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# Mortality reference points for the American Eel *(Anguilla rostrata)* and an application for evaluating cumulative impacts of anthropogenic activities

# Niveaux de référence pour la mortalité de l'anguille d'Amérique (*Anguilla rostrata*) et application pour l'évaluation des répercussions cumulatives des activités anthropogéniques

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# ABSTRACT

Canada has committed to using the Precautionary Approach (PA) in managing stocks. To be compliant with the PA, fishery management plans should include harvest strategies that incorporate a Limit Reference Point that defines the critical / cautious zones, and a Removal Reference that defines the maximum removal rate in the healthy zone. We propose that the Spawner Per Recruit (SPR) model should be the minimum default model considered to define fishing rate reference points for the American Eel (*Anguilla rostrata*). We discuss how the SPR approach can be extended to include complex life histories at the local scale, including those associated with the phenotypic plasticity of habitat use, stock complex dynamics, and cumulative impacts. The assumptions or estimates of natural mortality and probability of metamorphosing are relevant only for the age or size groups which are also vulnerable to the human activity being assessed. The derivation of these reference points and their use in management will benefit the species as a whole by ensuring that spawning escapement from each region would be proportional to abundance and conditioned by the life history characteristics of the region. Defining only mortality rate reference levels can be inadequate when stock biomass is low as it does not provide protection against depensatory effects which could express themselves at low biomass levels. Defining reference points is the first part of the larger assessment and management process. Assessing stock status of American Eel remains a challenge.

# RÉSUMÉ

Le Canada s'est engagé à appliquer l'approche de précaution à la gestion des stocks de poissons. Afin de nous conformer à cette approche, les plans de gestion des pêches doivent intégrer des stratégies incluant un niveau de référence limite définissant les zones critiques ou de prudence, ainsi qu'un niveau d'exploitation limite établissant le taux d'exploitation maximal dans la zone saine. Nous proposons que le modèle des géniteurs par recrue soit considéré comme le modèle de base par défaut définissant les niveaux de référence pour le taux de prise de l'anguille d'Amérique (*Anguilla rostrata*). Nous discutons de la façon dont ce modèle peut être développé afin d'inclure des cycles biologiques complexes à l'échelle locale, notamment les cycles associés à la plasticité phénotypique de l'utilisation de l'habitat, à la dynamique complexe du stock et aux répercussions cumulatives. Les hypothèses ou les estimations relatives à la mortalité naturelle et les probabilités de métamorphose sont pertinentes uniquement pour les groupes d'âge ou de taille qui sont également vulnérables à l'activité humaine évaluée. La dérivation de ces niveaux de référence et leur application à la gestion profiteront à l'espèce dans son ensemble en assurant que l'échappée de géniteurs de chaque région sera proportionnelle à l'abondance et conditionnée par les caractéristiques du cycle biologique de la région. Définir seulement que l'établissement de niveaux de référence pour le taux de mortalité peut s'avérer inadéquat lorsque la biomasse du stock est faible, car il n'offre aucune protection contre le mécanisme dépensatoire pouvant se déclencher à de faibles niveaux de biomasse. L'établissement de niveaux de référence constitue la première partie du processus général d'évaluation et de gestion. L'évaluation de l'état de l'anguille d'Amérique demeure un défi.

# INTRODUCTION

Canada, as signatory to the United Nations Agreement on Straddling and Highly Migratory Fish Stocks (UNFA) which came into force in 2001, has committed to using the Precautionary Approach (PA) in managing fish stocks. DFO completed a policy document entitled "A fishery decision-making framework incorporating the Precautionary Approach" which explains in detail how the precautionary approach will be put into practice (DFO 2009). To be compliant with the PA, fishery management plans should include harvest strategies that incorporate a Limit Reference Point that defines the critical / cautious zones and an Upper Stock Reference that delimits the cautious / healthy zones on the stock status axis, and a Removal Reference that defines the maximum removal rate in the healthy zone. The PA concept makes no distinctions among human-induced causes of animal death. It applies equally to mortality of animals from fishing, from passage through hydro-electric turbines, or from any other anthropogenic cause.

ICES (2001) provided the first proposal for mortality rate reference points for the American Eel (*Anguilla rostrata*) based on general principles developed and applied for other species. Using Spawning Per Recruit (SPR) analysis, ICES (2001) proposed F at 30%SPR as a limit removal rate reference point and F at 50%SPR as a target value. This was consistent with ICES (1997); for data poor situations a mortality rate which provides 30% of the virgin (F=0) SPR is a reasonable first estimate of $F_{lim}$ until further information is gathered. Considering uncertainties, a preliminary estimate for $F_{pa}$ could be 50%SPR.

In 2006, DFO and the two provincial governments responsible for eels in their jurisdictions (Ontario, Quebec) drafted a management plan with the long term objective to rebuild eel abundance to levels observed in the mid 1980s and with an immediate management objective of reducing mortality on eels by 50% (CEWG 2009). In the absence of reference levels for managing mortalities, it is unknown whether the short term objective of reducing mortality by 50% is appropriate to achieve the long-term goal of rebuilding abundance.

There are a number of reasons for the failure to date of establishing and implementing mortality rate reference points in eel management. These include: the observation that the American Eel has a plastic life history, there remain numerous mysteries in eel life history, eels are panmictic which makes stock and recruitment modeling difficult, and eels are exploited by a number of countries over a broad geographical range. Because of panmixia, some have advocated that watershed-based stock–recruitment relationships are inappropriate and that conservation and exploitation targets must be set on the basis of the entire panmictic stock, by incorporating a global assessment of metapopulation dynamics (De Leo et al. 2009; Vélez-Espino and Koops 2010). Difficulties of this approach include challenges in developing such complex models (De Leo et al. 2009), the lack of available assessments at the panmictic scale, and the necessity that management measures must be applied by national and sub-national authorities and scales across the American Eel's range of distribution.

De Leo et al. (2009) suggest that it is unlikely that a single population model can provide the realism required to account for the large geographic variability in demographic characteristics and provide the advice required to manage the diverse anthropogenic pressures. Since management of anthropogenic stresses to American Eel occurs at local rather than national and international scales, reference points and simple and cost-effective approaches to guide these management decisions are required at local scales.

Since the 2001 ICES report, there has been no progress in the definition of reference points for the American Eel. Meanwhile, the status of American Eel in eastern Canada has deteriorated

further in some areas, prompting COSEWIC to evaluate the status of the species in Canada in 2006 (COSEWIC 2006). Despite the precarious state of the species in some regions, COSEWIC evaluated the Canadian population of the species as "Special Concern."

This paper follows on the work reported in ICES (2001) in the development of mortality rate reference points to guide management of mortalities of eels from human activities. In the absence of alternate proposals for mortality reference points, we consider again the SPR model and apply it using life history characteristics of eels that occupy fresh waters that flow into the southern Gulf of St. Lawrence to define fishing rates consistent with $F_{SPR}$ reference levels for this region. Our intention is not to provide a definitive population assessment for eels of this region, but rather to demonstrate an approach and its methodology. We discuss how the SPR approach can be extended to include complex life histories at the local scale, including those associated with the phenotypic plasticity of habitat use (Thibault et al. 2006), and subpopulation dynamics as described by Vélez-Espino and Koops (2010), and finally how to incorporate cumulative impacts.

## VALUE OF REGIONAL SCALE REFERENCE LEVELS

ICES (2001) suggested that regional management can produce the same result as panmictic management if mortality reference points are developed to match regional demographic parameters. Under this approach, all local regions manage mortality as if spawners produced in their area are important in producing recruitment to their area. Once we accept that a prudent management action is to improve or ensure escapement, a strategy must be adopted to implement it.

There are two management choices to make based on how regional recruitment of eels occurs:
- Manage for regional escapement because regional recruitment depends upon regional escapement (regionally dependent spawner and recruitment hypothesis)
- Manage for panmictic recruitment because recruitment to the region depends upon total escapement of the species (panmictic dependent regional recruitment).

The hypothesis that regional recruitment depends specifically on silver eel escapement from that region is not tenable given recent and historic genetic data, which confirm the panmictic nature of American Eel reproduction. However, if a particular region contributes a substantial fraction of total spawner output, then a decreased escapement from that region could affect subsequent recruitment to that region. It has been widely suggested that the St. Lawrence basin formerly produced a substantial fraction of total American Eel spawner output (e.g. Casselman 2003). Although this hypothesis is based on assumptions that are unlikely to be valid (COSEWIC 2006), it is possible that other eel-producing regions could contribute high fractions of total spawn output.

**Consequences to regional recruitment of the management action dependent upon the recruitment - stock dependency hypothesis**

| | HYPOTHESES | |
|---|---|---|
| **MANAGEMENT ACTION** | No stock fidelity: regional recruitment is proportional to total panmictic escapement | Stock fidelity: regional recruitment is at least in part dependent upon regional escapement |
| Ensure only an overall sufficient panmictic escapement (can accept some regional over-exploitation) (requires international assessments and decisions) | **Possibly no regional overexploitation concerns** | **Likely to have regional overexploitation concerns** |
| Regional management of exploitation levels (requires regional assessments and decisions) | **Possibly no regional overexploitation concerns** | **Likely no regional overexploitation concerns** |

Prudent action under conflicting hypotheses is to choose the management action that minimizes a loss rather than maximizing a benefit. The loss to be avoided is recruitment collapse at the regional scale. This would be best assured by managing as if the regional stock fidelity hypothesis is true. If all, or even most, regions implement such an approach, eel conservation will be effective at a species-wide level. This is essentially the approach that is mandated by the European Union directive that is being implemented in most European countries (EU 2007). Given the uncertainty in the factors affecting recruitment of eels to eastern North America, prudence would dictate establishing region specific reference points.

## PROPOSED MODEL TO DEFINE MORTALITY RATE REFERENCE LEVELS

The proposed approach to define whether anthropogenic driven mortalities on eels are within acceptable levels is the Spawning biomass Per Recruit model (SPR) as described by Mace and Sissenswine (1993), summarized in National Research Council (1998), and applied to the American Eel in ICES (2001), Weeder and Uphoff (2009), and ICES (2010), and Fenske et al. (2011). ICES (2001) described with examples how mortality reference points based on SPR analyses could be derived which account for regional variation in life history features.

As originally proposed by ICES (2001), the fishing mortality rate that results in 30% SPR would be used as the limit mortality reference point and 50% SPR would be the value for rebuilding and long term management.

### What is SPR?

SPR is a model that uses the life history parameters of a species to calculate the ratio of spawner potential produced under a scenario of anthropogenic mortality relative to a scenario where anthropogenic mortality is zero. It does not require estimates of recruitment and as presented assumes there is no density dependence. In evaluating the effects of human-induced mortality, the same set of "average" life history parameters is used and the spawning biomass

which remains after human-induced impacts is compared to the spawning biomass expected in the absence of the human-induced mortalities (%SPR) (see the example in Table 1).

The life history parameters and assumptions of the SPR model as applied to eels include:

| Assumption or parameter | For American Eel |
|---|---|
| - ability to follow cohorts | Yes, by age-reading of otoliths |
| - weight-at-age or fecundity-at-age or weight-to-fecundity relationship | Yes, weight-at-age varies by sex, region, and habitat rearing conditions |
| - natural mortality at age | Limited, but weight-, temperature-, and density-based relations have been developed for the European Eel |
| - probability of maturing at age | Varies by sex and region, limited data but can make reasonable assumptions |
| - vulnerability at age or maturity stage to human-induced mortality | Limited, region and human activity specific but can make reasonable assumptions |

SPR analysis makes no assumption about the recruitment which is obtained from a spawning escapement. It only considers how many spawners are produced from recruited eels and assumes that the average life history characteristics are not modified by the relative size of the recruitment, i.e. no density dependent effects. It may be argued that this is not correct, and the analysis of Bevacqua et al. (2010) indicates that natural mortality at least does seem to vary with density for the European Eel, however, the presently precarious state of eel populations in some of the key northern areas of North America would suggest that there are likely negligible density dependent effects being manifested at this time.


## SPR ANALYSIS FOR EELS AND IMPACTS OF HUMAN ACTIVITIES

Due to the phenotypic plasticity of the American Eel and the association between demographic characteristics (sex ratio, growth rates, length at maturity, age at maturity, natural mortality) with geographic region and rearing habitat (Thibault et al. 2006; Jessop 2010; Vélez-Espino and Koops 2010), the reasonable approach is to do the SPR analysis at the geographic scale that provides a set of homogeneous life history characteristics (referred to as a stock complex).

In the following analysis, we show an example using life history characteristics of eels based on sampling from fresh waters flowing into the southern Gulf of St. Lawrence. We use information on size at age to make inferences on the probability of metamorphosing to the silver eel stage (maturing), length to weight relationships to convert length at age to weight at age, and water temperature data to populate the natural mortality parameters, based on theory described by Bevacqua et al. (2010). We estimate the spawning escapement that would occur after eels are subject to a fyke net fishery to define the fishing rate which would correspond to the mortality rate reference points of $F_{30\%SPR}$ and $F_{50\%SPR}$. Application of the SPR model to the freshwater drainages of the southern Gulf of St. Lawrence is hypothetical, because there is no fyke net fishery for eels in this area. This reflects the paper's main purpose, which is to demonstrate how the SPR approach works, rather than to generate management advice for a specific region. We conclude by addressing some of the more complex scenarios of eel life history and human impacts on eels to show how the simpler SPR analysis for one anthropogenic factor could be extended to multiple activities and cumulative impacts.

**The simple fishery model for the fresh waters of the southern Gulf**

<u>Weight and fecundity at age</u>

Because eels can be reliably aged with otoliths, it is possible to track cohorts, at least from the point of arrival as elvers. There are a large number of size and age data sets (see summaries in Cairns et al. 2007, 2008; synthesis in Jessop 2010) throughout the geographic range of the American Eel. Eels up to 30 years old have been interpreted from otoliths of animals from the southern Gulf (Fig. 1) with the oldest age in eastern Canada at 43 years (Cairns et al. 2008). Length at age is highly variable but seems to level off at age 11 in the freshwater derived samples and at age 7 in samples of eels from brackish and salt waters (Fig. 1; Lamson et al. 2009). Length and weight at age are also well documented and weight increases allometrically with length (Cairns et al. 2007; de Lafontaine et al. 2010).

Fecundity in the American Eel is not as well studied as for other fish species. Tremblay (2009) summarizes the results from four studies of fecundity at length and fecundity at weight relationships. Fecundity scales allometrically with length and weight. For a 1000 g female eel, mean fecundity based on relationships summarized by Tremblay (2009) varies between 7 and 12 million eggs.

For the scenarios examined, we used biomass of escaping eels as the surrogate for spawner output. Male eels are very rare in the southern Gulf of St. Lawrence. The choice of weight as a proxy for spawners means that both sexes are included, and allows the approach for deriving mortality reference levels to be applicable to all eel production areas regardless of the local sex-ratio.

<u>Probability of maturing</u>

The mechanisms which initiate silver eel metamorphosis are not well understood but silvering based on a threshold length and silvering based on age are both possible mechanisms (Jessop 2010; Vélez-Espino and Koops 2010). There can be a very broad age distribution from samples of female silver eels from a given region (Cairns et al. 2008). Size at migration of silver eels within the same region can also vary temporally; de Lafontaine et al. (2010) report an increase in mean weight of silver eels in commercial and experimental catches of the St. Lawrence River Estuary.

Individual eel growth is highly variable. The point at which yellow eels become silver eels and emigrate is most closely associated with size in the southern Gulf of St. Lawrence (Cairns et al. 2008). This means that rapidly growing eels leave at a younger age than slow growing eels. Animals which remain in an area and migrate at older ages are not always larger at the point of migration. Given the association between metamorphosis and size, slow growing eels generally take longer to reach the threshold size and turn silver. Under this model, the length-at-age curve derived from aging a sample of eels would rise until it reaches the length where silvering is triggered, and then would flatten with no further length increase. Such a pattern is observed in eel length-at-age plots in fresh waters of the southern Gulf of St. Lawrence, where mean size does not increase with age after 11 years (Fig. 1; Lamson et al. 2009). Despite the association between size and metamorphosis, it is also possible that the probability of metamorphosing increases with age, so that slow growing eels eventually metamorphose even at sizes below a critical value.

<u>Natural Mortality (M)</u>

Natural mortality (M) is a key component of the SPR analysis. ICES (2001) showed that the variability of the fishing rate at 30%SPR and 50%SPR was less than the variability in the assumed natural mortality rates so the conclusions on the mortality reference levels are reasonably robust to the assumptions of M.

| From ICES (2001) | $F_{30\%SPR}$ ($F_{lim}$) | $F_{50\%SPR}$ ($F_{pa}$) | Range of M examined |
|---|---|---|---|
| Southern stock profile – full recruitment at age 3 | 0.19 – 0.33 | 0.10 – 0.17 | 0.05 – 0.40 |
| Northern stock profile – full recruitment at age 3 | 0.09 – 0.11 | 0.05 – 0.07 | 0.05 – 0.40 |

The American Eel is a long-lived animal, particularly in the northern range of its distribution, attaining ages of over 40 years (Cairns et al. 2008), which suggests that natural mortality at least for the larger animals must be quite low. Hoenig (1983) suggests a relatively intuitive premise that the longevity and natural mortality rate in a species should be inversely related since animals from a species with a high mortality would not be expected to reach an old age. Hoenig described a relationship relating mortality (Z as annual instantaneous mortality rate) to maximum age ($t_{max}$) as:

$$\ln(Z) = a + b \ln(t_{max})$$
$$\text{with} \quad a = 1.46$$
$$b = -1.01$$

Based on the most frequently reported maximum age of 30 years for fresh waters of the southern Gulf (Cairns et al. 2008), the annual Z over the lifespan would be about 0.14 with a lifetime integrated value of 4.2.

Jensen (1996) showed how three special relations called Beverton and Holt life history invariants could be derived from maximization of the fecundity function that optimizes the trade-off between survival and fecundity. One of those invariants takes the form:

$$M * xm = C1$$
$$\text{where} \quad M \quad = \text{instantaneous natural mortality}$$
$$xm \quad = \text{mean age at maturity}$$
$$C1 \quad = \text{constant (1.65 or 2.0) (Jensen 1996).}$$

Although the mean age of the eel species across its range is not known, the most common mean age in the samples of female silver eels from eastern Canada was around 20 years (Jessop 2010). At this mean age at-maturity, the instantaneous mortality rate for females is in the range of 0.08 to 0.10.

The high fecundity of the eel is indicative of a species for which there is very poor survival of some life stages, presumably the fertilized egg and early life stages up to arrival on the coast. Ricker (1976) states that for a population at replacement, the reciprocal of the lifetime fecundity of a female provides a measure of M. That is for an "average" female to replace "herself", the average eggs produced during her lifetime must be sufficient to produce on average one female spawner. Assuming that the sex ratio of the eggs at fertilization is 50:50 (not unreasonable despite the environmental control of sex in eels), then half of the eggs would be female.

$$S \quad = \quad (0.5 * \text{Fecundity})^{-1}$$

Tremblay (2009) provides fecundity estimates for the American Eel from the northern portion of its distribution, ranging between 3.4 and 22.0 million eggs. For semelparous American Eel, the integrated survival rate from female eggs to female spawner would be 1 in 2 million to 1 in 10 million ($5 * 10^{-7}$ to $1 * 10^{-7}$), a lifetime integrated value (Z) of 14.5 to 16.0. This high lifetime Z value does not preclude a low natural mortality rate for larger eels but if mortality in larger eels is low, then mortality at sea of the eggs and larvae is very high. To put this in context, for Atlantic salmon, at replacement, the survival of one female egg to one female spawner equates to 1 per 2,500 or 0.04% (Chaput 2003).

## Metabolic theory estimates of M

Bevacqua et al. (2010) apply principles of metabolic theory, that link natural mortality to body mass and temperature, to estimate natural mortality of the European Eel. Their paper provides equations to estimate the mortality rate of an animal at unit mass (1 g) based on the average annual temperature of the environment of the animal; the warmer the temperature, the higher the mortality. They then describe a relationship between mass (g) and instantaneous mortality rate separately for male and female eels adjusted to three levels of relative density; as density increases, mortality increases. The relationships described by Bevacqua et al. (2010) were applied to data from eels of the southern Gulf of St. Lawrence.

Year-round in-river water temperatures are available from several sites in the Miramichi River and the Restigouche River (New Brunswick). Eels are found throughout these two rivers and the monitoring stations chosen are main stem river sites within the lower reaches of both rivers (Fig. 2). For example, the mean annual water temperature over the period 2008 – 2009 was just under 8ºC for the Miramichi River and just under 7ºC for the Restigouche River (Fig. 2).

Mean weights were modeled as an approximately linear function with age (about 52 g per year after age 3) representative of values from the southern Gulf: elver (age 0) of 0.17 g, age 1 of 18 g, age 5 of 265 g, age 10 of 528 g to age 25 at 1,308 g (D. Cairns, Unpubl. Data). Based on the mean annual water temperatures for these rivers, the predicted instantaneous mortality rate at unit mass is 0.26 – 0.65 ($\text{yr}^{-1}$) for female eels and 0.14 – 0.47 for male eels (equations in Fig. 1 of Bevacqua et al. 2010) for the slightly warmer Miramichi compared to 0.22 - 0.55 for females and 0.12 – 0.40 for males for the Restigouche (Table 2).

Based on this published relationship, M for a yellow eel with a mass of 100 g would be in the range of 0.03 to 0.05, decreasing to 0.01 to 0.02 for large silver eels of 1000 g body mass (Fig. 3; Table 2).

The integrated mortality rate from the elver stage (age 0; mass 0.18 g) to a 25 year old eel is in the range of 1.0 to 1.4 (depending on sex and density equations). Relating this to the total integrated mortality based on the fecundity relationship (Z = 14.5 to 16.0), then the percentage of the integrated lifetime mortality which occurs at sea, between the spawning female and the elver stage is greater than 90% (range of 90% to 97%).

Rerunning the same life history scenario examples in ICES (2001) but using the M values estimated from Bevacqua et al. (2010) gives $F_{30\%SPR} = 0.09$ and $F_{50\%SPR} = 0.05$ for the northern stock scenario.

## SPR model for the southern Gulf fishery example

The SPR analysis for evaluating a yellow eel fishery scenario in the fresh waters of the southern Gulf of St. Lawrence uses the following structure and data (Fig. 4; Table 3):

For age i = 0 to 25:

$$Catch_i = Yellow_i * (1 - exp(^{-F*PRi}))$$

where
Catch$_i$ = catch (in number) of yellow eels of age i in the fishery
Yellow$_i$ = abundance of yellow eels of age i prior to the fishery
F = fully recruited fishing rate
$PR$i = partial recruitment to the fishery at age i

The abundance of yellow eels at age i after the fishery is:

$$Yellow'_i = Yellow_i - Catch_i$$

The abundance of silver eels migrating at age i is:

$$Silver_i = Yellow'_i * Prob\_Silver_i$$

where
$Prob\_Silver_i$ = probability of yellow eel of age i metamorphosing to silver eel

The biomass of silver eels at age i is:

$$B\_Silver_i = Silver_i * Wt_i$$

where
Wt$_i$ = weight of silver eel at age i

The total spawner biomass is the sum of the biomass at age of silver eels:

$$Spawner\_Biomass = \sum_{i=0}^{25} B\_Silver_i$$

The catch in terms of silver eel equivalents is:

$$Catch\_Silver = \sum_{i=0}^{25} Catch_i * \Pr ob\_Silver_i * Wt_i$$

The cumulative mortality from fishing of silver eels (as percent of silver eel production) for the cohort:

$$Cumul\_mortality\_silver = Catch\_Silver / (Catch\_Silver + Spawner\_Biomass)$$

The following assumptions and input data :
- Males and females are combined (no distinction)
- Length at-age distributions from the data in Figure 1 for southern Gulf eels from freshwater habitat.
- Weight at length from the equation in Cairns et al. (2007)
  - Weight (g) = $7.006 \times 10^{-4}$ Length(cm)$^{3.2332}$
- Probability of metamorphosing to silver eels based on proportion of animals at age of length >= 70 cm up to age 10 years
  - for age 11+, probability of silvering = proportion of eels >= 70 cm over ages 11+
- Partial recruitment to fishing gear based on proportion of length at age >= 35 cm up to age 10, fully recruited for age 11+
- Fixed natural mortality at-age (Fig. 3) based on equations of Bevacqua et al. (2010), Miramichi annual water temperatures (Fig. 2), and mean weights at age from Cairns (Fig. 2)

- %SPR based on weight of silver eels escaping to the sea
- Fishing mortality occurs first, followed by metamorphosis / emigration and finally natural mortality for the non-migrating animals.

Uncertainties of some of the inputs (Table 3) were incorporated using Monte Carlo simulation (CrystalBall©) with the following distribution assumptions:
- Length at age drawn from lognormal distribution with parameters defined by the 5th to 95th percentiles at-age from Figure 1 for southern Gulf freshwater.
- Probability of metamorphosing drawn from a beta distribution with parameters set at age-specific sample size (< 70 cm; >= 70 cm) up to age 10
  - combined samples for age 11+
- Partial recruitment to fishing gear using beta distribution with parameters from samples at age up to age 10, fully recruited and no variation for age 11+
- Natural mortality as a triangular distribution based on low density to high density predictions of equations of Bevacqua et al. (2010) for females and Miramichi temperatures.

## Results of the SPR analysis for the southern Gulf fishery

The estimates of %SPR for sequentially increasing fishing rates for a hypothetical yellow eel fishery in fresh waters of the southern Gulf are shown in Figure 5. Based on the life history inputs for this scenario, the fishing mortality rate which would result in less than a 5% chance of being below 30%SPR (limit reference point) is F = 0.18 and the fishing rate that would result in a 50% chance of being below 50%SPR (target reference point) is at F < 0.12 (Fig. 5). The distributions of %SPR are quite narrow and reflect the limited uncertainty included in the model inputs. The yield, in terms of relative biomass of yellow eels caught, increases with F but levels off above F = 0.2 whereas the relative yield of silver eel equivalents is maximized at F = 0.2 (Fig. 5).

The effect of fishing not only reduces the overall abundance of the spawning stock but it also shifts the spawning stock biomass proportionally to younger ages. For this southern Gulf example, at F = 0 about 25% of the spawner biomass was derived from eel spawners aged 13 years and older. At F = 0.1 (50% SPR), eels aged 13 years and older contribute less than 18% to the spawner biomass and at F = 0.18 (30% SPR), these ages contribute less than 15% of the biomass.

The assumptions on M in the SPR analysis only affect the results of age groups which are vulnerable to the anthropogenic activities. In this scenario, the values of M for ages 0 to 2 have no effect on the SPR results because these ages groups are not recruited to the fishery and therefore not subjected to the anthropogenic mortality; we could have set M for these ages at any value without any consequence to the results of the analysis.

Sensitivity of results to M and probability of maturing (silver eel metamorphosis)

We examined the effect on the analysis of SPR of quadrupling M and approximately doubling the probability of metamorphosis (from a median value of 0.43 to 0.80) for ages 11+. The median estimates of the %SPR over the range of F (0.02 to 0.30) were essentially insensitive to the increase in the natural mortality parameter (Fig. 6). Increasing the probability of silver metamorphosis for eels aged 11+ has the effect of reducing the time they are exposed to the fishery and increasing the escapement. Consequently, increasing the probability of

metamorphosis results in a slight increase in F at $F_{lim}$ (95% chance of being above 30%SPR) of 0.21 versus 0.17 in the base scenario (Fig. 6).

Comparing a yellow eel fishery to a silver eel fishery

When a fishery occurs exclusively on silver eels, the animals are vulnerable to exploitation only once and the removal rate (F) corresponding to 50%SPR equals 0.69 (exploitation rate of 50%) and the removal rate corresponding to 30%SPR is F = 1.20 (exploitation rate of 70%). It seems counter-intuitive that such a high exploitation rate would be allowed on a long-lived species like the American Eel. However, the exploitation rate only occurs once on the cohort. This contrasts with the yellow eel fishery in which animals are exposed to exploitation in multiple years and the removal of yellow eels has a consequence to the potential production of silver eels in the future. The other consequence is the shift in the relative proportions at age of silver eels resulting from a yellow eel fishery which does not occur in the silver eel only fishery. In the yellow eel fishery, silver eel age is shifted to younger animals which are generally smaller, which contributes to a further loss of spawner biomass potential.

## Increasing the complexity of the SPR models to account for the phenotypic plasticity of eel phenotype and habitat use

One of the concerns with the assessment of eels is the large variability in phenotype characteristics within and across its geographic distribution. One well described phenotype variation is the differences in growth rates and size/age at maturity of male versus female eels (Jessop 2010; Vélez-Espino and Koops 2010). The SPR model can be readily adapted to this by simply treating the male and female life history parameters as separate streams and then summing them together to estimate spawner biomass after anthropogenic mortality has occurred (Fig. 7). Size at age, growth rate at age and age or size at metamorphosis to silver eels can be inferred from sampling data for each sex as was done for the previous example. Assuming that the life history characteristics by sex are known, the only additional piece of information required is an estimate of the relative abundance of males to females. In some northern areas, including the southern Gulf of St. Lawrence, there are very few male eels so excluding them from the SPR analysis may result in minimal bias.

There is increasing evidence of differences in growth rates and potentially sex determination based on the habitat utilized by eels, primarily freshwater versus brackish/marine waters (Jessop et al. 2004; Thibault et al. 2007; Cairns et al. 2009; Lamson et al. 2009; Vélez-Espino and Koops 2010). In particular, growth rates (cm per year) of eels in brackish and salt water are approximately double those of eels growing in fresh waters of the same watercourse (Cairns et al. 2009). The SPR modeling approach should be applied to regions where demographic characteristics are approximately homogeneous. Hence fresh water and brackish/salt waters should be considered as separate regions for the purpose of SPR modeling.

## Accounting for differential anthropogenic activities within a stock complex

Eels are broadly distributed in eastern Canada and in many locations they are not fished or subjected to other anthropogenic mortality. If eels in exploited and unexploited neighbouring areas have similar average life history characteristics (size at-age, growth rates, age/size at metamorphosis, temperature regimes), then an SPR analysis for the stock complex can be structured as shown in Figure 8. As with the scenario immediately above, information is required on the relative size of production from the impacted area vs. the unimpacted area. In the

absence of such information, relative watershed area might be a reasonable proxy for production to use for this type of analysis. If the exploited area is less than 50% of the stock complex area, then all the silver eels can be removed from the exploited portion without violating the $F_{50\%SPR}$ objective. If the exploited stock area is less than 30% of the stock complex area, then all the silver eels can be removed from the exploited area without violating the $F_{30\%SPR}$ limit reference point.

## Accounting for cumulative impacts

The question of cumulative impacts is relevant in many areas of eastern Canada, considering that eels in some watersheds are subject to various combinations of turbine mortality and fishing at different life history stages (elver, yellow eel, silver eel). Lake Ontario eels probably faced the most diverse and sequential anthropogenic pressures of any population in eastern Canada, historically being fished at the yellow eel stage within Lake Ontario, followed by passage through two hydro facilities and culminating in fishing pressure in the St. Lawrence Estuary at the silver eel stage during their spawning migration to the Sargasso Sea (Mathers and Pratt 2011). An illustration of that scenario is shown in Figure 9.

Given suitable information on size at age for the different life stages and migration probabilities, the cumulative impacts of multiple stressors can be assessed using the SPR model (Fig. 8). The output summaries are more complex to generate and interpret as they involve describing %SPR on two or more dimensions (one dimension for every anthropogenic activity being assessed). "What-if" scenarios could be run to assess the gains (or losses) in %SPR for candidate management actions.

An example %SPR analysis is shown in Figure 10, using the same life history input data for the southern Gulf but subjecting eels to yellow eel fisheries, then passage through turbines, and then silver eel fisheries. Two scenarios for turbine mortality are shown; mortality of 10% and mortality of 25% on the total migrating stock. The surface plots show the combinations of removal rates in the yellow eel fishery in an upper portion of the watershed, followed by a silver eel fishery in the lower river that would be consistent with the $F_{50\%SPR}$ and $F_{30\%SPR}$. At a turbine mortality rate of 25% and to respect the $F_{50\%SPR}$ objective, the fishing rate in the silver eel fishery should not be greater than $F = 0.4$ if there is no yellow eel fishery. The fishing rate in the yellow eel fishery should never be greater than $F = 0.06$ if there is no silver eel fishery (Fig. 10). If both fisheries are occurring, fishing rates in each should be much lower. At a turbine mortality rate of 10%, the $F_{50\%SPR}$ objective could be achieved if the fishing rate in the silver eel fishery was less than about $F = 0.6$ (if there is no yellow eel fishery) whereas the fishing rate in the yellow eel fishery should be less than $F = 0.09$ (if there is no silver eel fishery) (Fig. 10). With both fisheries operating, the fishing rates must be below those respective values. Alternate scenarios could be explored with the SPR model.

## DISCUSSION

In the present situation, it is possible to establish mortality reference points for American eel in eastern Canada. We propose using SPR as the model to define mortality rate reference points and to adopt F at 30%SPR as a limit mortality reference point and F at 50%SPR as the target mortality reference level, as indicated by ICES (2001). We propose that region or even watershed specific reference points should be developed based on the best available information on life history characteristics and habitat use. Despite the contention by some that only a global assessment model is appropriate for conserving eels, if the SPR principles are

applied consistently across the species range taking account of regional variation in life history characteristics, then the global conservation objective can be achieved.

We have shown how the SPR model can be used for a specific case of managing exploitation in a fishery. We also describe how the SPR model can be extended to account for sex-specific and habitat-specific variation in life history traits, partial vulnerability of eel stocks in a stock complex, and finally, cumulative mortalities on a stock. A good amount of life history information required to populate these analyses is already available or readily obtainable with dedicated monitoring programs. Two life history characteristics which are more difficult to obtain are natural mortality rates at age and probability of metamorphosis to silver eel at-age. The equations of Bevacqua et al. (2010) allow prediction of natural mortality in the European Eel on the basis of sex, weight, temperature and density. Given the close phylogenetic and ecological similarity of Atlantic eels, these equations may be considered applicable for the American Eel as well. However, the equations do not consider habitat salinity as a predictor of mortality. Cairns et al. (2009) showed that eels growing in fresh water in northeastern North America would need a natural mortality rate approximately half that of eels growing in brackish or salt water, in order for the two groups to produce the same number of silver eels per recruiting elver. Mortality rates were similar across salinity zones in the Hudson River Estuary (Cairns et al. 2009); however, data were sufficient for comparisons only at this single site, so it remains possible that eel mortality is lower in fresh water, which would compensate for the slow growth in that environment. The equations of Bevacqua et al. (2010) are primarily based on freshwater data (study sites consisted of five freshwater lakes and streams, one brackish-salt lagoon, and one hypersaline lagoon in which outflow is manipulated to favour salt production by evaporation).

The importance of the assumptions or estimates of natural mortality and probability of metamorphosing can be assessed through simulation. In the SPR analysis, both those values at-age are relevant only for the age or size groups which are also vulnerable to the human activity being assessed; for example elver and yellow eel survival rates are irrelevant in evaluating silver eel fisheries. Similarly, evaluating the consequence of an elver fishery as the only impact on the stock only requires an estimate of elver survival rate, all other parameters at older ages being inconsequential as the older ages are unaffected by the elver fishery.

Eel growth rates differ substantially between fresh and brackish/salt water (Lamson et al. 2009). Moreover, eel fishing is often permitted in one salinity zone but not the other. For these reasons fresh and brackish/salt populations should be modeled by SPR as separate production areas. However, eels commonly move between fresh and brackish/salt water during the yellow eel phase (see review by Lamson et al. 2006). In areas where this occurs, the SPR models will require modifications to accommodate such movements, and data to support the inputs to the model.

Natural mortality in the American Eel in eastern Canada must be low for yellow and silver eels, based on maximum ages observed and growth rates. ICES (2001) examined the effect of M on the derivation of the $F_{lim}$ and the $F_{pa}$ mortality reference points and concluded that the uncertainty in the reference points was less than the uncertainty range of natural mortality. In the example in this paper for the fresh waters of the southern Gulf, the %SPR analysis was insensitive to values of M but did change based on the assumed probability of silvering at age. The higher the probability of silvering after a critical age, the less time the cohort is exposed to the anthropogenic activity. The best and reasonable values should be used; based on the broad age distribution of silver eels from samples in eastern Canada, values of about 0.5 seem sufficient whereas a value of 0.8 is too high.

There is no reason at this stage to delay establishing mortality reference points for eels at a geographic scale that corresponds to the life history characteristics of the eel. The SPR analysis should be the minimum default model considered. The SPR model analysis can be extended to incorporate complex geographic structuring and multiple anthropogenic stressors. The accumulation of these reference points and their actioning will benefit the species as a whole by ensuring that spawning escapement from each region would be proportional to abundance.

Defining only mortality rate reference levels can be inadequate when stock biomass is low as it does not provide protection against depensatory effects which could express themselves at low biomass levels. Defining biomass reference points for the eel would be a challenge but efforts should be made to do so, particularly in some of the areas of concern in eastern Canada.

Defining reference points is the first part of the larger assessment and management process. The interest is in knowing whether the realized anthropogenic mortalities are within the defined reference levels. Assessing stock status relative to these reference points remains a challenge, as shown by the few targeted studies to assess mortality rates associated with fishing (Caron et al. 2003) or hydro dams (NYPA 1998).

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*Table 1.* *Hypothetical fish stock showing simple procedure for calculating %SPR for different levels of fishing rate.*

| | | | | Fishing rate 0 | | | |
|---|---|---|---|---|---|---|---|
| Age | Weight | Natural mortality | Abundance | Vulnerability to fishing | Biomass fished | Maturity | Spawner biomass |
| 1 | 10 | 0.8 | 100 | 0 | 0 | 0 | 0 |
| 2 | 50 | 0.4 | 20 | 0.1 | 0 | 0.1 | 100 |
| 3 | 100 | 0.2 | 12 | 0.5 | 0 | 0.5 | 600 |
| 4 | 125 | 0.1 | 10 | 1 | 0 | 0.8 | 960 |
| 5 | 140 | 0.1 | 9 | 1 | 0 | 1 | 1210 |
| 6 | 140 | 0.1 | 8 | 1 | 0 | 1 | 1089 |
| | | | | | | Total | 3958 |

| | | | | Fishing rate 0.1 | | | |
|---|---|---|---|---|---|---|---|
| Age | Weight | Natural mortality | Abundance | Vulnerability to fishing | Biomass fished | Maturity | Spawner biomass |
| 1 | 10 | 0.8 | 100 | 0 | 0 | 0 | 0 |
| 2 | 50 | 0.4 | 20 | 0.1 | 10 | 0.1 | 100 |
| 3 | 100 | 0.2 | 12 | 0.5 | 59 | 0.5 | 594 |
| 4 | 125 | 0.1 | 9 | 1 | 113 | 0.8 | 903 |
| 5 | 140 | 0.1 | 7 | 1 | 102 | 1 | 1024 |
| 6 | 140 | 0.1 | 6 | 1 | 83 | 1 | 829 |
| | | | **Spawner biomass per recruit** | | | | 3450 |
| | | | **%SPR (3450 / 3958)** | | | | 87.2% |

| Fishing rate | Spawner biomass | % SPR |
|---|---|---|
| 0 | 3958 | 100% |
| 0.1 | 3450 | 87% |
| 0.2 | 3003 | 76% |
| 0.3 | 2611 | 66% |
| 0.4 | 2272 | 57% |
| 0.5 | 1979 | 50% |
| 0.6 | 1729 | 44% |
| 0.7 | 1517 | 38% |
| 0.8 | 1339 | 34% |
| 0.9 | 1192 | 30% |

*Table 2.* *Instantaneous mortality rates of eels from fresh waters flowing into the southern Gulf of St. Lawrence based on the equations described in Bevacqua et al. (2010).*

| | | Miramichi | | Restigouche | |
|---|---|---|---|---|---|
| Mean annual water temperature | | 7.8 | | 6.9 | |
| Density range | | Mid | Low – High | Mid | Low – High |
| M (yr$^{-1}$) at unit mass | female | 0.43 | 0.26 – 0.65 | 0.37 | 0.22 – 0.55 |
| | male | 0.31 | 0.14 – 0.47 | 0.27 | 0.12 – 0.40 |
| M (yr$^{-1}$) for elver mass 0.17 g (age = 0) | female | 1.0 | 0.6 – 1.6 | 0.8 | 0.5 – 1.2 |
| | male | 0.7 | 0.3 – 1.1 | 0.6 | 0.3 – 0.9 |
| M (yr$^{-1}$) for eel mass 100 g (approx. 2 years post elver) | female | 0.05 | 0.03 – 0.08 | 0.04 | 0.03 – 0.06 |
| | male | 0.04 | 0.02 – 0.05 | 0.03 | 0.01 – 0.05 |
| M (yr$^{-1}$) for eel mass 500 g (approx. 9 - 10 years post elver) | female | 0.02 | 0.02 – 0.04 | 0.02 | 0.01 – 0.03 |
| | male | 0.02 | 0.01 – 0.03 | 0.02 | 0.01 – 0.02 |
| M (yr$^{-1}$) for eel mass 1000 g (approx. 20 years post elver) | female | 0.02 | 0.01 – 0.03 | 0.01 | 0.01 – 0.02 |
| | male | 0.02 | 0.01 – 0.02 | 0.01 | 0.01 – 0.02 |

*Table 3.* Input parameters for the Monte Carlo simulation to estimate SPR for a hypothetical fyke net fishery in fresh waters flowing into the southern Gulf of St. Lawrence. Values with an asterisk are added to ensure appropriate parameters to define the probability distributions.

| | | Natural mortality[2] | | Length range | | Prob. of silvering | | | Recruitment to fishery | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | In samples | | | In samples | | |
| Age | Mean weight at age[1] | low | high | 5th perc. | 95th perc. | Less 70 | >= 70 cm | Prob. >= 70 cm | < 35 cm | >= 35 cm | Prob. >= 35 cm |
| 0 | 0.2 | 0.593 | 1.460 | 6.2 | 10.7 | 124 | | 0 | 124 | 0 | 0 |
| 1 | 18.0 | 0.069 | 0.171 | 8.9 | 22.5 | 36 | | 0 | 36 | 0 | 0 |
| 2 | 106.0 | 0.031 | 0.076 | 13.4 | 29.0 | 32 | | 0 | 32 | 0 | 0 |
| 3 | 159.0 | 0.026 | 0.063 | 20.1 | 33.1 | 60 | | 0 | 58 | 2 | 0.03 |
| 4 | 212.0 | 0.022 | 0.055 | 22.7 | 34.8 | 89 | | 0 | 85 | 4 | 0.04 |
| 5 | 265.1 | 0.020 | 0.050 | 24.3 | 48.4 | 97 | | 0 | 68 | 29 | 0.30 |
| 6 | 317.9 | 0.019 | 0.046 | 25.4 | 54.1 | 99 | 1 | 0.010 | 43 | 57 | 0.57 |
| 7 | 370.7 | 0.017 | 0.043 | 26.5 | 62.3 | 74 | 1* | 0.013 | 22 | 52 | 0.70 |
| 8 | 423.3 | 0.016 | 0.040 | 29.3 | 67.6 | 38 | 1* | 0.026 | 7 | 31 | 0.82 |
| 9 | 475.9 | 0.015 | 0.038 | 40.0 | 66.1 | 20 | 1* | 0.048 | 1* | 20 | 0.95 |
| 10 | 528.5 | 0.015 | 0.036 | 29.1 | 74.4 | 15 | 2 | 0.133 | 1 | 16 | 0.94 |
| 11 | 580.9 | 0.014 | 0.035 | 63.5 | 88.6 | 125 | 95 | 0.432 | | | 1 |
| 12 | 633.3 | 0.014 | 0.033 | 51.2 | 78.3 | 125 | 95 | 0.432 | | | 1 |
| 13 | 685.7 | 0.013 | 0.032 | 48.8 | 76.8 | 125 | 95 | 0.432 | | | 1 |
| 14 | 737.9 | 0.013 | 0.031 | 55.1 | 86.7 | 125 | 95 | 0.432 | | | 1 |
| 15 | 790.1 | 0.012 | 0.030 | 60.5 | 81.4 | 125 | 95 | 0.432 | | | 1 |
| 16 | 842.2 | 0.012 | 0.029 | 61.6 | 83.8 | 125 | 95 | 0.432 | | | 1 |
| 17 | 894.3 | 0.012 | 0.028 | 56.3 | 80.1 | 125 | 95 | 0.432 | | | 1 |
| 18 | 946.3 | 0.011 | 0.028 | 61.4 | 81.9 | 125 | 95 | 0.432 | | | 1 |
| 19 | 998.2 | 0.011 | 0.027 | 58.0 | 81.9 | 125 | 95 | 0.432 | | | 1 |
| 20 | 1050.0 | 0.011 | 0.026 | 56.2 | 75.6 | 125 | 95 | 0.432 | | | 1 |
| 21 | 1101.8 | 0.010 | 0.026 | 63.4 | 109.8 | 125 | 95 | 0.432 | | | 1 |
| 22 | 1153.5 | 0.010 | 0.025 | 55.1 | 91.3 | 125 | 95 | 0.432 | | | 1 |
| 23 | 1205.1 | 0.010 | 0.025 | 59.5 | 80.5 | 125 | 95 | 0.432 | | | 1 |
| 24 | 1256.7 | 0.010 | 0.024 | 58.7 | 73.2 | 125 | 95 | 0.432 | | | 1 |
| 25 | 1308.2 | 0.010 | 0.024 | 63.2 | 72.8 | 125 | 95 | 0.432 | | | 1 |

1 mean weight at age from D. Cairns (DFO, Unpublished data)

2 Theoretical natural morality at-age based on equations of Bevacqua et al. (2010), and using the mean weights at-age from D. Cairns and the temperatures from the Miramichi River. Low represents theoretical M at low density, high represents theoretical M at high density (Bevacqua et al. 2010)
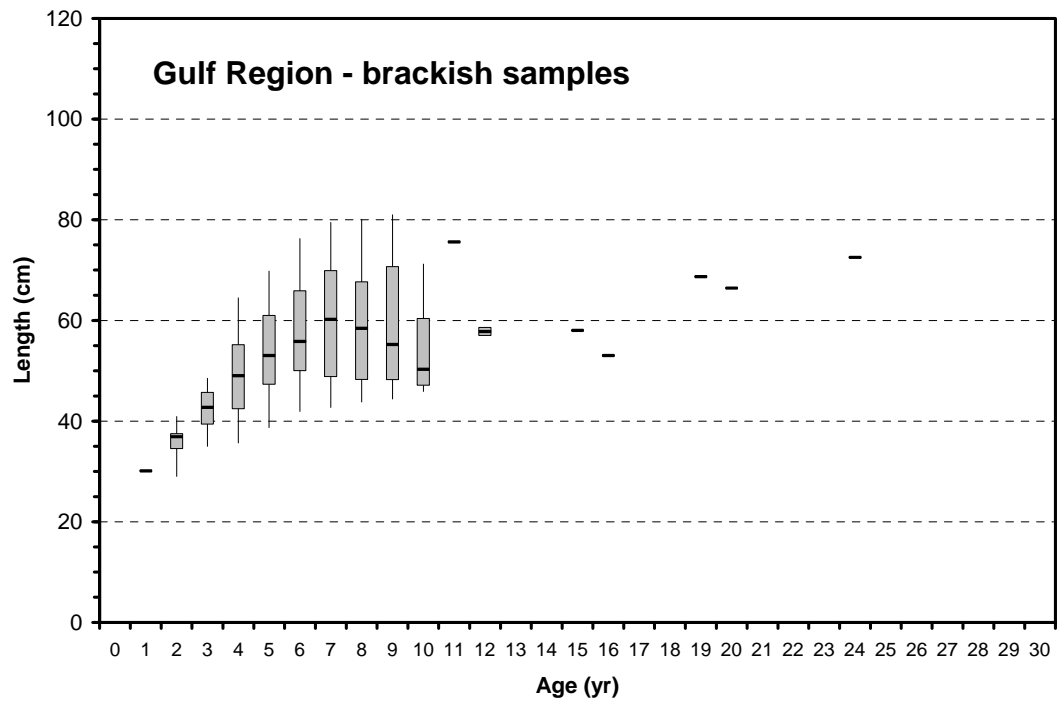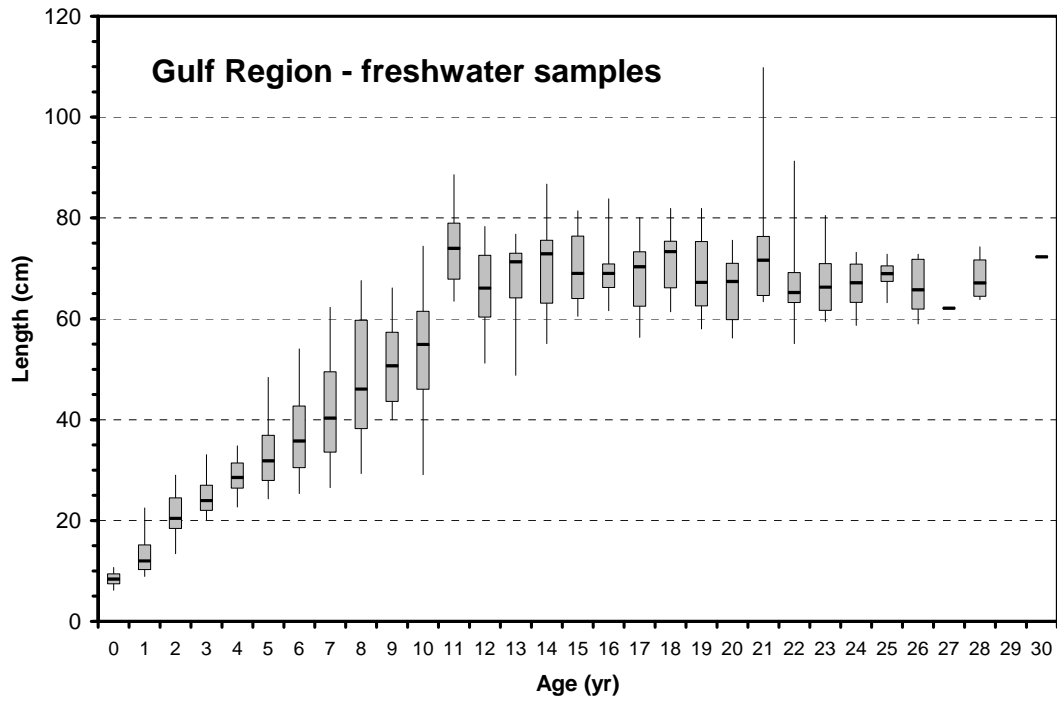
**Figure 1.** *Length at age distributions of American Eel from samples collected at freshwater sites (upper panel) versus brackish (or saltwater sites) (lower panel) from multiple sites within the southern Gulf (NB, NS, PEI) (D. Cairns DFO, unpubl data). Boxplots are interpreted as follows: vertical line is the $5^{th}$ to $95^{th}$ percentile range, the rectangle is the interquartile range and the horizontal dash is the median.*
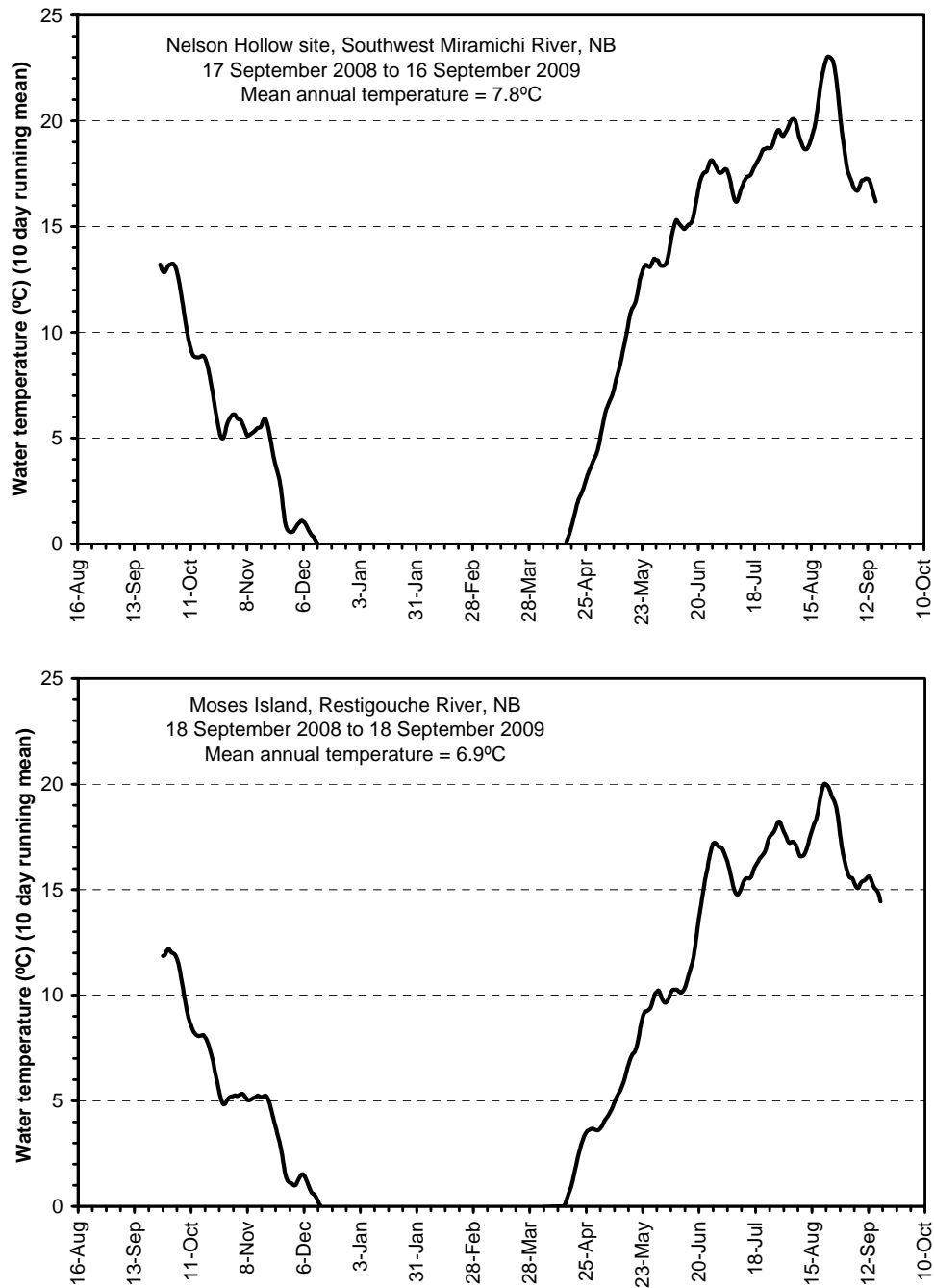
*Figure 2.* *Mean daily water temperature (10 day running mean) at two river sites in the southern Gulf of St. Lawrence during 2008 to 2009.*
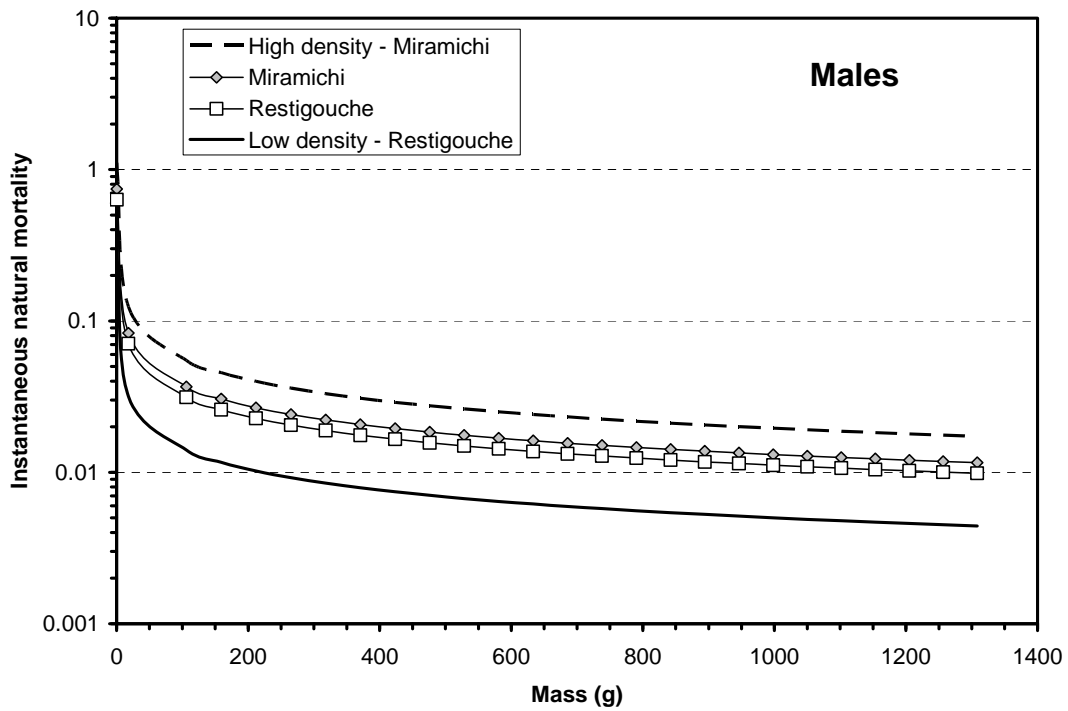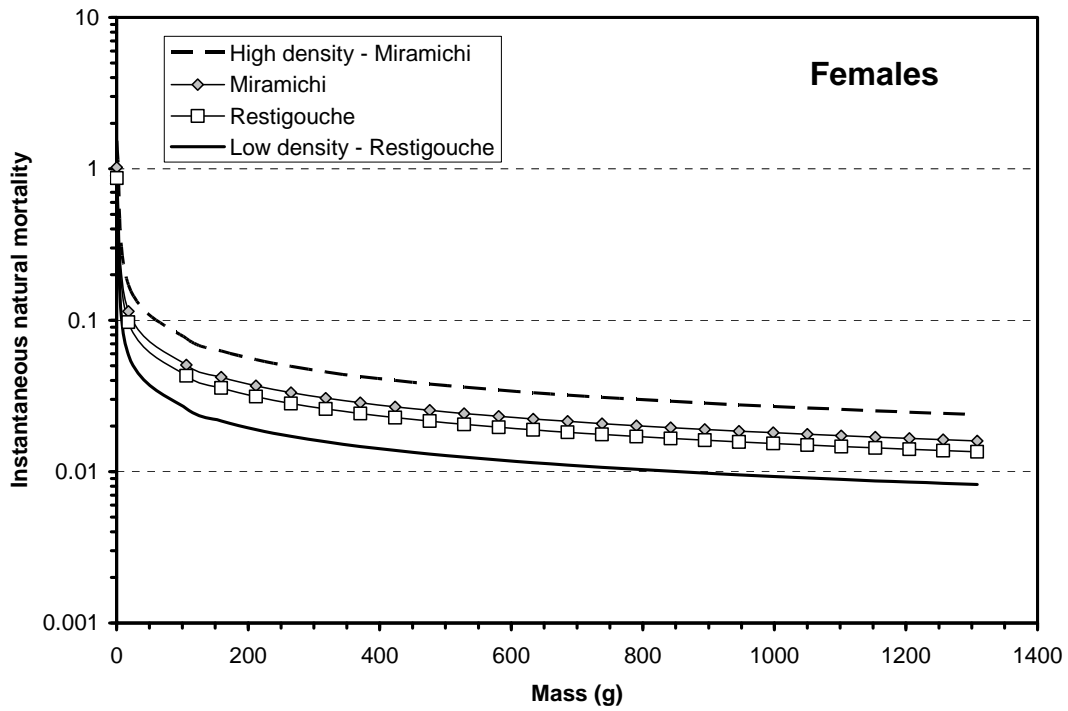
**Figure 3.** Predicted instantaneous natural mortality (yr$^{-1}$) at given mass for female eels (top) and male eels (bottom) based on the equations and relationships described in Bevacqua et al. (2010).
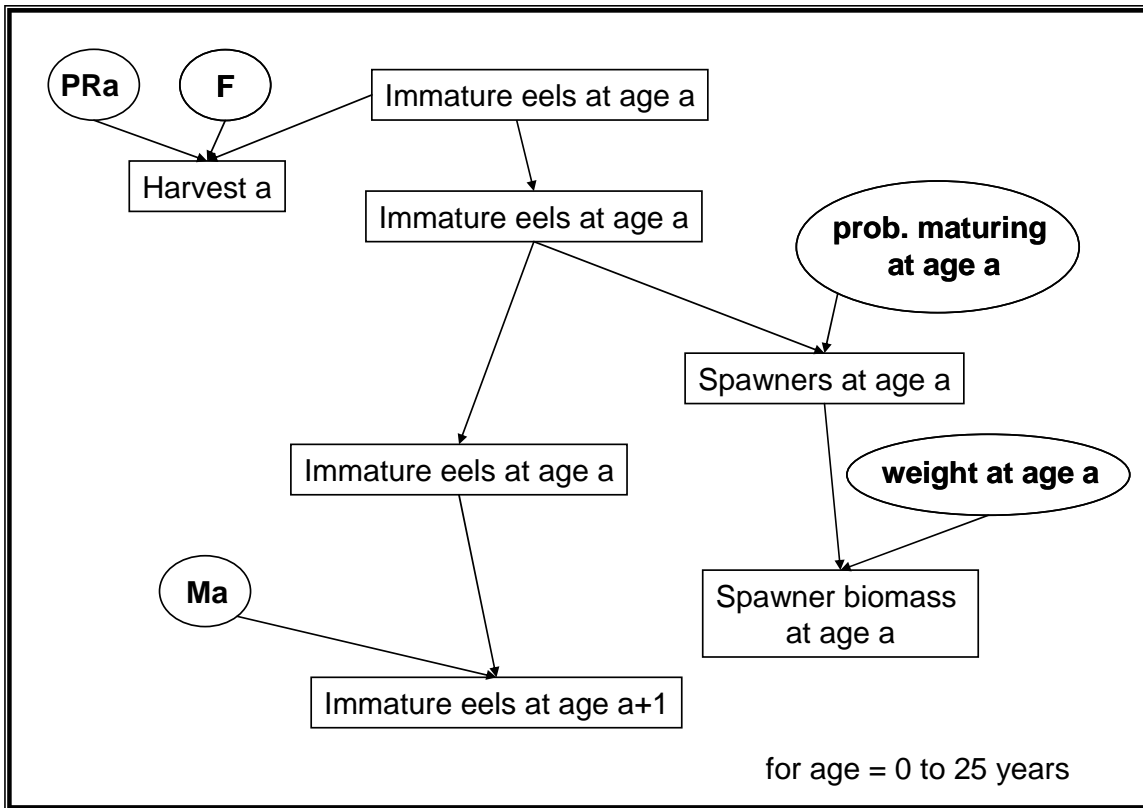
**Figure 4.** *SPR model for the fishery scenario in the southern Gulf of St. Lawrence. Ma is natural mortality at age a. F is the fishing mortality for the fully recruited age group and PRa is the partial recruitment for age a. The structure is the one shown in Table 1.*
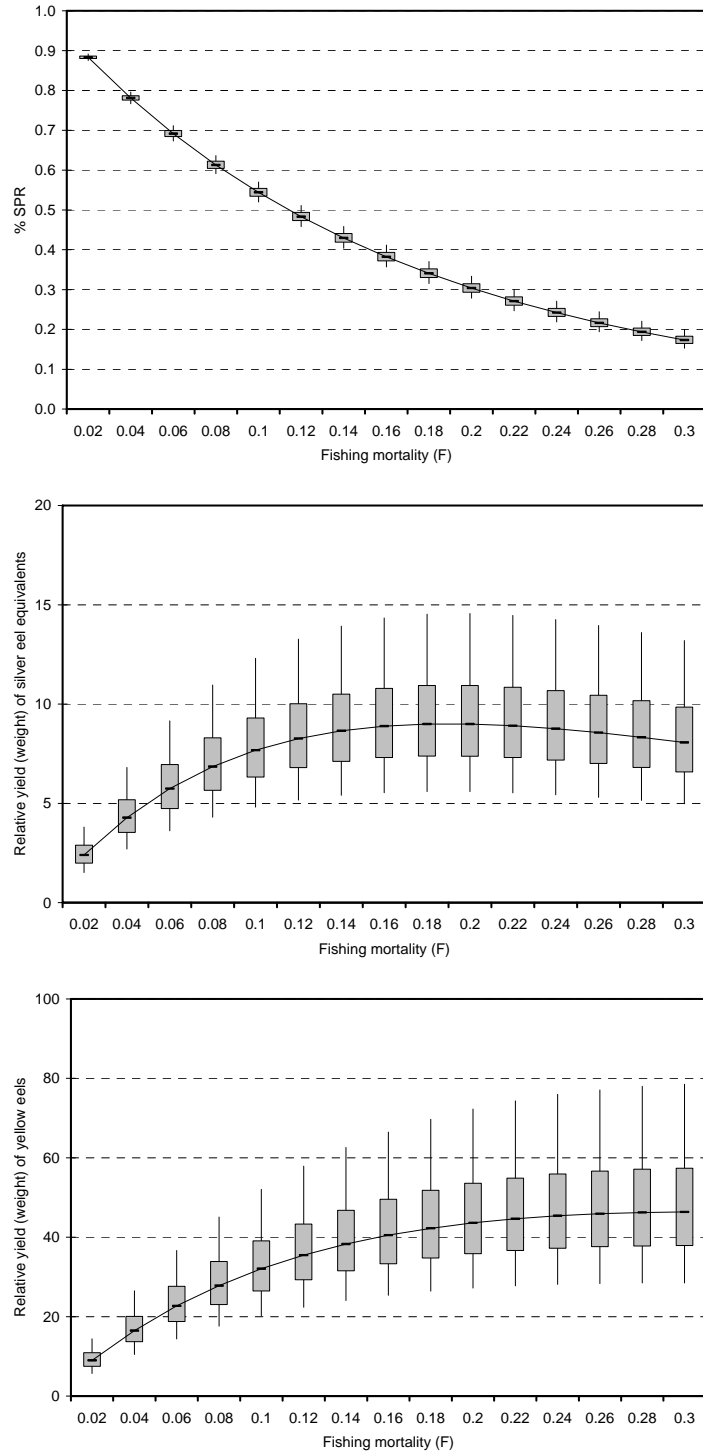
*Figure 5.* *%SPR calculation for the yellow eel fishery example of the southern Gulf based on the input parameters in Table 3 (upper), relative yield of silver eel equivalents (middle panel) and relative yield by weight of yellow eels (bottom panel). The F value is for fully recruited ages. Box plots are: vertical line is the 95% percentile range, the shaded rectangle is the interquartile range, the dash is the median from the Monte Carlo simulation.*
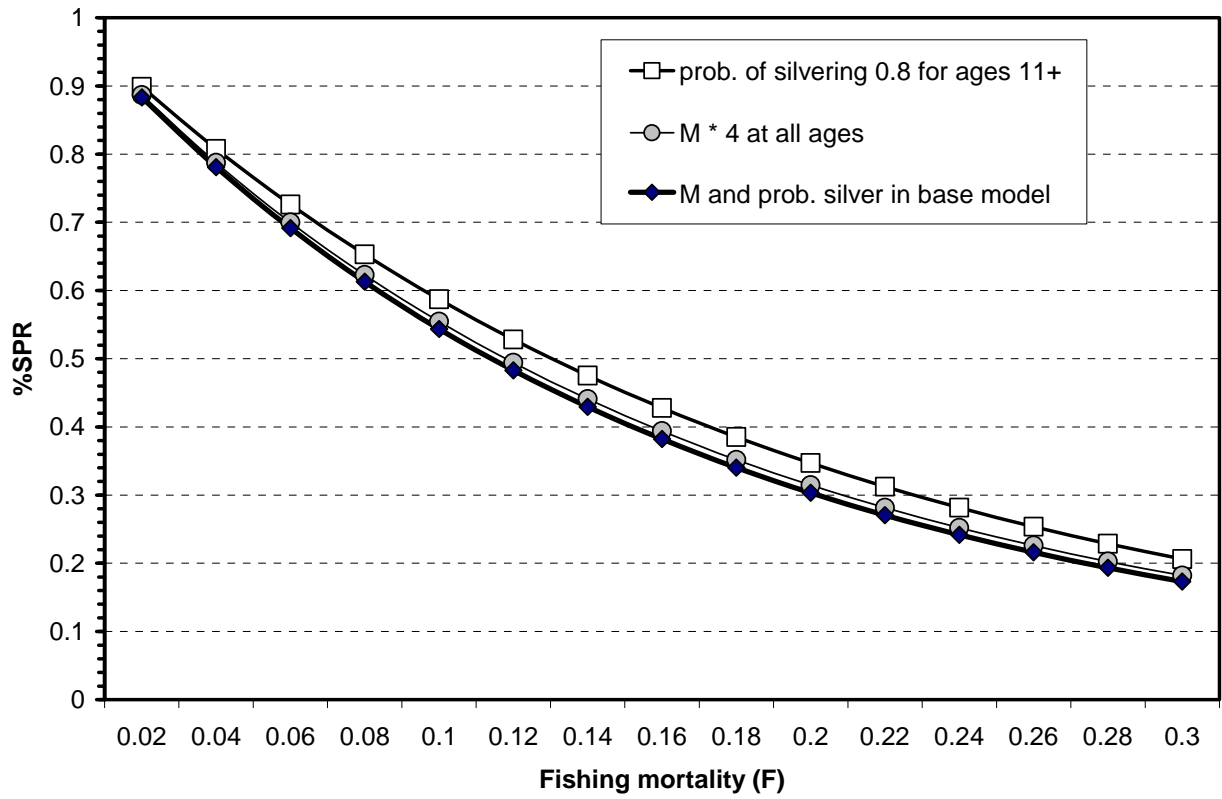
***Figure 6.*** *Sensitivity of %SPR results to assumptions of M and to probability of silvering at age 11+ relative to results from the base model. The F value is for fully recruited ages. The median values from the Monte Carlo simulation output are shown.*
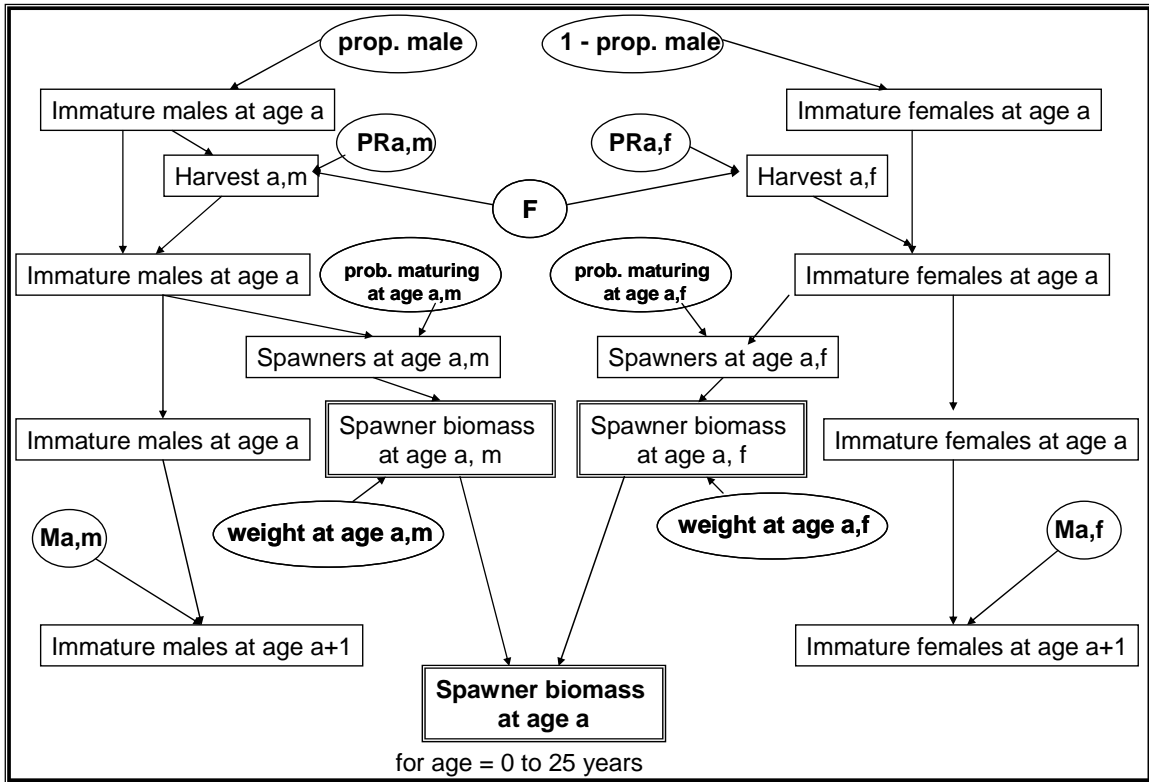
**Figure 7.** *SPR model structure to account for differences in life history characteristics of male and female eels. Acronyms as in Figure 4 with the addition of m or f to distinguish values for males and females, respectively.*
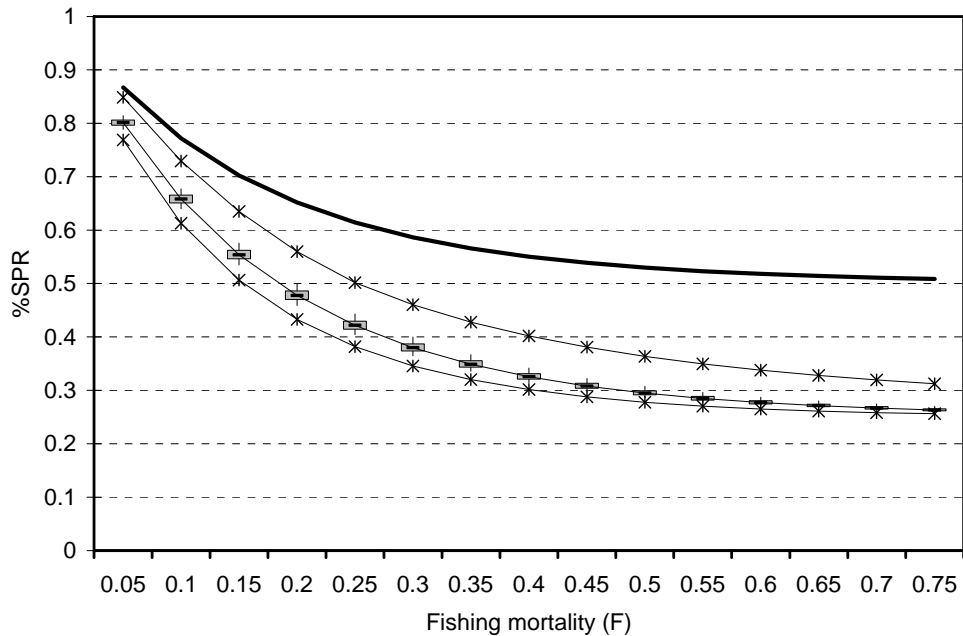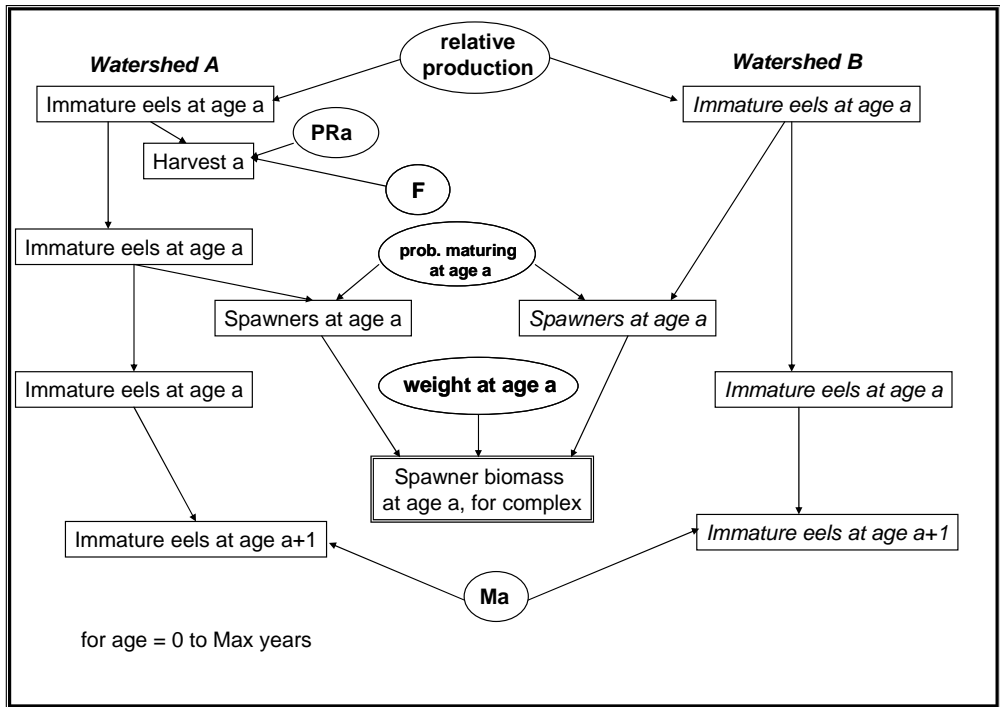
**Figure 8.** *SPR model structure (upper panel) to account for areas within an eel stock complex which are not subject to anthropogenic mortality. Watershed A has human activities which result in eel mortalities but Watershed B does not. Acronyms as in Figure 4. In the lower panel, box plots refer to the scenario where the exploited watershed is 75% of the total productive area of the complex. Box plots are as in Figure 5. The solid line is the median from the Monte Carlo simulations for the scenario where the exploited watershed is 50% of the total production area for the complex.*
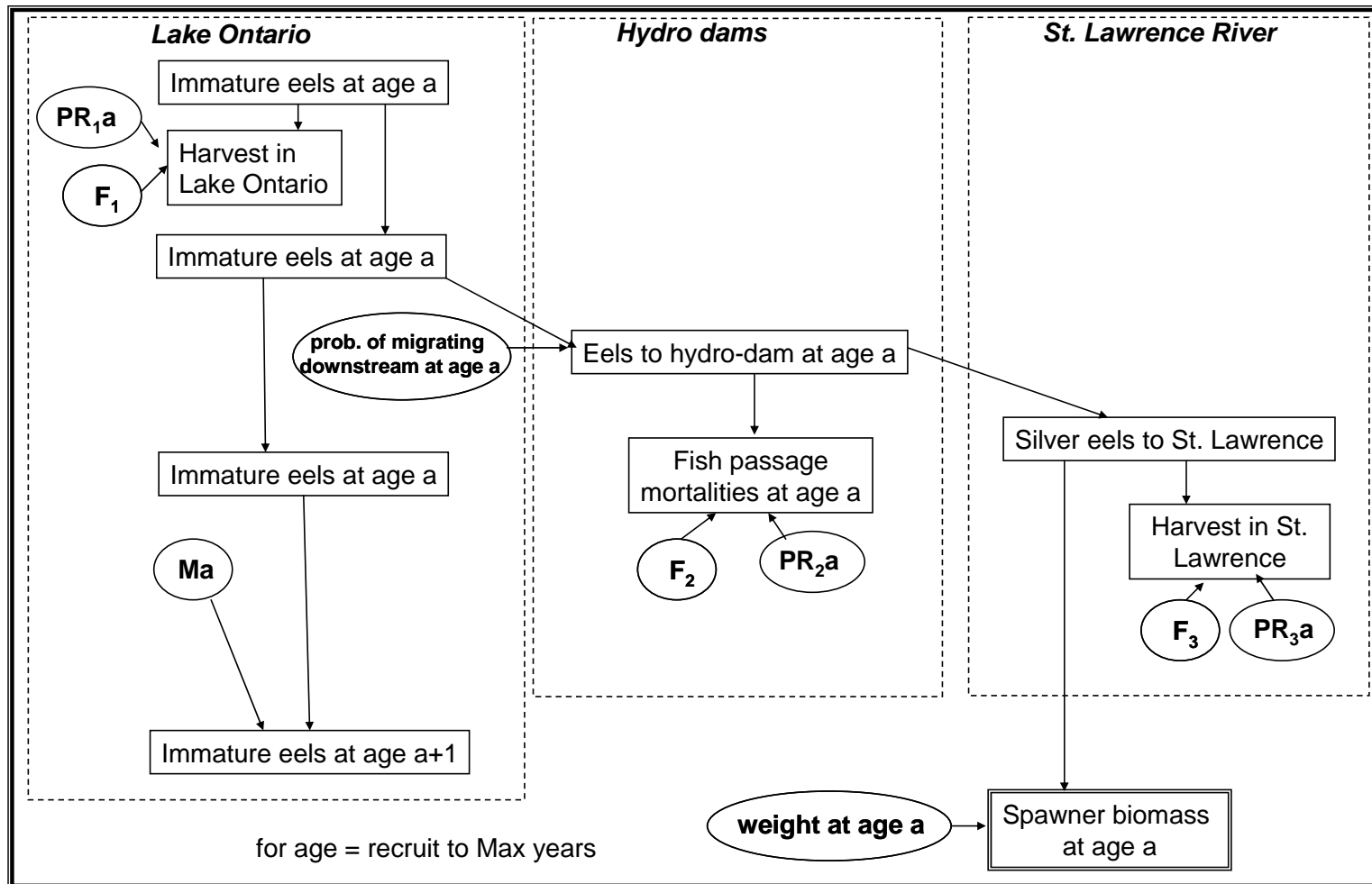
**Figure 9.** *SPR model structure example for an eel stock subjected to three sequential mortality stresses during its life in freshwater and subsequently during the silver eel migration to the spawning grounds. Acronyms as in Figure 4. Note for the hydro dam impacts, $F_2$ could represent the mortality rate of an eel passing through turbine and $PR_2a$ would be the proportion of the downstream run of eels that pass through the turbines (synonymous to partial recruitment vectors in fisheries). Also note that no natural mortality is modelled on the silver eel stage, but M could be incorporated at any stage in the model if it is considered appropriate.*
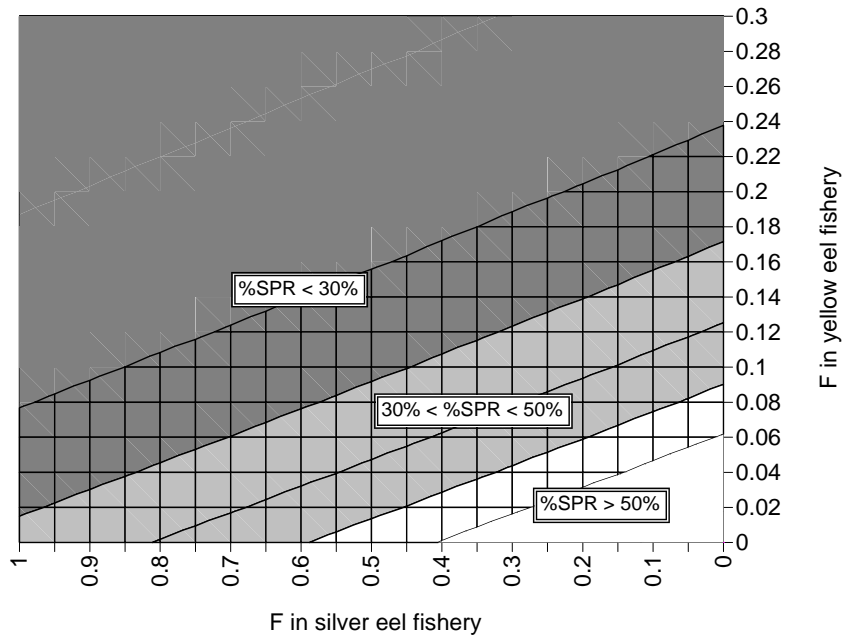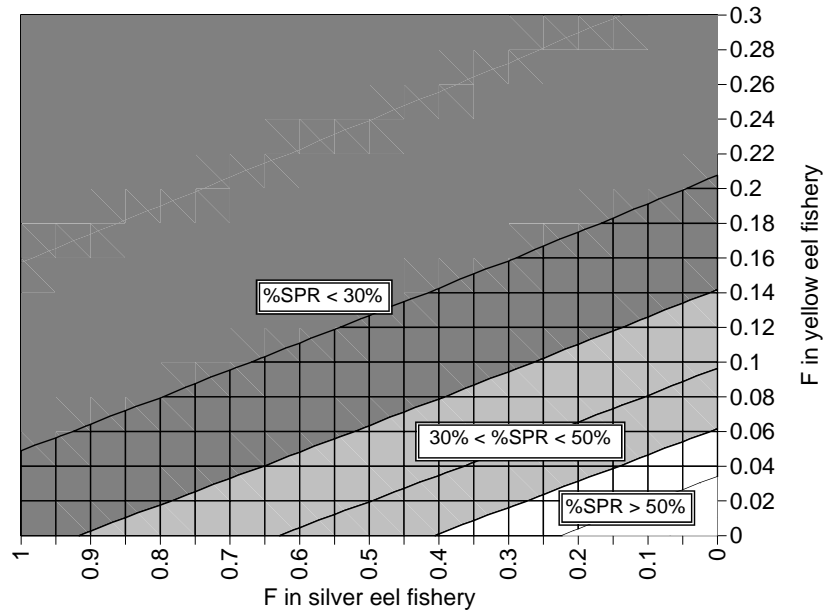
***Figure 10.*** *%SPR analysis of cumulative impacts of fishing at the yellow eel stage (yellow eel fishery) followed by fishing at the silver eel stage later and downstream in the migration (silver eel fishery) for two scenarios of turbine mortality of eels migrating from the rearing areas and the yellow eel fisheries to the downstream fishing locations as silver eels. Upper panel illustrates scenario with turbine mortality of 25% of the migration population, the lower panel scenario is for a turbine mortality of 10% of the migration population.*