ABSTRACT

Title of Document: ASSESSMENT OF LOCAL ABUNDANCE, DEMOGRAPHICS, HEALTH AND EXPLOITATION OF CHESAPEAKE BAY AMERICAN EEL

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The Chesapeake Bay supports the largest U.S. harvest of American eel *Anguilla rostrata*, yet little is known about the underlying production rates sustaining harvests. Demographic attributes were compared between six sub-estuaries and with an unexploited population in the Hudson River. A mark-recapture experiment in the Potomac River yielded growth, abundance, and production estimates. Sub-estuaries characterized by lower salinity had a lower proportion of females, and American eels were older, slower growing and showed increased parasitism. Female American eels were larger, older, and had higher growth rates than other gender types. Local abundances were 10-fold higher in the Potomac River estuary in comparison to the Hudson River, but growth rates were similar. Mortality rates were twice as high as those in the Hudson River estuary. The production model indicated American eel recruitment and biomass decreased substantially during the past 20 years.

ASSESSMENT OF LOCAL ABUNDANCE, DEMOGRAPHICS, HEALTH AND EXPLOITATION OF CHESAPEAKE BAY AMERICAN EEL

By

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Introduction

American Eel Life History

American eel *Anguilla rostrata* is an ecologically and economically important species. Because of their wide temperature and salinity tolerances, they occur in a variety of habitats including open ocean, brackish estuaries, and freshwater rivers, lakes, and streams. By some estimates American eels constituted as much as 25% of the historical fish biomass in east coast North American streams (ASMFC, 2004). Anguillid eels are opportunistic carnivores and their diet largely depends on their size and habitat but can include aquatic insects, fish, crustaceans, and worms (Tesch, 1977).

American eels are semelparous with a complex life history (Figure 0.1), 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 et al., 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 kilometers to spawning grounds. Leptocephali larvae drift on currents for about one 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 ASMFC 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 non-feeding adults called silver eels (Tesch, 1977).

American eels are sexually dimorphic in growth, maturation, and distribution. Male American eels are more common in the southern half of their distribution, primarily in estuarine habitats, while females are found throughout the range of the species, in freshwater and brackish water (Helfman et al., 1984; Helfman et al., 1987). American eel growth rates are higher in brackish water habitats than in freshwater (Cairns et al., in press), and American eels in brackish water tend to be younger than those in freshwater (Morrison and Secor, 2003). Male yellow eels have lower growth rates than females (Helfman et al., 1984; Oliveira, 1999; Oliveira and McCleave, 2002) and mature at a smaller size and age, whereas females are larger and older upon maturation (Oliveira, 1999; Oliveira and McCleave, 2002). Male American eels seldom exceed 45 cm TL whereas females can reach 100 cm or more in the northern reaches of their distribution. Oliveira (1999) found that female age at maturation is not correlated with latitude but that male age at maturation is correlated with latitude.

Population Stressors

During the past two decades, declining harvests and indications of population decline have prompted concerns about fishery and population sustainability

(Casselman, 2003). American eel catches in the US have been declining since the early 1980s (Figure 0.2; ASMFC, 2004). A reduction of more than 90% in yellow eel passage from the St. Lawrence River into Lake Ontario has caused particular concern about American eels over northern portions of their range (Casselman et al., 1997; Mathers et al., 1998). St. Lawrence River eels are predominantly female and may disproportionately contribute to the spawning population (Castonguay et al., 1994; ASMFC, 2004). Similarly, fishery independent surveys in the Chesapeake indicate that yellow eels have declined >50% over this same period (ASMFC, 2004).

Several population stressors have been identified as potentially affecting American eel health and abundance. Four broad categories include exploitation, parasitism, habitat loss, and climate changes. The yellow eel, silver eel, and in some regions glass eel phases are exploited by commercial fisheries, causing concern that harvest may be too high for population sustainability (ASMFC, 2004). Glass eels and silver eels migrate into and out of rivers and estuaries, which may serve as a physical and temporal bottleneck making them more vulnerable to fishing mortality and predation.

Parasitism by the non-native nematode *Anguillicola crassus* likely has consequences for eel health, but effects of parasitism are poorly understood. First identified in the U.S. in 1995, the parasite has spread rapidly and is now found as far north as Canada (Fries et al., 1996; Aieta and Oliveira, 2009). Parasite infection may affect eel behavior, growth, tolerance to changing environmental conditions, and reproductive ability (Kirk, 2003).

Habitat loss and degradation occurs on large and small spatial scales and causes large amounts of former habitat to be inaccessible. Dams block access to upstream habitat, thus increasing American eel density downstream of the barrier; barriers > 3 m high cannot be effectively negotiated (Wiley et al., 2004, Machut et al., 2007). Increased density of American eels below dams or barriers potentially causes density-dependent growth limitations (Machut et al., 2007). Dams also have detrimental effects on eels that do manage to migrate over or around them; turbine-induced mortality of migrating silver eels at hydroelectric dams has been estimated at 5-60% (ASMFC, 2000) and 5-30% (ASMFC, 2006).

Lastly, global climate change is another potential cause of declining abundance in American eels. Knights (2003), Friedland et al. (2007) and Bonhommeau et al. (2008) all suggested that worsening forage conditions and starvation of eel larvae may be linked to fluctuating primary productivity in the Sargasso Sea due to increasing sea surface temperature and vertical stratification of the water column that reduce nutrient availability. Recent increased sea surface temperature in the Sargasso Sea is not necessarily related to global warming but does suggest a mechanism for how changing oceanographic conditions might impact recruitment.

Objectives and Goals

American eels in the Chesapeake Bay have received little study, despite the fact that the majority of U.S. commercial landings come from the Chesapeake Bay states. My thesis goal was to improve understanding of American eel population dynamics in the Chesapeake Bay. The objectives of my research were 1) to compare

growth, mortality, and parasitism among several Chesapeake Bay tributaries, 2) to estimate local abundance and mortality in the Potomac River, and 3) to develop a model to assess the effect of exploitation on American eels in the Potomac River.

Objective 1

In Chapter 1, I detail the demographics of American eels from six sub-estuaries of the Chesapeake Bay. I dissected, aged, and identified gender for 850 American eels from summer and fall fishery catches to characterize different portions of the Chesapeake Bay habitat, then tested for seasonal, regional, and gender effects on eel growth, mortality, and health. I also use catch curves to estimate total loss rates of American eels for each sub-estuary. Using these individual demographic attributes, I compared sub-estuaries and bay regions to look for patterns in demographics and compared demographics data from American eels in the Chesapeake Bay to American eels in other portions of their range. This new data on growth, mortality, and health will fill in knowledge gaps regarding American eels in this highly exploited portion of their range. Data obtained from this demographics research was used to inform the age-structured production model developed in Chapter 3.

Objective 2

The Potomac River supports the largest American eel harvest of the Chesapeake Bay sub-estuaries. To better understand potential production underlying harvests of American eels in the Potomac River, in Chapter 2 I present a mark recapture experiment conducted in the summer and fall of 2007. I chose the Potomac River for the mark-recapture experiment for three key reasons: 1) the large harvest

obtained from the sub-estuary suggested that the Potomac River is a valuable and productive habitat in the Chesapeake Bay, 2) the Potomac River is a large, tidal river that resembles other key tributaries to the bay, and 3) the Potomac River Fisheries Commission (PRFC) maintains a detailed record on catch and effort, allowing for the development of a stock production model to complement the abundance estimates from the mark-recapture.

Using data obtained from the mark-recapture experiment I compare abundance in summer and fall 2007 to estimate the loss rate of American eels due to natural mortality, maturation, and fishing mortality. In addition, I use Passive Integrated Transponder (PIT) tagged eels to estimate growth rates for individual eels. Lastly, I compare estimates of loss rate, growth, and density of American eels in the Potomac River to other published estimates throughout their range.

Objective 3

My third objective was to develop a model to estimate abundance and mortality rates for American eels in the Potomac River and assess the effect of the fishery on American eels. I address this objective in Chapter 3, where I use data obtained in Chapters 1 and 2 to develop an age-structured stock assessment model for the Potomac River. The model used catch data from the PRFC, a fishery-dependent index of abundance, and fishery independent recruitment index; to assist in reconciling the opposing trends in the indices I allow catchability to vary over time in the model. Finally, I develop a Spawner Potential Ratio (SPR) model to assess the fishing mortality rates of female American eels with respect to the conservative biological reference point $F_{50\%}$. This model, though limited in scope, provides

estimated recruitment, abundance, and fishing mortality rates for American eels in the Chesapeake Bay, and provides evidence that fishing mortality and processes outside the scale of the Potomac River may be affecting American eels in the Potomac River.

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Figures

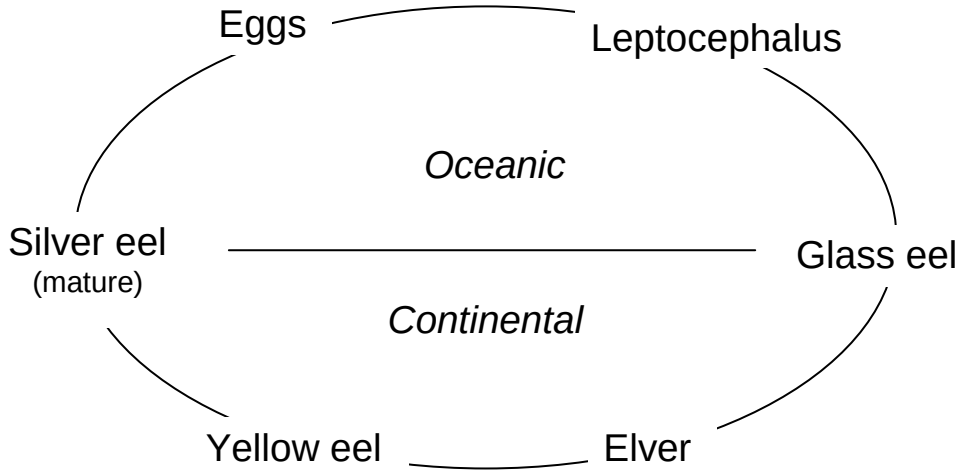

Figure 0.1. Life cycle of the American eel. The yellow eel phase may occur in fresh or brackish water.

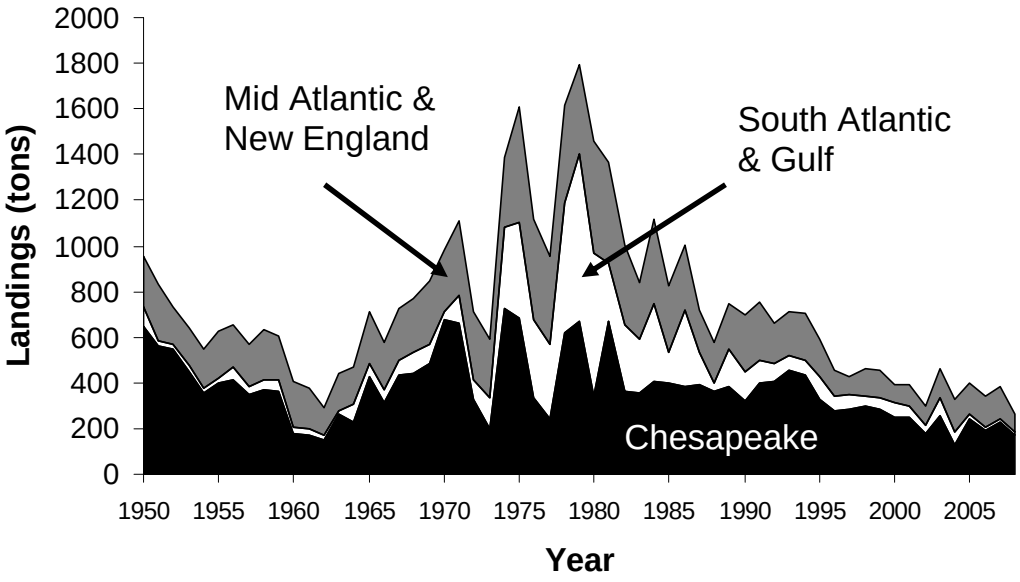

Figure 0.2. U.S. landings (tons) of American eel by region, 1950-2008 (NOAA Fishery Statistics, unpublished data).

Chapter 1: Demographics and parasitism of American eels in the Chesapeake Bay, USA

Abstract

The Chesapeake Bay supports the largest U.S. harvest of American eels, yet little is known about the underlying demographics and production rates that sustain these harvests. Sub-estuaries of the Chesapeake Bay (Sassafras, Chester, Choptank, Patuxent, Potomac, and James Rivers) are expected to provide varying growth habitats for yellow eels due to differences in land use, productivity, and salinity. By examining 850 American eels from six sub-estuaries of the Chesapeake Bay, I compared yellow eel length, age, growth, mortality, condition, and health (prevalence and incidence of parasitism) among six principal sub-estuaries of the Chesapeake Bay. Sub-estuaries supported substantial differences in American eel demographic attributes, including gender, length, weight, condition, age, growth, and parasitism. Across sub-estuaries, female American eels were larger, older, heavier, and had higher growth rates than male, intersexual, and undifferentiated eels. Gender ratios differed between sub-estuaries. The prevalence of male and intersexual eels in the upper Chesapeake Bay was higher than reported for other estuaries in South Carolina, Quebec, and the Hudson River in New York and similar to male prevalence in Georgia. Chesapeake Bay growth rates had a similar range but greater mean than other published estimates. Bay-wide growth rates ranged from 26.7-149.3 mm yr^{-1} and varied between sub-estuaries; the Choptank River had the highest mean growth rate (72.7 mm yr^{-1}) and the Chester River had the lowest (60.2 mm yr^{-1}). The patterns of growth rate estimates for eels by gender and salinity were similar to previous studies of American eel; brackish water supported higher growth rates and lower parasitism than freshwater. The prevalence of parasitized American eels varied between sub-estuaries, ranging from 17.8 to 72%, with no association between swimbladder damage or parasite presence and age or growth. Catch curve analysis revealed annual loss rate estimates of 0.405 – 0.636 yr^{-1} for sub-estuaries. These loss rates were not unrealistic for a productive population experiencing both natural and fishing mortality. Regional demographics differed between the upper bay (north of the Chesapeake Bay Bridge) and the lower bay, reflecting differences between sub-estuaries. Female prevalence, growth rates, and condition were lower; and parasite prevalence and intensity was higher in the less saline upper bay when compared to the lower bay, suggesting fundamental differences in the productivity and spawning contributions from these two regions.

Introduction

Harvests of American eels from the Chesapeake Bay are considerably larger than those elsewhere in the species' U.S. range (see Thesis Introduction, Figure 0.2), yet little is known about the underlying demographics of Chesapeake Bay eels. The Chesapeake Bay is a large estuary, with wide salinity, depth, and temperature gradients that provide a range of habitat conditions (Secor and Austin, 2006). Because >50% of freshwater non-tidal habitats have been potentially lost to American eels (Busch et al., 1998 as cited in ASMFC, 2000), the role of estuaries as primary growth habitats for yellow eels have become particularly important for fishery yields and species persistence (USFWS, 2007). Here, I examine how yellow eels vary in length, age, growth, mortality, condition, and health (prevalence and incidence of parasitism) among principal sub-estuaries of the Chesapeake Bay.

Previous research has shown that American eel size, gender, and habitat use vary substantially within and among estuaries (Helfman et al., 1987; Krueger and Oliveira, 1999; Oliveira, 1999). Female American eels generally mature at greater sizes and ages than males (Helfman et al., 1987; Oliveira, 1999), and growth rates in brackish habitats are greater than in tidal freshwater habitats of the same estuary (Helfman et al., 1984; Helfman, 1987; Morrison and Secor, 2003). Within an estuary, the distribution of gender and size of American eels can also vary greatly. American eels in the Potomac River were significantly larger and increasingly female with increasing distance upriver and upstream (Goodwin and Angermeier, 2003). Among estuaries, size at maturation increased with latitude for female American eels, but not for male American eels (Oliveira, 1999). Age at maturation of male American eels

was positively correlated with latitude, suggesting that male eel growth rates vary inversely with latitude (Oliveira, 1999). Indeed, previous studies indicated that growth rates tend to be higher in southern American eel habitats compared to northern habitats (Gunning and Shoop, 1962; Hansen and Eversole, 1984; Oliveira, 1999). Length of the growing season at different latitudes and differing food availability in freshwater and brackish habitats have been cited as possible explanations for differing growth rates (Gunning and Shoop, 1962; Wenner and Musick, 1975). Because American eels are panmictic (i.e., not exhibiting population structure among estuaries) differing growth rates cannot undergo selection based on regional habitat differences. Thus, it is critical to identify which regions (e.g. which estuary(s) or habitat types) are most important in contributing to yellow eel production and silver eel escapement.

American eels in the Chesapeake Bay are commonly infected with an exotic nematode parasite, *Anguillicola crassus*. In 1997, Chesapeake Bay watermen alerted scientists to the presence of "worms" in American eels. Barse and Secor (1999) identified the worms as *A. crassus* and their subsequent investigations of the Patuxent and Sassafras Rivers confirmed the presence of the parasite in the Chesapeake Bay for the first time. Originally found in Japanese eels *Anguilla japonica*, the parasite was first reported in the U.S. in 1995 (Fries et al., 1996), and since that time the parasite's range has extended throughout the U.S. and into Canada (Aieta and Oliveira, 2009). Infection by the parasite has been documented to have negative consequences for infected European, and potentially American, eels including thickening of the swimbladder wall, decreased appetite (van Banning and Haenen,

1990), and reduced swimming performance (Sprengel and Lüchtenberg, 1991). Concerns have arisen about the impact of *A. crassus* on American eel growth, mortality, condition, susceptibility to other infections, swimming behavior and spawning migration (USFWS, 2007). Previous studies have indicated that parasite prevalence and intensity is greater in tidal freshwater habitats than in brackish water (Morrison and Secor, 2003) and that salinity affects the infectivity of *A. crassus* (Kirk et al., 2000).

Evaluation of the likely effects of *A. crassus* on yellow eel demographics is hampered by the inability to evaluate the latent and cumulative effects of repeated infections. *A. crassus* has a rapid life cycle (Barse and Secor, 1999): it is possible for an eel to be infected by multiple stages of *A. crassus* and for an eel to be infected multiples times over the course of its life. Due to the short life cycle of the parasite, presence or absence of the parasite in the swimbladder is a short-term measure of infection. Damage to the swimbladder by current or previous infections of *A. crassus* is thought to be a more accurate measure of parasite pressure than parasite count (Lefebvre et al., 2002). The swimbladder degenerative index (SDI) was developed by Lefebvre et al. (2002) as an index of cumulative effects to swimbladder function.

Major sub-estuaries of the Chesapeake Bay are expected to provide varying growth habitats for yellow eels. The upper portion of the Chesapeake Bay and its sub-estuaries (Sassafras and Chester Rivers) are predominately freshwater or oligohaline (salinity levels < 10; White, 1989). In this region, most American eels are harvested in freshwater. Sub-estuaries in the middle and lower portions of the Chesapeake Bay (Choptank, Patuxent, Potomac, and James Rivers) have higher

salinity but harvest locations can range from 0-26 salinity, depending on the harvest location within the sub-estuary, season, and precipitation (White, 1989). The Potomac and Patuxent River samples in this study came from the oligohaline portions of each sub-estuary (J. Trossbach, pers. comm.). Sub-estuaries also differ in discharge rates and watershed land use that may affect American eel demographics (Pritchard and Schubel, 2001, Bilkovic et al., 2006). Benthic productivity of sub-estuaries likely varies as well, with differing foraging conditions for yellow eels based on salinity, bottom substrate, and prey species production and distribution.

I hypothesize that sub-estuary variations in habitat productivity and exploitation will result in measurable demographic differences in gender ratios, size and age structure, growth rates, and condition. This analysis was supported by laboratory-based analyses of age structure and swim bladder inspections of 850 yellow eels subsampled among six sub-estuaries (Figure 1.1; Sassafras, Chester, Choptank, Patuxent, Potomac, and James Rivers). Sub-estuary differences in demographics provided a comparative framework within which to evaluate possible associations between *A. crassus* parasitism and eel growth and mortality.

Methods

American eels harvested from six rivers and two seasons were donated by the Delaware Valley Fish Company (DVFC). Yellow stage American eels were harvested using baited two-chambered, 1.2 cm square mesh eel pots and transported in oxygenated tanks to the holding facility at DVFC. Approximately one hundred American eels each from the Sassafras River, Potomac River, and Chester River were

randomly selected by DVFC staff, frozen, and were received in July 2007. American eels at DVFC were not size graded at their facility, but size biases possibly occurred in those eels sold to DVFC. Interviews with a commercial fisher (J. Trossbach, pers. comm.) led me to believe that eels from the Potomac River were graded for size, where the smallest eels were sold for bait and were not provided to DVFC. Eels from the Patuxent River were received directly from a commercial fisher in June 2007 and were not graded. A fall sample of American eels from DVFC was received in December 2007, consisting of approximately one hundred American eels each from the Chester, Choptank, James, and Potomac Rivers. Fall sample American eels from the James and Potomac rivers were thought to be size graded because of the paucity of small eels (<30 cm) in those sub-samples (see Results).

To determine age, gender, condition and health, American eels were dissected and inspected for internal and external abnormalities. American eels from the DVFC were received frozen. American eels that we received directly from a commercial fisher were anesthetized in MS-222 and then frozen. Prior to dissection, eels were thawed overnight in a refrigerator or under cool flowing water. Eels were measured for total length (TL, mm), maximum girth (mm), and weight (0.1 g). Previous studies showed that freezing reduces eel length and weight by 1.2-3% and 1.9%, respectively (Morrison and Secor, 2003; Machut et al., 2007). All lengths and weights reported are based on uncorrected measurements. Fulton's condition factor (K) was calculated for each American eel (in g cm^{-3} 10^5; Ricker, 1975).

Each American eel was macroscopically inspected to determine gender according to Buellens et al.'s (1997) criteria. Four gender categories were identified:

female, male, intersexual, and undifferentiated. Undifferentiated gonads do not have identifiable oogonia or spermatogonia, and undifferentiated gonads can develop directly into an ovary. Intersexual gonads contain both female and male sex cells, and male American eels develop from intersexual gonads (Buellens et al., 1997). For fall American eel samples the gonads were examined to identify eels that may have been approaching sexual maturation. I removed and weighed the gonads that appeared large and well developed to determine the proportion of eels that may mature that year. According to Durif et al. (2005), a female exhibiting a gonado-somatic index of ≥1% may mature in the present year and subsequently undertake an oceanic spawning migration.

Each American eel was inspected for prevalence and intensity of *A. crassus* infection. The swimbladder was inspected internally and externally. The number of *A. crassus* worms were counted. Parasite prevalence was calculated as the percentage of infected eels for each sub-estuary; parasite intensity was calculated as the mean number of *A. crassus* among infected eels. I modified the SDI developed by Lefebvre et al. (2002). The original index score included three swimbladder criteria (swimbladder wall thickness, swimbladder wall transparency, and pigmentation and exudate). Each criterion was given a 0-2 score, two indicating the most severe damage. For my analysis I combined the score for the swimbladder wall thickness and swimbladder wall transparency only, and used this two-factor score, which was referenced as SBtt.

Direct aging occurred through enumeration of annuli in otoliths. Sagittal otoliths were removed, rinsed in tap water, rubbed clean, and air dried in a tissue

culture tray. One of the paired otoliths was randomly chosen and embedded in Streurs Epoxy resin. Embedded otoliths were glued to a microscope slide using Crystalbond adhesive, and a transverse section through the core was obtained using a low-speed wafering saw. The transverse section was polished on one side to reveal the core and annuli as described by Secor et al. (1991). To enhance the contrast of annuli, the polished otoliths were etched with 6% EDTA for 2-5 minutes, and then stained with a solution of 2% EDTA and 5% toluidine blue for 2-5 minutes. The excess stain was wiped off with a damp tissue (etching and staining methods modified from Morrison and Secor, 2003 and Graynoth, 1999). The glass eel transition check was assumed to equal age one (Morrison and Secor, 2003). Etched and stained otoliths were photographed under 10-X or 40-X magnification, and annuli were counted and marked with Photoshop image editing software. Each otolith image was aged at least two times.

Otolith-based aging has been validated in studies of American eels (Oliveira, 1996). Careful attention to establishing precision criteria can reduce the influence of poor otolith preparations and false annuli on aging errors (Campana, 2001). To assign an age to an individual each otolith was read multiple times. I compared the last two annuli counts for each American eel. If the two readings matched, that count was accepted as the assigned age. If the two readings did not match but differed by <2 years, then I accepted the most recent count as the assigned age. If the two readings differed by ≥ 2 years, then the otolith was read again. If the third reading matched one of the two previous readings, the "matched" count was assigned. If the third reading differed from either of the first two by <2 years, the third read was

accepted as the assigned age. Finally, if the third read differed from either of the first two by ≥2 years, that eel was excluded from further age-based analyses.

Mean annual growth rates were estimated by dividing eel TL by age (Oliveira, 1999, Morrison and Secor, 2003). To account for growth prior to entering the Chesapeake Bay region, I subtracted 57.1 mm and one year from the TL and age of each eel, based on the ten-year average length of glass eels entering the Little Egg Inlet, NJ (Sullivan et al., 2006).

The availability of sub-estuary samples from DVFC differed in summer and fall. Summer and fall sub-samples for the Chester River and Potomac River were combined for demographic analyses. To evaluate the role of Bay region (a proxy for salinity) on growth, condition, and parasitism I grouped the sub-estuaries into an upper bay and lower bay category. The Chester and Sassafras Rivers are upper bay sub-estuaries and the Choptank, James, Patuxent, and Potomac Rivers are lower bay sub-estuaries. To compare seasonal patterns in parasitism only the Potomac River and Chester River were considered.

Statistical analysis was done using software packages SAS v.9.3.1 and SYSTAT 12. I used one- and two-way ANOVA and ANCOVA among sub-estuary subsamples to test hypotheses regarding seasonal, regional, and gender effects on American eel growth, mortality, and health. Multiple mean comparison tests were done using Tukey multiple means comparison tests where indicated. Significance was tested at the 0.05 level. Age, length, growth rate, and weight data were $\log_e$ transformed to meet normality assumptions. For chi-square analysis on the proportion of females between bay region, only female American eels 20-40 cm were

considered to reduce bias created by size grading and differences between length distribution between regions. Because female American eels were significantly longer, older, and heavier than other genders and gender composition varied significantly between sub-estuaries, I focused on female American eels for comparison of sub-estuaries demographics. Catch curves were used to estimate loss rates for each sub-estuary (Ricker, 1975). Instantaneous loss rates were estimated as the slope of the descending limb for the $\log_e$ numbers versus age relationship. The fitted slope was stipulated to include all ages older than the mode in numbers at age. This catch curve analysis assumes non-trending recruitment and constant mortality across years and ages and no net immigration or emigration into fished regions of sampled sub-estuaries.

Results

Demographics

Ranges in length and age (n=850) among all sub-estuaries were 21.3-64.7 cm (mean=36.5 cm) and 3-11 years (mean=5.8 years). American eel weights ranged from 14.7 to 590.8 g (mean=98.8 g). There were significant gender differences in length, age, and weight; females were significantly longer (mean= 40.0 cm), older (mean=6.1 years) and heavier (mean weight 124.0 g) than other gender categories (Figure 1.2; ANOVA with Tukey multiple mean comparisons). Female was the most prevalent gender category, ranging from 34-100% among sub-estuaries (Figure 1.3). Chi-square analysis revealed that the proportion of females varied significantly between sub-estuaries ($p<0.001$) and that the proportion of female American eels 20-

40 cm in the upper bay (Chester and Sassafras Rivers) was significantly different (lower) than the proportion of females 20-40 cm in the lower bay (James, Potomac, Patuxent, and Choptank Rivers; $p<0.001$). Across all sub-estuaries and ages, females constituted 71.3% of the sample.

Females showed sub-estuary-specific differences in demographics: American eels in the James River were the largest (mean=47.0 cm) and the Patuxent River were the smallest (mean=36.0 cm; ANOVA with Tukey multiple mean comparisons, Table 1.1). Mean lengths by sub-estuary from largest to smallest were: James, Potomac, Choptank, Chester, Sassafras, and Patuxent. There were similar sub-estuary specific differences in weight and age but a greater number of significant contrasts between sub-estuaries were supported for length as a demographic response than age or weight (Table 1.1). Female American eels in the James River were the heaviest (mean 178.9 g, Table 1.1) and the Chester River females weighed the least (mean 89.2 g). Ages were not ranked across sub-estuaries in the same manner as length and weight. Sassafras and James River American eels were oldest (mean 6.8 years, Table 1.1) and significantly older than Chester, Choptank, and Patuxent River American eels (Tukey, $p<0.05$).

Demographics of female American eels were also different between the upper and lower bay regions. Females in the lower bay were significantly longer and heavier and had higher growth rates (see below) than females in the upper bay (Table 1.1; one-way ANOVA, $p<0.0001$). Mean age was not significantly different between bay regions (Table 1.1; one-way ANOVA, $p=0.99$).

Growth

Length-at-age for individual American eels was highly variable (Figure 1.4). For example, six-year-old eels ranged 23.2-64.7 cm TL. The overall range and mean growth rate for American eels (gender categories combined) in the Chesapeake Bay was 26.7-149.3 mm yr^{-1} and 67.5 mm yr^{-1}, respectively.

Mean growth rates varied by gender, bay region, and sub-estuary. For the Chesapeake Bay as a whole, female American eels exhibited the highest mean growth rates (71.4 mm yr^{-1}; Table 1.2) and were significantly different from intersexual and undifferentiated American eels (57.7 mm yr^{-1}, one-way ANOVA with Tukey correction, $p<0.0001$; and 48.5 mm yr^{-1}, $p<0.0001$; respectively). Males exhibited mean growth rates of 64.2 mm yr^{-1}, which was significantly different only from undifferentiated American eels ($p=0.05$). Growth rate in the upper bay region (57.3 mm yr^{-1} ±1.67 SE) was significantly lower than growth rate in the lower bay (65.2 mm yr^{-1} ±1.81 SE; ANOVA mixed model of Log_e growth with bay region and gender as fixed effects; $p<0.0001$).

Among sub-estuaries, growth rates in the Chester River were the lowest (60.2 mm yr^{-1}) and the Choptank River were the highest (72.7 mm yr^{-1}; ANOVA mixed model of log_e growth with sub-estuary and gender as class variables; Table 1.2). I also examined for trends in growth rates of all American eels by size class.

Growth rates of female American eels varied by sub-estuary and by bay region. Growth rates in the Choptank River (Table 1.1; 80.9 ±2.26 mm yr^{-1}) were the highest and the Sassafras River were the lowest (54.4 ±3.31 mm yr^{-1}). Female

American eels in the upper bay had significantly lower growth rates than females in the lower bay (Table 1.1; one-way ANOVA, $p<0.0001$).

Condition

The mean condition (*K*) of females (0.174 ±0.001) and males (0.174 ±0.006) was nearly identical (Table 1.2). Females exhibited a significantly higher condition index than intersexual American eels ($p<0.0001$ ANOVA with Tukey multiple mean comparison); all other pairings were not significantly different. Sub-estuary differences in condition were present (Table 1.2); the Patuxent River had the highest mean condition (0.199 ±0.003) and the Sassafras River had the lowest (0.161 ±0.002). There was a significant difference in condition (*K*) of American eels from the upper bay compared to the lower bay. Upper bay American eels had a mean condition of 0.170 (±0.003) and lower bay American eels had a mean condition of 0.183 (±0.003; $p<0.0001$, ANOVA).

Another estimate of condition was done using ANCOVA analysis of the $\log_e$ weight of American eels with $\log_e$ length as a covariate and gender, sub-estuary or bay region as class variables. This method of condition analysis detected no significant differences in the mean condition among gender categories (Table 1.2). There were significant differences between sub-estuaries and between the upper and lower regions of the Chesapeake Bay ($p<0.05$, Tukey multiple mean comparison test, Table 1.2). The Patuxent River American eels had significantly greater condition than all other sub-estuaries and the condition of American eels in the upper bay (4.28 ±0.009) was significantly lower than condition in the lower bay (4.35 ±0.007, $p<0.0001$).

Mortality

Estimated instantaneous loss rates ranged from 0.52 to 1.01 yr^{-1}, which occurred in the Choptank and Potomac Rivers, respectively (Table 1.3, Figure 1.5). These loss rates were equal to annual mortality rates of 0.41 – 0.64 yr^{-1}. Mean annual loss rate among sub-estuaries was 0.51 corresponding to an instantaneous rate of 0.72. The standard errors of the mean instantaneous loss rates were high and overlapping, indicating that there was no significant difference in loss rates between sub-estuaries or bay regions.

Parasitism

Prevalence of *A. crassus*-infected American eels in the Chesapeake Bay was 40.9% among all sub-estuaries, and parasite intensity ranged from 0-48 parasites per individual (mean 1.4, mode 0). For sub-estuaries combined, both parasite intensity and prevalence had significant negative correlations with size class ($p<0.0001$, $r>0.95$, Figure 1.6). For the Chesapeake Bay as a whole, 22.8% of American eels had evidence of both current (nematode present) and past (swimbladder damage) *A. crassus* infection and 52.0% of eels had either past or current evidence of *A. crassus* infection.

Sub-estuaries varied substantially in degree of parasitism (Table 1.4). The James River had the lowest prevalence (17.8%) of parasitized American eels and the Sassafras River had the greatest prevalence (72%). Chi-square analysis revealed that the sub-estuaries had significantly different parasite prevalence ($p<0.001$). Due to the relationship between size class and parasite intensity, I used ANOVA with sub-estuary and size class as fixed effects to adjust mean parasite intensity for each sub-

estuary; mean parasite intensity ranged from 2.0 to 4.0 worms per parasitized swimbladder (Table 1.4). A comparison of mean parasite intensity in upper bay sub-estuaries (mean 3.1, standard error [SE] 0.6) versus lower bay sub-estuaries (mean 2.7, SE 0.6) revealed no significant difference (ANOVA with bay region and length class as fixed effects; $p=0.43$). Chi-square analysis revealed that the prevalence of parasitized American eels in upper bay sub-estuaries (Chester and Sassafras, 52.1% prevalence) was significantly higher than lower bay sub-estuaries (34.3% prevalence; $p<0.001$).

Because females were larger and older than other gender categories (see Demographics, above), I limited analysis of demographic interactions with parasitism to females to avoid confounding effects. There was no significant association detected between incidence of the parasite and growth rate in females (ANCOVA using length-class as a covariate; $p=0.09$). Non-parasitized females had a mean growth rate of 74.0 mm yr^{-1} (2.1 SE); parasitized American eels had a mean growth rate of 71.2 mm yr^{-1} (2.3 SE). Further, no significant association was detected between the swimbladder damage score, SBtt, and growth rate (ANCOVA using length class as covariate, Tukey multiple means comparison, Figure 1.7). Female American eels with SBtt score of 0, 1, 2, 3, and 4 had mean growth rates (± SE) of 74.0 (2.13), 71.6 (4.69), 75.4 (3.27), 68.9 (4.28), and 68.6 (7.10) mm yr^{-1}, respectively. Similarly, there was no significant relationship between parasite presence and age (ANCOVA using length class as covariate, $p=0.2$) or SBtt and age (ANCOVA with Tukey multiple mean comparison test, Figure 1.8). Mean age (SE) of non-infected and infected American eels was 6.15 (0.16) and 6.30 (0.17) years,

respectively. Mean age (SE) of female American eels with SBtt scores of 0, 1, 2, 3, and 4 was 6.1 (0.16), 6.2 (0.35), 6.0 (0.24), 6.4 (0.32), and 6.7 (0.52) years, respectively.

Seasonal Parasitism

For those sub-estuaries sampled in both seasons, the Chester River had significantly lower parasite intensity in fall (mean intensity 1.85 ±0.76 parasites) than summer (mean 3.51, SE 0.69 parasites, $p<0.04$, ANCOVA, length class as covariate). The Potomac River also had lower parasite intensity in fall (mean 2.24, SE 0.42 parasites) than summer (mean 3.03, SE 0.50 parasites), but the difference was not significant ($p=0.10$). For the Chester and Potomac sub-estuaries combined, the mean swimbladder thickness and transparency (SBtt) score was significantly less in summer (mean 0.75, SE 0.07) than fall (mean 0.30, SE 0.07) samples ($p<0.001$, Kruskal-Wallis).

Discussion

Demographics

Sub-estuaries of the Chesapeake Bay supported substantial differences in American eel demographic attributes, including gender, length, weight, condition, age, growth, and parasitism. These differences likely reflect differences in sub-estuary foodwebs and abiotic conditions and are expected to have large influences on relative yields and spawner escapement from different portions of the Chesapeake Bay. In addition to sub-estuary differences in demographics, there was a broad

regional difference between the less saline upper bay and the more saline lower bay. The upper bay supported lower growth rates, higher parasite prevalence, and lower proportion of female American eels than the lower bay. Although harvest intensity is unknown at the level of sub-estuary or bay region, harvest rates may not be matched to underlying production differences between sub-estuaries across the Chesapeake Bay.

Previous research has indicated a link between American eel density and gender ratios, suggesting that environmental sex determination occurs in American eels. Krueger and Oliveira (1999) proposed that male American eels are associated with habitats where high elver density occurs and females derive from habitats with low elver densities (see also Davey and Jellyman, 2005). The environmentally responsive period of sex determination is yet unknown. Although evidence for differences in elver densities in the Chesapeake is lacking, a general view is that density declines with distance from the Sargasso Sea (Smogor et al., 1995). Thus I would have expected higher female densities in upper Chesapeake Bay sub-estuaries, but in fact observed the opposite. Females were most prevalent in the Patuxent, Potomac, and James sub-estuaries. The James River had a particularly high female ratio: 100 of the 101 sampled eels were female. Considering that Potomac and James River eels were size graded to a larger extent than other sub-estuaries (watermen sell smaller eels locally and retain larger ones for the dealer, see Methods), the proportion of female American eels in these systems was likely over-represented. Still, given the high proportion of females and the high density estimates (100-300 eels ha^{-1}) in the Potomac (see Chapter 2), environmental sex determination may be modulated by

more than densities alone, and further study on environmental sex determination in Chesapeake Bay and elsewhere is warranted.

The prevalence of male and intersexual American eels in upper Chesapeake Bay sub-estuaries was higher than that reported for other estuaries. Female American eels dominated (>95%) in the Hudson River estuary (Morrison and Secor, 2003), the Cooper River in South Carolina (Harrell and Loyacano, 1980; Hansen and Eversole, 1984), and the Matamek River in Quebec (Dolan and Power, 1977). However, some estuaries have had a higher prevalence of male American eels. Helfman et al. (1984) and Oliveira (1999) found male prevalence of ~36% in Georgia and ~90% in Rhode Island, respectively. Helfman et al. (1987) suggested that male American eels should predominate in brackish waters, but this was not supported by my results. The presence of male and female American eels in the Chesapeake Bay sub-estuaries suggested that the Chesapeake Bay may be contributing to both male and female spawner escapement.

Length and weight differences reflected differences in gender ratios among sub-estuaries. The relationship between length and gender is well established in the literature (Tesch, 1977; Helfman et al., 1987). Female American eels are larger and heavier, on average, than male American eels, and this was observed in my results. The mean length of American eels differed among bay regions and individual sub-estuaries. Excluding the James and Potomac Rivers, for which lengths probably reflect a bias due to size grading, American eels were largest in the Choptank and smallest in the Sassafras samples. The Sassafras River had the greatest proportion of

male and intersexual eels, and the Choptank River had the second greatest proportion of female eels; gender was clearly influencing mean length in sub-estuaries.

Inferences related to demographics were constrained by gear type and some amount of size grading among sub-estuaries. The gear was standardized by mesh size regulations across all sub-estuaries (12.7 mm mesh pots) and thus selected a similar size range as other studies, which used pots (26-69 cm, Hansen and Eversole, 1984; ~26-70 cm, Morrison and Secor, 2003; 15-65 cm, Ford and Mercer, 1986). Owens and Geer (2003) sampled American eels in the Virginia portion of the Chesapeake Bay with a wide variety of gears (bottom trawl, pots, and electroshocking) and observed a larger size range than that reported here: 6-77.6 cm (years 1997-2000; n=594). The sole use of pots to capture American eels in this study limited the capture of small eels and thus may have underrepresented male, intersexual, and undifferentiated eels in the sub-estuaries.

Although efforts were made to sub-sample without bias, the American eel samples represented harvest taken over a limited temporal and spatial scale for each sub-estuary. Further, it is important to note that these were samples taken from the commercial fishery, and are thus not necessarily representative of entire population. Because some of the sub-estuary samples were known to be size graded, this further limits inferences that can be drawn, particularly specific to the Potomac and James Rivers.

Age and Growth

I observed a fairly narrow age distribution for Chesapeake eels (90% of eels were between 4 and 8 years old), which could be explained by exploitation effects

(age truncation and growth compensation) and/or high underlying habitat productivity. The age range of eels in the Chesapeake was substantially younger than those from a study in the Hudson River, which used similar sampling and aging methods (3-38 years; Morrison and Secor, 2003). Growth rates were moderately lower in the Hudson River study (mean 54.8 mm yr^{-1} for Hudson River brackish water sites v. 67.5 mm yr^{-1} for the Chesapeake Bay). Two contributing factors may be lower productivity of the Hudson River (see Chapter 2) and/or lack of exploitation in the Hudson River. Exploitation in the Chesapeake Bay could result in increased growth rates if growth is density dependent. Density dependent growth in American eels has been has been suggested as the cause of decreased growth rates below dams or other barriers where densities are high (Machut et al., 2007). Interestingly, the age range in the Chesapeake Bay was similar to eels in South Carolina rivers (1-12 years, Hansen and Eversole, 1984; 0-15 years Harrell and Loycano, 1980), which are exploited but probably do not receive the same amount of directed fishing as in the Chesapeake Bay (NOAA unpublished harvest data). Owens and Geer (2003) found a few substantially older eels in the Virginia portion of the bay compared to the present study, with ages ranging from 1-18 years old, although similar to my study most were between 3 to 6 years of age.

American eel growth rates have been found to differ between genders (Helfman et al., 1984; Oliveira, 1999; Oliveira and McCleave, 2002) and my results support this conclusion (Table 1.2). Oliveira and McCleave (2002) suggested that male and female anguillid eels have different life history strategies; females benefit from maturing at larger size because fecundity increases with size and increased size

may confer greater diet breadth and survival advantages. Males do not obtain the large sizes of females but mature at smaller sizes. The present study supports this view on differing life history strategies. Female American eel growth rates in the Chesapeake Bay were greater than other gender categories and females obtained larger sizes. Growth rates between tributaries of the Chesapeake Bay had significant heterogeneity. However, the higher proportion of male and intersexual eels in the upper bay may indicate that this region is a source of male spawners.

Growth rates were related to bay region, a rough proxy for salinity levels. The salinity gradient in the Chesapeake Bay ranges from freshwater at the mouth of the Susquehanna River in the upper bay to full strength salt water at the mouth of the bay (lower bay). Lower growth rates, fewer females, and poorer condition of American eels in the upper bay may negatively affect fishery yields and female spawning potential from this portion of the Chesapeake Bay, and reinforces previous literature suggesting the freshwater habitats are less productive (Morrison and Secor, 2003) and support lower growth rates (Helfman et al., 1984) than brackish habitats. The mean Chesapeake Bay growth rate was double that found in most freshwater systems, and moderately greater than the brackish Hudson River estuary. Morrison and Secor (2003; see also Helfman et al., 1984) found that growth rates were higher in brackish water than in freshwater. Because we do not know the location of capture for the American eels in this study, correlations between growth rates and salinity can only be considered roughly. American eels in the Choptank River had the highest mean growth rates, suggesting that this system is a potentially productive habitat. The higher growth rates found in the Choptank River may be indicative of a river-specific

difference in growth potential, or a factor of the salinity zone within which eels were sampled. The majority (>70%) of American eel harvest in the Choptank River comes from brackish water (K. Whiteford, MD DNR, pers. comm.).

Heterogeneous growth rates in sub-estuaries may also reflect differing forage availability or environmental conditions. Anguillid eels are opportunistic carnivores, and their diet largely depends on their size and habitat but can include aquatic insects, fish, crustaceans, and worms (Tesch, 1977). The growth rate differences I observed may also reflect temperature differences between the upper and lower bay.

The range of growth rate estimates I found throughout the Chesapeake Bay were comparable to other studies, although the bay-wide mean growth rate estimate of 67.5 mm yr^{-1} for this study was greater than those in other published literature. The range of annual growth rates for a brackish system in South Carolina was 27-69 mm yr^{-1} (Hanson and Eversole, 1984). Growth estimates for the freshwater Hudson River ranged from 13-114 mm yr^{-1} (mean 33 mm yr^{-1}, Machut et al., 2007), and had a mean of 58.4 mm yr^{-1} in brackish water (Morrison and Secor, 2003). Mean growth rates of migrating female silver eels in Rhode Island were 39.8 mm yr^{-1}, and migrating male silver eels were 30.9 mm yr^{-1} (Oliveira, 1999).

Condition indices did not exhibit substantial differences among sub-estuaries but did show a similar trend to growth rate between bay regions. The Potomac and Patuxent Rivers had the highest condition by either index, yet the growth rates in these sub-estuaries were less than in the James and Choptank Rivers. Growth rates and condition were lower in the upper bay than in the lower bay.

Mortality

Loss rate estimates for each sub-estuary combine mortality from natural causes, maturation, and fishing. Thus any differences in estimated loss rates between sub-estuaries systems may indicate differences in natural mortality rates between rivers, differences in fishing mortality, or even differences between the number of eels maturing and emigrating to the Sargasso Sea. Some sub-estuaries also contained fall samples (Potomac and Chester River sub-estuaries) which could have biased age distributions due to the influence of new recruits growing into the fishery. Teasing apart these factors is not possible given the American eel's unique life history and lack of specific information related to fishing effort among sub-estuaries.

Catch curve estimates of morality assume that recruitment is not trending over time. This assumption likely oversimplifies the recruitment patterns in the Chesapeake Bay, especially given that recent recruitment indices indicated a decline during the past two decades (see Chapter 3). The narrow range of American eel ages present in the Chesapeake Bay limit the range of ages available for catch curve analysis; typically catch curves were based on 4-6 age-classes. This limited range added uncertainty to the loss rate estimates, contributing to high variances and lack of statistical sensitivity to tests related to sub-estuary differences (Table 1.4).

Despite limiting assumptions inherent in using loss rate as a measure of overall mortality, such estimates can be extremely useful in supporting fishery assessments and reference points for eels. Further, there are very few such estimates available for American eel. Morrison and Secor (2003) estimated 9-24% annual loss rate for American eels in the Hudson River, and cited an anonymous source with

estimates of 22% annual natural mortality on Prince Edward Island and 12-55% annual natural mortality for 10-year-old eels from a portion of the Gulf of St. Lawrence. By comparison, our average estimate of 34-59% loss rate from the catch curve analysis and 65.8-67.4% from seasonal change in abundance (see Chapter 2) may not be unrealistic for a productive population that is experiencing both natural and fishing mortality.

Parasitism

Parasitism prevalence by *A. crassus* has increased in the Chesapeake Bay since its first report (Barse and Secor, 1999). Initial reported estimates of 10-24% prevalence in the Patuxent and Sassafras Rivers, respectively, were substantially lower than the mean Chesapeake Bay prevalence (40.9%) and lower than the current estimates for the Patuxent (40.5%) and Sassafras Rivers (72.0%). Increasing parasite prevalence and intensity over time has also been noted in the Hudson River where parasite prevalence increased from <20% in 1997 to >60% in 2000 (Morrison and Secor, 2003). The tripling of parasite prevalence in the Hudson River over three years was similar to the three- to four-fold increase observed in the Sassafras and Patuxent sub-estuaries in the past decade. Studies have also indicated that the range of the parasite is increasing northward (Aieta and Oliveira, 2009).

The hatching, survival, and infectivity of *A. crassus* is negatively related to salinity (de Charleroy et al., 1989; Kirk et al., 2000). Chesapeake Bay parasite prevalence was significantly greater in the upper bay, where salinity is low, than in the lower bay where salinities are generally higher. The relationship between salinity and parasite presence was also observed in the Hudson River estuary as well

(Morrison and Secor, 2003); they found lower parasite intensity at brackish sites than freshwater sites. Parasite prevalence and incidence in the Chesapeake Bay tributaries was generally comparable to estimates for other rivers and estuaries in the published literature in the past decade. As stated previously, Morrison and Secor (2003) observed parasite prevalence increasing from <20% in 1997 to >60% in 2000. A later study of freshwater portions of the Hudson River found parasite prevalence of 32-52% (mean 39%) and mean parasite intensity of 2.4 (Machut et al., 2008). Parasite prevalence and intensity in North Carolina was 52% and 3.9 parasites, respectively, in samples drawn from 1998 and 1999 (Moser et al., 2001).

Mean parasite intensity of Chesapeake Bay American eel had a significant negative correlation with size class (Figure 6), opposite to the trend observed by Moser et al. (2001) in North Carolina. A negative association between size and parasite infection might occur if *A. crassus* diminished growth or increased mortality in infected American eels. However, I found that among sub-estuaries parasitism was unrelated to growth and mortality. In addition, American eels with or without swimbladder damage (based on the SBtt score) did not differ in age or growth rate. Although the strong correlation between parasite intensity and swimbladder damage index supports a cause and effect relationship, little is known about how rapidly swimbladder damage occurs with repeated infections and whether swimbladders can recover to a healthy condition. A controlled laboratory study of parasitism would be beneficial in our understanding of the effects of *A. crassus* parasitism on swimbladder histology and function in American eel.

Mean parasite intensity and swimbladder damage decreased between summer and fall for two Chesapeake Bay tributaries, a trend that was also identified by Lefebvre et al. (2002) for European eels. They hypothesized that the observed decrease in swimbladder damage may be due to mortality of infected eels, but the current study did not find evidence of increased mortality, which would have been evident through either differences in loss rates among sub-estuaries or a truncated age distribution of those individuals exhibiting heavily damaged swimbladders (see Figure 1.8). *A. crassus* life cycle duration is influenced by temperature; cooler water reduces hatching of the juvenile parasite, thus reducing recruitment of the parasite to intermediate hosts (De Charleroy et al., 1989; Höglund and Thomas, 1992). As fall approached, lower mean parasite intensity in the Chesapeake Bay tributaries may represent reduced parasite infection with cooler temperatures. A possible explanation for improved swimbladder condition during fall is that swimbladder damage is reversible within individuals within a several month span.

Conclusions and Implications

In summary, American eels in the Chesapeake Bay sub-estuaries and bay regions had different growth, gender, parasitism, and condition levels. The demographic diversity in the Chesapeake Bay region may be beneficial to the stability of a panmictic American eel population faced with a changing environment (Cairns et al., in press). The heterogeneity of sub-estuaries should be taken into consideration in future stock assessments and management plans. The high growth rates relative to other estuaries and mix of male and female eels among sub-estuaries all point to the

Chesapeake Bay as a central growth habitat for American eels, critical for sustained spawner escapement for American eel.

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Tables

Table 1.1. Mean TL, age, weight and overall growth rate for Chesapeake Bay female America eels by sub-estuary and bay region, 2007. Means with common superscripts are not significantly different from one another based upon a Tukey mean comparison test ($p<0.05$). Sub-estuaries are listed from north to south.

River	N	Mean TL (cm, (±SE))	Mean Age (yr, (±SE))	Mean Weight (g, (±SE))	Mean Growth Rate (mm yr^{-1}, (±SE))
Upper Bay	213	36.8 (0.58) ^{X}	6.1 (0.13) ^{X}	90.4 (5.92) ^{X}	65.2 (1.69) ^{X}
Sassafras	100	36.2 (1.09) ^{AB}	6.8 (0.24) ^{CD}	93.1 (11.75) ^{A}	54.4 (3.31) ^{A}
Chester	213	36.9 (0.59) ^{AB}	5.9 (0.14) ^{AB}	89.2 (6.40) ^{A}	68.7 (1.89) ^{B}
Lower Bay	537	41.2 (0.34) ^{Y}	6.1 (.069) ^{X}	135.5 (3.43) ^{Y}	73.2 (0.93) ^{Y}
Choptank	110	40.0 (0.75) ^{B}	5.4 (0.16) ^{A}	111.9 (8.13) ^{AB}	80.9 (2.26) ^{C}
Patuxent	121	36.0 (0.62) ^{A}	5.7 (0.14) ^{A}	107.0 (6.75) ^{A}	67.4 (1.86) ^{B}
Potomac	205	41.8 (0.48) ^{C}	6.3 (0.11) ^{BC}	136.9 (5.27) ^{B}	72.7 (1.47) ^{B}
James	101	47.0 (0.64) ^{D}	6.8 (0.14) ^{D}	178.9 (6.91) ^{C}	74.8 (1.90) ^{BC}

Table 1.2. Mean growth rate and condition for each gender, bay region, and sub-estuary of Chesapeake Bay American eels. Means with common superscripts are not significantly different from one another based upon a Tukey mean comparison test ($p<0.05$).

[1] Growth rates of each sub-estuary calculated using mixed model with gender and sub-estuary as fixed effects. Growth rates for each gender calculated using one-way ANOVA. Growth rates for bay region calculated using ANOVA with gender and bay region as fixed effects. [2]Condition (*K*) calculated as Fulton's condition index (Ricker 1975). Sub-estuary estuary differences tested using ANOVA with gender and sub-estuary as fixed effects. [3]ANCOVA condition uses ANCOVA analysis of the $\log_e$ weight eels with $\log_e$ length as a covariate and gender, bay region, or sub-estuary as class variables to test for differences in condition between sub-estuaries.

Gender/ Region	N	Mean Growth[1] Rate (mm yr^{-1}, (±SE))	Mean Condition[2] (*K*, $g \cdot m^{-3} \cdot 10^5$, (±SE))	ANCOVA Condition[3] Log_e Weight (g (±SE))
Female	605	71.4 (0.79) ^{C}	0.174 (0.001) ^{B}	4.33 (0.007) ^{A}
Male	19	64.2 (4.89) ^{BC}	0.174 (0.006) ^{AB}	4.30 (0.013) ^{A}
Intersexual	194	57.7 (1.45) ^{AB}	0.163 (0.002) ^{A}	4.36 (0.034) ^{A}
Undifferentiated	30	48.5 (3.65) ^{A}	0.165 (0.005) ^{AB}	4.32 (0.030) ^{A}
Upper Bay		57.3 (1.67) ^{X}	0.170 (0.003) ^{X}	4.28 (0.009) ^{X}
Sassafras	100	53.4 (2.18) ^{A}	0.166 (0.003) ^{A}	4.33 (0.017) ^{A}
Chester	213	60.2 (1.89) ^{AB}	0.161 (0.002) ^{AB}	4.30 (0.014) ^{A}
Lower Bay		65.2 (1.81) ^{Y}	0.183 (0.003) ^{Y}	4.35 (0.007) ^{Y}
Choptank	110	72.7 (2.34) ^{D}	0.167 (0.003) ^{AB}	4.32 (0.017) ^{A}
Patuxent	121	60.9 (2.29) ^{BC}	0.199 (0.003) ^{AB}	4.51 (0.017) ^{B}
Potomac	205	63.9 (2.07) ^{BC}	0.172 (0.003) ^{B}	4.34 (0.015) ^{A}
James	101	67.2 (2.52) ^{CD}	0.168 (0.003) ^{C}	4.30 (0.018) ^{A}

Table 1.3. Catch curve estimates of instantaneous mortality rate (*Z*) and annual mortality rate (*A*) for Chesapeake Bay sub-estuaries. Means with common superscript are not significantly different from one another based upon a Tukey mean comparison test ($p<0.05$). Sub-estuaries are listed from north to south.

River	Z (±SE)	A	Ages for analysis
Sassafras	0.623 (±0.53) ^{A}	0.464	6 to 10
Chester	0.572 (±0.93) ^{A}	0.436	6 to 11
Choptank	0.519 (±0.92) ^{A}	0.405	6 to 11
Patuxent	0.716 (±0.82) ^{A}	0.511	6 to 11
Potomac	1.009 (±0.62) ^{A}	0.636	7 to 11
James	0.879 (±0.34) ^{A}	0.585	8 to 11

Table 1.4. A. crassus parasite prevalence and mean intensity by Chesapeake Bay sub-estuary. Mean parasite intensity was adjusted for length and sub-estuary effects using ANOVA with size class and sub-estuary as fixed variables.

River	Parasite Prevalence (%)	Mean Parasite Intensity (±SE)	Parasite Range (n)
Sassafras	72.0	3.8 (±0.74)	0-23
Chester	42.3	2.9 (±0.69)	0-15
Choptank	39.1	2.1 (±0.79)	0-9
Patuxent	40.5	4.0 (±0.78)	0-48
Potomac	36.3	2.5 (±0.64)	0-10
James	17.8	2.0 (±1.07)	0-6

Figures

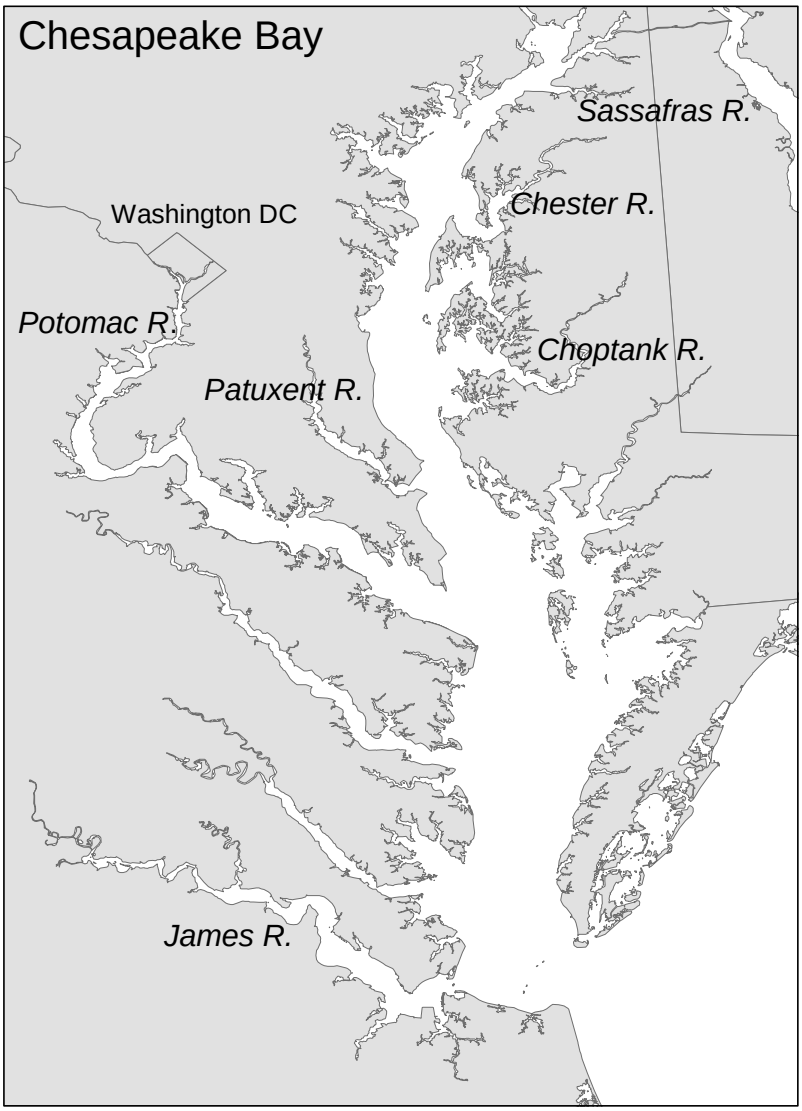
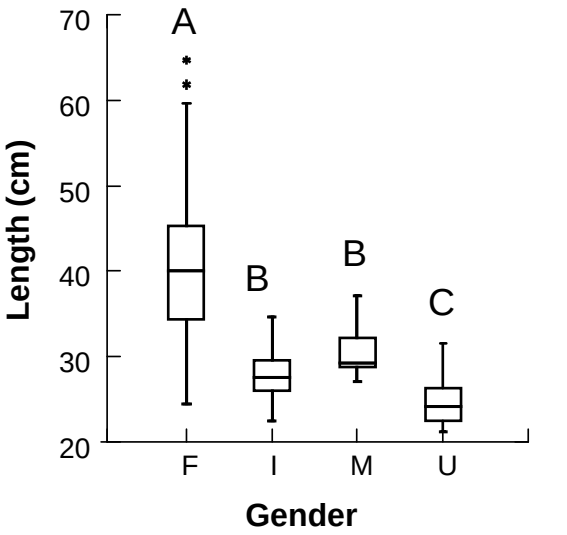


Figure 1.1. Map of sub-estuaries of the Chesapeake Bay sampled in 2007. The Potomac and Chester Rivers were sampled in summer and fall, the Sassafras and Patuxent were sampled in summer only, and the James and Choptank were sampled in fall only.


70
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30
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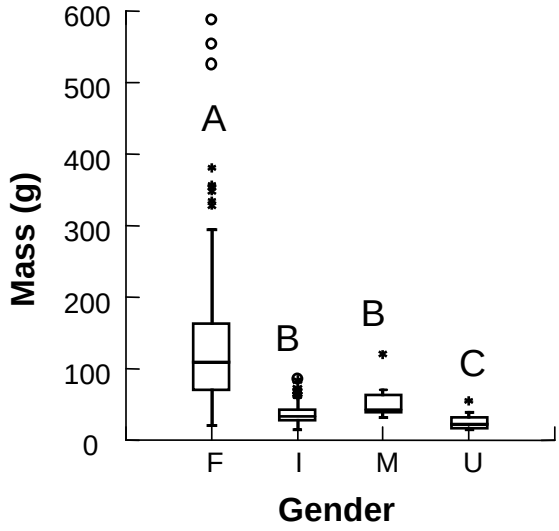
Length (cm)
A
B
B
C
F
I
M
U
Gender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Mass (g)
A
B
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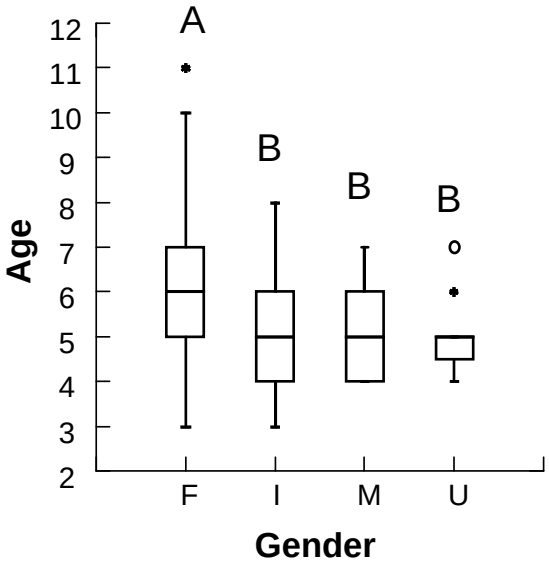
Gender


12
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Age
A
B
B
B
F
I
M
U
Gender

Figure 1.2. Mean TL (cm; a), mass (b), and age (c) of eels by gender categories for all sub-estuaries combined. Four gender categories are identified in American eels; female (*F*), male (*M*), intersexual (*I*), and undifferentiated (*U*). Boxes indicate the median (horizontal line), the first and third quartiles (box edges), ± 1.5 times the inner quartile range (whiskers), and outliers (stars). Significant differences between means ($p<0.05$) are indicated by a different letter.

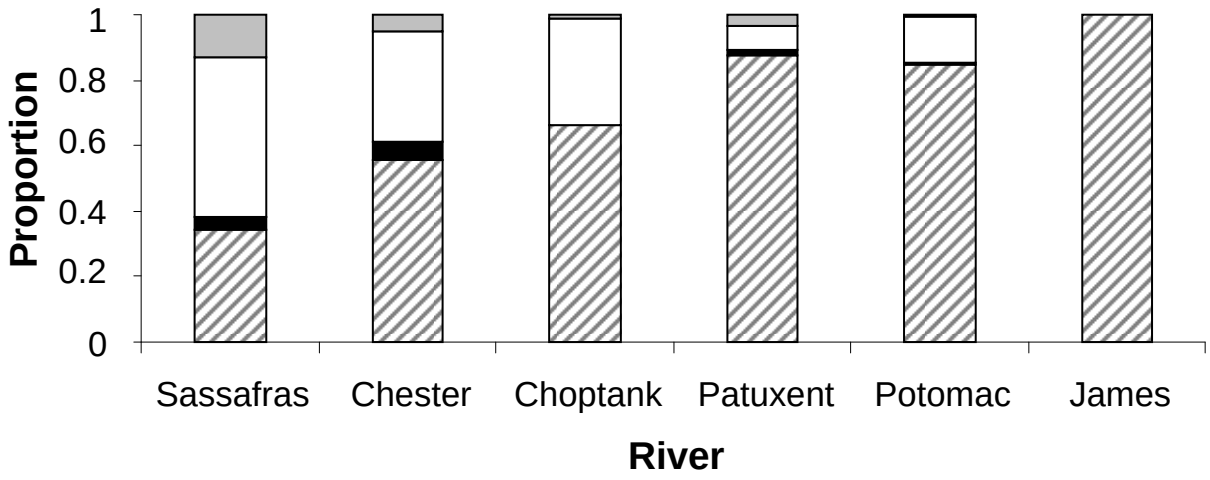

Figure 1.3. Proportion of each gender for each sub-estuary. Four gender categories are identified in American eels; female (hatched), male (black), intersexual (white), and undifferentiated (gray).

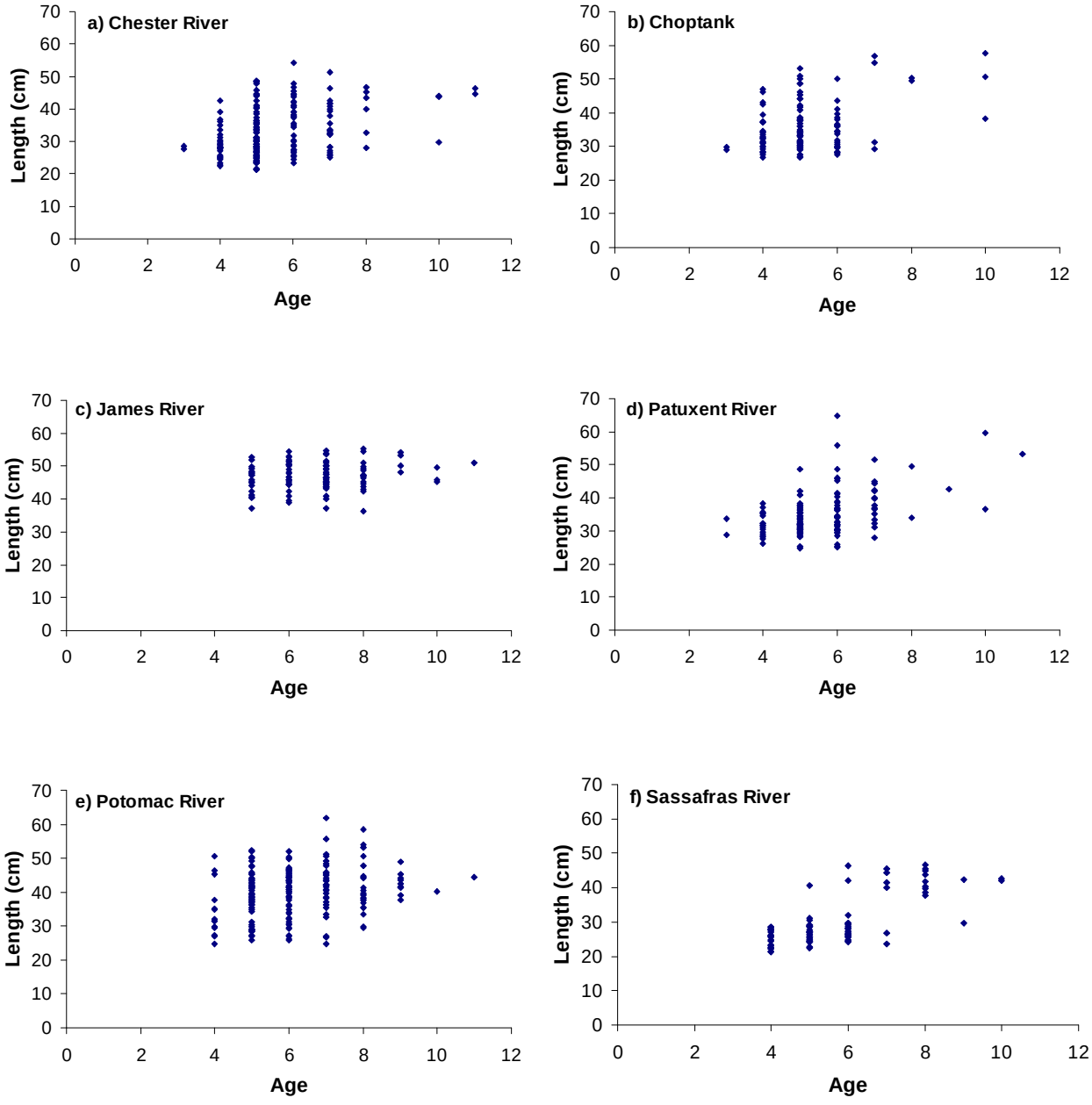

Figure 1.4. Length-at-age for Chesapeake Bay yellow eels for each sub-estuary.

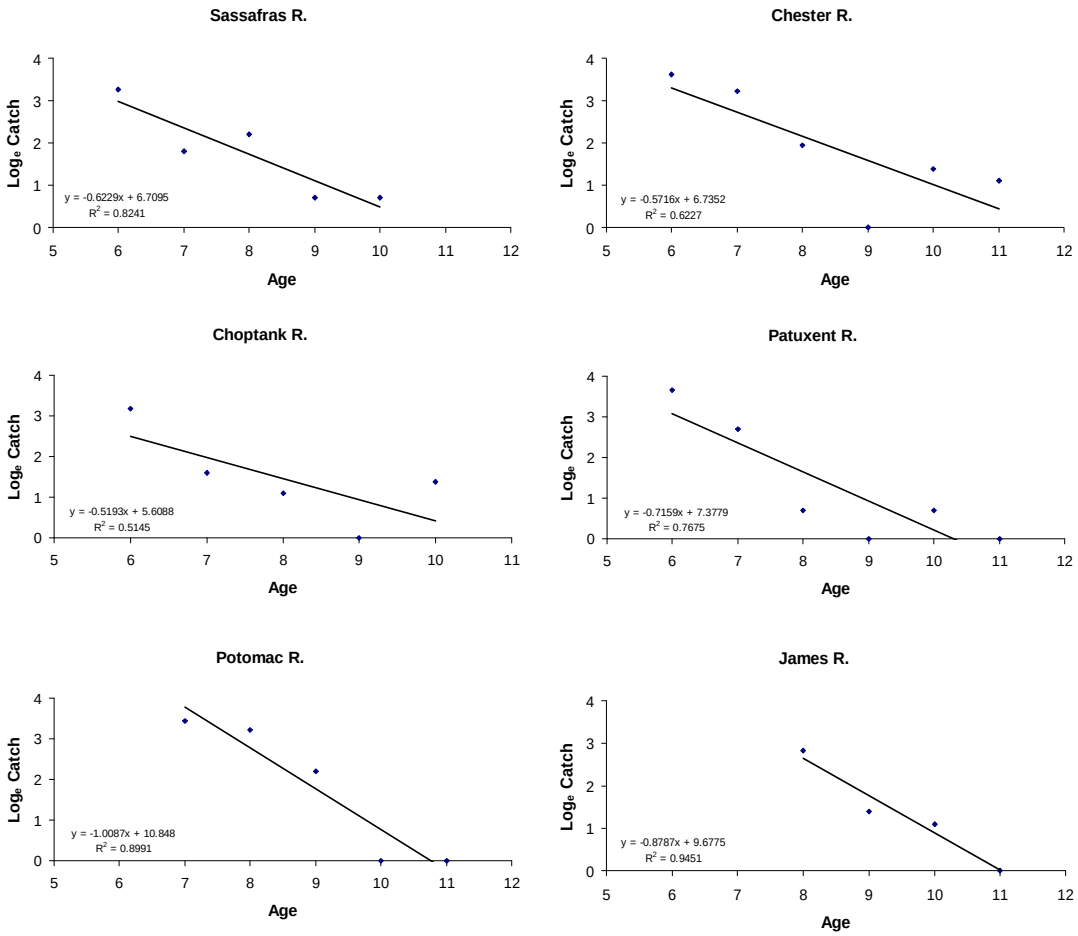

Figure 1.5. Catch curves for Chesapeake Bay yellow eels for each sub-estuary.

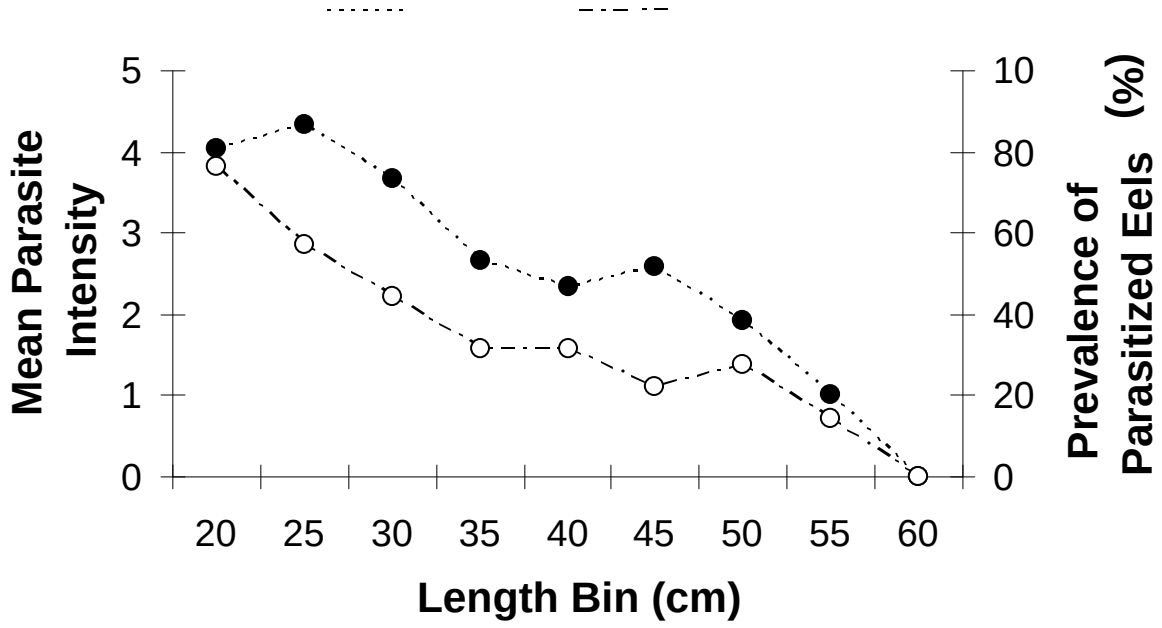

Figure 1.6. Mean parasite intensity (closed circles) and percent prevalence (open circles) versus American eel size class for all sampled Chesapeake Bay sub-estuaries combined.

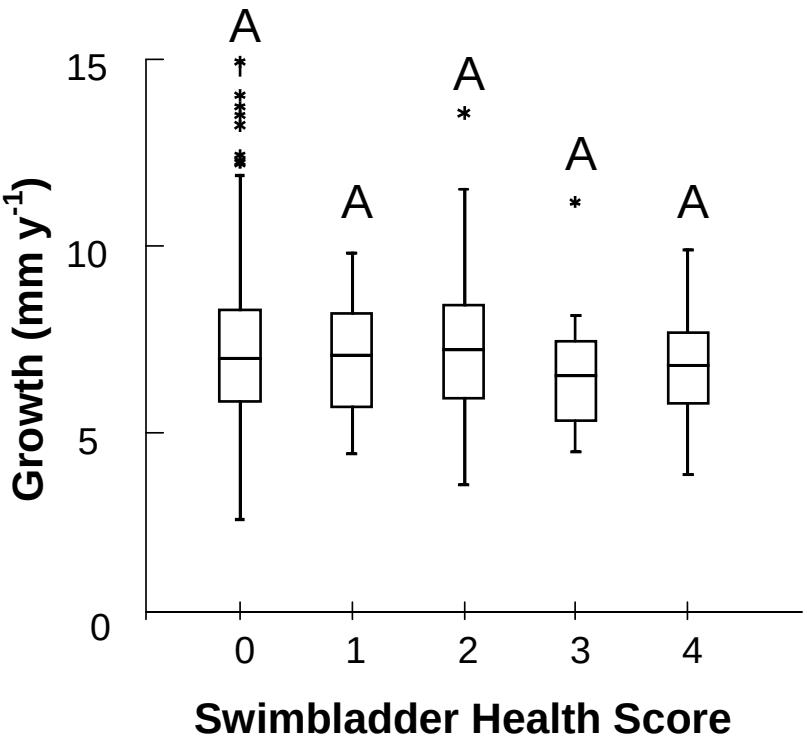

Figure 1.7. Growth rates of female American eel by swimbladder thickness and transparency score (*SBtt*). Boxes indicate the median (horizontal line), the first and third quartiles (box edges), ±1.5 times the inner quartile range (whiskers), and outliers (stars). Significant differences between means ($p<0.05$; Tukey multiple mean comparisons) are indicated by a different letter.

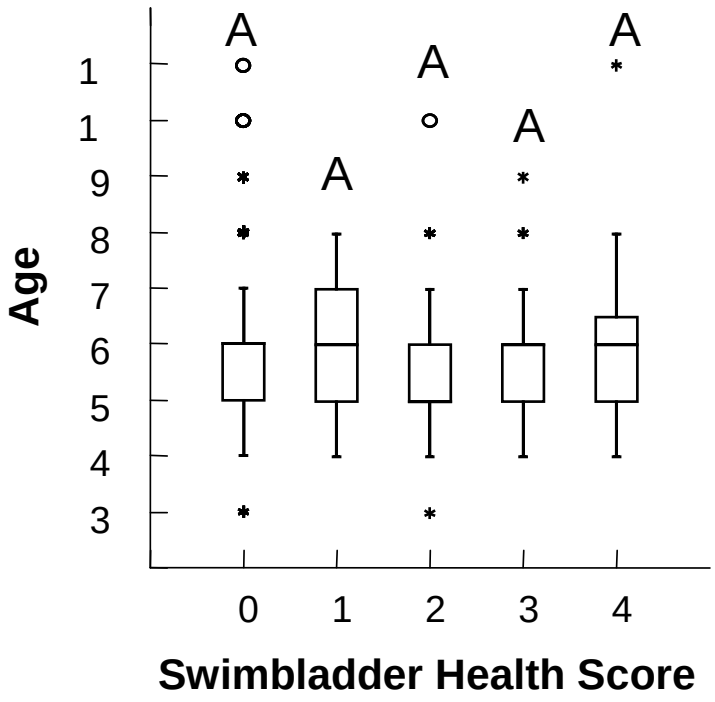

Figure 1.8. Mean female American eel age by swimbladder thickness and transparency (*SBtt*) score. Boxes indicate the median (horizontal line), the first and third quartiles (box edges), ±1.5 times the inner quartile range (whiskers), and outliers (stars). Significant differences between means ($p<0.05$; Tukey multiple mean comparisons) are indicated by a different letter.

Chapter 2: Local abundance and production of Potomac River Estuary American eels

Abstract

The Potomac River represents the center of American eel *Anguilla rostrata* distribution and supports among the most productive yellow eel fisheries (historically ~100 metric tons per year) in the U.S. To evaluate underlying production related to this fishery, a mark-recapture study was conducted in July and October of 2007 on the tidal, brackish portion of the Potomac River. The objective was to estimate abundance and growth to evaluate trends in seasonal yellow eel production and compare these to Hudson River estuary yellow eels, which are not exploited. Local abundances were higher in the Potomac River Estuary in comparison to the Hudson River, but growth rates were similar. Mortality rates, determined through catch curve analysis, were twice as high as those in the Hudson River estuary. If natural mortality rates are similar in both systems, then fishing mortality in the Potomac River is about equal to natural mortality. Production of eels in the Potomac may be greater due to underlying benthic production differences between the two ecosystems. Alternatively, if the Potomac River is not recruitment limited, higher mortality due to exploitation could result in higher production of yellow eels than in the Hudson River, which may be closer to carrying capacity.

Introduction

The decline of U.S. catches of American eel *Anguilla rostrata* during the past 20 years has prompted concern that harvest rates may be too high for population sustainability. In the 1970s, U.S. landings of American eel peaked at almost 1600 metric tons, but by 2001 harvest had fallen to about 400 metric tons. American eels are catadramous, panmictic, and semelparous (Avise et al., 2003; Tesch, 1977); all harvest occurs prior to spawning thus making fishing mortality a potential cause of declining American eel abundance (ICES, 2001; ASMFC, 2004; USFWS, 2007). Most exploitation occurs in estuaries on the yellow eel stage, yet little is known about the estuarine ecology of American eel. Here, I evaluate abundance and productivity of American eels in the Potomac River Estuary, which is centrally located within the species' range.

Declining abundance has been observed in other portions of the American eels' range. A >10-fold reduction in yellow eel passage from the St. Lawrence River into Lake Ontario has raised conservation concerns for the species (Casselman et al., 1997; Casselman, 2003) but other fishery-independent data indicates either a more moderate rate of decline during the past 20 years or no trend (ASMFC, 2004). Reasons for American eel stock decline are not fully understood but lack of spawner escapement, poor habitat quality, reduced habitat availability due to dams, global climate change and lethal or sub-lethal effects of parasitism infection have been discussed in addition to overexploitation (Castonguay et al., 1994; Haro et al., 2000; Knights, 2003; Friedland et al., 2007).

Access to approximately 25-84% of the historically available habitat for American eels is now partially or completely impeded by small and large dams (ASMFC, 2000; USFWS, 2007), so understanding the growth and mortality of American eels in estuaries and tidal rivers is critical to management of the species. Estuaries and the brackish portions of rivers are recognized as productive American eel habitats (Helfman, 1987), but the American eel population in the Chesapeake Bay, the largest North American estuary, has received little attention. The USFWS (2007) concluded that listing American eels as a Federally threatened or endangered species was not warranted, based in part on the conclusion that American eels can complete their life cycle without entering freshwater and that brackish and marine habitats can be highly productive.

Within the Chesapeake Bay, the Potomac River supports the single largest yellow eel fishery. From 1950 to 2007, 16% of U.S. American eel catches and 32% of catches in Chesapeake Bay came from the Potomac River (Potomac River Fisheries Commission [PRFC], unpublished data). The fishery is predominately commercial and is conducted primarily using two-chambered eel pots (>98% of the catch by weight), with a small number of eels taken in pound nets. The PRFC regulates harvest and licensing on the river and maintains a database on catch and effort statistics.

Historically high yield in the Potomac River and its central location within the range of American eel suggest that the Potomac could be a critical growth habitat for yellow eels. The Potomac River is a large, productive tributary of the Chesapeake Bay. The tidal portion of the river extends approximately 180 river km to the

Washington, D.C. border and is broken into three regions; the tidal freshwater zone, the transition zone, and the mesohaline estuarine region (Fig. 2.1; Jaworski, 2007). The mesholine estuarine region of the river extends 80 km upstream from the mouth of the river and is characterized by salinities of 5 to 18 ‰. The transition zone extends 47 km further upstream, with salinities ranging from 0.5 to 10 ‰.

The Hudson and Potomac Rivers share physical characteristics that allow for comparisons of production, abundance, and growth. Located in the Mid-Atlantic region, both rivers contain large freshwater and brackish tidal components that are partially mixed. The Potomac and Hudson River estuaries also have similar watershed areas (36,784 km^2 and 34,706 km^2 respectively), and discharge rates (326 and 388 $m^3 s^{-1}$ respectively; Paul, 2001). Since 1976 the harvest of American eels has been banned in the Hudson River due to polychlorinated biphenyl (PCB) contamination. The ban includes commercial and recreational harvest, with the exception of a small bait fishery, and the long-term closure allowed us to compare estuarine yellow eel production between the Potomac and Hudson River estuaries, which represented exploited and unexploited stocks. The Potomac River is a productive system with high nutrient inputs and high primary production (Boynton et al., 1982; Jaworski, 2007), and despite fisheries occurring there, I predict that growth and production rates and abundance will be greater than in the Hudson River estuary.

The objectives of this study were: 1) estimate early summer and fall local abundances in brackish portions of the Potomac River estuary; 2) estimate annual growth, mortality, and production rates; 3) compare local abundance and production rates between the Potomac and Hudson River estuaries. To fulfill these objectives I

conducted a mark-recapture experiment in the Potomac River in 2007 and compared my estimates of growth rate, production and mortality to published estimates from the Hudson River.

Methods

Mark-Recapture Experiment

To estimate local abundance, we conducted a mark-recapture experiment in the early summer (June 25-July 12) and fall (September 28-October 14) of 2007. Consulting with a knowledgeable local waterman (J. Trossbach, pers. comm.), I chose three sites within the mesohaline estuary region and oligohaline zone of the Potomac River that (1) corresponded to historical high yield fishing locations, (2) occurred over river depths 2 - 8 m, and (3) accommodated a 6.4 km long string of pots (Figure 2.1).

At each site, 75 cylindrical two-chamber, 1.2 cm mesh eel pots baited with razor clams were set on a trot line in a grid-and-line configuration (Figure 2.2), and surface and bottom water quality measurements (dissolved oxygen, salinity, and temperature) were obtained with a YSI handheld meter. The pot set consisted of five sections, each with 15 baited pots. Based on Morrison and Secor (2004), local abundance was estimated for the centrally located three lines of grid pots. These pots were closely spaced at 50 m intervals to saturate the area. Lines of pots were set upstream and downstream of the grid to measure bait attraction of American eels into the grid. During the summer experiment, captured yellow eels at Site 1 experienced lethal hypoxia. Therefore, an alternative site (Site 4) was chosen for the fall sampling

when it became evident that eels had still not re-colonized Site 1. The alternative site was a trot line set by the commercial waterman for the purpose of harvest; the site consisted of a line of 18 pots spaced at ~40 meter intervals with no grid section.

Sampling at each site in each season occurred over a four-day sequence. On day one, baited pots were set into the grid-and-line configuration (Figure 2.2). After a one night soak, pots were retrieved one section at a time. Each American eel was anesthetized with MS-222, measured (nearest mm TL), and given a site- and section-specific freeze-brand (described below). American eels were allowed to recover from the anesthetic and were released into the middle of the section where they had been caught. Yellow eels exhibit trap-shy behavior the day following capture (Morrison and Secor 2004), so no pots were fished on day two. On day three, we set 45 baited pots back into the central grid, using GPS to relocate the original pot sites. Pots were soaked one night, and then on day four the pots were retrieved and captured American eels were inspected for brands and PIT tags. We recorded the number of newly captured and recaptured American eels for each section of the grid. In the fall, all American eels were checked for evidence of past brands.

Liquid nitrogen brands were applied according to Sorenson et al. (1983). A copper rod with a 0.75 cm changeable copper die screwed to one end was pressed to the skin of the anesthetized eel. The copper rod was seated in a 4-L thermos of liquid nitrogen; by applying the copper die to the eel's skin for 3 to 5 seconds, a brand was marked upon the skin. Previous studies of branded and eels held in the laboratory showed that brands were visible for at least 30 days and American eels showed no adverse effects from the branding process (Morrison and Secor, 2003). Brands from

the summer mark-recapture experiment were still visible on some American eels captured three months later at the fall mark-recapture sites, and were distinguishable from recent brands by their larger size and indistinct edges.

Local American eel abundance at each site was estimated with a modified Lincoln-Peterson method,

$$N = \frac{(M+1)(C+1)}{R+1} - 1, \tag{2.1}$$

where N is the estimate of total population size, M is the total number of individuals captured and marked in the grid on the first visit, C is the total number of individuals captured in the grid on the second visit, and R is the number recaptured in the grid on the second visit (Seber, 1982). We calculated the estimated abundance with branded eel data and excluded PIT tagged American eels (see below) to avoid possible adverse effects of PIT tagging on recapture rates. The variance of estimated N was

$$\mathrm{var}(N) = \frac{(M+1)(C+1)(M-R)(C-R)}{(R+1)^2(R+2)}, \tag{2.2}$$

(Seber, 1982). We evaluated immigration between sites by examining eels for brands that were specific to sections outside sampling grid or site; these individuals were removed from the abundance estimates. Ingress into the sampling grid from the upstream and downstream sampling lines was calculated as the number of eels marked outside the grid on day 2 that were recaptured in the grid on day 4 divided by the recapture rate of marked eels in the grid. The estimated abundance of American eels in the sample grid was reduced by the number of American eels attracted to the sampling grid from the upstream or downstream lines. To estimate American eel density at each site, we assumed a 50 m x 50 m attraction area centered at each pot,

with symmetrical coverage of the sampling grid to estimate the area sampled by the grid. The estimated American eel abundance in the sampling grid was divided by the area sampled to estimate density (American eels ha^{-1}).

Growth

During summer sampling, we measured and injected 80 American eels at each site with PIT tags into the visceral cavity using a hypodermic needle. Tagging in the visceral cavity rather than in the dorsal musculature was necessary due to the potential for tagged American eels to be used for human consumption. We estimated daily summer growth rates of recovered PIT tagged American eels by dividing the change in length by the number of days at large.

Loss and Production Rate

I used catch curve analysis to obtain loss rate estimates for comparison to similar estimates for the Hudson River (Morrison and Secor, 2003), and for comparison to loss rate estimates based on changing seasonal abundance estimates. I had obtained 850 American eels representing six sub-estuaries of the Chesapeake Bay from the Delaware Valley Fish Company (see Chapter 1), including 97 and 108 eels from the Potomac River in summer and fall of 2007, respectively. I used standard aging techniques (Secor, 1991; Morrison and Secor, 2003) to section, polish and age the otoliths and determine catch-at-age for each season's sample. Instantaneous annual mortality rates were estimated using catch curves. The regression used catch-at-age data beginning at an age one year past the age of peak catch through the oldest age in the catch. Non-trending recruitment, constant mortality, and constant catchability across years and ages were assumed (Ricker, 1975; Hilborn and Walters,

1992). Because American eels in the Potomac River were subject to a commercial fishery, catch-curve mortality estimates include mortality due to fishing and natural causes and emigration from the sampling region (or the Potomac River due to maturation). Net loss rates were estimated from the mark-recapture experiment by calculating the percent decrease in abundance at the study sites between summer and fall.

We estimated production rates for the three Potomac River sites to allow comparison with production in the Hudson River and for comparison with outputs from the age-structure production model developed for the Potomac River (see Chapter 3). Mean biomass throughout the year was estimated as

$$B = \frac{B_0(e^{G-Z} - 1)}{(G - Z)}, \tag{2.3}$$

where B_0 is the initial biomass per hectare of American eels at the site, G is the mean instantaneous growth rate as measured by PIT tagged American eel growth, and Z is the instantaneous mortality estimate from the catch-curve analysis. Because only length measurements were taken in the field, B_0 for each site was calculated by converting length measurements to weight estimates based on the length (cm)–weight (g) relationship of Chesapeake Bay American eels analyzed in Chapter 1 ($W=0.0012TL^{3.1}$, $N=850$, $r^2=0.96$). Then, the mean individual biomass for each site was multiplied by the abundance estimate from the mark-recapture experiment.

Results

Mark-Recapture Experiment

Captured American eels ranged from 20.1 to 97.0 cm TL (Fig. 2.3), with a mean of 31.6 cm, and a median of 30.2 cm. This size range is representative of harvested eels throughout the Chesapeake Bay (see Chapter 1). The minimum mesh size for American eel pots was regulated by the PRFC to select eels greater than 15.2 cm, the minimum legal size. I did not catch American eels smaller than this minimum legal size.

A total of 4952 American eels were branded at sites 2, 3, and 4 over the duration of the investigation, with an overall recapture rate of 22%. The mark-recapture grid sites had salinities ranging from 5.9 to 12.2‰; summer and fall bottom temperatures ranged 23.6-27.6 C and 20.8-27.1 C, respectively. Dissolved oxygen (DO) levels at Site 1 ranged 0.3-10.4 mg L^{-1} (4.1-135.7% saturation). Site 2 and Site 3 had summer DO levels of 1.65 to 6.7 mg L^{-1} (21.7-83.5% saturation) and fall DO levels of 4.53-8.31 mg L^{-1} (56.3-104.6% saturation). The depth at Site 4 was greater than water quality probes could reach, so bottom temperatures and DO levels were not recorded for that site.

Ingress of American eels into the sampling grid at Sites 2 and 3 ranged from 0-151 eels per site (Table 2.1). Only four American eels out of 623 recaptured with brands were recaptured at a different sampling site from where there were originally branded (<1%); one American eel moved from Site 1 in summer to Site 2 in summer (one week at large), two moved from Site 2 in summer to Site 3 in summer (one week

at large), and one American eel originally branded at Site 2 in summer was recaptured at Site 3 in Fall (~3 months at large).

The summer ingress-adjusted abundance estimate was 2,589 and 2,875 American eels for Sites 2 and 3, respectively (Table 2.1). Fall abundance estimates were much lower; with 886 and 946 American eels at Sites 2 and 3, respectively. Because Site 4 was not set up to estimate ingress, overall abundance was not adjusted for bait attraction. Here fall abundance was estimated at 2,116 eels. Density estimates between seasons ranged from 79-256 eels ha^{-1} for Sites 2 and 3, and was 470 American eels ha^{-1} for Site 4.

Seasonal Abundance

American eel abundance and density showed strong seasonal trends. The estimated ingress-adjusted abundance of American eels at Sites 2 and 3 was significantly greater in summer than fall (Z-test, $p<0.001$), resulting in a 66.6% average decrease in abundance through the fishing season. The density of American eels at Site 2 dropped from an estimated 230 American eels ha^{-1} in summer to 79 American eels ha^{-1} in fall, while the American eels' density at Site 3 decreased from 156 to 83 American eels ha^{-1} over the same time period (Table 2.1).

Growth

Returns of PIT tagged American eels were low. Of the 240 American eels tagged in summer, only 5 were recaptured in the fall (2% recapture rate). A similarly low return rate was observed with branded eels: only 2% of American eels captured in the fall had visible brands from summer. Growth was highly variable, ranging

from 18 to 108 mm during the ~3 months at large, representing daily growth rates of 0.19 to 1.15 mm d^{-1}, with an average of 0.52 mm d^{-1}.

Loss and Production Rate

The annual instantaneous loss rate estimate from catch curve analysis was 0.55 (±SE 0.45) for summer and 0.82 (±0.39) for fall (Figure 2.4). This corresponds to a total mean annual loss rate of 64% yr^{-1} for the Potomac River. This estimate combines mortality due to fishing and natural causes and emigration. A coarse estimate of seasonal mortality was derived from the change in abundance between summer and fall from the mark-recapture estimates. The decrease in abundance between summer and fall was 65.8% for Site 2 and 67.4% for Site 3.

Production estimates based on summer abundance for Sites 2 and 3 were 26.7 kg $ha^{-1}yr^{-1}$ and 23.2 kg ha^{-1} yr^{-1}, respectively. Production estimates based on fall abundance for Sites 2, 3, and 4 were 8.5 kg ha^{-1} yr^{-1}, 9.2 kg ha^{-1} yr^{-1}, and 43.1 kg ha^{-1} yr^{-1}, respectively.

Discussion

Mark-Recapture Experiment

American eel density in the Potomac River was much higher than in the Hudson River estuary. Previous work in the Hudson River (Morrison and Secor, 2004) estimated densities of 5 to 18 American eels ha^{-1} in brackish water sites. Estimates from the White Oak River estuary in North Carolina were similar to the Hudson River, 4 to 14 American eels ha^{-1} (Hightower and Nesnow, 2006). These

numbers are much less than the 230 to 256 American eels ha^{-1} summer densities or 79 to 83 American eels ha^{-1} fall densities estimated in my study. The brackish water sites sampled by Morrison and Secor (2003) on the Hudson River comprised similar river depths, substrates, and salinities to those found at the Potomac River study sites (Table 2.2). The White Oak River estuary is a substantially smaller system.

The large differences in American eel density between the Hudson and Potomac rivers suggest that there may be large differences in the productivity of these estuaries. Primary productivity is often used as an indicator of a system's capacity for production. In the Mid-Chesapeake Bay, mean daily phytoplankton production and chlorophyll concentrations are higher than in the Hudson River (Table 2.2). Estimates of summer chlorophyll concentrations specifically in the Potomac River regularly exceeded 20 mg L^{-1} (20,000 mg m^{-3}; Chesapeake Bay Monitoring website: http://www.dnr.state.md.us/Bay/monitoring/mon_mngmt_actions/chapter5.html). These primary production rate differences between systems likely support higher fishery production in the Potomac than in the Hudson River (Houde and Rutherford, 1993; Monaco and Ulanowicz, 1997; Nixon and Buckley, 2002).

The mark recapture estimator used here depended upon a closed population assumption. I attempted to correct for any bait attraction of eels into the sampling grid by directly measuring ingress and adjusting the local abundance estimate accordingly. Ingress rates, or the number of eels attracted to the grid divided by the number of eels marked outside the grid, ranged 0 to 14% and were less than those observed for the Hudson River, where 32% of the eels marked outside the grid were found recaptured within the grid within a six-day period (Morrison and Secor, 2004).

Movements of branded eels among study sites were very low. Only four eels were observed at a site different from where they were originally branded (< 1%). Thus tagging data indicated that yellow eels show local fidelity to the region corresponding to the grid size (c. 11.25 ha), similar to home ranges observed throughout the Hudson River estuary (Morrison and Secor, 2003).

I observed a strong influence of hypoxia on yellow eel abundance and behavior. At Site 1, on the morning of day two of the summer mark-recapture experiment, I measured extreme hypoxia in bottom waters (1.21 mg L^{-1} or 11.5% saturation on Day 2). Many pots that had been set the previous day were pulled up empty or containing dead eels, particularly in the deep section of the grid (depth 3.7-6.1 m, total dead eels=58). On day four, hypoxic conditions continued and 21 of 45 grid pots were empty when retrieved. The early morning hypoxic events were believed to be due to a diel DO sag, the result of a large phytoplankton bloom that I observed when setting pots. Such diel hypoxic cycles in estuaries are increasingly recognized as an important constraint on growth and nursery habitats within estuaries (Breitburg, 2002; Tyler et al., 2009). Three weeks after the initial visit to Site 1, I returned and sampled the grid during normoxic conditions. I captured 1537 eels, but only five that had brands from the original Site 1 tagging. During fall, no brands from the first day's tagging were observed. These eels likely perished, migrated to new and more suitable habitats, or were caught by eelers.

The influence of hypoxia on eel habitat suitability has been infrequently noted. Despite the fact that eels can respire cutaneously and survive in air better than in poorly oxygenated water, they are no more tolerant to hypoxic water than other

fishes (Tesch, 1977). In a study on small Japanese eels (*Anguilla japonica*, mean weight 2 g), dissolved oxygen levels of 1.0 $mg \cdot L^{-1}$ were found to be lethal (Yamagata et al., 1983), and there is well documented evidence of European eels (*Anguilla anguilla*) escaping poor water quality conditions by crawling onto shore (Tesch, 1977). In addition, European eels parasitized by the swimbladder parasite *Anguillicola crassus* have increased mortality under severe oxygen stress than non-parasitized eels (Lefebvre et al., 2007). American eels in the Potomac River are frequently infected with *A. crassus* (Chapter 1).

Growth

Growth was highly variable, and this has been found in other studies of American eels (Morrison and Secor, 2003; Cairns et al., in press). The average growth rate, 0.52 $mm \cdot d^{-1}$, indicated that individuals below the minimum size caught by the pots (~15-20 cm TL) in summer probably recruited to the fishery by the fall sampling period. Thus, the closed population assumption between the summer and fall sampling periods was likely violated as new recruits would occur in the fall experiment and fall abundances were likely over-estimated in comparison to the summer abundance.

Returns of PIT tagged American eels were much lower than expected. Only 2% of American eels PIT tagged in the summer were recaptured in the fall. This low recapture rate could be due to two factors; 1) the tagging of American eels in the visceral cavity may have been stressful or lethal, leading to increased mortality of PIT-tagged American eels, or 2) the presence of a commercial fishery increased mortality on all eels and few PIT-tagged American eels were recaptured because they

had been caught in the commercial fishery. Morrison and Secor (2003) PIT tagged American eels in the dorsal musculature in 1998, and in the visceral cavity in 1999. They found that 72 of 81 eels retained PIT tags in the visceral cavity when recaptured two months later, supporting high rates of tag retention and post-tagging survival. Support for the second factor can be gleaned from the low number of American eels branded in summer that were recaptured in fall showing evidence of summer brands. Of the 1249 eels branded in the grid during my summer Potomac River sampling, only 25 American eels were recaptured in the fall grid sites with evidence of summer brands. While it is possible that brands faded between summer and fall or were missed in our examination, I feel my careful examination of the American eels makes this unlikely.

Growth rates in the Potomac River were higher than in the Hudson River (Morrison and Secor, 2003). Growth rates for both river systems were estimated over summer months (June/July through September/October in Potomac River, June through August for Hudson River) and mean temperatures over months and years sampled in both rivers were within 1° C. Hudson River daily growth estimates for 14 brackish water American eels at large for two months averaged 0.44 mm d^{-1}, whereas the Potomac River growth rates averaged 0.52 mm d^{-1}(n=5) and were more variable. Morrison and Secor (2003) observed that Hudson River American eel growth in brackish water sites was 30 mm yr^{-1} greater than American eels in freshwater. Given that the tidal Potomac River is large, and growth rates were slightly higher than the Hudson River, results indicate that the Potomac River is a more productive habitat for American eels.

Loss and Production Rate

There are few loss rate estimates for American eels in the published literature. Morrison and Secor (2003) estimated 9-24% annual loss rate for American eels in the Hudson River, and cite an anonymous source with estimates of 22% annual natural mortality on Prince Edward Island and 12-55% annual natural mortality for 10-year-old eels from a portion of the Gulf of St. Lawrence. By comparison, our average estimate of 64% from the catch curve and 66-67% net loss from changing abundance is not unrealistic for a productive population experiencing natural and fishing mortality. One of the assumptions of catch curve analysis is that recruitment is not trending over time. This assumption was likely violated because recruitment declined over time in Virginia waters of Chesapeake Bay (Chapter 3). Because of the small range of American eel ages present in the Potomac River the range of ages available for catch curve analysis was small, typically our catch curves were based on 4-6 age-classes. This limited range adds uncertainty to our loss rate estimates, although they were not unreasonably high for a population that is commercially fished.

Production estimates of American eels in the Potomac River (8.5-43.1 kg ha^{-1} yr^{-1}) were greater than those of the Hudson River (1.10-1.77 kg ha^{-1} yr^{-1}in brackish sites) but biomass estimates from the Potomac River were similar to estimates from European eel biomass estimates (Barak and Mason, 1992). The ten-fold difference in American eel density and the 10- to 20-fold difference in production between the Potomac and Hudson River estuaries cannot be completely explained by the two- or three-fold difference in primary production in the two estuaries. One possible explanation for the difference in production is that assuming the Potomac River is not

recruitment limited; the fishery on the Potomac River American eel population has kept the population below carrying capacity, increasing the productivity of the stock by keeping the population in a growth phase. Historically high and long-term fishing yields in the Chesapeake Bay region suggest that Chesapeake Bay is a highly productive region for American eels.

Management Implications

The Potomac River American eel fishery may not be tracking species trends in productivity and abundance. While the worldwide catches of American eels have been decreasing since the early 1980s, harvest in the Chesapeake Bay has been fairly stable (NMFS Annual Landings Query; Chapter 3), showing only moderate declines. A stable landings history suggests that high production specific to the Potomac River estuary may be able to sustain high fishing rates.

Morrison and Secor (2003) suggested that freshwater portions of rivers should be set aside and kept free from commercial fishing as American eel "reserves" and that brackish habitats be fished, due to their higher abundances and higher growth rates. My research supports these conclusions, but the freshwater reserve concept has some problems. Pound net fisheries for silver eels in brackish estuaries must be minimized to avoid catching silver eels that are migrating out of freshwater habitats. Freshwater habitats are frequently obstructed by dams that can impede the migration of eels upstream and significantly reduce eel condition beyond habitat barriers (Busch et al., 1998; USFWS, 2007; Machut et al., 2007), making freshwater regions less reliable as spawning or production reserves. However, the idea of freshwater reserves is supported by evidence of hypoxia in estuarine habitats. As hypoxia can cause

stress and mortality in fishes (Breitburg, 2002), and is common in estuarine environments, a freshwater reserve would help buffer the effects of estuarine degradation. The USFWS (2007) decision to not list American eels as an Endangered or Threatened Species was based in part on evidence that estuarine production of eels was sufficient to counteract the freshwater habitat lost due to dams. On average, American eel densities in brackish habitats were greater than in freshwater habitats (Morrison and Secor 2004), indicating that brackish habitat may help counteract the loss of some freshwater habitat. As world climates change and population centers continue to grow and impact our coastal estuaries, both freshwater and brackish water may be crucial to American eel survival.

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Tables

Table 2.1. Summary of field sites. Site 4 was originally a pot line set by the waterman assisting with field work; when Site 1 failed in fall, we used this set. Estimated abundances have been corrected for ingress due to bait attraction.

Site	Season	Total N branded	Unadjusted M-R abundance estimate	Proportion of grid eels recaptured	Number eels marked outside grid recap. in grid	Adjusted estimated abundance of eels	Standard deviation of abund. estimate (±)	Est. density (eels/ha)	PIT tags retrieved
2	Summer	1343	2663	0.315	10	2589	273.6	230	
	Fall	387	886	0.380	0	886	68.2	79	2
3	Summer	1922	3026	0.312	47	2875	139.7	256	
	Fall	631	955	0.219	4	937	99.5	83	3
4	Fall	669	2116	0.148		2116	160.7	470	

Table 2.2. Comparison of physical features and production of the Hudson River and Potomac River estuaries. Sample sites for both studies had a fine grain clay and silt substrate. [a]Morrison and Secor 2004, [b]Boynton et al. 1982.

River	Tidal reach	River width at Sample sites	Temperature range at sites, C	Depth range at sites	Salinity at sites	Phytoplankton productivity ($g\ C\ m^{-2}\ d^{-1}$)	Chlorophyll a ($mg\ m^{-3}$)
Potomac	180 km	3-6 km	20.6-29.1	2-6 m	3.6-12.9	~1.0[b] (in Mid-Chesapeake Bay)	~7.5[b]
Hudson	255 km	0.5-5 km	mean 24±2[a]	2-10 m[a]	0-20[a]	~0.5[b]	~2.5[b]

Figures

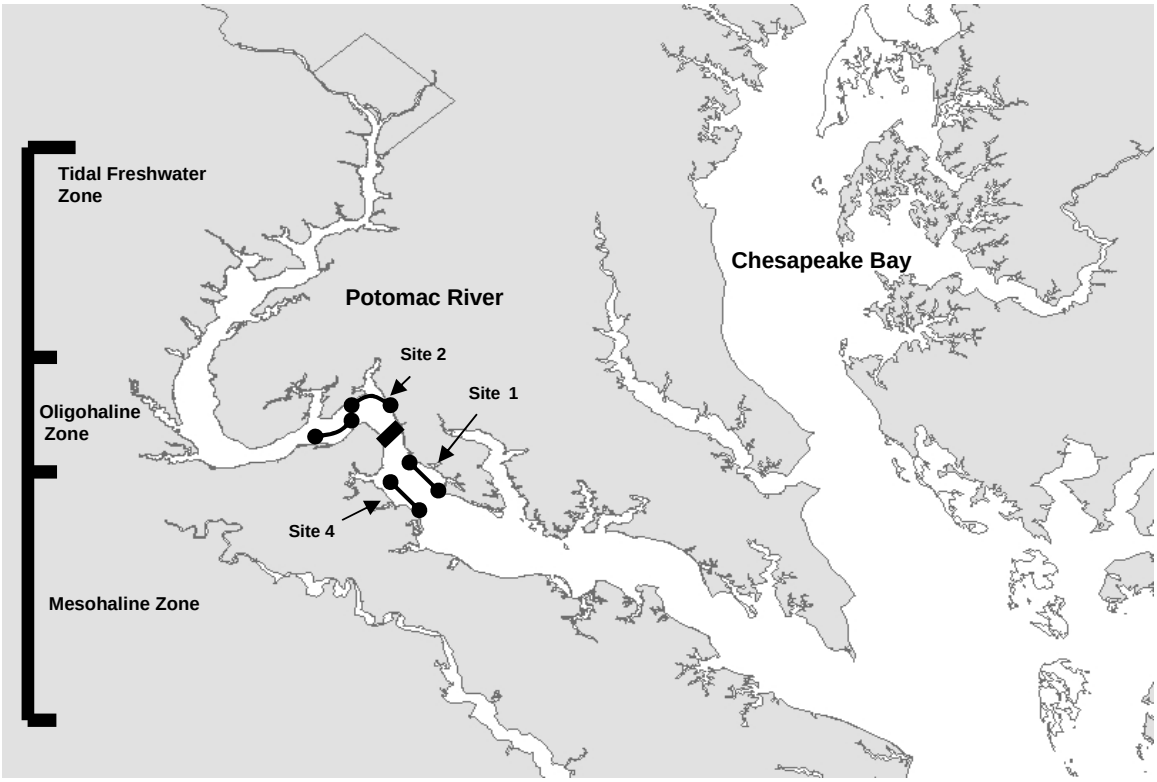

Figure 2.1. The Potomac River tributary of Chesapeake Bay, USA. Field sites are indicated by the black line between solid circles. The thick black bar indicates the Rt. 301 Bridge between Maryland and Virginia. River divisions based on salinity are indicated on the left axis (Jaworski et al., 2007).

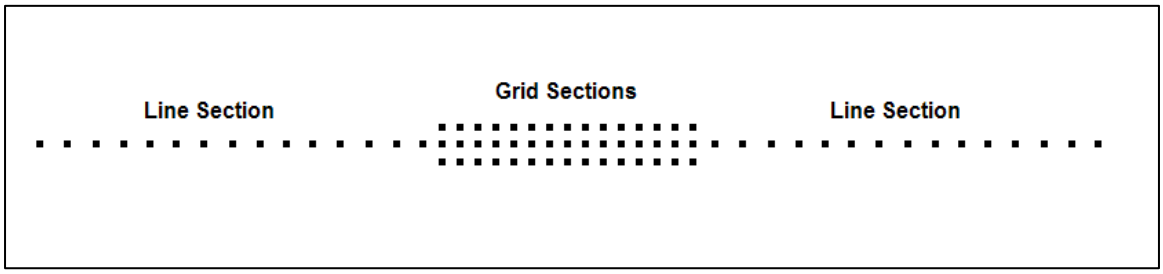

Figure 2.2. Eel pot configuration for day one of field work. Sites 1, 2, and 3 were sampled using a grid-and-line layout. The grid consisted of three sections, each section made up of one line of 15 pots, each pot and line spaced 50 m apart. A line of pots extending upstream and downstream of the grid consisted of 15 pots each. Line pots were spaced 200 m apart and the first line section pot was placed 50 m from the last grid pot. The total pot set was 6.4 km long for each site.

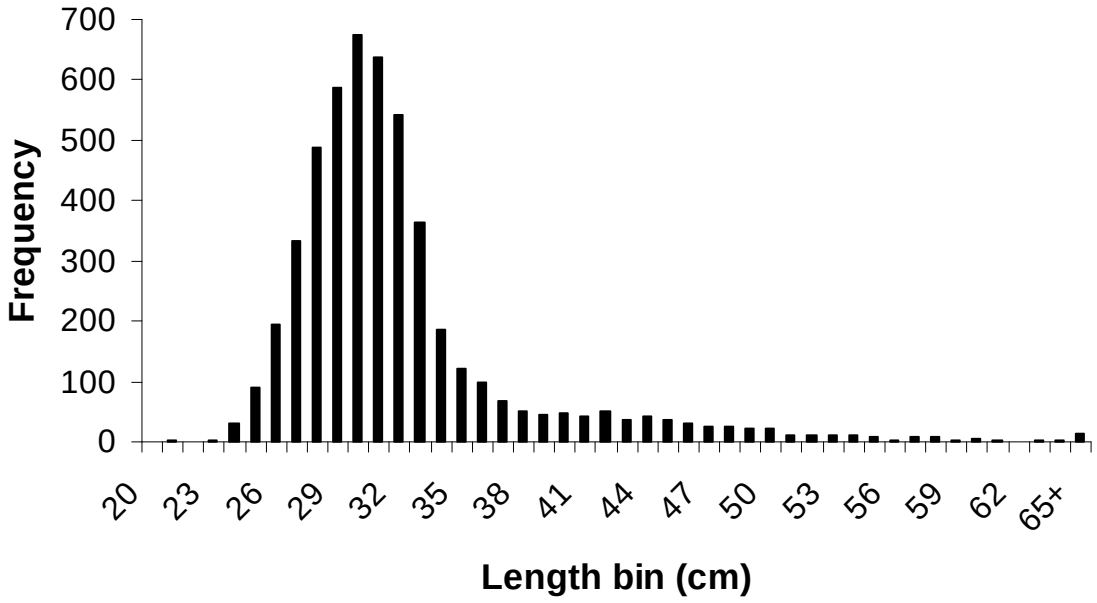

Figure 2.3. Length frequency distribution for branded American eels in the Potomac River. All sites and seasons were combined. The captured American eel length range was 20.1 - 97.0 cm TL; mean length was 36.1 cm.

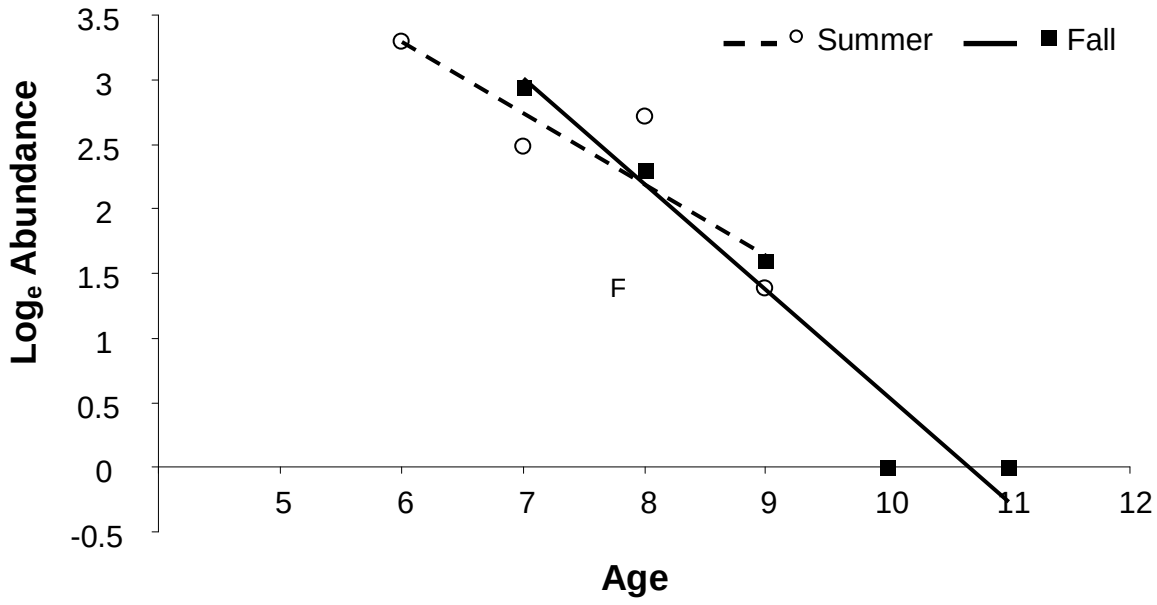

Figure 2.4. Catch curves for the summer (open circle, dashed line) and fall (solid square, solid line) samples (Chapter 1) from the Potomac River. Ages 6-9 and 7-11 were used in summer and fall catch curves, respectively. Instantaneous mortality estimates of 0.55 (summer) and 0.82 (fall) were calculated, with a total annual mortality rate estimated as 64% per year for the oligohaline zone samples of the Potomac River. Trendline equation for summer is Log_e N = -0.5505*age + 6.5979, R^2 = 0.7921; for fall, Log_e N = -0.8191*age + 8.7436, R^2 = 0.9372.

Chapter 3: Age-structured production model for American eels in the Potomac River, Maryland

Abstract

Since 1964, an average of 16% of the U.S. commercial harvest of American eel has come from the Potomac River, yet little is known about the population dynamics or abundance in this system. To examine the effect of fishing on American eel abundance in the Potomac River, I developed an age-structured production (ASP) model for 1980-2008 and a biological reference point (BRP) model. The model included natural mortality, fishing mortality, and gender- and age-specific estimates of maturation mortality and selectivity. Preliminary results from the ASP model indicated that American eel abundance had decreased substantially, while annual fishing mortality rates ranged 4.1-41.9% and increased over time. Average estimated recruitment and biomass for 2004-2008 were 13.0 and 11.7% of 1980 levels, respectively. The average estimated abundance for 2004-2008 was 13.3% of the 1980 abundance. In all years except one, the F_{50}% BRP was not met. Sensitivity analysis revealed that the model was moderately sensitive to changes in natural mortality, standard deviation for fishery and recruitment CPUE indices, and initial fishing mortality, but several sensitivity analyses remain to be conducted. Synchronous declining recruitment of American eels in the Potomac River, St. Lawrence River, Canada, and in European eels in Den Oever, Netherlands suggested that large-scale oceanic processes have affected Anguillid eel recruitment in the North Atlantic.

Introduction

American eel *Anguilla rostrata* is a common species on the east coast of North America that inhabits coastal and inland brackish and freshwater systems from Greenland to Venezuela (Tesch, 1977; Helfman et al., 1987). Ecologically, American eels are opportunistic carnivores, and historically comprised as much as 25% of total fish biomass in portions of their east coast range (Atlantic States Marine Fishery Commission [ASMFC] 2004). As a semelparous and panmictic species, local recruitment dynamics may not be closely tied to local abundance (Tesch, 1977; Wirth and Bernatchez, 2003). Adult American eels throughout their range spawn in the Sargasso Sea, and larvae are distributed along their range by oceanic currents (Kleckner and McCleave, 1980). 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).

American eel abundance and recruitment have declined in the past 25 years (ASMFC, 2000). In 2004 a petition for the listing of American eel as an endangered species was filed with the U.S. Fish and Wildlife Service (USFWS). The USFWS found that the listing was not warranted, citing the stability of glass eel recruitment over the past 15 years, the resilience of the widely distributed and panmictic species, and the ability of American eels to complete their life cycle in marine and estuarine waters as justification (UWFWS, 2007). In Canada, American eels are considered a "species at risk" and in Ontario, Canada they are being considered for an "endangered" listing by The Committee on the Status of Endangered Wildlife in Canada (MacGregor et al., 2008). Speculation about the cause of decline centers on

diminished recruitment, disease and parasitism, overharvest, and habitat degradation (Haro et al., 2000).

Many of the potential causes for declining American eel abundance are interrelated. Declining American eel recruitment may be tied to changing oceanic conditions encountered on spawning grounds in the Sargasso Sea, as suspected in the European eel *Anguilla anguilla* (ICES, 2001; Freidland et al., 2007; Bonhommeau et al., 2008). Declining recruitment may also be caused by reduced spawner escapement, which may be caused by over-harvest, mortality from hydro-electric dams, and increased mortality due to disease and parasitism on the yellow-phase juvenile or maturing silver eel stages (ICES, 2001). Reduced habitat availability and quality may be due to the number of dams impeding migration into upstream, freshwater habitats throughout the American eel range, and pollution (Busch et al., 1998; Castonguay et al., 1994). Increased urbanization in U.S. watersheds may also negatively affect habitat quality and American eel condition (Roth et al., 1996; Foley et al., 2005; Machut et al., 2007).

American eel is an economically important species in the Potomac River; harvest in the Potomac River comprises 32% of the Chesapeake Bay harvest and 16% of the total U.S. harvest on average during the past 57 years (Potomac River Fisheries Commission [PRFC], unpublished data). The majority of American eel are caught in baited, cylindrical, two-chambered pots (>98% of the catch by weight) set on trot lines in the oligohaline portion of the Potomac River (PRFC, unpublished data). The American eel fishery is primarily commercial, with most eels sold for export to Europe and Asia (Foster, 1981). Smaller commercially caught eels are frequently

sold for bait in the catfish, cobia, and striped bass recreational fisheries (J. Trossbach, pers. comm.). Few American eels are captured and retained by recreational fishermen, and recreational harvest is considered negligible (ASMFC, 2004). Since peak harvest in the 1980s, total harvests throughout their U.S. range have declined about 75% (NOAA, unpublished data). The Potomac River is near the center of the range of American eels and is highly productive compared to other U.S. estuaries (Chapter 2).

Despite the large harvest of American eels taken annually from the Chesapeake Bay region, little is known about the population dynamics of American eels in the region. Data on American eel natural mortality, abundance, age-at-maturity, and gear selectivity are fragmented and not available for all areas of their range. Despite the panmictic population, there are often regional differences in growth rate, gender ratios, and maturation age (Helfman et al., 1984; Oliveira, 1999).

My goal was to develop a model to estimate the effect of fishing on the Potomac River American eel sub-stock and develop biological reference points to aid in management of the fishery. To address these objectives, I constructed an age-structured production (ASP) model for the Potomac River using data from the PRFC, my field and lab data, and Virginia Institute of Marine Science (VIMS) trawl survey data. Because of concerns about the potential for American eels to experience depensation at low population size, the management of American eel based on spawner escapement has been suggested (ICES, 2001). I developed a spawner per recruit model to estimate the threshold $F_{50\%}$ where 50% of virgin spawning potential is protected. I then compared the model-estimated fishing mortality rates to the rates

that would be protective of 50% of the unfished spawning potential of female American eels.

Methods

Stock Assessment Model

A sex-specific ASP model was developed to obtain abundance and mortality rate estimates for American eels in the Potomac River. The ASP model followed cohorts of fish through time and consisted of two parts: a process submodel and an observation submodel. The process submodel described the population processes, while the observation submodel described the observations of the population. This state-space approach allowed for assumed errors in process and the observations. The model's parameters were estimated using maximum likelihood.

The American eel ASP model included years 1980-2008 and ages 4-11+; the "plus" group served as an aggregate category for ages 11 and older. The model years were chosen to cover the range of available catch and recruitment data and modeled ages reflected the ages of American eels observed in the Potomac River (Chapter 1). Male and female American eels had different demographic rate parameters (see Chapter 1) and were tracked separately in the model. Four stages of sexual development were identified in American eels (Buellens et al., 1997); female, male, intersexual and undifferentiated. For gender-specific parameters, male and intersexual American eels are termed 'male' and female and undifferentiated are termed 'female'. All symbols used in equations are described in Table 1.

Process Submodel

The process model described how recruitment and abundance of American eels changes over time. Recruitment (abundance at age four) was estimated for each year and sex by estimating median recruitment and year-specific deviations.

(3.1) $$R_{y,g} = \overline{R}e^{\delta_y} s_g$$

The model was parameterized in this way to reduce correlations among parameters. I assumed a 1:1 gender ratio for the first age in the model. This ratio was supported by the bay-wide proportion of 51.4% female for age-4 eels (Chapter 1 data).

Abundance-at-age (*N*) was modeled with the assumption that catch-at-age is known without error and that all of the catch happens in a pulse halfway through the year. For the first year in the model, abundance was estimated using an assumed equilibrium instantaneous fishing mortality of 0.105 prior to 1980,

(3.2) $$N_{y=1,a+1,g} = N_{y=1,a,g} e^{-(F_{init}S_{a,g}+M)}(1-m_{a,g}).$$

The age-11+ group for the first year of the model was estimated as the solution to the infinite series for abundance for ages older than 11,

(3.3) $$N_{y=1,a=11+,g} = \frac{N_{y=1,a=11,g} e^{-(F_{init}S_{a=11,g}+M)}\left(1-m_{a=11,g}\right)}{1-e^{-(F_{init}S_{a=11,g}+M)}\left(1-m_{a=11,g}\right)}.$$

For subsequent model years abundance was estimated as

(3.4) $$N_{1,a+1,g} = \left(N_{1,a,g} e^{\frac{-M}{2}} - C_{y,a,g}\right) e^{\frac{-M}{2}}\left(1-m_{a-1,g}\right).$$

The plus-group was modeled as the number of age-10 eels that survive plus survival of those in the plus group from the previous year,

$$N_{y+1,a,g} = \left(N_{y,a,g} e^{\frac{-M}{2}} - C_{y,a,g} \right) e^{\frac{-M}{2}} \left(1 - m_{a,g}\right) + \left(N_{y,a-1,g} e^{\frac{-M}{2}} - C_{y,a-1,g} \right) e^{\frac{-M}{2}} \left(1 - m_{a-1,g}\right). \quad (3.5)$$

This is a common approach used in this type of model (e.g., de Bruyn et al., 2008), and the instantaneous catch assumption is called Pope's approximation (MacCall, 1986). This assumption was reasonable because the fishery primarily occurs between April and October, while natural mortality is thought to occur throughout the year. In cases of moderate and low fishing mortality, Pope's approximation is a reasonably accurate, simplifying approximation (MacCall, 1986; Quinn and Deriso, 1999). Instantaneous natural mortality in the model was assumed to be 0.15, based on estimates from the Hudson River. Using the original Morrison and Secor (2003) Hudson River data, I used the St. Lawrence River and Chesapeake Bay recruitment indices to adjust the Hudson River abundance at age data and recalculated the catch curves because of the observed decline in recruitment. The adjusted mean annual loss rate estimate was 0.44 yr^{-1}. The Hudson River natural mortality estimates did not separate mortality due to maturation. Because maturation mortality was considered separately from natural mortality in the ASP model, the natural mortality estimate I chose was less than estimates from the Hudson River. Natural mortality was assumed to be constant across ages and years.

The last term in the abundance-at-age equation represents the loss of individuals from the population due to maturation because American eels are semelparous. To obtain maturation-at-age estimates for male and female American eels, I used maximum likelihood estimation to fit observed age-at-maturation from two sources of data on American eel maturation in the Chesapeake Bay: my dissection of the ~400 Chesapeake Bay eels collected in fall 2007 (see Chapter 1),

and estimates of mean ages-at-migration for male and female American eels from Goodwin (1999; see Appendix 1 for details). Due to the lack of male eels older than age eight in my Chesapeake Bay samples (Chapter 1), I assumed a maturation-at-age of 0.99 for male American eel ages 8-11.

American eel biomass was calculated as the mass of eels at the middle of the year, which accounts for effects of natural mortality before the fishing,

$$B_{y,g} = \sum_{a} N_{y,a,g} \overline{w}_{a,g} e^{\frac{-M}{2}} . \quad (3.6)$$

Mean mass-at-age for female and male American eels was calculated using the mass and age data collected from all sampled Chesapeake Bay sub-estuaries (see Chapter 1; Figure 3.1a). Mass-at-age data for male and intersexual American eels was available for ages 3-8, and I extrapolated mean mass-at-age for male and intersexual eels aged 9-11 using the regression equation from ages 3-8.

Spawner biomass (*SB*) is the biomass of maturing female American eels in a given year that survived natural mortality and were not harvested,

$$SB_y = \sum_{Ages} \left(N_{y,a} e^{-\frac{M}{2}} - C_{y,a} \right) e^{-\frac{M}{2}} w_a m_a . \quad (3.7)$$

Equation variables were for female eels only but otherwise were the same as described for ASP model. The model assumed that mean mass-at-age did not change over time.

Because catch-at-age data were not available, catch-at-age (in numbers) for each gender was calculated from total catch (in mass), selectivity, and mass-at-age,

$$C_{y,a,g} = \frac{\dfrac{X_y S_{a,g} \overline{w_{a,g}} N_{y,a,g} e^{\frac{-M}{2}}}{\sum_g \left(S_{a,g} \overline{w_{a,g}} N_{y,a,g} e^{\frac{-M}{2}} \right)}}{\overline{w_{a,g}}}. \tag{3.8}$$

Selectivity-at-age was estimated using the fishery independent data in Owens and Geer (2003). Because size-at-age is different for males and females, selectivity-at-age was modeled separately. For female selectivity-at-age I calculated the proportion of American eels greater than 320 mm for each age in the model, assuming a normal distribution and standard deviations from Owens and Geer (2003) for American eels in Virginia waters of Chesapeake Bay (Figure 3.1b). I chose 320 mm as the fully selected size based on the frequency distribution of lengths for Potomac River eels captured during my field work (Chapter 2). Peak frequency of capture occurred at 320 mm in field samples. Male American eels were smaller at age on average than females (Chapter 1). The length-frequency distributions for male American eels were very similar for ages 4-8. Thus, I assumed a constant selectivity pattern for male American eels. Based on the laboratory dissection data of Potomac River eels (Chapter 1), mean total length of male American eels was 73.3% smaller than age-4 females. Assuming a linear relationship, male selectivity-at-age should be about 73.3% of female selectivity-at-age 4, 0.423 (Figure 3.1b).

The fishing mortality rate was calculated as the estimated catch-at-age divided by the exploitable biomass,

$$F_{y,a,g} = \frac{C_{y,a,g}}{N_{y,a,g} e^{\frac{-M}{2}}}. \tag{3.10}$$

The exploitation rate of American eels was calculated as the total observed catch divided by total biomass,

$$U_y = \frac{X_y}{B_y}. \tag{3.11}$$

Observation Submodel

The observation model makes predictions that can be compared to the data to estimate parameters. A recruitment index was estimated for each model year to compare with the VIMS trawl survey data,

$$\hat{I}_y = R_y q_1. \tag{3.12}$$

Additionally, the model-predicted fishery CPUE was proportional to exploitable biomass,

$$\hat{C}PUE_y = B_y q_{2,y}. \tag{3.13}$$

Fishery catchability (q_2) was estimated for each year using an effort dependent catchability model (Wilberg et al., *in submission*),

$$q_{2,y} = \alpha E_y^{\beta}. \tag{3.14}$$

Effort dependent catchability occurs when additional units of effort result in lower catchability than previous units of effort. This may occur because of gear interaction, localized stock depletion, or when additional effort directed at the fishery is in sub-optimal locations because the optimal locations are already occupied. I chose to use time-varying catchability instead of constant catchability because there were fewer trends in the residuals, and I was not satisfied with the assumption of constant catchability over time given the decrease in the number licensed eel fishermen over

the model years. Other fisheries have been found to have effort dependent catchability as well; in the Australian prawn fishery knowledge of prawn behavior and technological advances led to increased catchability over time (Ellis and Wang, 2006).

Model Fitting

The model was built in AD Model Builder and parameters were estimated using maximum likelihood. The model was fitted by finding the set of parameters that minimized the negative log likelihood function (-*LL*). The negative log likelihood function contained components for the recruitment index, the fishery CPUE index, and female abundance-at-age data in 2007.

The first likelihood component (L_1) used the observed recruitment index to model predicted recruitment for each year,

$$L_1 = n_1 \log_e \sigma_1 + \frac{\sum \left(\log_e(I_y) - \log_e(\hat{I}_y)\right)^2}{2\sigma_1^2}, \tag{3.15}$$

where,

$$\log_e q_1 = \frac{1}{n_1} \sum_y \left(\log_e I_y - \log_e B_y\right). \tag{3.16}$$

I assumed that the observed abundance index was log-normally distributed and that the standard deviation (σ_1) for recruitment (on the log scale) was 0.4. The generalized linear model estimates for the standard deviation of the log-scale recruitment index was about 0.2, but I used 0.4 because the recruitment index was not specific to the Potomac River. Recruitment catchability was assumed to be constant for the model years. The fishery-independent recruitment index time series was

selected to minimize effects due to changing gear and was thought to have reasonably constant catchability. I used analytic solution of the maximum likelihood estimate of catchability for the recruitment index.

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

$$L_2 = n_2 \log_e \sigma_2 + \frac{\sum \left(\log_e(CPUE_y) - \log_e(\hat{C}PUE_y)\right)^2}{2\sigma_2^2} \quad . \tag{3.17}$$

I assumed that this abundance index was log-normally distributed with a log-scale standard deviation (σ_2) of 0.3.

The third likelihood component (L_3) compared the observed and predicted proportional abundance-at-age for female American eels ages 7-11 using a multinomial likelihood function,

$$L_3 = -n_e * \sum_{a=7-11} p_{observed} * \log_e \hat{p} \, . \tag{3.18}$$

The overall negative log likelihood function combined components for the recruitment and CPUE indices,

$$-LL = L_1 + L_2 + L_3 \, . \tag{3.19}$$

Data

The ASP model required catch data, a recruitment index, and an index of abundance for the remaining ages. Catch (kg) and catch per unit effort (CPUE, in kg/pot) from the Potomac River commercial fishery were available from the PRFC during 1980-2008 and 1988-2008, respectively. The recruitment index was developed from log-transformed catch data ($\log_e$(catch+0.01)) from York, James, and

Rappahannock Rivers in months April through September and years 1980-2008 from the VIMS trawl survey. American eels 20-40 cm were used in the index, to best correspond to the size range of age-4 eels from the Chesapeake Bay sampling data (Chapter 1). The recruitment index was standardized using a generalized linear model that included year, river, depth, and a river*depth interaction. No comparable long-term survey exists for the Potomac River. Using the VIMS trawl data to develop the recruitment index was a reasonable choice based on the proximity to the Potomac River and because the size range of eels caught in the survey overlapped the size of age-4 eels in the ASP model. The index of recruitment allowed the ASP model to avoid the assumption that recruitment was dependent on the local spawning stock.

Early model versions predicted a large proportion of the population in the 11+ age group, which conflicted with aging information from the Potomac River (Chapter 1). Abundance-at-age data for females aged 7-11 from the Potomac River were obtained from Chapter 1 dissection data. The inclusion of Potomac River abundance-at-age data led to model outputs of proportions-at-age that more closely resembled observed values.

Sensitivity Analysis

Because of the uncertainty around the assumed values for some of the model parameters, I performed sensitivity analyses on one variable at a time to examine effects of different natural mortality estimates, different values of standard deviation for recruitment and fishery CPUE indices on model outputs, and for different values of initial fishing mortality. I increased and decreased each variable by one-third or

one-half and compared estimates of total abundance and male and female mean fishing mortality for 2008 to those from the base model.

Reference Points

Biological reference points (BRP) are fishing level targets or limits that establish acceptable levels of catch or biomass that will allow a species to self-regenerate. My goal was to assess the fishing mortality of yellow-phase American eels in the Potomac River with respect to a conservative BRP, $F_{50\%}$, where 50% of the virgin spawning potential was protected (Punt et al., 2008).

A spawning potential ratio (SPR) model for semelparous species was developed. Parameters of the SPR model were the same as those for females in the ASP model. SPR was calculated as the spawning stock biomass per recruit of American eels in a fished population (SSB/R_F) divided by the spawning stock biomass per recruit in an unfished population (SSB/R_U),

$$SPR = \frac{SSB/R_F}{SSB/R_U}. \tag{3.20}$$

The SSB/R_F of American eels in a fished population was

$$SSB/R = \sum_{ages}^{\infty} N_a e^{-\sum_{i=4}^{a-1} FS_i + M} w_a \prod_{i=4}^{a-1} (1 - m_i). \tag{3.21}$$

The SSB/R_U for an unfished population was the same as equation 3.21 with fishing mortality equal to zero. For computational ease the infinite series solution was used in calculating the SSB/R for the age-11+ group.

Results

Fishery Trends

Commercial harvest of American eels in the Potomac River declined since peaking in the late 1970s and early 1980s (Figure 3.2). Eel pots were the primary gear used for harvest; greater than 98% of reported catches during 1976-2008 were from eel pots. There was a decline in the number of watermen who held eel pot licenses and in the number of license holders who reported catches (Figure 3.3). Between 1988 and 2008, the number of active (i.e., those that reported catch of American eels), license-holding fishermen declined from 50 to 15. There was a corresponding decline in the amount of effort reported, from more than 142,000 eel pots in 1988 to less than 49,000 eel pots in 2008. The mean observed fishery CPUE increased slightly between 1988 and 2008 and was at the highest level in the Potomac River in 2007 (Figure 3.4a). The recruitment CPUE index decreased substantially during 1980-2008 (Figure 3.4b).

Preliminary Model Results

The ASP model fit the observed fishery CPUE and recruitment indices reasonably well, but some residual patterns were present (Figure 3.5). Observed and predicted recruitment CPUE decreased over model years. In 17 of the most recent 19 years, model predictions for recruitment CPUE were greater than observed recruitment CPUE. In contrast to the recruitment CPUE index, fishery CPUE increased slightly over model years. Estimated fishery CPUE fit reasonably well to observed values. Standardized residuals for fishery CPUE showed little trend and 95% of observations were within one standard deviations of the mean (Figure 3.5a).

Standardized residuals for recruitment indicated a trend of reduced deviation through time, and four observations were greater than one standard deviation from the observed value (Figure 3.5b).

Preliminary estimates indicated that abundance declined substantially during 1980-2008. Estimated abundance across age classes of American eels was relatively high from 1980 to 1984 then began a steady decline in 1985. The average estimated abundance for 2004-2008 was 2.4 million eels, which was only 13.3% of the 1980 abundance (Table 3.2). There were differences between male and female abundance over time; females were more abundant from 1980 to 1998, but during 1999-2008 male and female abundances were nearly equal. These differences were driven by the different selectivity and maturation patterns for male and female eels. Estimated biomass decreased over time in a similar pattern as abundance (Figure 3.6). The 2004-2008 average estimated biomass was 11.7% of the 1980 biomass. Estimated recruitment showed a strong decreasing pattern; average recruitment for 2004-2008 was only 13.0% of the 1980 estimate in 2008 (Figure 3.7). The estimated sex ratio of American eels in the model was skewed heavily towards female eels for ages 9-11+ because of the assumed maturation of most males at age eight.

Estimated fishing mortality and exploitation rates across ages increased over time (Figures 3.8 and 3.9). Estimates of instantaneous fishing morality rates ranged 0.04-0.42 across years and ages. The estimated instantaneous fishing mortality rate for both genders during 1980-2008 averaged about 0.16, similar to natural mortality. Female American eels had consistently greater fishing mortality rates (range 0.06-0.42) than males (range 0.04-0.18; Figure 3.8). Estimated fishery catchability was

fairly constant from 1988 to 2001, and then increased during 2002-2007 as effort decreased (Figure 3.10).

Reference Points

Estimated spawner biomass followed the same decreasing pattern as abundance and biomass, but with an approximately 4-year lag (Figure 3.11). Estimated spawner biomass in 2008 was 3.9% of 1980 level. The estimated F was higher than $F_{50\%}$ in all modeled years except 1981. Between 1993 and 2008, the estimated SPR has been below 20%.

Sensitivity Analysis

The model was only moderately sensitive to estimates of natural mortality, standard deviation for fishery and recruitment CPUE indices, or initial fishing mortality (Table 3). A 33-67% increase in natural mortality caused estimated fishing mortality rates for female and male American eels in 2008 to decrease by approximately 5-10% and abundance to increase by 10-20%. A similar magnitude decrease in natural mortality caused estimated fishing mortality rates for female and male American eels in 2008 to increase by approximately 7-15% and abundance to decrease by 10-20%. Decreasing the standard deviation for the recruitment by 50% resulted in an approximately 6% increase in fishing mortality and a 6.2% decrease in 2008 total abundance. Increasing the standard deviation for the fishery CPUE index by 50% resulted in a 16.9% decrease in 2008 abundance and increased instantaneous female and male fishing mortality by about 30% each. Changing the initial fishing mortality estimate had little effect on estimated fishing mortality or abundance for 2008.

Discussion

Both the American eel sub-stock and the American eel fishery in the Potomac River have undergone changes in the past 27 years. Based on the preliminary model estimates, American eel biomass, abundance, and recruitment declined substantially since the early 1980s, yet fishery CPUE and estimated catchability increased in recent years. The sub-stock dynamics of Potomac River American eels were affected by processes outside the Potomac River, largely evidenced by the decline in recruitment, as well as locally high fishing mortality in recent years.

The decline in recruitment was of a similar magnitude and on the same time scale as the decline in abundance seen in American eels in the St. Lawrence River in Canada (Casselman et al., 1997; Mathers et al., 1998). Since the 1970s, the number of American eels ascending eel ladders at the Moses-Saunders Hydroelectric Dam at Cornwall, Ontario has declined by about 99%. Both the lower Chesapeake Bay recruitment index and the St. Lawrence abundance indices peaked in the early 1980s. Similar declines in recruitment have been observed in European eel *Anguilla anguilla* populations (Bonhommeau et al., 2008), a species that shares spawning grounds in the Sargasso Sea with American eel (McCleave, 1993).

The coincidence of the decline in three distant regions of anguillid eels points to large-scale processes as an important component of declining American eel recruitment. Recruitment is often affected by spawning stock biomass and larval survival (Myers and Barrowman, 1996). For American eels, spawning stock biomass may be too low, possibly due to overharvest (ASMFC 2000), habitat loss (Busch et

al. 1998, ASMFC 2000), changing oceanic conditions, or increasing natural mortality. If the *A. crassus* parasite affects American eels similarly to European eel *Anguilla anguilla*, mortality due to parasitism or during the spawning migration has been suggested (Kirk, 2003; Palsta et al., 2007). Larval eel survival may also be affected by oceanic conditions. Knights (2003), Friedland et al. (2007) and Bonhommeau et al. (2008) all suggested that worsening forage conditions and starvation of eel larvae may be linked to fluctuating primary productivity in the Sargasso Sea. Productivity fluctuations may have been due to increasing sea surface temperature and vertical stratification of the water column that reduced nutrient availability to surface waters where eel leptocephali occur. These studies suggest that changes in productivity and currents could result in poor food availability for larval eels, alteration of the larval migration back to continental waters, or lead to diminished larval condition that would negatively affect recruitment. Such a large-scale process is consistent with the wide-ranging decrease in recruitment observed in American eels as well as in European eels, and points to changing oceanic conditions as a contributing cause of declining abundance for European and American eels.

Few comparable models have been developed for American eels in other portions of their range, so it has been difficult to evaluate the effect of fishing mortality on abundance or recruitment outside the Potomac River. Additionally, few natural mortality estimates for American eels exist (but see Morrison and Secor, 2003). The estimates from the ASP model were similar to loss rates estimates from catch curve analysis in the Potomac River and other Chesapeake Bay sub-estuaries. Catch curve estimates of mortality for the Potomac River (Chapter 2) indicated a 64%

annual loss rate that included natural mortality, fishing mortality, and loss due to maturation. Other Chesapeake Bay sub-estuaries had annual loss rate estimates of approximately 41-59% (Chapter 1). Catch curve analysis of the Owens and Geer (2003) published data indicated a similar loss rate (~69%) in the James, York, and Rappahannock Rivers (ages 4-18; 0.01 added to adjust ages of no catch).

The discovery of the swimbladder parasite *A. crassus* in American eels did not coincide with the onset of declining abundance, suggesting that parasitism may not be a primary cause of declining abundance. *A. crassus* were first identified in American eels in the U.S. in 1995 (Fries et al., 1996) and American eel recruitment began to decline as early as 1985 in the Potomac River. While it is possible that the parasite went unnoticed for a decade, this seems unlikely. *A. crassus* was identified in European eels in 1982 (Peters and Hartmann, 1986), more than a decade before it was discovered in the U.S. and thereby alerting U.S. researchers to the possibility of its spread. Also, there has been no evidence of direct lethal effects by *A. crassus* on American eel. My previous work was not able to identify a relationship between parasitism and increased mortality or decreased eel condition in the Chesapeake Bay (Chapter 1), which was consistent with other studies (Moser et al., 2001; Machut and Limburg, 2008). There has been suggestion that swimbladder damage caused by *A. crassus* may affect the ability of silver eels to complete their spawning migration, which is thought to occur at substantial depth (Sprengel and Lüchtenberg, 1991; Kirk, 2003). Paltra et al. (2007) found that *A. crassus* infection severely impaired swimming performance of silver eels.

During the past two and a half decades, Potomac River American eel catches decreased, CPUE increased, and fishermen left the fishery. This may have left only the "best" fishermen in the fishery and it was possible that a fishery retaining only the "successful" fishermen lead to increased CPUE and catchability over time. The model-estimated catchability increase that began in 2002 corresponded with the sharp reduction in the number of fishermen who reported eel harvests and a steep decline in effort. In 2002, the number of fishermen reporting American eel harvest in the Potomac River dropped to 12 from 28 in 2001. As fishermen leave a fishery, reduced competition for productive fishing sites and reduced gear interaction may increase eel catchability (Hilborn and Walters, 1992). Changing catchability over time may have made fishery CPUE a less accurate predictor of abundance so allowing catchability to change over time in the model was necessary and allowed the model to converge given the conflicting trends in recruitment and CPUE indices.

The ASP model was moderately sensitive to assumptions regarding natural mortality and the fishery and recruitment CPUE indices. Additional sensitivity analyses regarding maturation-at-age for American eels would improve confidence in the preliminary model results. Research leading to improved estimates of natural mortality and maturation-at-age rates, and further study of upstream migration patterns of American eels would improve the model estimates. Similarly, the development of a fishery-independent catch-at-age index and a recruitment index for the Potomac River would allow for increased confidence in model estimates of abundance and fishing mortality.

Management Implications

Given the differing growth, gender ratios, and density of American eels in other regions, stock assessments should be conducted to compare production in the Potomac River to other systems where eels are harvested. Assessment and reference point models similar to those developed here could be applied in other regions. Describe necessary additional data. For the future of the American eel stock, it is imperative to assess the status of the stock relative to fishing in other regions and to reduce fishing mortality to meet target reference points. The ASP model indicated that annual fishing mortality rates below 10% would be protective of the spawning potential. My previous chapters indicated that the Chesapeake Bay was a highly productive habitat for American eels, and comparisons of the abundance in the Chesapeake region to other regions may indicate whether stock protection efforts should be targeted to regions with above-average contribution to spawning stock. For the conservation of the species, evidence of large scale influences on recruitment suggested that American eels throughout their range should be managed as a single population, supporting the conclusion reached by Wirth and Bernatchez (2003).

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Tables

Table 3.1. Parameters, data, and variables for Potomac River American eel assessment model.

Variables	*Description*
a	Age
A	Plus group for maximum age used in the model (11)
$B_{y,a}$	Exploitable biomass (kg) for year *y* and age *a*
$C_{y,a}$	Catch (number of individuals) for year *y* and age *a*
e^{δ_y}	Deviation for American eel recruitment
E_y	Fishery effort for year *y* (in 10,000 pots nights fished)
F	Fishing mortality
F_{init}	Equilibrium fishing mortality prior to 1980
g	Gender (female or male)
I_y	Recruitment index ($\log_e$ number of eels per tow) for year *y*
m_a	Proportion of eels aged *a* that will mature that year
M	Natural mortality rate
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 gender *g*
p	Proportional abundance-at-age for third likelihood component
q_1	Catchability for recruitment CPUE
$q_{2,y}$	Catchability for fishery CPUE
R_y	Estimated recruitment of American eels in year y
$\overline{R}$	Median recruitment of American eels over range of model
s	Sex ratio of age-4 American eels
$S_{a,g}$	Selectivity-at-age for eels age *a* and gender *g*
SB_y	Spawner biomass (female kg) for year *y*
$\overline{w}_{a,g}$	Mean weight-at-age for eels age *a* and gender *g*
X_y	Observed catch (kg) for year *y*
y	Year
α , β	Parameters of effort-dependent catchability
σ_1	Standard deviation for recruitment index
σ_2	Standard deviation for CPUE index

Table 3.2. Model estimates of American eel abundance-at-age (10,000s) during 1980-2008 in the Potomac River

	Age							
Year	4	5	6	7	8	9	10	11+
1980	511.7	399.0	306.2	232.4	174.6	66.5	46.2	79.0
1981	865.1	393.2	300.3	227.3	170.7	64.4	44.7	76.3
1982	561.5	676.5	302.7	228.6	171.3	64.6	44.8	76.6
1983	489.4	435.6	515.4	227.8	170.3	63.9	44.3	75.5
1984	1027.0	376.7	328.5	383.5	167.7	62.3	43.0	73.3
1985	301.7	776.9	277.9	238.5	275.4	58.9	40.4	68.6
1986	399.6	235.3	596.1	210.7	179.1	101.5	40.8	68.6
1987	327.8	307.1	177.2	442.8	154.9	64.4	68.2	66.8
1988	99.9	252.0	231.3	131.6	325.5	55.6	43.2	83.3
1989	186.6	77.7	192.4	174.5	98.3	119.8	38.2	78.8
1990	229.1	140.3	56.9	138.5	124.2	33.9	76.8	67.9
1991	150.8	173.1	103.3	41.2	99.2	42.6	21.9	86.1
1992	173.8	113.6	127.0	74.6	29.4	33.4	27.4	62.3
1993	170.0	131.2	83.6	91.9	53.4	9.8	21.6	52.3
1994	198.8	121.4	89.8	55.8	60.7	15.7	5.6	38.0
1995	238.2	129.4	73.5	52.4	32.1	13.7	7.1	17.6
1996	300.6	164.6	84.9	47.1	33.3	7.5	7.2	11.7
1997	231.5	203.9	105.3	52.9	29.2	7.1	3.7	8.7
1998	215.8	166.8	141.2	71.5	35.6	6.9	4.1	6.5
1999	145.1	151.1	111.3	91.9	46.1	8.3	3.7	5.2
2000	156.2	104.5	104.5	75.3	61.7	11.8	4.8	4.7
2001	91.1	107.0	67.7	65.8	47.0	14.5	6.0	4.5
2002	109.6	59.1	64.5	39.4	38.0	9.4	6.5	4.4
2003	146.4	75.2	38.4	40.9	24.8	8.0	4.8	5.2
2004	116.9	100.1	48.6	24.2	25.7	5.1	4.1	4.7
2005	76.3	80.3	65.2	30.8	15.3	5.4	2.6	4.2
2006	66.1	52.6	52.5	41.5	19.5	3.3	2.8	3.2
2007	72.9	46.4	35.1	34.3	26.9	4.5	1.8	3.0
2008	0.4	48.7	29.1	21.4	20.7	5.6	2.1	2.1

Table 3.3. Results of sensitivity analyses for alternate natural mortality rates (M), standard deviation estimates for the fishery (SD_F) and recruitment (SD_R) CPUE indices, and initial fishing mortality ($F_{initial}$) used in the ASP model for yellow-phase American eels in the Potomac River. The baseline model estimates for total abundance (N; 1,000,000s) in 2008, and mean instantaneous female and male fishing mortality ($\overline{F}$; percent) for 2008 are provided. The proportional change in abundance (ΔN; percent change) and mean instantaneous fishing mortality ($\Delta\overline{F}$) between the baseline and the adjusted model are displayed for comparison.

	Baseline	Adjusted	N	ΔN	$\Delta\overline{F}$ Females	$\Delta\overline{F}$ Males
Baseline			13.0		35.7	16.5
M	0.15	0.05	10.5	-19.2	15.1	15.2
		0.10	11.8	-9.2	6.7	6.7
		0.20	14.3	10.4	-5.3	-5.5
		0.25	15.6	20.3	-9.8	-9.7
SD_R	0.4	0.2	12.2	-6.2	6.2	6.1
		0.6	13.3	2.3	3.9	4.2
SD_F	0.3	0.2	15.9	22.3	-22.4	-22.4
		0.4	10.8	-16.9	30.5	30.3
$F_{initial}$	0.10	0.05	13.1	-0.8	1.1	1.2
		0.15	13.0	0.0	-0.6	-0.6

Figures

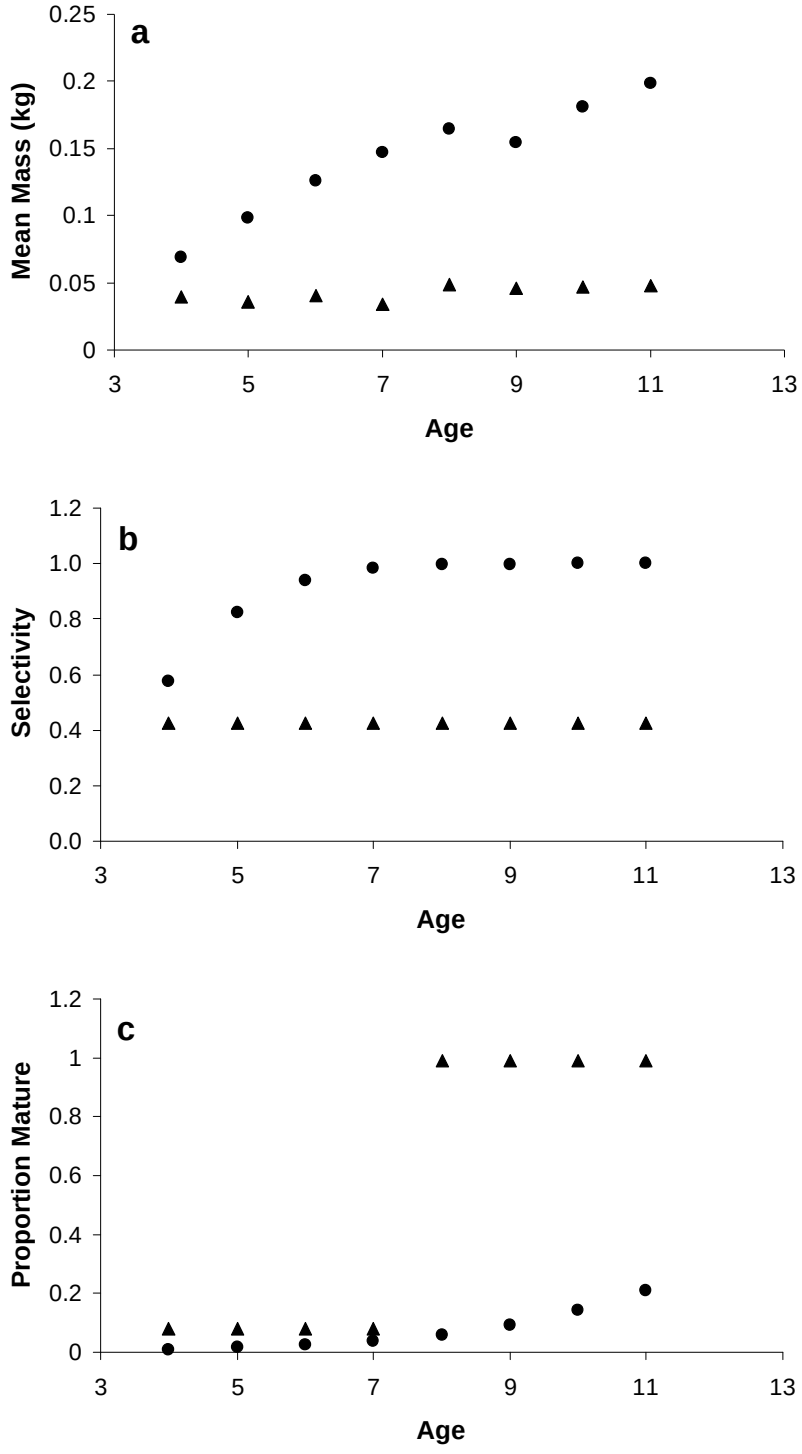

Figure 3.1. Mean mass-at-age (a), selectivity-at-age (b), and maturity-at-age (c) used in the ASP model for female (circle) and male (triangle) American eels.

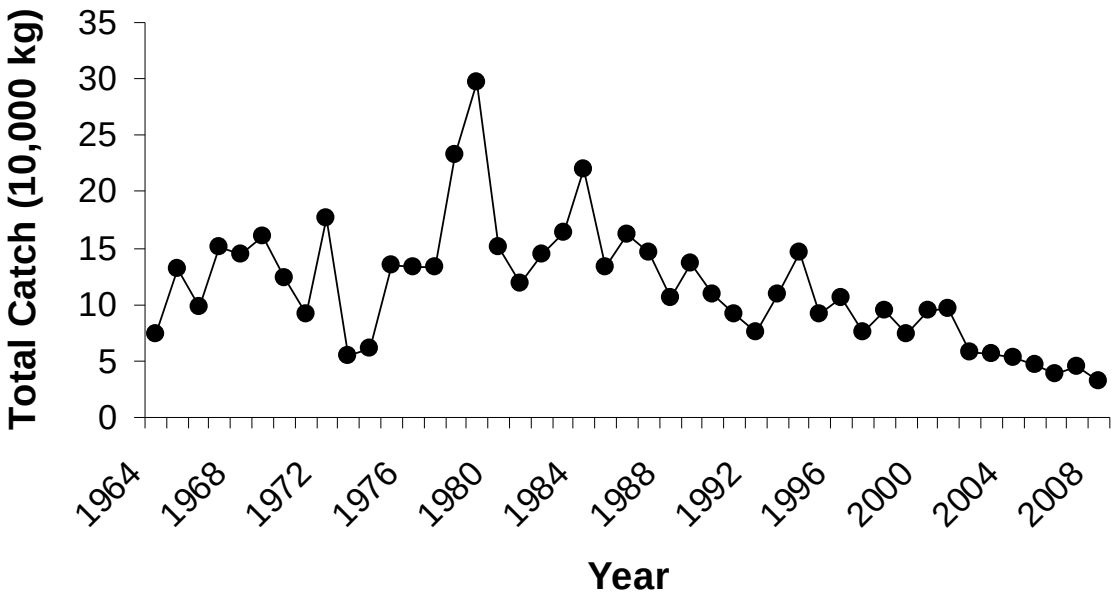

Figure 3.2. Total catch (in 10,000 kg) of American eels in the Potomac River, 1964-2008 (PRFC, unpublished data).

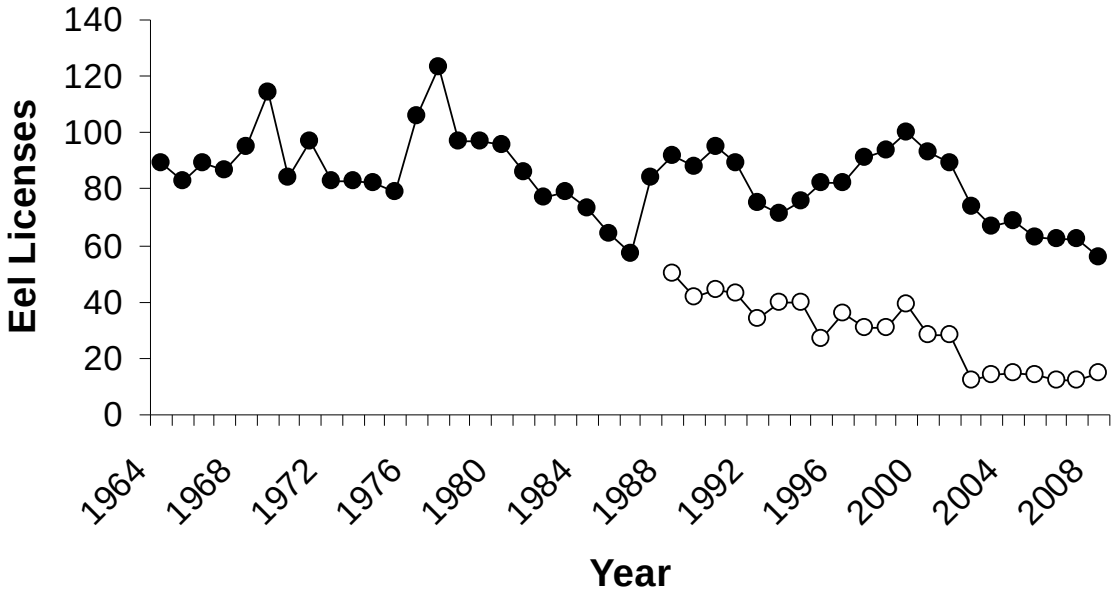

Figure 3.3. Number of licensed American eel pot fishermen in the Potomac River (dark circles, 1964-2008) and number of American eel pot licenses that reported catches (open circles, 1988-2008).

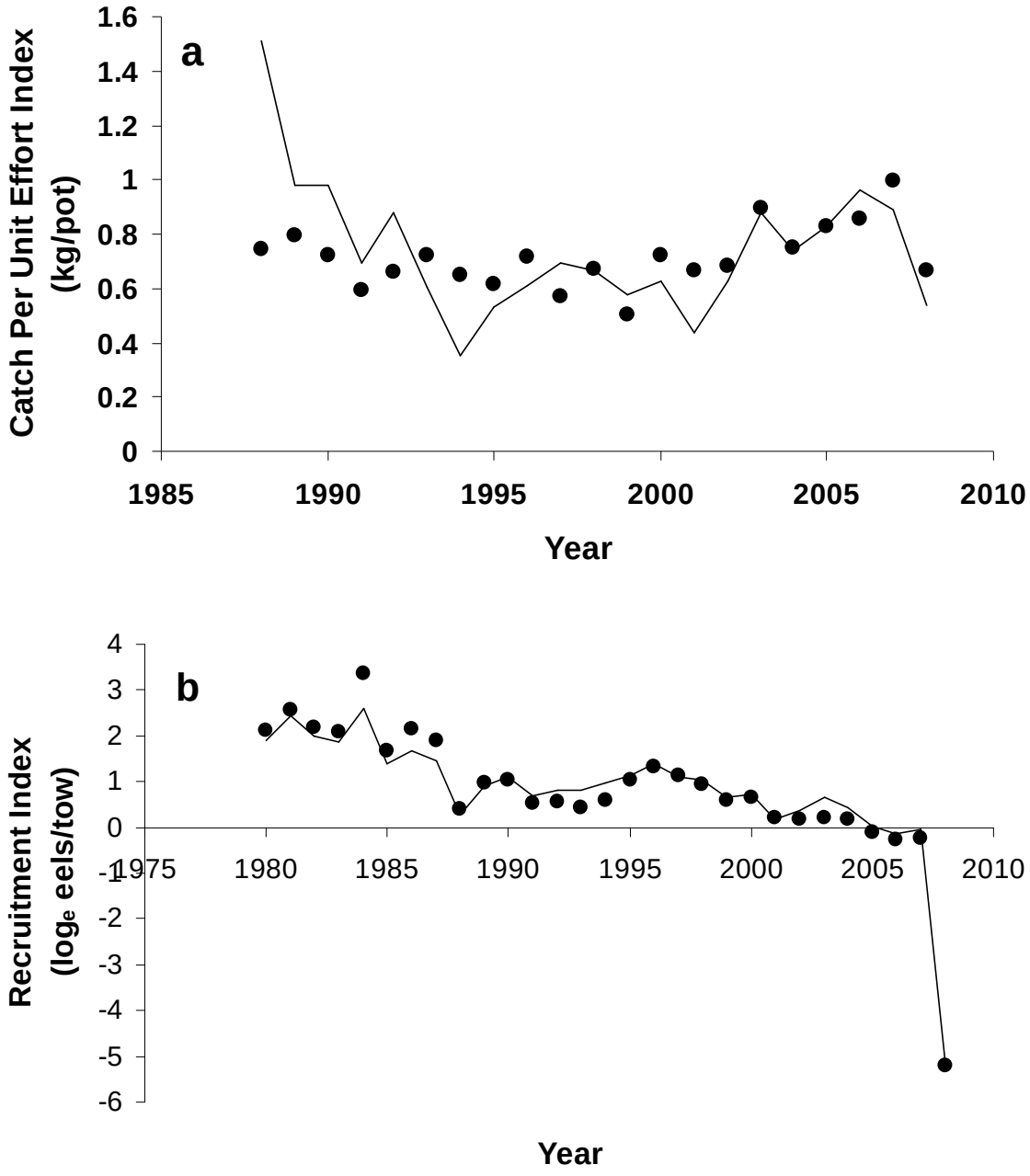

Figure 3.4. Observed and estimated CPUE for the fishery (a) and recruitment (b). Model estimates are represented by the solid lines and observed data by circles.

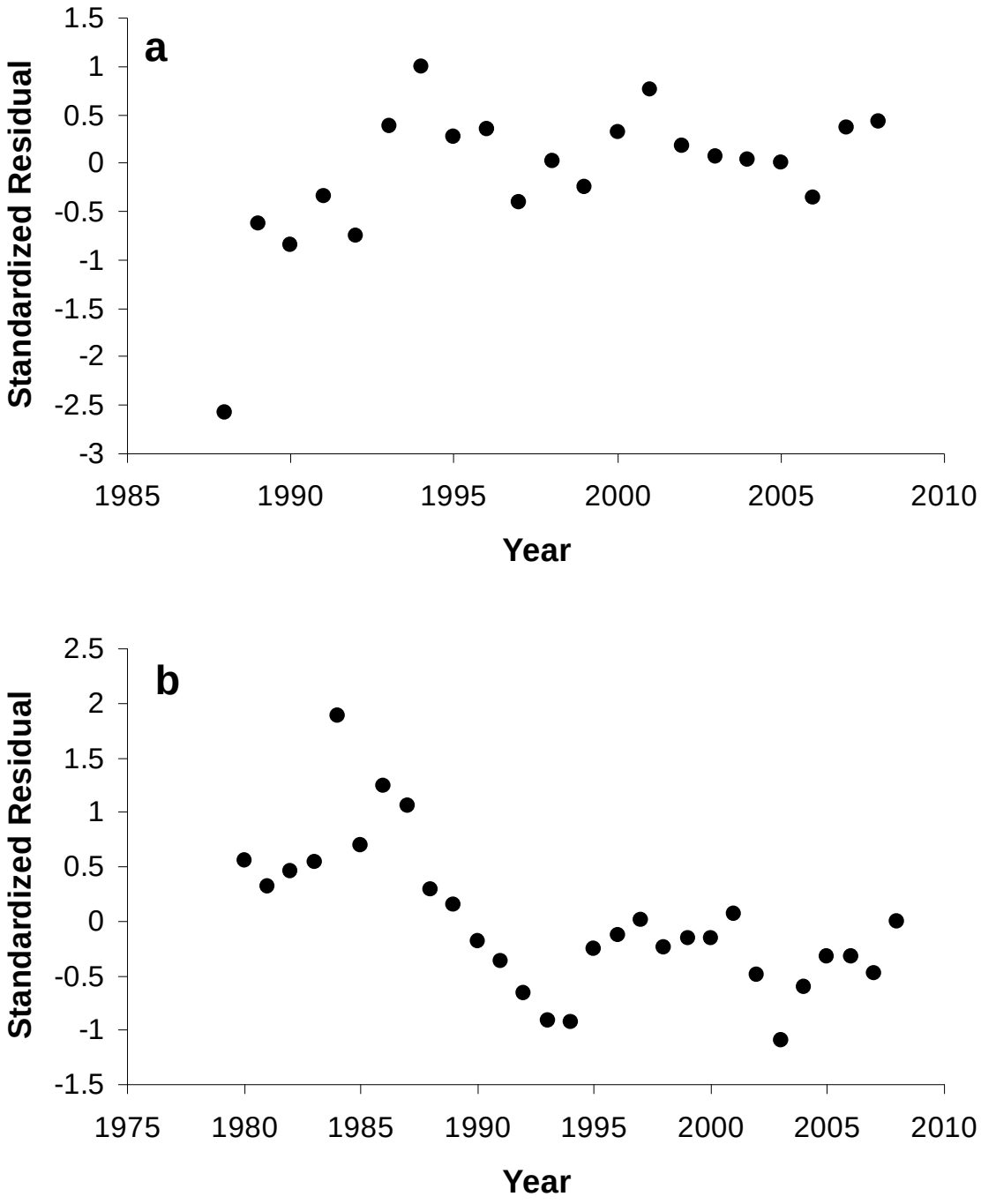

Figure 3.5. Standardized residuals for fishery (a) and recruitment (b) CPUE.

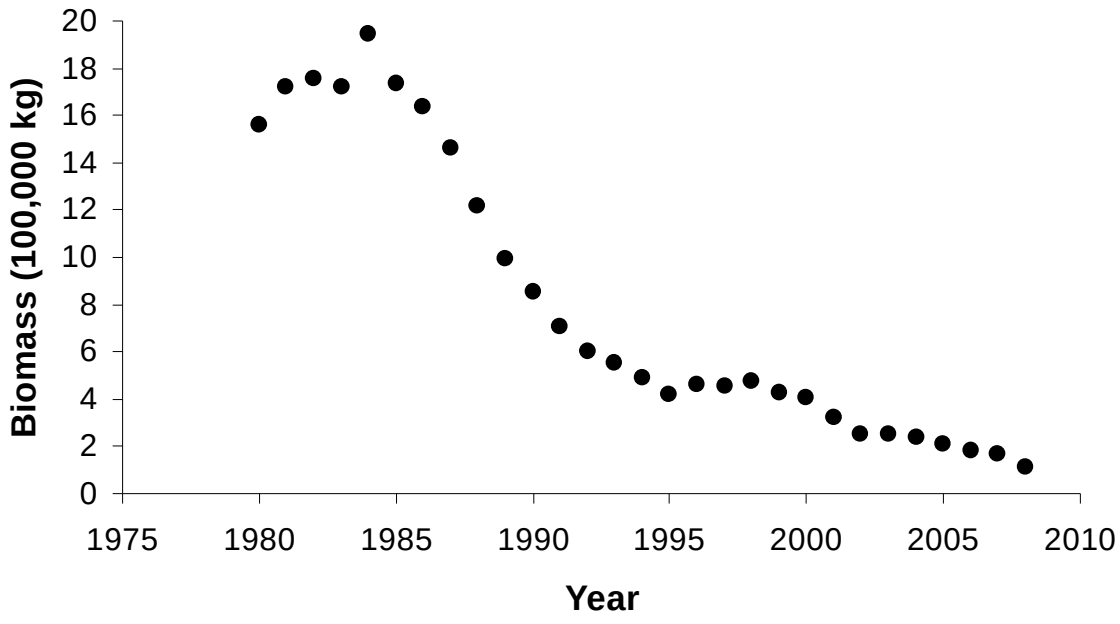

Figure 3.6. Estimated biomass (100,000 kg) of American eels in the Potomac River, 1980-2008.

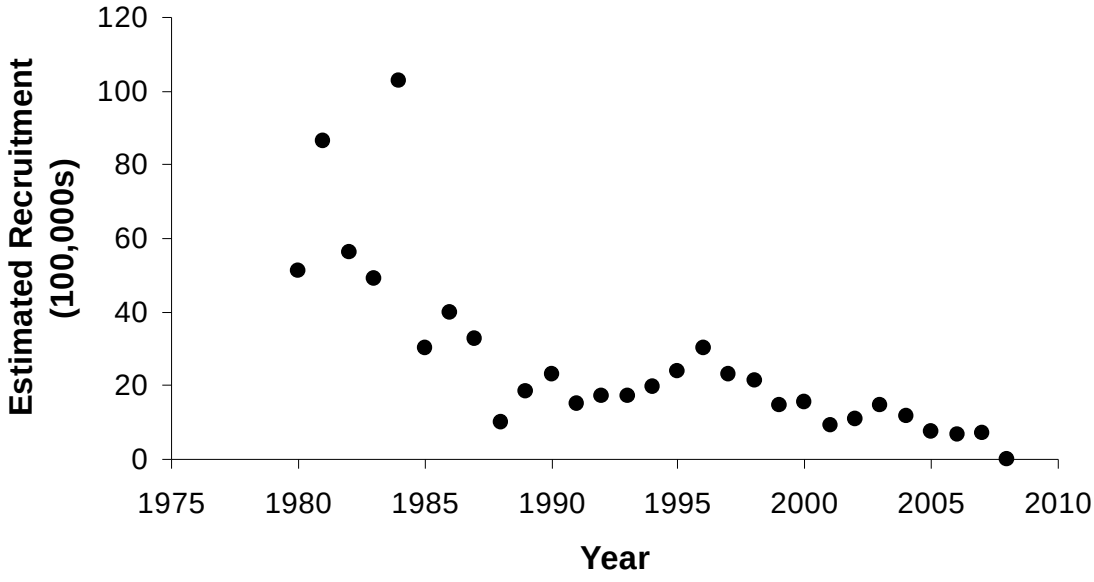

Figure 3.7. Estimated recruitment (abundance at first age in model) of American eels in the Potomac River, 1980-2008.

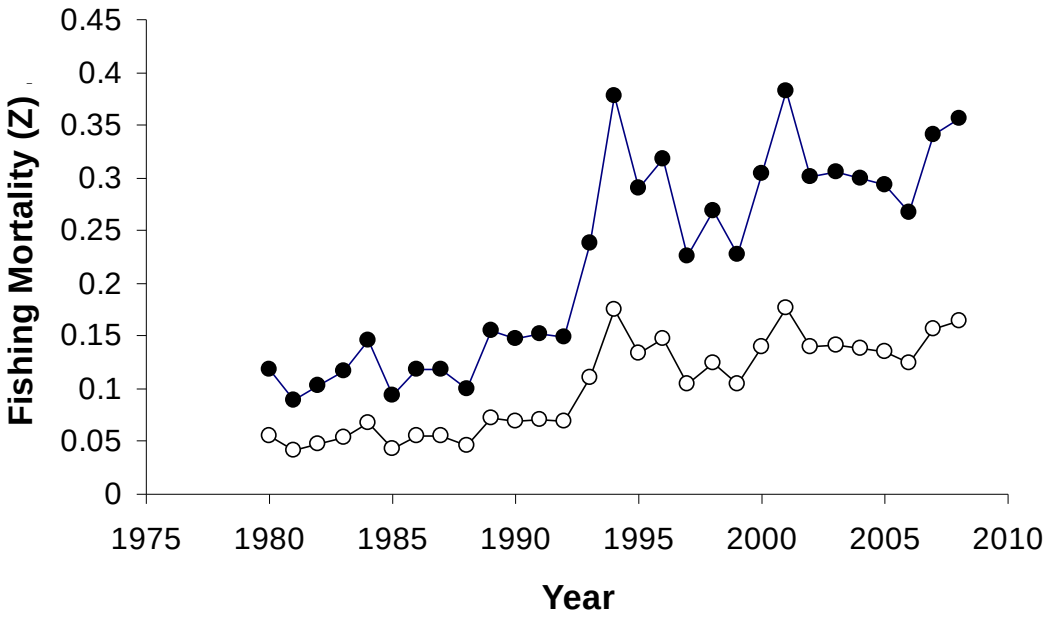

Figure 3.8. Estimated instantaneous fishing mortality rate for female (dark circles) and male (open circles) American eels in the Potomac River, 1980-2008.

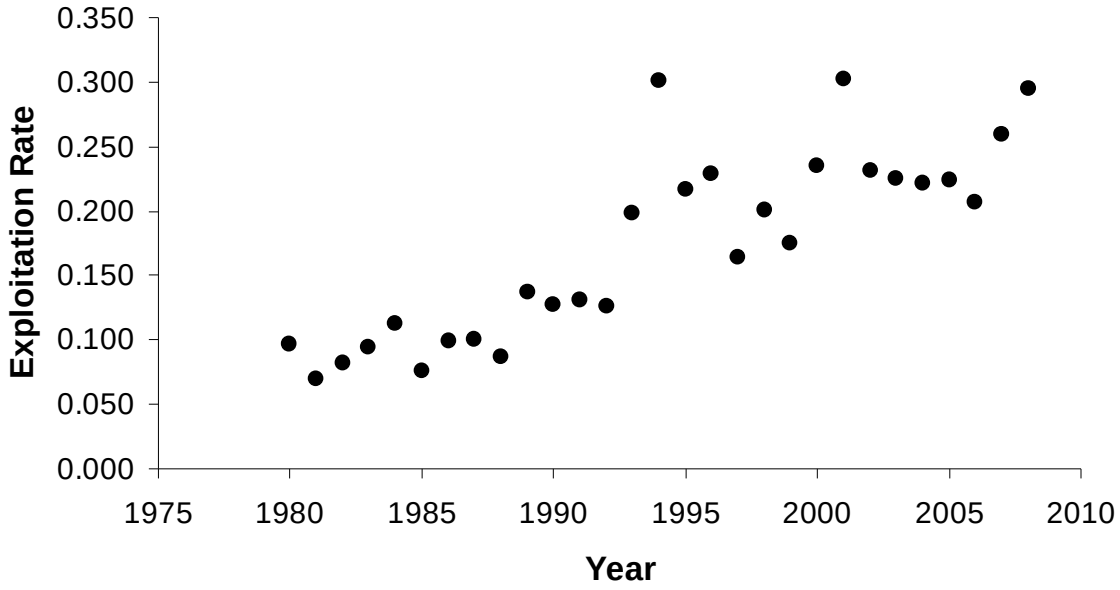

Figure 3.9. Estimated exploitation rate for American eels in the Potomac River, 1980-2008.

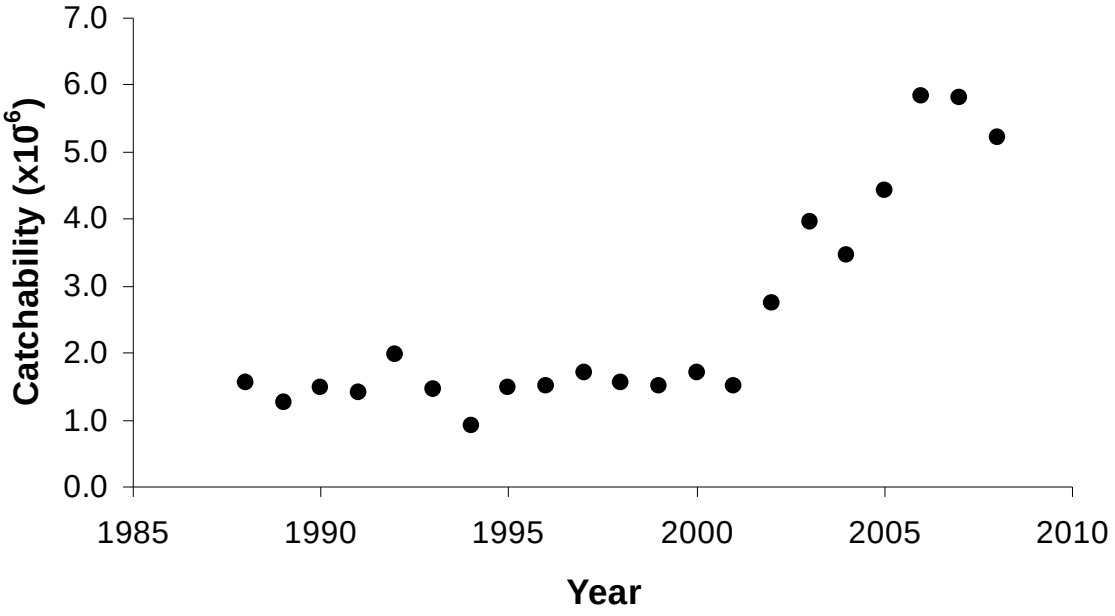

Figure 3.10. Estimated catchability of American eels in the Potomac River, 1980-2008.

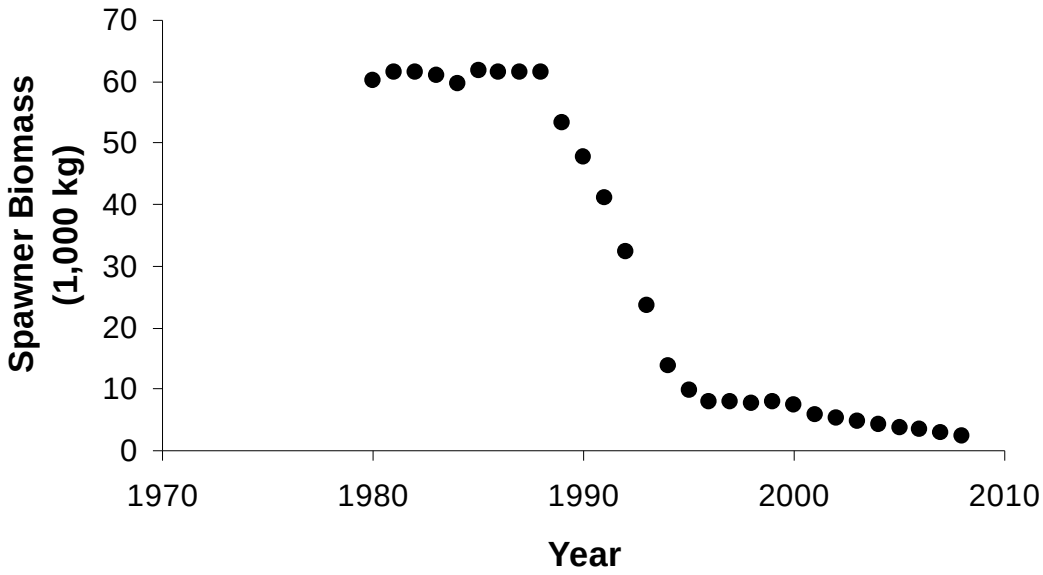

Figure 3.11. Estimated spawner biomass (1,000 kg) for female American eels from the Potomac River, 1980-2008.

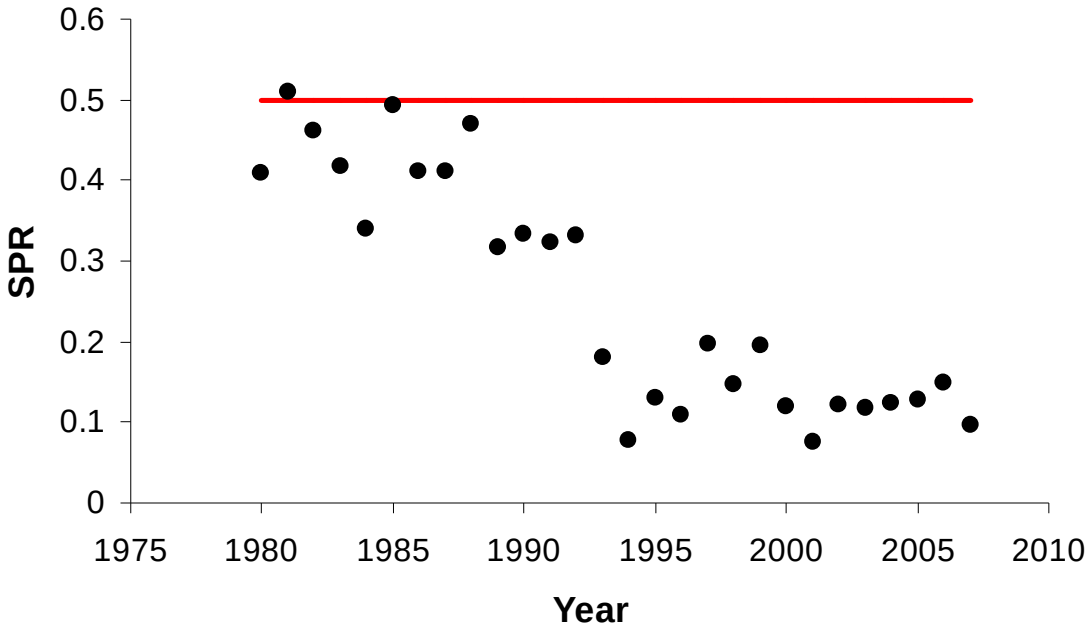

Figure 3.12. Estimated spawning potential ratio (SPR). The estimated SPRs (circles) were compared to the conservative reference point, $F_{50\%}$, where 50% of the virgin biomass is protected (solid line).

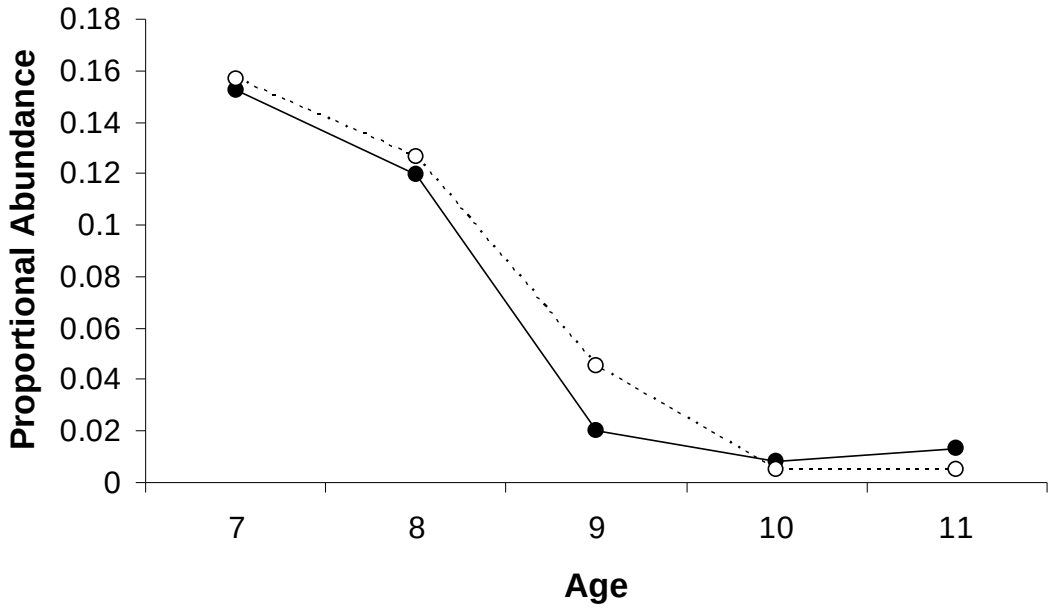

Figure 3.13. Comparison of the model-estimated age composition in 2007 (dark circles) to the observed age composition (open circles, data from eel dissections done for Chapter 1) for Potomac River American eels in 2007.

Appendices

Appendix 1. Estimation of maturation-at-age for female and male American eels in the Potomac River.

To obtain maturation-at-age estimates for male and female American eels, I used maximum likelihood estimation to fit observed age at maturation from two sources of data on American eel maturation in the Chesapeake Bay: my dissection of approximately 400 Chesapeake Bay eels collected in fall 2007 (see Chapter 1), and estimates of mean ages at migration for male and female American eels from Goodwin (1999).

Data

I used gonad dissection data from the Chester, Choptank, James, and Potomac Rivers fall samples, 2007. A total of 345 female eels aged 4-11 were macroscopically inspected (Table A.1). Female eel gonads were examined to identify eels that may be approaching sexual maturation. I removed and weighed gonads that appeared large and well developed to determine the proportion of eels that may mature that year. According to Durif et al. (2005), a female exhibiting a gonado-somatic index of ≥1% may mature in the present year and subsequently undertake an oceanic spawning migration. To increase the sample size I selected eels with a gonado-somatic index ≥0.9%.

For male maturation-at-age I used my American eel dissection data from the Chester, Choptank, James, Patuxent, Potomac, and Sassafras Rivers differently than for the female maturation-at-age. A total of 185 male and intersexual eels aged 3-8 were examined (Table A.2). Male European eels, and presumable American eels,

develop directly from intersexual eels (Buellens et al. 1997). Because I used only macroscopic examination for the gender identification, I was conservative in the differentiation between male and intersexual eels. Only gonads that fit the macroscopic observations of male eels detailed in Buellens et al. (1997) were termed males. Because of the low number of male American eels in my samples, I assumed that any American eel deemed male would mature and migrate in the current year. Thus, I used the ratio of male to intersexual eels at each age to estimate the proportion mature.

I also used the Goodwin (1999) estimate of mean age of silver eels in Potomac River tributaries. Goodwin (1999) conducted electroshocking surveys in 1996-1998 in ten Potomac tributaries and identified six silver eels, of which two male and two female silver eels were aged. The mean age for silver female eels in the Potomac was 8.0 (sd=4.2) and the mean age for male silver eels in the Potomac was 6.5 (sd=0.7).

Model

Abundance-at-age (N_a) for female American eels was modeled using

$$N_{a+1} = N_a e^{-M}\left(1 - m_a\right), \quad \text{(A.1)}$$

where M is natural mortality and m_a is the proportion of eels that mature at a given age

$$m_a = \frac{1}{1 + e^{\left(-\alpha * (a - \beta)\right)}}, \quad \text{(A.2)}$$

and where α is the 50% maturation age and β is the slope at 50% maturation age. M was assumed to be 0.15, based on data from the Hudson River (Morrison and Secor,

2003). Maturation-at-age for male American eels was modeled using the same model as females, but maturation-at-age was assumed constant over ages.

AIC indicated that the single parameter model (AIC=16.4) was a bitter fit than the two-parameter model (AIC=18.5) used for male maturation-at-age.

The likelihood function included a binomially distributed component (L1) for the maturation at age data and a normally distributed component (L2) for the mean age of maturation. Using the two data inputs for each gender, I used Solver to minimize the negative of the $\log_e$ likelihood for each gender. Solve for α and β.

(A.3) $$-LL = \log_e(L_1) + \log_e(L_2)$$

Results

The estimated maturation-at-age for female and male American eels is given in Tables A.1 and A.2. For female American eels, the 50% maturation age, α, was 13.8 and slope at the 50% maturation age, β, was 0.47. For male American eels, the proportion maturing at each age was 8.0%. Due to the lack of male eels older than age eight in my Chesapeake Bay samples, I assumed a maturation-at-age of 0.99 for male eels aged 8-11 for the ASP model.

Table A.1. Data and results of female maturation-at-age model.[1]N mature refers to the number of examined female American eels (N examined) with a gonado-somatic index ≥0.9% (data from Chapter 1).

Age	N examined	N Mature[1] (observed)	Estimated Proportion Mature (model output)
3	0	0	0.006
4	31	1	0.010
5	106	1	0.015
6	93	2	0.024
7	63	3	0.039
8	31	2	0.061
9	9	0	0.094
10	10	0	0.143
11	2	2	0.211

Table A.2. Data and results of male maturation-at-age model. [1]Number of male and intersexual eels observed in the Chester, Choptank, James, Patuxent, Potomac, and Sassafras Rivers in 2007 (data from Chapter 1). Because of the low sample size of male eels, both summer and fall data were combined.

Age	N Male[1] (observed)	N Intersexual[1] (observed)	Proportion Mature (model output)
3	0	4	0.080
4	5	49	0.080
5	5	57	0.080
6	4	45	0.080
7	1	12	0.080
8	0	3	0.080
9	0	0	0.080
10	0	0	0.080
11	0	0	0.080

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