An age- and sex-structured assessment model for American eels (*Anguilla rostrata*) in the Potomac River, Maryland

Kari H. Fenske, Michael J. Wilberg, David H. Secor, and Mary C. Fabrizio

Abstract: American eel (*Anguilla rostrata*) and European eel (*Anguilla anguilla*) populations have declined since the 1980s prompting concern about their status and the causes of decline, but stock assessment approaches to estimate effects of fishing on these populations are lacking. Since 1964, 16% of United States commercial American eel harvest came from the Potomac River, yet American eel abundance, production, and fishing mortality is poorly understood in this system. We developed an age- and sex-structured assessment model for 1980–2008 and compared results with the $F_{50\%}$ biological reference point (BRP). The model included natural mortality, fishing mortality, and sex- and age-specific maturation mortality and selectivity. Between 1980 and 2008 estimated recruitment, biomass, and abundance decreased 82%–89%. In all years since 1993, the exploitation rate exceeded the $F_{50\%}$ BRP. The model was moderately sensitive to changes in natural mortality, standard deviation for fishery and recruitment catch-per-unit-effort indices, and initial fishing mortality. The multidecadal decline in recruitment in Chesapeake eels matches those reported elsewhere for American and European eels, suggesting large-scale processes have affected anguillid eel recruitment in the North Atlantic.

Résumé : Les populations d'anguilles d'Amérique (*Anguilla rostrata*) et d'Europe (*Anguilla anguilla*) ont décliné depuis les années 1980, ce qui a généré des préoccupations sur leur statut et les causes de leur déclin; il n'existe, néanmoins, pas d'études d'évaluation des stocks pour estimer les effets de la pêche sur ces populations. Depuis 1964, 16 % de la récolte commerciale américaine d'anguilles d'Amérique s'est faite dans le fleuve Potomac, bien que l'abondance, la production et la mortalité due à la pêche dans ce système restent mal comprises. Nous avons mis au point un modèle d'évaluation structuré d'après l'âge et le sexe pour 1980–2008 et comparé nos résultats aux points de référence biologiques (BRP) $F_{50\%}$. Le modèle inclut la mortalité naturelle, la mortalité due à la pêche, ainsi que la mortalité reliée à la maturation et la sélectivité spécifiques à l'âge et au sexe. Entre 1980 et 2008, le recrutement, la biomasse et l'abondance estimés ont décru de 82–89 %. Au cours de toutes les années depuis 1993, le taux d'exploitation a dépassé le BRP $F_{50\%}$. Le modèle est modérément sensible aux changements dans la mortalité naturelle, la déviation standard dans les indices des pêches et de capture par unité d'effort du recrutement et la mortalité initiale de la pêche. Le déclin sur plusieurs décennies du recrutement des anguilles dans la baie de Chesapeake correspond à ceux signalés ailleurs pour les anguilles d'Amérique et d'Europe, ce qui laisse croire que des processus à grande échelle affectent le recrutement des anguilles de la famille des Anguillidae dans l'Atlantique Nord.

[Traduit par la Rédaction]

Introduction

American eel (*Anguilla rostrata*) and European eel (*Anguilla anguilla*) populations have decreased substantially since the 1980s (Casselman 2003; Dekker 2003), such that there is considerable concern about their conservation (United States Fish and Wildlife Service 2007; MacGregor et al. 2008). In 2004 the Ontario government closed the American eel commercial fishery for all of Ontario, including Lake Ontario and portions of the St. Lawrence River (MacGregor et al. 2008), and in 2008 American eel was designated as an endangered species in that system (MacGregor et al. 2009). Speculation about the causes of population decline centers on diminished recruitment, disease and parasitism, overharvest, and habitat degradation (Haro et al. 2000). Testing these alternative hypotheses is complicated by the American eel's wide distribution and lack of population structure throughout its range (i.e., panmixia; Tesch 1977). Regional effects (overfishing, habitat degradation, turbine mortality) may not be closely tied to range-wide population consequences be-

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cause local recruitment is probably not related to local spawner abundance (Tesch 1977; Avise 2003; Wirth and Bernatchez 2003). However, given American eel life history, regional sources of mortality should have cumulative consequences on range-wide spawner abundance (MacGregor et al. 2009).

American eels are semelparous with a complex life history, which complicates typical approaches for assessing stock status and developing reference points for fishery management. American eels inhabit coastal and inland brackish and freshwater systems from Greenland to Venezuela (Tesch 1977; Helfman et al. 1987). The American eel population is thought to be panmictic based on life history and genetic evidence (Williams et al. 1973; Williams and Koehn 1984; Avise 2003). Adult (silver) eels from throughout their range migrate to the Sargasso Sea to spawn; those from the farthest reaches of their range migrate thousands of kilometres to spawning grounds. Leptocephalus larvae drift on currents for about 1 year until reaching the continental waters of South, Central, and North America (Helfman et al. 1987; McCleave et al. 1987). Upon reaching shelf waters, leptocephali metamorphose into juvenile-stage, unpigmented glass eels (see Atlantic States Marine Fisheries Commission 2000 for definition of life history stages). As pigmentation develops, the young eels are termed elvers and make their way into bays, rivers, and estuaries. Elvers, once fully pigmented, are termed yellow eels (Tesch 1977). The yellow eel stage is the primary feeding and growth phase for the eel. After approximately 3 to 30+ years (Jessop 1987), the eels mature into nonfeeding adults called silver eels (Tesch 1977).

A recently proposed management tactic for anguillid eels matches regional anthropogenic effects like fishing mortality with regional productivity (International Council for the Exploration of the Sea 2006; Bark et al. 2007; Robinet et al. 2007). Sustainably managing all subcomponents of a population as independent stocks is robust to the underlying source–sink population dynamics (Tuck and Possingham 2000; Wilberg et al. 2008). Until population-wide management can be coordinated, individual regions should manage harvest and other anthropogenic mortality sources at locally sustainable levels. Here we develop an age- and sex-structured assessment (ASSA) model for an American eel stock occurring in the Potomac River region, Chesapeake Bay (Fig. 1) and evaluate whether regional harvests are sustainable based upon best estimates of regional spawner production.

Despite the recent attention American eel has received, few population models exist (e.g., De Leo and Gatto 1995), and relatively little is known about American eel production and abundance. Most commonly used stock assessment models have been developed for iteroparous species with well-defined population structure. These models are not well suited to American eel because American eels are semelparous with overlapping generations, panmictic with a common spawning ground in the Sargasso Sea such that local recruitment is probably not related to local stock size, and catadromous with extremely little data from the oceanic portion of their life cycle that would indicate the size of the spawning stock. Additionally, American eel are relatively data-poor; although data collection is improving, there are almost no fishery-independent indices of abundance, length composition or age structure of the harvest, or maturation or sex ratio data available for most of the American eel range (Electric Power Research Institute 1999). We have developed a stock assessment model that requires relatively little data but can be applied to American eel and many other anguillid eel species because it explicitly models American eel's semelparous life history and does not include assumptions about a stock–recruitment function.

Our goal was to estimate the effect of fishing on American eel and develop fishing mortality biological reference points (BRP) to aid in management of the fishery. To address these objectives, we applied the ASSA model to the Potomac River eels using fishery-dependent catch and effort data, demographic data collected in 2007, and a fishery-independent index of recruitment. The Potomac River is near the center of the range of American eels and is a highly productive growth habitat compared with other USA estuaries (Fenske 2009). Harvest of yellow eels in the Potomac River region comprised 16% of the total USA harvest (by mass) on average during the past 57 years (A.C. Carpenter, Potomac River Fisheries Commission (PRFC), P.O. Box 9, Colonial Beach, VA 22443, USA, unpublished data). Results from the stock assessment were compared with the BRP to evaluate sustainability of the fishery.

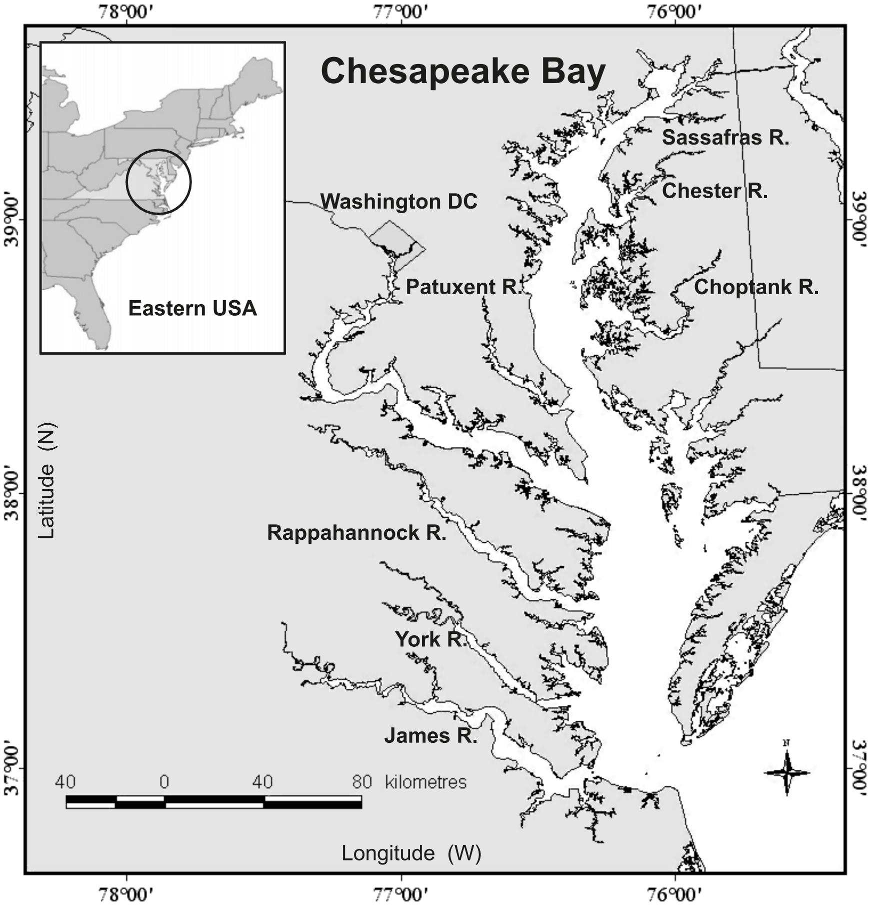
Materials and methods

Data

The ASSA model was fitted to an index of abundance based on commercial fishery catch per unit effort (CPUE, $kg \cdot pot^{-1}$), a recruitment index based on a fishery-independent trawl survey, and proportional abundance-at-age data for 2007. A recruitment index was required for this model because a stock–recruitment relationship cannot be determined. Catch (kg) and fishery-dependent CPUE data were available from the PRFC during 1980–2008 and 1988–2008, respectively. Commercial harvests declined after peaking in the late 1970s and early 1980s (Fig. 2), similar to declining harvest across the entire North American range (MacGregor et al. 2009). Eel pots were the primary fishing gear accounting for >98% of reported catches during 1976–2008. Between 1988 and 2008, the number of active (i.e., those that reported catch) license-holding fishers declined from 50 to 15 (Fig. 2). Reported effort showed a corresponding decline from more than 142 000 reported eel pot lifts in 1988 to less than 49 000 in 2008.

Data on recruitment were available from the Virginia Institute of Marine Science (VIMS, Gloucester Point, Virginia) trawl survey, which used a stratified random survey in the lower Chesapeake Bay, collected between April and September in the York, James, and Rappahannock rivers, which are principal habitats (Tuckey and Fabrizio 2010; Fig. 1). The recruitment index was standardized using a general linear model that included year, river, depth, and a river by depth interaction and expressed as the log-transformed catch of 300–400 mm eels ($\log_e(\text{catch} + 0.01)$). Otolith-based aging indicated that 300–400 mm eels corresponded well to age-4 (Fenske 2009), but there was a broad range of ages potentially present within this size bracket. We chose age-4 as the recruitment age because age-4 was common in the fishery, but age-3 fish were very rare (Fenske 2009). Because length-at-age was highly variable, we also evaluated indices of

Fig. 1. Sub-estuaries of the Chesapeake Bay. Inset shows location in eastern USA.



recruitment from the VIMS survey for alternative size ranges: 200–400, 250–350, and 200–300 mm. These showed approximately the same trend as the one using 300–400 mm eels. Survey-caught eels are not regularly aged in the Chesapeake Bay region, leading to uncertainty regarding age structure of the recruitment index. Although no long-term fishery-independent survey exists for the Potomac River, the use of a recruitment index from other adjacent major Chesapeake Bay tributaries was reasonable based on their proximity to the Potomac River.

We sampled the commercial catch for proportional abundance-at-age in 2007. Otoliths from 168 females from the Potomac River eel pot fishery in 2007 were aged following the methods of Morrison and Secor (2003). Only relatively large females were present in the sample because it had been size graded, where the smallest eels were sold as bait prior to our inspection. Ages 7–11 were chosen for inclusion in the model because they were fully selected to the gear based on inspection of the catch curve, which resulted in a sample size of 60 individuals. Only 1 year of proportional abundance-at-age data was available because management agencies do not sample the catch for age or size composition in the Potomac River.

Stock assessment model

The ASSA model estimated abundance and exploitation rates and was sex-specific because American eels have sexually dimorphic growth and maturation. Females are larger and older at maturation and have higher growth rates (Tesch 1977; Helfman et al. 1987; Oliveira 1999). The model has underlying age-structured dynamics, assumes that total catch is known without error, and is fitted to an aggregate index of abundance. Catch reports for American eels in the Potomac River are thought to be quite accurate during the period included in the model (A.C. Carpenter, PRFC, Colonial Beach, VA 22443, USA, personal communication, 2010). The model included years 1980–2008 and ages 4 to 11+; the “plus” group served as an aggregate category for ages 11 and older. Some parameters were estimated outside the ASSA model, including natural mortality and age- and sex-specific maturation, selectivity, and mean individual mass. Because American eels are semelparous, they mature, leave their juvenile habitat, and spawn only once. Maturation mortality was included in the model to allow estimation of female spawner escapement. We approximated the 95% confidence intervals of model estimates as the maximum likelihood estimate (MLE) ± 2 times their asymptotic standard errors.

The process model described how abundance changed over time (see Table 1 for variable definitions). Recruitment (abundance at age-4) was estimated for each year and sex by the product of the sex ratio and overall recruitment for each year:

$$(1) \qquad R_{y,g} = T_y s_g$$

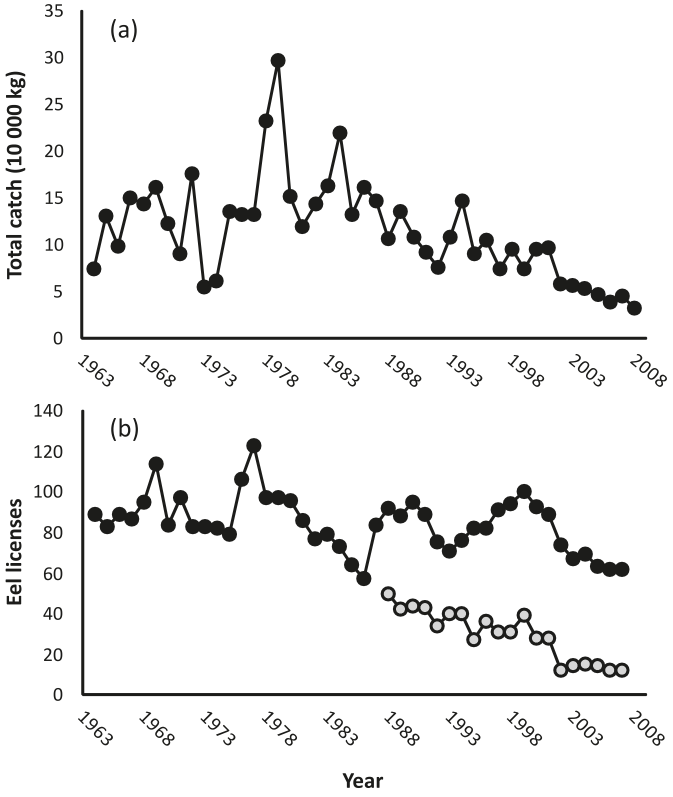


Fig. 2. (*a*) Total catch (in 10 000 kg) of American eels in the Potomac River, 1964–2008 (A.C. Carpenter, Potomac River Fishery Commission, P.O. Box 9, Colonial Beach, VA 22443, USA, unpublished data). (*b*) Number of licensed American eel pot fishers in the Potomac River (black circles, 1964–2008) and number of American eel pot licenses that reported catches (grey circles, 1988–2008).

We assumed a 1:1 sex ratio for age-4 eels. Recruitment was estimated as a free parameter for each year. We took this approach because local recruitment may not be tied to local spawning stock abundance. The model did not include any penalty on deviations for mean recruitment because recruitment had declined substantially in some regions, and we did not want to cause attenuation of the parameter estimates.

Abundance-at-age in1980 was calculated assuming the Potomac stock was in equilibrium. Abundance in the next age was equal to the product of abundance in the previous age, the exponential mortality model where fishing mortality-at-age and sex was based on fishery selectivity, and the proportion of individuals that did not mature:

$$(2)\qquad N_{1980,a+1,g} = N_{1980,a,g}\,\mathrm{e}^{-M}(1 - S_{a,g}U_{\mathrm{init}})(1 - m_{a,g})$$

Maturation mortality occurred after other natural mortality sources, and the equilibrium exploitation rate was estimated during model fitting. Abundance in the age-11+ group in 1980 was calculated using the solution to the infinite series for abundance for ages 11 and older:

$$(3)\qquad N_{1980,11+,g} = \frac{N_{1980,10,g}\,\mathrm{e}^{-M}(1 - S_{10,g}U_{\mathrm{init}})(1 - m_{10,g})}{1 - \mathrm{e}^{-M}(1 - S_{11+,g}U_{\mathrm{init}})(1 - m_{11+,g})}$$

For subsequent model years (1981–2008), abundance-at-age was calculated assuming the catch occurs instantaneously halfway through the year:

$$(4)\qquad N_{y+1,a+1,g} = (N_{y,a,g}\,\mathrm{e}^{-0.5M} - C_{y,a,g})\,\mathrm{e}^{-0.5M}(1 - m_{a,g})$$

Abundance of age-11+ eels was calculated as the sum of surviving age-10 and age-11+ eels from the previous year.

$$(5)\qquad \begin{aligned} N_{y+1,11+,g} = {} & (N_{y,11+,g}\,\mathrm{e}^{-0.5M} - C_{y,11+,g})\,\mathrm{e}^{-0.5M} \\ & \times (1 - m_{11+,g}) + (N_{y,10,g}\,\mathrm{e}^{-0.5M} - C_{y,10,g}) \\ & \times \mathrm{e}^{-0.5M}(1 - m_{10,g}) \end{aligned}$$

Because catch-at-age data were not available, catch-at-age (in numbers) for each sex was calculated from the product of total catch (in mass) and the proportional biomass of each age and sex class weighted by selectivity and converted from mass to numbers:

$$(6)\qquad C_{y,a,g} = \frac{X_y\,S_{a,g}\,N_{y,a,g}\,\mathrm{e}^{-0.5M}}{\sum\limits_g \sum\limits_a (S_{a,g}\,\overline{w}_{a,g}\,N_{y,a,g}\,\mathrm{e}^{-0.5M})}$$

Total biomass just prior to fishing was calculated as the product of abundance, mean mass, and survival during the first half of the year:

$$(7)\qquad B_y = \sum_g \sum_a N_{y,a,g}\overline{w}_{a,g}\,\mathrm{e}^{-0.5M}$$

Biomass of spawning females (SB) was calculated as the sum of maturing females over ages that survived and were not harvested:

$$(8)\qquad \mathrm{SB}_{y,g} = \sum_a (N_{y,a,g}\,\mathrm{e}^{-0.5M} - C_{y,a,g})\,\mathrm{e}^{-0.5M}\overline{w}_{a,g}m_{a,g}$$

Exploitable biomass was the biomass vulnerable to the fishery:

$$(9)\qquad \widetilde{B}_y = \sum_g \sum_a N_{y,a,g}\,S_{a,g}\overline{w}_{a,g}\,\mathrm{e}^{-0.5M}$$

The annual exploitation rate for the Potomac stock was calculated as total observed annual catch divided by total biomass in that year:

$$(10)\qquad U_y = \frac{X_y}{B_y}$$

The observation model made predictions that were compared with the observations to estimate parameters. A recruitment index was estimated for each model year to compare with the standardized age-4 recruitment index:

$$(11)\qquad \widehat{I}_y = T_y q_1$$

where the MLE of catchability was

$$(12)\qquad \log_{\mathrm{e}} q_1 = \frac{1}{n_1}\sum_y (\log_{\mathrm{e}} I_y - \log_{\mathrm{e}} N_{y,4})$$

The estimated fishery CPUE index included density-dependent catchability:

Table 1. Parameters, data, and variables for Potomac River American eel assessment model.

Variable	Description
a	Age (i is also an age subscript in spawning potential ratio (SPR) calculations)
A	Plus group for maximum age (11) used in the model
y	Year
g	Sex
f	Female
B_y	Total biomass (kg) for year y
$\widetilde{B}_y$	Exploitable biomass (kg) for year y
$C_{y,a,g}$	Catch (number of individuals) for year y, age a, and sex g
E_y	Fishery effort for year y (in 10 000 pot nights fished)
I_y	Recruitment index ($\log_e$ number of eels per tow) for year y
$m_{a,g}$	Proportion of eels of age a and sex g that will mature that year
M	Natural mortality rate (year^{-1})
n_e	Effective sample size for abundance-at-age data
n_1	Number of years of data for the first likelihood component
n_2	Number of years of data for the second likelihood component
$N_{y,a,g}$	Numbers-at-age a in year y for sex g
p	Proportional abundance-at-age for third likelihood component
q_1	Catchability for recruitment index
$q_{1,y}$	Catchability for fishery catch-per-unit-effort (CPUE) index
$R_{y,g}$	Estimated recruitment of American eels in year y for sex g
s_g	Sex ratio of age-4 American eels
$S_{a,g}$	Selectivity-at-age for eels age a and sex g
SB_y	Spawner biomass (female kg) for year y
$\mathrm{SB}/R_{\mathrm{F}}$	Spawner biomass per recruit for fished population
$\mathrm{SB}/R_{\mathrm{U}}$	Spawner biomass per recruit for unfished population
SPR	Spawning potential ratio
T_y	Total recruitment, sexes combined, in year y
U_{init}	Equilibrium exploitation rate prior to 1980
U_y	Exploitation rate in year y
$\overline{w}_{a,g}$	Mean mass-at-age (kg) for individual eels age a and sex g
X_y	Observed catch (kg) for year y
α, β	Parameters of effort-dependent catchability
σ_1	Standard deviation for recruitment index
σ_2	Standard deviation for fishery CPUE index
σ_{rw}	Standard deviation for catchability in the random walk model
σ_{wn}	Standard deviation for catchability in the white noise model

$$(13) \qquad \widehat{\mathrm{CPUE}}_y = \widetilde{B}_y\, q_{2,y}$$

where fishery catchability was estimated for each year using a density-dependent catchability model (Paloheimo and Dickie 1964; Wilberg et al. 2010):

$$(14) \qquad q_{2,y} = \alpha \widetilde{B}_y^{\beta}$$

Density-dependent catchability has been observed in fishery-dependent indices of abundance for many stocks and can be caused by nonrandom search by fishers on a contagiously distributed stock and by gear saturation (Wilberg et al. 2010). We used a density-dependent catchability model for fishery CPUE because it was very robust to changes in the standard deviation (SD) of the CPUE index.

Model fitting

The model was constructed in AD Model Builder (Otter Research Ltd., Sidney, British Columbia), and parameters were estimated using maximum likelihood estimation. The model was fitted by minimizing the negative log likelihood function (–LL), which contained components for the recruitment index (L_1), the fishery CPUE index (L_2), female proportional abundance-at-age in 2007 (L_3), and a penalty to constrain the equilibrium exploitation rate in the first year (L_4):

$$(15) \qquad -\mathrm{LL} = L_1 + L_2 + L_3 + L_4$$

The first likelihood component (L_1) compared the observed and predicted recruitment index for each year:

$$(16) \qquad L_1 = n_1 \log_{\mathrm{e}} \sigma_1 + \frac{\sum \left[\log_{\mathrm{e}}(I_y) - \log_{\mathrm{e}}(q_1 \widehat{N}_{y,a=4})\right]^2}{2\sigma_1^2}$$

We assumed that errors in the recruitment index were lognormally distributed with an SD (on the log scale) of 0.3. This value was slightly greater than the estimated standard error of the log-scale recruitment index (~0.2), but because the recruitment index was not specific to the Potomac River, we wanted to capture the potential for additional variation. Additionally, the estimated precision of the index of recruitment

(0.2) is a lower threshold for the relationship between the recruitment index and actual recruitment because it only includes variability in survey catch (Wilberg et al. 2010).

The second likelihood component (L_2) compared the observed and predicted fishery CPUE index:

$$(17)\qquad L_2 = n_2 \log_{\mathrm{e}} \sigma_2 + \frac{\sum \left[\log_{\mathrm{e}}(\mathrm{CPUE}_y) - \log_{\mathrm{e}}(\widehat{\mathrm{CPUE}}_y)\right]^2}{2\sigma_2^2}$$

We assumed errors in the fishery CPUE index were lognormally distributed with a log-scale SD of 0.3 and tested the sensitivity of the model to this assumption. We chose this SD so that the fishery CPUE index would have an equal weight to the recruitment index. An SD of 0.3 is somewhat higher than 0.15–0.2 recommended by Francis et al. (2003) for commercial fishery-dependent indices in New Zealand.

The third likelihood component (L_3) compared the observed and predicted proportional abundance-at-age for female ages 7–11 in 2007 using a multinomial likelihood function (Fournier and Archibald 1982):

$$(18)\qquad L_3 = -n_{\mathrm{e}} \sum_{a=7}^{11} p_a \log_{\mathrm{e}} \widehat{p}_a$$

Because effective sample size is typically lower than the number of individuals aged (Crone and Sampson 1998), we selected an effective sample size for proportional abundance-at-age that was half the number of American eels aged (n = 30).

A penalty on the equilibrium exploitation rate prior to the first year of the model was necessary to estimate the parameter. The number of days fished during 1976–1979 was 20% higher than in 1980. Thus, we included a lognormal penalty on the equilibrium (median) exploitation rate, which was 20% higher than the 1980 exploitation rate and a log-scale SD of 0.3:

$$(19)\qquad L_4 = \frac{0.5\left[\log\left(u_{\mathrm{eq}}\right) - \log\left(1.2u_{1980}\right)\right]^2}{0.09}$$

This was the highest level of coefficient of variation (CV) we could choose and still have the model converge.

Biological reference points (BRP)

In addition to the ASSA model, we developed a spawning potential ratio (SPR) model for female American eels to estimate an exploitation rate BRP and compared the estimated exploitation rates with the BRP. The SPR model predicted the equilibrium spawning biomass of females produced per female recruit:

$$(20)\qquad \mathrm{SB}/R_F = \sum_{a=4}^{\infty} \left[\mathrm{e}^{\sum_{i=4}^{a-1} -M} \, \overline{w}_{a,f} m_{a,f} \prod_{i=4}^{a-1} (1 - S_{i,f}u)(1 - m_{i,f}) \right]$$

Values for the parameters of the SPR model (natural mortality, maturation-at-age, selectivity-at-age, and mass-at-age) were identical to those for females in the ASSA model. SPR was calculated as the (female) spawning biomass per recruit of American eels in a fished population divided by the spawning stock biomass per recruit in an unfished population:

$$(21)\qquad \mathrm{SPR} = \frac{\mathrm{SB}/R_{\mathrm{F}}}{\mathrm{SB}/R_{\mathrm{U}}}$$

The $\mathrm{SB}/R_{\mathrm{U}}$ for an unfished population was calculated using eq. 20, but with the exploitation rate set equal to zero. We calculated $F_{50\%}$, the exploitation rate that results in a 50% reduction of the SPR (Quinn and Deriso 1999), and the estimated SPR for each year. $F_{50\%}$ has been suggested as a precautionary reference point for European eel (International Council for the Exploration of the Sea 2001).

Parameters estimated outside of the model

American eel are a relatively data-poor species, and published estimates of biological parameters such as selectivity, maturation, and natural mortality are rare or vary substantially by region. Additionally, the age- or size-structured data that are necessary to estimate these parameters during model fitting are not available for the Potomac River. Few estimates of natural mortality exist for American eels. Instantaneous natural mortality was assumed to be 0.24 year^{-1}, based on catch curve estimates from the unfished American eel stock in the Hudson River. To obtain this estimate, we conducted catch curve analysis based on Hudson River data from Morrison and Secor (2003), but catches-at-age were first rescaled by the observed decline in recruitment in the Chesapeake Bay and St. Lawrence River (Casselman et al. 1997). Estimated maturation mortality was subtracted from the catch curve mortality estimates to obtain the natural mortality estimate.

Female maturation-at-age is thought to be length-based (Vøllestad and Jonsson 1986; De Leo and Gatto 1996). We estimated maturation-at-age for females by fitting a logistic model to data from American eels collected throughout the Chesapeake Bay. Gonads of 345 females, aged 4–11, were collected in fall 2007 from the Chester, Choptank, James, and Potomac rivers and macroscopically inspected. A female exhibiting a gonado-somatic index (GSI) $\geq$1% may mature in the present year and subsequently undertake an oceanic spawning migration (Durif et al. 2005). We assumed females with a GSI $\geq$ 0.9% (19% of female sample) would mature that year. Female maturation-at-age never exceeds 20% in our estimation. This was similar to the finding of De Leo and Gatto (1996), who found that the percentage of European eel females maturing reached an asymptote at approximately 10%–30%·year^{-1} in the systems and years they considered. Our assumed upper level of maturation-at-age is consistent with the maximum observed age of 18 in Chesapeake Bay (Owens and Geer 2003).

Male maturation-at-age was estimated using data collected from eels sampled in the Chester, Choptank, James, Patuxent, Potomac, and Sassafras rivers in 2007. Gonad development of 185 male and intersexual eels aged 3–8 was examined macroscopically. Male European eels, and presumably American eels, develop directly from intersexual eels (Buellens et al. 1997). Males were identified on the basis of gonad morphology as described in Buellens et al. (1997) (i.e., gonads with individual, overlapping lobes). Male American eel are thought to use a “time minimization” strategy, where they mature and migrate at the earliest possible age (Oliveira 1999). Given this strategy, we assumed that any American eel that was identifiable as male would mature in the current year. We used the ratio of male to intersexual eels at each age to estimate the proportion mature, and maturation was constant over ages 4–7. Owing to the lack of male or intersexual American eels older than 8 years in the Chesapeake Bay samples, we assumed a maturation-at-age of 0.99 for males aged 8–11 (Fig. 3). This was a similar result to De Leo and Gatto (1996), who found that by age 4–7 years, all males had likely matured.

Mean individual mass-at-age for female and male American eels was calculated using the mass and age data collected from the Chester, Choptank, James, Patuxent, Potomac, and Sassafras rivers (Fenske 2009; Fig. 3). Because of a lack of older males in samples, we extrapolated mean mass-at-age for male and intersexual eels aged 9–11 using a linear mass-at-age regression from ages 3 to 8.

Because age-specific catch data were not available for the Potomac River, we estimated fishery selectivity outside of the model fitting. Eel pots with a 12.7 mm mesh are the primary gear used in the commercial fishery in the Potomac River. To calculate female selectivity-at-age, we fit a von Bertalanffy growth curve to female length-at-age data from Owens and Geer (2003; for ages 1–3) and length-at-age data from 2007 collected by Fenske et al. (2010) (for ages 4–11). Male length-at-age was modeled as a linear function using length-at-age data collected in 2007 (Fenske 2009). We then calculated the proportion of male and female American eels greater than 270 mm for each age in the model, assuming a normal distribution and the SDs of length-at-age from Owens and Geer (2003). The 270 mm threshold size was chosen as the midpoint between the minimum length (220 mm) commonly retained by eels pots with 12.7 mm mesh and a minimum length (320 mm) that should always be retained by the pots. These length thresholds were based on a length–girth relationship developed from measurements of 820 eels from the Chesapeake Bay in 2007 (Fenske 2009). Male eels were never fully selected in the model, which was reasonable because some may mature before reaching the size of full selection used in this model (Oliveira 1999).

Sensitivity analyses

We performed sensitivity analyses to examine the effects of our assumed natural mortality rate, the SDs for both indices of abundance, selectivity, and time-varying catchability model for fishery CPUE. For natural mortality and the SD of the fishery CPUE index, we increased and decreased the values by 20%–50% and compared these alternate model outputs with the base model (the ASSA model specified in the methods). In addition we tested the sensitivity of the model to two different selectivity patterns by choosing a larger (320 mm) and a smaller (220 mm) length threshold for calculating selectivity-at-age. These alternate length thresholds represented the length at which eels were fully selected to the gear and the length at which less than 0.1% were retained by the gear, respectively.

We conducted sensitivity analyses of four alternative models for fishery catchability: white noise, random walk, effort-dependent, and constant. Each catchability pattern was run with three values for the SD of the recruitment index (0.2, 0.3, 0.4). The white noise model (i.e., random variation about a constant mean on the log scale) was

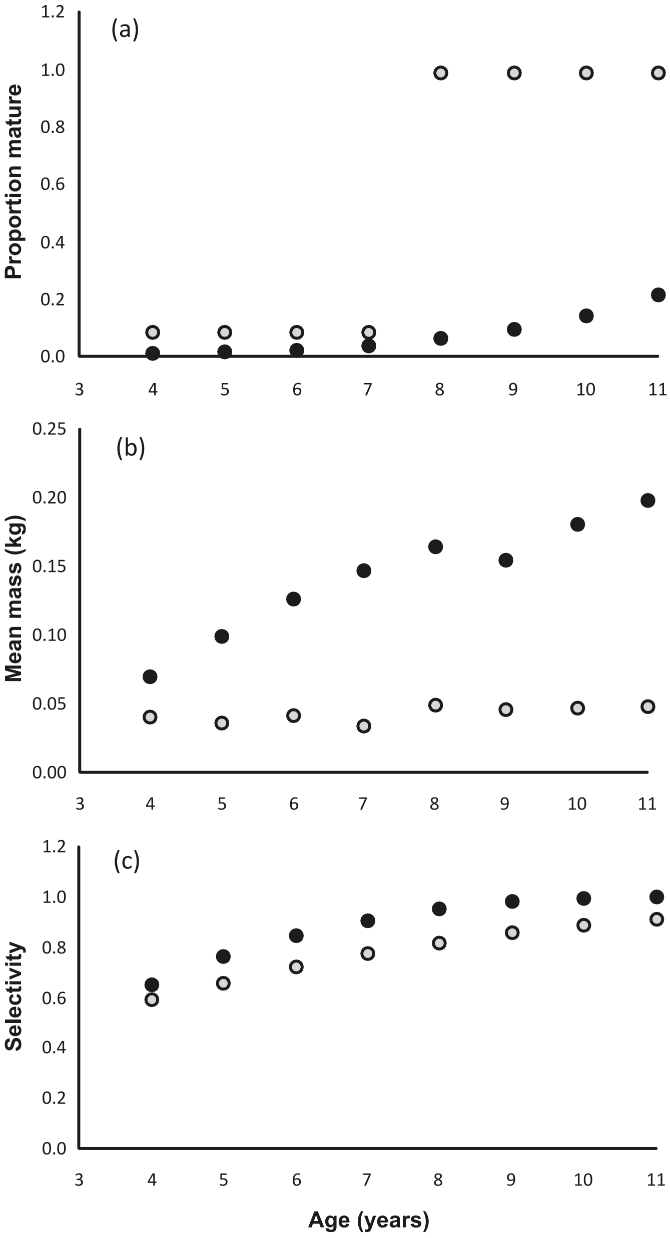


Fig. 3. Mean maturity-at-age (*a*), mass-at-age (*b*), and selectivity-at-age (*c*) used in the age- and sex-structured assessment (ASSA) model for female (black circles) and male (grey circles) American eels. Data came from published literature and laboratory dissections of American eel in the Chesapeake Bay.

$$q_{2,y} = \overline{q}_2 \, \mathrm{e}^{\delta_y} \tag{22}$$

The white noise model also required an additional likelihood component for the annual deviations from mean catchability:

$$L_5 = \frac{1}{2\sigma^2_{\mathrm{wn}}} \sum_{y=1988}^{2008} \delta_y^2 \tag{23}$$

We used two values for the SD of the process errors, 0.25 and 1.0.

The random walk catchability model was

$$(24)\qquad q_{2,y+1} = q_{2,y}\ \mathrm{e}^{\delta_y}$$

The random walk catchability model also required an additional likelihood component:

$$(25)\qquad L_5 = \frac{1}{2\sigma_{\mathrm{rw}}^2}\sum_{y=1989}^{2008}\delta_y^2$$

We used two values for the SD of the process errors: 0.25 and 1.0. For the random walk catchability model, $q_{2,1988}$ is an estimated parameter.

The effort-dependent catchability model was

$$(26)\qquad q_{2,y} = \alpha E_y^{\beta}$$

where α and β were estimated parameters. The last catchability model assumed constant catchability for fishery CPUE.

For all sensitivity analyses, we compared the following with the base model values: the estimates of average total abundance during 1980–2008, total abundance in the first and last year of the model, average exploitation rate during 1980–2008, and exploitation rate in 2008.

Results

The ASSA model fit the observed fishery CPUE index, recruitment index, and proportion-at-age reasonably well, but a slight residual pattern was present in the fit to the fishery CPUE index (Fig. 4). Predicted fishery CPUE increased 11.9% during 1988–2008, in contrast with the recruitment index. Residuals for fishery CPUE showed a U-shaped pattern with positive residuals at the beginning and end of the time series and negative residuals in the middle. Observed and predicted recruitment indices decreased substantially during 1980–2008, and the model fit the observed index nearly perfectly when the recruitment index was the only source of data. Model predictions of the age composition in 2007 showed the same pattern of decreasing proportions with increasing age as the observed proportions-at-age (Fig. 4).

Estimated female spawner biomass declined to 6.4% of its 1980 value (Fig. 5). The estimates had a large CV early in the time series, but the uncertainty decreased with more data. The primary reason for the large amount of uncertainty in the first year was due to U_{init} (median 0.17; 95% confidence interval (CI) 0.04–0.68). Estimated abundance (in numbers) declined substantially to 7.8% of its 1980 value during 1980–2008 (Table 2). Estimated abundance was relatively high from 1980 to 1984 then began to steadily decline in 1985. The estimated abundance in the Potomac River in 2008 was less than 2.4 million American eels. Estimated recruitment in 2008 was 17.7% of the 1980 value (Table 2; MLE q_1: 5.72×10^{-9}, 95% CI: 4.60×10^{-9} to 6.85×10^{-9}). Estimated catchability in the fishery increased steadily during 2002–2008 as American eel biomass decreased (Fig. 5), and the parameters of the density-dependent catchability function had relatively narrow 95% CIs (MLE α: 7.42×10^{-6}, 95% CI: 6.00×10^{-6} to 9.17×10^{-6}; MLE β: –1.05, 95% CI: –1.22 to –0.88).

In contrast with abundance, estimated exploitation rate increased over time (Fig. 5). The exploitation rate that corresponded to the BRP $F_{50\%}$ was 0.14 year^{-1}. The exploitation rate for fully selected females was higher than the $F_{50\%}$ reference point since 1993. Between 1996 and 2008, the estimated exploitation rate was higher than $F_{30\%}$: 0.25 year^{-1}.

Sensitivity analysis

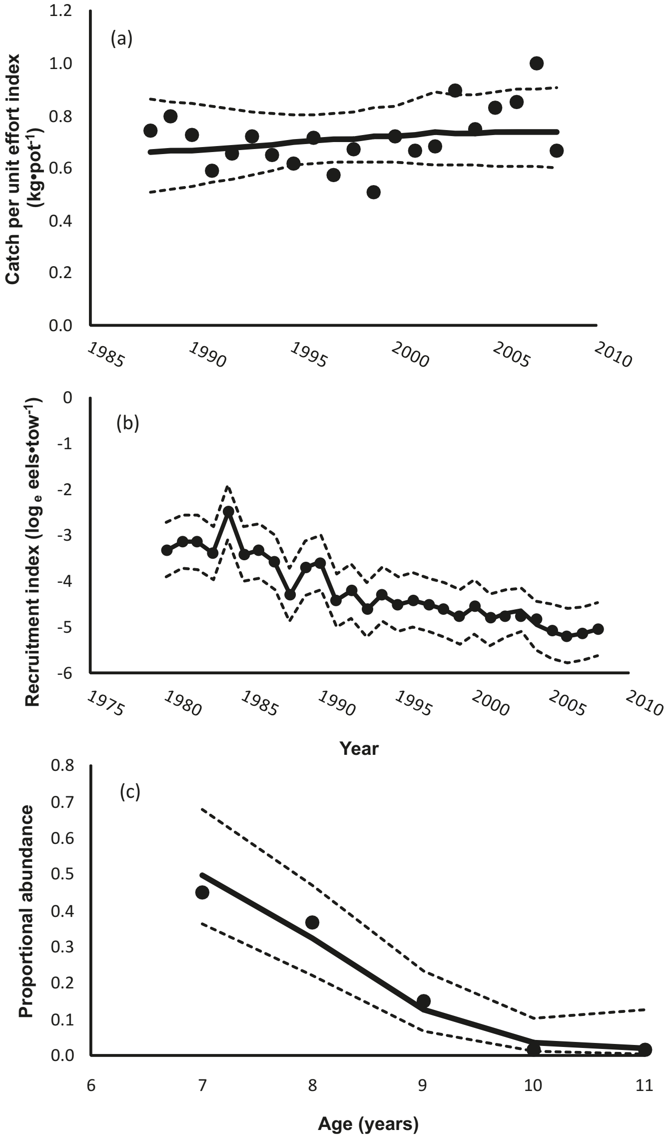
Most of the models with different catchability assumptions were very sensitive to the assumed SD of the recruitment index (Table 3). However, two notable exceptions were the density-dependent catchability model and the white noise model with a log-scale SD of 1.0. These two models were insensitive to assumed SD of the recruitment index, with a small (3%–13%) difference in range of estimated mean abundance across the range of assumed SD for the recruitment index. In comparison, the constant, effort-dependent, random walk, and white noise (with log-scale SD of 0.25) catchability models were more sensitive to assumed recruitment index SD, with a large range (43%–80%) of differences in estimated mean abundance across models. In several catchability scenarios, the model would not converge on a solution. Abundance in the first and last years showed a similar pattern to average abundance, and exploitation rate showed the opposite pattern.

The model was moderately sensitive to assumptions of natural mortality, the SDs of fishery CPUE and recruitment indices, and selectivity patterns, based on the percent difference of the base model and alternative model results (Table 4). A 25% increase in natural mortality caused estimated exploitation rates in 2008 to decrease by approximately 13% and abundance in 2008 to increase by 15% over the base model. A 17%–38% decrease in natural mortality caused estimated exploitation rates for females and males in 2008 to increase by approximately 9%–29% and 2008 abundance to decrease by 10%–24%. Increasing or decreasing the minimum size for the selectivity estimates by 19% caused changes of 13%–43% for 2008 abundance and 13%–30% for exploitation rate (Table 4). Increasing or decreasing the SD for the fishery CPUE index by 50% resulted in mean abundance and mean exploitation rates changing by <2% and <5%, respectively. Changing the SD for fishery CPUE also resulted in changes to how well the recruitment index was fitted, but the model was always matched the observed recruitment index very closely (median absolute value of percent deviation $\leq$ 0.2%).

Discussion

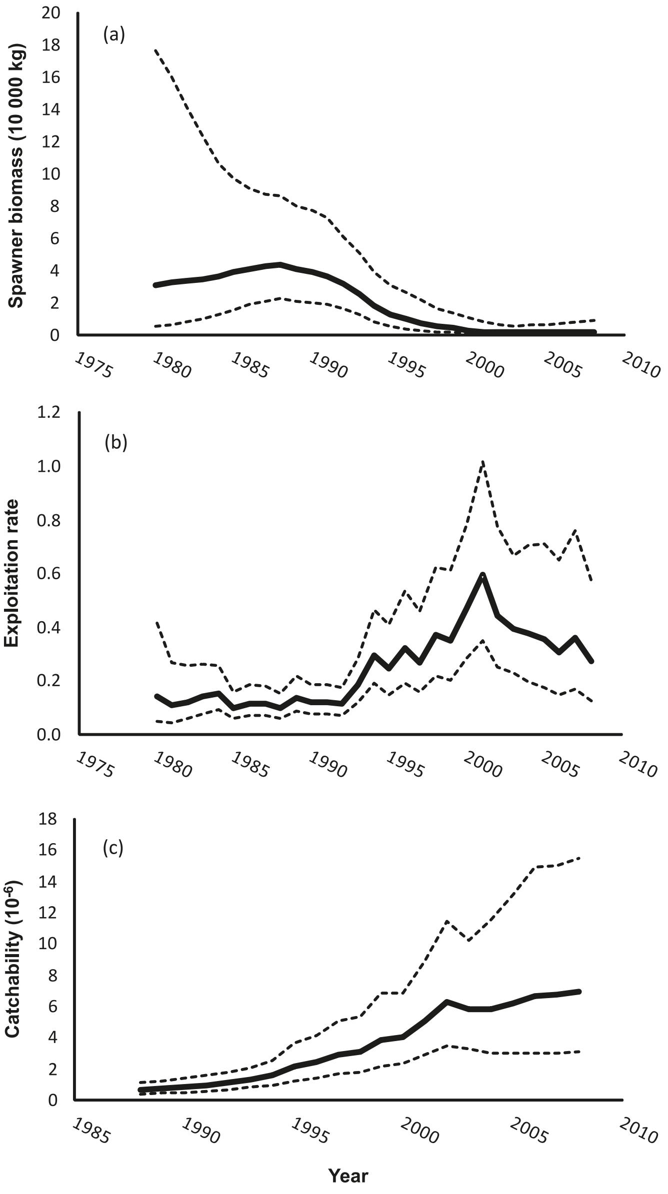
We detected a substantial decline in American eel abundance in the Potomac River between 1980 and 2008. The decline was of a similar magnitude and on the same time scale as the decline in abundance seen in other parts of the American eel's range and for European eel (Casselman et al. 1997; Committee on the Status of Endangered Wildlife in Canada 2006; International Council for the Exploration of the Sea 2006). Since the 1970s, the number of yellow-phase American eels ascending eel ladders at the Moses–Saunders Hydroelectric Dam at Cornwall, Ontario, has declined by about 99%. Between 1980 and 2008, the Chesapeake Bay recruitment index from the VIMS trawl survey has declined by 82%, and the 2006 Atlantic States Marine Fisheries Commis-

Fig. 4. Model fit for observed and estimated fishery catch per unit effort (CPUE) (*a*), recruitment CPUE (*b*), and female age composition in 2007 (*c*). Model estimates are represented by the solid lines and observed data by solid circles. The 95% confidence intervals for the predicted CPUE and age composition are indicated by dashed lines.



sion stock assessment for American eel also indicated that the stock was "at or near documented low levels" (Atlantic States Marine Fisheries Commission 2006). Similar declines in abundance and recruitment have been observed for European eel (Dekker 2000; International Council for the Exploration of the Sea 2006), a species that shares spawning grounds in the Sargasso Sea with American eel (McCleave 1993). The coincidence of declining recruitment and abundance in three distant regions of anguillid eels points to large-scale (population-wide) processes as an important component of anguillid population dynamics. The decline predicted by the model also serves as a diagnostic; the model results were consistent with observed declines in American eel recruitment in the Chesapeake Bay and elsewhere.

Fig. 5. (*a*) Estimated spawner biomass (10 000 kg) for female American eels from the Potomac River, 1980–2008. (*b*) Estimated exploitation rate for female American eels in the Potomac River, 1980–2008. (*c*) Model-estimated catchability of American eels in the Potomac River, 1988–2008. For all figures, the 95% confidence intervals for the predicted parameter are indicated by the dashed lines.



The abundance estimates from our ASSA model were heavily influenced by trends in the recruitment index from tributaries of the lower Chesapeake Bay, and the model fit the recruitment index nearly exactly (absolute value of the median deviation was 0.1%). We believe these abundance estimates reflect a true decline in abundance of yellow-phase American eels. Our model indicated that female spawner escapement from the Potomac River decreased by 94% between 1980 and 2008. For American eels, spawning stock biomass may have decreased to levels that impair recruitment, possibly due initially to overharvest (Atlantic States Marine Fisheries Commission 2000; de Lafontaine et al. 2010), habitat

Table 2. Age- and sex-structured assessment model estimates of American eel abundance-at-age (×10 000) during 1980–2008 in the Potomac River.

	Age								
Year	4	5	6	7	8	9	10	11+	Total
1980	641.0	429.6	282.2	182.0	115.1	39.1	22.9	26.3	1738.0
1981	760.6	432.6	284.6	183.7	116.2	39.5	23.2	26.6	1867.1
1982	760.4	527.4	295.8	191.9	121.9	41.7	24.6	28.2	1991.9
1983	593.6	521.8	356.3	196.7	125.5	43.2	25.5	29.3	1891.9
1984	1451.4	402.1	347.2	233.0	126.4	43.7	25.8	29.8	2659.4
1985	583.5	972.5	264.2	223.8	147.3	43.2	25.6	29.7	2289.9
1986	627.8	408.3	671.9	180.2	150.4	53.9	27.3	31.8	2151.5
1987	489.6	432.7	277.2	449.5	118.6	53.8	33.2	33.1	1887.7
1988	240.2	338.0	294.3	185.8	296.4	42.6	33.2	37.3	1467.8
1989	431.4	168.2	233.7	201.0	125.0	109.1	26.9	40.6	1336.0
1990	486.8	292.4	112.0	153.0	129.2	43.8	65.3	36.5	1319.0
1991	211.7	334.6	197.9	74.7	100.3	46.2	26.8	57.7	1049.9
1992	261.7	145.6	226.7	132.0	49.0	35.9	28.3	46.6	925.8
1993	174.7	181.0	99.3	152.3	87.3	17.7	22.2	41.9	776.4
1994	243.1	114.1	115.5	61.9	92.9	28.7	9.9	32.4	698.6
1995	194.1	144.7	65.2	63.5	32.9	25.8	13.6	17.8	557.6
1996	213.7	120.6	86.9	38.0	35.9	9.7	13.3	14.6	532.7
1997	193.3	124.4	67.1	46.4	19.5	9.3	4.4	11.5	476.0
1998	174.2	117.7	73.0	38.1	25.5	5.4	4.6	7.0	445.6
1999	147.4	96.9	61.9	36.6	18.2	6.0	2.3	4.4	373.6
2000	184.6	83.4	52.1	31.8	18.0	4.4	2.6	2.6	379.4
2001	140.0	92.8	38.8	22.6	12.9	3.4	1.5	1.6	313.5
2002	161.6	61.1	36.1	13.6	7.2	1.7	0.8	0.6	282.8
2003	172.9	83.8	29.5	16.4	5.8	1.3	0.6	0.5	310.9
2004	124.5	94.2	43.0	14.4	7.6	1.2	0.5	0.4	285.7
2005	108.0	68.9	49.3	21.4	6.9	1.6	0.5	0.3	256.9
2006	98.1	61.0	37.0	25.2	10.5	1.5	0.7	0.3	234.3
2007	103.3	57.8	34.4	20.1	13.2	2.6	0.7	0.4	232.7
2008	113.4	58.1	30.9	17.5	9.8	3.1	1.1	0.5	234.4
2009	—	69.0	34.1	17.5	9.6	2.6	1.5	0.7	—

Note: Recruitment in 2009 was not estimable, but abundance-at-age for the remaining ages is presented.

loss (Busch et al. 1998; Atlantic States Marine Fisheries Commission 2000), changing oceanic conditions, or increasing natural mortality. Mortality or curtailed spawning migrations due to impoundments, turbine mortality, or infection by the *Anguillicola crassus* parasite could be further depressing reproduction (McCleave 2001; Kirk 2003; Palstra et al. 2007). Changing oceanic conditions may have depressed marine primary production, leading to poor feeding conditions and reduced survival for eel leptocephali (Friedland et al. 2007; Bonhommeau et al. 2008).

A petition to list American eel as an endangered species in the USA was filed in 2004, but the US Fish and Wildlife Service (USFWS) found that the listing of American eel was not warranted (United States Fish and Wildlife Service 2007). A central rationale for USFWS not to list American eels as endangered centered on stable trends of glass eel (earliest juvenile stage) abundance indices (United States Fish and Wildlife Service 2007). Indeed, glass eel indices from New Jersey, North Carolina, and two in Nova Scotia, all beginning in the mid- to late 1980s, indicate no trend in recruitment over time (Sullivan et al. 2006; Committee on the Status of Endangered Wildlife in Canada 2006). For a long-lived species, a recruitment index of 15 years may be insufficient to capture population trends. These glass eel trends are counter to the observed changes in yellow eel abundance from Chesapeake Bay and other estuaries and demonstrate the difficulty in assessing American eel status based on a single life stage. If the glass eel indices are a true representation of eel population abundance, then declining yellow eel abundances would be attributable to decreasing survival between the glass eel and yellow eel phases. Although speculative, the decreased size of glass eels observed in New Jersey since the mid 1980s and decreased energetic status of European eel elvers (Edeline et al. 2006; Sullivan et al. 2006) could point to decreased survival between the glass eel and yellow eel phases. Alternatively, because glass eel abundance is highly variable from year to year, trends are difficult to detect, and recruitment indices based on yellow-phase eels may be more reliable. We used CPUE of 300–400 mm American eels in the VIMS trawl survey in Virginia tributaries of Chesapeake Bay as an index of age-4 recruitment in the Potomac River and examined indices based on three alternative size ranges. Use of a size-based index of abundance from a neighboring region presented two problems: (*i*) multiple ages comprised our index of abundance because of large overlaps in size at age for American eels (Owens and Geer 2003; Fenske et al. 2010), and (*ii*) the survey samples tributaries of Chesapeake Bay south of the Potomac River, which are under different

Table 3. Sensitivity analyses of recruitment variance for different catchability models within the age- and sex-structured assessment (ASSA) model.

	Adjusted						
Model	R_{var}	σ_{rw} or σ_{wn}	N_{1980}	$\overline{N}$	N_{2008}	$\overline{U}$	U_{2008}
Baseline DD	—	—	173.8	99.9	23.4	0.21	0.23
	0.2	—	176.5	101.5	24.0	0.21	0.22
	0.4	—	171.5	98.6	22.9	0.22	0.23
ED	0.2	—	244.1	149.2	44.9	0.11	0.10
	0.3	—	57.1	63.4	21.4	0.27	0.24
	0.4	—	50.8	50.6	18.6	0.35	0.29
CN	0.2	—	360.7	219.2	81.6	0.07	0.05
	0.3	—	49.6	44.7	23.9	0.40	0.21
	0.4	—	NC				
RW	0.2	0.25	356.0	214.8	74.8	0.07	0.06
	0.3	0.25	53.7	54.6	26.7	0.32	0.18
	0.4	0.25	NC				
	0.2	1.00	193.4	116.4	33.3	0.16	0.14
	0.3	1.00	159.4	101.7	32.2	0.17	0.15
	0.4	1.00	54.8	66.0	26.3	0.27	0.19
WN	0.2	0.25	335.2	200.9	69.1	0.08	0.06
	0.3	0.25	55.4	58.1	27.7	0.30	0.17
	0.4	0.25	NC				
	0.2	1.00	187.3	109.3	29.2	0.18	0.17
	0.3	1.00	174.1	102.8	29.4	0.19	0.17
	0.4	1.00	156.2	94.6	29.4	0.20	0.17

Note: The ASSA model assumed density-dependent (DD, baseline model) catchability with recruitment variance (R_{var}) of 0.3, but effort-dependent (ED), constant (CN), random walk (RW), and white noise (WN) catchability were also run. The first row represents the baseline model estimates for abundance in 1980 (N_{1980}, 100 000 eels); average abundance over years, ages, and sexes ($\overline{N}$, 100 000 eels); abundance in 2008 (N_{2008}, 100 000 eels); mean exploitation rate across year, ages, and sexes ($\overline{U}$); and average exploitation rate for 2008 (U_{2008}). Subsequent rows identify the adjusted recruitment variance value and indicate the model responses with respect to the baseline estimate. Models that did not converge are indicated by NC in the table.

Table 4. The model estimates from sensitivity analyses of alternative natural mortality rates (*M*), selectivity patterns, and standard deviation estimates for the fishery (SD_F) CPUE index used in the ASSA model for yellow-phase American eels in the Potomac River.

	Baseline	Adjusted	N_{1980}	$\overline{N}$	N_{2008}	$\overline{U}$	U_{2008}	% Dev
Baseline	—	—	173.8	99.9	23.4	0.21	0.23	0.1
M	0.24	0.15	148.0	88.3	17.7	0.23	0.29	0.1
		0.2	162.8	94.9	21.0	0.22	0.25	0.1
		0.3	190.2	107.7	26.9	0.21	0.20	0.1
Selectivity	270	220	160.4	91.5	20.4	0.24	0.26	0.1
		320	226.0	131.8	33.5	0.16	0.16	0.1
SD_F	0.3	0.2	172.8	99.5	23.1	0.22	0.23	0.2
		0.4	174.1	100.0	23.6	0.21	0.22	<0.1

Note: The first row represents the baseline model estimates for abundance in 1980 (N_{1980}, 100 000 eels); average abundance over years, ages, and sexes ($\overline{N}$, 100 000 eels); abundance in 2008 (N_{2008}, 100 000 eels); mean exploitation rate across year, ages, and sexes ($\overline{U}$); average exploitation rate for 2008 (U_{2008}); and median absolute value of the percent deviation between observed and predicted values for the recruitment index (% Dev). Subsequent rows identify the adjusted parameter value and indicate the difference in model response with respect to the baseline estimate.

regulations and potentially have different fishing mortality than the Potomac River so that the age composition may be different even if recruitment is the same. We thought it was reasonable to assume that the index represented age-4 American eels because they should be the dominant age class in the 300–400 mm range. To test the sensitivity of the model to an alternative model formulation that treated the index as a multiple-age index, we conducted two sensitivity analyses that assumed selectivity patterns for the VIMS trawl survey index. We conducted one run that assumed the selectivity of the "recruitment index" was equal for all ages across sexes and another run where we assumed that selectivity was equal for ages 4–6, but was zero for older ages. The results of these sensitivity analyses were similar to the base model. Estimated average abundance was 36% lower for the model with equal selectivity across all ages and 24% lower for the model with equal selectivity for ages 4–6. Abundance in the last year was much less sensitive to selectivity assumptions for the recruitment index, and both sensitivity runs were within 10% of the base model. We strongly recommend enhanced sampling and aging of American eels to increase certainty in recruitment indices.

Fishing mortality was an important component affecting the stock dynamics of American eels in the Potomac River, and current exploitation rates are too high if the goal is to match local anthropogenic effects with local productivity. The exploitation rates estimated by the ASSA model were much greater than $F_{50\%}$ for the past 16 years and greater than $F_{30\%}$ for the past 13 years. Additionally, estimated exploitation rates since 1996 were 12%–149% greater than the natural mortality rate (0.24 year^{-1}), which has been suggested as an upper threshold for sustainable fishing (Williams and Shertzer 2003). The total mortality rates estimated in the base model (natural mortality, maturation, and exploitation combined) were similar to total mortality estimates in the Chesapeake Bay (46%–76%·year^{-1}; Weeder and Hammond 2009) and indicate high mortality for American eel in the Chesapeake Bay region. Several sustainable levels of anthropogenic mortality for anguillid eels have been suggested. $F_{40\%}$ was recently adopted by the European Union for managing European eel stocks (Council Regulation (EC) 2007). $F_{50\%}$ has been suggested as a precautionary reference point for European eel (International Council for the Exploration of the Sea 2001), and given the observed decline in American eel and the difficulty in managing a data-poor, semelparous, and panmictic species, we suggest that a conservative reference point of $F_{50\%}$ is warranted for American eel.

Few comparable assessment models have been developed for American or European eels (e.g., De Leo and Gatto 1995), in part because of a lack of data. American eel landings are not routinely sampled for age or length composition (Atlantic States Marine Fisheries Commission 2006). Indices of abundance are only available in some parts of their range, and sex ratio, growth, and maturation can vary substantially among regions. Because of the data-poor situation of American eel fisheries, we made several assumptions about the selectivity, effective sample sizes, and SDs. In particular, we estimated selectivity outside of the model fitting, and estimated abundance was sensitive to changes in fishery selectivity. We believe we bracketed the range of potential gear selectivity patterns in our sensitivity analyses. However, fishing practices, such as decisions about where and when to fish, can also affect selectivity by targeting areas with the desired size of fish. We also specified the maturation schedule. Ideally, information on the age or size distribution of outmigrating silver eels would be used to estimate maturation at age (e.g., De Leo and Gatto 1995). Data on silver eels were not available for the Potomac River and are not routinely collected throughout most of the American eel's range. Finally, the model can easily be modified to include additional mortality sources, such as effects of turbine mortality on outmigrating silver eels, which are an important source of mortality in regions outside the Potomac River (McCleave 2001; Verreault and Dumont 2003). To model a system in which female spawner escapement was reduced by turbine mortality, eqs. 8 and 20 would be modified by multiplying SB or SB/R by $1 - \rho\tau$, where ρ is the proportion of the stock that must pass through turbines during outmigration and τ is the mortality rate from passing through a turbine. For the purpose of estimating SB/R under conditions of no additional anthropogenic mortality, ρ or τ should be set to zero.

The recruitment index and fishery CPUE index had conflicting trends that had to be reconciled within the model. This conflict among indices of abundance resulted in large differences among estimates for models with different assumptions about fishery catchability and observation error variance. Estimates from statistical catch-at-age models with different catchability assumptions have been shown to be highly sensitive to time-varying catchability (Wilberg and Bence 2006), so our results were not surprising. However, the density-dependent catchability model had remarkably consistent estimates of abundance and fishing mortality when different levels of observation error were assumed. Fishery CPUE data had little effect on estimated recruitment, perhaps implying that fishery CPUE was more informative about changes in catchability than population abundance. Density-dependent catchability has been observed in a substantial number of other fisheries (Wilberg et al. 2010) and is expected when fishers are able to target aggregations of fish (Paloheimo and Dickie 1964; Ellis and Wang 2007). Therefore, we used insensitivity of the model to observation error variance and the theoretical basis for density-dependent catchability as justification for selecting the density-dependent catchability model over the others. Continued development of methods for selecting among competing assessment models (e.g., Wilberg and Bence 2008) is necessary to develop robust model selection methods when candidate models differ in how they model random effects (e.g., deviations in catchability over time).

Declining American eel abundance and recruitment have raised concerns regarding the viability of the species under current management (Atlantic States Marine Fisheries Commission 2000). Because of variations in growth, maturation, sex ratios, and density of American eels throughout their range and a lack of population-wide abundance and recruitment indices, it is not feasible to develop a whole population model at this time. Although humans have little control over the oceanic phase of American eel life history, the status of the stock can be assessed relative to fishing in other regions, and fishing mortality (or other anthropogenic sources) can be reduced to meet target reference points and to promote adequate spawner escapement. However, a comprehensive, range-wide management plan for American eel is necessary to achieve sustainability because relative contributions to the spawning stock from different regions are unknown. One potential range-wide management plan is to assess and manage all regions of the range for locally sustainable anthropogenic mortality (e.g., harvest and turbine mortality). Managing all portions of a metapopulation sustainably is a robust management strategy under uncertainty about spatial dynamics (Tuck and Possingham 2000; Wilberg et al. 2008). While regional assessment and management has not been specifically evaluated for American eels, the approach could protect the population in each portion of its range and allow individuals from all areas to contribute to the spawning stock. The ASSA model proposed here could be applied in other regions, to the whole population if data became available, or to other anguillid eel stocks. This model could be a first step towards assessing American eel and reducing exploitation in regions where spawner escapement is too low.

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