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Testing Location-Specific Mortality Reference Points for American Eel (*Anguilla rostrata*) in a Meta-Population Model

Madison E. Brook, Adam S. van der Lee, Marten A. Koops

Fisheries and Oceans Canada
Great Lakes Laboratory for Fisheries and Aquatic Sciences
867 Lakeshore Rd.
Burlington, ON L7S 1A1

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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

Despite its broad distribution which includes the east coast of Canada and the United States of America, American Eel (*Anguilla rostrata*) share one common breeding ground with a panmictic population structure. An age-structured matrix model was used to construct a meta-population model with zones defined along the east coast of North America to test the effect of managing the meta-population at a regional level. A variety of possible assumptions about density-dependence, leptocephali survival and leptocephali dispersal were examined. Mortality reference points that resulted in a silver eel escapement (ESC) of 50% (F_{50} mortality reference points) were generated for each zone assuming independence, and then implemented in the meta-population model to observe the ESC of the total meta-population and the individual zones. While elver fishery F_{50} values were mostly successful in meeting targets of 50% ESC, eel F_{50} values more often resulted in populations falling below their targets, indicating that mortality reference points generated assuming independent populations may not achieve management objectives when the meta-population structure is considered. Under some leptocephali dispersal scenarios, northern zones consistently had low silver escapement, and were therefore considered more sensitive to the overall status of the meta-population than the more southern zones.

INTRODUCTION

American Eel (*Anguilla rostrata*) is a wide-ranging species found all along the east coast of North America, and as far inland as Lake Ontario (COSEWIC 2012). Their range of life history characteristics are similarly broad, with dramatic differences in growth rate, length-at-maturity, fecundity, etc. across latitudes (Cairns et al. 2014; Vélez-Espino & Koops 2010). Leptocephalus (eel larval stage) migrate from the spawning grounds in the Sargasso Sea along the east coast of North America where they turn into glass eel (transparent, small eel) upon reaching the Coastal Shelf, and then into pigmented elvers further inland (Cairns et al. 2014). Eel spend most of their lives as yellow eel, living in freshwater, brackish, or saline environments, until they mature and metamorphose into silver eel (Cairns et al. 2014). Silver eel from all locations, migrate back to the Sargasso Sea to breed, after which they die (Cairns et al. 2014). A lack of genetic population structure across its geographic range (Ulmo Diaz et al. 2023) supports conclusions of American Eel as a panmictic species. While panmixia suggests consideration of the entire species as a single population with local sub-populations, little is known about how leptocephali distribute to continental waters (Ulmo Diaz et al. 2023).

In Canada, American Eel was assessed as Threatened by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) (COSEWIC 2012). However, it has not been listed under Schedule 1 of the *Species at Risk Act*, with fisheries in multiple locations in Quebec and along the east coast (Cairns et al. 2014). Management of fisheries species by Fisheries and Oceans Canada (DFO) uses a sustainable fisheries framework that includes both mortality and stock status reference points (DFO 2006). Mortality reference points are instantaneous fishing mortality rates (F) intended to result in a population size that meets or exceeds stock status reference points (DFO 2006). For American Eel, silver eel escapement (ESC) has been used to estimate mortality reference points for American Eel (Brook et al. 2024), where a 50% ESC ratio (ESC_{50}) is used as the upper stock reference point (mortality reference point of F_{50}), and a 30% ESC ratio (ESC_{30}) is used as the limit reference point (mortality reference point of F_{30}) (Brook et al. 2024). Spawner-per-recruit (SPR: the proportion of silver eel to recruits) has also been used to estimate mortality reference points (Bradford et al. 2022; ICES 2001). Previous analyses have estimated F_{50} values for elver fisheries to be approximately 0.67 (Brook et al. 2024; Bradford et al. 2022). Conservative eel mortality reference points range is approximately 0.07 – 0.23 for F_{50} values, though these can vary across geographic zones in Canada and by the minimum fishing size (Brook et al. 2024; Bradford et al. 2022; ICES 2001). Furthermore, these estimates are highly dependent on assumptions made about the density-dependent mechanisms in the model: when there are more density-dependent mechanisms, the mortality reference points can increase beyond the ranges outlined above (Brook et al. 2024).

Fisheries are typically managed regionally and independently (DFO 2019; DFO 2012). Therefore the mortality reference points are typically generated while assuming the population is an individual, isolated population. This assumes that all leptocephali produced by the silver eel from a location will return to that same location. Because of the panmictic nature of American Eel, this is not necessarily true. While some leptocephali may return to the same location their mother is from, others may disperse to different locations. Over time, this could mean changes to the number of leptocephali arriving at different sub-populations, and implies that fishing one area could affect other areas that are not directly being affected. It has not been directly tested how effective the mortality reference points generated on independent populations perform when implemented in a meta-population structure. Therefore, a full interpretation of the American Eel population would be a meta-population with sub-populations along the Eastern coast of North America (e.g., Young & Koops 2014), ideally including locations like Greenland and the Caribbean (Ulmo Diaz et al. 2023; Cairns et al. 2014).

The objectives were to

1. determine whether managing zones as local populations (i.e. fishing zones using mortality reference points calculated from independent population assumptions) produces consistent results when applied to a meta-population structure;
2. evaluate how the meta-population responds to excess mortality in some zones, and if the response depends on the life stage affected (i.e. eel vs. elvers) and
3. investigate how the meta-population responds if mortality is reduced in one or more zones.

The general sensitivity of the meta-population to individual zone life history characteristics was also examined. An age-structured matrix meta-population was used, with seven zones along the east coast of North America. Alternative leptocephali dispersal assumptions were applied to consider their influence on responses to fishing mortality.

METHODS

The structure and parameterization of the meta-population model presented here is based on the individual population models used by Brook et al. (2024) to identify mortality reference points for Canadian locations based on life history. While the meta-population model extends beyond the geographic coverage of the Brook et al. (2024) models, a consistent model structure was applied with location-specific parameterization from the literature.

LIFE HISTORY

Due to data availability, the model is based primarily on data from freshwater female eel. Previously defined geographic zones were based on approximate management boundaries and life history (Figure 1; Cairns et al. 2014). Zone-specific life history traits were determined primarily based on data from the literature (Table 1; Cairns 2020; Cairns et al. 2014). The four Canadian zones (SL, NG, SG and SF) approximately represented the St. Lawrence basin, Newfoundland, PEI and Nova Scotia, respectively (Figure 1). The American zones represented drainages to the Atlantic Ocean along the East Coast. Due to a lack of data, no zones were defined north of the NG (e.g. Greenland) or south of the USA (e.g. Caribbean).

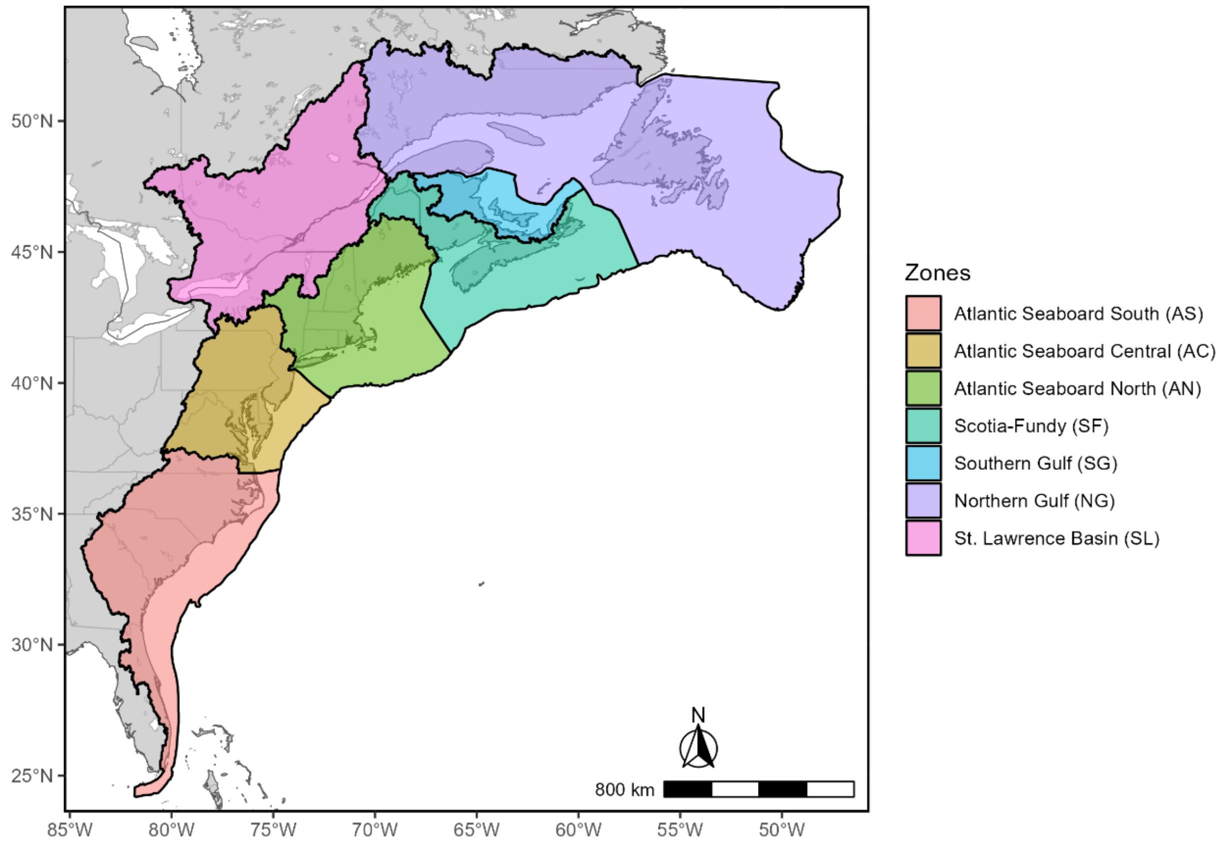

Figure 1. Boundaries used to define zones in the meta-population model (data from Cairns et al. 2014).

Growth rate

A biphasic growth curve was used to model length at age *a* (Brook et al. 2024):

$$length_{a,x} = \left\{ \begin{array}{ll} gr_x \times a + el_x & a < a_{b,x} \\ gr_x \times a_{b,x} + el_x & a \geq a_{b,x} \end{array} \right\}, \qquad (1)$$

where gr_x is the annual growth rate in mm/year for zone *x*, *el* is the elver length in mm in zone *x*, and $a_{b,x}$ is the inflection point of the piecewise function for zone *x*. The mean silver length for a given zone is equal to the second half of the piecewise function. For zones SF, SG and NG, there was sufficient data to directly calculate a biphasic growth equation using data from Cairns (2020). For the other locations, the growth rates were calculated by converting literature growth rates (Cairns et al. 2014) to biphasic growth rates (Brook et al. 2024), and the silver lengths were equal to the mean of the literature values (Cairns et al. 2014). All locations were assumed to share the same mean elver length of 63 mm (Jessop 2010).

Probability of Silvering

The probability of silvering in a given zone at a given age ($\gamma_{a,x}$) determines the number of eel likely to mature into a silver eel, and migrate out of the zones to spawn in the Sargasso Sea. The inverse of this is the probability of staying a yellow eel ($1-\gamma_{a,x}$). The underlying mechanism of determining the probability of silvering assumed that all zones start with a 10% probability of silvering at age 5 (the youngest possible silver age, below which $\gamma_{a,x}$ is set to 0), which increases 1% per year thereafter (Brook et al. 2024). This is then converted into a logistic equation to give the probability of silvering at age *a* using a simulation with zone-specific growth rates and silver lengths so that:

$$\gamma_{a,x} = \frac{1}{(1+e^{-0.5(a-int_x)})} \quad , \tag{2}$$

where the int_x parameter controls the inflection point along the x-axis of the equation for each zone, and the steepness of the curve is constant across locations (-0.5) (Brook et al. 2024).

Length-weight

A population-wide length-weight relationship was derived from fitting relationships to subsets of a large dataset of Canadian length-weight data, due to a lack of length-weight data from American locations (Brook et al. 2024; Cairns 2020). The final relationship for generating weight estimates from length was:

$$W = 2.0 \times 10^{-7}(L^{3.35}) \ , \tag{3}$$

where *W* is weight in g and *L* is length in mm.

Survival

Mortality for a given age *a* and zone *x* ($M_{a,x}$) was estimated using the Lorenzen (1996) equation (Brook et al. 2024; ASMFC 2012). The Lorenzen equation models instantaneous mortality rate as a function of weight, such that:

$$M_{a,x} = \eta \times 3.00 \times {W_{a,x}}^{-0.288} \ , \tag{4}$$

where η is an adjustment factor that affects the shape and maximum survival of the curve (Brook et al. 2024; ASMFC 2012). This equation was used to estimate the survival of yellow eel and silver eel due to a lack of data on American Eel survival rates. Elver annual survival (σ_E) was set to 0.0055 (Jessop 2000).

Leptocephali survival was solved for based on population stability (e.g. so that the population growth rate, λ, equals 1). It is not known how leptocephali survival may vary among zones, therefore, two scenarios were investigated. In scenario 1, leptocephali survival was solved for independently in each zone, giving each zone a unique survival value. This scenario closely replicates the structure of the independent population models (Brook et al. 2024). In scenario 2, a single leptocephali survival rate was solve for, which was scaled by the approximate duration of the migration from the Sargasso Sea to each zone (e.g. the migration from the Sargasso Sea to AS takes approximately 11 months, while the migration to SL takes approximately 17-18 months, Cairns et al. 2014). Leptocephali survival was scaled such that scaling constant was equal to 1 in AS (the closest zone the Sargasso Sea) and equal to 0.5 in SL (the farthest from the Sargasso Sea); the other zones were interpolated based on distance ($Scale_{L,x}$, Table 1).

Fecundity

Fecundity was defined based on a range-wide fecundity-length relationship. Using Canadian data from Tremblay (2009) and American data from Barbin & McCleave (1997), the data appeared to share a common trend, and differences among location-specific relationships is likely due to a different range in lengths. The fecundity of a female from a given zone (f_x) is defined as:

$$log_{10}(f_x) = 2.05 + 2.56(log_{10}(sl_x)), \tag{5}$$

where *sl* is the mean silver length of the zone in cm.

Proportion of Females

There is wide variation in the proportion of females within sub-populations of American Eel across its distribution (Cairns et al. 2014). While it is generally believed there are no naturally occurring males from the SL zone, some males have been found in every other zone (Cairns et al. 2014). Sex ratios are thought to be affected by variables such as salinity or density, but neither have been proven to cause significant changes (Côté et al. 2015; Cairns et al. 2014). Mean sex ratios from freshwater locations were used as the proportion of females for each zone (Cairns et al. 2014), though these means reflect the locations tested for sex ratios, and may not be representative of a zone as a whole (Table 1).

Table 1. Mean life history traits for each zone. For AS, AC, AN and SL, the growth rates were solved using the conversion between literature growth rates and biphasic growth rates (Brook et al. 2024). Water attraction proportions were taken from Young & Koops (2014). $Scale_{L,x}$ refers to the leptocephali survival scaling that could be applied to the common survival value based on distance from the Sargasso Sea.

Zone	Growth rate (mm/year)	Silver Length (mm)	Proportion female	Water Attraction Proportion	$Scale_{L,x}$	Life History Sources
AS	113.8	629	0.923	0.1901	1	Cairns et al. (2014)
AC	86.9	740	0.734	0.1217	0.95	Cairns et al. (2014)
AN	53.3	510	0.328	0.09880	0.86	Cairns et al. (2014)
SF	42.6	489	0.868	0.06270	0.75	Cairns (2020); Cairns et al. (2014)
SG	52.4	692	0.986	0.02740	0.64	Cairns (2020); Cairns et al. (2014)
NG	50.3	666	0.978	0.2340	0.63	Cairns (2020); Cairns et al. (2014)
SL	66.9	918	1	0.2653	0.5	Cairns et al. (2014)

Leptocephali Dispersal

The mechanism for leptocephali dispersal between zones is largely unknown, other than that there is sufficient mixing of genetics to be considered panmictic with no identified population structure (Ulmo Diaz et al. 2023; Miller et al. 2015). In an attempt to cover a realistic range of possibilities, three main variables could be changed to alter how the leptocephali dispersed to continental waters among zones: whether each zone in the meta-population had an independent leptocephali survival value or the meta-population shares one common leptocephali survival value that was scaled (see survival section above), the underlying leptocephali dispersal (*distr*) to the zones, and whether there are maternal effects contributing to the distribution (*m*).

Young & Koops (2014) examined a variety of mechanisms for leptocephali dispersal in their American Eel meta-population model, including the possibility of maternal effects. Maternal effects (*m*) describes a measure of natal homing, where offspring are more likely to return to the maternal zone than other zones. For example, if *m* was equal to 0.9 (90% maternal effects), then 90% of the offspring produced by females from a given zone will return to that zone, with the remaining 10% being distributed according to the underlying distribution.

The underlying leptocephali dispersal (*distr*) in the model was water attraction. Water attraction assumes that leptocephali distribute themselves based on the size of the available freshwater habitat in each zone: the larger the area of water each zone has, the more leptocephali go to that zone (Young & Koops 2014) (Table 1). The water attraction dispersal could be used as the primary dispersal mechanism, or used in conjunction with the maternal effects. An “infilling” dispersal mechanism was also examined. Infilling dispersal also used water attraction as an underlying dispersal, but as the density of leptocephali decreased, fewer leptocephali successfully traveled northward up the east coast. A 5% maternal effect was used in the infilling scenarios, so the population was not solely reliant on the infilling mechanism. In total, there were 6 leptocephali dispersal scenarios tested (Table 2).

Table 2. Leptocephali dispersal scenarios examined.

	Leptocephali survival options	
	Unique Leptocephali Survival	**Scaled Shared Leptocephali Survival**
Leptocephali dispersal options	90% maternal effects	90% maternal effects
	Water Attraction	Water Attraction
	Infilling	Infilling

Density-Dependence

Density-dependence in elver survival affected the zones individually using the Beverton-Holt equation:

$$d_{x,t} = \frac{\sigma_{E,x\ \lambda=max} / \sigma_{E,x_{\lambda=1}}}{1 + b_{dd,x} / K_{E,x} \times N_{E,x,t}}, \tag{6}$$

where $d_{x,t}$ is the compensation applied to the elvers in zone *x*, $b_{dd,x}$ is the density-dependent factor that is solved so that when a given zone is at its elver carrying capacity K_E, $d_{x,t}$ is equal to 1. This method of assigning density-dependence uses two measurements of the elver survival σ_E: one when the discrete time population growth rate (λ) for a zone is 1 (population is stable and does not change over time) and one when the elver survival is such that $\lambda = \lambda_{max}$. λ_{max} is the theoretical maximum population growth rate of the meta-population, and was estimated using an allometric equation (Randall & Minns 2000). $N_{E,x,t}$ is the number of elver in a zone at time *t*.

Because the elver survival density-dependence occurs during the elver stage, an assumption must be made about the timing of the elver fishery relative the timing of the density-dependence. If the density-dependence occurs after the fishery, $N_{E,x,t}$ is reduced based on the fishing mortality in that zone (See Brook et al. 2024). This assumption can have dramatic implications for fisheries and mortality reference points (Brook et al. 2024), so both assumptions were examined in the meta-population model.

Density-dependence was also optionally included in somatic growth rate (Brook et al. 2024). Based on the presumption that lower density leads to less competition for resources and therefore faster growth (as possibly seen in Ontario; EPRI (2018)), the number of yellow eel in each zone could affect the density-dependent growth rate $gr_{a,x,t}$ such that:

$$gr_{a,x,t} = \begin{cases} gr_{max,x} - gr_{K,x} * \frac{Na_{a,x,t}}{K_{Y,x}} & \frac{Na_{a,x,t}}{K_{Y,x}} < \frac{gr_{min,x} - gr_{max,x}}{-gr_{K,x}} \\ gr_{min,x} & \frac{Na_{a,x,t}}{K_x} \geq \frac{gr_{min,x} - gr_{max,x}}{-gr_{K,x}} \end{cases}. \tag{7}$$

Based on Brook et al. (2024), the growth rate for an age *a* eel in zone *x* in time *t* ($gr_{a,x,t}$) is determined by its growth rate when the zone is at K ($gr_{K,x}$), its maximum growth rate ($gr_{max,x}$;

equal to $gr_{K,x}$ * 2), and its minimum growth rate ($gr_{min,x}$; equal to $gr_{K,x}$ / 2). $Na_{a,x,t}$ is the mean density of yellows that age class *a* has experienced over its lifetime, and K_{Yx} is the number of yellows when the zone *x* is at *K*. When the ratio of number of yellow eel to the carrying capacity is larger than where the first half of the piecewise function intersects with the minimum growth rate, the growth rate is equal to that minimum growth.

Changing the growth rate every year based on the density can affect the probability of silvering and the survival at age. To change the probability of silvering, the inflection point parameter *int* (Equation 2) becomes both age and time dependent such that:

$$int_{a,x,t} = e^{(\alpha_x * \frac{Na_{a,x,t}}{K_{Y,x}})} + \beta_x \ , \tag{8}$$

where α_x and β_x are life history-dependent parameters that are solved for so that when $Na_{a,x,t}$ is equal to K_{Yx}, the $int_{a,x}$ is equal to its value at $gr_{K,x}$. When survival is affected via changing of growth rates based on density, the density-dependent growth rate ($gr_{a,x,t}$) for each age is used to calculate the mean length at age *a*, which is converted to weight (Equation 3) and used in the survival equation (Equation 4). Overall, the three different density-dependent scenarios were "Elver DD." (density-dependence only in the elver survival), "Elver + Silv. DD" (density-dependence in elver survival and the probability of silvering), and "Elver + Silv. + Mort. DD" (density-dependence in elver survival, probability of silvering and mortality).

POPULATION STRUCTURE

Model structure

The meta-population was constructed as an age-structured matrix model, with the exception of the silver stages (S_x), which consisted of multiple age-classes. The model was structured as a pre-breeding model, so individuals recruit as elvers and the egg and leptocephali stages are included in the recruitment term. All zones have an elver stage (E_x) that lasted one year, and the yellow eel stage (Y_x) which was the majority of the American Eel lifespan (Equation 10). Each zone had the same maximum age (a_{max}) of 25, which means each zone's matrix dimensions were equal to 25 + 1 by 25 + 1. For each zone, stage-1 represents the elvers in that zone, and stage-26 is the number of silvers in that zone. There are seven zones in the model, corresponding to Figure 2. While each zone has its own life history, the processes experienced by all zones were the same.

A given zone demographic matrix has the equation:

$$\boldsymbol{M_x} = \begin{bmatrix} 0 & 0 & 0 & \dots & 0 & 0 & R_{e,x\to x} \\ E_x & 0 & 0 & \dots & 0 & 0 & 0 \\ 0 & Y_{2,x} & 0 & \dots & 0 & 0 & 0 \\ 0 & 0 & Y_{3,x} & \dots & 0 & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots & \vdots \\ 0 & 0 & 0 & \dots & Y_{a_{max-1},x} & 0 & 0 \\ 0 & 0 & 0 & \dots & S_{a_{max-1},x} & S_{a_{max},x} & 0 \end{bmatrix}, \tag{9}$$

where $R_{e,x\to x}$ is the leptocephali produced by silvers from zone *x* that return to zone *x*, E_x is the transition through the elver stage, the Y_x stages move through the yellow eel ages, and S_x is the silver stage.

The dispersal matrix ***D*** determines how the leptocephali move between stages:

$$\boldsymbol{D}_{\boldsymbol{x}\rightarrow\boldsymbol{y}} = \begin{bmatrix} 0 & 0 & 0 & \dots & 0 & 0 & R_{e,x\rightarrow y} \\ 0 & 0 & 0 & \dots & 0 & 0 & 0 \\ 0 & 0 & 0 & \dots & 0 & 0 & 0 \\ 0 & 0 & 0 & \dots & 0 & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots & \vdots \\ 0 & 0 & 0 & \dots & 0 & 0 & 0 \\ 0 & 0 & 0 & \dots & 0 & 0 & 0 \end{bmatrix}, \tag{10}$$

where $R_{e,x\rightarrow y}$ is the leptocephali produced by silvers from zone *x* that disperse to zone *y*.

The demographic and dispersal matrices are combined into the projection matrix A:

$$\boldsymbol{A} = \begin{bmatrix} \boldsymbol{M}_{\boldsymbol{AS}} & \boldsymbol{D}_{\boldsymbol{AC}\rightarrow\boldsymbol{AS}} & \boldsymbol{D}_{\boldsymbol{AN}\rightarrow\boldsymbol{AS}} & \boldsymbol{D}_{\boldsymbol{SF}\rightarrow\boldsymbol{AS}} & \boldsymbol{D}_{\boldsymbol{SG}\rightarrow\boldsymbol{AS}} & \boldsymbol{D}_{\boldsymbol{NG}\rightarrow\boldsymbol{AS}} & \boldsymbol{D}_{\boldsymbol{SL}\rightarrow\boldsymbol{AS}} \\ \boldsymbol{D}_{\boldsymbol{AS}\rightarrow\boldsymbol{AC}} & \boldsymbol{M}_{\boldsymbol{AC}} & \boldsymbol{D}_{\boldsymbol{AN}\rightarrow\boldsymbol{AC}} & \boldsymbol{D}_{\boldsymbol{SF}\rightarrow\boldsymbol{AC}} & \boldsymbol{D}_{\boldsymbol{SG}\rightarrow\boldsymbol{AC}} & \boldsymbol{D}_{\boldsymbol{NG}\rightarrow\boldsymbol{AC}} & \boldsymbol{D}_{\boldsymbol{SL}\rightarrow\boldsymbol{AC}} \\ \boldsymbol{D}_{\boldsymbol{AS}\rightarrow\boldsymbol{AN}} & \boldsymbol{D}_{\boldsymbol{AC}\rightarrow\boldsymbol{AN}} & \boldsymbol{M}_{\boldsymbol{AN}} & \boldsymbol{D}_{\boldsymbol{SF}\rightarrow\boldsymbol{AN}} & \boldsymbol{D}_{\boldsymbol{SG}\rightarrow\boldsymbol{AN}} & \boldsymbol{D}_{\boldsymbol{NG}\rightarrow\boldsymbol{AN}} & \boldsymbol{D}_{\boldsymbol{SL}\rightarrow\boldsymbol{AN}} \\ \boldsymbol{D}_{\boldsymbol{AS}\rightarrow\boldsymbol{SF}} & \boldsymbol{D}_{\boldsymbol{AC}\rightarrow\boldsymbol{SF}} & \boldsymbol{D}_{\boldsymbol{AN}\rightarrow\boldsymbol{SF}} & \boldsymbol{M}_{\boldsymbol{SF}} & \boldsymbol{D}_{\boldsymbol{SG}\rightarrow\boldsymbol{SF}} & \boldsymbol{D}_{\boldsymbol{NG}\rightarrow\boldsymbol{SF}} & \boldsymbol{D}_{\boldsymbol{SL}\rightarrow\boldsymbol{SF}} \\ \boldsymbol{D}_{\boldsymbol{AS}\rightarrow\boldsymbol{SG}} & \boldsymbol{D}_{\boldsymbol{AC}\rightarrow\boldsymbol{SG}} & \boldsymbol{D}_{\boldsymbol{AN}\rightarrow\boldsymbol{SG}} & \boldsymbol{D}_{\boldsymbol{SF}\rightarrow\boldsymbol{SG}} & \boldsymbol{M}_{\boldsymbol{SG}} & \boldsymbol{D}_{\boldsymbol{NG}\rightarrow\boldsymbol{SG}} & \boldsymbol{D}_{\boldsymbol{SL}\rightarrow\boldsymbol{SG}} \\ \boldsymbol{D}_{\boldsymbol{AS}\rightarrow\boldsymbol{NG}} & \boldsymbol{D}_{\boldsymbol{AC}\rightarrow\boldsymbol{NG}} & \boldsymbol{D}_{\boldsymbol{AN}\rightarrow\boldsymbol{NG}} & \boldsymbol{D}_{\boldsymbol{SF}\rightarrow\boldsymbol{NG}} & \boldsymbol{D}_{\boldsymbol{SG}\rightarrow\boldsymbol{NG}} & \boldsymbol{M}_{\boldsymbol{NG}} & \boldsymbol{D}_{\boldsymbol{SL}\rightarrow\boldsymbol{NG}} \\ \boldsymbol{D}_{\boldsymbol{AS}\rightarrow\boldsymbol{SL}} & \boldsymbol{D}_{\boldsymbol{AS}\rightarrow\boldsymbol{SL}} & \boldsymbol{D}_{\boldsymbol{AN}\rightarrow\boldsymbol{SL}} & \boldsymbol{D}_{\boldsymbol{SF}\rightarrow\boldsymbol{SL}} & \boldsymbol{D}_{\boldsymbol{SG}\rightarrow\boldsymbol{SL}} & \boldsymbol{D}_{\boldsymbol{NG}\rightarrow\boldsymbol{SL}} & \boldsymbol{M}_{\boldsymbol{SL}} \end{bmatrix}. \tag{11}$$

A is a 182 x 182 matrix (7 zones multiplied by the maximum age of 25 + 1). The population vector ***n*** shares this length of 182, where each zone's population abundance is tracked (the first 26 values are the abundances of each age class in zone 1, the next 26 are zone 2, etc.).

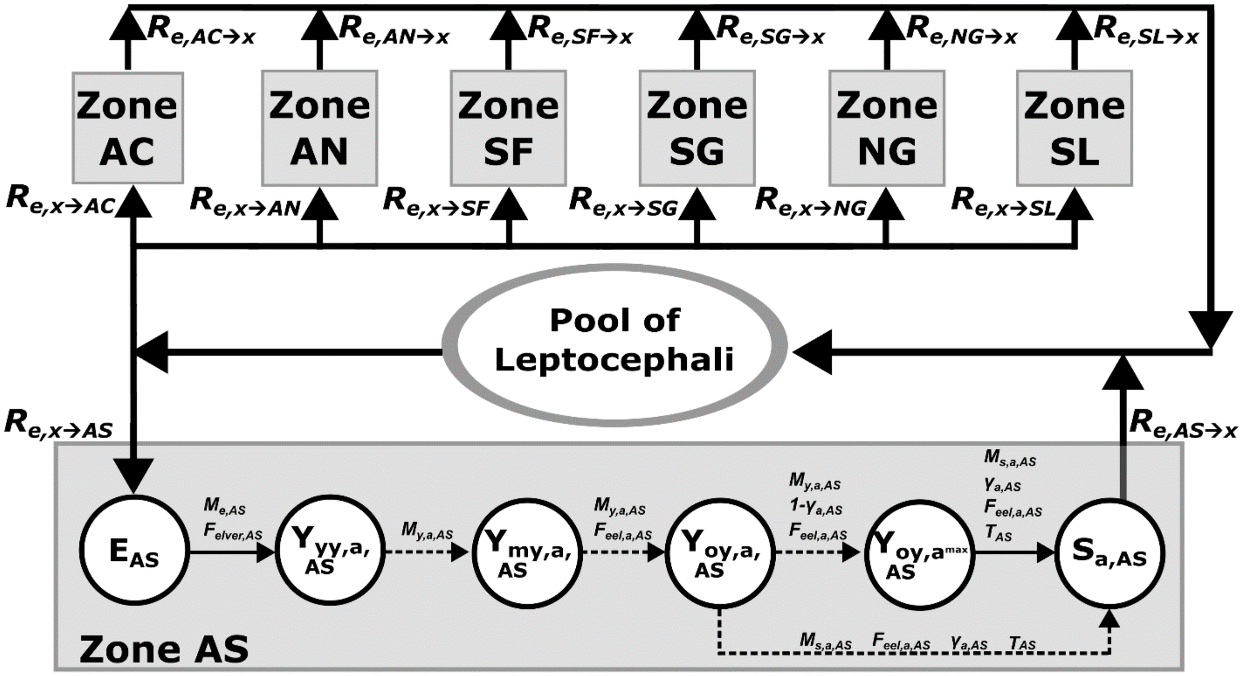

*Figure 2. Model diagram for meta-population model. Processes occurring within each matrix **M** (see Equation 9) has been expanded for the AS zone, but all zones have the same equations and processes. The subscript yy denotes young yellow eel; my are moderately aged yellows that are not large enough to silver; and oy are yellow eel large enough to silver.*

The meta-population moves through time in yearly increments *t* by:

$$\boldsymbol{n}_{t+1} = \mathbf{A}_{N,t}\boldsymbol{n}_t, \tag{12}$$

The matrix ***A*** changes every year based on the density at time *t*.

The recruitment parameters (R_e), where and how many offspring from each zone go to all the zones, are determined by different combinations of the above variables. The number of leptocephali that return to same zone *x* where the silver eel originate from is given by:

$$Re_{x\rightarrow x} = f_x \times \sigma_{L,x} \times m + f_x \times \sigma_{L,x} \times (1-m) \times distr_x \,, \qquad (13)$$

and the number of leptocephali produced by silvers in zone *x* but disperse to zone *y* is:

$$Re_{y\rightarrow x} = f_y \times \sigma_{L,x} * (1-m) * distr_x. \qquad (14)$$

where f_y is the fecundity value in zone *y*, $distr_x$ is the distribution of leptocephali going to zone *x*, *m* is the maternal effects, and $\sigma_{L,x}$ is the leptocephali survival in zone *x* (either solved independently or scaled from one common value).

Each zone receives a number of leptocephali every year based on the number of silvers ($N_{S,x,t}$) in the population:

$$N_{L,x,t} = Re_{x\rightarrow x} \times N_{S,x,t} + \sum_{y=1}^{6}(Re_{y\rightarrow x} \times N_{S,y,t}). \qquad (15)$$

When the number of silvers is equal to the number of silvers when the meta-population is at K ($N_{S,x,t} = K_{S,x}$) in Equation 15, then Equation 15 is used to calculate the number of leptocephali each zone receives when the population is at K ($K_{L,x}$). The total number of leptocephali in the meta-population when at *K* ($K_{L,total}$) is the sum of $K_{L,x}$ across all zones.

Knowing the total number of leptocephali in the meta-population is important when using the Infilling dispersal scenario (Table 2), where the density of leptocephali affects the dispersal probabilities to the zones. The number of leptocephali in the meta-population as a whole at time *t* is equal to:

$$N_{L,total,t} = \sum_{x=1}^{7}(N_{L,x,t}). \qquad (16)$$

Starting in the most southern zone (AS, x=1) moving northward (until SL, x=7), the number of leptocephali dispersing to zone *x* at *K* ($K_{L,x}$) is subtracted by the number of leptocephali available ($N_{L,avail,x,t}$), giving the new total of available leptocephali. For AS, the number of leptocephali available is the $N_{L,total,t}$, because it is the most southern zone. Subtracting $K_{L,1}$ from this total gives the number of leptocephali that could go to the next most northern zone, AC, and so on:

$$N_{L,avail,x+1,t} = N_{L,avail,x,t} - K_{L,x}, \qquad (17)$$

The ratio of $N_{L,avail,x,t}$ and $K_{L,x}$ is used to determine the modifier on the distribution of leptocephali for zone *x* (mod_x). If the available leptocephali is less than $K_{L,x}$, then the modifier was equal to the available leptocephali for that zone divided by the $K_{L,x}$ for that zone. All zones where the available leptocephali was less than 5% of the proportion at *K* was set to a modifier minimum of 0.05:

$$mod_{x,t} = \begin{cases} 1 & \frac{N_{L,avail,x,t}}{K_{L,x}} \geq 1 \\ \frac{N_{L,avail,x,t}}{K_{L,x}} & \frac{N_{L,avail,x,t}}{K_{L,x}} < 1 \ AND \ \frac{N_{L,avail,x,t}}{K_{L,x}} > 0.05 \\ 0.05 & \frac{N_{L,avail,x,t}}{K_{L,x}} \leq 0.05 \end{cases} \qquad (18)$$

where $mod_{x,t}$ is the modifier to be applied to the underlying leptocephali dispersal. The *mod* values are multiplied by the underlying leptocephali dispersal of water attraction (Table 1), and then rescaled to sum to 1 :

$$distr_{x,t} = {(mod_{x,t} \times wat.attr_{x})}\Big/{\textstyle\sum_{y=1}^{7}(mod_{y,t} \times wat.attr_{y})}. \tag{19}$$

When using the Infilling dispersal scenario, the $distr_{x,t}$ is recalculated at every timestep. For the other options, it stays static during simulations.

Though life history varies among locations, the equations that determine the transition matrix through each stage/age are consistent, and the same as Brook et al. (2024). The elver stage in zone x is given by:

$$E_x = (prop_{f,x} \times e^{-(F_{elver,x})} \times \sigma_{E,x}) \times d_{x,t} \;, \tag{20}$$

where $\sigma_{E,x}$ is the annual elver natural mortality rate, $F_{elver,x}$ is the instantaneous fishing mortality rate of elvers in zone *x*, $prop_f$ is the proportion of females in zone *x* (Table 1, Cairns et al. 2014), and $d_{x,t}$ is the density-dependent compensation (Equation 6). The yellow stage for zone *x* is given by:

$$Y_{a,x} = \left(1 - \gamma_{a,x}\right) \times e^{-(M_{y,a,x} + F_{eel,a,x})} \;, \tag{21}$$

where 1-γa,x is the probability of not silvering, My,a,x is the age-specific natural mortality rate of age a in zone x (Equation 4). Feel,a,x is the age and zone specific instantaneous fishing mortality rate. Every age had its own Feel value, based on the proportion of eel expected to be larger than the minimum fishing size (see Brook et al. 2024 for more detail). The silver transition at age a is:

$$S_{a,x} = \gamma_{a,x} \times e^{-(M_{s,a,x} + F_{eel,a,x} + T_x)} \;, \tag{22}$$

where $\gamma_{a,x}$ is the probability of silvering, $M_{s,a,x}$ is the age and zone silver natural mortality rate, and *T* is the zone-specific turbine mortality rate.

Population Model Analysis

Stochastic Analysis

To account for uncertainty in the life history parameterization, stochasticity was included for several key variables with their value randomly drawn from specified distributions for each simulation replicate. Uncertainty in the growth rate and silver length were based on the Canada-wide standard deviations (7.95 mm/year and 89mm, respectively (Brook et al. 2024)). Based on approximately two multiplied by the standard deviation, growth rates were drawn from a uniform distribution where the growth rate at K was equal to the mean value from Table 1 ± 15 mm/year, and the mean silver length was ± 175 mm. The proportion of females in each zone were drawn from a beta distribution, which bounds the prediction between 0 and 1. A standard deviation of 0.025 was used for all zones, which corresponded to an approximate range of ± 0.1 from the mean proportion of female (Table 1), with the exception of the SL zone which was held constant at 100% females for all simulations. It is generally understood that no males occur in the SL zone, except for eel that were displaced during a transport experiment (Pratt & Threader 2011).

Uncertainty in other life history variables followed the methods of Brook et al. (2024). Fecundity was calculated using Equation 5 then varied assuming a normal distribution and a coefficient of variation (CV) of 10% (Brook et al. 2024). λ_{max} was drawn from a uniform distribution, ranging from 1.2 – 1.5 (Randall & Minns 2000, Brook et al. 2024), though each zone had the same λ_{max} for a given simulation replicate. Each zone had a unique elver length, which followed a uniform distribution, with a minimum size of 57 mm and a maximum of 69 mm (Brook et al. 2024; Jessop 2010). Survival values were independent among zones, with the η parameter drawn from a uniform distribution between 0.063 and 0.21, giving a maximum survival value between

~90 – 97% (Equation 4). Elver survival varied uniformly between 0.0052 and 0.0057 (Jessop 2000).

Calculating F_{50} mortality reference points

The mortality reference point F_{50} was determined for each zone, under the assumption that it was an independent population (Brook et al. 2024, Bradford et al. 2022). This was done by randomly generating the life history as described above (Table 1), and running simulations until each zone had a sample size of 50 data points with a silver escapement value (ESC) of between 0.49 and 0.51. The median F value of this sample was used as the F_{50} value (same methods as Brook et al. 2024). For eel fisheries, each zone was assumed to have the same minimum eel fishing size of 300 mm, which was chosen as a moderate minimum size, while ensuring no simulation replicates had a silver length smaller than the minimum fishing size. The median $F_{extinct}$ was also calculated according to the methods in Brook et al. (2024), representing the smallest fishing mortality rate that would result in the population eventually becoming extinct (Brook et al. 2024).

To observe how leptocephali dispersal options affect zone-specific carrying capacities and how the populations respond to fishing mortality rate, a 125 year simulation was run using the mean life history data (no stochasticity in life history). The timeline for these simulations started in 1900, with all populations fished at their calculated eel F_{50} values. After 75 years (in 1975), a 40% annual turbine mortality was introduced to the SL zone (COSEWIC 2012). In the year 2000, elver fisheries in AN and SF (representing Maine and Nova Scotia) (Cairns et al. 2014) were also applied fishing at F_{50}, and the simulation continued to 2025. This simulation was to visualize the effects of various sequential additions of anthropogenic mortalities, as well as the different leptocephali survival and dispersal options. It was not intended to directly mimic a timeline of historical anthropogenic mortality.

F_{50} management in a meta-population

Each stochastically generated simulation was fished at the independently derived F_{50} values for 50 years for both eel fisheries and elver fisheries. 100 stochastic trials were run for each leptocephali and density-dependence scenario. The silver escapement (ESC) of the zones and populations were recorded, where the zone escapement is:

$$ESC_x = \frac{N_{S,x,after}}{N_{S,x,before}}, \tag{23}$$

Where $N_{S,x}$ is the number of silver eel in zone x, which is determined both before and after fishing mortality is applied to the population. The total meta-population escapement is:

$$ESC_{total} = \frac{\sum_{i=1}^{7} N_{S,x,after}}{\sum_{i=1}^{7} N_{S,x,before}}. \tag{24}$$

ESC values close to 0.5 indicate that the independently generated F_{50} values can be used to manage the meta-population for the same ESC target.

Excess Mortality and Recovery simulation

Simulations were used to investigate how excess mortality occurring in one or multiple zones may impact the status of the meta-population or other zones. These simulations estimate how many zones need to be strongly impacted before effects are seen on a meta-population level, as well as determine how individual zones react as more and more zones face excess mortality. The abundance of the meta-population after fishing eel at F_{50} for 50 years was the starting point of the simulations. Excess mortality was simulated by setting the fishing level of a random zone to $F_{extinct}$ (i.e. just past the threshold for overfishing). That zone was fished at its $F_{extinct}$ value for an additional 50 years, and the ESC measured. Then, again starting from the abundance of the F_{50} trial, an additional zone was randomly chosen to be fished at $F_{extinct}$ (total of 2 zones experiencing excess mortality), and the simulation run for 50 years. This was repeated until all seven zones were subject to excess mortality. Excess mortality was applied to both the elver and eel life-stages to determine if the life-stage impact affected the population response. In elver trials, the eel continued to be fished at their F_{50}.

The recovery simulations were conducted similarly, but in the reverse order as the excess mortality simulation. These simulations were used to determine if there is a threshold number of zones that must recover before effects are seen in both a zone and total meta-population level. The starting abundance used was the result of fishing all zones at their $F_{extinct}$ (either eel or elver) after 50 years. In a random order, one of the zones was chosen to be fished at their F_{50} instead (for eel trials) or for the fishing to stop (for elver trials) for an additional 50 years, until no zones were experiencing excess mortality. 100 stochastic simulations were run for both simulations.

Sensitivity analysis

A sensitivity analysis was conducted to determine the sensitivity of ESC (both meta-population wide and zone-specific ESC) to changes in life history in one of the zones. Based on previous sensitivity analysis (Brook et al. 2024), five life history parameters were selected to be perturbed: growth rate, silver length, fecundity, yellow and silver eel survival, and the proportion of females in each zone. A matrix was randomly generated, and, one at a time, each zone life history parameter was perturbed, and the resulting ESCs recorded. Each life history was perturbed ± 10%, with the exception of the proportion of females, due to its beta distribution. Instead, the proportion of females was perturbed using the 2.5 and 97.5% quantiles assuming a beta distribution, using the randomly chosen value as the mean and a standard deviation of 0.025. This was repeated until each life history variable had been tested 100 times for each zone.

RESULTS

The calculated independent zone F_{50} values varied depending on the density-dependent mechanisms and type of fishery. The "Elver DD" model had the smallest F_{50} values, and the mortality reference points increased as the number of density-dependent mechanisms increased (Table 3 and 4). When density-dependence occurred after the elver fishery, the F_{50} values were much larger than if the density-dependence occurred before the fishery. The $F_{extinct}$ values show the inverse of this trend; additional density-dependent mechanisms lowered the $F_{extinct}$ values. The $F_{extinct}$ values for elvers were calculated assuming the eel fishery was being managed at its F_{50} value for use in the simulations, which occasionally led to $F_{extinct}$ values smaller than the F_{50} values when only elvers were fished. This was done to ensure that the $F_{extinct}$ value for elver fisheries take into account the mortality to eel for the excess mortality trials: if $F_{extinct}$ was calculated assuming only elver mortality, the $F_{extinct}$ would be overestimating the amount of mortality the population could sustain and still be able to replace itself when the eel fishing was included in the simulation.

Table 3. Summary of elver fishery F_{50} and $F_{extinct}$ values calculated assuming independent zones for use in simulations. Note that $F_{extinct}$ was calculated assuming that eel were being fished at their F_{50}.

Density Model	**Fishery timing**	**Zone**	**F_{50}**	**$F_{extinct}$**
Elver DD	DD occurs AFTER elver fishery	AS	2.3	2.03
		AC	2.99	1.93
		AN	2.86	2.25

Density Model	**Fishery timing**	**Zone**	F_{50}	$F_{extinct}$
		SF	2.88	2.14
		SG	3.14	2.13
		NG	3.44	2.32
		SL	3.67	2.25
	DD occurs BEFORE elver fishery	AS	0.646	2.03
		AC	0.657	1.93
		AN	0.661	2.25
		SF	0.667	2.14
		SG	0.671	2.13
		NG	0.672	2.32
		SL	0.676	2.25
Elver + Silv. DD	DD occurs AFTER elver fishery	AS	2.11	2.05
		AC	2.20	2.26
		AN	1.95	2.35
		SF	2.46	2.29
		SG	2.47	2.46
		NG	2.45	2.14
		SL	2.39	2.19
	DD occurs BEFORE elver fishery	AS	0.709	2.05
		AC	0.749	2.26
		AN	0.827	2.35
		SF	0.915	2.29
		SG	0.899	2.46
		NG	0.915	2.14
		SL	0.828	2.19
Elver + Silv. + Mort. DD	DD occurs AFTER elver fishery	AS	2.08	1.88
		AC	2.22	2.18
		AN	2.26	2.20
		SF	2.37	1.96
		SG	2.65	2.41
		NG	2.81	2.59
		SL	2.78	2.35
	DD occurs BEFORE elver fishery	AS	0.89	1.88
		AC	1.01	2.18
		AN	1.12	2.20
		SF	1.25	1.96
		SG	1.33	2.41
		NG	1.25	2.59
		SL	1.21	2.35

Table 4. Summary of eel fishery F_{50} and $F_{extinct}$ values calculated assuming independent zones for use in simulations.

Density Model	**Zone**	F_{50}	$F_{extinct}$
Elver DD	AS	0.0976	0.528
	AC	0.0890	0.587
	AN	0.125	1.08
	SF	0.153	1.15
	SG	0.0832	0.773

Density Model	**Zone**	F_{50}	$F_{extinct}$
	NG	0.0810	0.777
	SL	0.0682	0.638
Elver + Silv. DD	AS	0.105	0.463
	AC	0.101	0.51
	AN	0.133	0.727
	SF	0.174	0.860
	SG	0.105	0.589
	NG	0.110	0.579
	SL	0.0906	0.540
Elver + Silv. + Mort. DD	AS	0.118	0.469
	AC	0.115	0.497
	AN	0.162	0.691
	SF	0.224	0.942
	SG	0.129	0.552
	NG	0.130	0.568
	SL	0.109	0.516

125 YEAR VISUALIZATION

Which leptocephali survival and dispersal mechanisms were used affected the initial meta-population stable state distribution (Figure 3; Supplemental Data 1). When a shared leptocephali survival was used, the AS zone population often was the largest zone, though when the dispersal was the 90% maternal effects scenario the SL zone was the largest by far. When each zone had its own, unique leptocephali survival, NG consistently had the largest population, and in general the zone abundances were more similar. While the Infilling and Water Attraction scenarios had similar initial conditions, their behaviour changed under different fishing conditions. Notably, after anthropogenic mortality was applied, the more northern zones like SL and NG had smaller final population sizes in the Infilling scenarios than the Water Attraction scenarios.

While the behaviour of the scenarios were different, the overall trends between them were similar. When eel were fished at their F_{50}, the number of silver eel declined quickly and stabilized (Figure 3; Supplemental Data 1). In 1975, when turbine mortality was introduced to the simulation in the SL zone, the number of silver eel in the SL decreased. In 2000, introduction of elver fisheries in the AN and SF zone largely affected just those zones. These overall trends were consistent regardless of the density-dependent mechanisms in the model, and the timing of elver density-dependence (Supplemental Data 1).

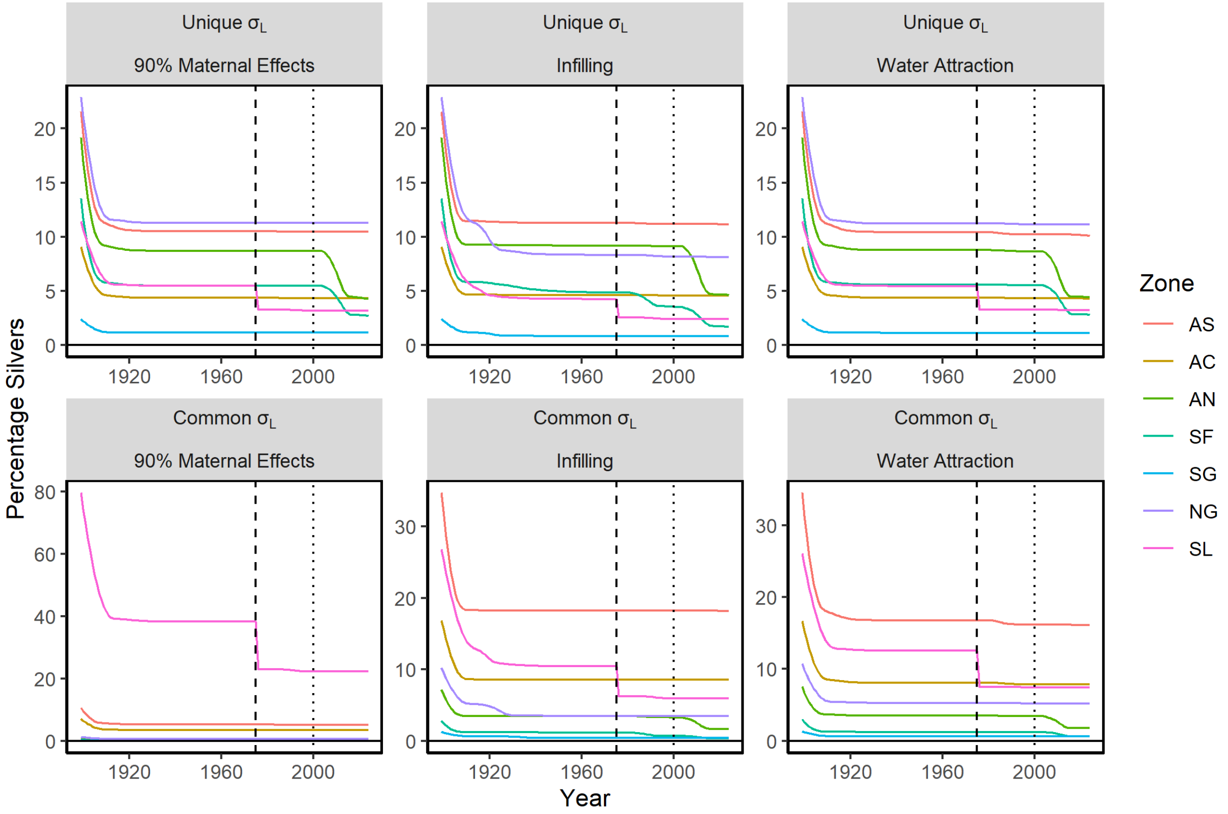

Figure 3. Silver eel relative percentage when eel are fished at F_{50}, with the "Elver DD" density-dependent model. This simulation assumes the elver density-dependence occurs before the elver fishery, when applicable. The dashed line shows when turbine mortality was introduced to the SL zone; the dotted line shows when elver fisheries began operating in the AN and SF zones.

MANAGING ZONES AT F_{50}

Under most scenarios, managing the meta-population using F_{50} values calculated from independent populations results in a total meta-population ESC at or near 50%, especially when density-dependence was only in the elver survival. For elver fisheries, when density-dependence occurs before the fishery, the ESC values were almost all at 50%, with the exception of the Infilling dispersal assumption (Table 5; Figure 4). Under the Infilling assumption, the four most northern zones (SL, NG, SG and SF) are consistently below their target (Figure 5). On the other hand, the ESC values are much more variable when the density-dependence in elver survival occurs after the fishery (Table 6, Figure 6). Under this assumption, the total meta-population ESC was as low as 0% in most of the dispersal and leptocephali survival assumptions (Figure 6). The variance around the ESC for individual zones was very high, though they do show the same overall trends as when density-dependence happens before the fishery (Figure 7).

Eel fisheries were more variable than the elver fishery when density-dependence occurs before the fishery, but not as variable as elver fisheries when the density-dependence occurs after the fishery. Again, the Infilling dispersal assumption had the lowest total meta-population ESC values (Figure 8), and the most northern zones were consistently below their target (Figure 9). However, the ESC values also tended to be lower than their target in zones AN and SF when fished at their eel F_{50} (Table 7; Figure 9). For all fisheries, variability in the outputs increased as more density-dependent mechanisms were included in the model, and the ESC values in northern zones under the Infilling dispersal mechanism tended to be smaller (Supplemental Data 2).

For most leptocephali survival and dispersal assumptions, there were no large differences between zone-specific outputs (e.g. the SG zone did not behave differently than the NG zone), with the exception of AN and SF being consistently below their target for eel fisheries. However, under the Infilling dispersal assumption, the ESC values of the northern zones SL, NG, SG and SF were consistently lower compared to the other zones (Figure 5, 7 and 9). This pattern occurred for both eel and elver fishing, and for all density-dependent mechanisms (Supplementary Data 2). Therefore, under the Infilling dispersal assumption, fishing all zones using F_{50} values calculated assuming independent populations is particularly unlikely to result in 50% silver escapement in the northern part of American Eel range.

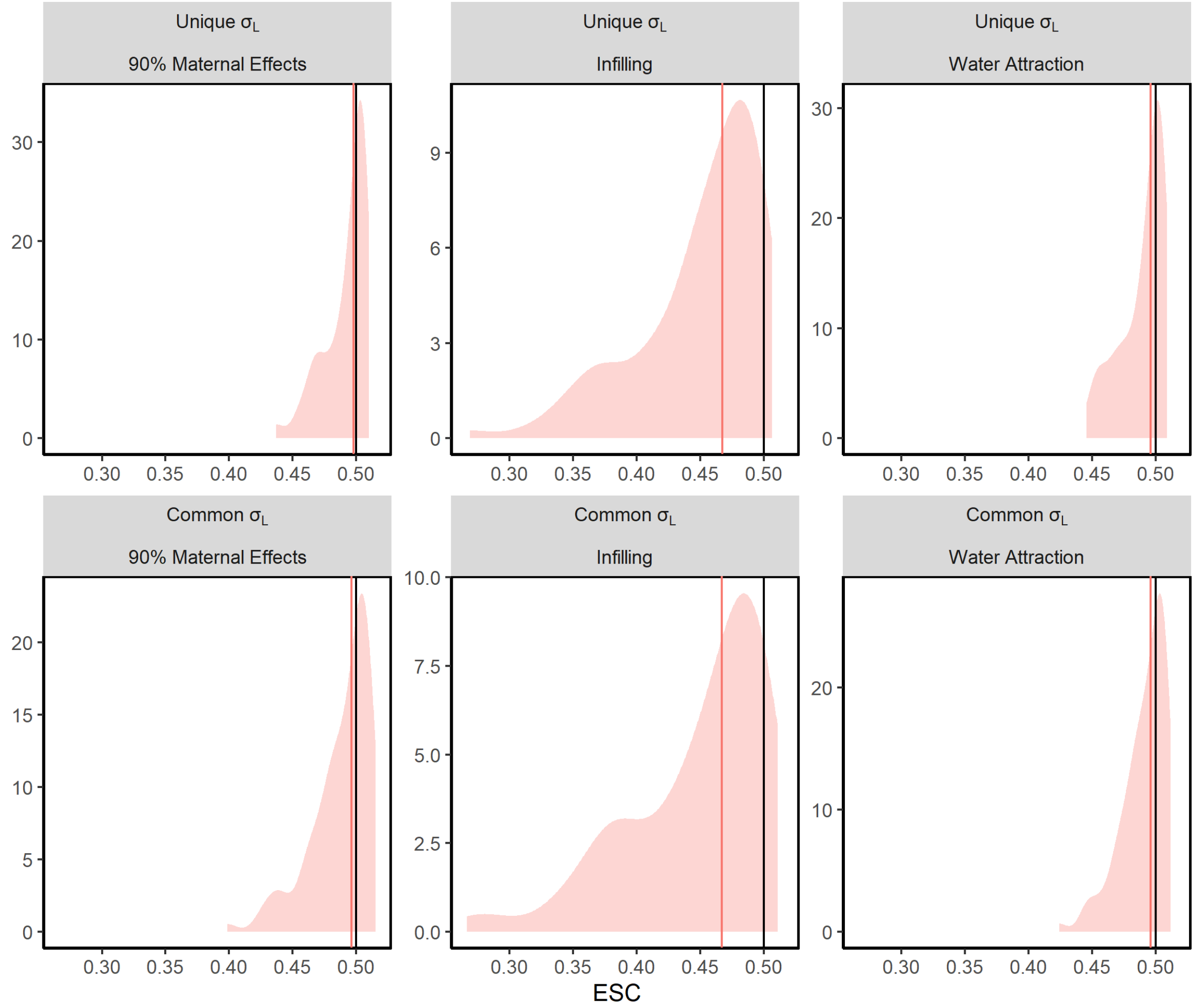

Figure 4. Distribution of ESC values for the entire meta-population when each zone is fished at its elver F_{50} when the density-dependent model is “Elver DD”, and the density-dependence occurs before fishing. The solid black line is the target of ESC_{50}, and the solid red line is the median of the distribution.

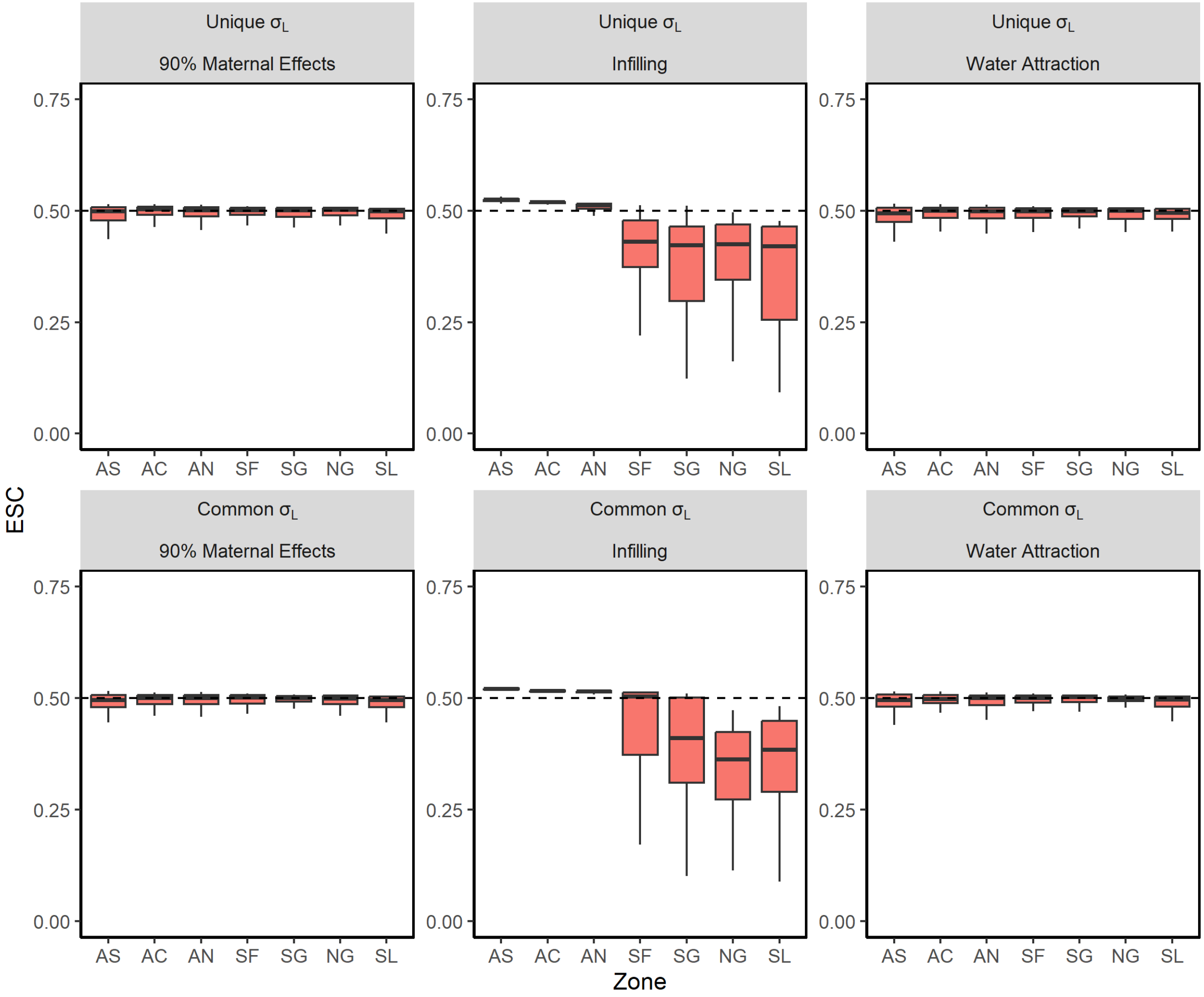

Figure 5. Distribution of ESC values of each zone, when each zone is fished at its elver F_{50} *when the density-dependent model is "Elver DD" and the density-dependence occurs before fishing.*

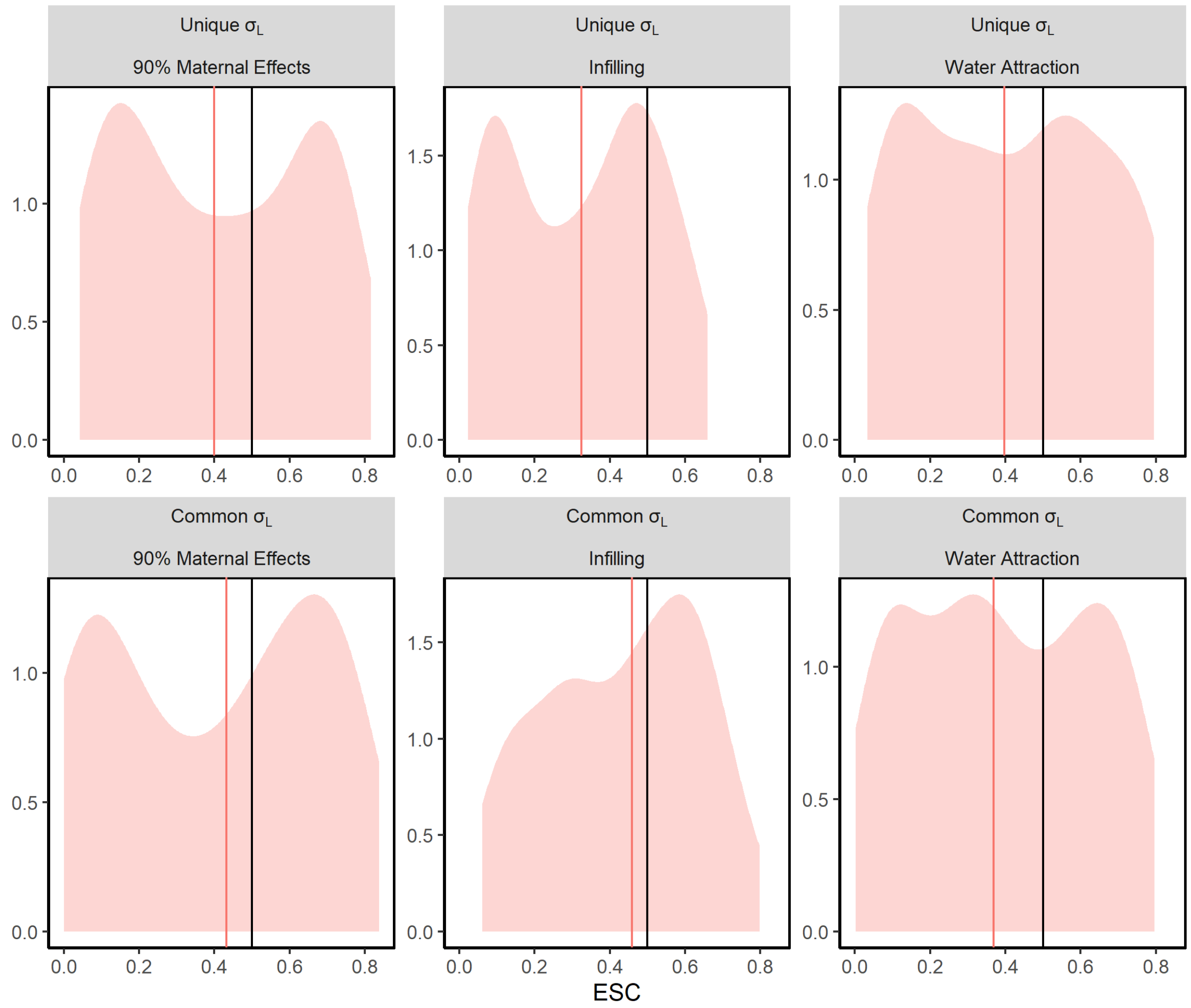

Figure 6. Distribution of ESC values for the entire meta-population when each zone is fished at its elver F_{50} when the density-dependent model is "Elver DD", and the density-dependence occurs after fishing. The solid black line is the target of ESC_{50}, and the solid red line is the median of the distribution.

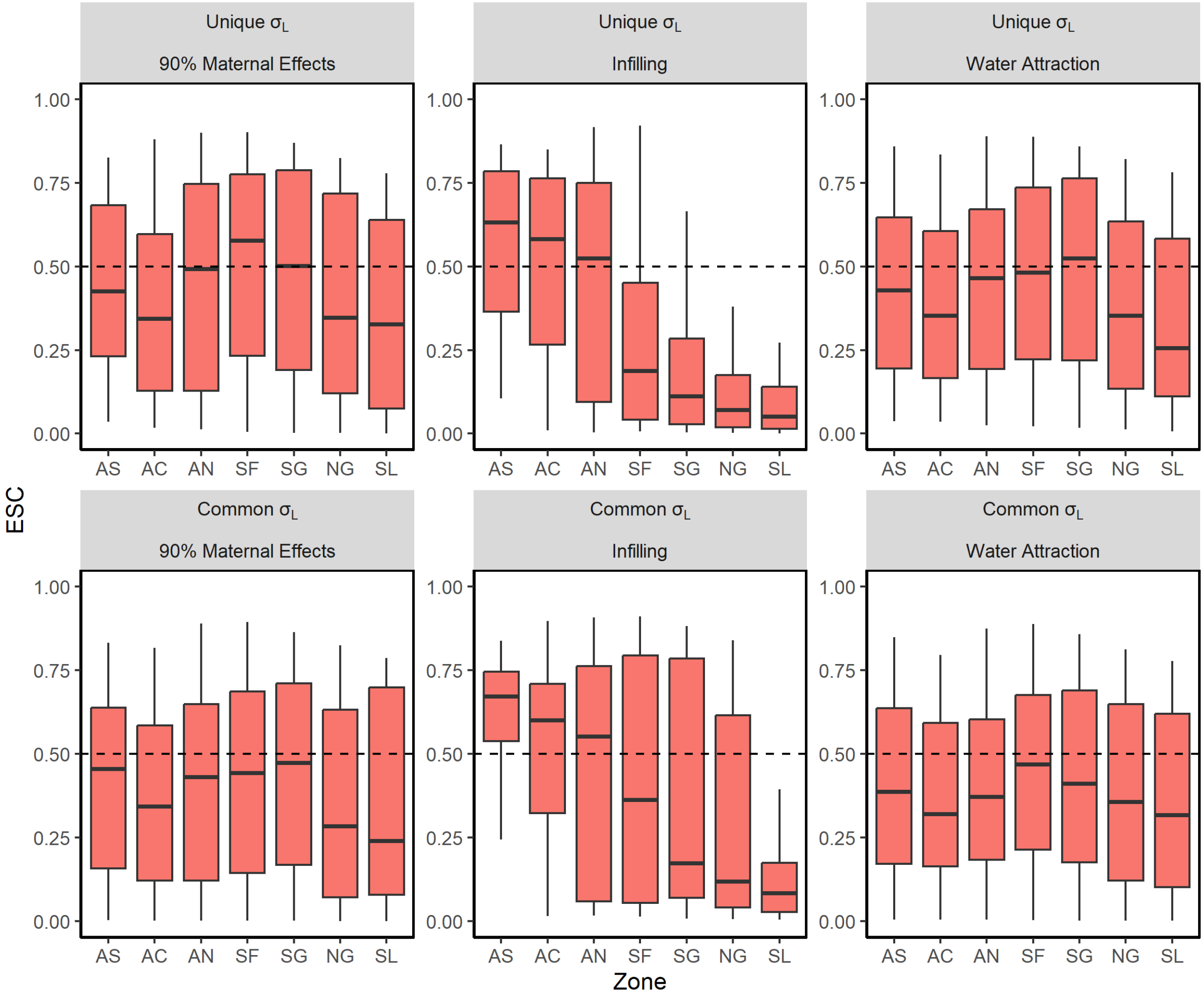

Figure 7. Distribution of ESC values of each zone, when each zone is fished at its elver F_{50} when the density-dependent model is “Elver DD” and the density-dependence occurs after fishing.

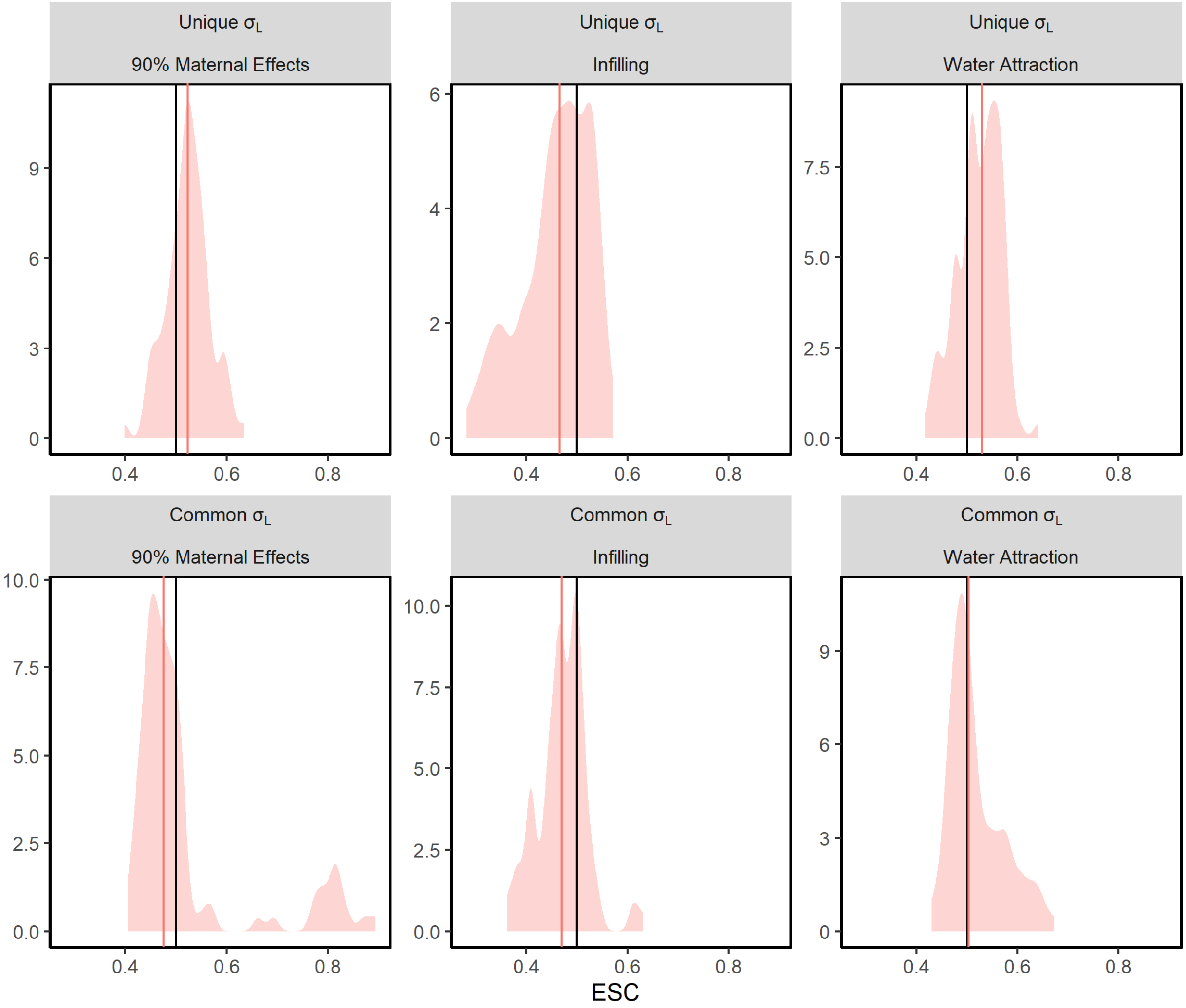

Figure 8. Distribution of ESC values for the entire meta-population when each zone is fished at its eel F_{50} when the density-dependent model is "Elver DD". The solid black line is the target of ESC_{50}, and the solid red line is the median of the distribution.

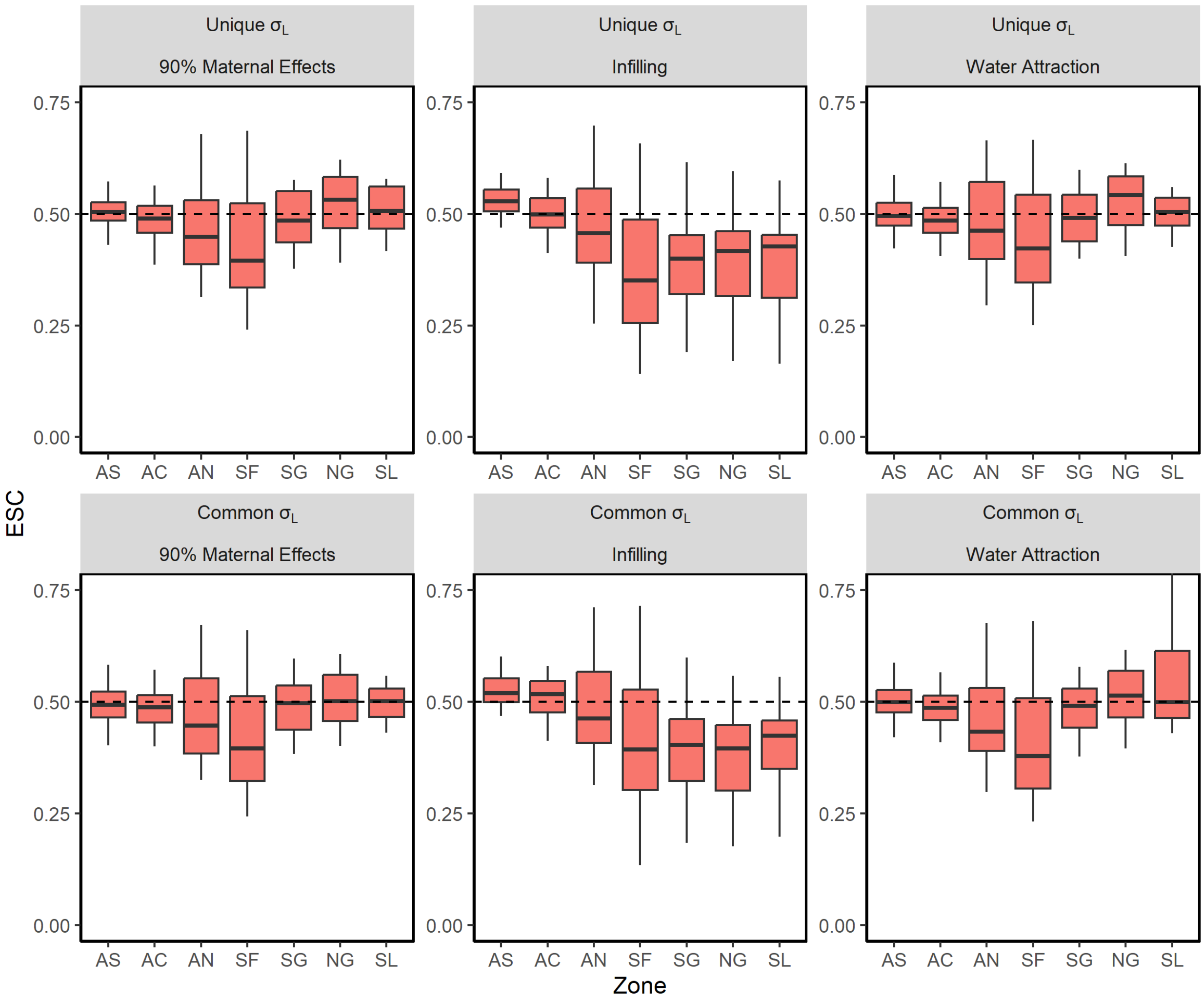

Figure 9. Distribution of ESC values of each zone, when each zone is fished at its eel F_{50} when the density-dependent model is "Elver DD".

Table 5. Median outputs across zones when elver fisheries were fished at F_{50} for 50 years. These results assume the density-dependence occurs before the fishery. The "Total" zone refers to the meta-population as a whole. Italicised values are 5% below their target; bold values are 10% below their target.

			Elver DD	**Elver + Silv. DD**	**Elver + Silv. + Mort. DD**
Survival	**Distribution**	**Zone**	***ESC***	***ESC***	***ESC***
Unique Leptocephali Survival	90% maternal effects	Total	0.50	0.49	0.50
		AS	0.50	0.49	0.46
		AC	0.50	0.50	0.49
		AN	0.50	0.50	0.48
		SF	0.50	0.48	0.55
		SG	0.50	0.48	*0.44*
		NG	0.50	0.48	0.50
		SL	0.50	0.49	0.45
	Water Attraction	Total	0.50	0.49	0.49
		AS	0.49	0.49	0.48
		AC	0.50	0.49	0.48

			Elver DD	**Elver + Silv. DD**	**Elver + Silv. + Mort. DD**
Survival	**Distribution**	**Zone**	***ESC***	***ESC***	***ESC***
		AN	0.50	0.49	0.47
		SF	0.50	0.49	0.52
		SG	0.50	0.47	*0.44*
		NG	0.50	0.46	0.49
		SL	0.49	0.48	*0.44*
	Infilling	Total	0.47	***0.37***	***0.38***
		AS	0.52	0.53	0.51
		AC	0.52	0.53	0.53
		AN	0.51	0.50	0.49
		SF	*0.43*	***0.22***	***0.22***
		SG	*0.42*	***0.23***	***0.18***
		NG	*0.43*	***0.22***	***0.20***
		SL	*0.42*	***0.23***	***0.19***
Common Leptocephali Survival	90% maternal effects	Total	0.50	0.48	*0.42*
		AS	0.50	0.49	*0.45*
		AC	0.50	0.50	0.46
		AN	0.50	0.49	0.48
		SF	0.50	0.48	0.48
		SG	0.50	0.48	*0.42*
		NG	0.50	0.46	0.46
		SL	0.50	0.49	*0.42*
	Water Attraction	Total	0.50	0.48	*0.45*
		AS	0.50	0.49	0.46
		AC	0.50	0.50	0.48
		AN	0.50	0.49	0.50
		SF	0.50	0.48	0.50
		SG	0.50	0.47	0.46
		NG	0.50	0.48	0.49
		SL	0.50	0.49	*0.44*
	Infilling	Total	0.47	*0.41*	***0.37***
		AS	0.52	0.53	0.51
		AC	0.52	0.53	0.51
		AN	0.51	0.51	***0.40***
		SF	0.50	***0.22***	***0.17***
		SG	*0.41*	***0.20***	***0.15***
		NG	***0.36***	***0.21***	***0.15***
		SL	***0.38***	***0.26***	***0.17***

Table 6. Median outputs across zones when elver fisheries were fished at F_{50} for 50 years. These results assume the density-dependence occurs after the fishery. The "Total" zone refers to the meta-population as a whole. Italicised values are 5% below their target; bold values are 10% below their target.

			Elver DD	**Elver + Silv. DD**	**Elver + Silv. + Mort. DD**
Survival	**Distribution**	**Zone**	***ESC***	***ESC***	***ESC***
Unique Leptocephali Survival	90% maternal effects	Total	*0.40*	0.50	0.47
		AS	*0.43*	*0.42*	*0.45*
		AC	***0.34***	0.47	0.55
		AN	0.49	0.65	0.60
		SF	0.58	0.51	0.61
		SG	0.50	*0.44*	***0.34***
		NG	***0.35***	0.49	***0.38***
		SL	***0.33***	0.51	***0.34***
	Water Attraction	Total	*0.40*	0.52	*0.44*
		AS	*0.43*	0.49	0.47
		AC	***0.35***	0.55	0.50
		AN	0.46	0.62	0.51
		SF	0.48	0.53	0.57
		SG	0.52	0.51	0.48
		NG	***0.35***	0.49	***0.37***
		SL	***0.26***	0.51	***0.34***
	Infilling	Total	***0.32***	***0.40***	***0.26***
		AS	0.63	0.63	0.59
		AC	0.58	0.67	0.59
		AN	0.52	0.73	*0.43*
		SF	***0.19***	***0.15***	***0.083***
		SG	***0.11***	***0.10***	***0.050***
		NG	***0.07***	***0.083***	***0.033***
		SL	***0.05***	***0.087***	***0.039***
Common Leptocephali Survival	90% maternal effects	Total	*0.43*	0.46	***0.32***
		AS	*0.45*	*0.44*	*0.43*
		AC	***0.34***	*0.44*	0.50
		AN	*0.43*	0.59	***0.40***
		SF	*0.44*	*0.41*	***0.40***
		SG	0.47	*0.45*	*0.44*
		NG	***0.28***	0.46	***0.31***
		SL	***0.24***	0.48	***0.25***
	Water Attraction	Total	***0.37***	*0.45*	***0.36***
		AS	***0.39***	*0.45*	***0.38***
		AC	***0.32***	0.47	***0.39***
		AN	***0.37***	0.54	*0.42*
		SF	0.47	*0.43*	*0.42*
		SG	*0.41*	*0.45*	***0.35***
		NG	***0.36***	*0.45*	***0.34***
		SL	***0.32***	*0.43*	***0.25***
	Infilling	Total	0.46	*0.43*	*0.43*
		AS	0.67	0.62	0.65
		AC	0.60	0.65	0.67
		AN	0.55	0.72	0.64
		SF	***0.36***	***0.17***	***0.12***
		SG	***0.17***	***0.12***	***0.094***
		NG	***0.12***	***0.072***	***0.048***

			Elver DD	**Elver + Silv. DD**	**Elver + Silv. + Mort. DD**
Survival	**Distribution**	**Zone**	***ESC***	***ESC***	***ESC***
		SL	***0.083***	***0.084***	***0.051***

Table 7. Median outputs across zones when eel fisheries were fished at F_{50} for 50 years. The "Total" zone refers to the meta-population as a whole. Italicised values are 5% below their target; bold values are 10% below their target.

			Elver DD	**Elver + Silv. DD**	**Elver + Silv. + Mort. DD**
Survival	**Distribution**	**Zone**	***ESC***	***ESC***	***ESC***
Unique Leptocephali Survival	90% maternal effects	Total	0.52	0.52	0.52
		AS	0.50	0.50	0.49
		AC	*0.49*	0.49	0.51
		AN	*0.45*	0.48	0.50
		SF	***0.39***	*0.45*	*0.44*
		SG	*0.48*	0.50	0.51
		NG	0.53	0.48	0.51
		SL	0.51	0.50	0.51
	Water Attraction	Total	0.53	0.51	0.51
		AS	0.49	0.51	0.49
		AC	0.48	0.50	0.51
		AN	0.46	0.48	0.47
		SF	*0.42*	*0.44*	*0.42*
		SG	0.49	0.51	0.49
		NG	0.54	0.48	0.51
		SL	0.50	0.51	0.50
	Infilling	Total	0.47	*0.41*	*0.43*
		AS	0.53	0.53	0.52
		AC	0.50	0.52	0.53
		AN	0.46	0.48	0.49
		SF	***0.35***	***0.25***	***0.22***
		SG	***0.40***	***0.29***	***0.31***
		NG	*0.42*	***0.28***	***0.31***
		SL	*0.43*	***0.29***	***0.32***
Common Leptocephali Survival	90% maternal effects	Total	0.48	0.49	0.48
		AS	0.49	0.50	0.50
		AC	0.49	0.50	0.51
		AN	*0.45*	0.48	0.48
		SF	***0.40***	*0.45*	*0.41*
		SG	0.50	0.50	0.48
		NG	0.50	0.48	0.51
		SL	0.50	0.50	0.51
	Water Attraction	Total	0.50	0.51	0.50
		AS	0.50	0.50	0.51
		AC	0.49	0.50	0.49
		AN	*0.43*	0.49	0.50
		SF	***0.38***	0.46	***0.40***
		SG	0.49	0.50	0.50
		NG	0.51	0.50	0.50
		SL	0.50	0.50	0.51
	Infilling	Total	0.47	*0.44*	*0.45*
		AS	0.52	0.53	0.53

			Elver DD	**Elver + Silv. DD**	**Elver + Silv. + Mort. DD**
Survival	**Distribution**	**Zone**	***ESC***	***ESC***	***ESC***
		AC	0.52	0.52	0.52
		AN	0.46	0.52	0.47
		SF	***0.39***	***0.31***	***0.30***
		SG	***0.40***	***0.28***	***0.31***
		NG	***0.40***	***0.28***	***0.30***
		SL	*0.42*	***0.32***	***0.33***

EXCESS MORTALITY

The results of excess mortality on the eel and elver stages showed similar patterns in total population ESC values (Figures 10, 13, and 16). When the number of zones experiencing excess mortality increased, the meta-population wide ESC decreased. While the medians varied among density-dependent mechanism (Supplemental Data 2), the trends were similar. Assumptions about leptocephali survival and dispersal affected the rate and variability of the declines. The Infilling and Water Attraction dispersal scenarios mostly declined linearly, while the 90% maternal effect scenario had a plateau effect when a common leptocephali survival parameter was used (Figures 10, 13, and 16). Under this assumption, when only a few zones were subject to excess mortality (i.e. 1-3), the median ESC values did not change dramatically (Figure 16). As the number of zones subject to excess mortality increased, there was increased variability only after approximately two zones were impacted, which remained until all zones were impacted. This was likely caused by differences in which zones in particular were subject to the excess mortality.

The life stage impacted did not change the pattern in zone-specific ESC values (Figures 11, 12, 14, 15, 18 and 20). When only one zone faced excess mortality, there was little change to the median ESC values of the individual zones in general. However, when approximately two to five zones of the metapopulation were faced with excess mortality, most of the zones show a high degree of variability. As the number of zones that have excess mortality increases, it becomes more likely that any given zone faces the mortality, leading to the band of variation. Beyond approximately five zones facing excess mortality, the ESC of all the zones tend to decrease to be very small.

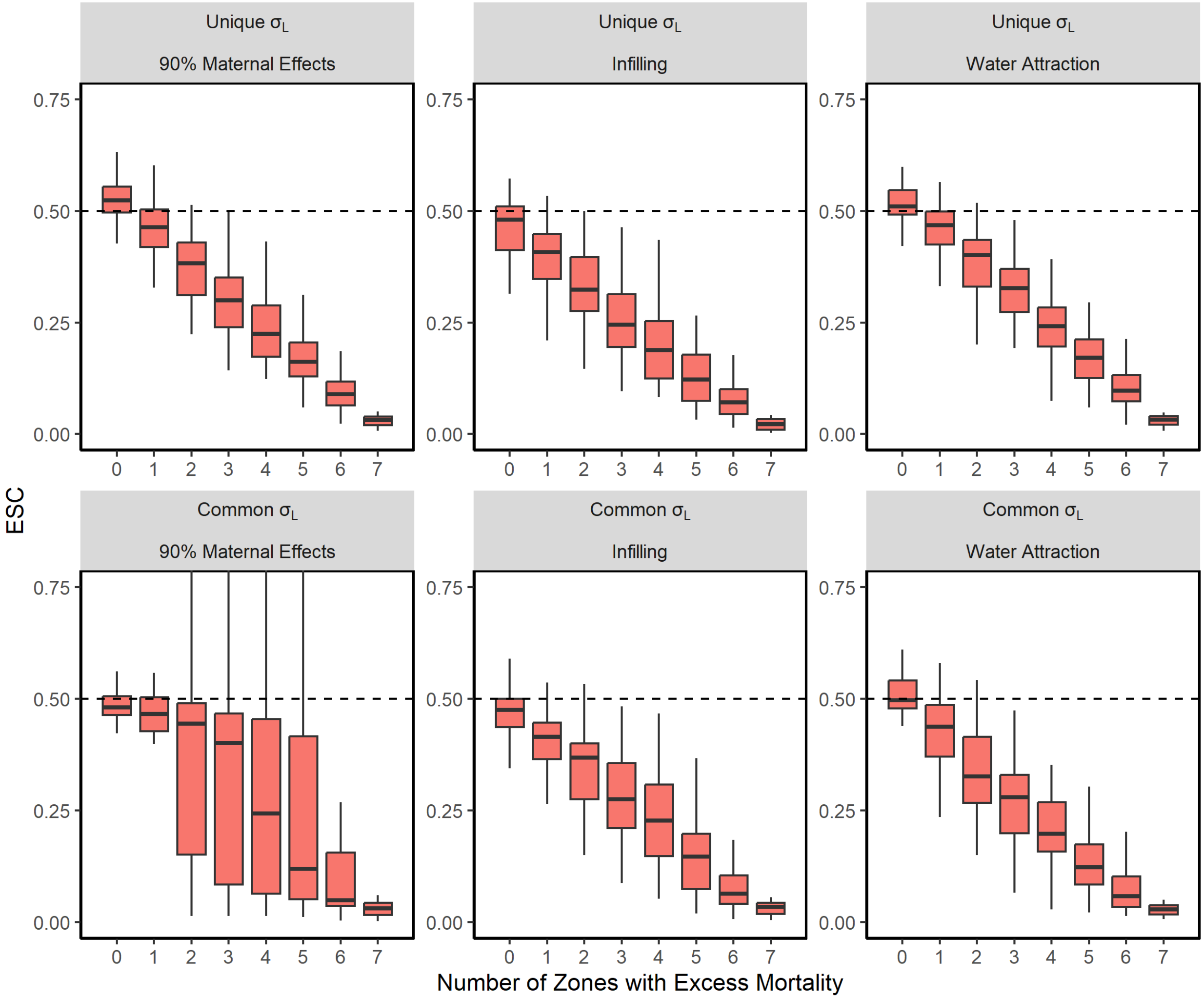

Figure 10. Effects of excess mortality on the elver stage on the total meta-population ESC values across different leptocephali survival and distribution options using the "Elver DD" density-dependent model. This simulation assumes that elver density-dependence happens before the elver fishery.

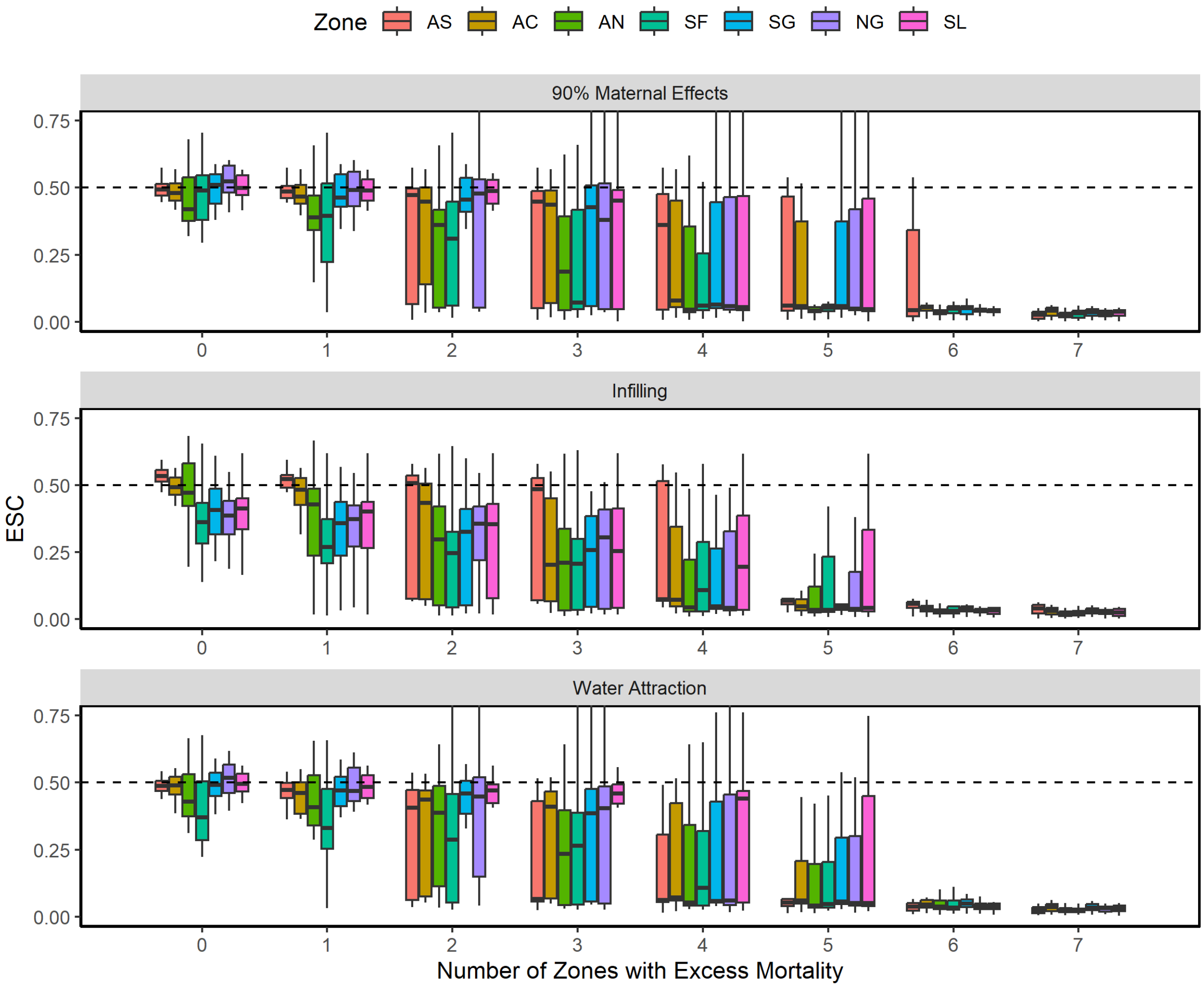

Figure 11. Effects of excess mortality on the elver stage on the zone meta-population ESC values assuming a common leptocephali survival and the "Elver DD" density-dependent model is used. This simulation assumes that elver density-dependence happens before the elver fishery.

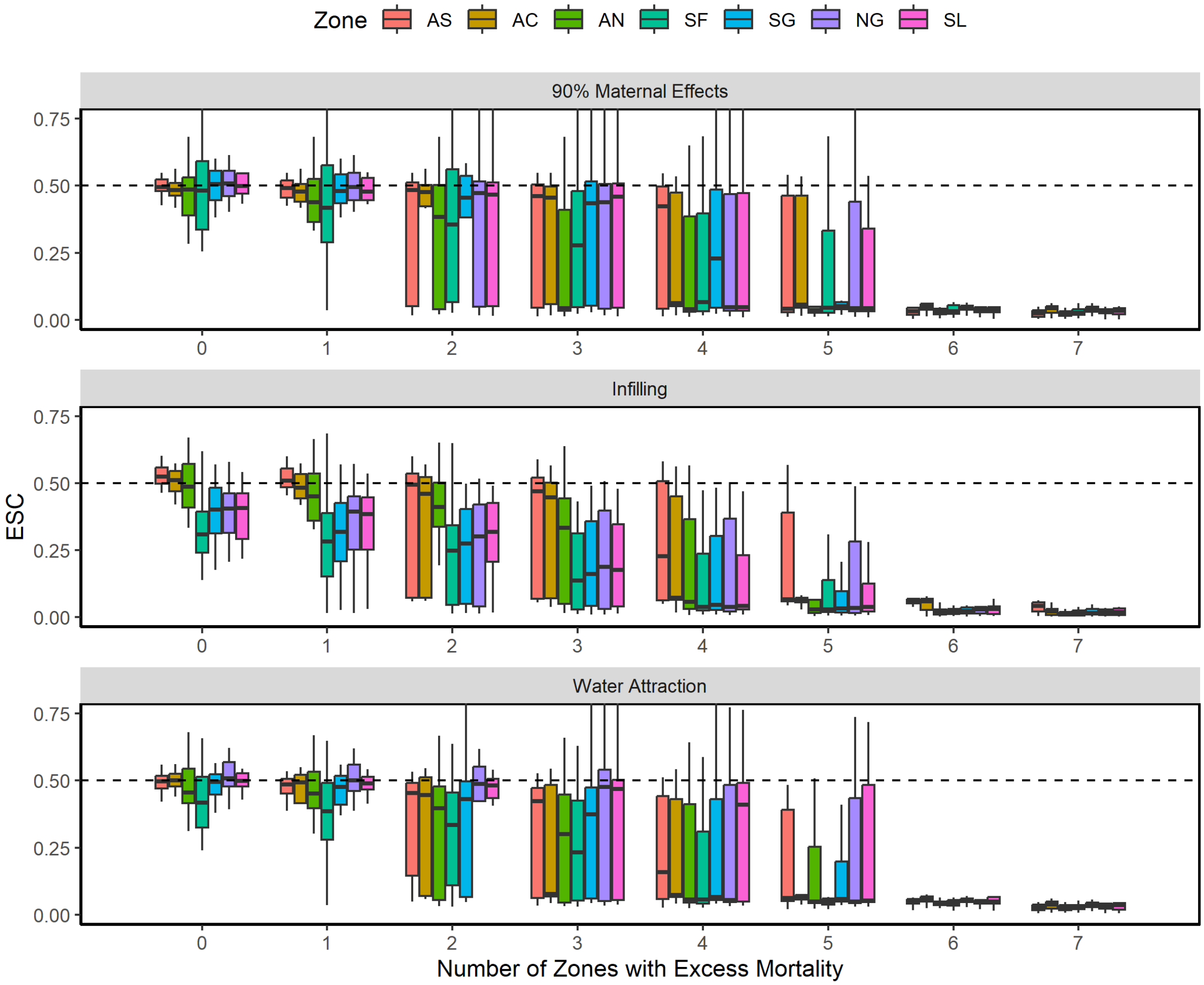

Figure 12. Effects of excess mortality on the elver stage on the zone meta-population ESC values assuming a each zone has a unique leptocephali survival and the “Elver DD” density-dependent model is used. This simulation assumes that elver density-dependence happens before the elver fishery.

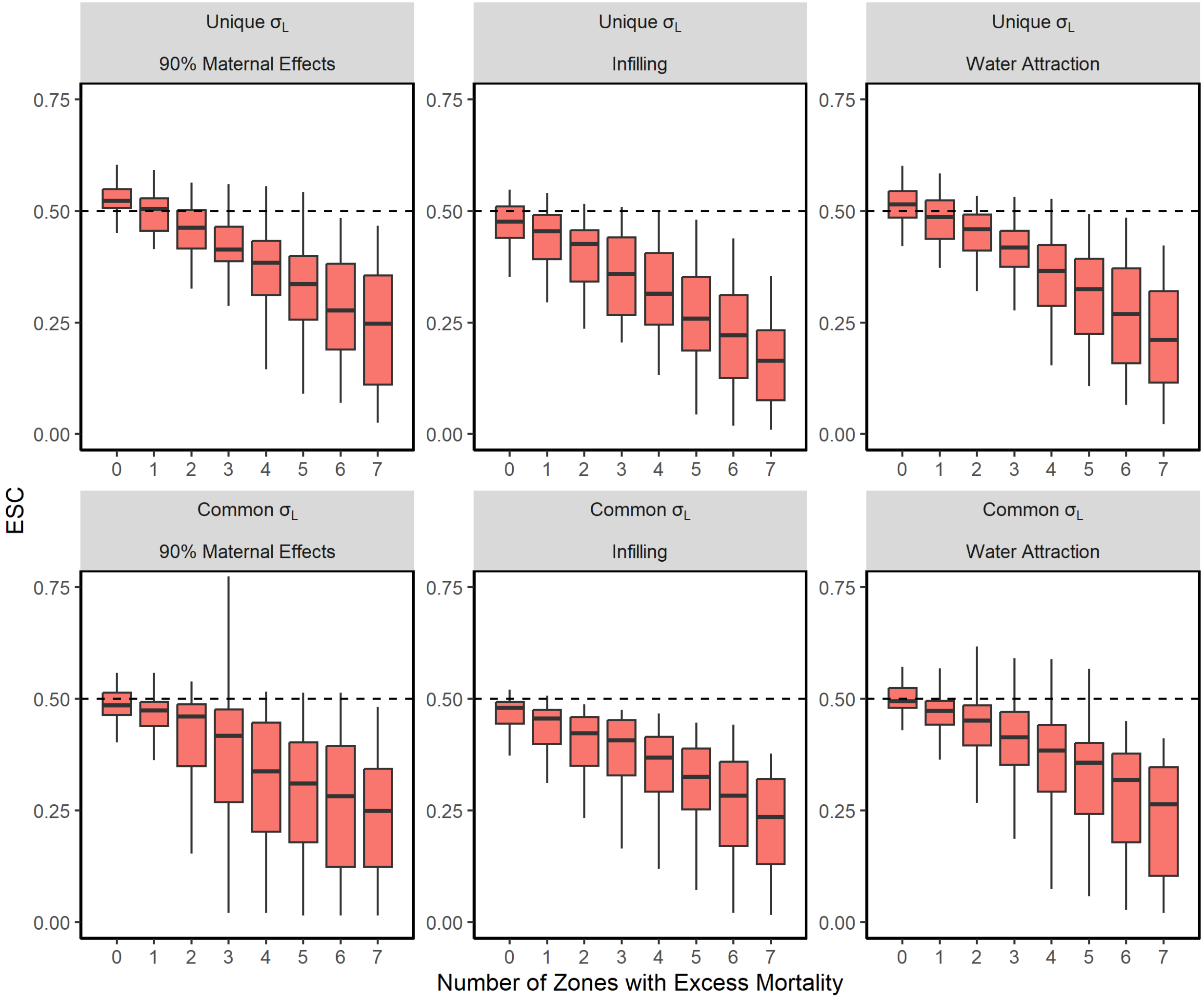

Figure 13. Effects of excess mortality on the elver stage on the total meta-population ESC values across different leptocephali survival and distribution options using the “Elver DD” density-dependent model. This simulation assumes that elver density-dependence happens after the elver fishery.

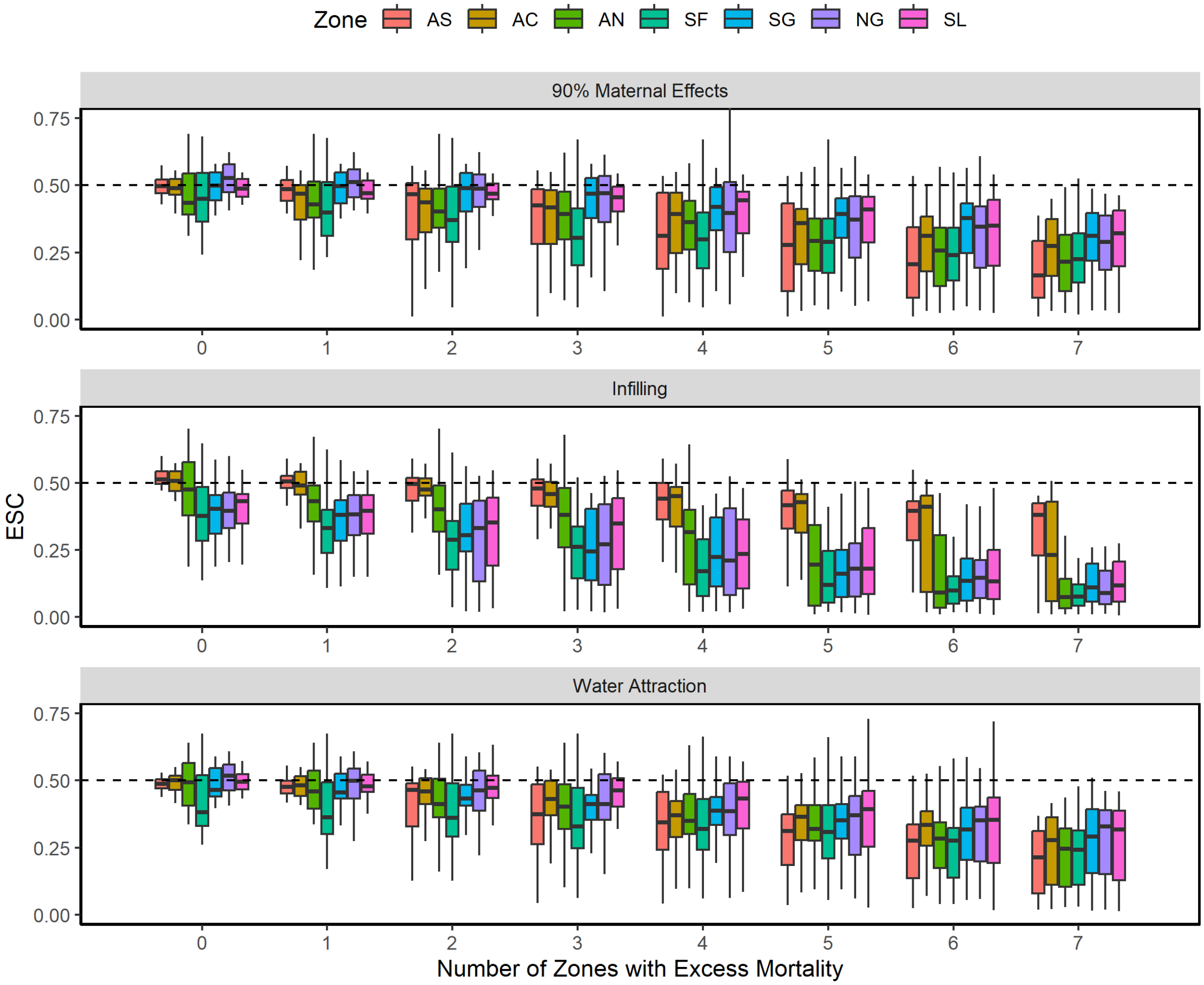

Figure 14. Effects of excess mortality on the elver stage on the zone meta-population ESC values assuming a common leptocephali survival and the “Elver DD” density-dependent model is used. This simulation assumes that elver density-dependence happens after the elver fishery.

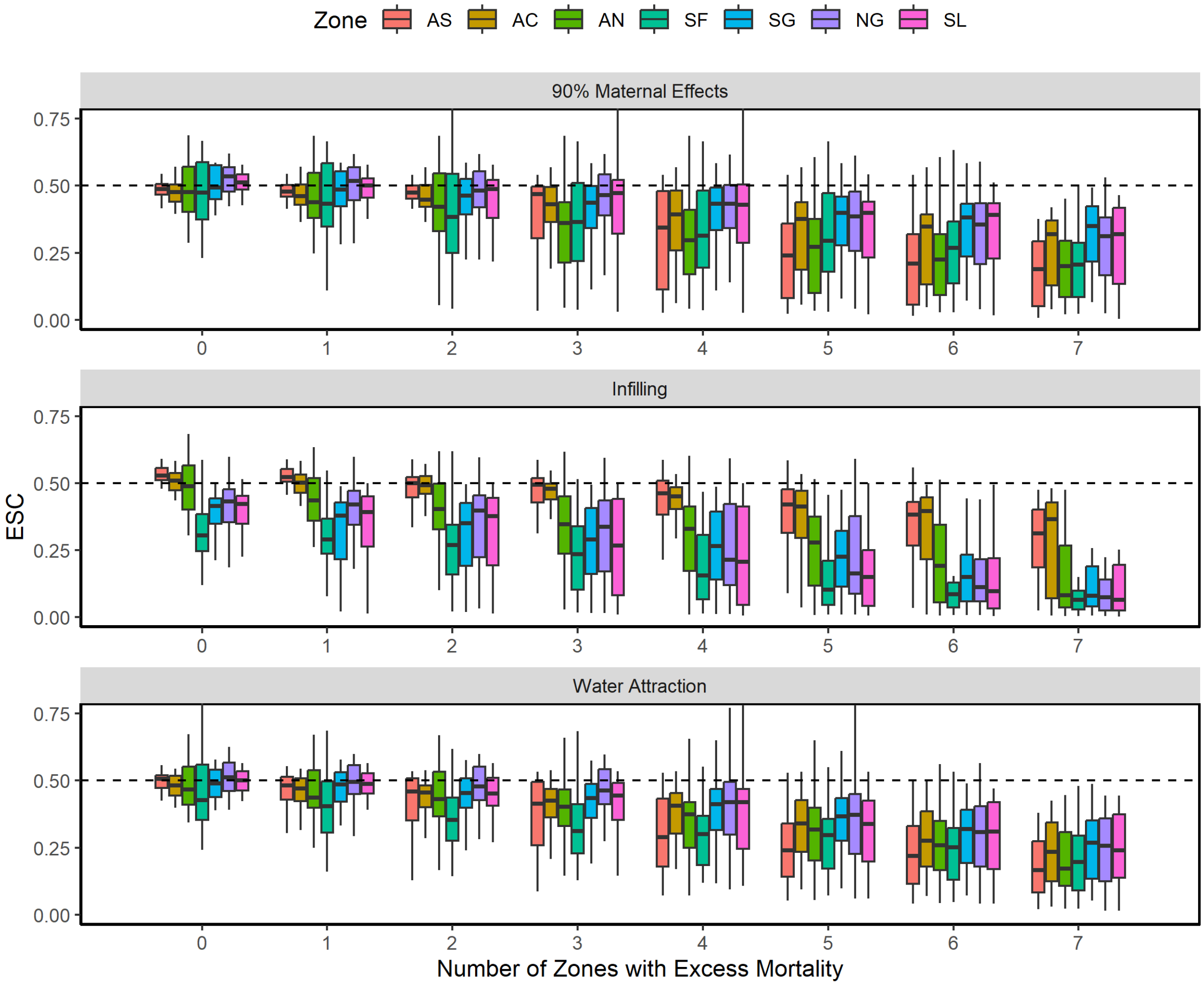

Figure 15. Effects of excess mortality on the elver stage on the zone meta-population ESC values assuming a each zone has a unique leptocephali survival and the “Elver DD” density-dependent model is used. This simulation assumes that elver density-dependence happens after the elver fishery.

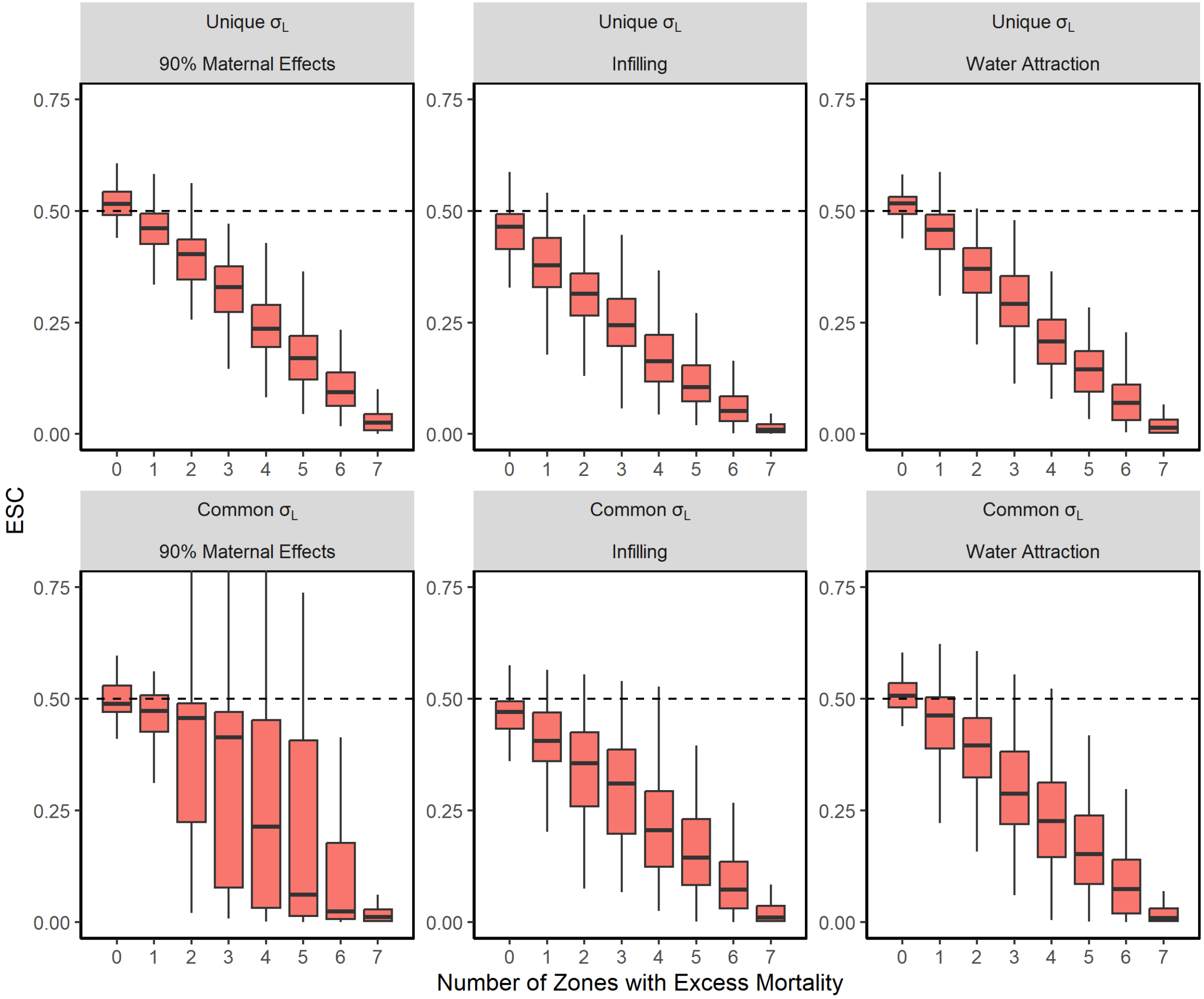

Figure 16. Effects of excess mortality on the eel stage on the total meta-population ESC values across different leptocephali survival and distribution options using the "Elver DD" density-dependent model.

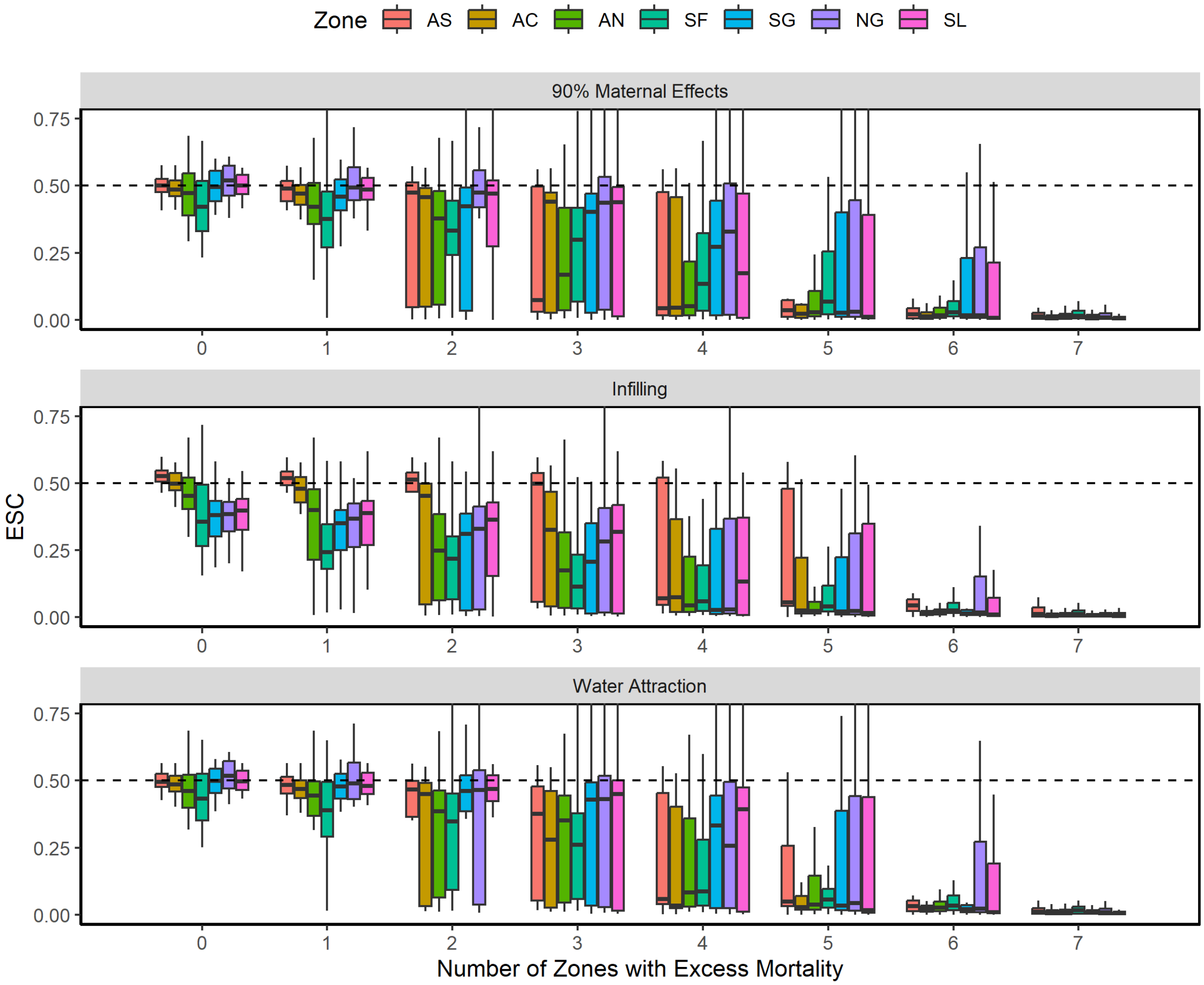

Figure 17. Effects of excess mortality on the eel stage on the zone meta-population ESC values assuming a common leptocephali survival and the "Elver DD" density-dependent model.

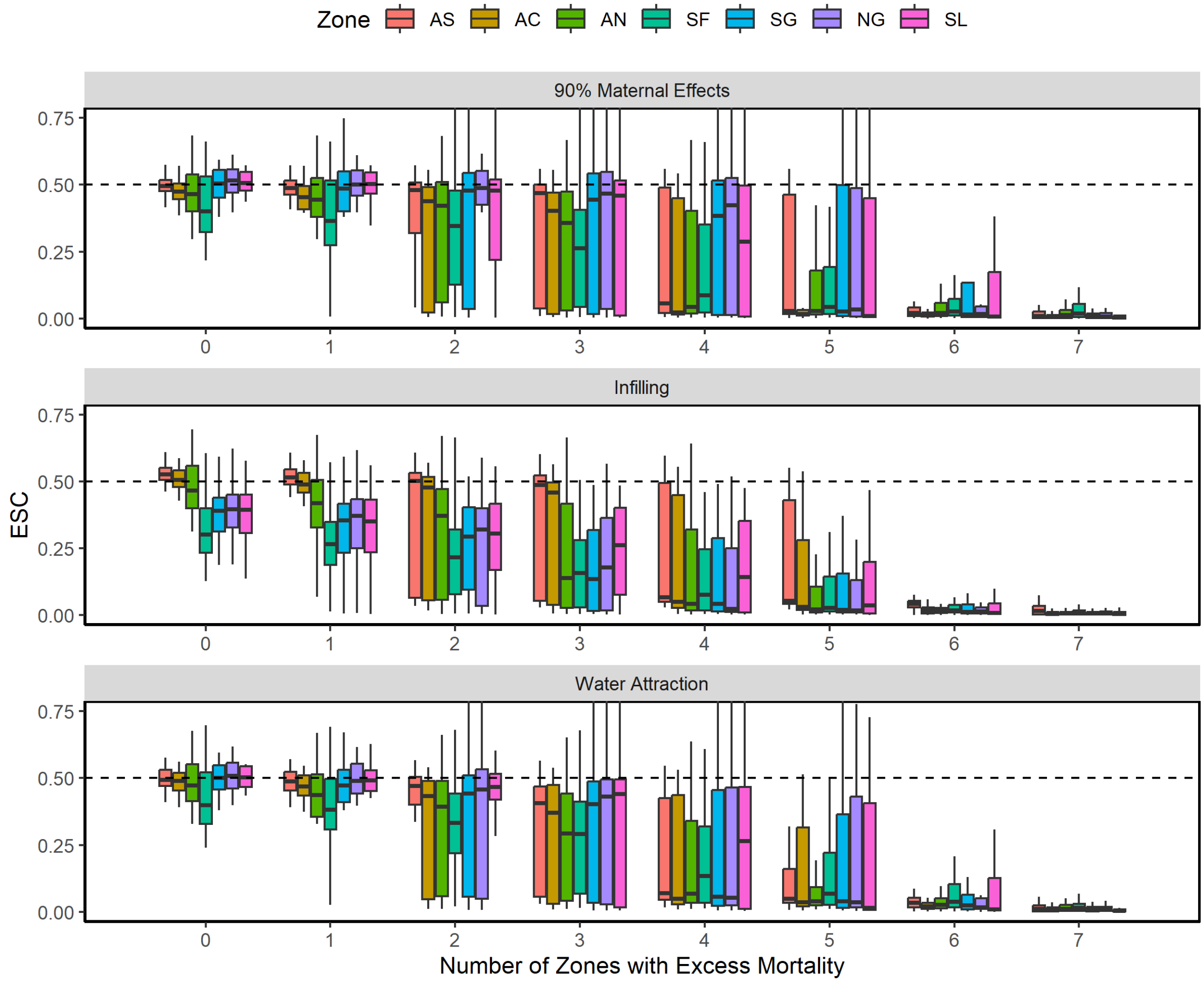

Figure 18. Effects of excess mortality on the eel stage on the zone meta-population ESC values assuming each zone has a unique leptocephali survival and the "Elver DD" density-dependent model.

RECOVERY

The recovery simulations showed similar outcomes to the excess mortality simulations but in reverse, regardless of density-dependent mechanisms or fishery type Figures 19 - 21, (Supplemental Data 2). As the number of zones experiencing excess mortality decreased (therefore more zones recovered), the ESC values for the total meta-population increased (Figures 19 - 21). The Infilling and Water Attraction dispersal scenarios generally had meta-population wide ESC increase linearly as the number of recovered zones increased, while the 90% maternal effects combined with a common leptocephali survival scenario often showed a non-linear pattern. Under that assumption, there was often large variability as the number of recovered zones increased before the population median jumped near its target of 50% ESC. When density-dependence occurred after the elver fishery (Figure 20), the resulting ESC was more variable and less steep, similar to what was seen in the excess mortality simulations (Figure 13).

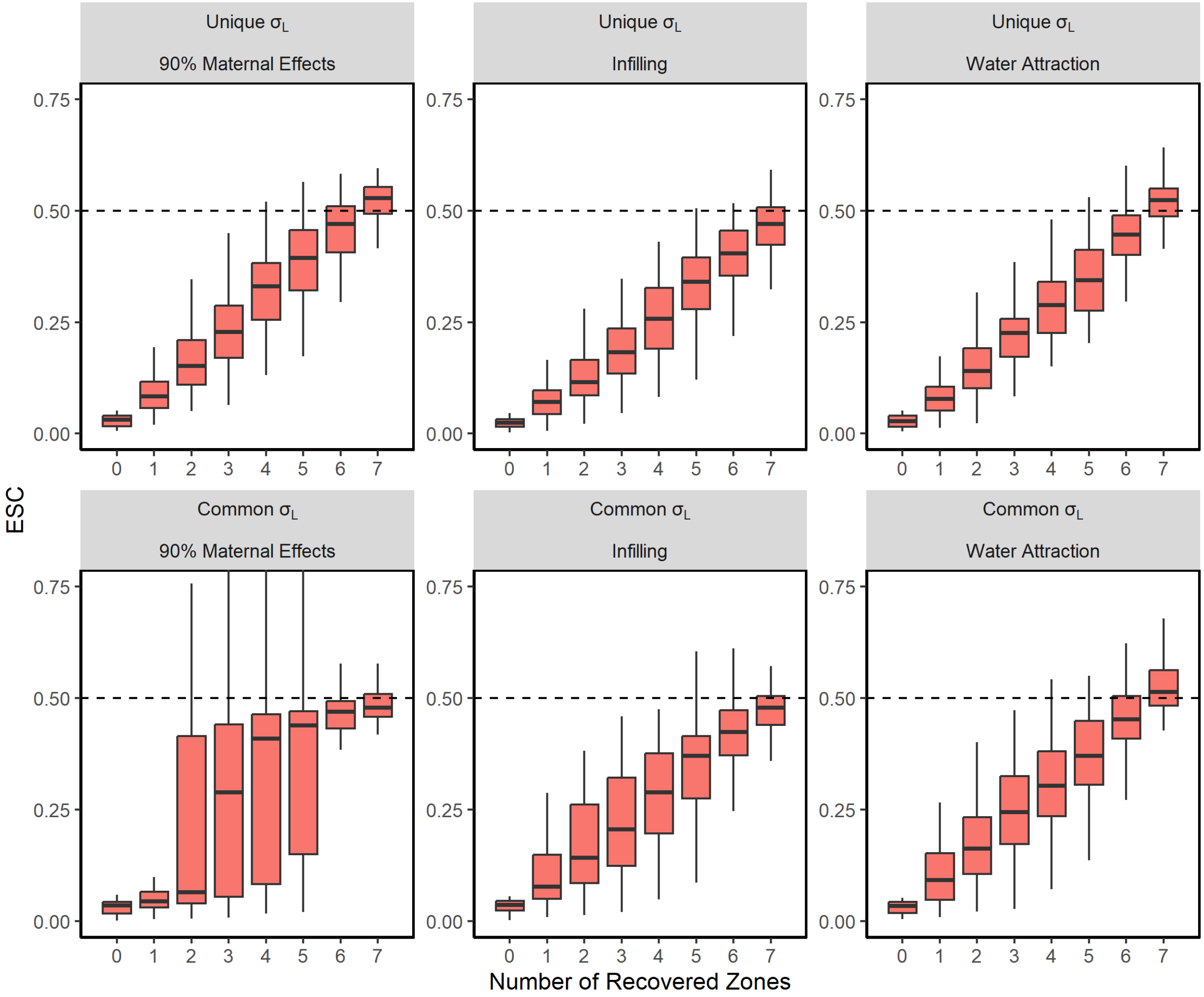

Figure 19. Effects of reducing excess mortality on the elver stage on the total meta-population ESC values across different leptocephali survival and distribution options using the "Elver DD" density-dependent model. This simulation assumes elver density-dependence occurs before the fishery.

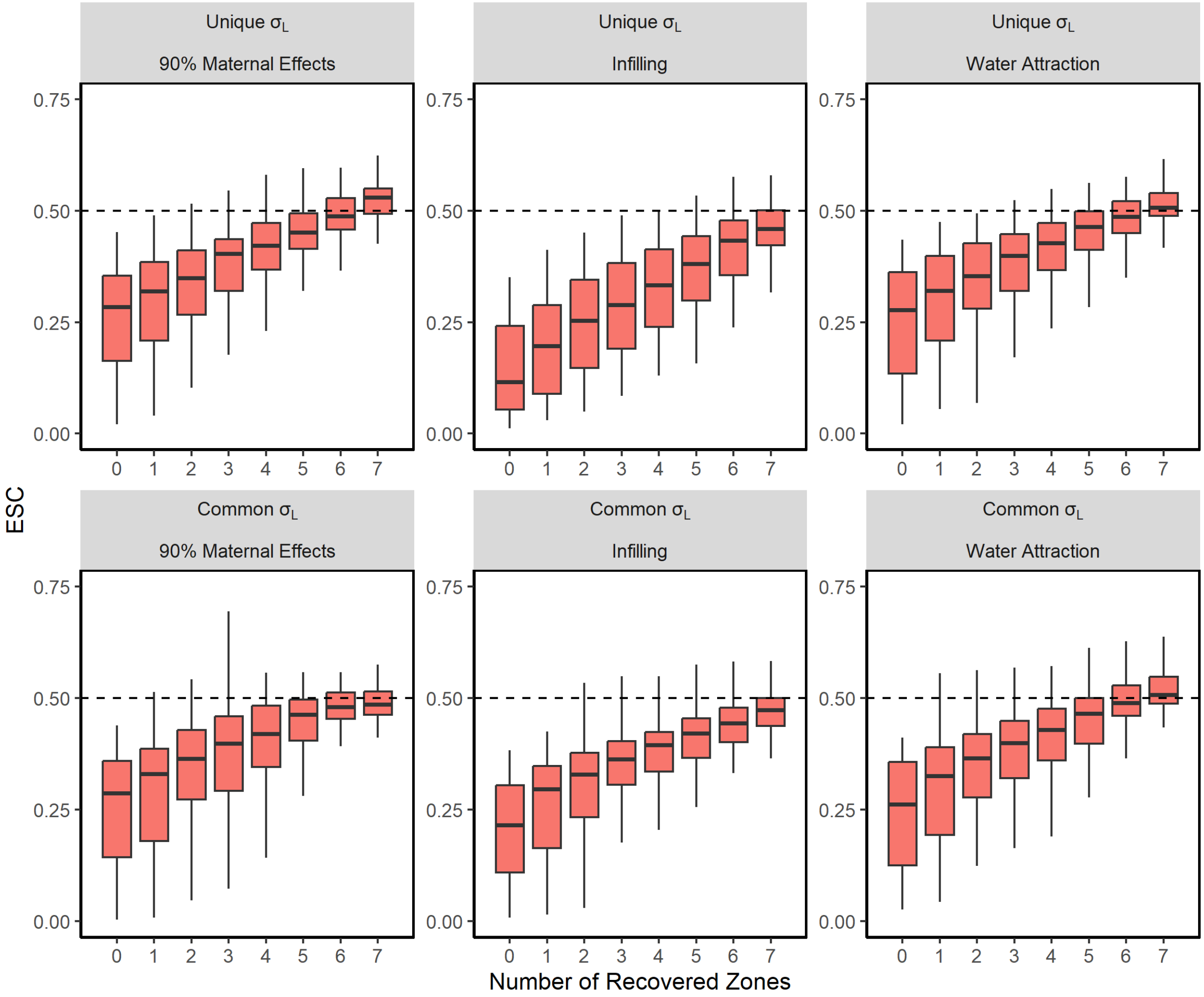

Figure 20. Effects of reducing excess mortality on the elver stage on the total meta-population ESC values across different leptocephali survival and distribution options using the "Elver DD" density-dependent model. This simulation assumes elver density-dependence occurs after the fishery.

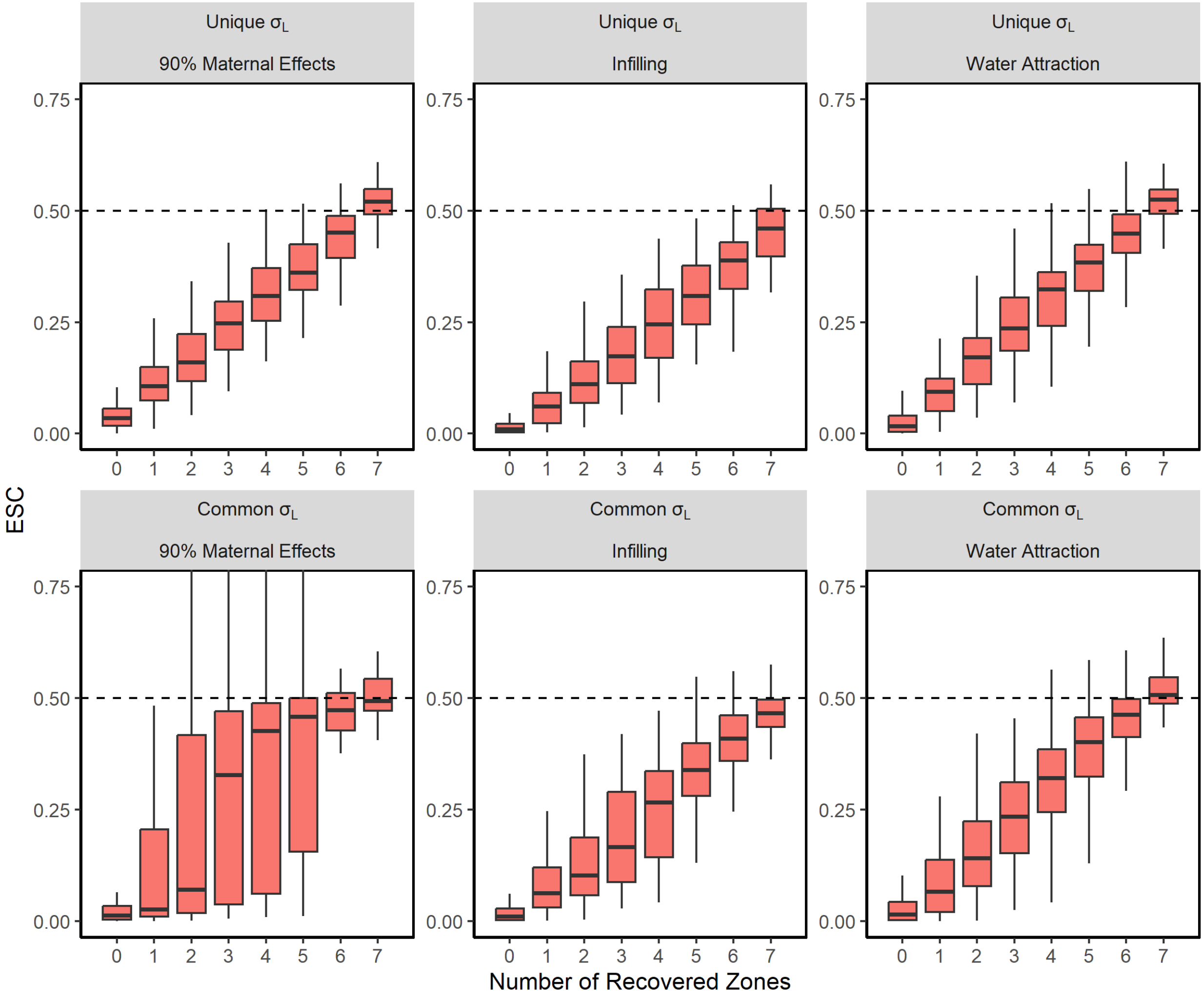

Figure 21. Effects of reducing excess mortality on the eel stage on the total meta-population ESC values across different leptocephali survival and distribution options using the "Elver DD" density-dependent model.

SENSITIVITY ANALYSIS

In general, the results of the sensitivity analysis was highly variable among leptocephali survival and dispersal assumptions (Figures 22, 23 and 24). The results from simulations with the Infilling dispersal were very similar to those with the Water Attraction dispersal option, here only Water Attraction results are displayed. The change in the total meta-population ESC was more variable under unique, independent leptocephali survivals, and was generally most variable under the 90% maternal attraction (Figure 22). Under the Water Attraction dispersal option, changing either the growth rate or silver length of one of the zones had the largest potential impact on the total meta-population ESC. The fecundity, proportion female and survival had a much smaller effect. While the median percent change in ESC values were all very close to 0, perturbations to growth rate or silver length could occasionally result in larger changes to the meta-population as a whole.

Under the 90% maternal effect leptocephali dispersal, the other life history variables were also more sensitive (Figure 22). There was relatively little variability when the meta-population shared one common leptocephali survival, but large amounts of variation regardless of life history parameter being perturbed when each zone had a unique leptocephali survival. Overall, the proportion of female and fecundity appeared to have relatively less effect on the meta-population ESC than growth rate, silver length and eel survival.

A similar pattern of life history parameter effect on the model was observed in the individual zone ESC values (Figure 23 and 24). Both leptocephali survival scenarios were combined due to similarities. Under the Water Attraction dispersal scenario (Figure 23), changes to growth rate and silver length affected the percent change in the ESC the most. Fecundity and proportion female did not have large effects on the ESC, and eel survival was somewhere in between those extremes. Under the 90% maternal effects dispersal assumption, most of the life history parameters were quite variable (Figure 24). However, under both assumptions, changes to a given zone's life history variable had the largest effect on that zone, though some changes could affect others. For example, changing the silver length in SL was more likely to affect the other zones than changing the silver length in SF (Figure 23, 24). In general, AN, SF and SG were the least likely to affect other zones when their life history was perturbed (Figure 23 and 24).

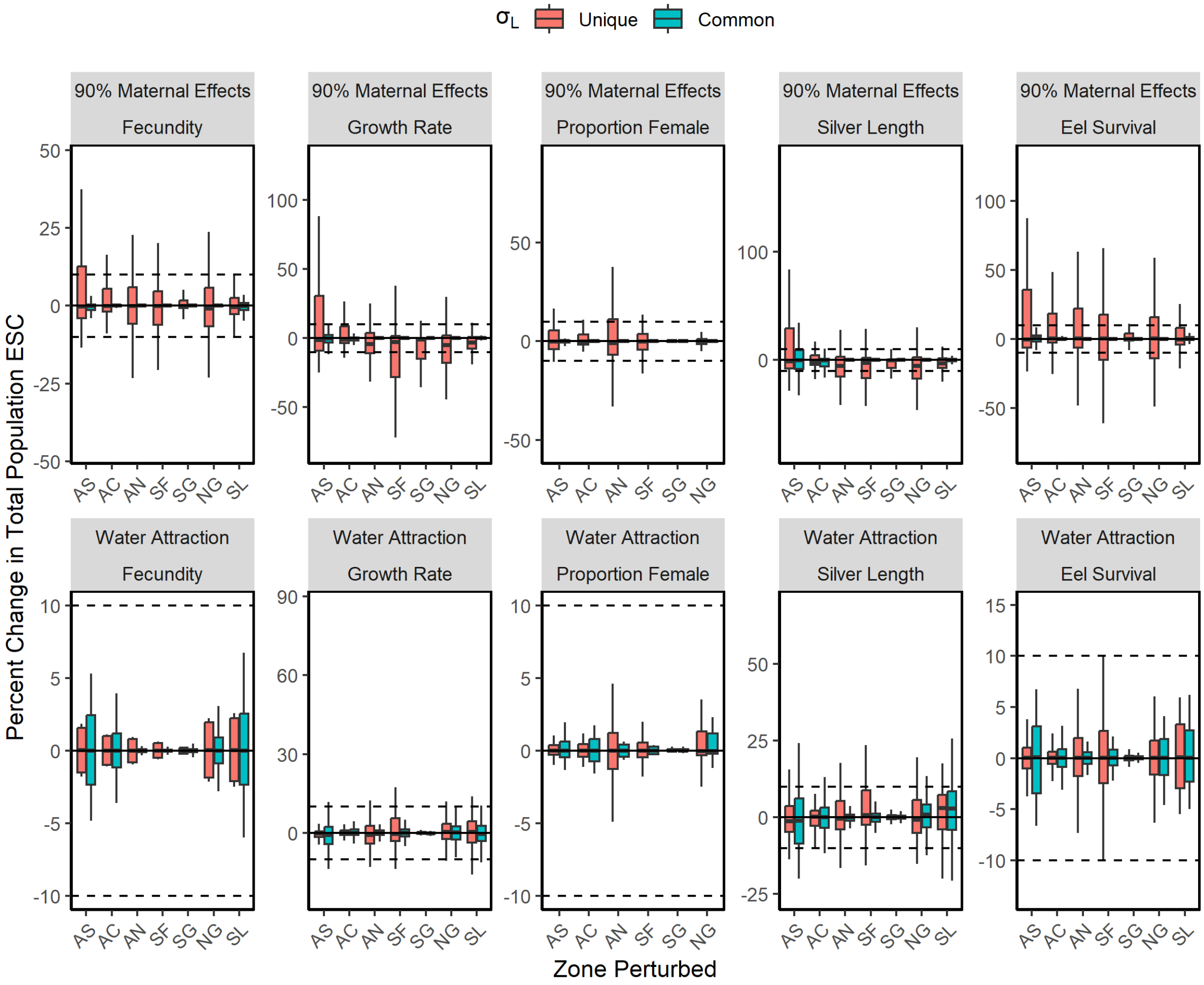

Figure 22. Percent change in the total meta-population ESC under different combinations of life history variable and zone perturbations. Each variable was changed +-10%, while the proportion female was changed based on its 2.5 and 97.5% quantiles.

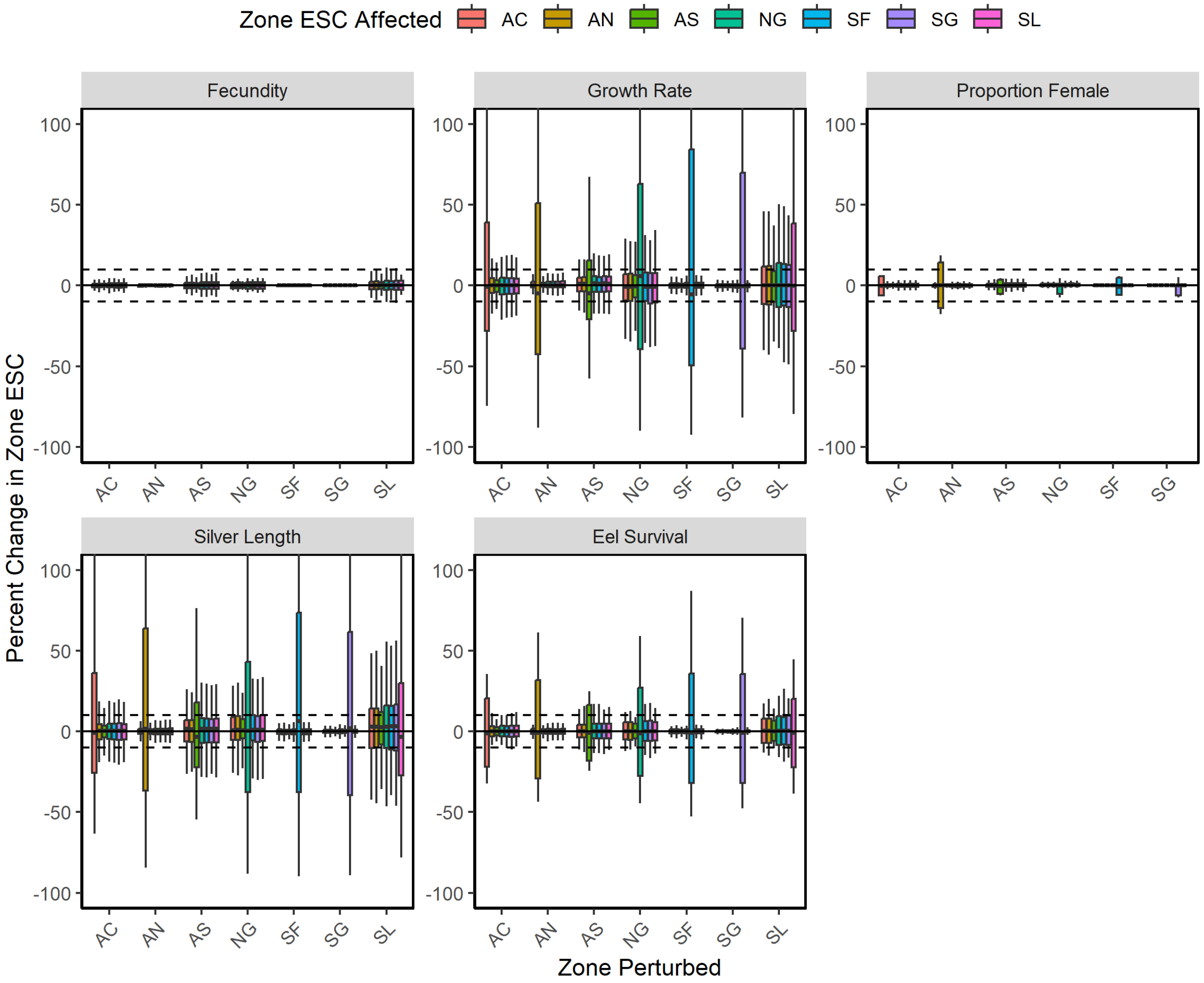

Figure 23. Percent change in the individual zone ESC values using the water attraction dispersal scenario under different combinations of life history variable and zone perturbations. Each variable was changed ± 10%, while the proportion female was changed based on its 2.5 and 97.5% quantiles.

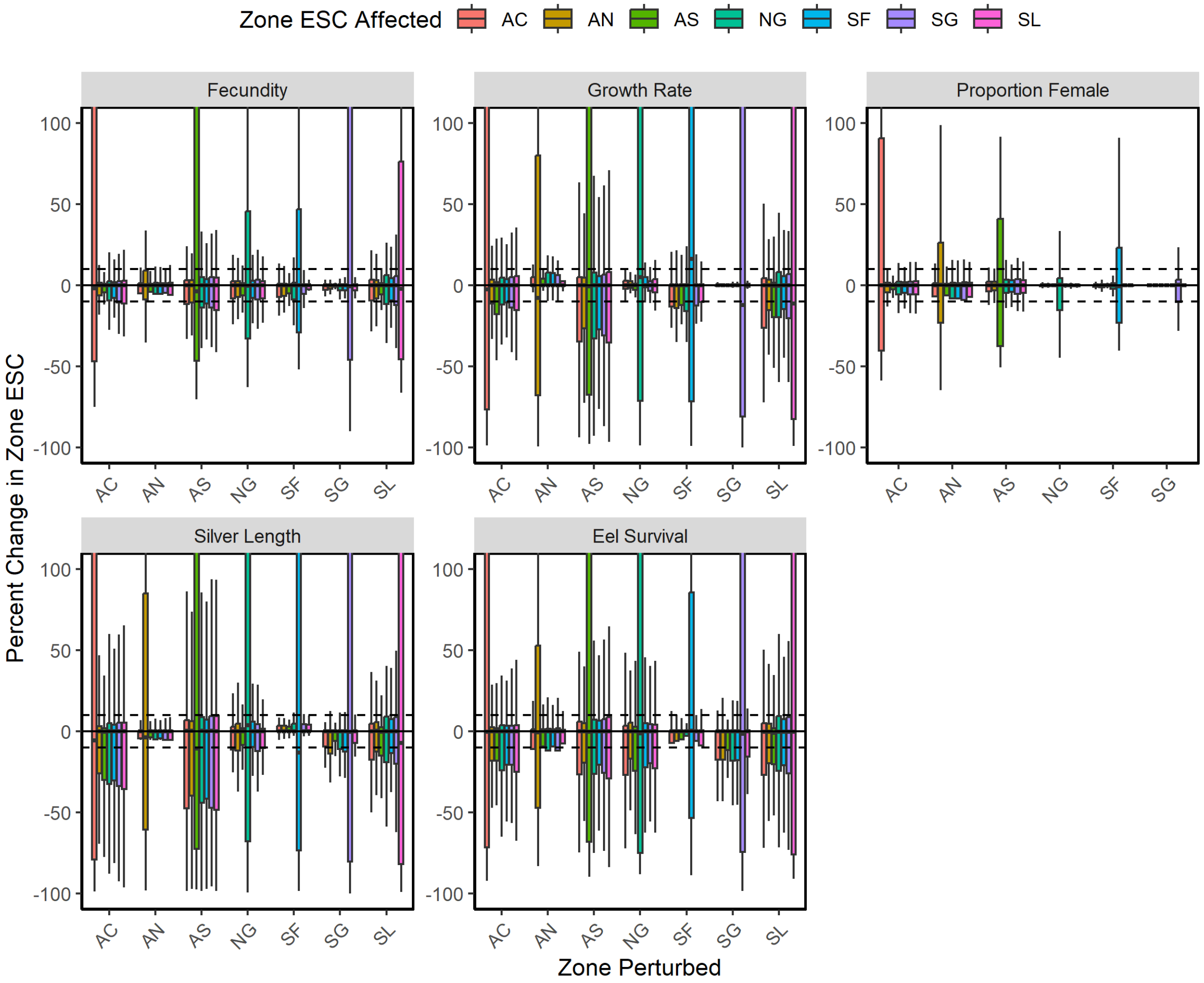

Figure 24. Percent change in the individual zone ESC values using the 90% maternal effect dispersal scenario under different combinations of life history variable and zone perturbations. Each variable was changed ± 10%, while the proportion female was changed based on its 2.5 and 97.5% quantiles.

DISCUSSION

USE OF INDEPENDENT MORTALITY REFERENCE POINTS

Whether fishing at the independently-derived F50 values successfully led to an ESC of 50% for the whole meta-population or for specific zones depended largely on the type of fishery. For elver fisheries, when it was assumed that density-dependent compensation in elver survival occurred before any fishery activity, the ESC values were typically very close to their target of 50% for both the entire meta-population and for individual zones (Table 5, Figure 4 and 5). This indicates F50 worked as intended despite the meta-population structure. However, when its assumed that the elver density-dependence occurs after the elver fishery, the results were much more variable. Estimates of zone ESC were regularly <40% (Table 6), and there was a large variance around median total meta-population and zone estimates of ESC across replicates (Figure 6 and 7). This is consistent with results from Brook et al. (2024), which found that the F50 values were much larger and more variable when density-dependence occurs after the elver fishery. Because the F50 values were much higher when it was assumed that density-dependence occurs after the fishery, it is more precautious to assume the density-dependence occurs before the fishery.

Eel fishery results were not as consistent as elver fishery results. While most zones approximately met their target ESC of 50%, SF and AN were often below this target (Table 7, Figure 9). These zones had the largest F_{50} values (Table 4) and the smallest silver lengths of the zones (Table 1). It is possible that setting F_{50} values assuming zone independence resulted in overestimates of the mortality reference points more than in the other zones. Both fisheries saw an increase in the number of zones with ESC estimates <50% when there were more density-dependent mechanisms included in the simulation. This may be due to the increased variability in mortality reference points as the number of density-dependent mechanisms increase (Brook et al. 2024).

The Infilling leptocephali dispersal scenario had unique behaviour compared to the other distribution options when considering the individual zone ESC when fishing at F_{50}. Regardless of the type of fishery, the amount of density-dependence, or the leptocephali survival, the northern Canadian zones (SL, NG, SG and SF) consistently had a lower ESC value compared to the other zones when infilling was used (Tables 5, 6 and 7). This indicates that, if there is a mechanism that limits northern migration of leptocephali, the population sizes in more northern zones will be more dependent on the relative status of the entire meta-population than southern zones. It also indicates that, even if all other zones had ESC values at or near 50%, parts of the northern range would not be able to achieve the same target.

EXCESS MORTALITY AND RECOVERY SIMULATIONS

The life-stage impacted and density-dependent mechanisms in the simulation did not appear to affect how sensitive the meta-population was to either excess mortality (Figures 10, 13 and 16) or ability to recover (Figures 19 - 21). However, assumptions made about the leptocephali survival and dispersal affected the “tipping point” of the meta-population: how many zones needed to experience excess mortality or recover before a trend was observed in the entire meta-population. In the case of a 90% maternal effect with a common leptocephali survival (these simulations had one zone that was much larger than the others by relative carrying capacities, see Figure 3 and Supplemental Data 1), the ESC was variable only after a few zones either had excess mortality or were recovering (as opposed to showing an immediate effect). This is likely because, as more zones were affected, the probability of the largest zone being affected increased, which largely drove the meta-population total ESC trends.

The zone-specific ESC values for excess mortality simulations, with some exceptions, did not show clear differences among the zones (Figures 11, 12, 14, 15, 17, 18). When an intermediate number (e.g. 3 – 5) of zones were subject to excess mortality, the ESC values were quite variable, likely depending on which combination of zones experienced excess mortality. However, as more zones (e.g. 6 – 7) were subject to excess mortality, this variability decreased, and ESC declined. This indicates that under most leptocephali survival and dispersal assumptions, the meta-population was relatively resilient to a few zones experiencing excess mortality. An exception to this trend was the northern zones under the Infilling dispersal scenario, whose ESC values were consistently smaller than other zones. In general, the results indicated that if all or most zones are independently managed well, the meta-population as a whole does well.

UNCERTAINTIES

The method by which leptocephali disperse to continental waters and their survival rate is largely unknown and therefore a variety of leptocephali dispersal mechanisms and survival assumptions were tested. While all scenarios tested have a reasonable basis, it is unknown which one (or which combinations) are the most realistic, or if alternative mechanisms not tested are possible. Results that were common across scenarios (e.g. fishing the meta-population with elver F_{50} values generally returns values near 50%), gives some confidence in the inferences despite the uncertainties. All scenarios showed decreased total ESC when the number of zones being affected by excess mortality increased, though they differed on how many zones needed to be affected before population-wide changes were observed. Under high maternal effects (i.e. zones are largely independent with limited mixing), population-wide effects may not be observed until several zones are impacted. The results that differed most greatly among scenarios was how the northern zones were impacted following anthropogenic harm. For example under the infilling dispersal assumption, the ESC values of northern zones decreased much more than the other zones, even before excess mortality trials (e.g. Figure 9). While this pattern only occurred in 2 of the 6 scenarios, it is worth emphasizing given the status of American Eel in the SL zone (Cornic et al. 2021; COSEWIC 2012).

While a reasonable range of assumptions were tested regarding leptocephali dispersal, it was not feasible to test every possibility. All the scenarios tested used an underlying water attraction hypothesis, even when infilling or maternal effects modified its relative strength in the model. However, it is also possible that the underlying distribution is distance-based, where leptocephali are less likely to migrate farther north regardless of density. The scenarios also all assumed a constant leptocephali dispersal, though it is likely that environmental conditions impact the dispersal of leptocephali year-to-year (Jessop 2020). Long term potential changes caused by climate change were also not included in the model, though changes to ocean currents may impact leptocephali migration patterns and success (Drouineau et al. 2018; Rypina et al. 2016).

While somatic growth rate and silver length consistently had relatively high sensitivity to the model ESC, the variation of these sensitivity values depended on leptocephali survival and dispersal assumptions (Figure 22). This is also the case when considering the sensitivity of life history changes between zones (Figures 23 and 24), where sensitivity values were occasionally very large (particularly for the zones where the life history was changed for the sensitivity test). This variability makes it difficult to draw overall conclusions on the sensitivity of these and other parameters in the model, due to the underlying uncertainty around leptocephali dispersal and survival.

Males were not included in the model structure, under the assumption that there will be a sufficient number of males that make it to the Sargasso Sea to fertilize the eggs, and that only the number of female eel is relevant for population state. However, it is possible that the overall reproductive success of the meta-population is sensitive to the number of males available, creating a possible population growth rate bottleneck if there are insufficient males that survive to migrate to the Sargasso Sea. Current understanding of where males come from is incomplete. The available data indicate that some locations producing very few (if any) males, while the AN zone is comprised primarily of males (Table 1). If the majority of male eel originate from just a few locations in the meta-population, the population may be more sensitive to anthropogenic mortality in those zones than other locations. The reason for the widely varying sex ratios is not well understood, with density (Cairns et al. 2014; Krueger & Oliveira 1999) being proposed as a possible mechanism (though Côté et al. (2015) found no relationship between density and sex ratio). Determining what drives the sex differentiation in eel is necessary both for gathering additional life history data for male eel to include in future models, but also to provide a better understanding of the distribution of male American Eel.

This analysis only includes anthropogenic fishing mortality as a source of increasing mortality for American Eel populations, but there are a variety of factors that could affect their mortality.

The simulations assumed a constant carrying capacity (K) in each zone, but habitat degradation, or inaccessibility due to damming, may reduce the K values. Furthermore, damming, even if some young eel and elvers can climb over the dam, may introduce additional density-dependent effects to the population (Camhi et al. 2021), and turbine mortality can be a significant source of anthropogenic mortality during return migrations in locations like the SL (COSEWIC 2012).

A lack of data available to fit growth curves required the growth rates for the Atlantic zones (AS, AC, AN) and the SL to be estimated using the growth rate conversion in Brook et al. (2024). This conversion takes growth rates from the literature (generally calculated assuming constant growth over the eel lifespan) and converts them to biphasic growth rates (Brook et al. 2024). However, there is an error associated with this conversion, and no data to verify how accurate it is. This method resulted in a very high growth rate for the AS zone (though the AS zone typically has higher growth rates relative to other zones, Cairns et al. (2014)). Furthermore, there was insufficient data to include zones in the more southern range of American Eel, like the Caribbean (Ulmo Diaz et al. 2023) or most extreme northern areas like Greenland (Cairns et al. 2014), as a result, the meta-population model did not encompass the full geographic range of American Eel. Similarly, only freshwater data were used in the model due to data limitations.

The population of American Eel in Canada has decreased over time (van der Lee & Koops 2024). Overall, the results of these meta-population simulations suggest that this could be caused by a combination of effects, including anthropogenic mortality both within and outside Canada. While fisheries are managed independently, the effect of American Eel panmictic population structure on mortality reference points, and the potential to achieve management objectives, needs to be considered if the ultimate goal is recovery and protection of sustainable American Eel fisheries.

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SUPPLEMENTAL DATA 1 – 125 YEAR SIMULATIONS

The 125 year simulations included eel and elver fishing, and turbine mortality in SL. They were completed to visualize how assumptions about leptocephali survival and dispersal affect the number of yellow and silver eel and the number of elvers arriving in each zone. The number of elvers and eel were scaled so that when the meta-population was at its carrying capacity, the total number was equal to 100 (i.e. "100%" of the amount at K). These assumptions also affect the relative carrying capacities between the zones when the meta-population as a whole is in its stable state. In general, when a common leptocephali survival is used, AS zone has the largest number of yellow eel, due to the scaling of the leptocephali survival. When each zone used a unique leptocephali survival, NG had the largest number of yellow eel. SG zone consistently had the smallest number of yellow eel, relative to the other zones.

Under most circumstances, the number of elvers going to each zone did not dramatically decrease when eel were fished at F_{50}. Because the F_{50} values are generally well above $F_{extinct}$, the number of reduced leptocephali caused by the fishing is largely replaced by the compensation from elver density-dependence (and growth density-dependence if it is included), so the number of elvers does not decrease dramatically. An exception to this are the Infilling scenarios, where the SL and other northern zones can experience a decrease in elvers due to the decreasing overall number of leptocephali in the meta-population. In general, the patterns between the density-dependent options were similar.

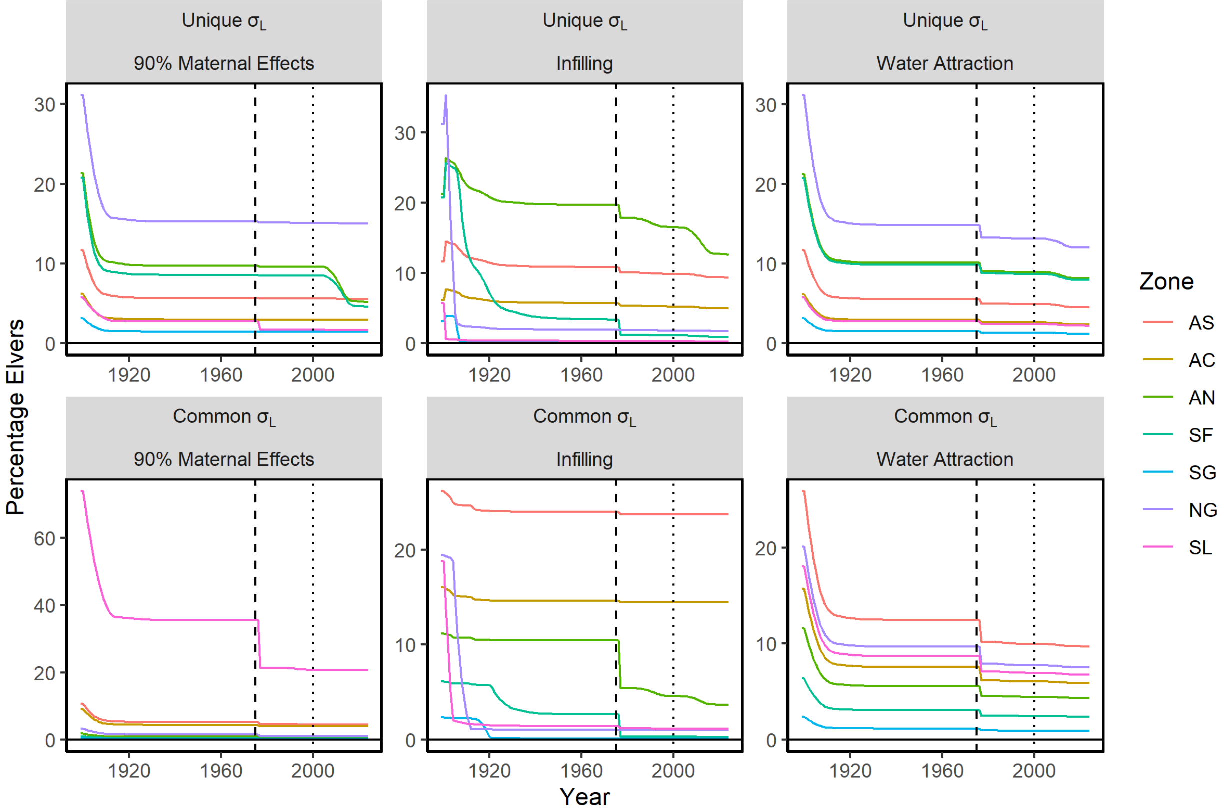

Figure S1.1. Elver relative percentage when eel are fished at F_{50}, with the "Elver DD" density-dependent model. This simulation assumes the elver density-dependence occurs before the elver fishery, when applicable. The dashed line shows when turbine mortality was introduced to the SL zone; the dotted line shows when elver fisheries began operating in the AN and SF zones.

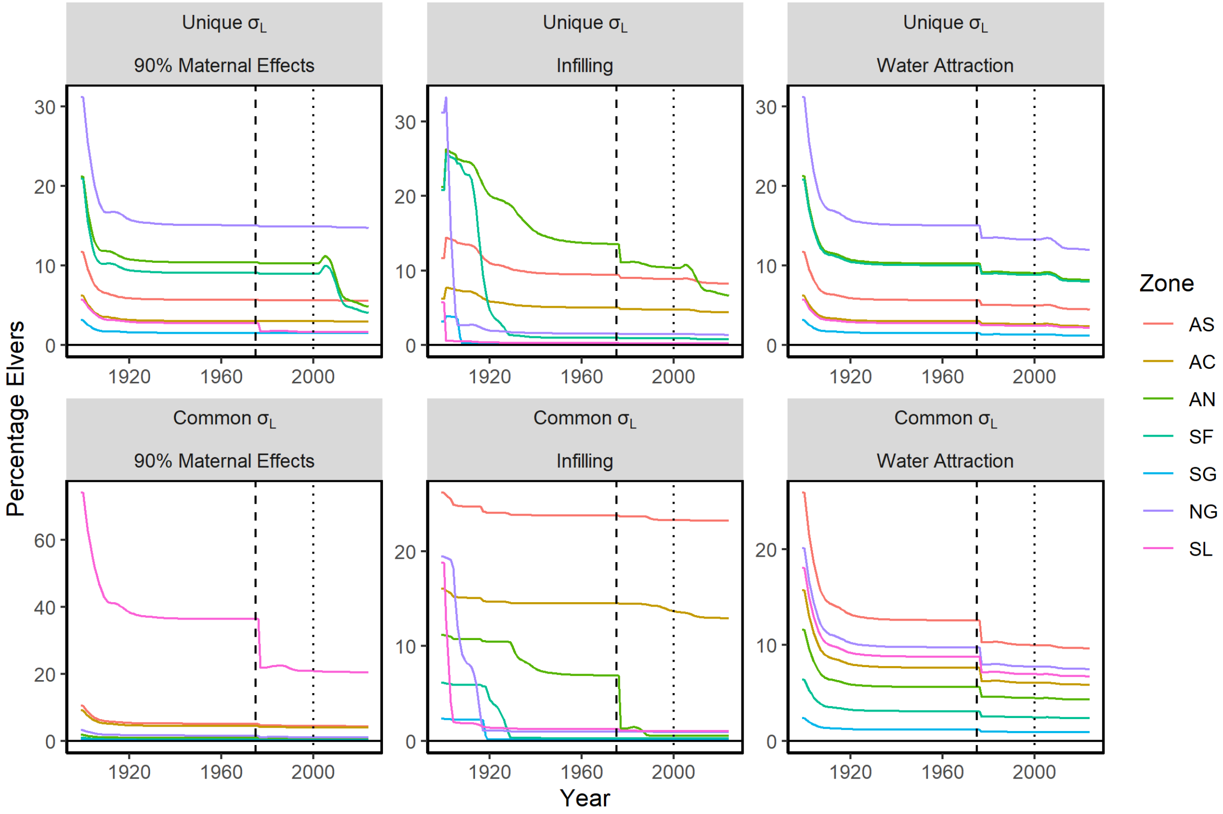

Figure S1.2. Elver relative percentage when eel are fished at F_{50}, with the "Elver + Silv. DD" density-dependent model. This simulation assumes the elver density-dependence occurs before the elver fishery, when applicable. The dashed line shows when turbine mortality was introduced to the SL zone; the dotted line shows when elver fisheries began operating in the AN and SF zones.

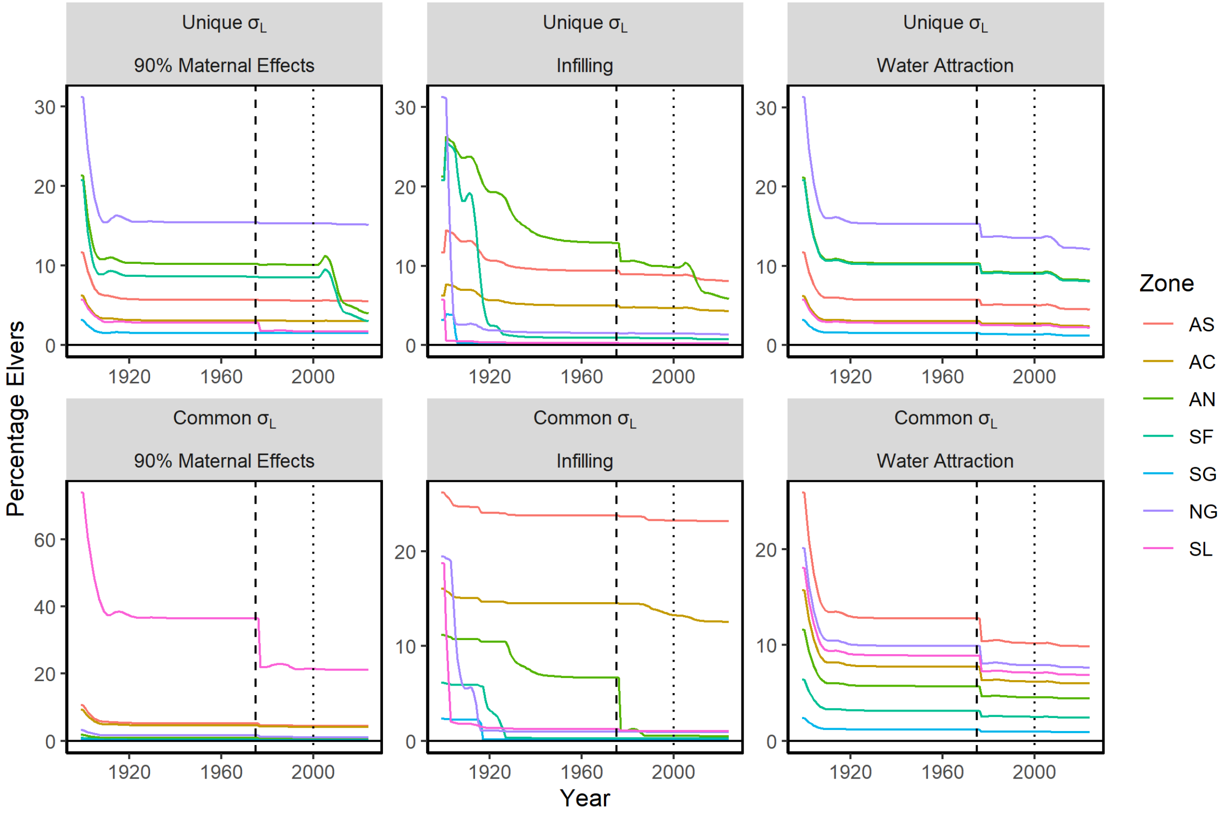

Figure S1.3. Elver relative percentage when eel are fished at F_{50}, with the "Elver + Silv. + Mort. DD" density-dependent model. This simulation assumes the elver density-dependence occurs before the elver fishery, when applicable. The dashed line shows when turbine mortality was introduced to the SL zone; the dotted line shows when elver fisheries began operating in the AN and SF zones.

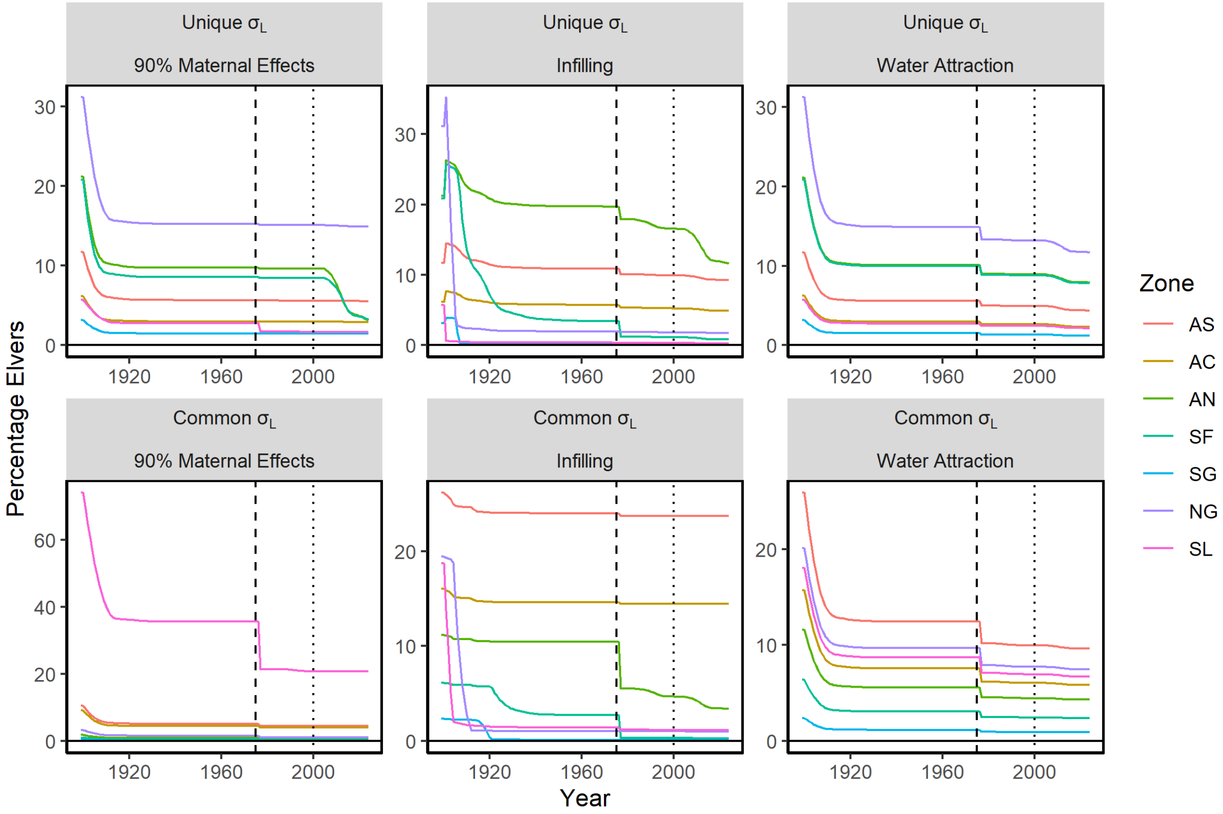

Figure S1.4. Elver relative percentage when eel are fished at F_{50}, with the "Elver DD" density-dependent model. This simulation assumes the elver density-dependence occurs after the elver fishery, when applicable. The dashed line shows when turbine mortality was introduced to the SL zone; the dotted line shows when elver fisheries began operating in the AN and SF zones.

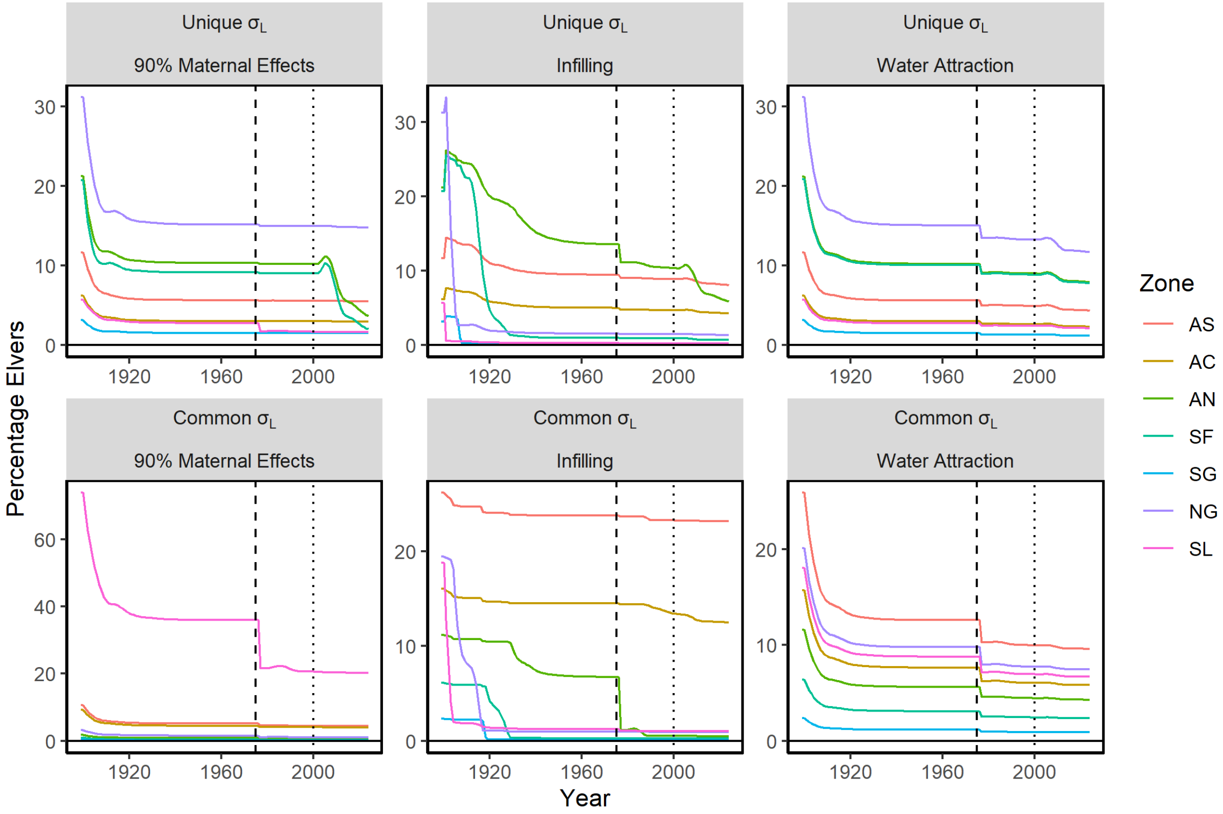

Figure S1.5. Elver relative percentage when eel are fished at F_{50}, with the "Elver + Silv. DD" density-dependent model. This simulation assumes the elver density-dependence occurs after the elver fishery, when applicable. The dashed line shows when turbine mortality was introduced to the SL zone; the dotted line shows when elver fisheries began operating in the AN and SF zones.

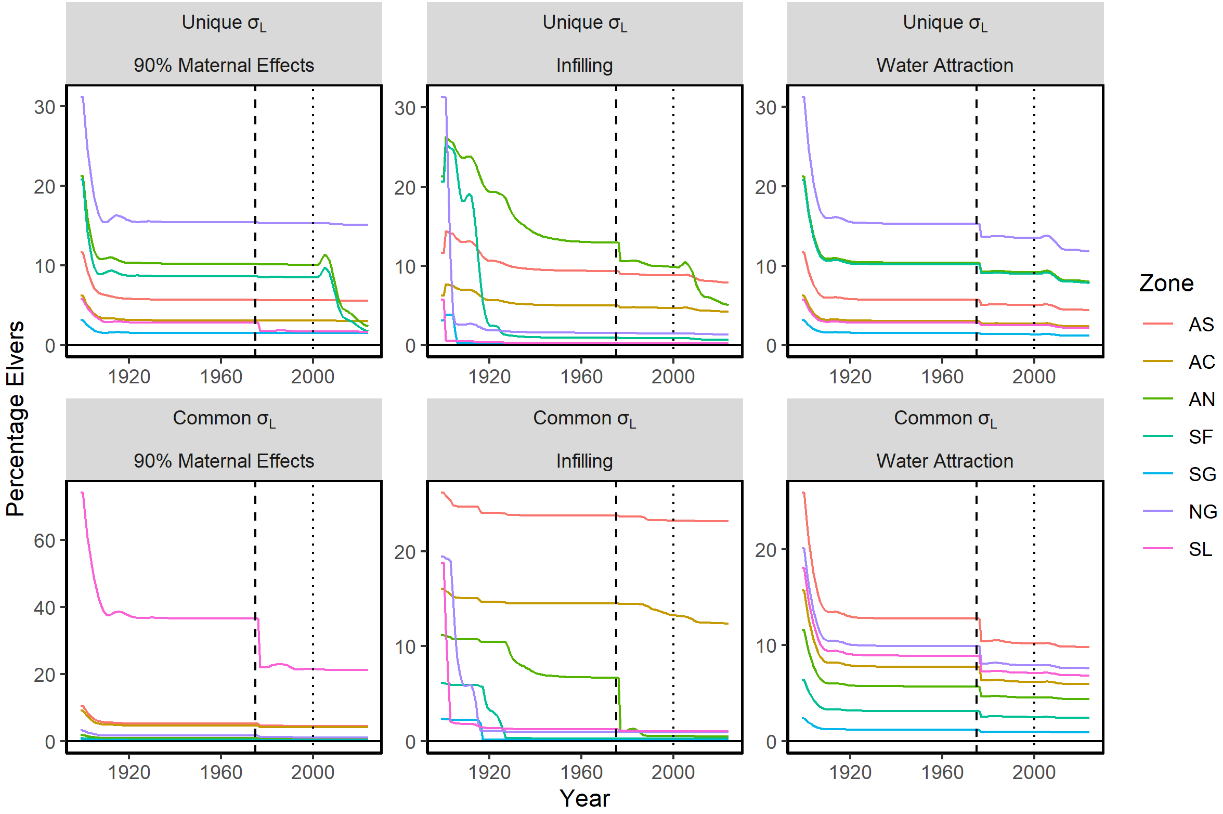

Figure S1.6. Elver relative percentage when eel are fished at F_{50}, with the "Elver + Silv. + Mort. DD" density-dependent model. This simulation assumes the elver density-dependence occurs after the elver fishery, when applicable. The dashed line shows when turbine mortality was introduced to the SL zone; the dotted line shows when elver fisheries began operating in the AN and SF zones.

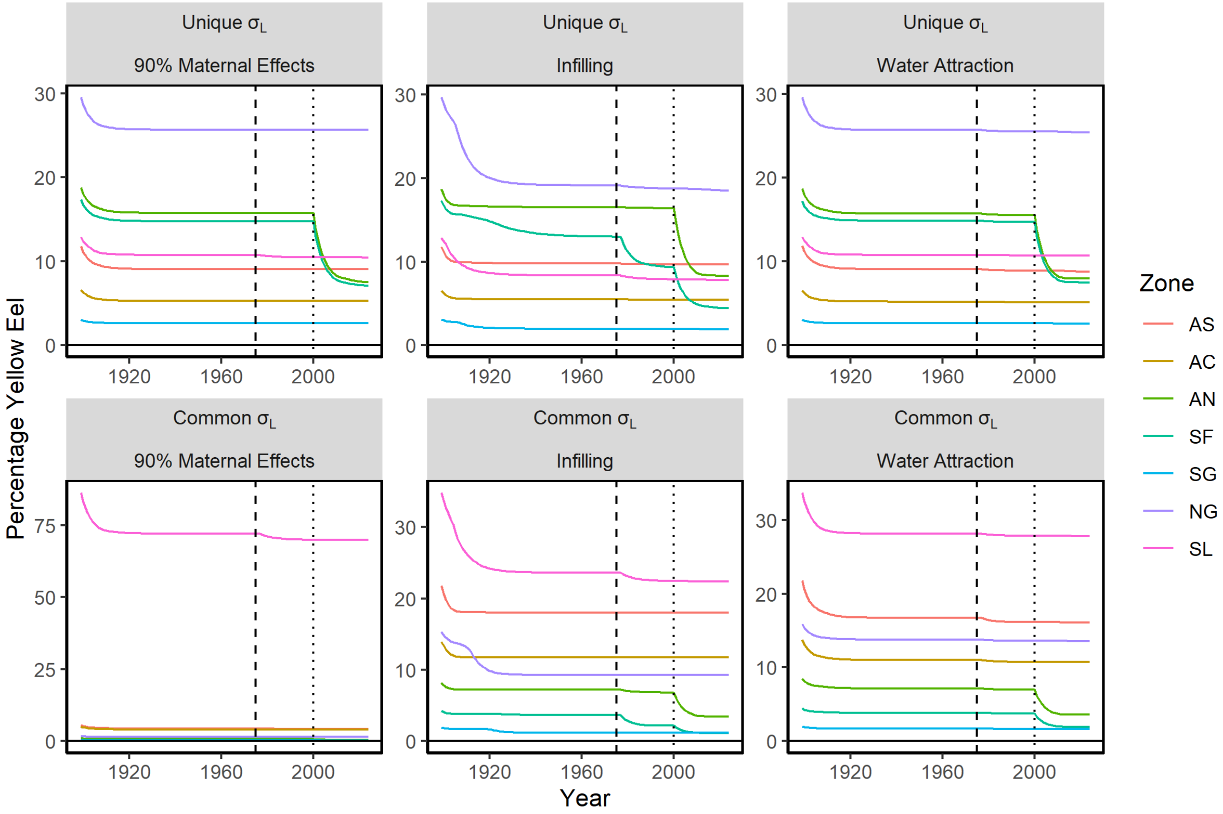

Figure S1.7. Yellow eel relative percentage when eel are fished at F_{50}, with the "Elver DD" density-dependent model. This simulation assumes the elver density-dependence occurs before the elver fishery, when applicable. The dashed line shows when turbine mortality was introduced to the SL zone; the dotted line shows when elver fisheries began operating in the AN and SF zones.

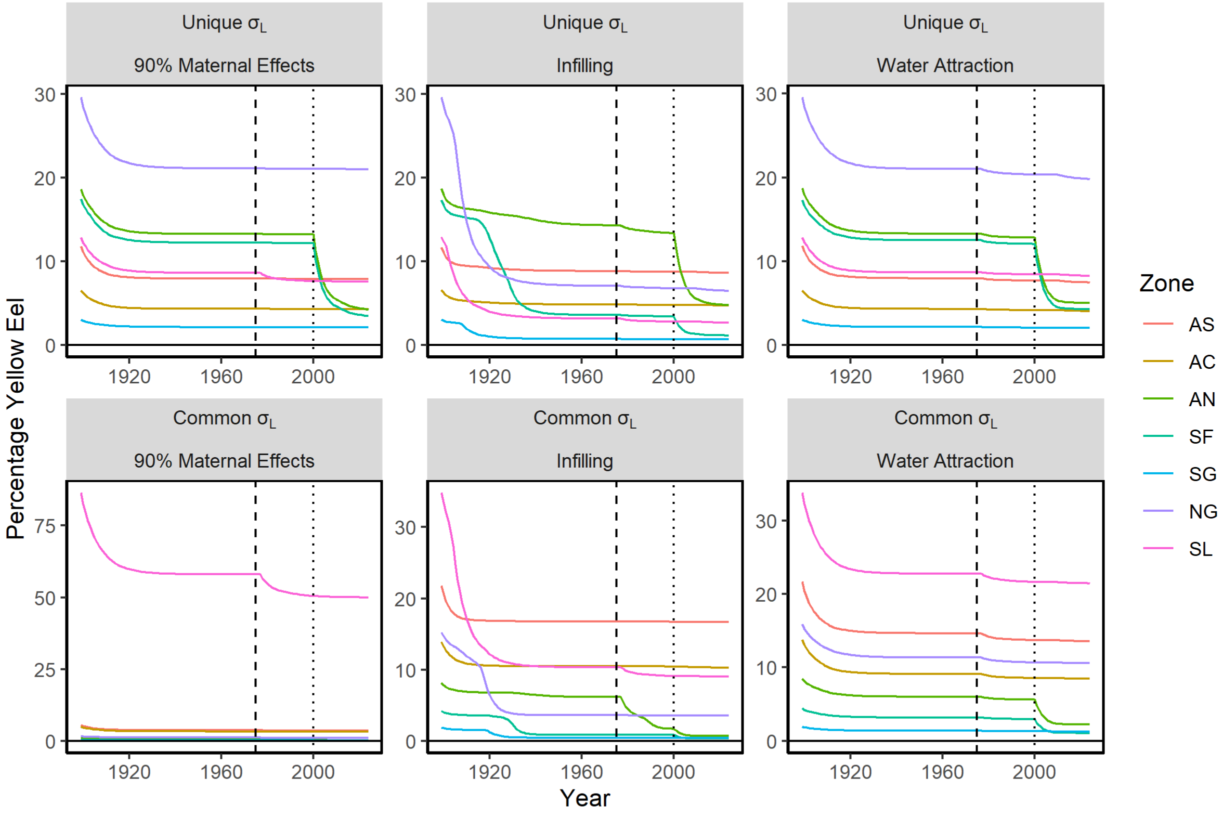

Figure S1.8. Yellow eel relative percentage when eel are fished at F_{50}, with the "Elver + Silv. DD" density-dependent model. This simulation assumes the elver density-dependence occurs before the elver fishery, when applicable. The dashed line shows when turbine mortality was introduced to the SL zone; the dotted line shows when elver fisheries began operating in the AN and SF zones.

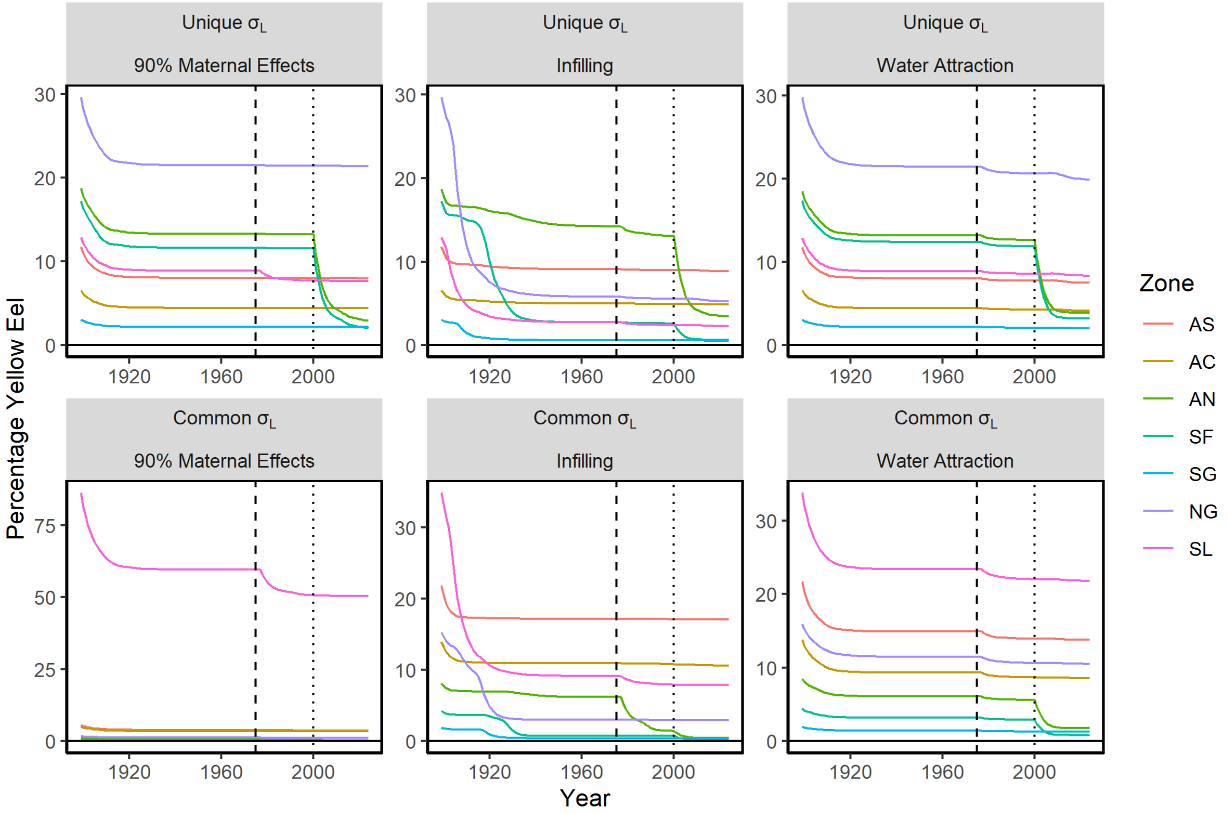

Figure S1.9. Yellow eel relative percentage when eel are fished at F_{50}, with the "Elver + Silv. + Mort. DD" density-dependent model. This simulation assumes the elver density-dependence occurs before the elver fishery, when applicable. The dashed line shows when turbine mortality was introduced to the SL zone; the dotted line shows when elver fisheries began operating in the AN and SF zones.

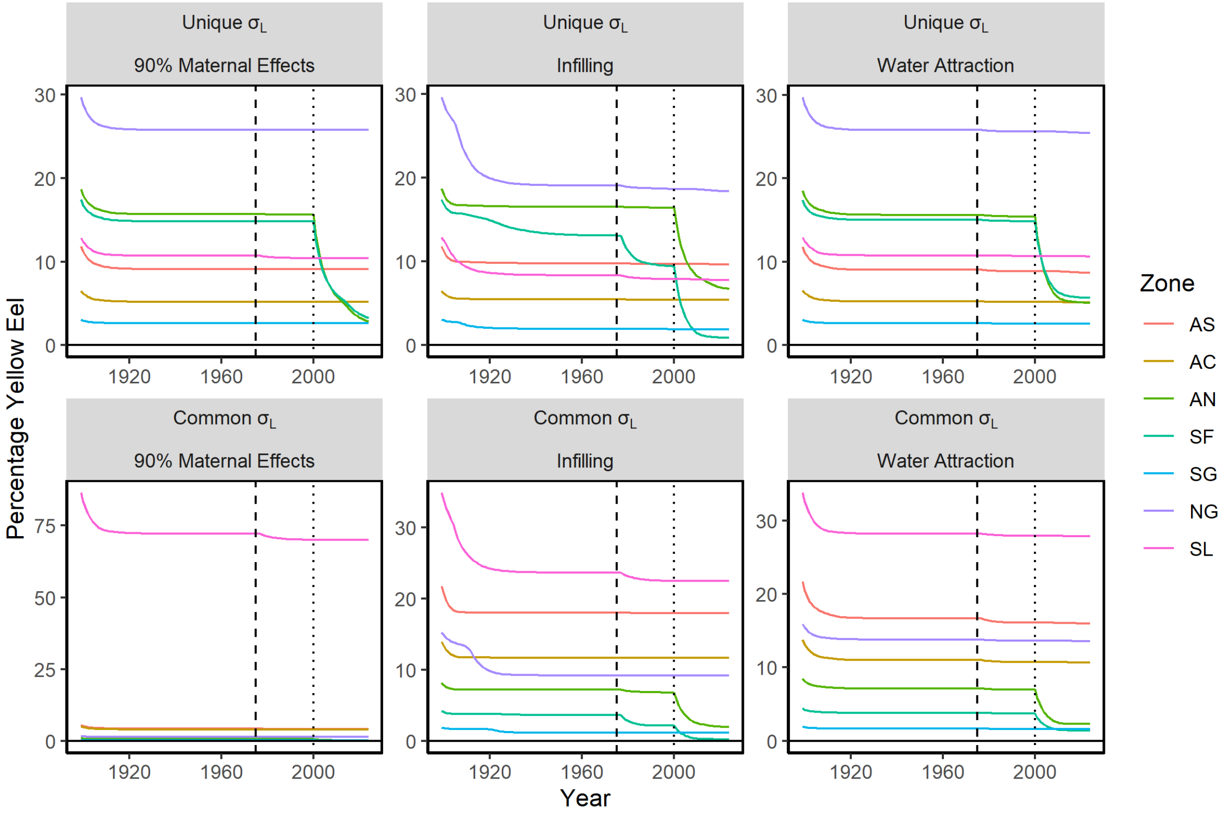

Figure S1.10. Yellow eel relative percentage when eel are fished at F_{50}, with the “Elver DD” density-dependent model. This simulation assumes the elver density-dependence occurs after the elver fishery, when applicable. The dashed line shows when turbine mortality was introduced to the SL zone; the dotted line shows when elver fisheries began operating in the AN and SF zones.

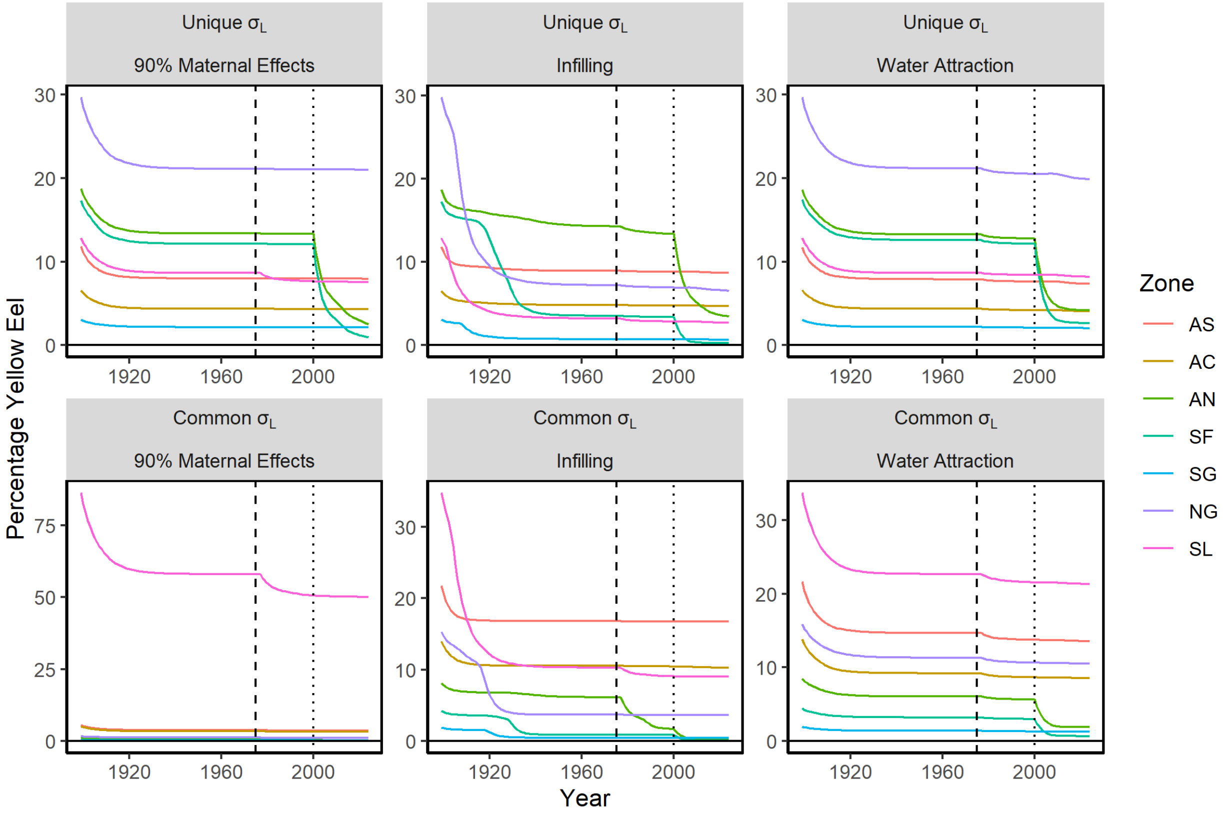

Figure S1.11. Yellow eel relative percentage when eel are fished at F_{50}, with the "Elver + Silv. DD" density-dependent model. This simulation assumes the elver density-dependence occurs after the elver fishery, when applicable. The dashed line shows when turbine mortality was introduced to the SL zone; the dotted line shows when elver fisheries began operating in the AN and SF zones.

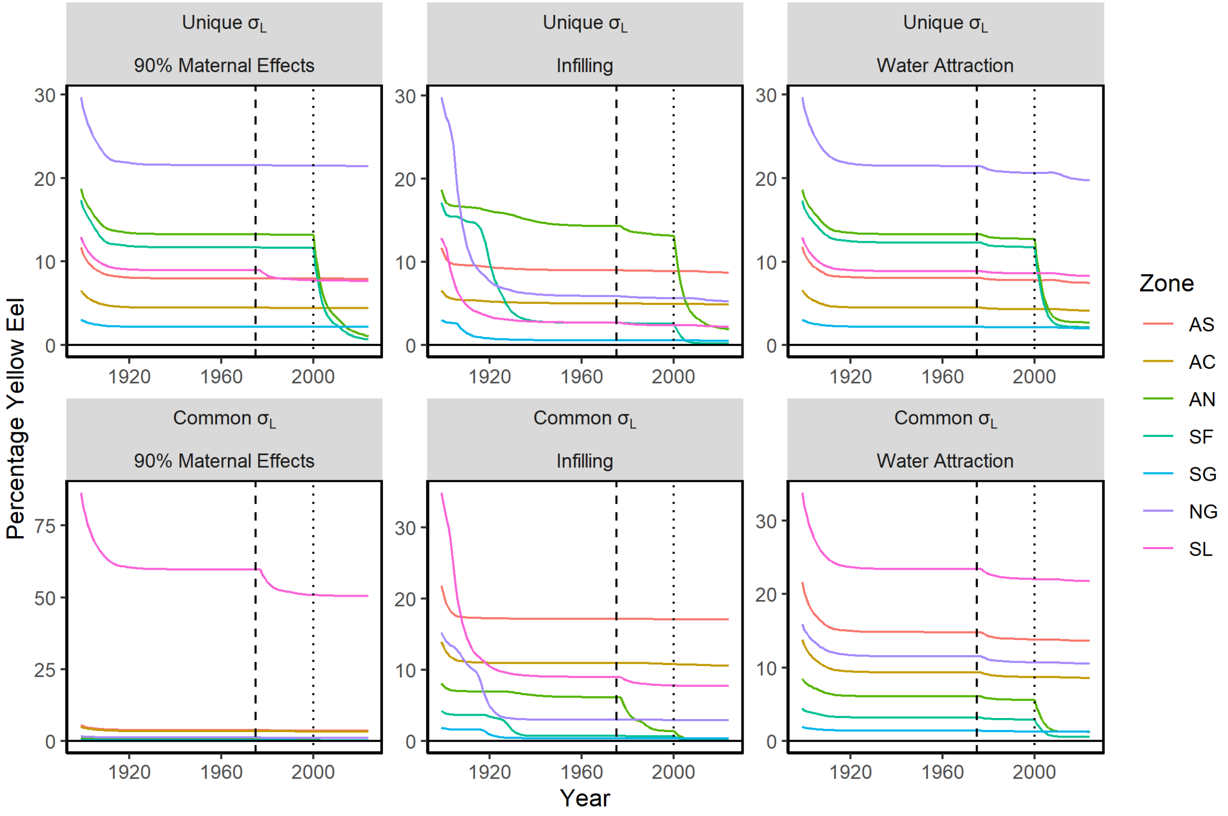

Figure S1.12. Yellow eel relative percentage when eel are fished at F_{50}, with the “Elver + Silv. + Mort. DD” density-dependent model. This simulation assumes the elver density-dependence occurs after the elver fishery, when applicable. The dashed line shows when turbine mortality was introduced to the SL zone; the dotted line shows when elver fisheries began operating in the AN and SF zones.

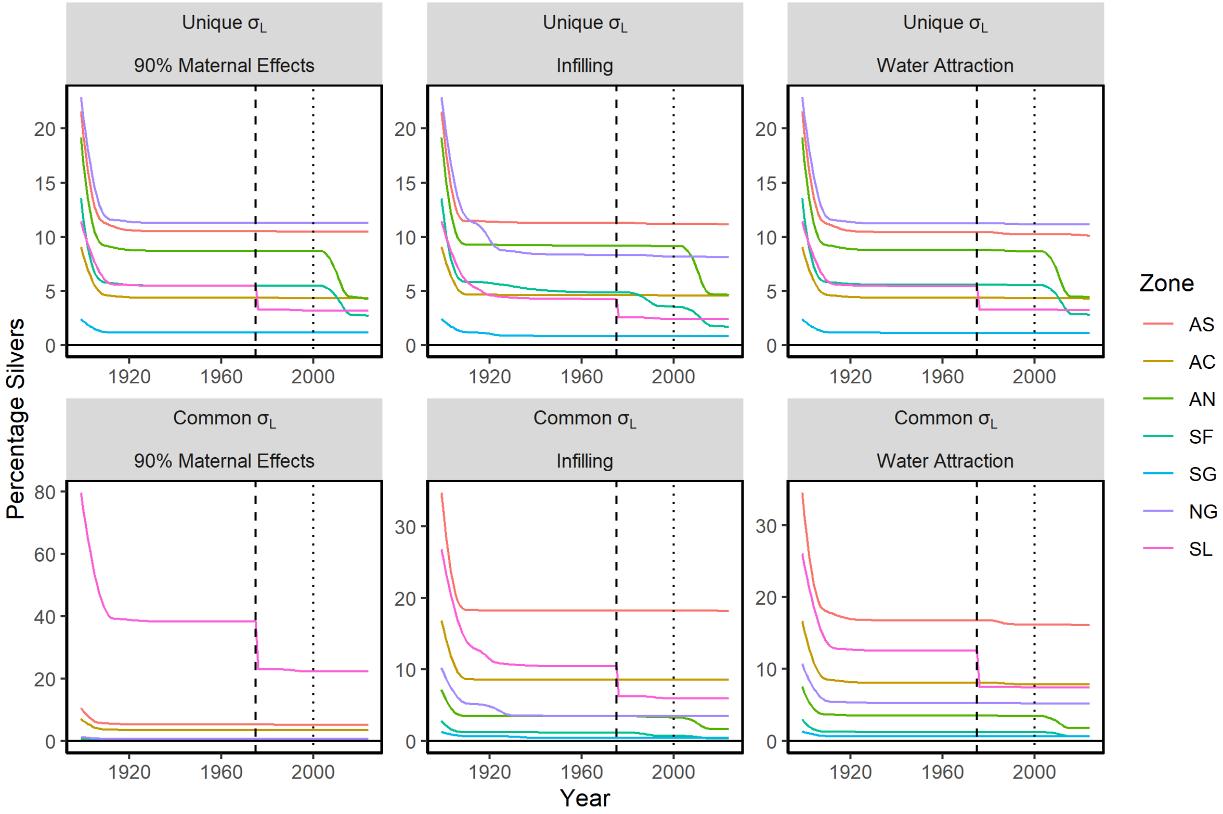

Figure S1.13. Silver eel relative percentage when eel are fished at F_{50}, with the "Elver DD" density-dependent model. This simulation assumes the elver density-dependence occurs before the elver fishery, when applicable. The dashed line shows when turbine mortality was introduced to the SL zone; the dotted line shows when elver fisheries began operating in the AN and SF zones.

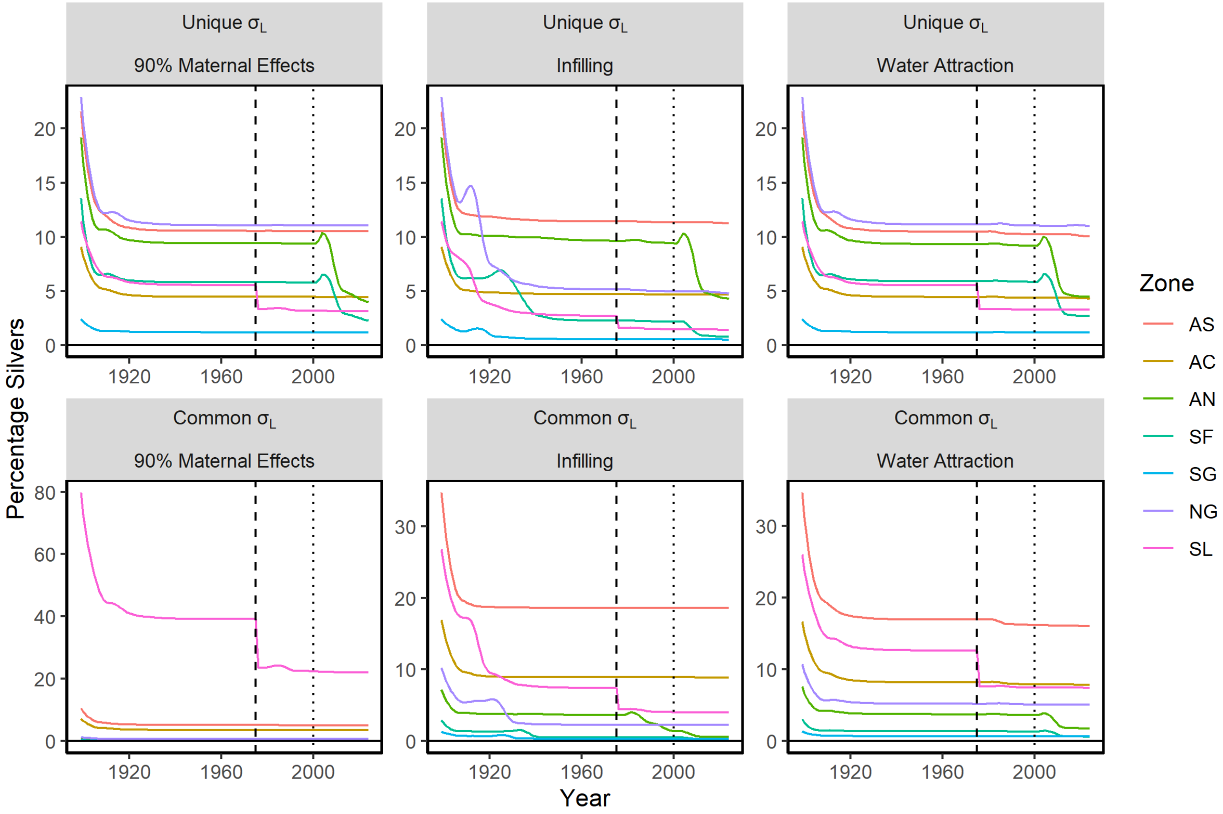

Figure S1.14. Silver eel relative percentage when eel are fished at F_{50}, with the "Elver + Silv. DD" density-dependent model. This simulation assumes the elver density-dependence occurs before the elver fishery, when applicable. The dashed line shows when turbine mortality was introduced to the SL zone; the dotted line shows when elver fisheries began operating in the AN and SF zones.

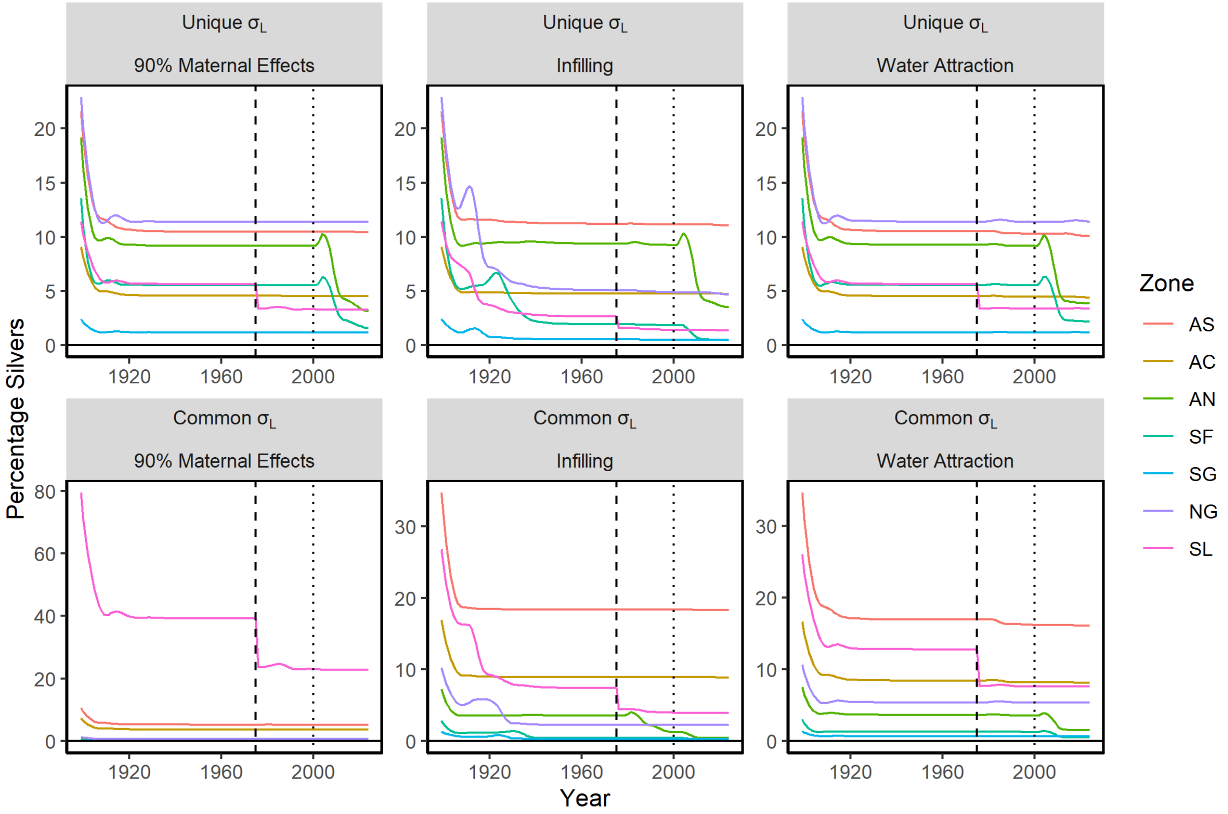

Figure S1.15. Silver eel relative percentage when eel are fished at F_{50}, with the "Elver + Silv. + Mort. DD" density-dependent model. This simulation assumes the elver density-dependence occurs before the elver fishery, when applicable. The dashed line shows when turbine mortality was introduced to the SL zone; the dotted line shows when elver fisheries began operating in the AN and SF zones.

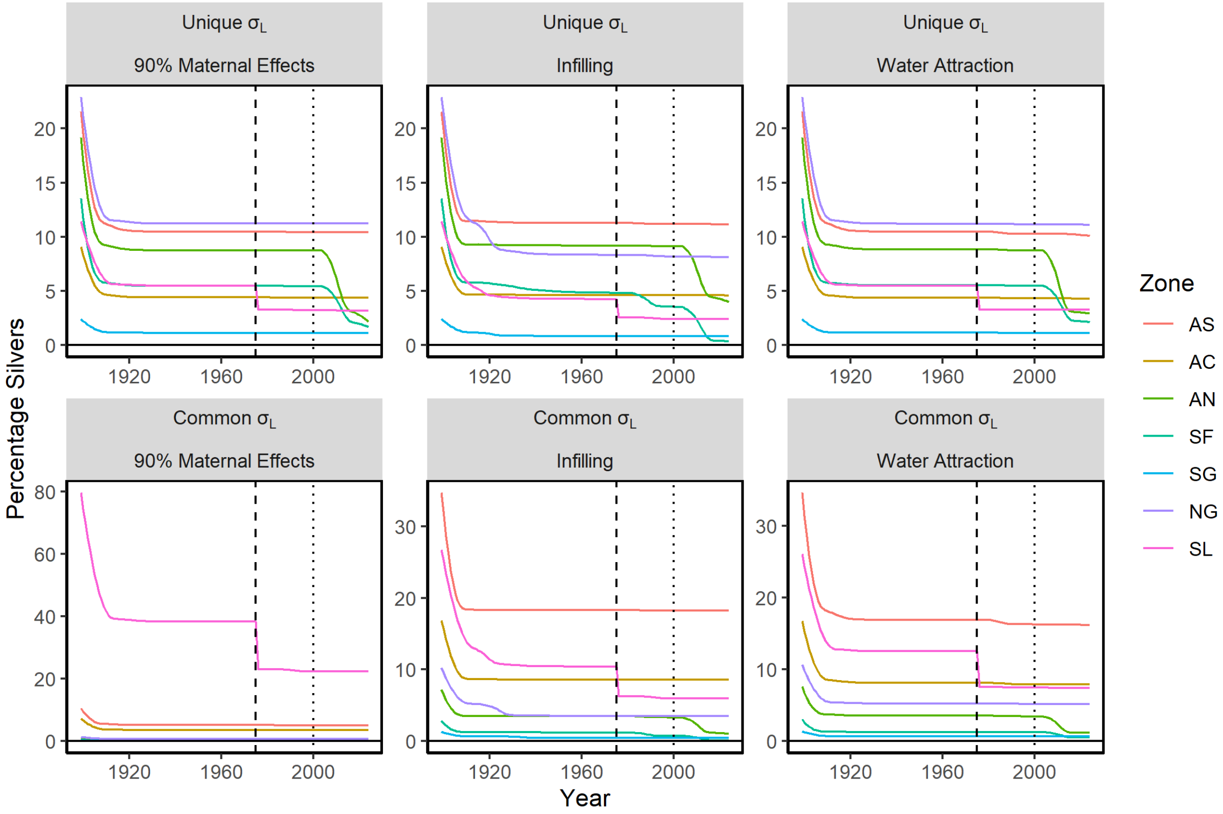

Figure S1.16. Silver eel relative percentage when eel are fished at F_{50}, with the "Elver DD" density-dependent model. This simulation assumes the elver density-dependence occurs after the elver fishery, when applicable. The dashed line shows when turbine mortality was introduced to the SL zone; the dotted line shows when elver fisheries began operating in the AN and SF zones.

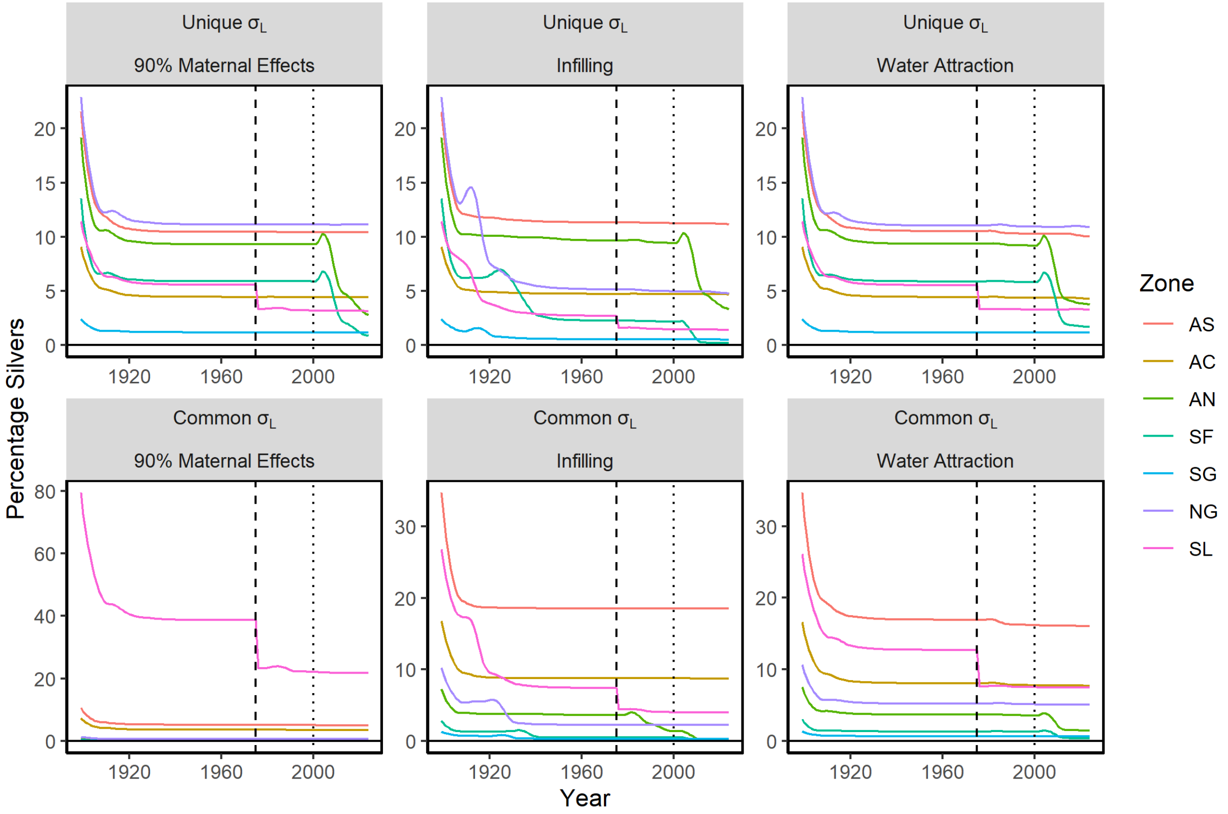

Figure S1.17. Silver eel relative percentage when eel are fished at F_{50}, with the "Elver + Silv. DD" density-dependent model. This simulation assumes the elver density-dependence occurs after the elver fishery, when applicable. The dashed line shows when turbine mortality was introduced to the SL zone; the dotted line shows when elver fisheries began operating in the AN and SF zones.

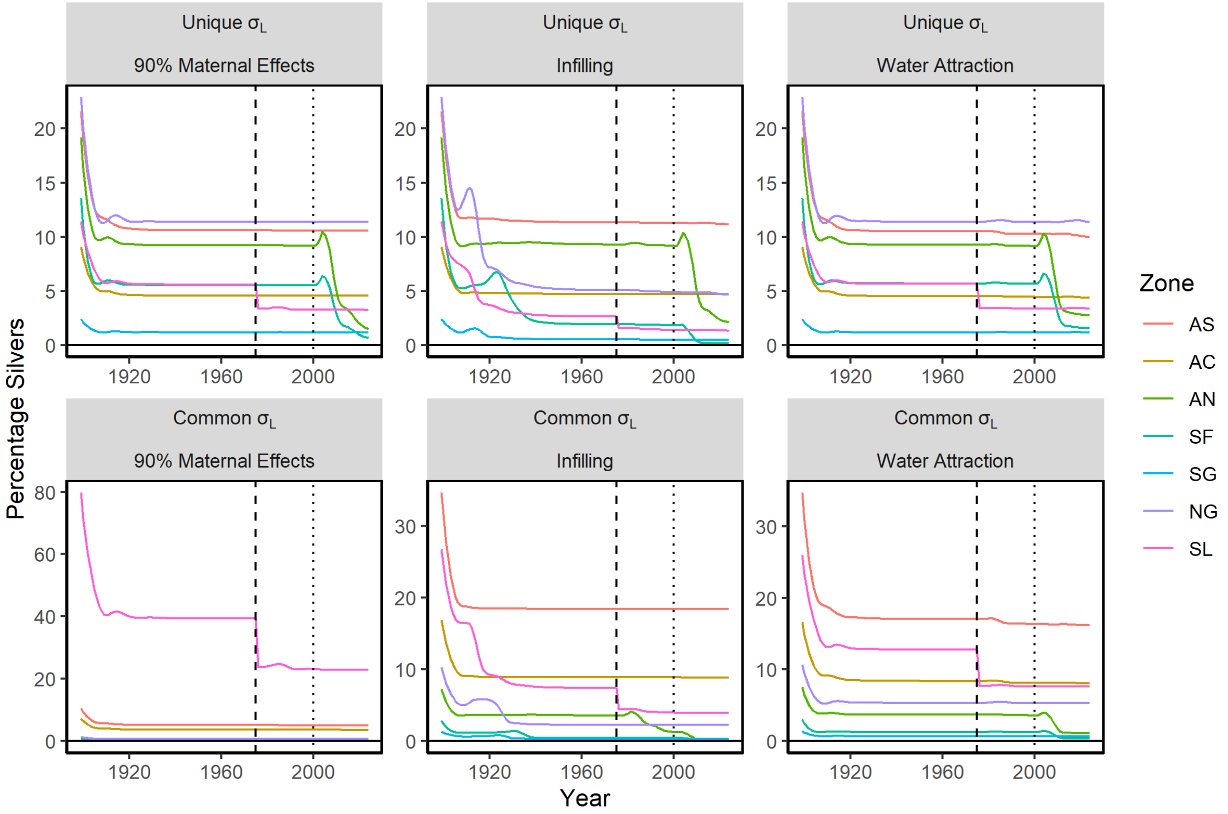

Figure S1.18. Silver eel relative percentage when eel are fished at F_{50}, with the "Elver + Silv. + Mort. DD" density-dependent model. This simulation assumes the elver density-dependence occurs after the elver fishery, when applicable. The dashed line shows when turbine mortality was introduced to the SL zone; the dotted line shows when elver fisheries began operating in the AN and SF zones.

SUPPLEMENTAL DATA 2 – OTHER DENSITY-DEPENDENT MECHANISMS

Overall, the simulation outputs did not dramatically differ when more density-dependent mechanisms were added to the model. The addition of more density-dependence mechanisms generally added more variability to the output, but in the case of the F_{50}, excess mortality and recovery simulations, the overall patterns did not differ between the “Elver DD”, “Elver + Silv. DD” or “Elver + Silv. + Mort. DD” trials.

MANAGING ZONES AT F_{50}

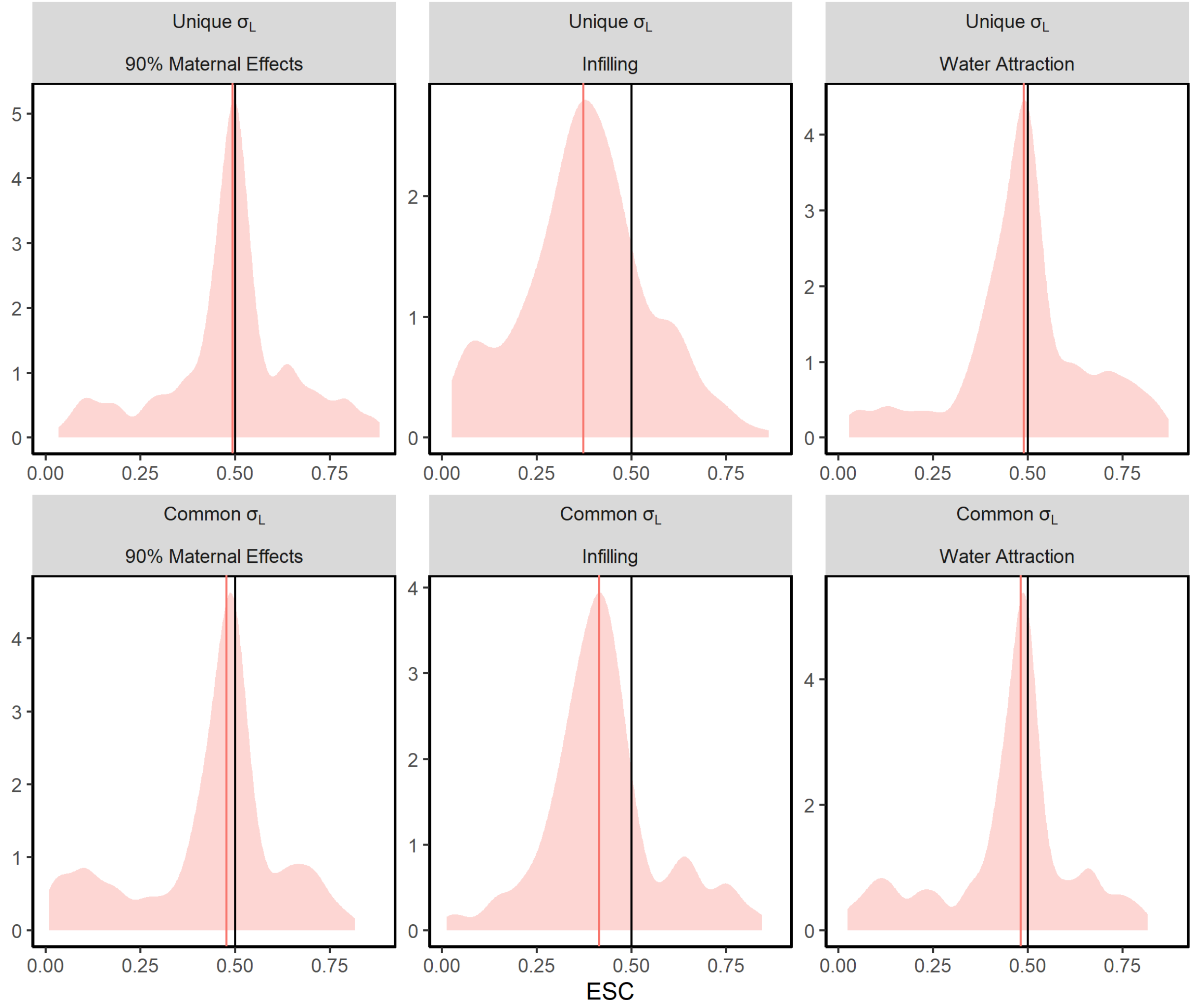

Figure S2.1. Distribution of ESC values for the entire meta-population when each zone is fished at its elver F_{50} when the density-dependent model is “Elver. + Silv. DD”, and the density-dependence occurs before fishing. The solid black line is the target of ESC_{50}, and the solid red line is the median of the distribution.

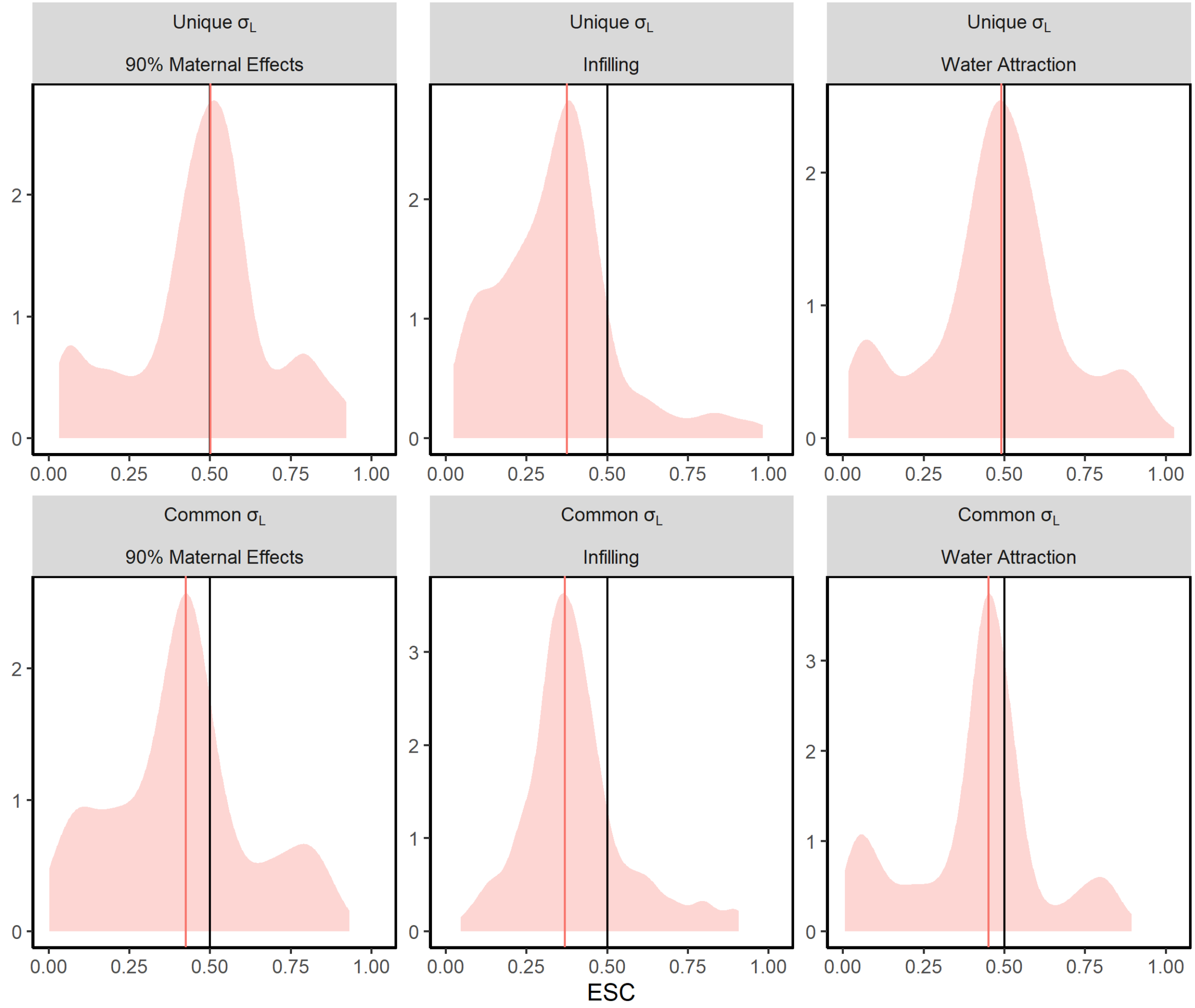

Figure S2.2. Distribution of ESC values for the entire meta-population when each zone is fished at its elver F_{50} when the density-dependent model is "Elver. + Silv. + Mort. DD", and the density-dependence occurs before fishing. The solid black line is the target of ESC_{50}, and the solid red line is the median of the distribution.

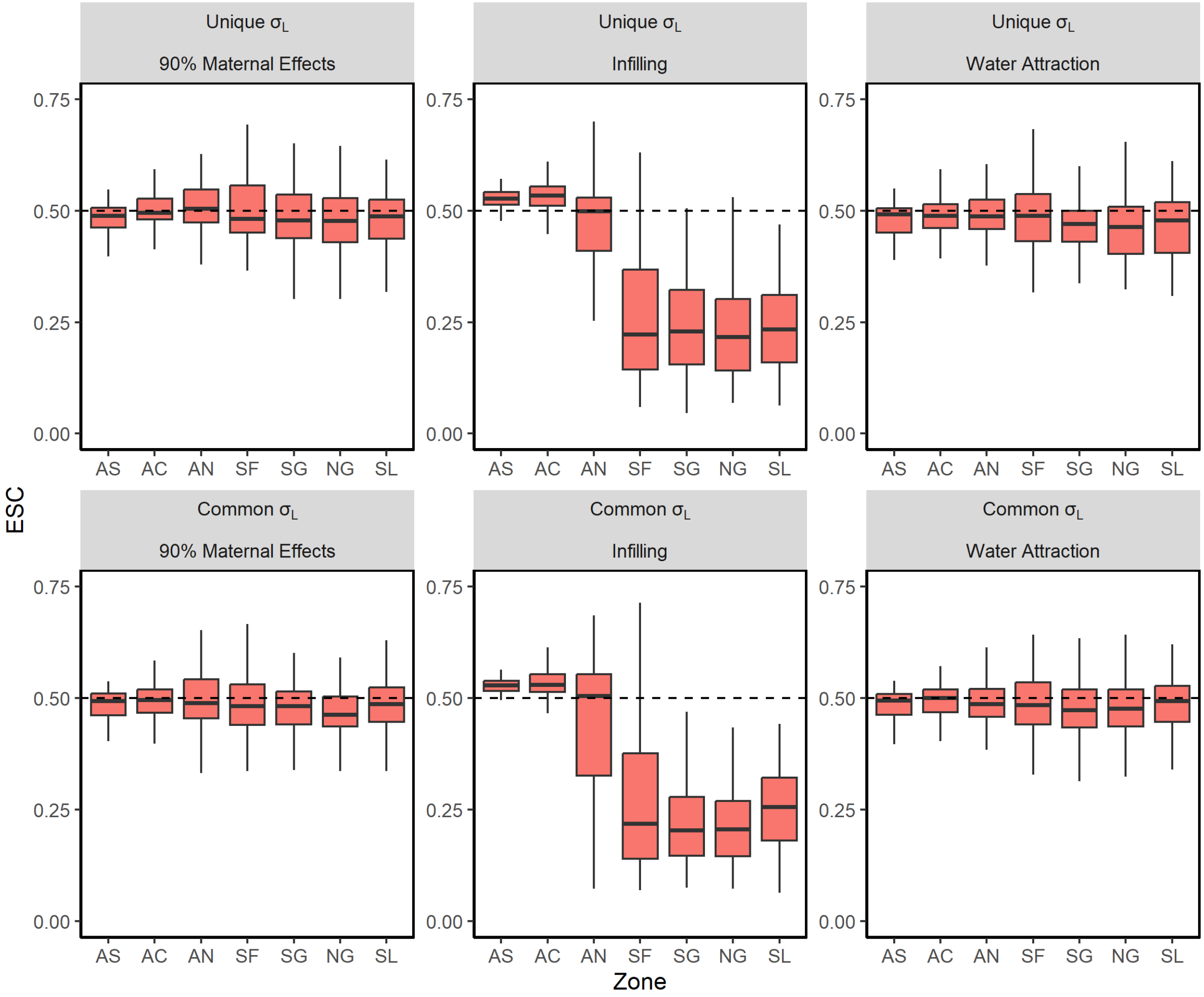

Figure S2.3. Distribution of ESC values of each zone, when each zone is fished at its elver F_{50} when the density-dependent model is "Elver + Silv. DD" and the density-dependence occurs before fishing.

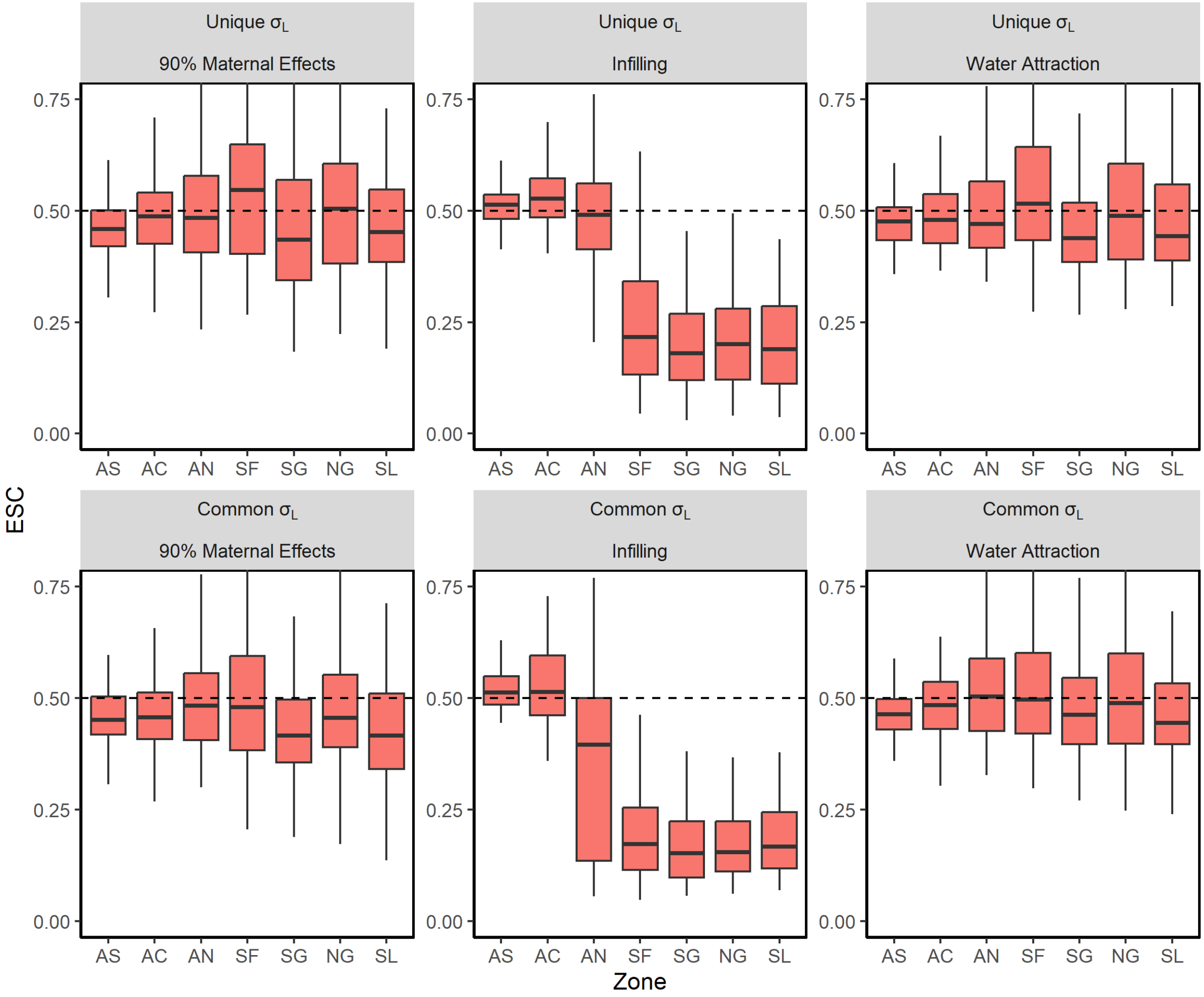

Figure S2.4. Distribution of ESC values of each zone, when each zone is fished at its elver F_{50} when the density-dependent model is "Elver + Silv. + Mort. DD" and the density-dependence occurs before fishing.

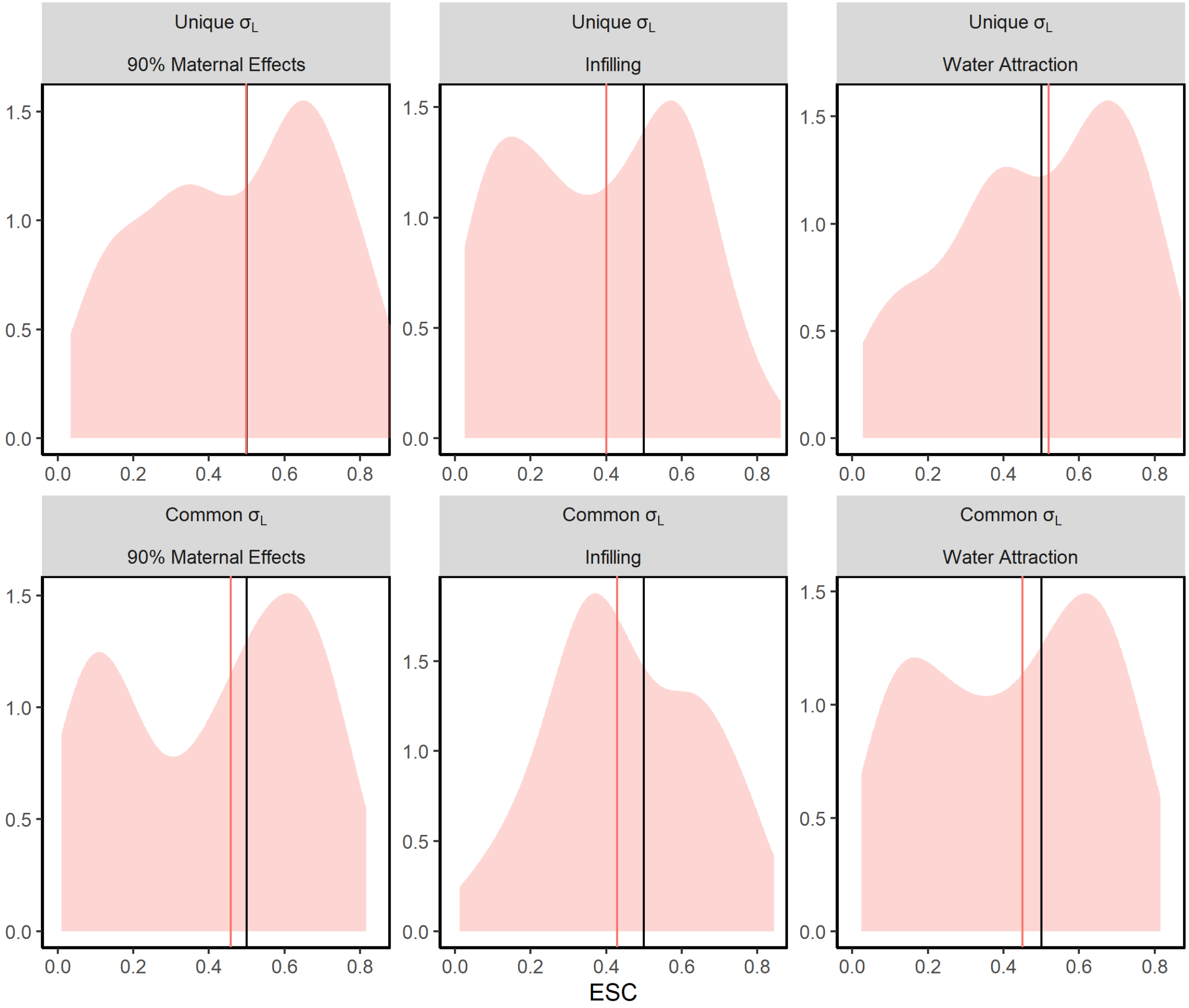

Figure S2.5. Distribution of ESC values for the entire meta-population when each zone is fished at its elver F_{50} when the density-dependent model is "Elver. + Silv. DD", and the density-dependence occurs after fishing. The solid black line is the target of ESC_{50}, and the solid red line is the median of the distribution.

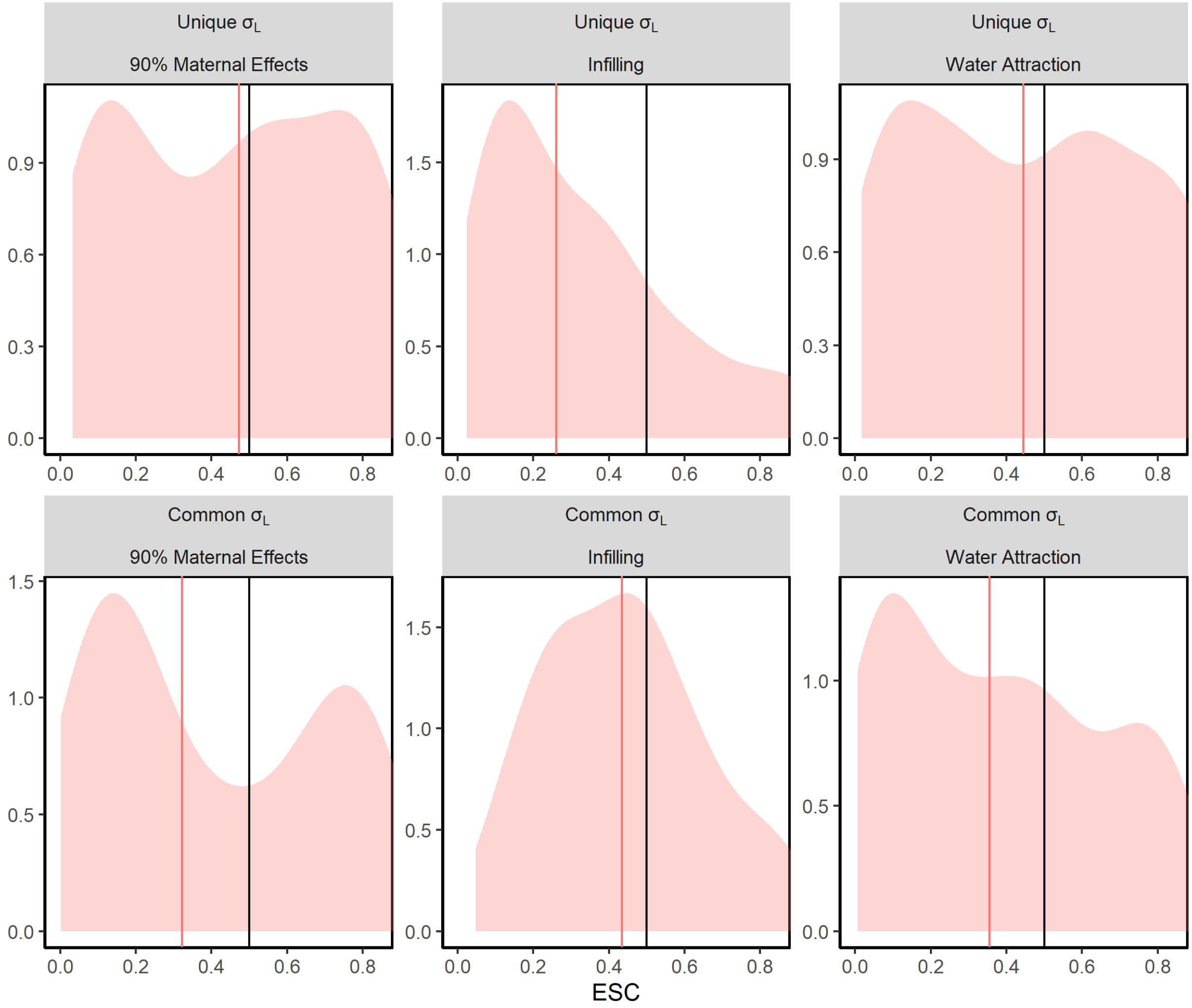

Figure S2.6. Distribution of ESC values for the entire meta-population when each zone is fished at its elver F_{50} when the density-dependent model is "Elver. + Silv. + Mort. DD", and the density-dependence occurs after fishing. The solid black line is the target of ESC_{50}, and the solid red line is the median of the distribution.

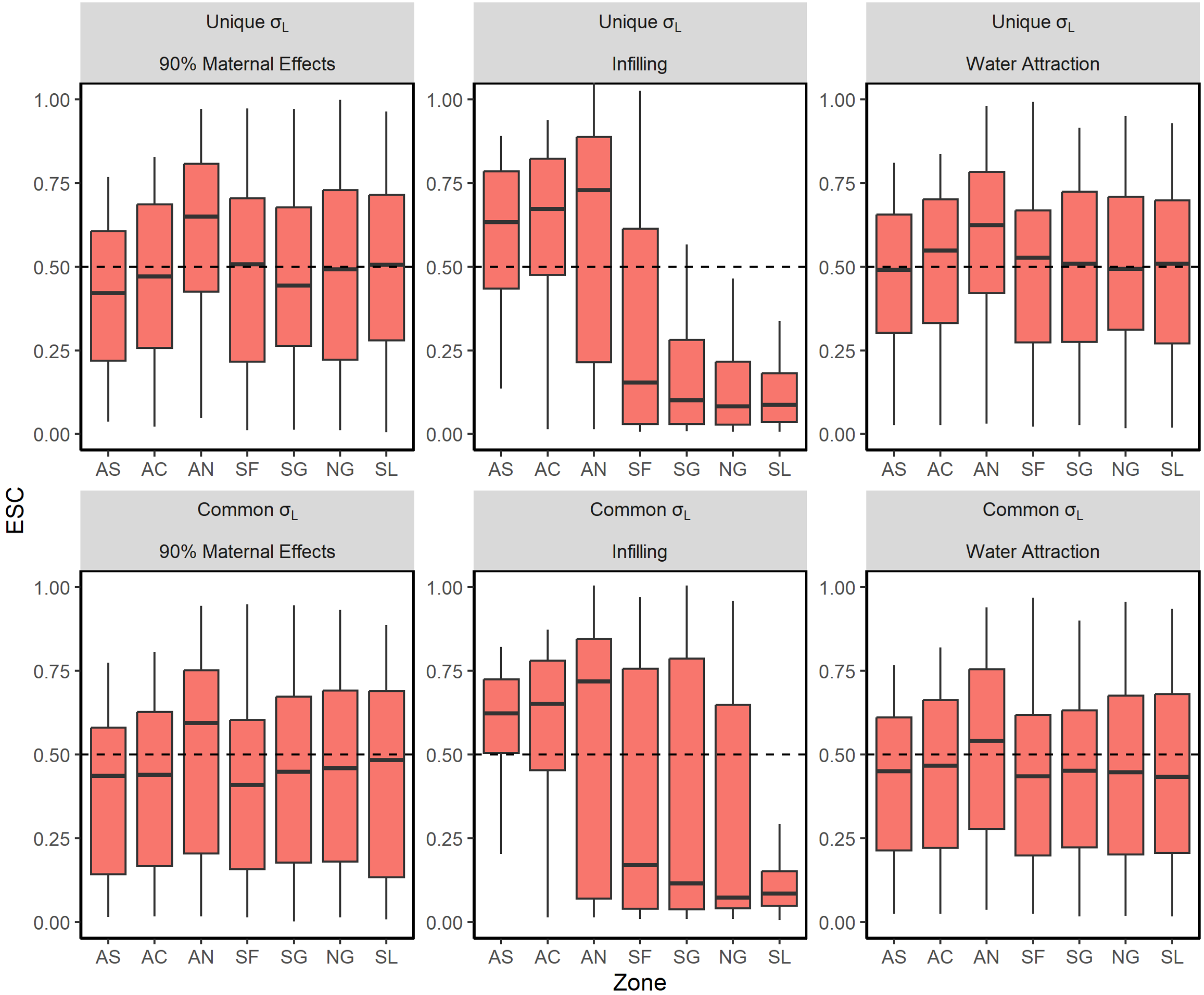

Figure S2.7. Distribution of ESC values of each zone, when each zone is fished at its elver F_{50} when the density-dependent model is "Elver + Silv. DD" and the density-dependence occurs after fishing.

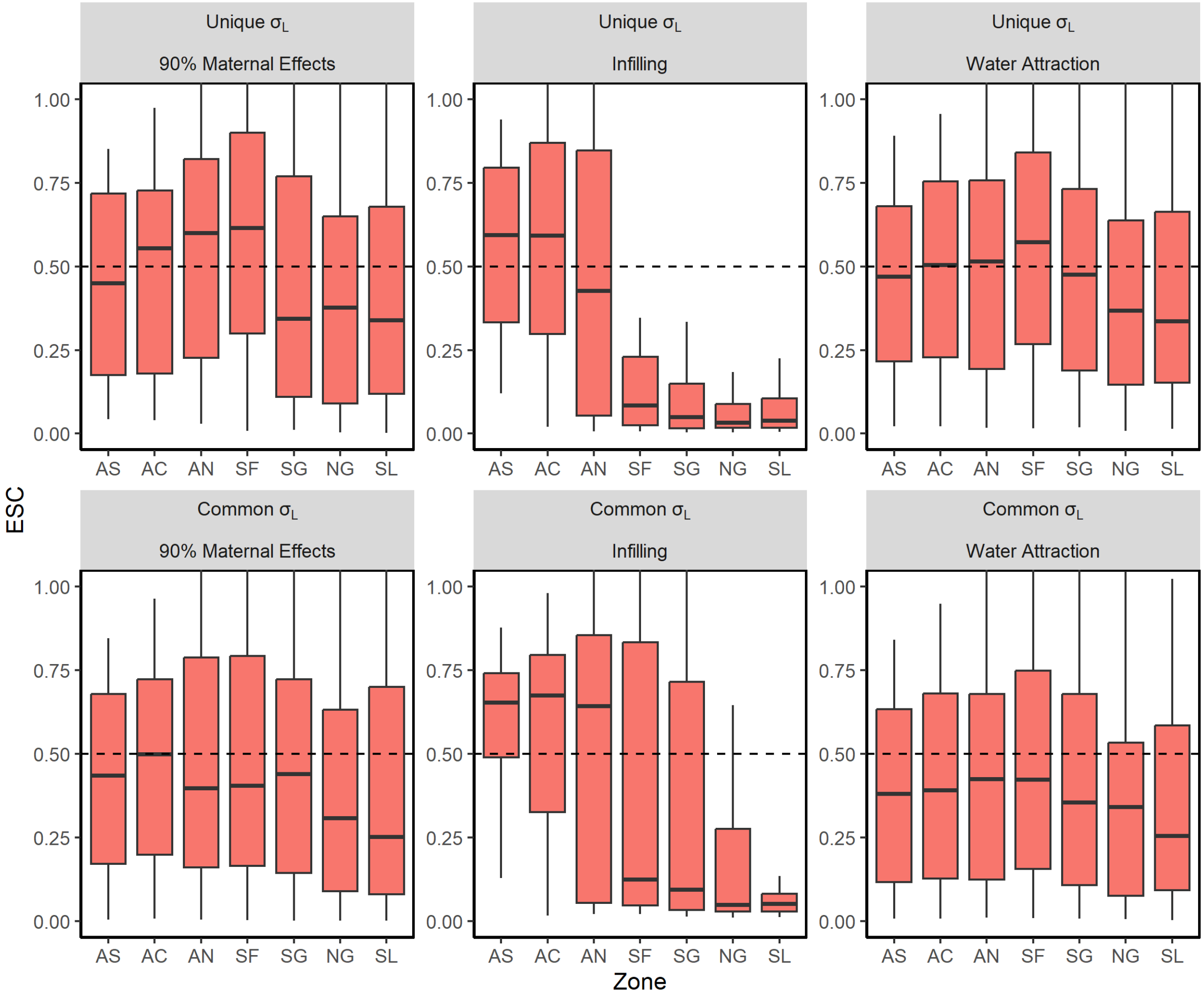

Figure S2.8. Distribution of ESC values of each zone, when each zone is fished at its elver F_{50} when the density-dependent model is "Elver + Silv. + Mort. DD" and the density-dependence occurs after fishing.

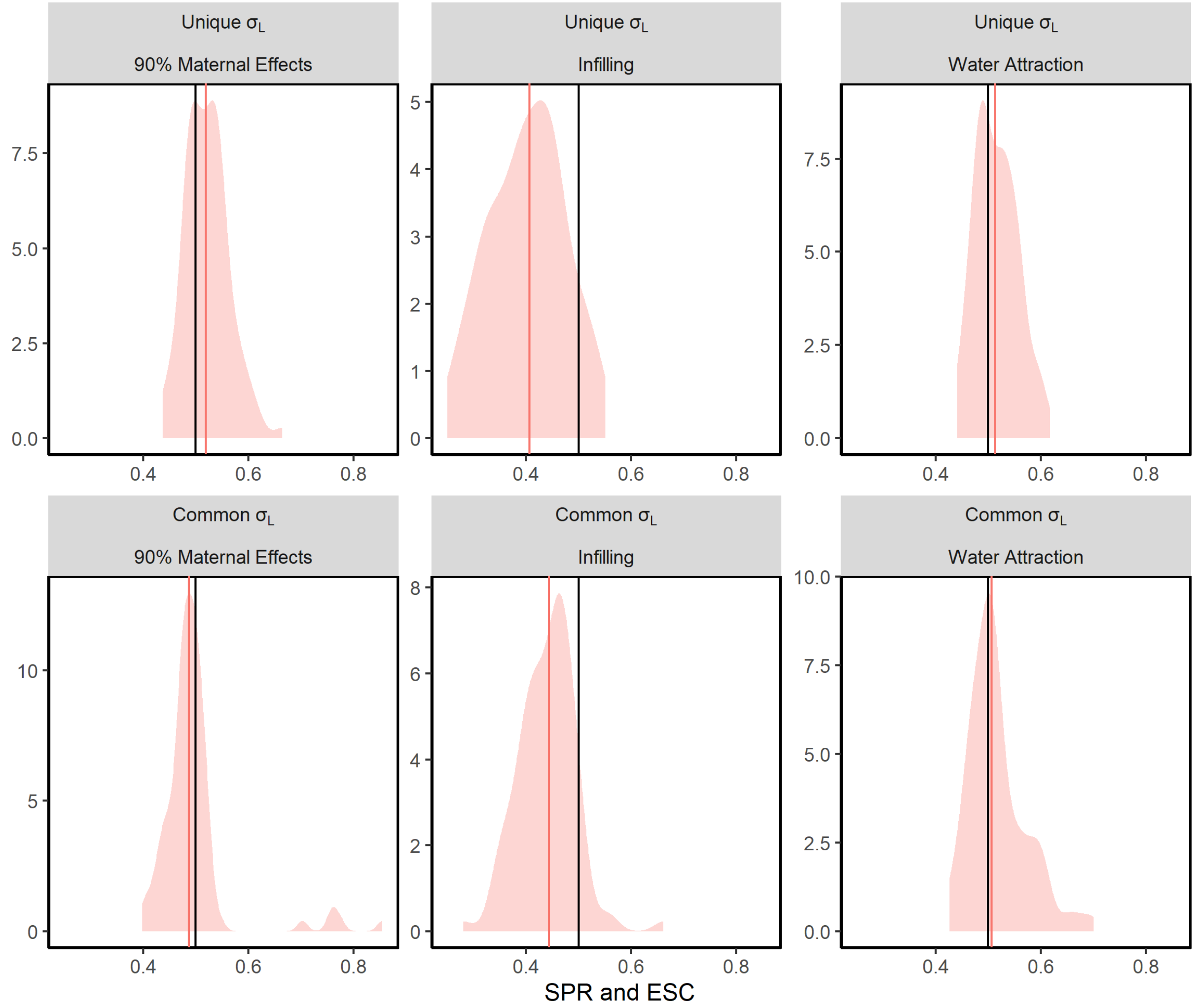

Figure S2.9. Distribution of ESC values for the entire meta-population when each zone is fished at its eel F_{50} when the density-dependent model is "Elver + Silv. DD". The solid black line is the target of ESC_{50}, and the solid red line is the median of the distribution.

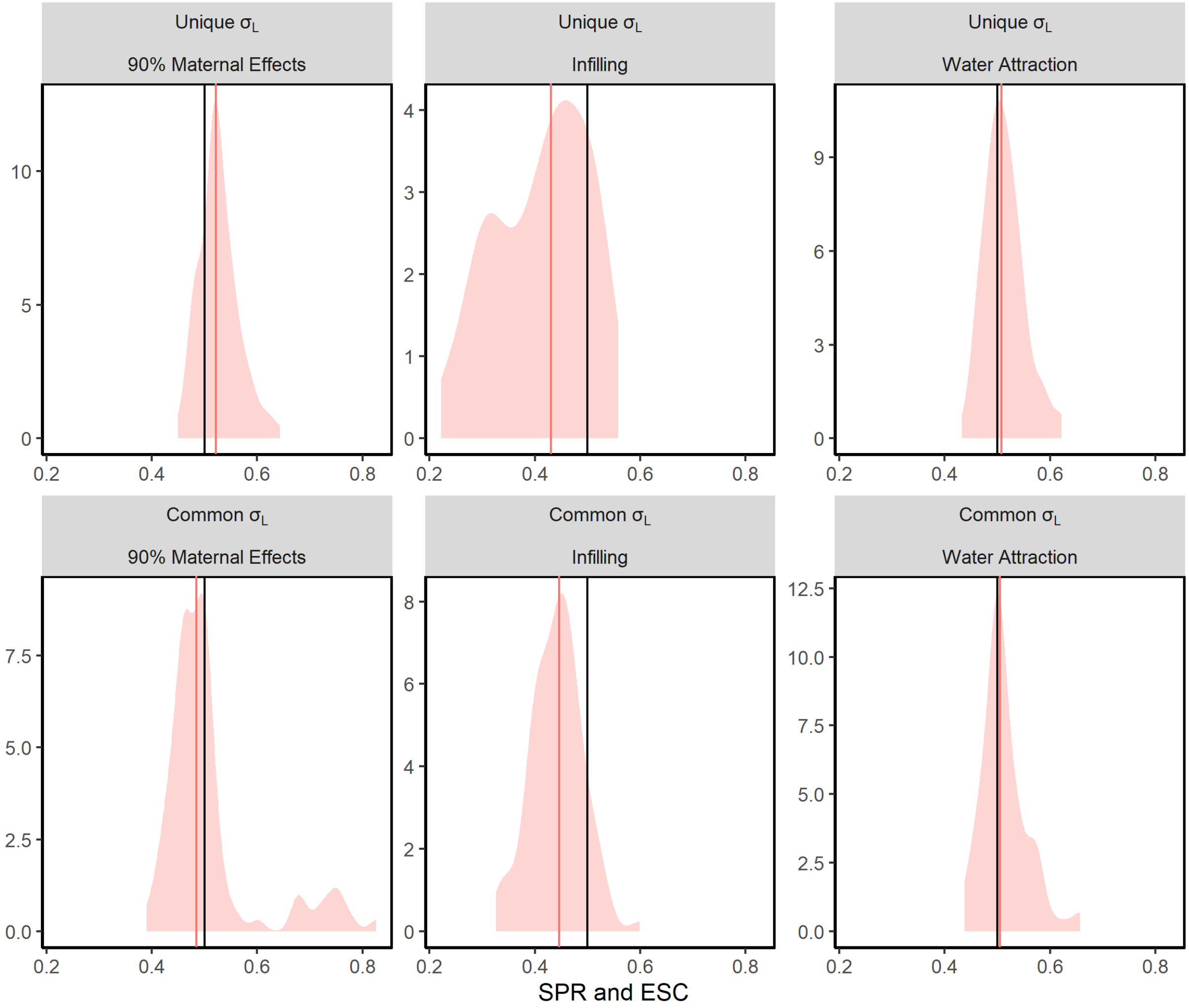

Figure S2.10. Distribution of ESC values for the entire meta-population when each zone is fished at its eel F_{50} when the density-dependent model is “Elver + Silv. + Mort. DD”. The solid black line is the target of ESC_{50}, and the solid red line is the median of the distribution.

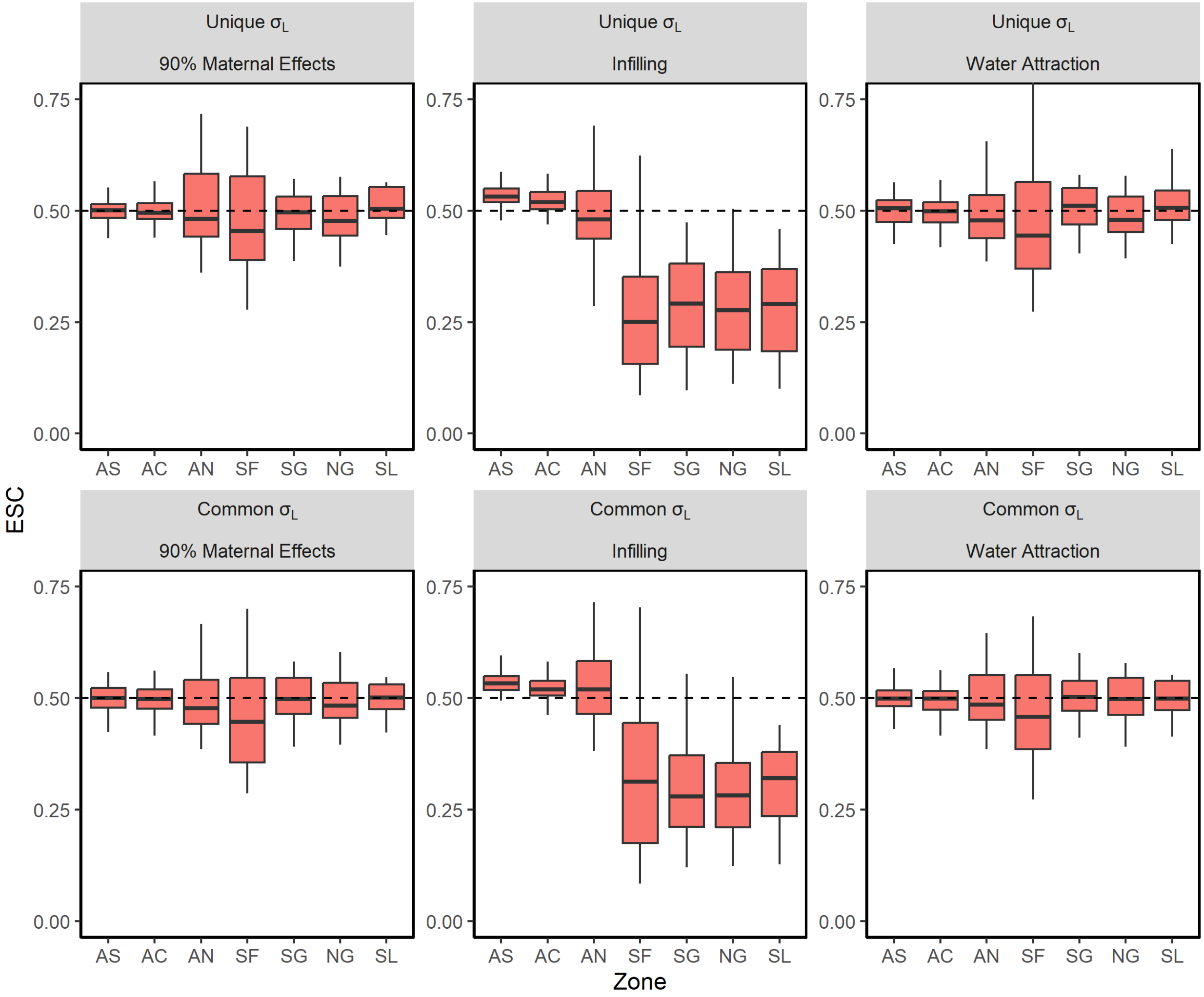

Figure S2.11. Distribution of ESC values of each zone, when each zone is fished at its eel F_{50} when the density-dependent model is "Elver + Silv. DD".

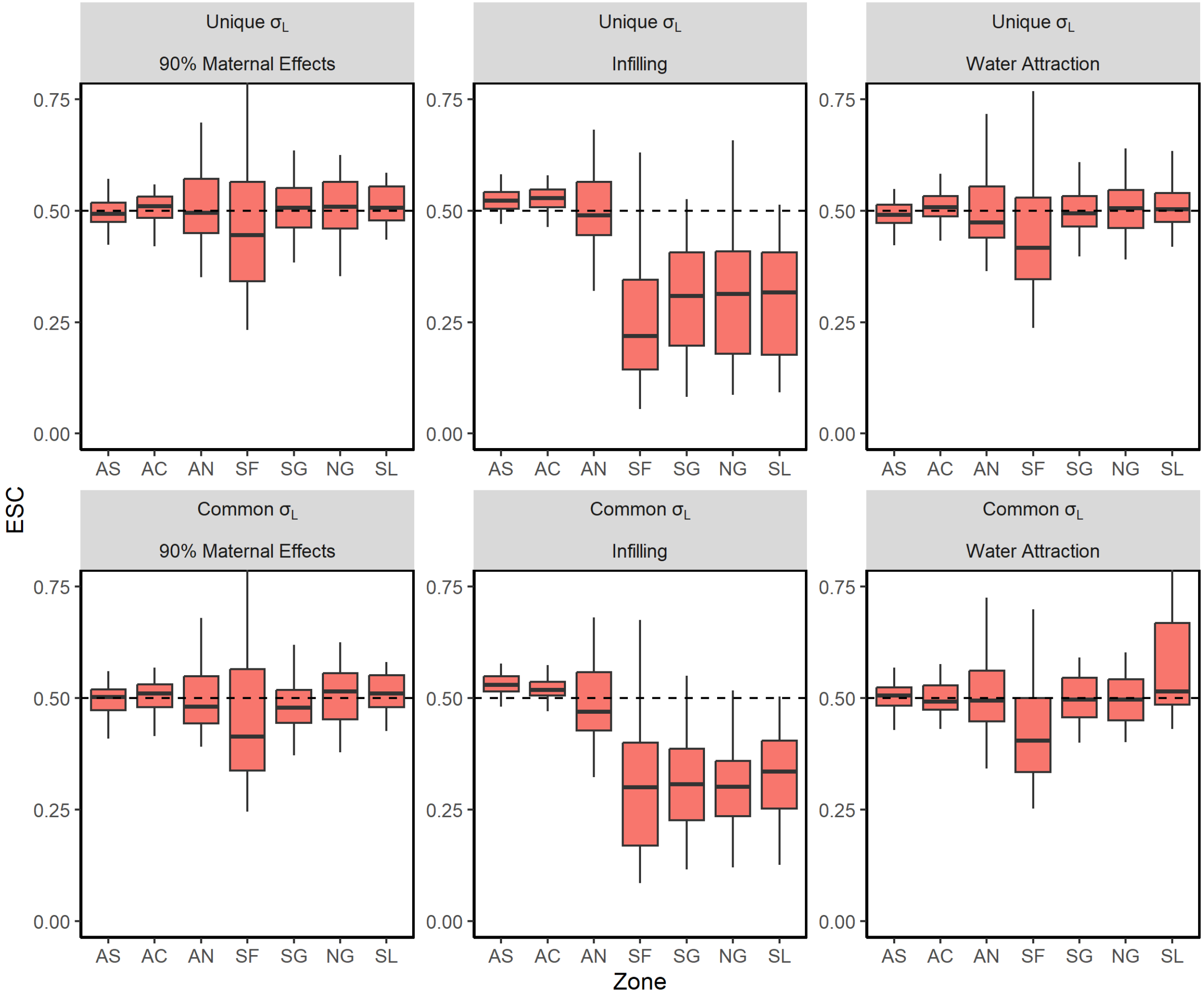

Figure S2.12. Distribution of ESC values of each zone, when each zone is fished at its eel F_{50} when the density-dependent model is "Elver + Silv. + Mort. DD".

EXCESS MORTALITY

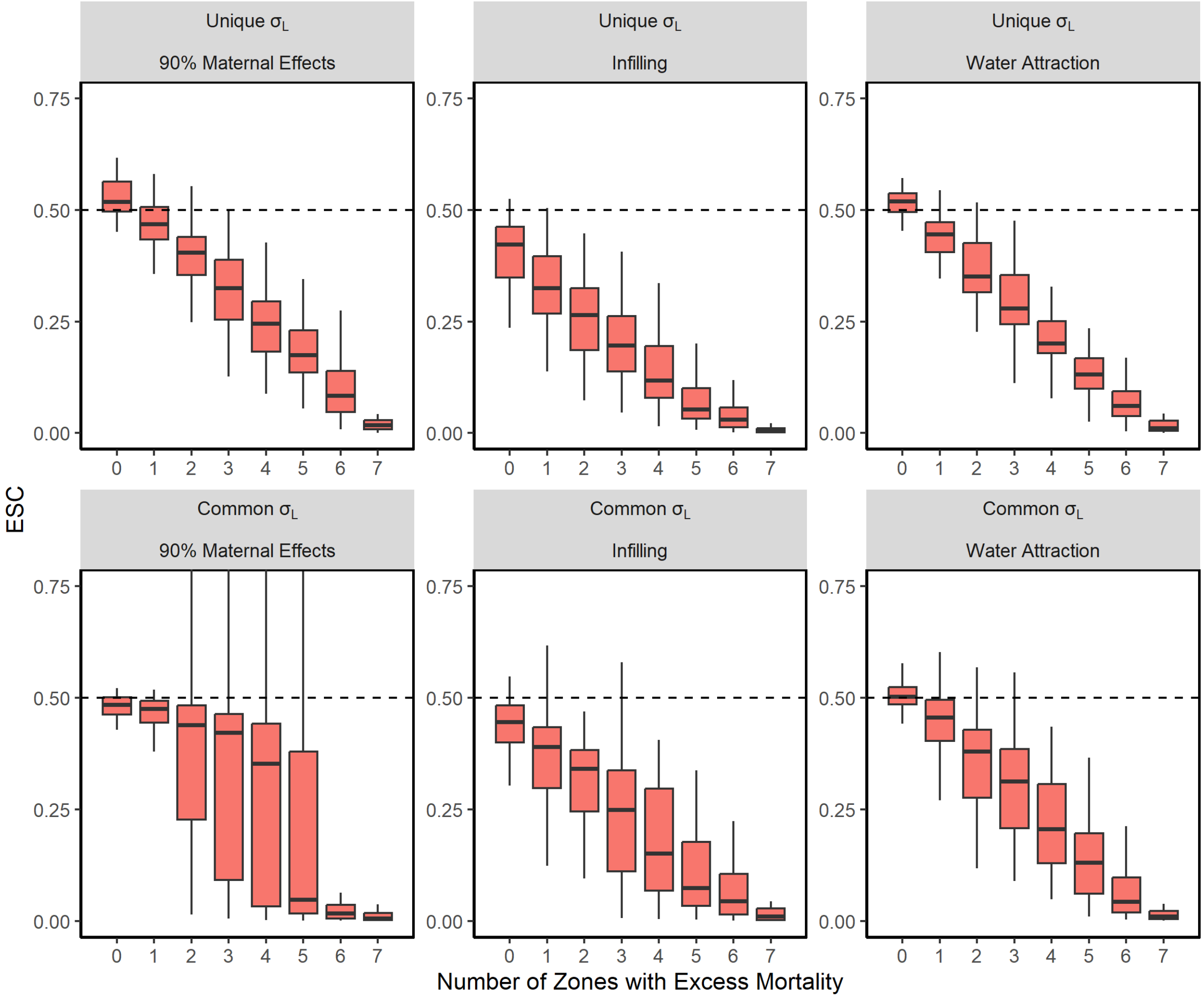

Figure S2.13. Effects of excess mortality on the elver stage on the zone meta-population ESC values across different leptocephali survival and distribution options using the “Elver + Silv. DD” density-dependent model. This simulation assumes that elver density-dependence happens before the elver fishery.

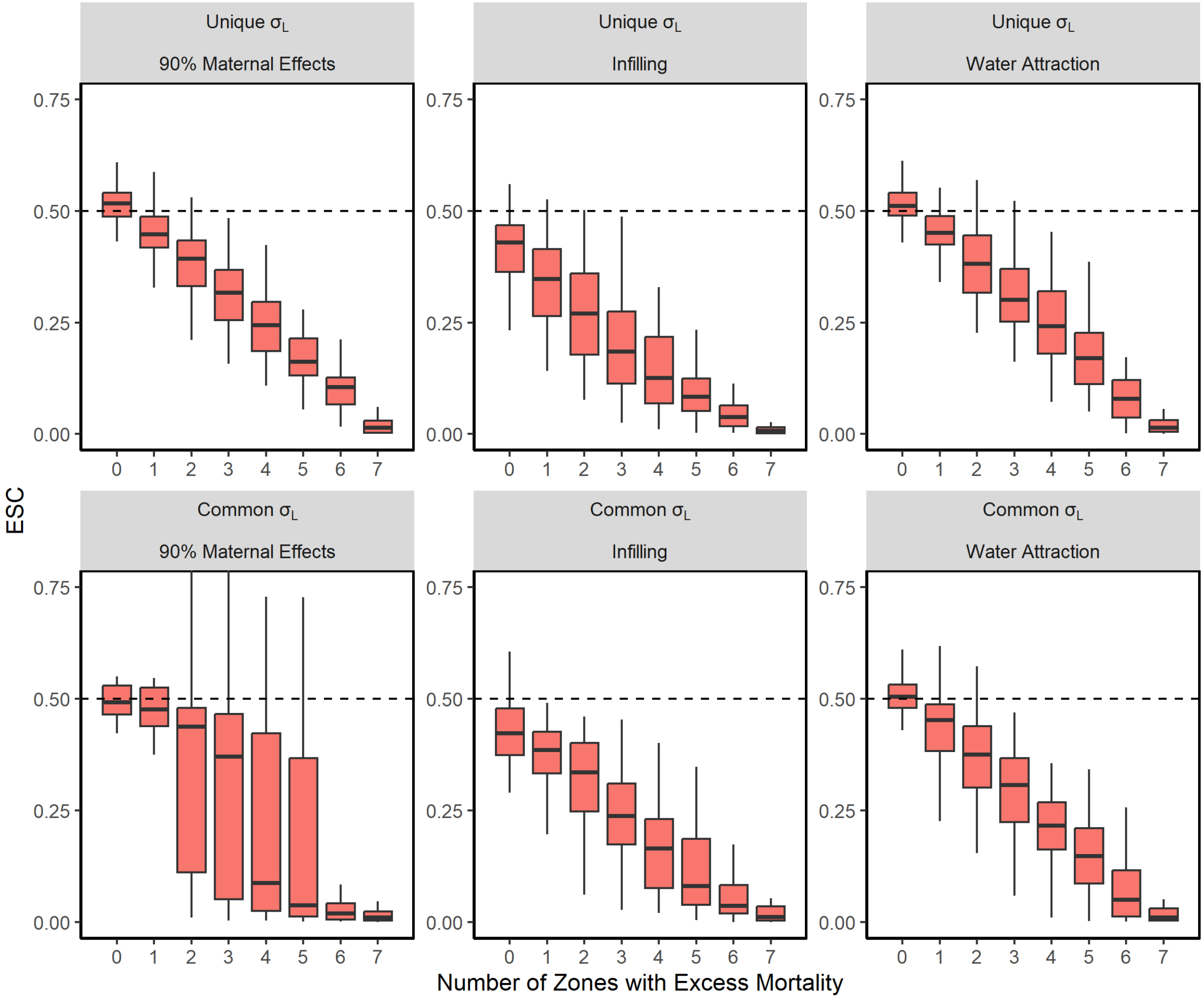

Figure S2.14. Effects of excess mortality on the elver stage on the zone meta-population ESC values across different leptocephali survival and distribution options using the "Elver + Silv. + Mort. DD" density-dependent model. This simulation assumes that elver density-dependence happens before the elver fishery.

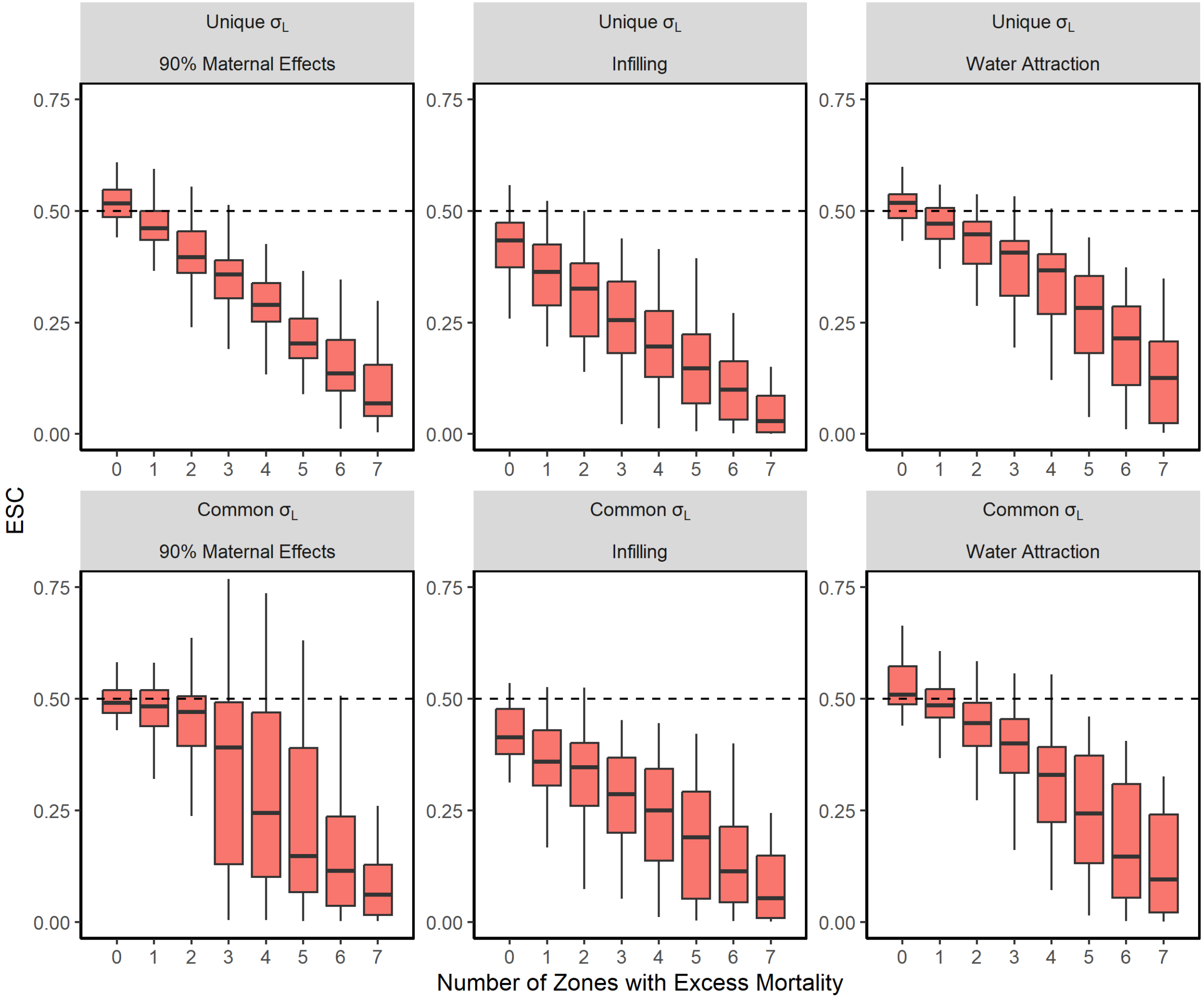

Figure S2.15. Effects of excess mortality on the elver stage on the zone meta-population ESC values across different leptocephali survival and distribution options using the “Elver + Silv. DD” density-dependent model. This simulation assumes that elver density-dependence happens after the elver fishery.

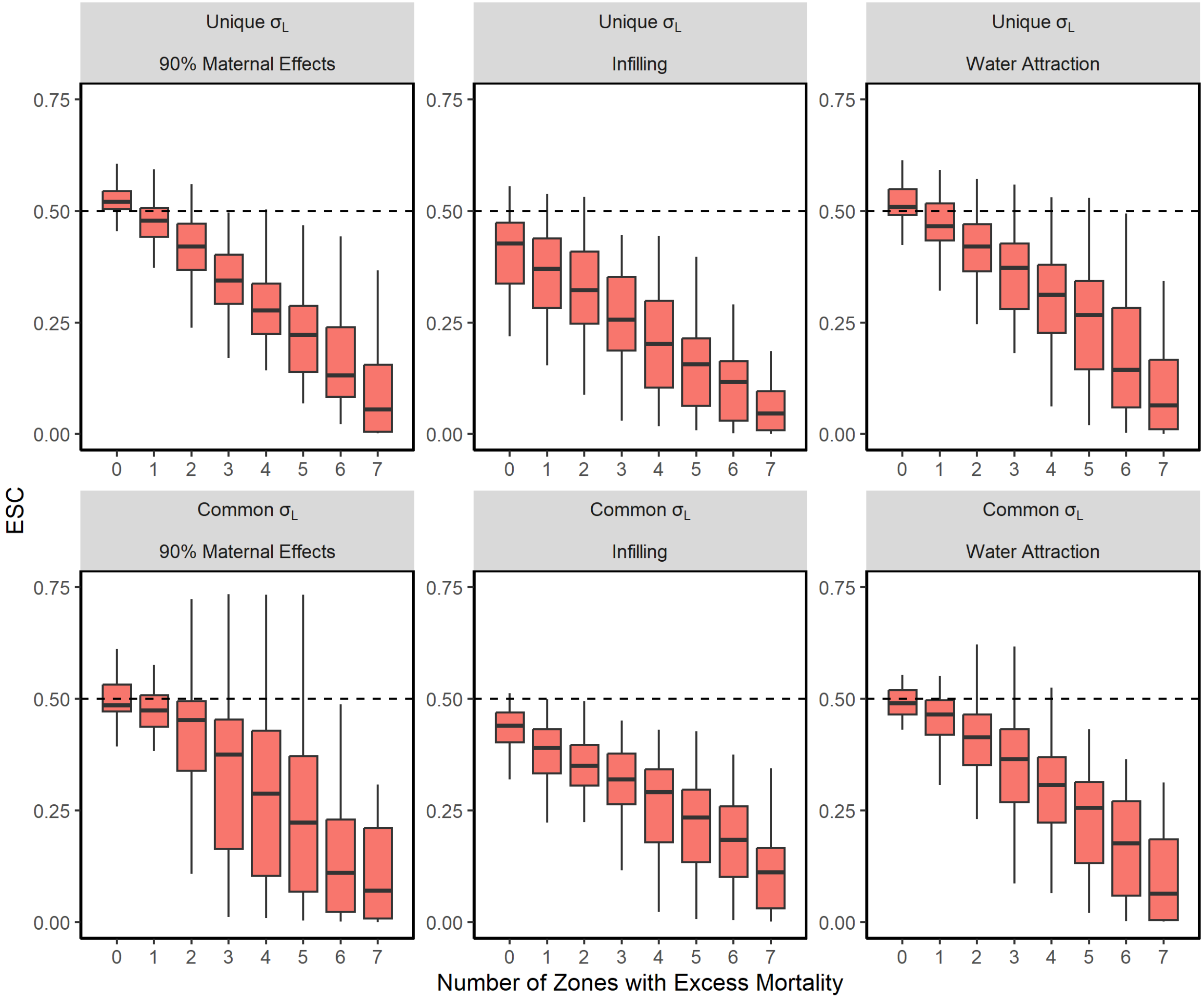

Figure S2.16. Effects of excess mortality on the elver stage on the zone meta-population ESC values across different leptocephali survival and distribution options using the "Elver + Silv. + Mort. DD" density-dependent model. This simulation assumes that elver density-dependence happens after the elver fishery.

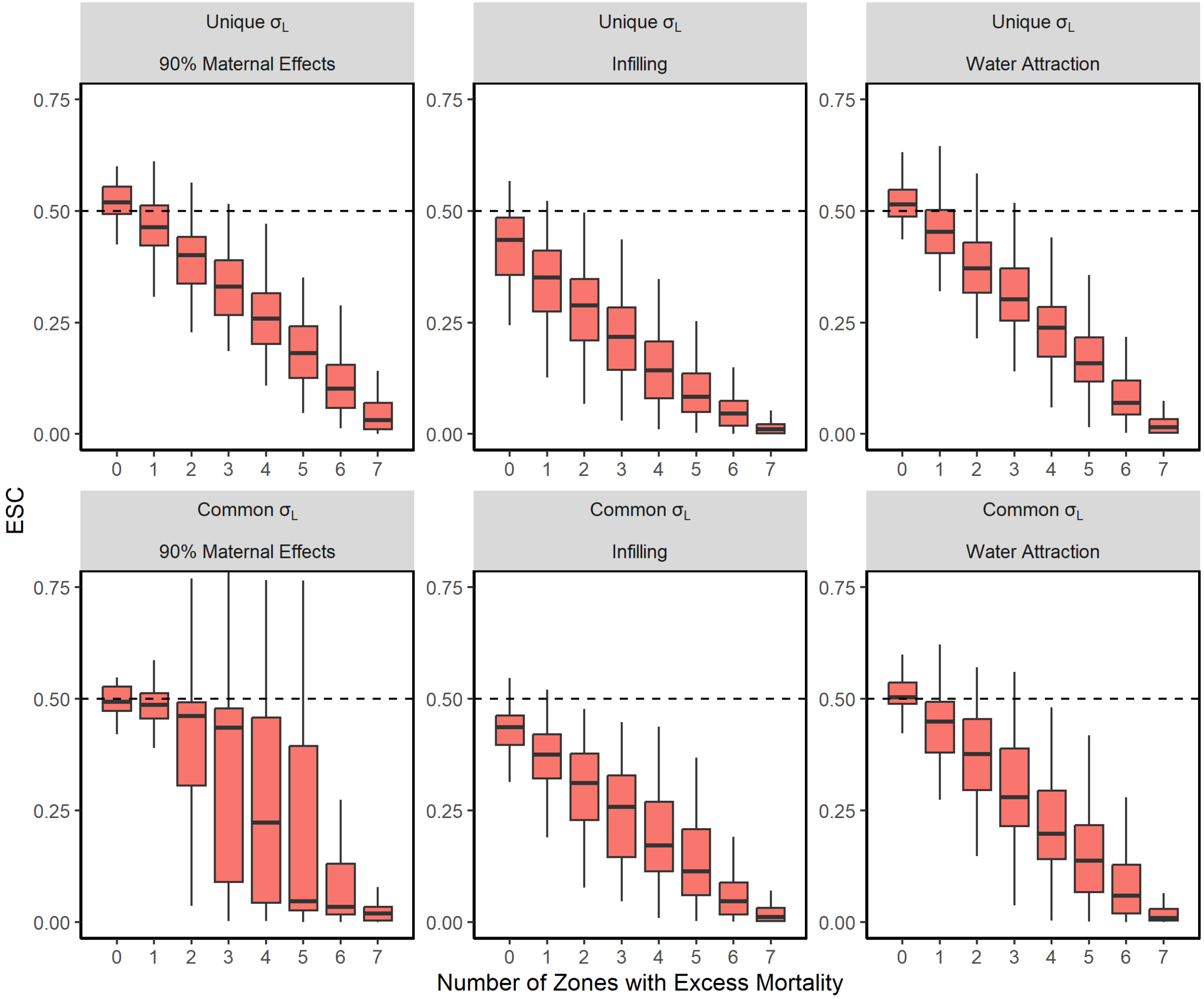

Figure S2.17. Effects of excess mortality on the eel stage on the zone meta-population ESC values across different leptocephali survival and distribution options using the "Elver + Silv. DD" density-dependent model.

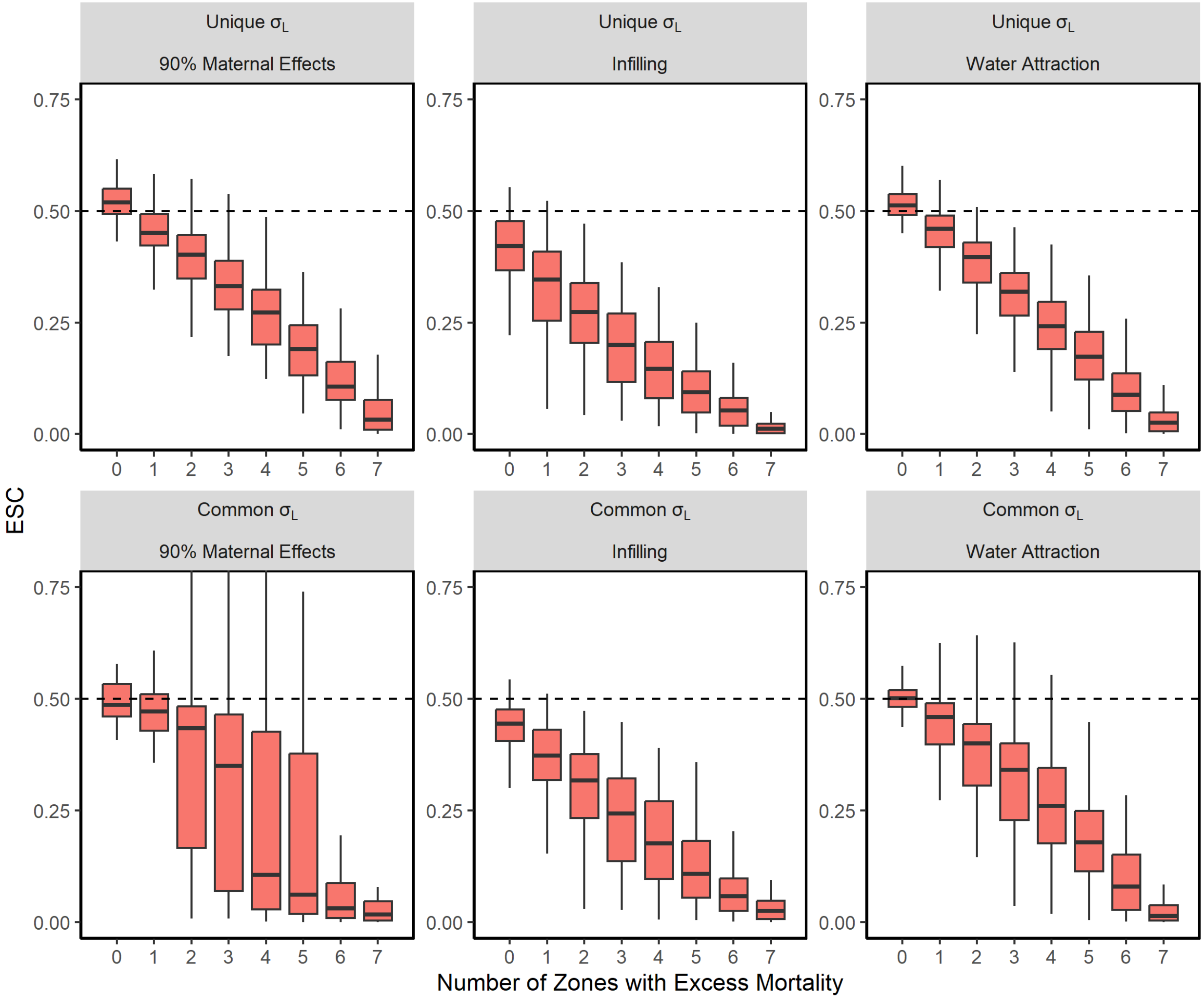

Figure S2.18. Effects of excess mortality on the eel stage on the zone meta-population ESC values across different leptocephali survival and distribution options using the "Elver + Silv. + Mort. DD" density-dependent model.

RECOVERY

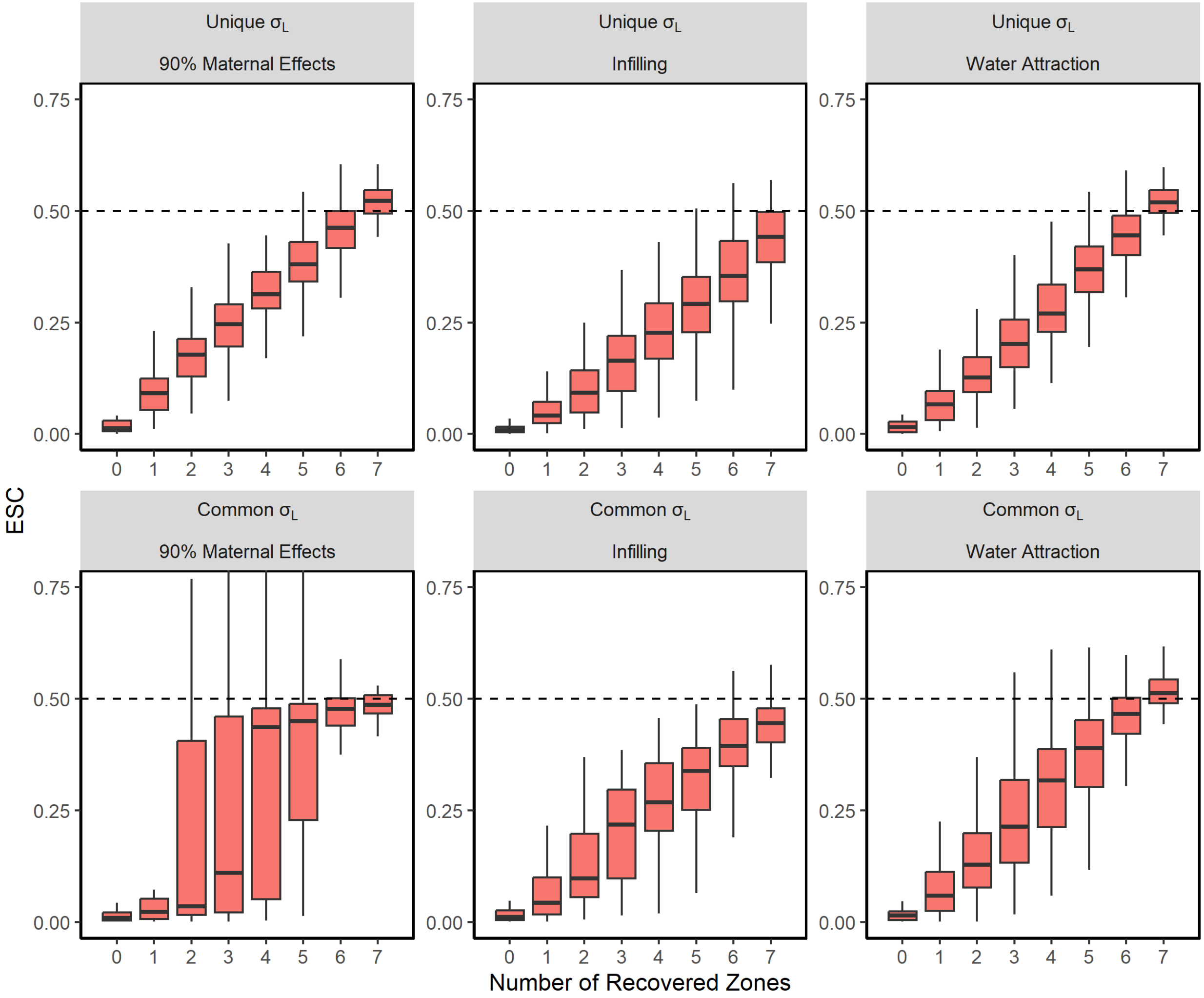

Figure S2.19. Effects of reducing excess mortality on the elver stage on the total meta-population ESC values across different leptocephali survival and distribution options using the "Elver + Silv. DD" density-dependent model. This simulation assumes elver density-dependence occurs before the fishery.

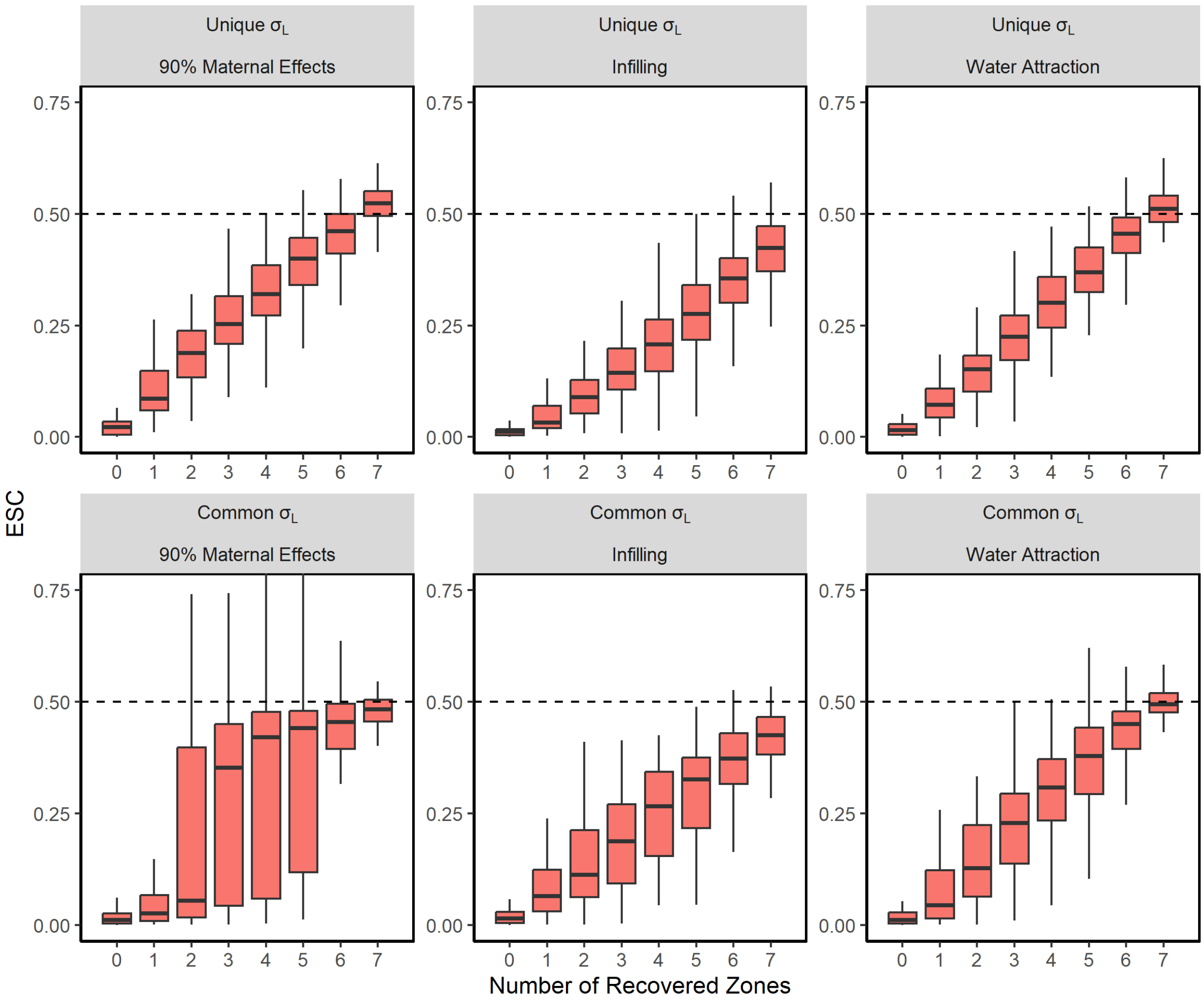

Figure S2.20. Effects of reducing excess mortality on the elver stage on the total meta-population ESC values across different leptocephali survival and distribution options using the "Elver + Silv. + Mort. DD" density-dependent model. This simulation assumes elver density-dependence occurs before the fishery.

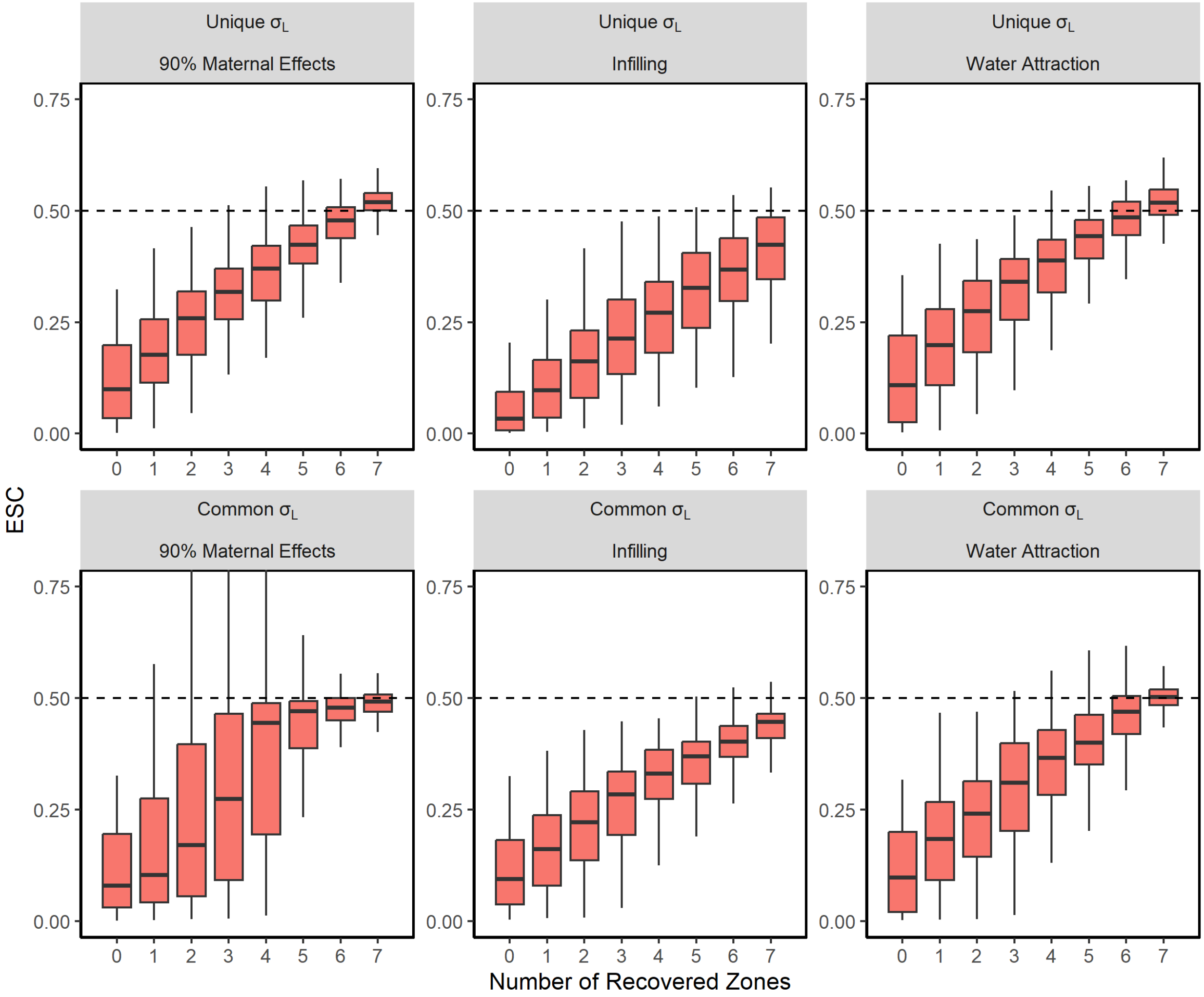

Figure S2.21. Effects of reducing excess mortality on the elver stage on the total meta-population ESC values across different leptocephali survival and distribution options using the "Elver + Silv. DD" density-dependent model. This simulation assumes elver density-dependence occurs after the fishery.

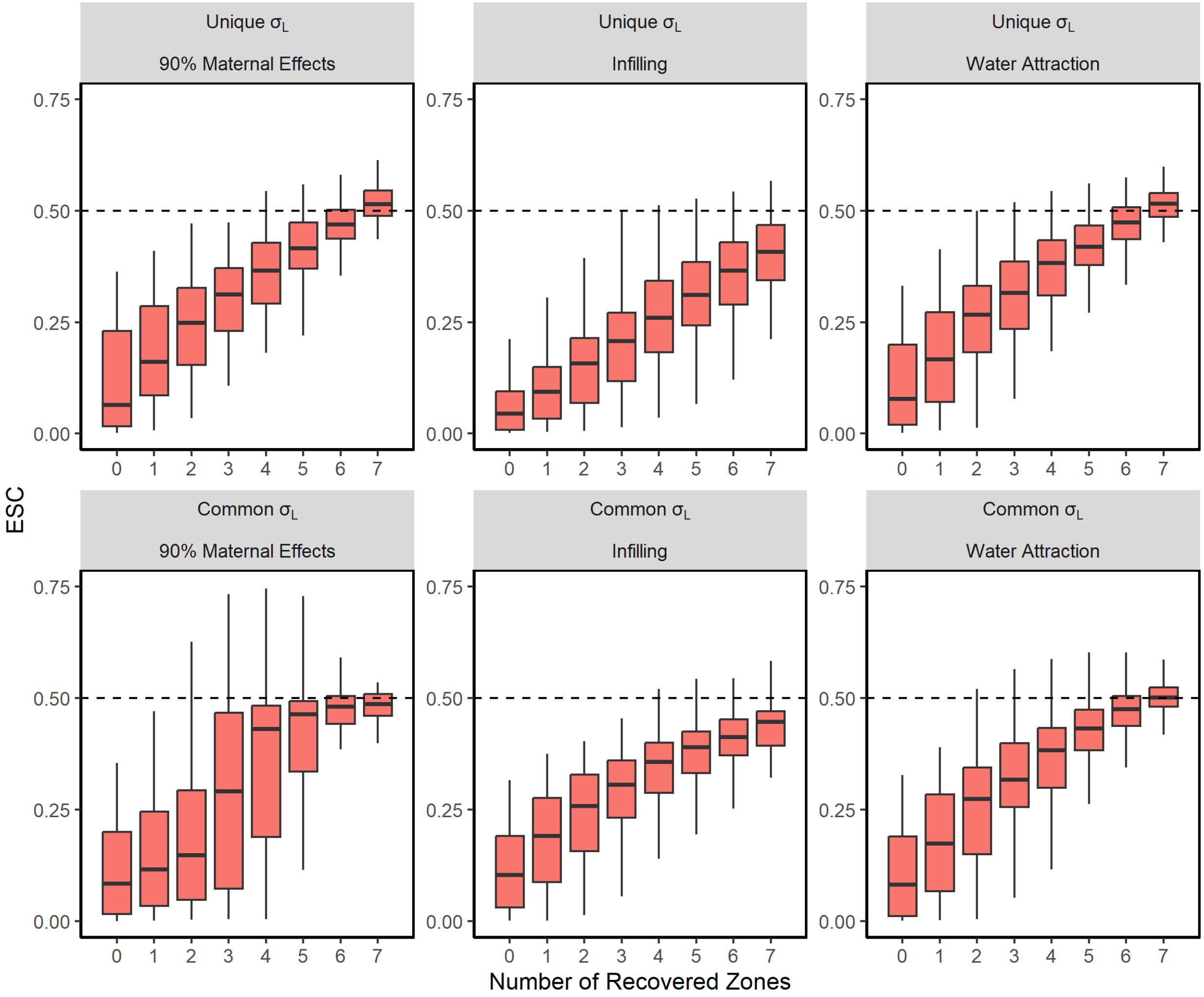

Figure S2.22. Effects of reducing excess mortality on the elver stage on the total meta-population ESC values across different leptocephali survival and distribution options using the "Elver + Silv. + Mort. DD" density-dependent model. This simulation assumes elver density-dependence occurs after the fishery.

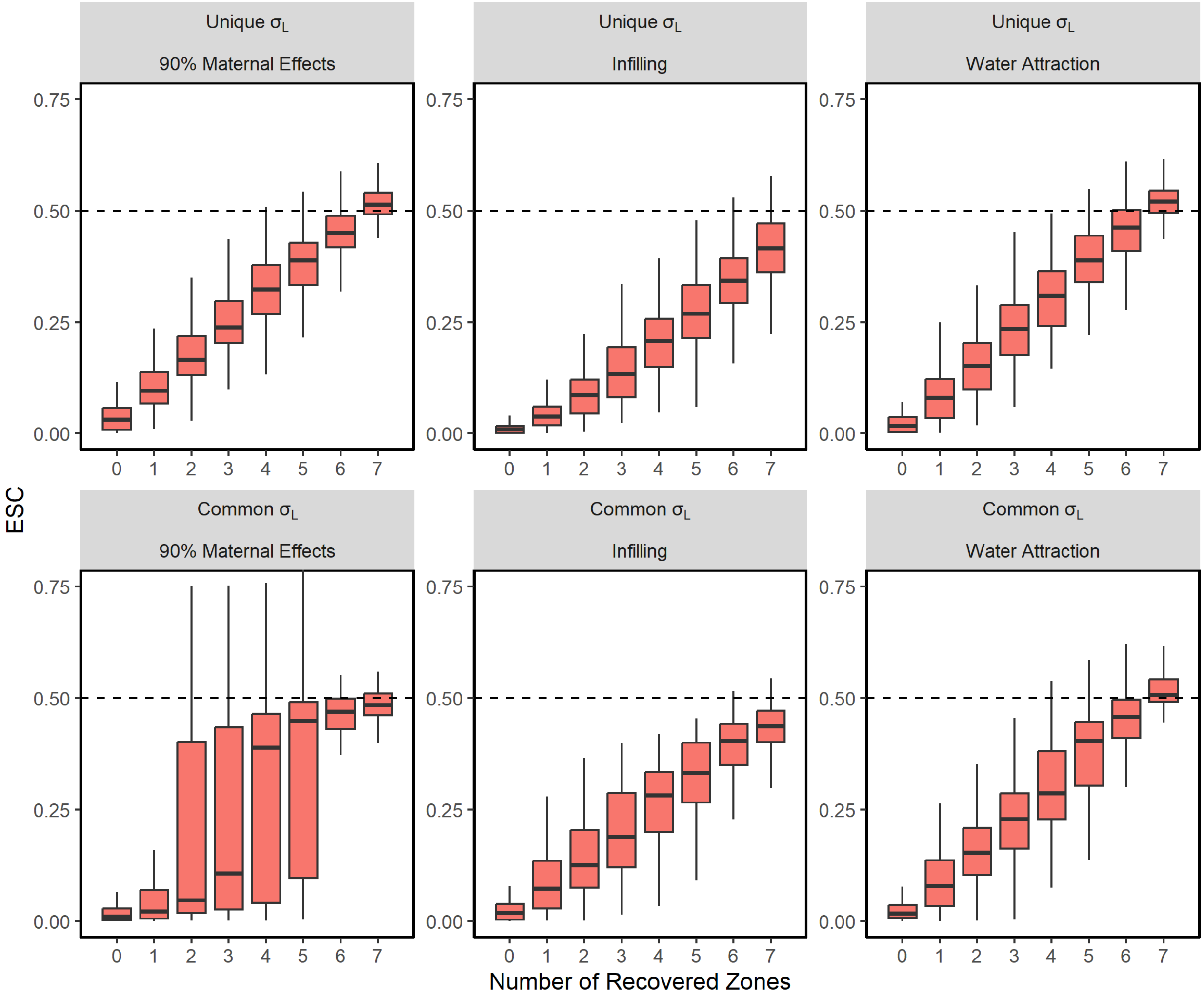

Figure S2.23. Effects of reducing excess mortality on the eel stage on the total meta-population ESC values across different leptocephali survival and distribution options using the "Elver + Silv. DD" density-dependent model.

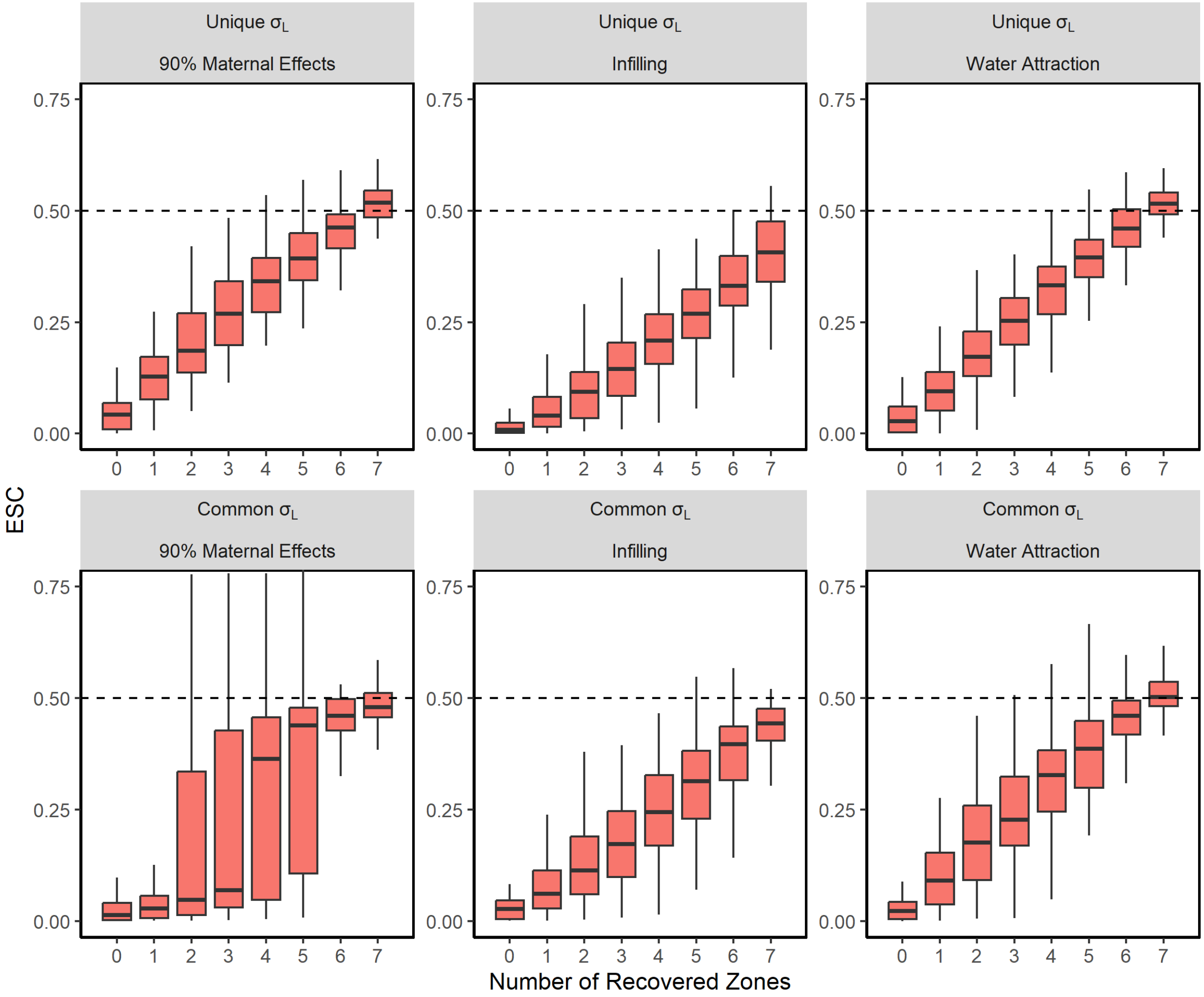

Figure S2.24. Effects of reducing excess mortality on the eel stage on the total meta-population ESC values across different leptocephali survival and distribution options using the "Elver + Silv. + Mort. DD" density-dependent model.