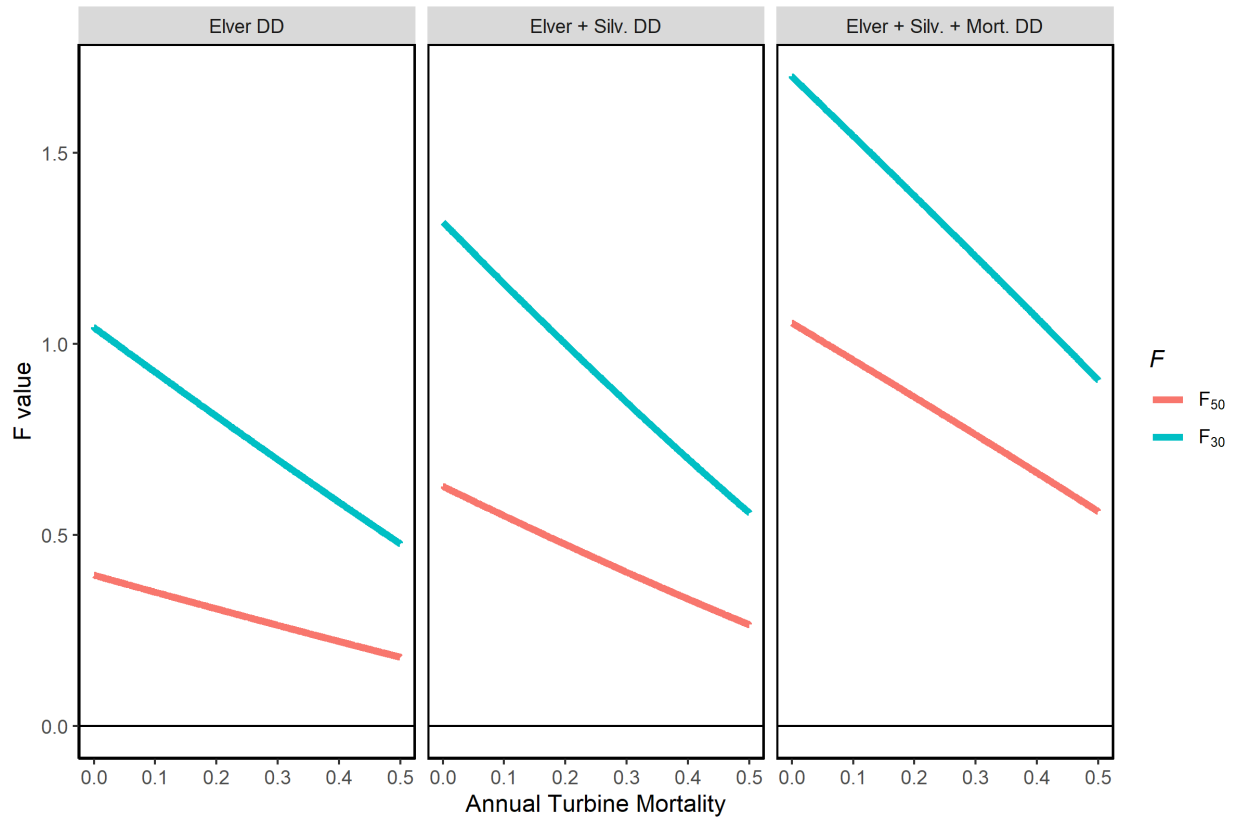


Figure 9. Relationship between annual turbine mortality and mortality reference points for elver fisheries, as derived from multiple linear regressions in Table 7. These regressions assume density-dependence occurs before the fishery.

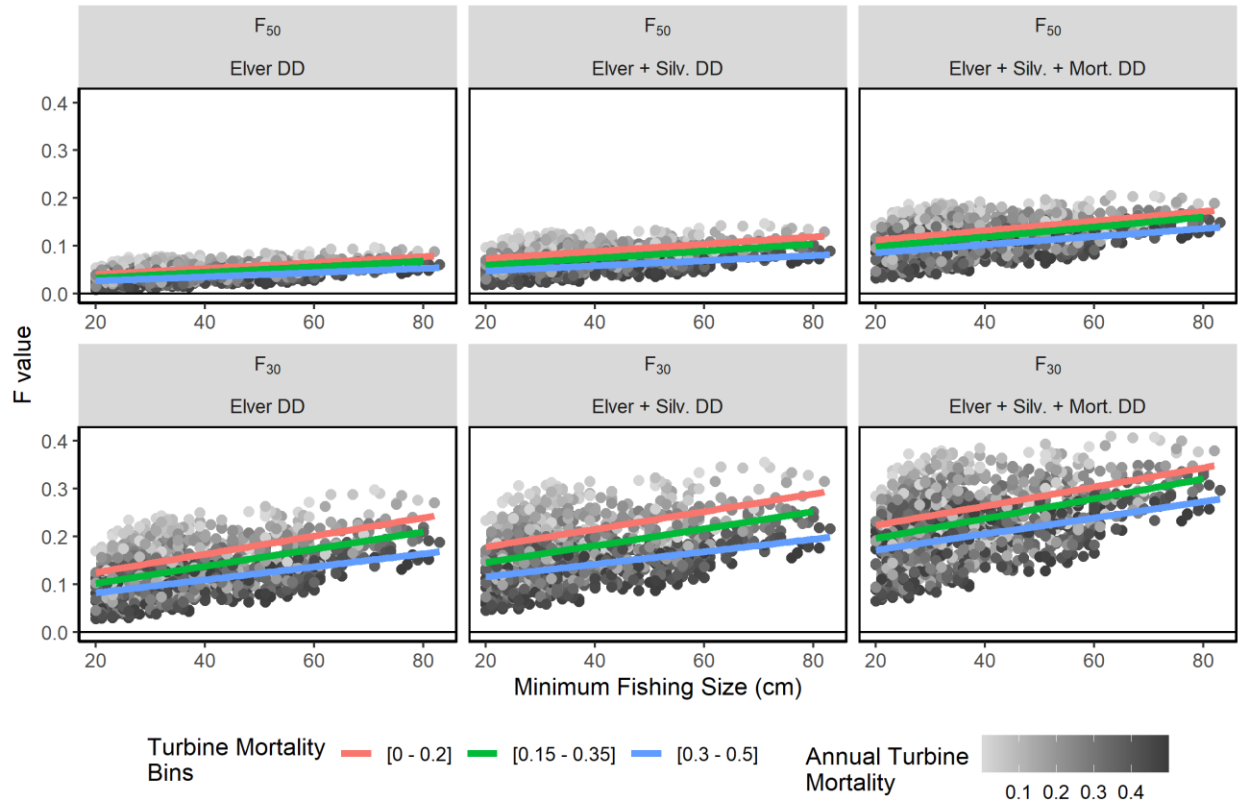


Figure 10. Relationship between minimum fishing size, mortality reference points and annual turbine mortality for eel fisheries, as derived from multiple linear regressions in Table 7. The fit lines on the graph are linear regression fits to binned annual turbine mortalities, showing the different responses across turbine mortality.

PREDICTING MORTALITY REFERENCE POINTS

Instantaneous turbine mortality (T) (e.g. $T = 0.69$ for an annual turbine mortality of 50%) was included as possible parameters in the multiple regression. Silver length (SiL) was chosen as the life history variable to also include as a covariate, and minimum fishing size in mm (MS) was included in regressions for eel fisheries. The response variable, F , was log transformed to improve linearity of the model. Models were fit to the general form:

$$F = e^{(\alpha + \beta_{ESC} + \beta_T + \beta_{SiL} + \beta_{MS})}, \quad (21)$$

where α (intercept) and each β_i are reported in Table 7. If a parameter is not reported, that means it was not an important predictor of F , and was removed from the regression for that variable. For the regressions, only elver fisheries where the density-dependence occurs before the fishery are presented. The shape of the relationship between F and ESC did not support the use of linear regressions to make predictions when the density-dependence occurred after the fishery (residuals consistently non-normal despite transformations). Because of the large sample size ($n = 3,500$), the data were split so that ~50% was training data, and the remaining 50% was testing data. The training data were used to fit the regressions (so each regression has a sample size of approximately 1750), while the test data were used to visualize the predictive ability of the regressions (Appendix 3).

Most models had very high R^2 values (range of 0.82 – 0.90; Table 7), with the exception of elver fisheries when there is density-dependence in elver survival, silvering probability and yellow eel

mortality, which had an R^2 of 0.67. These high values indicate all models do a good job of predicting the mean output. In general, the more density-dependent compensation in the model, the smaller the R^2 . The predicted F values tend to be smaller, underestimating the mortality reference points compared to Canada-wide values found using the population model (Table 8; Table 3 and 4). When only zone differences were considered (Table 3), the more density-dependent compensation was included in the model, the larger the expected mortality reference points were (Table 8).

Examples using the regression parameters in Table 7 and Equation 21 are as follows. For a population with an average silver length of 600 mm, a minimum fishing size of 350 mm, and an instantaneous turbine mortality rate of 0.29, the elver mortality reference limit for an ESC target of 50% would be:

$$F = e^{(1.50 + (-4.85 \times 0.5) + (-1.13 \times 0.29))}$$

$$F = 0.29$$

For an eel fishery, the F_{50} could be estimated as:

$$F = e^{(0.173 + (-5.65 \times 0.5) + (-0.994 \times 0.29) + (-0.00189 \times 600) + (0.00291 \times 350))}$$

$$F = 0.047$$

Table 7. Parameters from chosen multiple linear regression models to predict F with silver length (SiL) in mm as a life history covariate. ESC is the silver escapement target, and T is the instantaneous turbine mortality rate, and MS is the minimum fishing size in mm.

| Density Model | Fish Type | R^2 | Parameter values | Std. Error | |
|--------------------------|--------------------|--------|--------------------------|-----------------------|--------|
| Elver DD | Elver | 0.88 | $B_{ESC} = -4.85$ | 0.0425 | |
| | | | $\beta_T = -1.13$ | 0.0413 | |
| | | | $\alpha = 1.50$ | 0.0201 | |
| | Eel | 0.90 | $B_{ESC} = -5.65$ | 0.0474 | |
| | | | $\beta_T = -0.994$ | 0.0392 | |
| | | | $\beta_{SiL} = -0.00189$ | 5.47×10^{-5} | |
| $\beta_{MS} = 0.00291$ | | | 7.47×10^{-5} | | |
| Elver + Silv. DD | Elver | 0.82 | $B_{ESC} = -3.72$ | 0.0421 | |
| | | | $\beta_T = -1.24$ | 0.0526 | |
| | | | $\alpha = 1.39$ | 0.0251 | |
| | Eel | 0.86 | $B_{ESC} = -4.44$ | 0.0431 | |
| | | | $\beta_T = 1.03$ | 0.0478 | |
| | | | $\beta_{SiL} = -0.00159$ | 6.49×10^{-5} | |
| | | | $\beta_{MS} = 0.00233$ | 8.53×10^{-5} | |
| | | | $\alpha = 0.121$ | 0.0419 | |
| | | | Elver + Silv. + Mort. DD | Elver | 0.67 |
| | $\beta_T = -0.910$ | 0.0681 | | | |
| | $\alpha = 1.25$ | 0.0330 | | | |
| | Eel | 0.84 | | $B_{ESC} = -3.47$ | 0.0379 |
| $\beta_T = -0.627$ | | | | 0.0496 | |
| $\beta_{SiL} = -0.00169$ | | | | 7.07×10^{-5} | |
| $\beta_{MS} = 0.00233$ | | | | 9.46×10^{-5} | |
| $\alpha = 0.600$ | | | | 0.0449 | |

Table 8. Predicted F_{50} and F_{30} values for multiple linear regressions. The predicted mortality reference point, as well as the estimated F values \pm of the target ESC were provided. For eel fisheries, a minimum fishing size of 350 mm was assumed in this table.

| Density Model | Fish Type | ESC target | F (F value at ± 0.01 of target) |
|--------------------------|-----------|------------|--|
| Elver DD | Elver | 50 | 0.40 (0.38 – 0.41) |
| | | 30 | 1.0 (0.99 – 1.1) |
| | Eel | 50 | 0.050 (0.047 – 0.052) |
| | | 30 | 0.15 (0.14 – 0.16) |
| Elver + Silv. DD | Elver | 50 | 0.63 (0.60 – 0.65) |
| | | 30 | 1.3 (1.3 – 1.4) |
| | Eel | 50 | 0.087 (0.084 – 0.091) |
| | | 30 | 0.21 (0.20 – 0.22) |
| Elver + Silv. + Mort. DD | Elver | 50 | 1.1 (1.0 – 1.1) |
| | | 30 | 1.7 (1.7 – 1.7) |
| | Eel | 50 | 0.12 (0.12 – 0.13) |
| | | 30 | 0.25 (0.24 – 0.26) |

RISK MAP MATRICES

Each cell of the risk maps (Figures 11-15) shows the probability of the ESC being either above 0.5 (F_{50} plots) or 0.3 (F_{30} plots) for the Canada-wide data. Lower probabilities indicate the population is less likely to meet the target ESC at the end of the simulation (10 years for the eel fisheries and 25 years for the elver fishery). Unlike the mortality reference point analysis, the risk map analysis does not assume that the population is starting from a healthy baseline, and therefore includes a more robust depiction of risk. For both fisheries, there was an increased probability of meeting the target when the initial starting ESC values were larger. When density-dependence in the elver stage occurred before the fishery, there was relatively little variation in its risk map compared to the other simulations (Figure 12). This is because of the relatively little variation in the relationship between ESC and fishing mortality under these assumptions (Figure 6). The minimum fishing size of eel fisheries had a large impact on the variance in the probabilities (Figures 13-15). At larger minimum fishing sizes (e.g. Figure 15), there was a greater probability of meeting stock status targets.

Across all simulation scenarios, there was often a < 50% likelihood of achieving the stock status target when fishing at F_{50} or F_{30} , particularly when the initial stock status was poor. Ideally, the probability of meeting the target ESC should be high when fishing at the mortality reference point. There was a much greater likelihood of achieving stock status targets when anthropogenic mortality was held to the 10% quantile of reference limit estimates (Table 4).

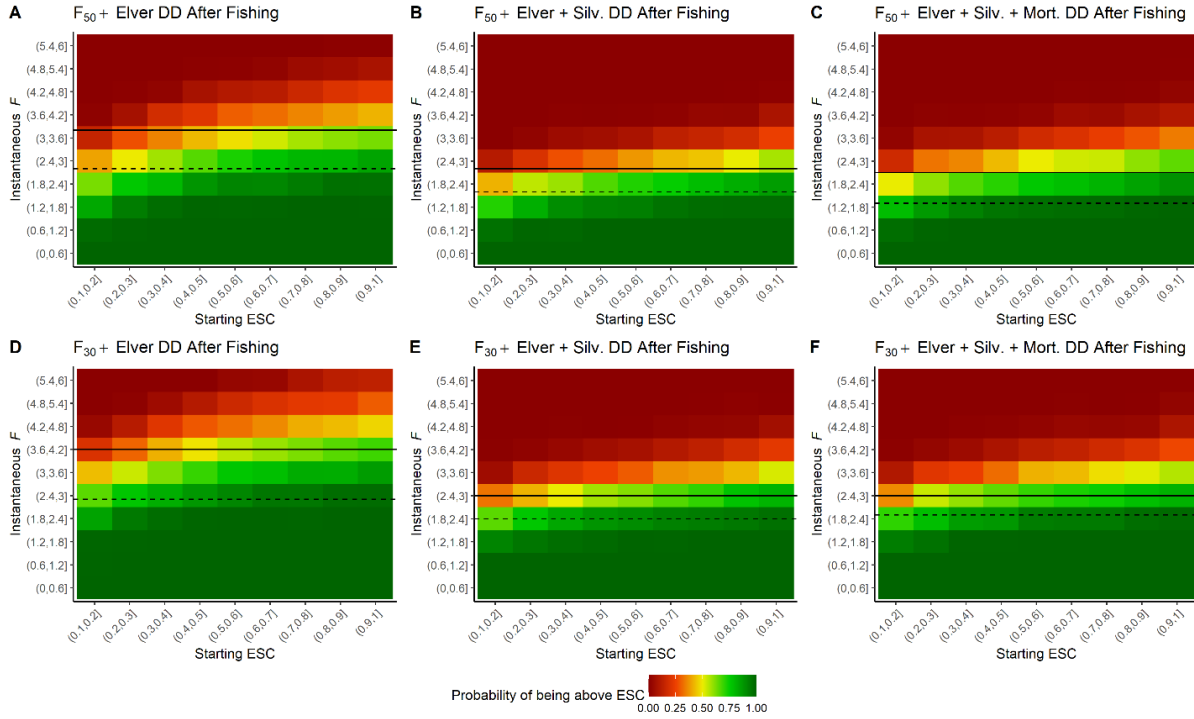


Figure 11. Risk matrices of elver fisheries when density-dependence occurs after fishing for Canada-wide data. Horizontal solid lines show the F_{50} and F_{30} mortality reference points, while the dashed lines show the 10% quantile of those mortality reference points from Table 3. Each cell is the probability of meeting or exceeding the target silver escapement (50% in panels A-C or 30% in panels D-F) over 25 years.

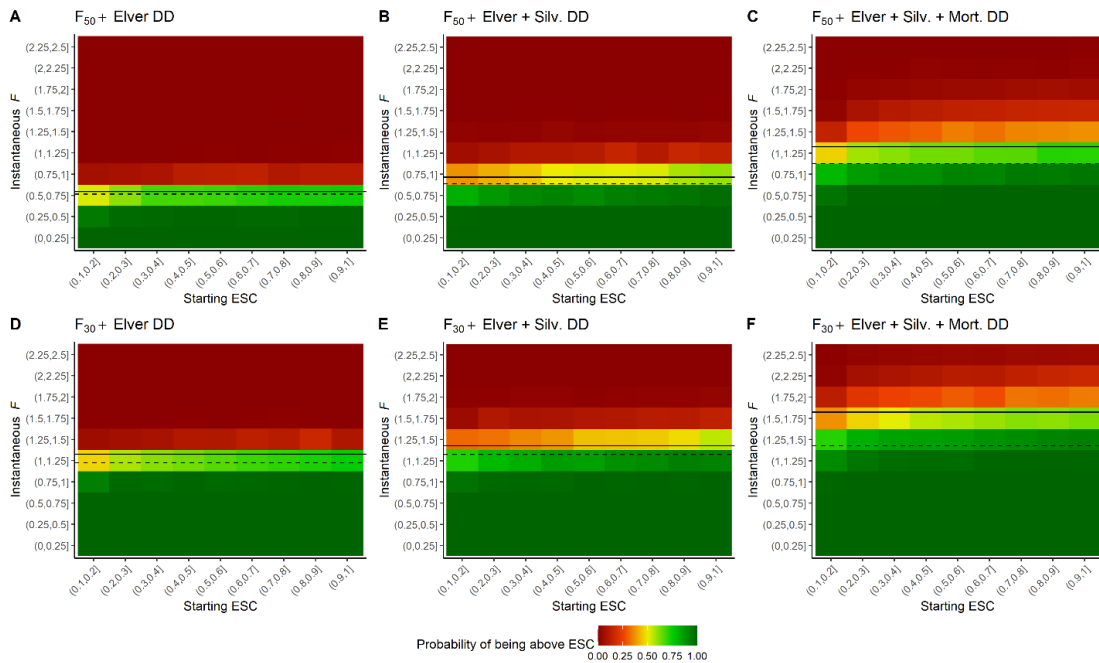


Figure 12. Risk matrices of elver fisheries when density-dependence occurs before fishing for Canadian-wide data. Horizontal solid lines show the F_{50} and F_{30} mortality reference points, while the dashed lines show the 10% quantile of those mortality reference points from Table 3. Each cell is the probability of meeting or exceeding the target silver escapement (50% in panels A-C or 30% in panels D-F) over 25 years.

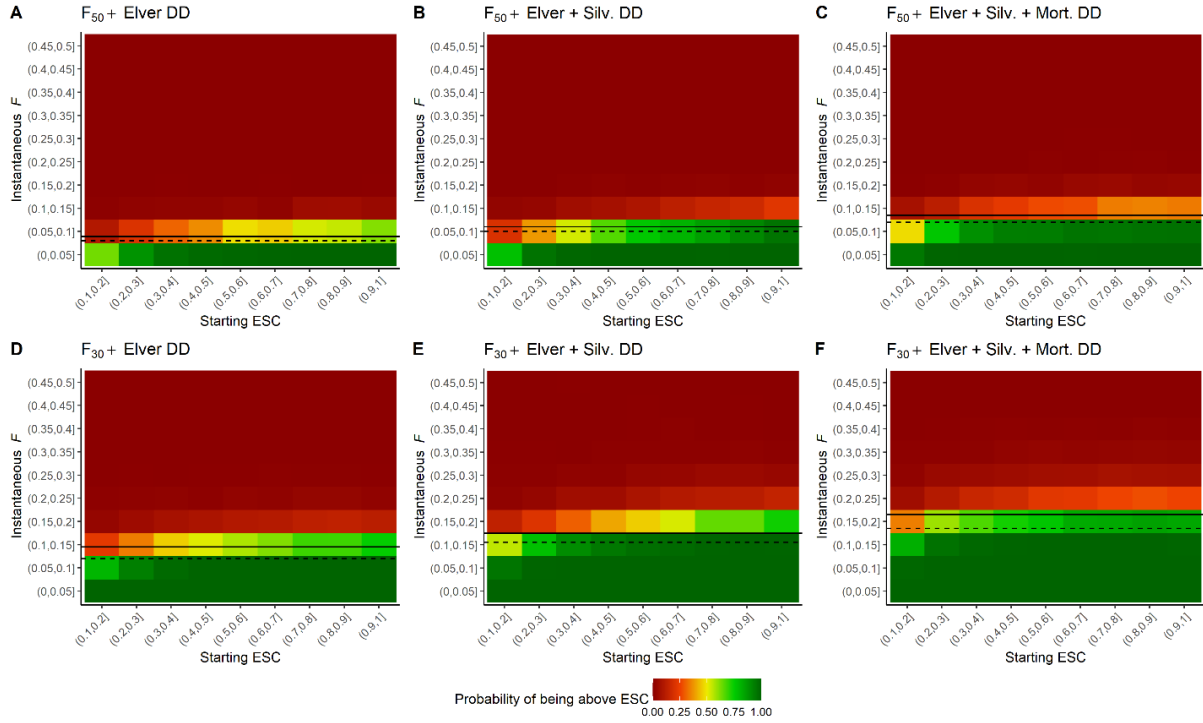


Figure 13. Risk matrices of eel fisheries when the minimum fishing size is 200 mm. Horizontal solid lines show the F_{50} and F_{30} mortality reference points, while the dashed lines show the 10% quantile of those mortality reference points from Table 3. Each cell is the probability of meeting or exceeding the target silver escapement (50% in panels A-C or 30% in panels D-F) over 10 years.

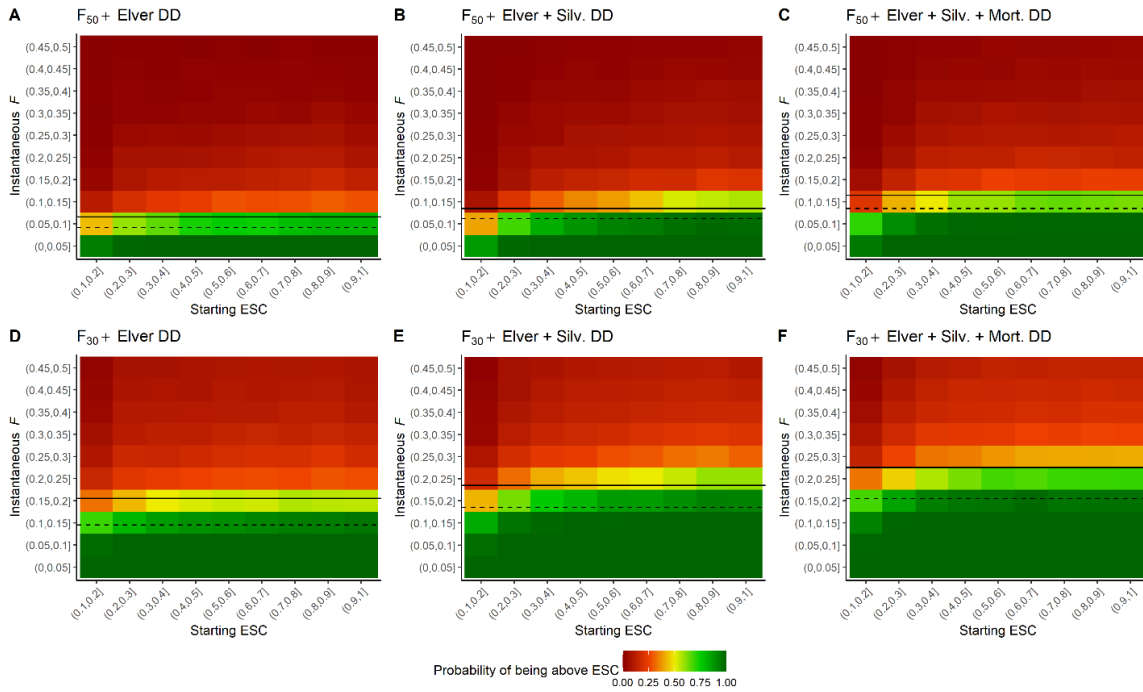


Figure 14. Risk matrices of eel fisheries when the minimum fishing size is 350 mm. Horizontal solid lines show the F_{50} and F_{30} mortality reference points, while the dashed lines show the 10% quantile of those mortality reference points from Table 3. Each cell is the probability of meeting or exceeding the target silver escapement (50% in panels A-C or 30% in panels D-F) over 10 years.

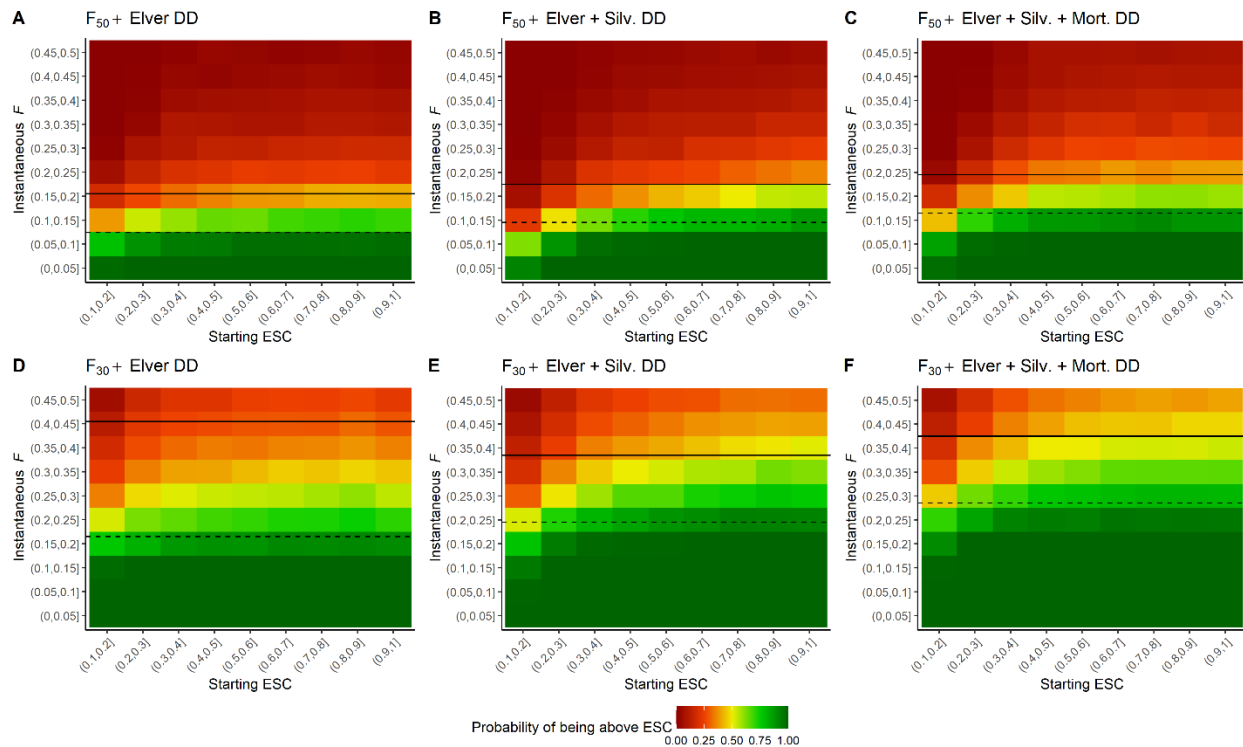


Figure 15. Risk matrices of eel fisheries when the minimum fishing size is 530 mm. Horizontal solid lines show the F_{50} and F_{30} mortality reference points, while the dashed lines show the 10% quantile of those mortality reference points from Table 3. Each cell is the probability of meeting or exceeding the target silver escapement (50% in panels A-C or 30% in panels D-F) over 10 years.

SENSITIVITY

The elasticity of λ analysis shows the proportional effect of perturbations to life history values on the population growth rate. In general, life history parameters that only affect one age-class do not have large effects on the population growth rate (e.g. elver and silver related variables). Fecundity and leptocephali survival also have small elasticities (mean values all less than 0.07). Yellow life history variables were more important, with survival rate of younger eel producing greater elasticities than older eel survival rate (Figure 16). This may be partly driven by the length of time spent in each class: the average length of time spent in the young yellow stage is 4 years (age range of 4 – 8), with the moderate yellow stage average length being 6 years (age range of 7 – 17 years). The old yellow stage can last from the agebreak to the maximum age of the population (average of 13 years spent in this category), the true average length will be smaller than that, as yellow eel mature and silver.

Sensitivity analysis reveals that the number of silver eel was most sensitive to silver length (Figure 17). A proportional change in silver length of 10%, can cause a much larger percent change in the resulting number of silver eel. Reproduction-related variables such as fecundity and leptocephalus survival have an approximately equivalent effect on silver number: a 10% change in one of those variables results in a 10% change in the number of silver eel. While survival values had a large effect on the population growth rate (Figure 16), a change in any survival has a proportionately smaller direct impact on the number of silver eel. The life history traits of growth rate and elver length had a similar magnitude of change as the reproduction variables, but investigation of the correlations demonstrates that this is due to the stochasticity

in the fecundity and mortality variables, not a sensitivity to growth rate or elver length themselves (Appendix 4).

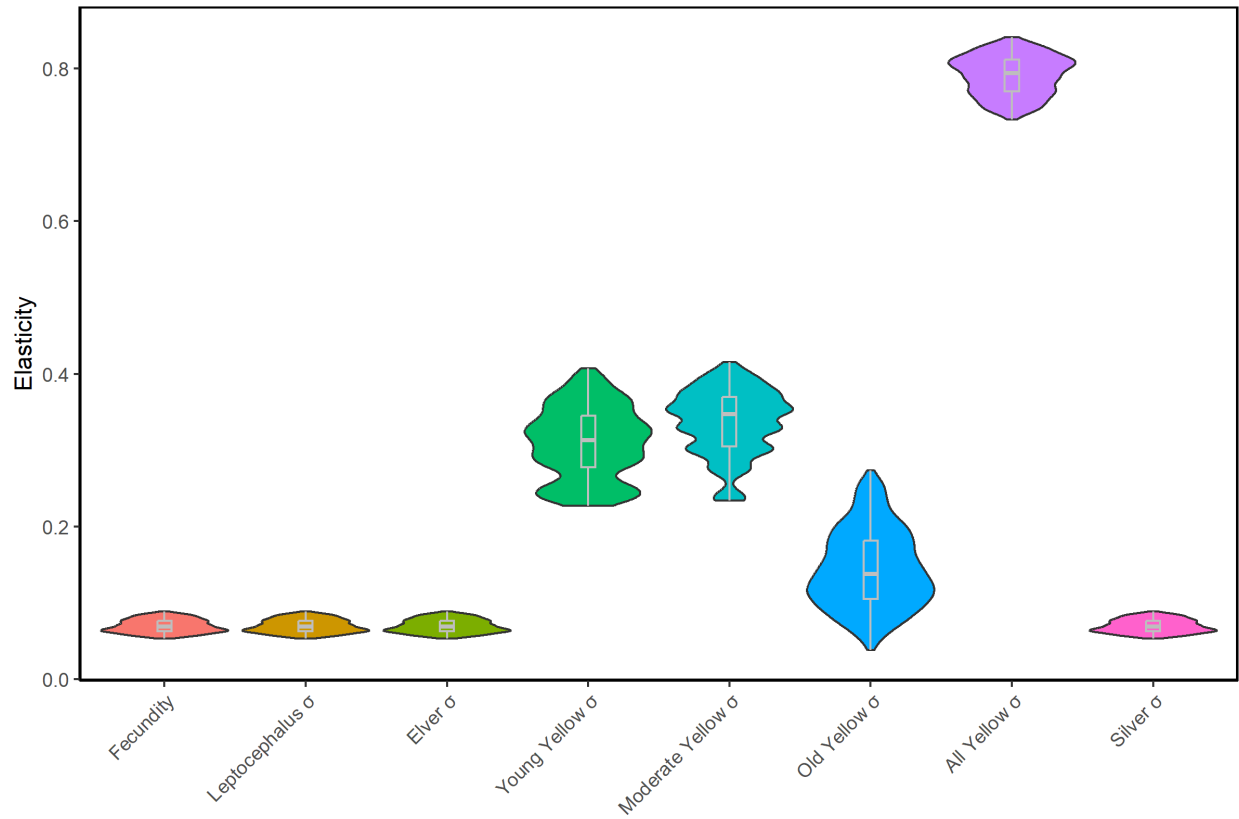


Figure 16. Elasticities of λ to life history variables. The larger the elasticity, the larger the proportional change that variable has on the population growth rate. σ represents the annual survival.

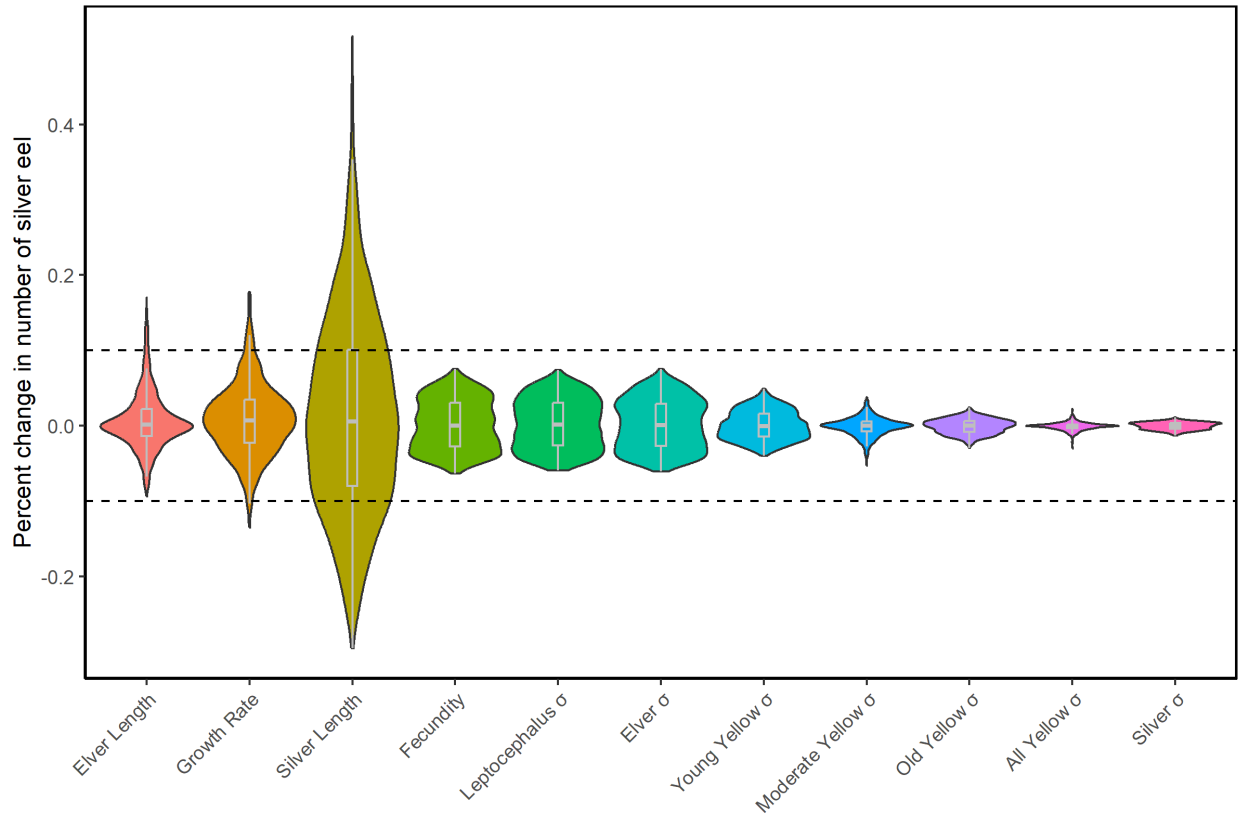


Figure 17. Sensitivities showing the percent change of the number of silver eel given a percent change of $\pm 10\%$ for life history variables. The larger the percent change in silver eel numbers, the larger the influence that variable has on the ESC output of the model. The dashed lines show the $\pm 10\%$ percent change.

DISCUSSION

MORTALITY REFERENCE POINTS

Regardless of the inclusion of turbine mortality or the type of fishery, the model with density-dependence in only the elver survival acting before the elver fishery (“Elver DD”) had the smallest estimated mortality reference points, making these reference points the most precautionary. Mortality reference points from this density-dependent model generally align with other mortality reference points estimated for American Eel populations. Bradford et al. (2022) SPR-based mortality reference points in the Maritimes region found F_{50} and F_{30} for elver fisheries to be 0.69 and 1.2 respectively (compared to this model when density-dependence in elvers happens before the fishery output of 0.67 and 1.2; Table 3). F_{50} and F_{30} for eel fisheries were 0.09 and 0.166 with a minimum fishing size of 350 mm (Bradford et al. (2022) (compared to this model output of 0.091 and 0.18 for Canada-wide data; Table 4). The model outputs for most zones for eel fisheries were also similar to Chaput & Cairns (2011), which found an F_{50} of 0.12 and an F_{30} of 0.18. ICES, (2001) also estimated F_{50} and F_{30} reference points for eel in the “northern range” of American Eel, with ranges of 0.06 – 0.118 for F_{50} and 0.09 – 0.18 for F_{30} .

The reference points for eel in the SF zone were higher than the values found in the literature, with a F_{50} of 0.21 and F_{30} of 0.36 (Table 4) when the minimum fishing size was 350 mm. This is likely because the SF zone has the smallest average silver length and small associated

growth rates, which was associated with smaller mortality reference points. Also, the smallest SF silver length was equal to the minimum fishing size, meaning that a subset of large yellow eel and fully grown silver eel would not be susceptible to fishing mortality, leading to an increase in the fishing rate for those simulations. On the other hand, the SL zone consistently had the smallest mortality reference point estimates (Table 4) compared to the other zones, likely due to its large average silver length. Mortality reference points from the other density-dependent models (“Elver + Silv. DD” and “Elver + Silv. + Mort. DD”) are generally higher than literature values. Furthermore, when the minimum fishing size was 200 mm, mortality reference points tended to be smaller than the literature values (when the density-dependent effect was only in elvers) with F_{50} of 0.064 and F_{30} of 0.12 for Canada-wide. The mortality reference points were much larger when the minimum fishing size was 530 mm: F_{50} of 0.18 and F_{30} of 0.43 (Table 4). The variability around the reference points increased at larger minimum fishing sizes.

$F_{extinct}$ is the fishing mortality where the population cannot support itself. Ideally mortality reference points should be considerably smaller than $F_{extinct}$ to avoid risking the possibility of fishing to the point of extinction. When there are more density-dependent mechanisms, the $F_{extinct}$ values tend to be smaller (Table 5). Despite this, eel mortality reference points were generally well below $F_{extinct}$ levels across density-dependent assumptions (Table 5). Similarly, when the elver density-dependence occurs before the elver fishery, the mortality reference points were not close to $F_{extinct}$, for either F_{50} or F_{30} values. However, when the density-dependence in the elver stage occurred after the elver fishery, the mortality reference points were very similar to $F_{extinct}$ (Table 5). This is because of the shape of the relationship between F and ESC (Figure 6 and Figure 8), which initially declined slowly with F which then accelerated as F approach $F_{extinct}$. The proximity of the F_{50} and F_{30} to the $F_{extinct}$ in this scenario indicates that using those values to set mortality reference points may jeopardize the population as there is very little margin for error.

If significant density dependence acts after fishing mortality has occurred, under most levels of fishing mortality there will be very little change in the population size until F approaches $F_{extinct}$, and the population is at risk of going extinct (Figure 6 and 8). Under these circumstances, the size of the population is no longer sensitive to fishing mortality, and could no longer be used as an indicator of population status or to set mortality reference points. If it is the case that large density-dependence occurs after elver fishing mortality, mortality reference points may have to be set using alternative means (e.g. based on a proportion of $F_{extinct}$, which is not sensitive to density-dependence timing, though additional investigation into the feasibility of this approach would be needed). In other words, the sustainable fisheries framework, which sets reference points based on stock status, would have to be reconsidered (for American Eel as well as any species with significant density-dependence post-fishery activity). For American Eel, setting mortality reference points assuming that elver density-dependence occurs before the fishery minimizes the risks associated with being wrong about this assumption, given uncertainties about the timing of density-dependence.

In addition, the risk maps (Figure 11 - 15) support using lower mortality reference points. After 10 years (for eel fisheries) or 25 years (for elver fisheries), fishing at the mortality reference point only had approximately a 50% chance or lower of meeting the ESC target. If the mortality reference points were lowered (the example shown in the figures shows the 10% quantile), the probability of meeting the target ESC increases, which increases the confidence in achieving the goal of the mortality reference point. This is of particular importance given that the initial ESC of the population affects the probability of meeting the target ESC after the time period. If the population is not starting from a large ESC, the probability of meeting the target is already decreased, so it is particularly important to reduce the mortality reference limit. The relative abundance of American Eel in Canada has decreased > 50% since the 1980s (van der Lee &

Koops 2024), so this adjustment of mortality reference points may be very important to promote stock recovery.

The results suggest that elvers could be fished at a higher rate than eel, as the population is generally less sensitive to elver fishing mortality. However, because changes to the elver stock take time to be expressed through the population, the time horizon that is considered when determining the effect of fishing strongly influences the conclusion. The impacts of elver fishing needs to be considered after a sufficient period of time, otherwise one might conclude no significant change to population size, when it is more accurate to say that the changes have not had time to affect the population. Given the recent historical highs of elver imports in China (Shiraishi & Kaifu 2024), and the panmictic nature of the population (Ulmo Diaz et al. 2023; Cairns et al. 2014), it is important to consider that the effects of elver fishing will continue to affect the population for many years to come.

PREDICTING MORTALITY REFERENCE POINTS

The multiple linear regression analysis demonstrates that mortality reference points can be estimated for populations based on limited life history and turbine mortality data. The regression for eel fisheries could additionally be used to estimate how changes to the minimum fishing size could affect the mortality reference point. However, while these equations output an F value, as discussed above, it may be necessary to reduce this value to increase the confidence in meeting the target ESC, and to account for a decreased initial stock size or general uncertainty around the estimate.

Turbine mortality had an important impact on predicted mortality reference points (Figure 9 and Figure 10). For locations with turbine mortality, the fishing mortality reference points should be adjusted to account for the increased silver mortality. When density-dependence was only in the elver survival (especially for eel fisheries), high turbine mortality predicted F_{50} values very close to 0, indicating that under that under the considered management scenarios these combinations of turbine mortality and life history effectively left no scope for fishing mortality to reach the target ESC_{50} . This is of particular interest in the St. Lawrence basin region, where turbine mortality for some out-migrating silver eels has been estimated to be as high as 40% (COSEWIC, 2012). To adequately adjust mortality reference points to account for turbine mortality, gaining a thorough understanding of the turbine mortality that eel face as a whole across watersheds is important (e.g. in an area with multiple turbines, not all eels will have to pass through multiple turbines to leave to spawn).

SENSITIVITY

The elasticity of λ analysis suggests that yellow eel are the stage that have the strongest impact on population growth rates (Figure 15). This is likely because fishing affects yellow eel across multiple cohorts every year, and there are multiple years for a given eel cohort to be affected by fishing mortality. On the other hand, elver fisheries affect only one age class in the model, lessening their impact on the population growth rate. If elver fisheries affected more than one age class, their elasticity would increase, the mortality reference points would have to be reduced to account for the effect across multiple years.

The elasticities were generally higher for younger and moderately aged eel than the elasticities of older eel (Figure 15). This may be due to the life history of American Eel; as yellow eel age, they are more likely to silver and leave the population to spawn, and do not re-enter the population. Those age class densities are therefore smaller a portion of the cohort has already silvered, lessening the effect on the population when fished. This supports the existence of a minimum fishing size that protects young yellow eel.

The sensitivity to number of silver eel demonstrated that the model was most sensitive to silver length (Figure 16). This is likely because silver length directly impacts the calculation of other life history parameters (fecundity and survival). Therefore, a 10% change in silver length also affects two other life history variables, compounding its influence in the model. Changes to variables that directly impact the ratio of elvers to silvers (fecundity and leptocephali survival) have approximately an equivalent sensitivity, where a 10% change in the life history parameter leads to an approximate 10% change in the number of silver eel. On the other hand, variables that affect the number of silver eel more indirectly, like survival values, have a smaller effect when perturbed.

UNCERTAINTIES

Uncertainty in the life history parameters was minimized in multiple ways. Canadian-specific data were used as much as possible for life history values like growth rates, silver length, fecundity, etc. to ensure the data were relevant. In stochastic trials, these life history parameters were varied across replicates, in a further attempt to capture the variance and likely range around these estimates. However, if the variance around these life history parameters was underestimated, the resulting variance around the mortality reference points would be too narrow, and may not reflect the true range of the population. Other possible uncertainty could come from the simplifying assumptions about the length of American Eel migrations: the model assumed leptocephalus and silver migrations both lasted one year. If these migrations took longer, there would be additional delay in the population response to fishing mortality (and the reverse if the migrations were faster).

Despite the range of life history tested, the life history of males, or eel that occupy brackish or saline environments, was not represented in the model. There was insufficient information to parameterize the model based on these life history strategies, however, it is known that they are different from freshwater female eel. Males generally mature at smaller sizes than female eel (Cairns et al. 2014), meaning the length of time they are susceptible to fishing is much different and would decrease their fishing elasticity. Eel in saline environments tend to grow and mature faster than freshwater eel (Cairns et al. 2014), so their mortality reference points would likely differ.

A large source of uncertainty in the model was the mortality of American Eel. There was insufficient measured mortality data to use in the model, instead parameterized weight-based mortality equations were used (Bevacqua et al. 2011; Lorenzen 1996). While the range of annual survival of adult yellow eel (approximately 90% – 97%) appears reasonable, there is more uncertainty around the survival of younger eel and elvers. Lin & Jessop (2020) estimated daily elver M during an elver fishery to average 0.029/d. Applying these methods across Canada at locations where elvers are not fished may help provide additional estimates of elver survival in Canada. Furthermore, leptocephali survival has not been measured and was completely unknown. It was found by solving for the rate that allows the population matrix model to reach stability.

Environmental variability or climate change projections were not directly investigated. American Eel may be especially susceptible to multiple climate change factors due to spending time in both open ocean and continental waters during their life cycle, and therefore are affected by alterations in both habitats (Drouineau et al. 2018). For example, turbine mortality on silver eel migration might increase with decreased precipitation causing water levels to drop (Drouineau et al. 2018). In particular, changes to ocean currents have the possibility to seriously affect American Eel populations (Drouineau et al. 2018). Natural changes to ocean currents can change the success of leptocephali reaching the continental shelf by a factor of two (Rypina et al. 2016), so further alterations to ocean currents, especially the Gulf Stream, has the

possibility to drastically affect leptocephali migrations. Furthermore, changes to ocean temperature may decrease food available to the leptocephali to consume, increasing mortality rates in the leptocephalus stage (Miller et al. 2016). Additional research on both the survival and expected response to climate change of leptocephali will be increasingly important when trying to assess future population responses.

The model assumed a constant fishing rate with no interannual variation. Variation in fishing pressures across years could change the expected ESC dramatically. Based on the general exponential decay shape (Figure 6), small changes in F can have large changes in resulting ESC. This is particularly important for elver fisheries, which experienced such high levels of poaching in the Maritimes fishery in 2023 that the fishery was closed (Withers 2023a). It is estimated that at least 4.5 metric tonnes of elvers were illegally exported out of Canada (Withers 2023b). Precautionary setting of mortality reference limits is important, given the uncertainty of the fishing mortality applied to the population.

Three potential density-dependence mechanisms were included in the model. There were no empirical data available to inform these relationships; therefore, the mechanisms investigated were theoretical. The way in which density-dependence was included in the model had important impacts on model results, such as estimates of ESC reference points. While the implemented density-dependent mechanisms are consistent with responses of American Eel in some locations, it is not clear if the mechanisms adequately represent how density-dependence functions in extant American Eel populations. Furthermore, the timing of potential density-dependent effects are unknown, so what the timing of elver density-dependent survival should be relative to the fishery is not clear. However it is well supported in the results that it is more precautionary to use the mortality reference points assuming the density-dependence occurs before the fishery, which are much smaller than the $F_{extinct}$ estimates.

Genetic evidence supports the American Eel population being panmictic (Ulmo Diaz et al. 2023), which suggests the current model structure of an independent freshwater population is inaccurate. Instead, the American Eel dynamics at a location may be influenced by dynamics at other locations. The extent to which local dynamics are influenced by other locations may be dependent on how leptocephali are distributed back to continental waters from the spawning grounds (Young & Koops 2014). For the purpose of identifying mortality reference points, the next question that needs to be addressed is if making management decisions at a local level (e.g. based on the presented population modelling) meets similar management objectives in a panmictic population.

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APPENDIX 1 – LIFE HISTORY

BIPHASIC GROWTH MODEL

When data were available, it was filtered to include freshwater female eel data, which included data from Scotia Fundy (SF), Southern Gulf (SG) and Northern Gulf (NG) (Cairns 2020) (Figure A1.2). Both a biphasic growth model and a von Bertalanffy model were considered as potential growth models. The overlap in prediction intervals between both models (Figure A1.1) indicated the models have very similar length predictions, so the choice to use the biphasic growth model was based on the parameter output.

The Canada-wide standard deviations for determining variance around the growth rates and silvering lengths in the stochastic trials was based on the mean standard deviations across zones (Table A1.1). Standard deviations (sd) for growth rates and silver lengths were estimated using the normal distribution and the prediction intervals of the biphasic growth, and were calculated as:

$$sd = \frac{\text{max value} - \text{min value}}{2 * 1.96}, \quad (\text{A1.1})$$

where the *max value* and *min value* refer to the range of prediction intervals around growth rates and silver lengths.

The average standard deviation around growth rate was 7.95 mm/year, and the average standard deviation around silver length was 89 mm (Table A1.1).

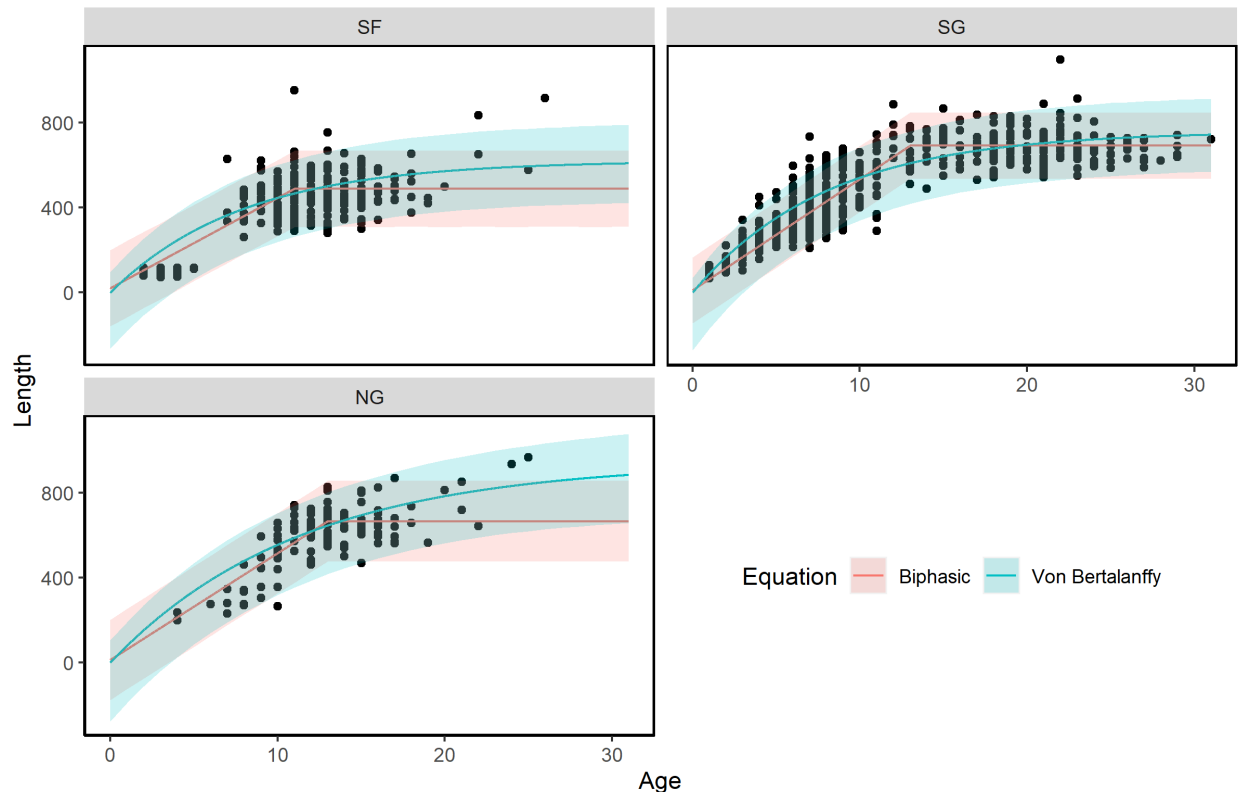


Figure A1.1. Comparison of von Bertalanffy equation to biphasic growth rate prediction intervals. Different shaded regions reflect the different equations.

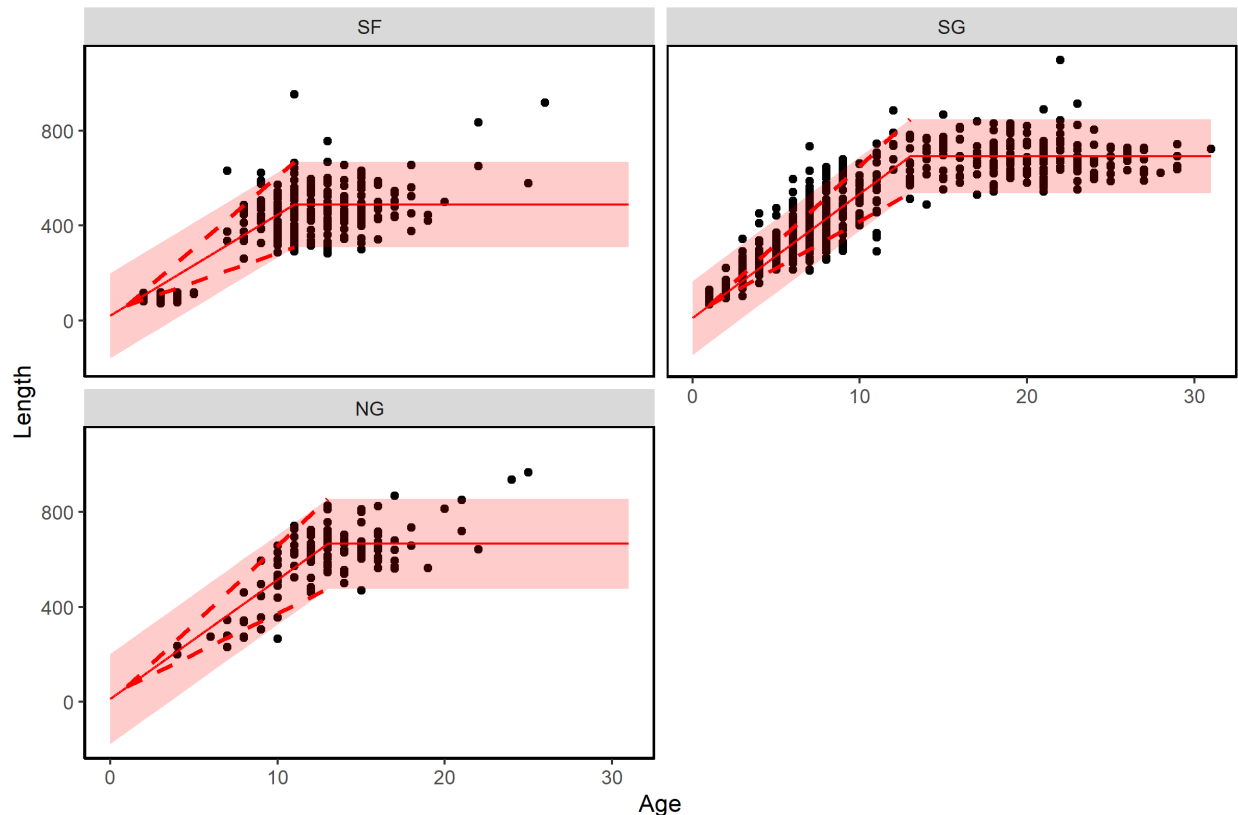


Figure A1.2. Biphasic plots for three geographic zones in Canada. The shaded areas show the prediction interval around the biphasic curve; the dashed red lines show the minimum and maximum growth rates used to calculate the standard deviation for growth rates. The ages in the plot have been adjusted to reflect elvers as age 1; common notation is to record them as age 0.

Table A1.1. Mean and standard deviations of growth rates and silver lengths for the geographic regions in Canada based on the biphasic growth model.

| Zone | Growth rate (sd) (mm) | Silver length (sd) (mm) | Age break |
|---------------|--------------------------|----------------------------|-----------|
| Scotia Fundy | 42.6 (9.16) | 489 (91.6) | 10 |
| Southern Gulf | 52.4 (6.60) | 692 (79.5) | 12 |
| Northern Gulf | 50.3 (8.07) | 666 (96.8) | 12 |

Because the biphasic model assumes a period of no growth at older ages, biphasic growth rates will be faster than literature growth rates - which generally assume constant growth rates until silvering. Simulations were run to allow for conversion between the different growth rate options. Based on recorded growth rates, mean silver lengths and mean silver ages, a distribution of eel that are likely to silver was generated. The Canada-wide standard deviation of 89 mm was used to add variance to average silver length from the literature (Cairns et al. 2014). A relationship of silver age to the standard deviation around silver age was used to determine the standard deviation for silver ages (Figure A1.3). A biphasic curve was fit to the simulated data, and the literature growth rates compared to the new biphasic growth rates (Figure A1.4). When using the equations for the multiple linear regressions to predict fishing mortality rate reference points, the literature growth rates need to be converted to biphasic growth rates before being used in the equations.

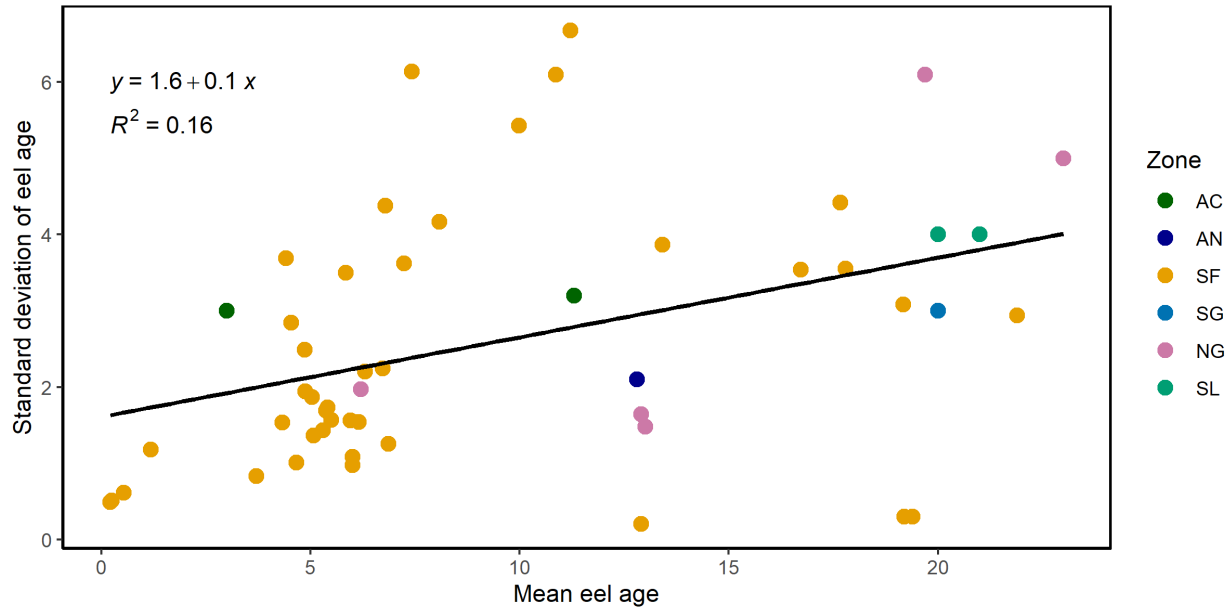


Figure A1.3. Relationship of mean eel age to standard deviation. Data come from Jessop et al. (2009); Tremblay (2009); Cairns et al. (2007); Goodwin & Angermeier (2003); Oliveira (1999); Jessop (1987); Bouillon & Haedrich (1985). Only datasets with a minimum sample size of 10 were used.

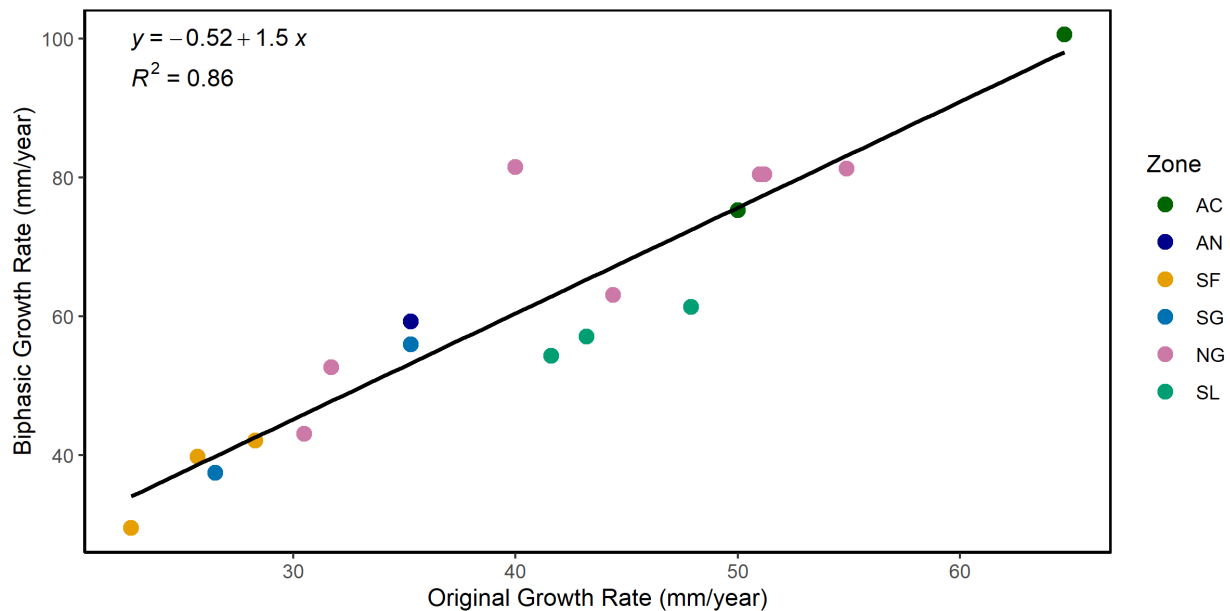


Figure A1.4. Conversion between growth rates that are assumed to be constant throughout life (x-axis; “Original Growth Rate”) and the growth rate in the biphasic model (y-axis; “Biphasic Growth Rate”). Because the biphasic model does not assume constant growth, the growth rates are always larger than values found in the literature that use a constant growth model.

PROBABILITY OF SILVERING

A model that described the ages and lengths at which eel transitioned from yellow to silver eel was needed to determine the average silvering probability for each age. The output for this

model should ideally correspond with the available data on silver eel length and age and the shape of the length-age distributions for yellow eel.

Three possible methods describing the likelihood of transitioning from a yellow eel into a silver eel were investigated. The first model assumed that eel silvered upon reaching silvering length. The second model assumed that once an eel reached its silvering length, it had a constant 10% probability of silvering every year. The third model assumed that the probability of silvering was initially 10% at the earliest silvering age, with the probability of silvering increasing 1% every year thereafter. For example, if the earliest possible silvering age was 5 years, then an eel of silvering length would have a 15% probability of silvering at age 10.

The simulated distribution of silver lengths were similar to the observed distribution data for all models (Figure A1.5); however, there was a large difference in the age distributions (Figure A1.6). In the model where eel silvered when they first reached their silvering length (“At Silver Length”), the resulting distribution of silver ages was too narrow when compared to a distribution of actual silver ages. In the case of the SG zone, the average age of the simulated silvers was also too small. However, when the probability was held constant at 10% (“Constant 10%”), the distribution was flatter, and the SF zone had much older silvers present compared to the observed data. In general, the model where the probability of silvering started at 10% at the earliest silvering age and increased 1% every year did the best job approximating the shape of the distribution of silver ages (Figure A1.6).

The same pattern occurred when considering the number of yellow eel in the various simulations (Figure A1.7). When eel mature upon reaching silver length, there is no representation of older, larger eel in the resulting yellow distribution. Alternatively, a constant 10% probability of silvering after the silver length has been reached produced an overrepresentation of older eel not seen in the observed data, with ages up to 50 years. The model where the probability of silvering increases as eel age most closely represented the age-length distribution data, allowing for the representation of a few older individuals.

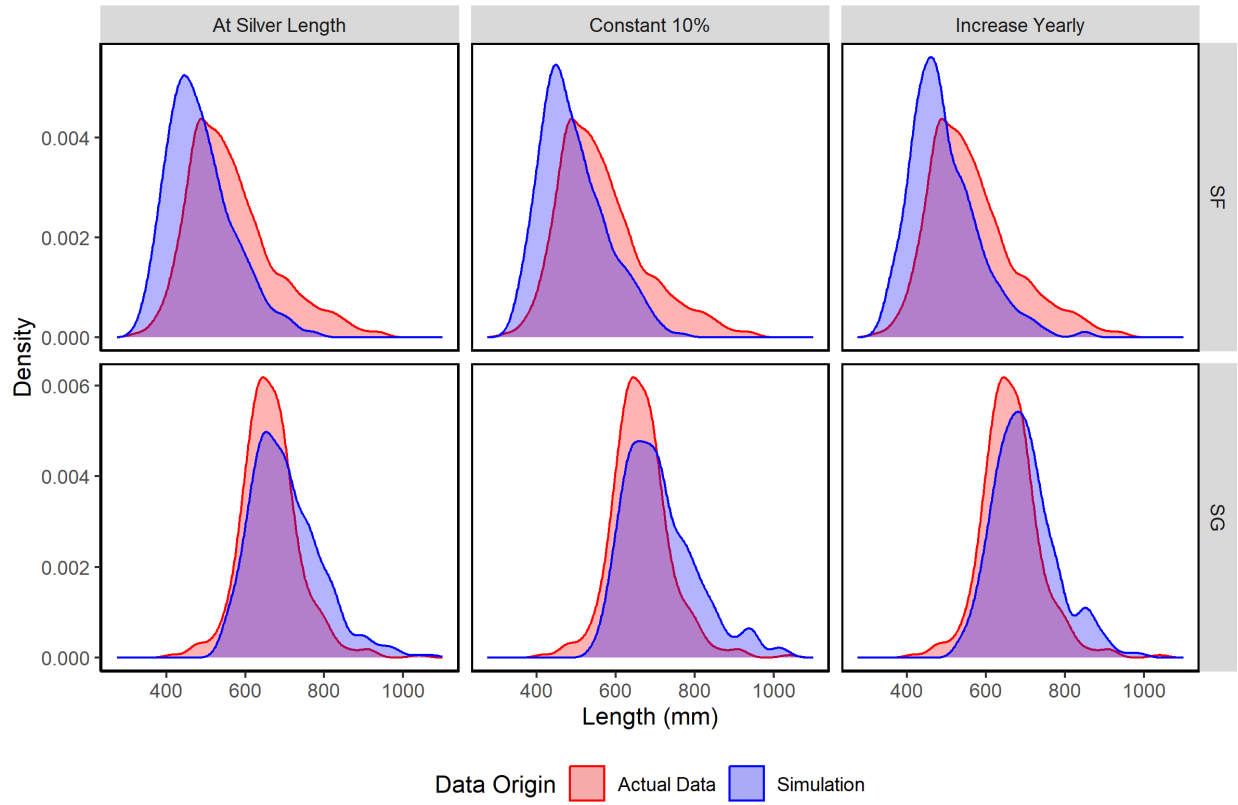


Figure A1.5. Comparison of silver length distributions across different probability of silvering models and geographic zones. All models and zones are relatively similar.

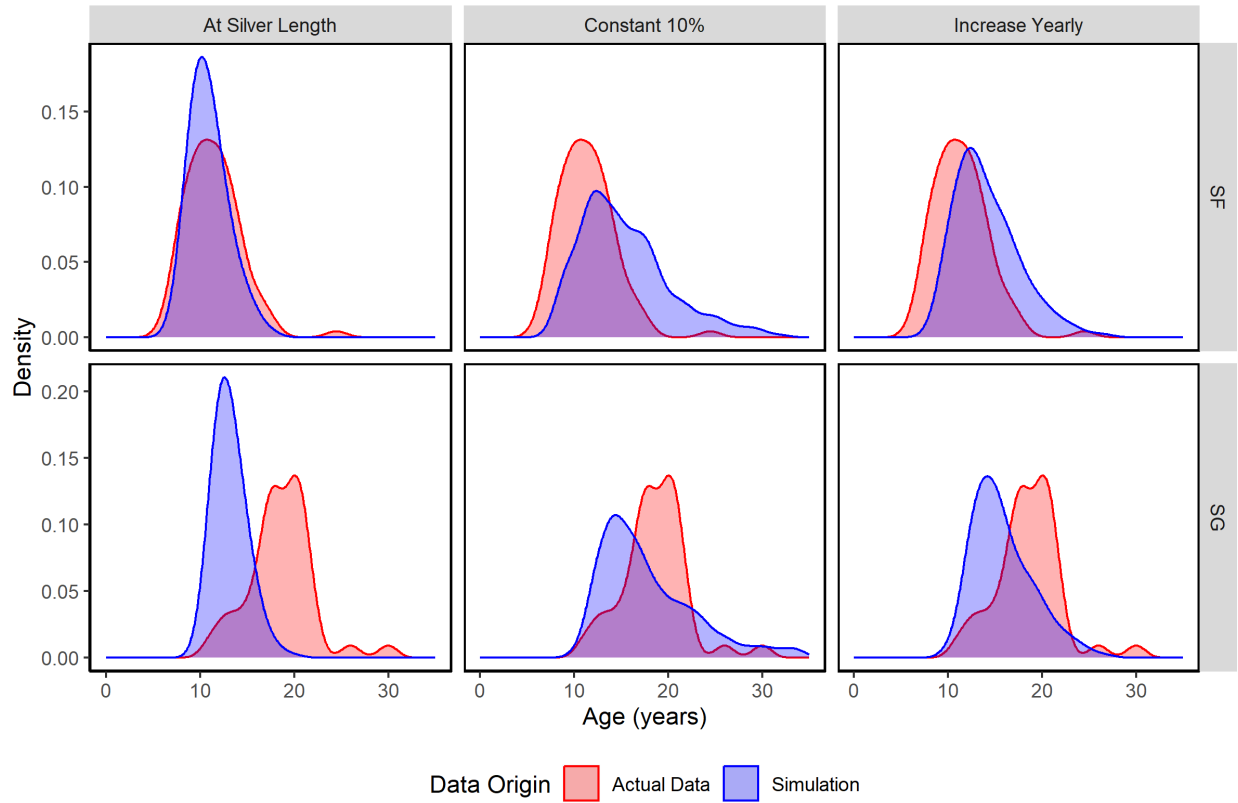


Figure A1.6. Comparison of silver age distributions across different probability of silvering models and geographic zones. The model with maturation as soon as silver lengths are reached was consistently too narrow, and the model with a constant 10% probability of silvering was typically too broad.

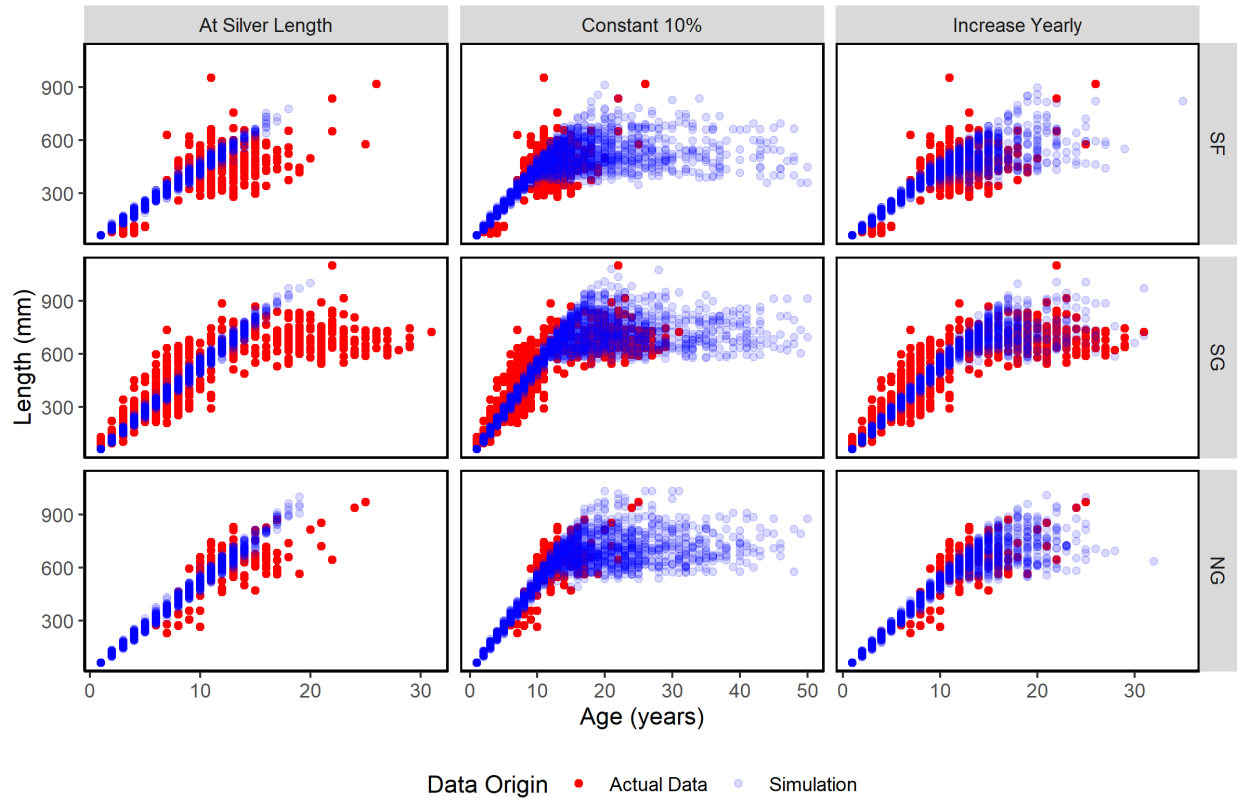


Figure A1.7. Age-length relationships of yellow eel across various geographic zones and models for determining the probability of silvering. Note the different x-axis scales between the models; the “Constant 10%” has a wider range than the others.

LENGTH-WEIGHT RELATIONSHIP

Subsetting the length-weight data affected the resulting shape of the regression (Figure A1.8). When very short eel were removed from the data (removing SG’s large influence on the curve), and every location had the same number of data points, the curve was slightly steeper.

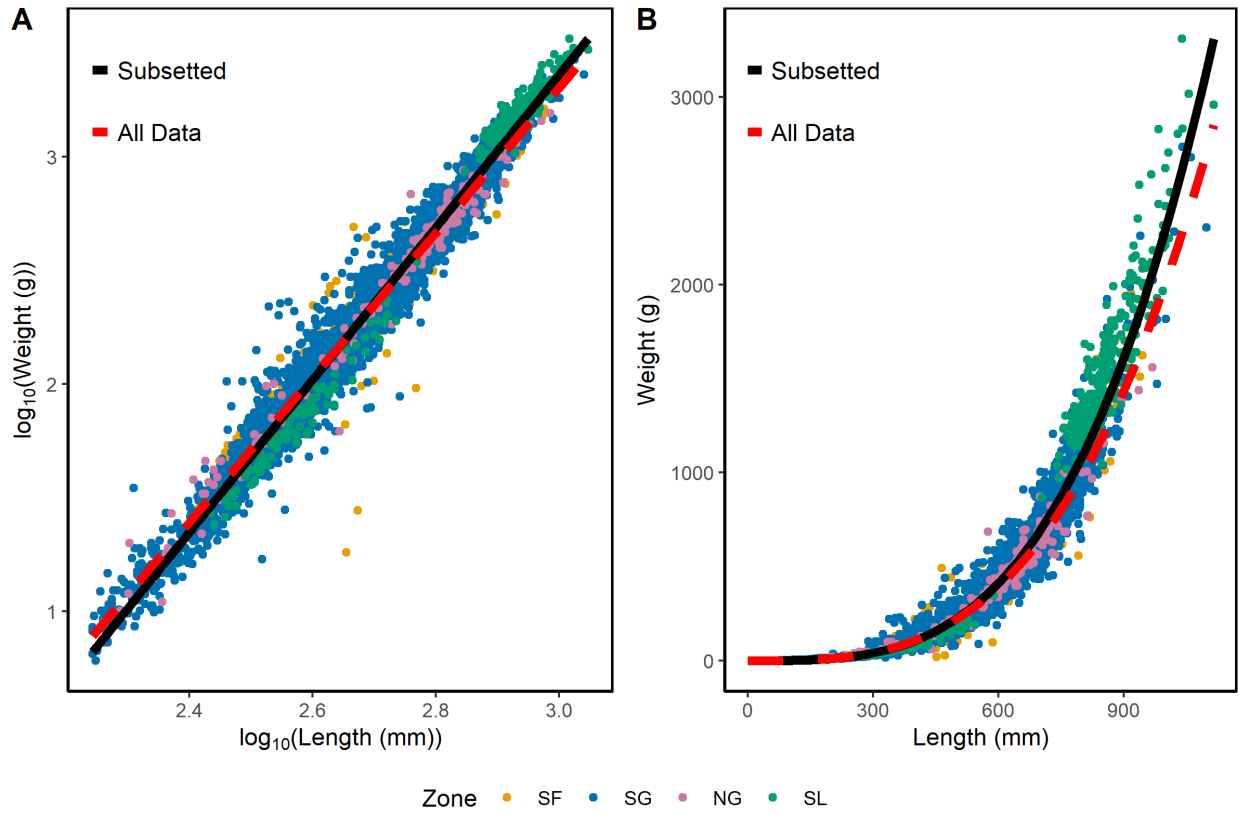


Figure A1.8. Transformed and untransformed relationship between length and weight. Regressions performed on the entire dataset are the dashed red line, while the solid black line shows the resulting curve from the subsetted data simulations.

APPENDIX 2 – MAXIMUM SUSTAINABLE YIELD, SPR AND ESC

The use of maximum sustainable yield (MSY), spawner per recruit (SPR) or silver escapement (ESC) as the basis for defining the limit reference point and upper stock reference point were investigated. To test the difference, 1,000 simulations of elver and eel fisheries, for each of the density-dependent groups, were conducted. The life history values were held constant at the Canadian average (growth rate = 55 mm/year, silver length = 725 mm, no variance in fecundity, mortality or λ_{max}), while the fishing mortality rate was varied for each simulation. The ESC and SPR ratio was recorded for each simulation.

The yellow eel biomass was calculated by multiplying the population vector by the average weight expected at each age (based on the biphasic growth curve in Equation 1, and the length-weight relationship in Equation 2). This was completed across density-dependent assumptions, different minimum fishing lengths, and different elver density-dependence timings. Yield was calculated by multiplying the biomass by the annual fishing mortality (and in the case of eel fisheries, was then summed). Both biomass and yield were scaled so that the maximum value was equal to 1, to allow for easier comparisons.

Fishing mortality reference points were calculated slightly differently depending on the method. For both SPR and ESC metrics, the fishing mortality that resulted in the respective output being closest to either 0.5 or 0.3 was considered the reference point (Upper Stock Reference and Limit Reference Point respectively, see Figure 1). For the MSY approach, the biomass at MSY was used (BMSY), where the fishing mortality that resulted in 80% of BMSY was considered the Upper Stock Reference and 40% BMSY was considered the Limit Reference Point.

For eel fisheries, it is clear that ESC based mortality reference points are more precautionary (Figure A2.1). An MSY approach appears riskier for eel fisheries, as it is consistently much larger than the other options, and results in very low escapement of the population. While ESC and SPR mortality reference points are similar, the ESC prediction is consistently slightly smaller, and therefore the most precautionary to use when setting mortality reference points. Furthermore, while SPR and ESC-based metrics are similar, they are affected by the λ_{max} of the simulation (Figure A2.2). When λ_{max} decreases, there is a larger difference between the ESC and SPR metric, with SPR being biased higher than ESC. This difference is larger when there are more density-dependent mechanisms in the simulation (Figure A2.2).

For elver fisheries, the answer is less obvious which metric should be preferred (Figure A2.3). If the density-dependence in elver survival occurs before the fishery, then ESC is more precautionary than MSY approaches. However, if the density-dependence occurs after the fishery, MSY tends to result in smaller mortality reference points. As discussed in the paper, there are a number of concerns associated with assuming density-dependence occurs after fishery activity. Therefore, ESC was used as a common metric of determining mortality reference points for both eel and elver fisheries.

When fishing eel, ESC and yellow eel biomass have a non-linear relationship, which was mostly linear at high ESC values, but declined sharply at low ESC (Figure A2.4). This supports the use of ESC₃₀ as the lower reference limit; at ESCs below 0.3 the population biomass is expected to decline rapidly. The shape of the non-linear relationship between yellow eel biomass and ESC was similar across the different density-dependent assumptions, though they differ slightly under different minimum fishing size conditions. It is possible that future monitoring of American Eel could use yellow eel biomass as an approximation of the silver eel escapement, based on the relationship between them.

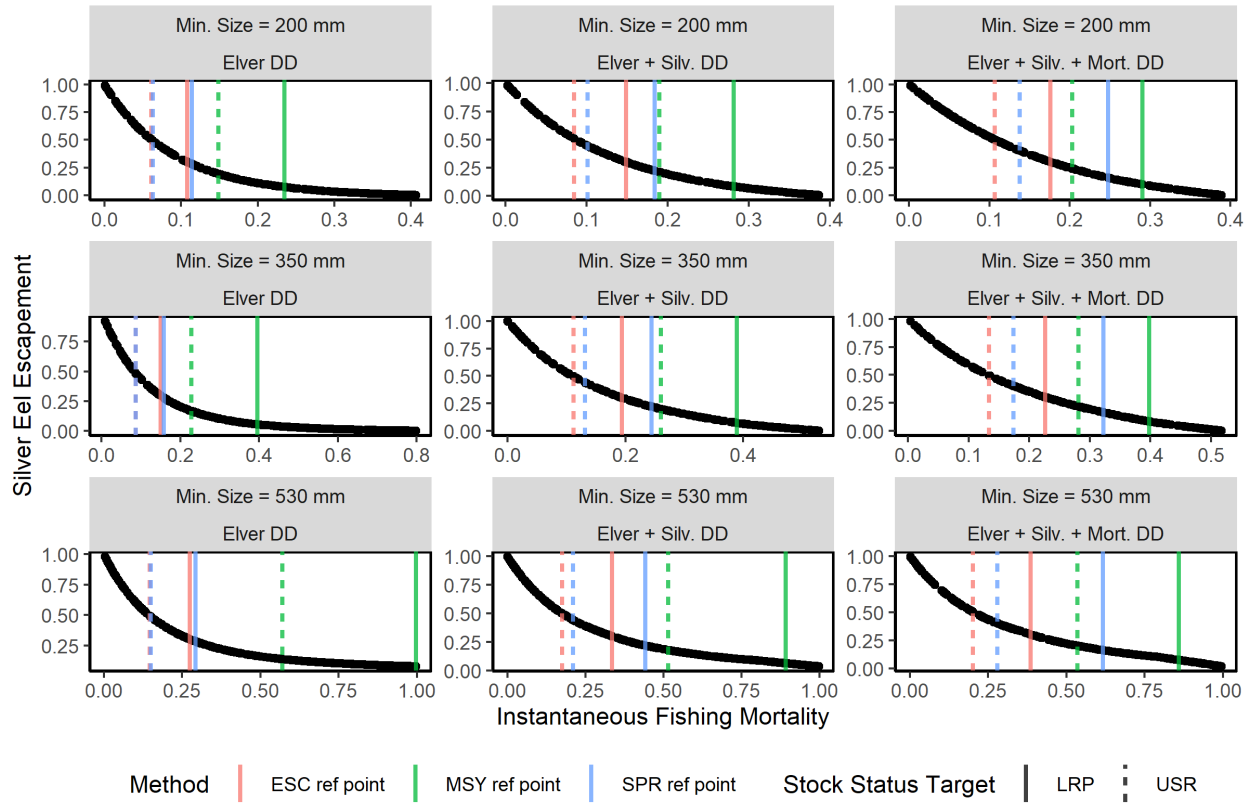


Figure A2.1. Mortality reference points for eel fisheries calculated using different metrics. The vertical lines are mortality reference points, coloured by which metric was used to calculate them. Solid lines represent LRP mortality reference points, while the dashed lines represent the mortality reference point associated with the USR. This simulation had a lambda λ_{max} of 1.3.

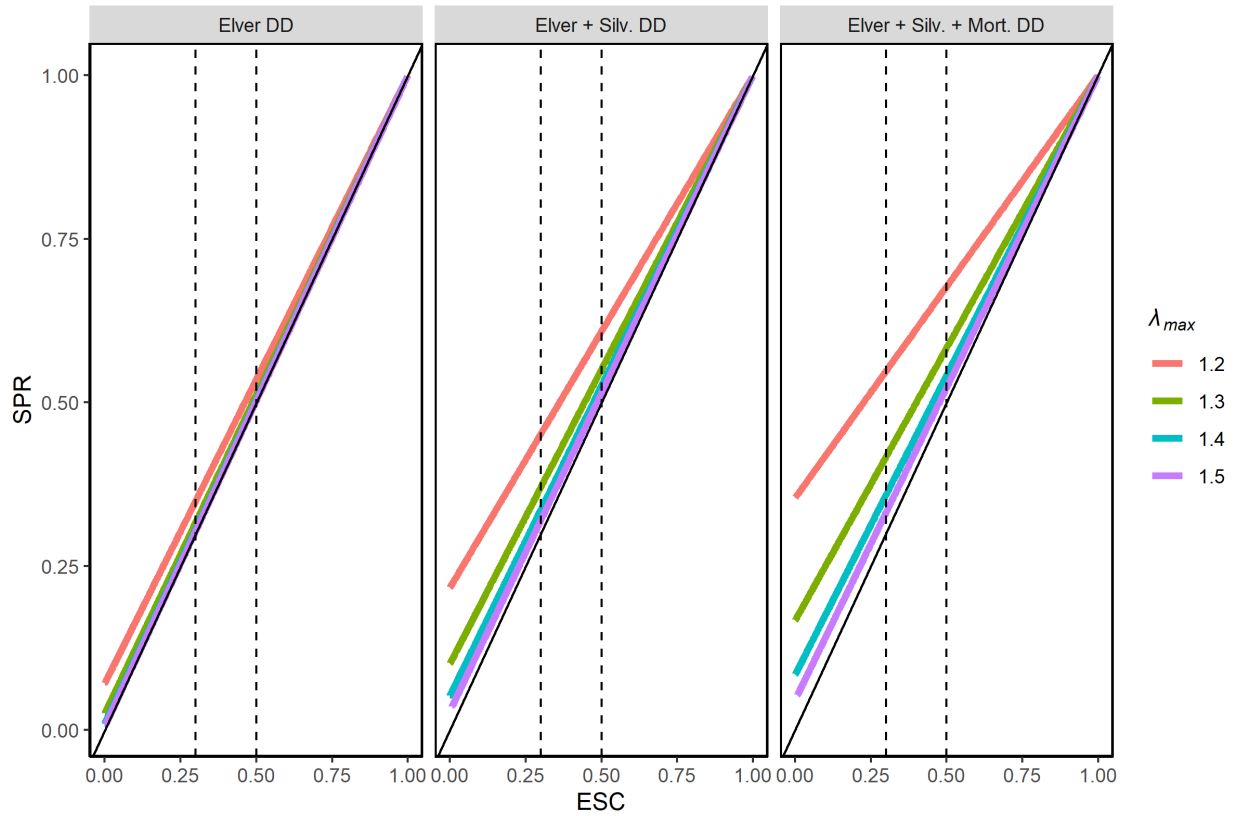


Figure A2.2. Relationship between ESC and SPR for eel fisheries across different density-dependent scenarios. The solid black line reflects a slope of 1, reflecting equivalence between the measurements. The dashed lines show the ESC level of 0.5 and 0.3 used as the upper stock reference and limit reference point.

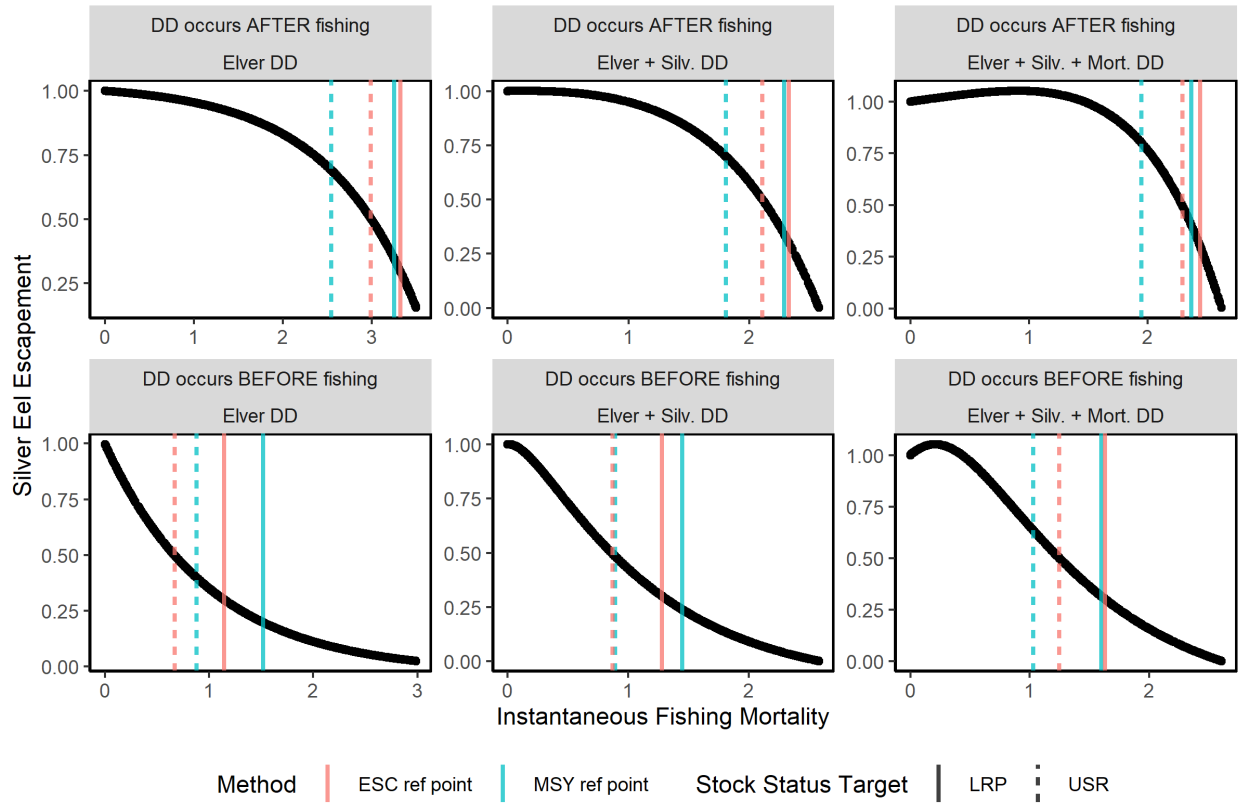


Figure A2.3. Mortality reference points for elver fisheries calculated using different metrics. The vertical lines are mortality reference points, coloured by which metric was used to calculate them. Solid lines represent LRP mortality reference points, while the dashed lines represent the mortality reference point associated with the USR. This simulation had a lambda λ_{max} of 1.3.

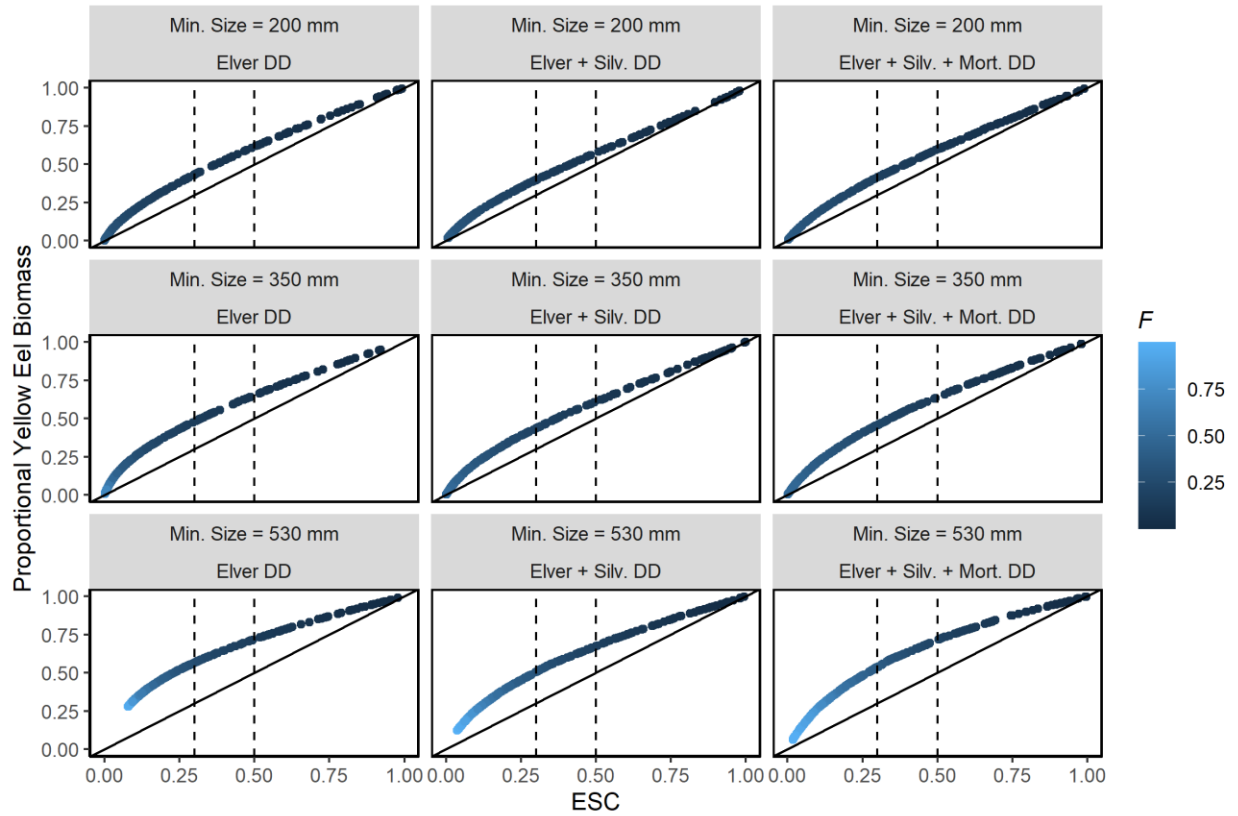


Figure A2.4. Relationship between ESC and the proportional yellow eel biomass for eel fisheries and density-dependent models across different minimum fishing sizes. The solid line reflects a slope of 1, reflecting equivalence between the measurements. The dashed lines show the ESC level of 0.5 and 0.3 used as the upper and limit reference points.

APPENDIX 3 – MULTIPLE LINEAR REGRESSION FIGURES

When the data used in the multiple linear regressions was split into training and testing data, the testing data (seen below) was used to observe how well the regressions performed on new data. The following plots show these diagnostic plots for the different density-dependent and regression for eel and elver fisheries. While the regressions tend to overestimate the fishing mortality at very small escapement values, they are fairly consistent over the range of escapement values likely to be considered for reference points (Figure 1).

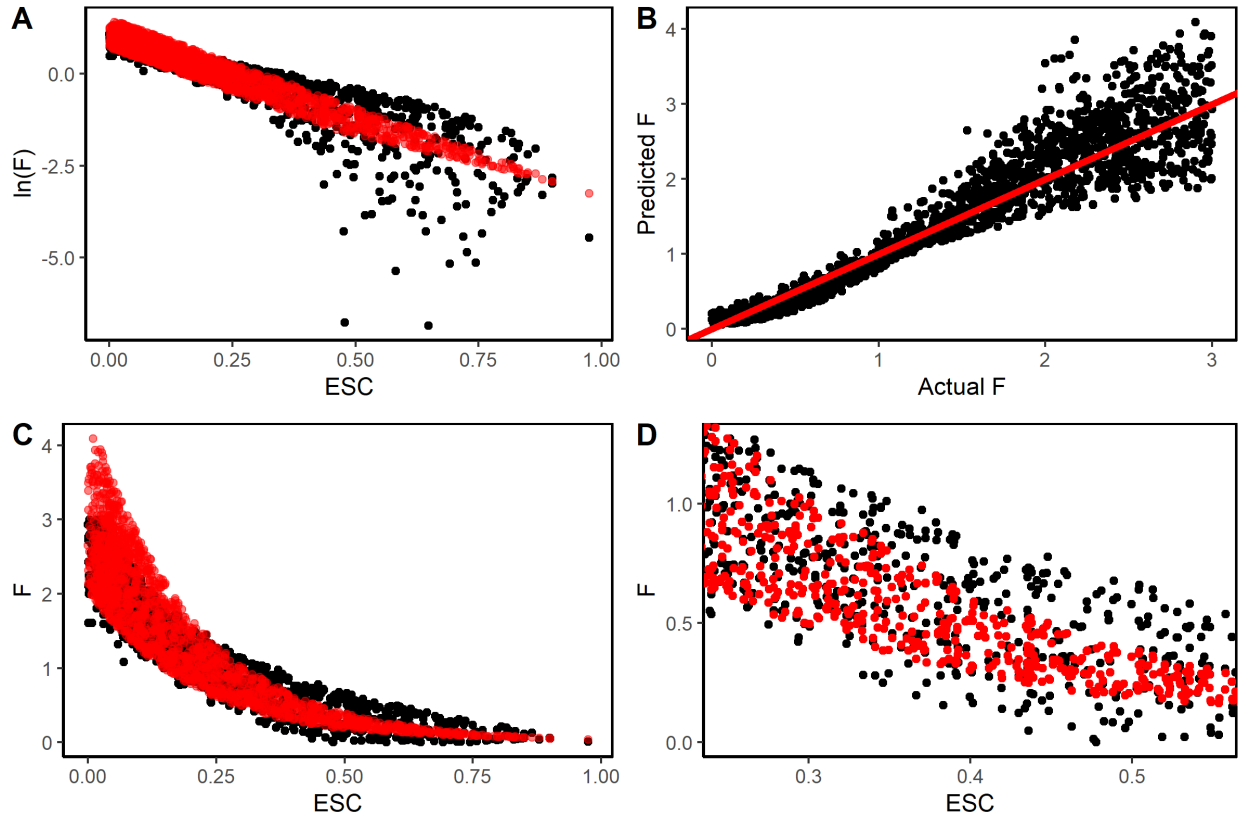


Figure A3.1. Multiple linear regression observations for elver fisheries, assuming density-dependence is in the elver stage only (“Elver DD”). Red points represent the predicted values from the test, while black points represent the actual value of the test data. Panel A shows the relationship between ESC and the log-transformed fishing mortality. Panel B shows the results between the actual F values and the F values the regression predicted. Panel C shows the relationship between the ESC and the untransformed F value across the entire range of ESC, while panel D shows the relationship only in ESC values likely to be of interest: between 0.25 and 0.55.

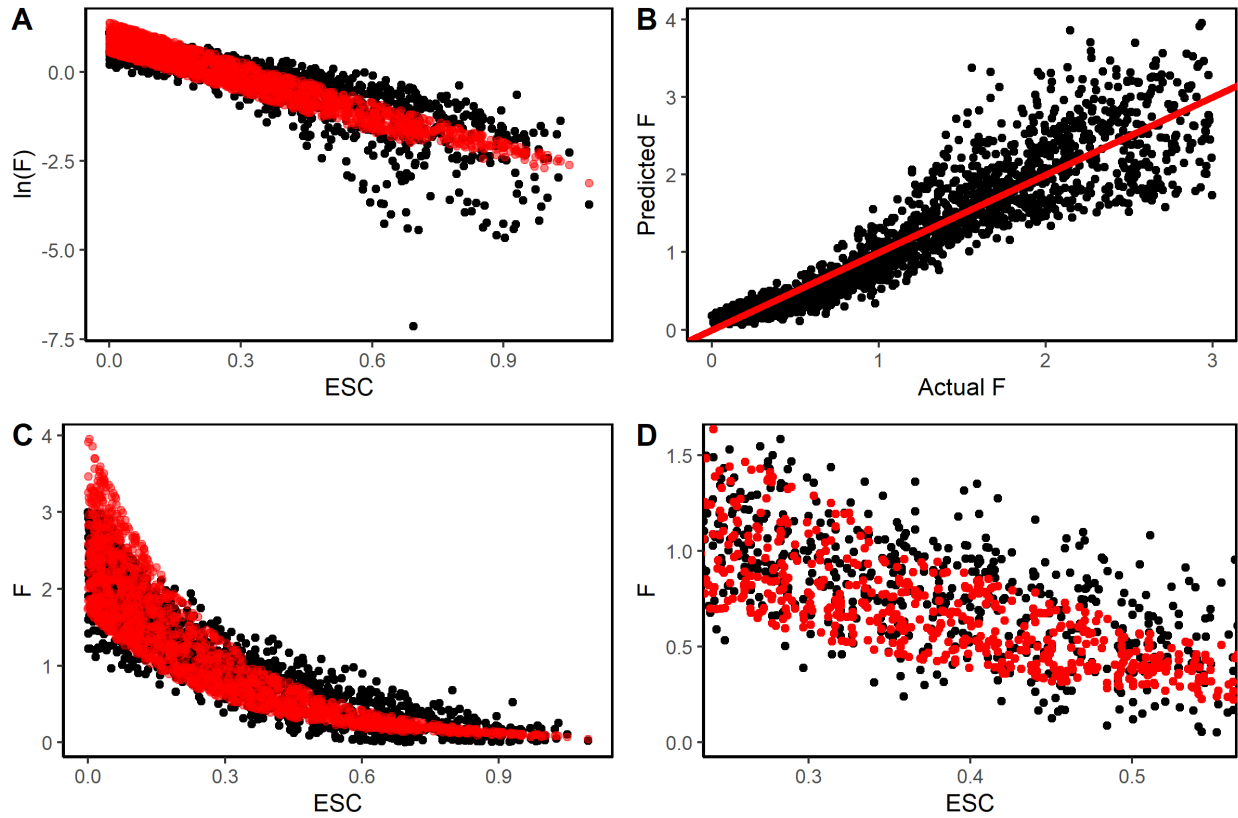


Figure A3.2. Multiple linear regression observations for elver fisheries, assuming density-dependence is in the elver stage and the probability of silvering (“Elver + Silv. DD”). Red points represent the predicted values from the test, while black points represent the actual value of the test data. Panel A shows the relationship between ESC and the log-transformed fishing mortality. Panel B shows the results between the actual F values and the F values the regression predicted. Panel C shows the relationship between the ESC and the untransformed F value across the entire range of ESC, while panel D shows the relationship only in ESC values likely to be of interest: between 0.25 and 0.55.

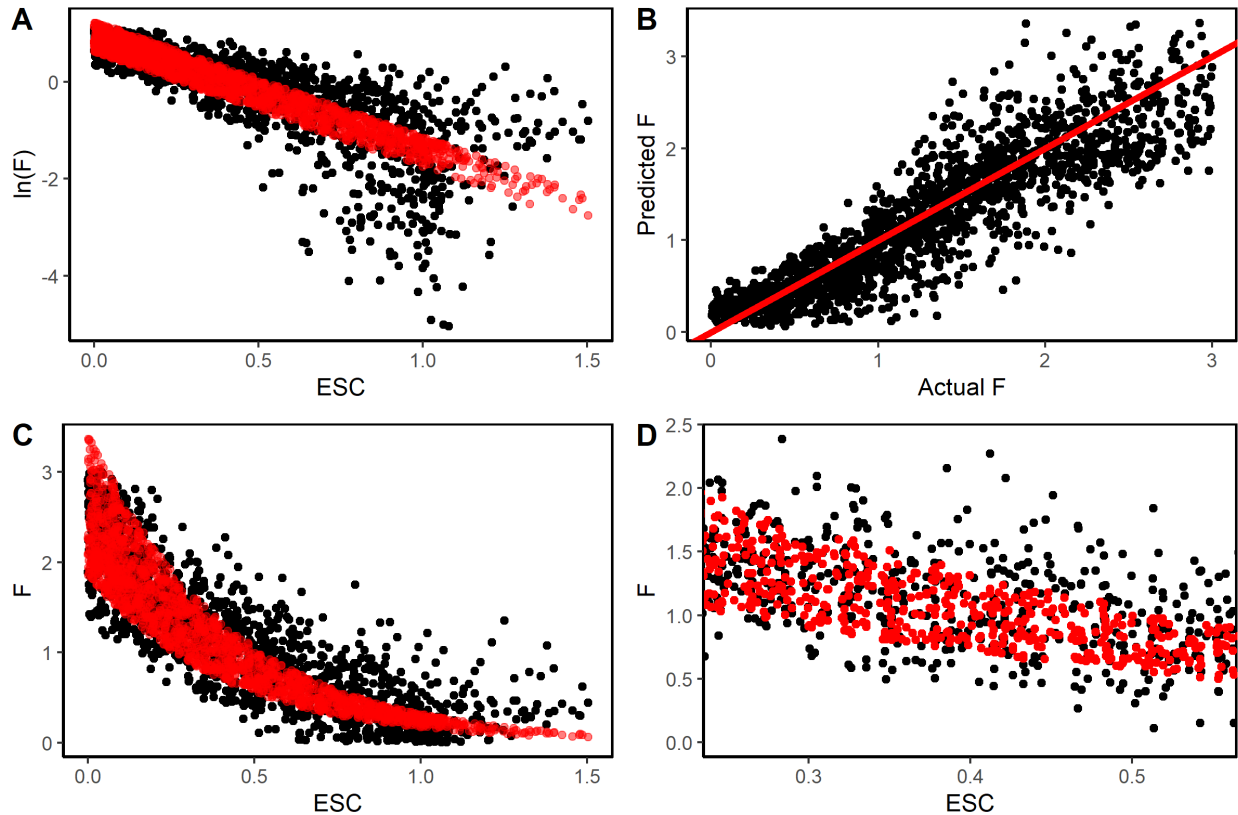


Figure A3.3. Multiple linear regression observations for elver fisheries, assuming density-dependence is in the elver stage and the probability of silvering (“Elver + Silv. + Mort. DD”). Red points represent the predicted values from the test, while black points represent the actual value of the test data. Panel A shows the relationship between ESC and the log-transformed fishing mortality. Panel B shows the results between the actual F values and the F values the regression predicted. Panel C shows the relationship between the ESC and the untransformed F value across the entire range of ESC, while panel D shows the relationship only in ESC values likely to be of interest: between 0.25 and 0.55.

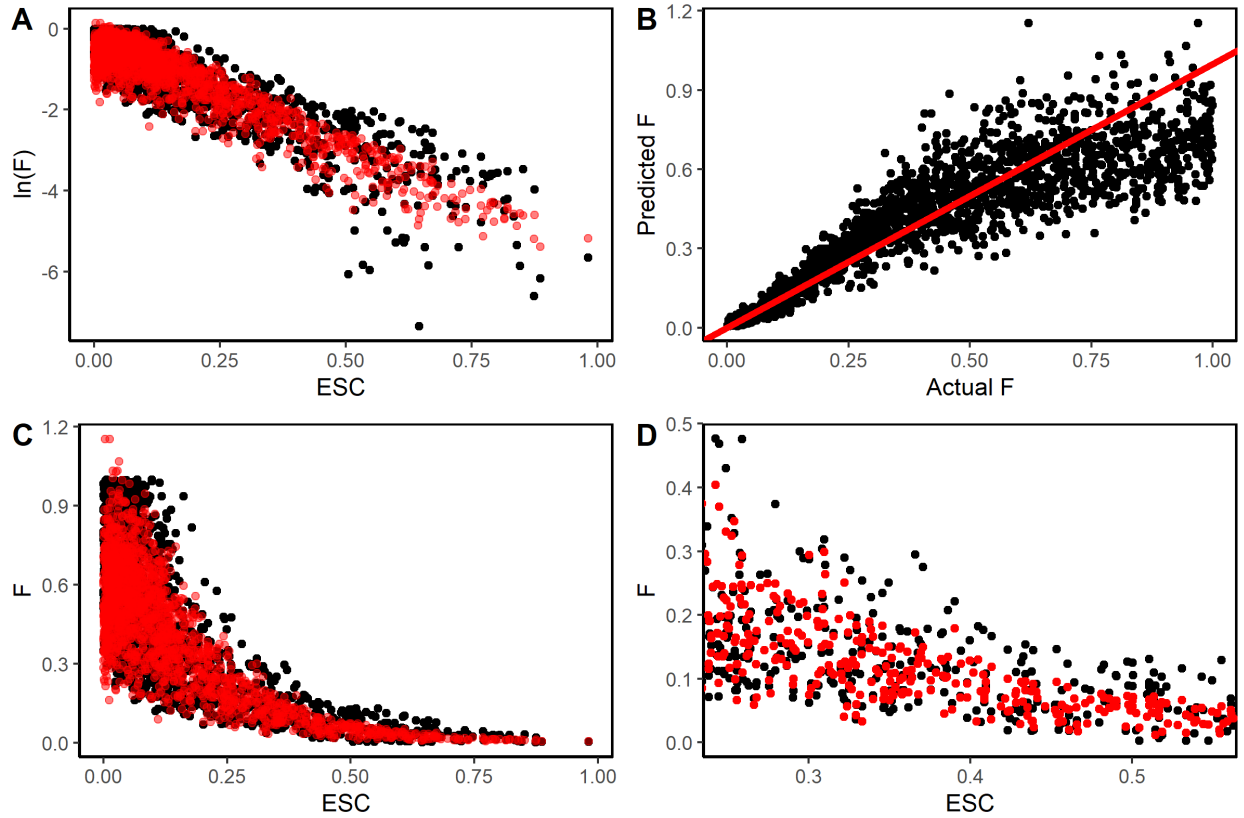


Figure A3.4. Multiple linear regression observations for eel fisheries, assuming density-dependence is in the elver stage only ("Elver DD"). Red points represent the predicted values from the test, while black points represent the actual value of the test data. Panel A shows the relationship between ESC and the log-transformed fishing mortality. Panel B shows the results between the actual F values and the F values the regression predicted. Panel C shows the relationship between the ESC and the untransformed F value across the entire range of ESC, while panel D shows the relationship only in ESC values likely to be of interest: between 0.25 and 0.55.

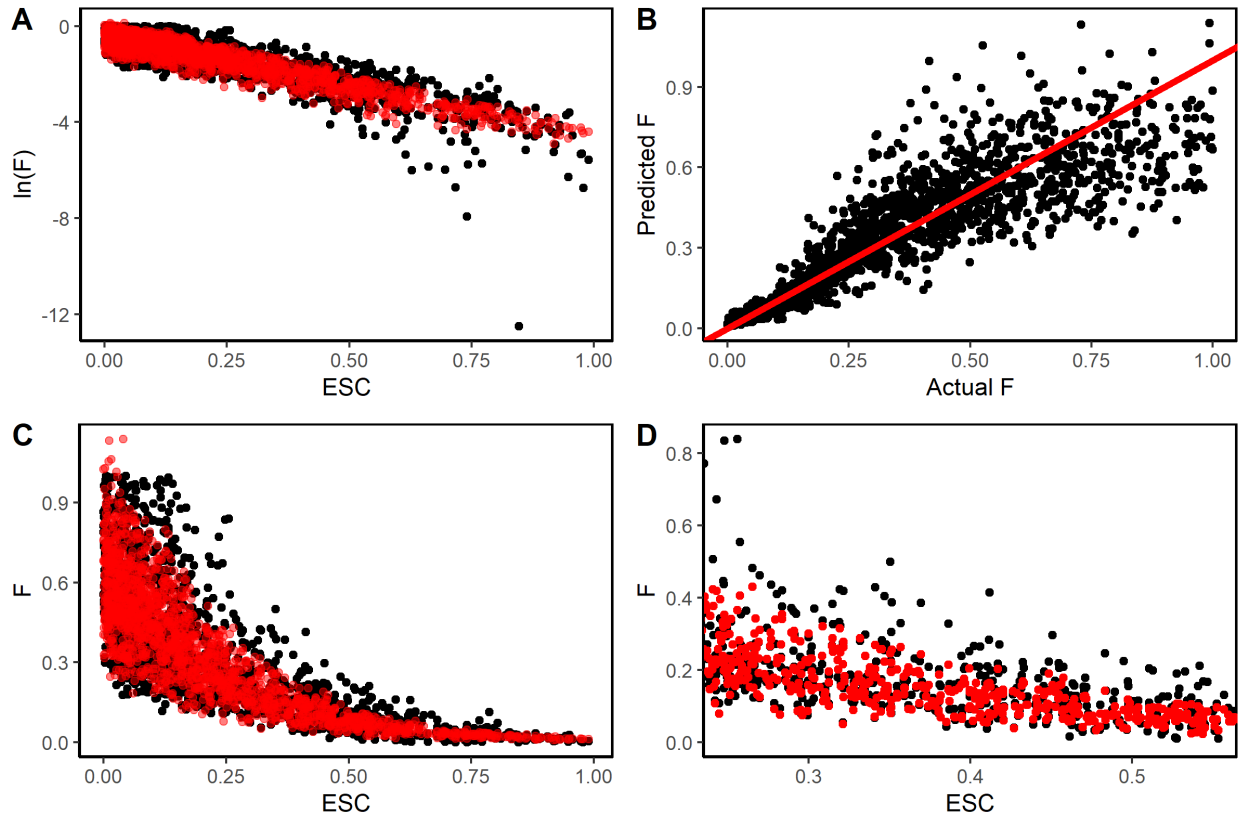


Figure A3.5. Multiple linear regression observations for eel fisheries, assuming density-dependence is in the elver stage and the probability of silvering (“Elver + Silv. DD”). Red points represent the predicted values from the test, while black points represent the actual value of the test data. Panel A shows the relationship between ESC and the log-transformed fishing mortality. Panel B shows the results between the actual F values and the F values the regression predicted. Panel C shows the relationship between the ESC and the untransformed F value across the entire range of ESC, while panel D shows the relationship only in ESC values likely to be of interest: between 0.25 and 0.55.

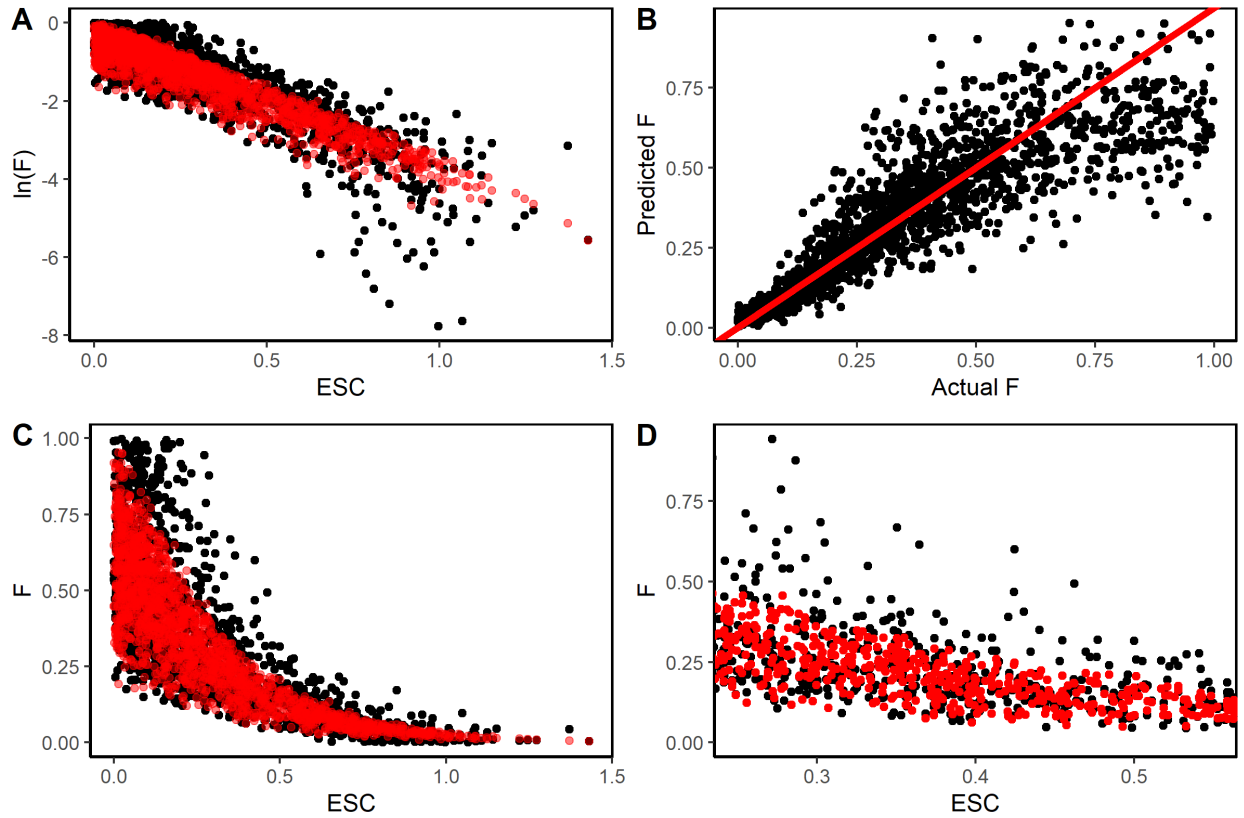


Figure A3.6. Multiple linear regression observations for eel fisheries, assuming density-dependence is in the elver stage and the probability of silvering (“Elver + Silv. + Mort. DD”). Red points represent the predicted values from the test, while black points represent the actual value of the test data. Panel A shows the relationship between ESC and the log-transformed fishing mortality. Panel B shows the results between the actual F values and the F values the regression predicted. Panel C shows the relationship between the ESC and the untransformed F value across the entire range of ESC, while panel D shows the relationship only in ESC values likely to be of interest: between 0.25 and 0.55.

APPENDIX 4 – CORRELATION OF SENSITIVITIES

While the grouped effect on the percent change in life history variable's effect on the percent change in the number of silver eel is shown in Figure 16, this can also be visualized as a correlation. Figure A4.1 shows the correlation between the life history variables and the percent change in the number of silver eel. Silver length caused the largest percent changes, likely due to its effects on fecundity and survival values. While elver length caused relatively large percent changes in the number of silver eel, it was uncorrelated to the percent change in the parameter itself, indicating this large effect is caused by the stochasticity in the silver mortality, not the change in the parameter itself. Growth rate was correlated with silver length and fecundity (and mildly with the maximum survival rate) (Table A4.1), while silver length was highly correlated with fecundity and maximum survival. When the partial correlations are considered (Table A4.2), the largest correlation was between fecundity and silver length, likely because fecundity is calculated from silver length (Equation 4).

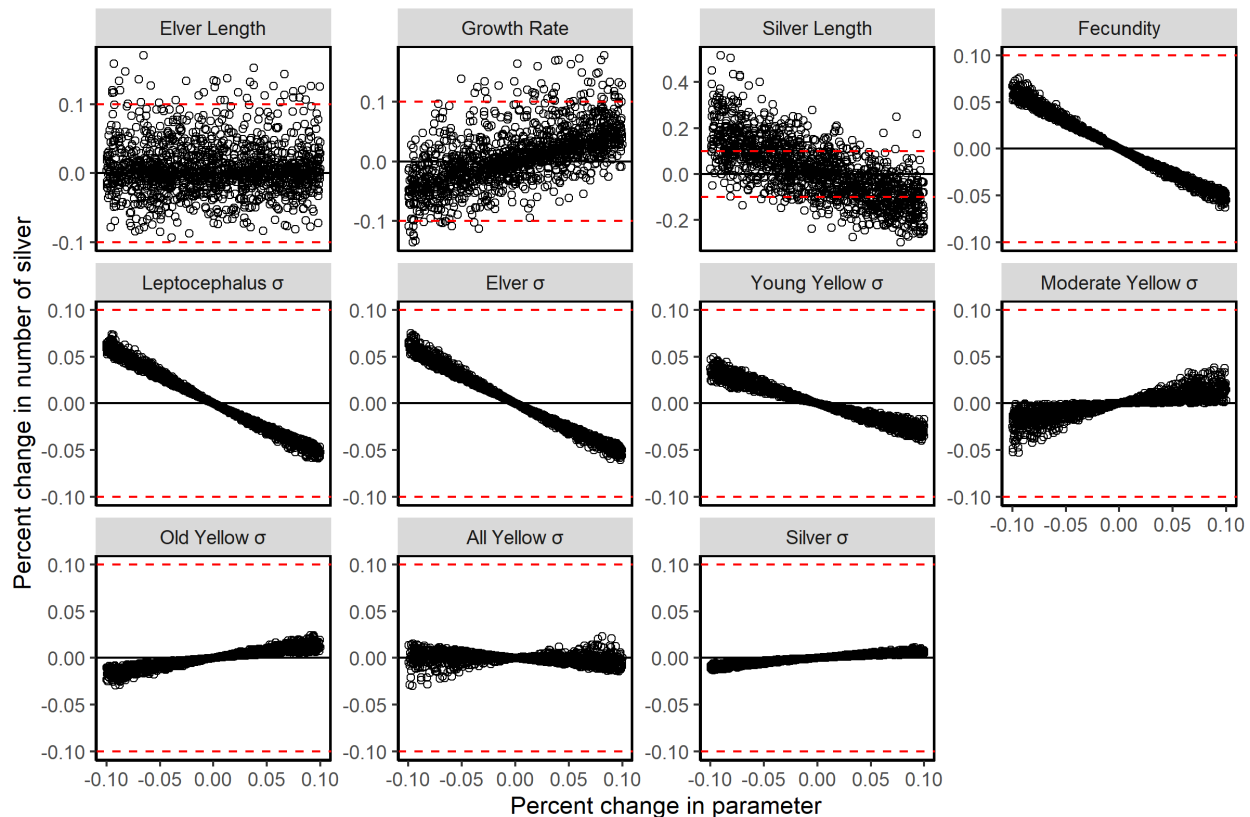


Figure A4.1. How the percent change in given parameters causes a percent change in the number of silver eel. Red dotted line show the corresponding 10% percent change in number of silver eel. Survival values were converted to their instantaneous version before perturbations.

Table A4.1. Correlation between variables. Correlations over 0.5 are italicized.

| | Growth Rate | Silver Length | Elver Length | Fecundity |
|------------------------|--------------------|----------------------|---------------------|------------------|
| Growth Rate | - | - | - | - |
| Silver Length | <i>0.68</i> | - | - | - |
| Elver Length | 0.017 | 0.0082 | - | - |
| Fecundity | <i>0.64</i> | <i>0.97</i> | 0.0056 | - |
| Maximum | 0.45 | <i>0.62</i> | 0.0057 | <i>0.58</i> |
| Silver Survival | | | | |

Table A4.2. Partial correlations between variables. Correlations over 0.5 are italicized.

| | Growth Rate | Silver Length | Elver Length | Fecundity |
|------------------------|--------------------|----------------------|---------------------|------------------|
| Growth Rate | - | - | - | - |
| Silver Length | 0.31 | - | - | - |
| Elver Length | 0.014 | 0.0059 | - | - |
| Fecundity | -0.11 | <i>0.93</i> | -0.0077 | - |
| Maximum | 0.032 | 0.26 | -0.00058 | -0.091 |
| Silver Survival | | | | |