

Demographics and Parasitism of American Eels in the Chesapeake Bay, USA

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Abstract.—The Chesapeake Bay supports the largest U.S. harvest of American eels *Anguilla rostrata*, yet little is known about the underlying demographics and production rates that sustain these harvests. Chesapeake Bay subestuaries (Sassafras, Chester, Choptank, Patuxent, Potomac, and James rivers) are expected to provide productive but varying growth habitats for yellow-stage American eels due to differences in land use, prey availability, and salinity. We compared length, age, growth, mortality, condition, and health (prevalence and incidence of parasitism by the swim bladder nematode *Anguillicola crassus*) of yellow American eels ($n = 850$) in the six principal subestuaries. As has been observed for other systems, female American eels in the Chesapeake Bay were larger, older, and heavier and had higher growth rates than male, intersexual, or undifferentiated American eels. Prevalence of male and intersexual individuals in the upper bay region was higher than that in the lower bay and higher than that reported for estuaries in South Carolina, Quebec, and the Hudson River, New York. American eel demographic attributes (gender, length, weight, condition, age, growth, and parasitism) differed substantially among the subestuaries. Individual growth rates ranged from 26.7 to 149.3 mm/year; the Choptank River had the highest mean growth rate (72.7 mm/year), and the Chester River had the lowest (60.2 mm/year). Estimated instantaneous loss rates (0.52–1.01 per year) did not vary systematically among subestuaries. Prevalence of parasitized American eels ranged from 17.8% to 72.0% and was higher in the upper bay subestuaries than in the lower bay. Swim bladder damage and *Anguillicola crassus* presence were not associated with American eel age or growth rate. In summary, female prevalence, growth rates, and condition were lower and parasite prevalence and intensity were higher in the less-saline upper bay than in the lower bay, suggesting fundamental differences in the productivity and spawning contributions between these two regions.

Harvests by weight of American eels *Anguilla rostrata* from the Chesapeake Bay are considerably larger than elsewhere in the species' U.S. range, prompting the view that the Chesapeake Bay should support more-productive growth habitats for juveniles than other systems (Secor et al. 2006). On average, 54% of the U.S. American eel harvest during 1950–2008 was from the Chesapeake Bay (NMFS 2009), yet little is known about the underlying demographics of Chesapeake Bay American eels. The Chesapeake Bay is a large, eutrophic estuary with wide salinity, depth, and temperature gradients that provide a range of habitat conditions (Kemp et al. 2005; Secor and Austin 2006). The Chesapeake Bay and other estuaries may play a key role in recovery of American eels because more than 50% of freshwater nontidal habitats have potentially been lost (Busch et al. 1998). Here, we examine growth habitats in the Chesapeake Bay, focusing on how yellow-stage American eels vary in

length, age, growth, mortality, condition, and health (prevalence and intensity of parasitism by the exotic swim bladder nematode *Anguillicola crassus*) among principal subestuaries of the Chesapeake Bay.

Because American eels are panmictic (i.e., not exhibiting population structure among estuaries), they do not undergo selection for differing growth rates based on regional habitat differences. Thus, it is critical to identify which regions (e.g., estuaries or habitat types) are most important in contributing to production of yellow American eels and escapement of silver (sexually mature) American eels. American eel size, gender, and habitat 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, 1987; Morrison and Secor 2003; Cairns et al. 2009; Jessop et al. 2009). Within an estuary, the distribution of gender and size of American eels can also vary greatly. American eels in nontidal portions of the Potomac River were not only significantly larger but also increasingly female with increasing distance

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upriver and upstream (Goodwin and Angermeier 2003). Among estuaries, size at maturation was greater with increasing latitude for female American eels but not for males (Oliveira 1999). Age at maturation of male American eels was positively correlated with latitude, suggesting that growth rates for males vary inversely with latitude (Oliveira 1999). Previous studies indicated that American eel growth rates tended to be higher in southern habitats than in northern habitats (Gunning and Shoop 1962; Hansen and Eversole 1984; Oliveira 1999). The length of the growing seasons at different latitudes and differences in 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).

Major subestuaries of the Chesapeake Bay are expected to provide a variety of growth habitats for yellow American eels. The upper portion of the Chesapeake Bay and its subestuaries (Sassafras and Chester rivers) are predominately freshwater or oligohaline (salinity levels < 10‰; White 1989). In this region, most American eels are harvested in freshwater. Subestuaries in the middle and lower portions of the Chesapeake Bay (Choptank, Patuxent, Potomac, and James rivers) have higher salinity, and harvest locations can range from 0‰ to 26‰ salinity depending on the location within the subestuary, season, and amount of precipitation (White 1989). Subestuaries also differ in discharge rates and watershed land use (Pritchard and Schubel 2001; Bilkovic et al. 2006), both of which can affect American eel demographics (Machut et al. 2007). Benthic productivity of subestuaries probably varies as well, with the foraging conditions for yellow American eels differing according to salinity, bottom substrate, and prey availability (Minello et al. 2003).

Growth habitats in the Chesapeake Bay could be compromised by disease. American eels in the Chesapeake Bay are commonly infected with *Anguillicola crassus*. The parasite was first reported in the USA in 1995 (Fries et al. 1996), and the range has since been extended throughout the USA and into Canada (Aieta and Oliveira 2009). Negative consequences, including thickening of the swim bladder wall and reduced swimming performance, have been documented in *Anguillicola crassus*-infected European eels *Anguilla anguilla* and could potentially occur in American eels (Palstra et al. 2007). Concerns have arisen about the impact of *Anguillicola crassus* on American eel growth, mortality, condition, susceptibility to other infections, swimming behavior, and spawning migration (USFWS 2007). *Anguillicola crassus* has a rapid life cycle (Barse and Secor

1999); American eels can be infected by multiple stages of the parasite, and an individual can be infected many times over the course of its life. Due to the short life cycle of the parasite, presence or absence of the parasite in the swim bladder may be an incomplete measure of infection. Previous studies indicate that parasite prevalence and intensity are greater in tidal freshwater habitats than in brackish water (Morrison and Secor 2003) and that salinity negatively affects the infectivity of *Anguillicola crassus* (Kirk et al. 2000).

We hypothesized that yellow American eels would experience higher growth rates in the Chesapeake Bay than in other estuaries and that subestuaries within the Chesapeake Bay would exhibit measurable demographic differences in gender ratios, size structure, age structure, growth rates, and condition. A laboratory-based analysis was conducted on age structure and swim bladder infections of 850 yellow American eels sampled from six subestuaries (Sassafras, Chester, Choptank, Patuxent, Potomac, and James rivers). Subestuary differences in demographics provided a comparative framework within which to evaluate possible associations between *Anguillicola crassus* parasitism and American eel growth and mortality.

Methods

The Delaware Valley Fish Company (DVFC) donated 850 yellow-stage American eels from six rivers for use in this study. American eels were harvested using baited, two-chambered, 12.7-mm-mesh eel pots and were transported in oxygenated tanks to the holding facility at DVFC. Approximately 100 American eels each from the Sassafras, Potomac, and Chester rivers (representing June–July harvests) were randomly selected from holding tanks by DVFC staff in July 2007 and were stored frozen. Similarly, November–December samples (about 100 each) from the Potomac, Chester, James, and Choptank rivers were selected. American eels at DVFC were not size-graded at the facility, but size-grading possibly occurred before the fish were sold to DVFC. Interviews with a commercial fisher (J. Trossbach, personal communication) indicated that American eels from the Potomac and James rivers were graded for size, with the smallest American eels being sold for bait and not provided to DVFC; few fish smaller than 30 cm were observed in these samples. American eels from the Patuxent River were received directly from a commercial fisher in June 2007 and were not graded. Samples from the Sassafras, Chester, and Choptank rivers showed a size distribution similar to that of the Patuxent River subsample and thus were assumed to have not been size-graded prior to sale to DVFC. To evaluate the role of bay region (a proxy for salinity) on growth, condition, and parasit-

ism, we grouped the subestuaries into upper bay (Chester and Sassafra rivers) and lower bay (Choptank, James, Patuxent, and Potomac rivers) categories.

American eels were measured for total length (TL, mm), maximum girth (mm), and mass (0.1 g) and then were inspected for internal and external abnormalities. Previous studies showed that freezing reduces length and weight of American eels by 1.2–3.0% and 1.9%, respectively (Morrison and Secor 2003; Machut et al. 2007). All TLs and masses reported are based on uncorrected measurements. Fulton's condition factor (K) was calculated for each individual ($K = 100 \times [\text{mass, g}]/[\text{TL, cm}]^3$; Ricker 1975).

Each American eel was macroscopically inspected to determine gender according to Buellens et al. (1997). Four gender categories were identified: female, male, intersexual, and undifferentiated. Undifferentiated gonads do not have identifiable oogonia or spermatogonia and can develop directly into an ovary. Intersexual gonads contain both female and male sex cells, and American eels with intersexual gonads can develop into males (Buellens et al. 1997). Chi-square analysis was used to test for differences among proportions of females among subestuaries and between bay regions; to reduce bias created by size-grading and differences in length distribution between regions, only female American eels of 20–40 cm TL were considered.

Each swim bladder was inspected internally and externally, and the number of *Anguillicola crassus* present was counted. For samples from each subestuary, parasite prevalence (Bush et al. 1997) was calculated as the percentage of infected American eels. Parasite intensity was calculated as the mean number of *Anguillicola crassus* among infected individuals (Bush et al. 1997). We used chi-square analysis to test for differences in parasite prevalence among subestuaries and between bay regions. To determine statistical significance of mean parasite intensity among subestuaries or between bay regions, we used analysis of variance (ANOVA) with subestuary or bay region and size-class as fixed effects and we performed Tukey's multiple comparison test. To compare seasonal patterns in parasitism, only the Potomac and Chester rivers were considered.

Damage to the swim bladder by current or previous infections of *Anguillicola crassus* is thought to be a more-accurate measure of parasite pressure than parasite count (Lefebvre et al. 2002). The swim bladder degenerative index was developed by Lefebvre et al. (2002) as an index of cumulative effects on swim bladder function. To measure long-term cumulative effects of parasitism and to test whether parasite infection affected growth or mortality rates, we modified the index as follows. The original index

included three swim bladder criteria: (1) swim bladder wall thickness, (2) swim bladder wall transparency, and (3) pigmentation and exudates. We felt that the third metric corresponded better with parasite incidence than with swim bladder condition, and so we excluded it from the analyses. For our analysis, we combined the scores for swim bladder wall thickness and swim bladder wall transparency only, resulting in a composite score (SBtt) of 0–4 (0 = no damage, 4 = greatest damage). To examine effects of swim bladder damage (as SBtt) and parasite incidence (presence or absence) on growth rate and age, we used analysis of covariance (ANCOVA) with size-class as a fixed effect and we performed Tukey's multiple comparison test. We used chi-square analysis to test for independence of the metrics for swim bladder wall thickness and swim bladder wall transparency.

The American eels were aged directly through enumeration of annuli in otoliths. Otolith-based aging has been validated in studies of American eels (Oliveira 1996). Sagittal otoliths were prepared in the transverse plane as described by Morrison and Secor (2003). To enhance the contrast of annuli, the polished otoliths were etched with 6% EDTA for 2–5 min and then were stained with a solution of 2% EDTA and 5% toluidine blue for 2–5 min. The check representing the transition from the leptocephalus stage to the glass eel stage was assumed to equal age 1 (Morrison and Secor 2003). Photographs of etched and stained otoliths under 10 \times or 40 \times magnification were annotated for annuli incidence by using Adobe Photoshop image editing software. Two readers initially examined a similarly prepared (i.e., Morrison and Secor 2003) set of 25 otoliths representing the Hudson River. Sequential training sessions and independent interpretations were made to ensure that the two readers could consistently interpret annuli structure. Subsequently, each otolith image was aged at least two times by the more-experienced reader without knowledge of the American eel's length, weight, or gender. At least two annuli counts were made for each American eel. If the two readings matched, that count was accepted as the assigned age (60.4% of otoliths). If the two readings differed by less than 2 years (29.5% of otoliths), then we used the most recent of the two counts as the assigned age, assuming that accuracy and consistency improved with increased experience. If readings differed by 2 years or more (7.0% of otoliths), then a third blind read was made and accepted when it matched one of the previous reads. If the third reading differed from either of the first two readings by less than 2 years, the third read was accepted (2.5% of otoliths). Finally, if the third reading differed from either of the first two by 2 years or more, that individual otolith sample was discarded (0.6% of otoliths).

TABLE 1.—Mean (SE) total length (TL), age, mass, growth rate, and condition factor (*K*) for female Chesapeake Bay American eels by subestuary (river) and bay region in 2007. Means with common letters are not significantly different (Tukey’s multiple comparison test, *P* > 0.05; the letters z and y pertain to comparisons between regions, the letters a–d to comparisons among subestuaries. Subestuaries are listed from north to south.

Bay region and river	<i>n</i>	TL (cm)	Age (years)	Mass (g)	Growth rate (mm/year)	<i>K</i>
Upper bay	313	36.8 (0.58) z	6.1 (0.13) z	90.4 (5.93) z	65.2 (1.69) z	0.163 (0.002) z
Sassafras	100	36.2 (1.09) ab	6.8 (0.24) cd	93.1 (11.75) a	54.4 (3.31) a	0.170 (0.004) bc
Chester	213	36.9 (0.59) ab	5.9 (0.14) ab	89.2 (6.40) a	68.7 (1.89) b	0.161 (0.002) c
Lower bay	537	41.1 (0.34) y	6.1 (0.07) z	135.3 (3.43) y	73.2 (0.93) y	0.177 (0.001) y
Choptank	110	40.0 (0.75) b	5.4 (0.16) a	111.9 (8.13) ab	80.9 (2.26) c	0.167 (0.003) bc
Patuxent	121	36.0 (0.62) a	5.7 (0.14) a	107.0 (6.75) a	67.4 (1.86) b	0.198 (0.003) a
Potomac	205	41.8 (0.48) c	6.3 (0.11) bc	136.9 (5.27) b	72.7 (1.47) b	0.174 (0.002) b
James	101	47.0 (0.64) d	6.8 (0.14) d	178.9 (6.91) c	74.8 (1.90) bc	0.168 (0.003) bc

Mean annual growth rate was estimated by dividing TL by age (Oliveira 1999; Morrison and Secor 2003) and assuming linear growth (Hansen and Eversole 1984; Graynoth 1999; Morrison and Secor 2003). To account for growth that occurred before entry into the Chesapeake Bay region, we subtracted 57.1 mm from the TL and 1 year from the age of each American eel based on the average length for glass-eel-stage American eels entering the Little Egg Inlet, New Jersey, over a 10-year period (Sullivan et al. 2006). Growth rate differences (1) among gender categories and (2) among subestuaries for female American eels only were analyzed by one-way ANOVA and Tukey’s multiple comparison test. Growth rates among subestuaries were analyzed by ANOVA and using subestuary and gender as fixed effects. Growth rate differences between bay regions were compared by ANOVA using bay region and gender as fixed effects. Catch curves were calculated for each subestuary to obtain loss rate estimates (Ricker

1975). Here, loss rate is defined as any American eel losses from the local population, including natural mortality, fishing mortality, and emigration related to spawning.

For all statistical analyses, significance was tested at the 0.05 level. Age, length, growth rate, and weight data were log_e transformed to meet normality assumptions. Statistical significance of *K*, mean length, age, and mass among subestuaries and between bay regions was analyzed using ANOVA with Tukey’s multiple comparison test in the Statistical Analysis System version 9.3.1 (SAS Institute, Inc., Cary, North Carolina). Contrasts between bay region and subestuaries were conducted with female American eels only (Table 1) and with all gender categories (Table 2).

Results

Demographics

Length and age ranges for American eels from the Chesapeake Bay were 21.3–64.7 cm TL (mean = 36.5 cm TL) and 3–11 years (mean = 5.8 years), respectively; mass ranged from 14.7 to 590.8 g (mean = 98.8 g). Females were significantly longer (mean = 40.0 cm TL), older (mean = 6.1 years), and heavier (mean = 124.0 g) than other gender categories (Figure 1). Females constituted the most prevalent gender category, ranging from 34% to 100% among subestuaries (Figure 2). The proportion of females varied significantly between subestuaries (df = 5, *P* < 0.001), and the proportion of 20–40-cm female American eels in the upper bay (Chester and Sassafras rivers) was significantly lower than that in the lower bay (James, Potomac, Patuxent, and Choptank rivers; df = 1, *P* < 0.001). Across all subestuaries, females constituted 71.3% of the sample.

Female size and age differed among subestuaries (Table 1). Subestuaries listed in descending order of female mean lengths were the James (mean = 47.0 cm TL), Potomac, Choptank, Chester, Sassafras, and

TABLE 2.—Mean (SE) American eel growth rate and condition factor (*K*) for each gender, by Chesapeake Bay region and subestuary in 2007 (genders combined). Means with common letters are not significantly different (Tukey’s multiple comparison test, *P* > 0.05); the letters z and y pertain to comparisons between regions, the letters a–d to comparisons among genders and subestuaries.

Gender or region	<i>n</i>	Growth rate (mm/year)	<i>K</i>
Female	605	71.4 (0.79) c	0.174 (0.001) b
Male	19	64.2 (4.89) bc	0.174 (0.006) ab
Intersexual	194	57.7 (1.45) ab	0.163 (0.002) a
Undifferentiated	30	48.5 (3.65) a	0.165 (0.005) ab
Upper bay		57.3 (1.67) z	
Sassafras	100	53.4 (2.18) a	
Chester	213	60.2 (1.89) ab	
Lower Bay		65.2 (1.81) y	
Choptank	110	72.7 (2.34) d	
Patuxent	121	60.9 (2.29) bc	
Potomac	205	63.9 (2.07) bc	
James	101	67.2 (2.52) cd	

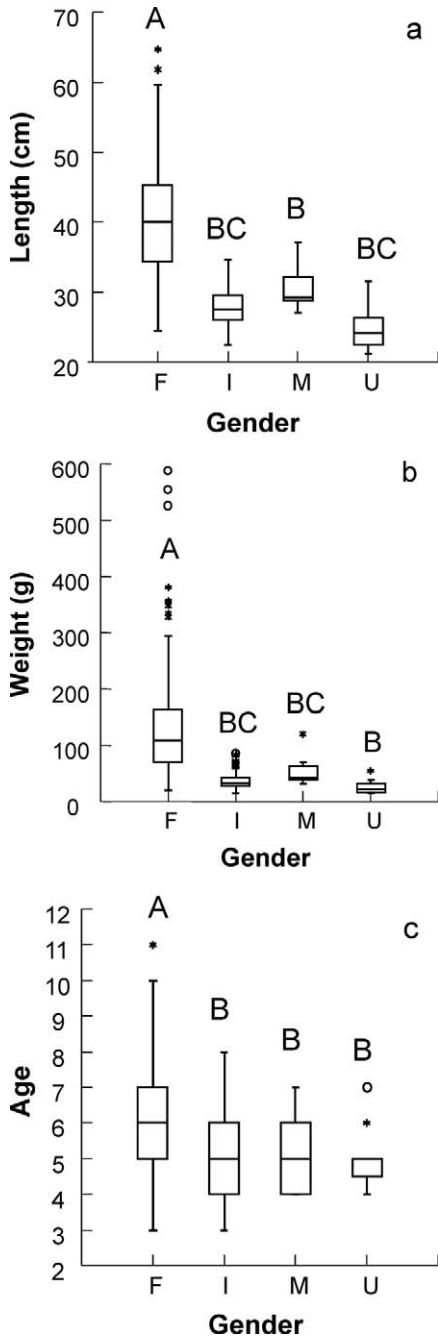


FIGURE 1.—Mean (a) total length (TL, cm); (b) weight (g); and (c) age (years) of American eels in each gender category (F = female, I = intersexual, M = male, U = undifferentiated) for all Chesapeake Bay subestuaries combined (horizontal line in each box = median; lower edge of box = first quartile; upper edge of box = third quartile; whiskers = ± 1.5 times the interquartile range; asterisks and open circles = outliers). Significant differences between means ($P < 0.05$) are indicated by differing letters.

Patuxent (mean = 36.0 cm TL) rivers. Similarly, female mass was greatest in the James River (mean = 178.9 g) and least in the Chester River (mean = 89.2 g). Ages ranked by subestuaries differed from the patterns for length and weight. Females from the Sassafras and James rivers were significantly older (mean = 6.8 years) than females from the Chester, Choptank, and Patuxent rivers. 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; $df = 1, 603, P < 0.0001$). Mean age was not significantly different between bay regions ($df = 1, 576, P = 0.99$).

Growth and Condition

Length at age for individual American eels was highly variable (Figure 3), differing based on gender, bay region, and subestuary. As an example of this variability, American eels that were estimated to be 6 years old ranged from 23.2 to 64.7 cm TL. The overall range and mean of growth rates for American eels (gender categories combined) in the Chesapeake Bay were 26.7–149.3 and 67.5 mm/year, respectively. Female American eels exhibited the highest mean growth rate (71.4 mm/year; Table 2), which was significantly different from those of intersexual and undifferentiated individuals (57.7 and 48.5 mm/year, respectively; $df = 3, 786, P < 0.0001$). Males exhibited a mean growth rate of 64.2 mm/year, which was significantly different only from that of undifferentiated American eels ($P = 0.05$). The mean ($\pm SE$) growth rate in the upper bay region (57.3 ± 1.67 mm/year) was significantly lower than that in the lower bay (65.2 ± 1.81 mm/year; $df = 1, 790, P < 0.0001$). Among subestuaries, the growth rate was lowest in the Chester River (60.2 mm/year) and highest in the Choptank River (72.7 mm/year; Table 2) when all genders were included in the analyses. Female growth rate (mean $\pm SE$) was highest in the Choptank River (80.9 ± 2.26 mm/year; Table 1), lowest in the Sassafras River (54.4 ± 3.31 mm/year), and significantly higher in the lower bay region than in the upper bay (Table 1; $df = 1, 576, P < 0.0001$).

The mean $\pm SE$ K -values of females (0.174 ± 0.001) and males (0.174 ± 0.006) were nearly identical (Table 2). Females exhibited a significantly higher K -value than intersexual American eels ($df = 3, 844, P < 0.0001$); all other pairings were not significantly different. Subestuary differences in female K were present (Table 1); the Patuxent River had the highest mean ($\pm SE$) K (0.198 ± 0.003), and the Chester River had the lowest (0.161 ± 0.002). The K of female American eels from the upper bay (0.163 ± 0.002)

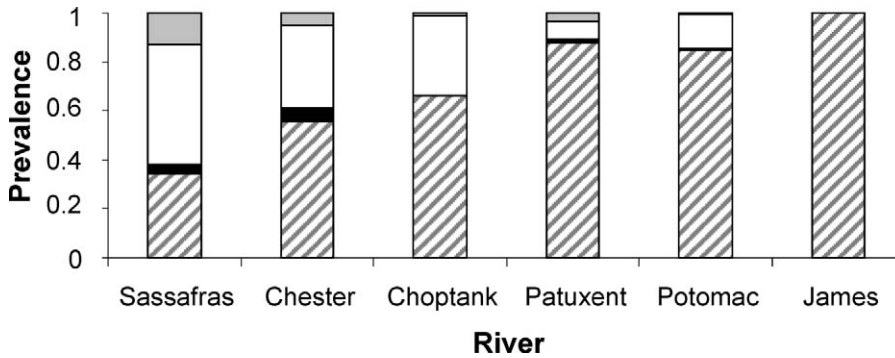


FIGURE 2.—Percent gender composition (hatched = female; black = male; white = intersexual; gray = undifferentiated) of American eels from each Chesapeake Bay subestuary.

differed significantly from the K for the lower bay (0.177 ± 0.001 ; $df = 1, 603$, $P < 0.0001$; Table 1).

Loss Rates

Estimated instantaneous loss rates (gender categories combined) ranged from 0.52 per year in the Choptank River to 1.01 per year in the Potomac River (mean [all subestuaries] = 0.72 per year; Figure 4). The SEs of the mean instantaneous loss rates were high and overlapping, indicating that any difference in loss rates between subestuaries or bay regions was not significant.

Parasitism

Prevalence of *Anguillicola crassus*-infected American eels in the Chesapeake Bay was 40.9% among all subestuaries, and parasite intensity ranged from 1 to 48 parasites/infected individual (mean = 3.5 parasites/individual; mode = 1 parasite/individual). For all subestuaries combined, both parasite intensity and prevalence had significantly negative correlations with size-class ($r > 0.95$, $P < 0.0001$; Figure 5); 52.0% of American eels had evidence of either past or current *Anguillicola crassus* infection.

Subestuaries varied substantially in degree of parasitism (Table 3). American eels in the James River had the lowest prevalence (17.8%), and those in the Sassafras River exhibited the greatest prevalence (72.0%). Chi-square analysis detected significant differences in parasite prevalence among subestuaries ($df = 5$, $P < 0.001$). Mean parasite intensity among subestuaries ranged from 2.0 to 4.0 parasites/infected individual (Table 3). A comparison of mean (\pm SE) parasite intensity in upper bay subestuaries (3.1 ± 0.6 parasites/infected individual) with that in lower bay subestuaries (2.7 ± 0.6 parasites/infected individual) was not significant ($df = 1, 337$, $P = 0.43$). Parasite prevalence in upper bay subestuaries (52.1%), howev-

er, was significantly higher than that in lower bay subestuaries (34.3%; $df = 1$, $P < 0.001$).

Because females were larger and older than other gender categories, the analyses of demographic interactions with parasitism were limited to females to avoid the confounding effects of size. We detected no significant association between incidence of *Anguillicola crassus* and female American eel growth rate ($df = 1, 566$, $P = 0.10$) or between parasite incidence and female age ($df = 1, 566$, $P = 0.25$). Females lacking parasites had a mean (\pm SE) growth rate of 74.0 ± 2.1 mm/year and a mean age of 6.2 ± 0.2 years; parasitized females had a mean growth rate of 71.3 ± 2.3 mm/year and a mean age of 6.3 ± 0.2 years. No significant association was detected between SBtt and growth rate ($df = 4, 553$, $P = 0.51$) or between SBtt and age ($df = 4, 553$, $P = 0.60$). Swim bladder wall thickness and transparency metrics were independent ($df = 4$, $P < 0.01$).

For those subestuaries that were sampled in both seasons, the Chester River had significantly lower parasite intensity in fall (mean \pm SE = 2.3 ± 0.6 parasites/infected individual) than in summer (4.16 ± 0.35 parasites/infected individual; $df = 1, 89$, $P = 0.009$). The Potomac River also had lower parasite intensity in fall (mean \pm SE = 2.1 ± 0.30 parasites/infected individual) than in summer (3.0 ± 0.34 parasites/infected individual; $df = 1, 72$, $P = 0.034$). For the Chester and Potomac River subestuaries combined, the mean (\pm SE) SBtt score was significantly higher in summer (0.27 ± 0.3) than in fall (0.13 ± 0.03 ; $df = 1, 414$, $P = 0.002$).

Discussion

Chesapeake Bay as Growth Habitat

Here, we provide evidence that the Chesapeake Bay harbors productive and diverse growth habitats for American eels. There was a broad difference in growth

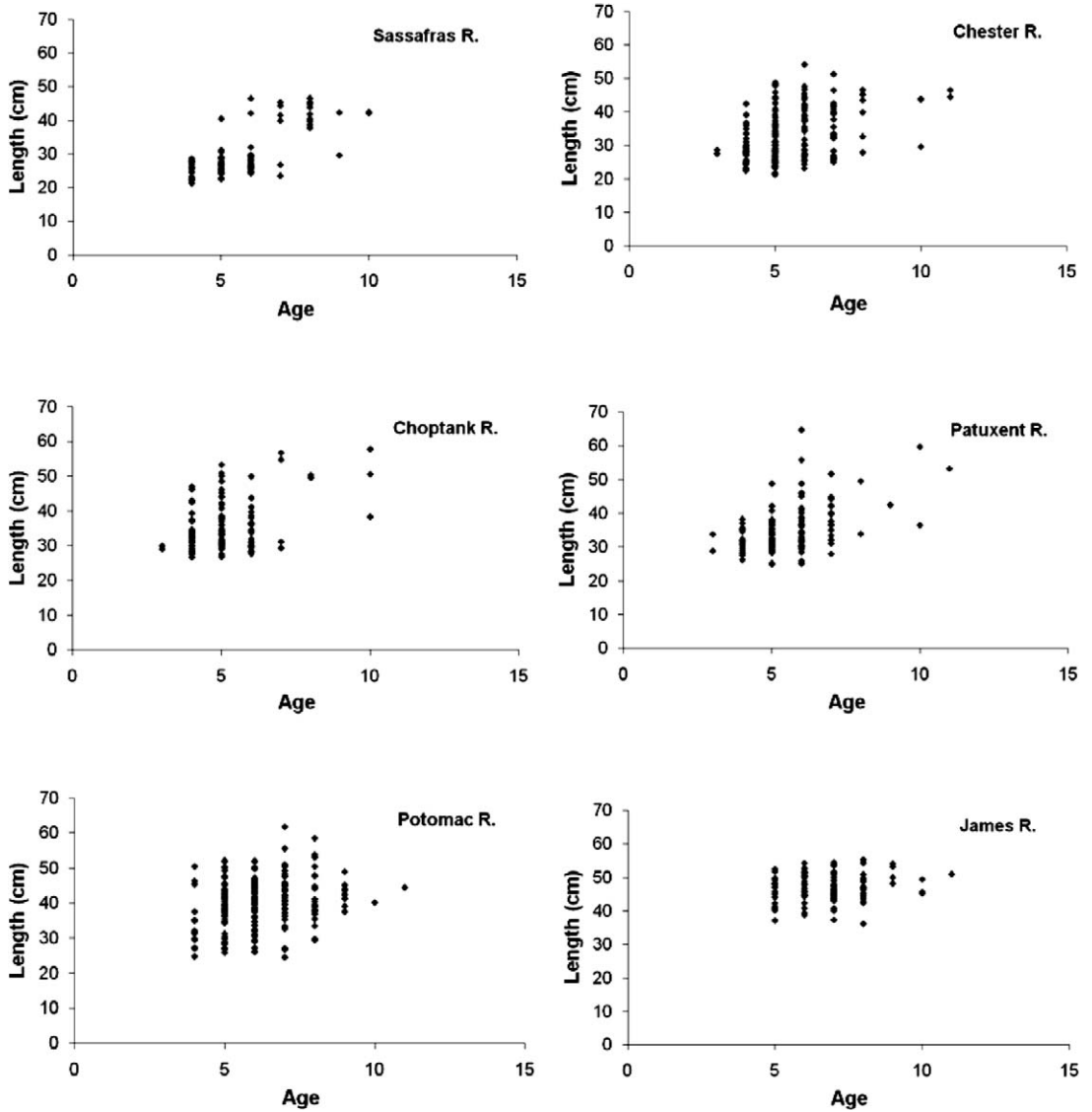


FIGURE 3.—Total length at age for yellow-stage American eels from each Chesapeake Bay subestuary sampled in 2007.

rates between bay regions, suggesting that growth habitats might be associated with salinity levels. The salinity gradient in the Chesapeake Bay ranges from freshwater at the mouth of the Susquehanna River (upper bay) to nearly full-strength seawater (salinity = 32‰) at the mouth of the bay (Murdy et al. 1997). 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 coarsely considered. Still, American eels in the Choptank River, where the majority (>70%) of American eel harvest comes from brackish water, had the highest mean

growth rates (K. Whiteford, Maryland Department of Natural Resources, personal communication). Conversely, lower growth rates, fewer females, and more poorly conditioned American eels were observed in the upper bay. These differences mirror previous literature findings that freshwater supports less-productive growth habitats than brackish water (Helfman et al. 1984; Morrison and Secor 2003; Cairns et al. 2009; Jessop et al. 2009).

The mean growth rate estimate for American eels in the Chesapeake Bay was generally greater than those reported elsewhere. The range of annual growth rates

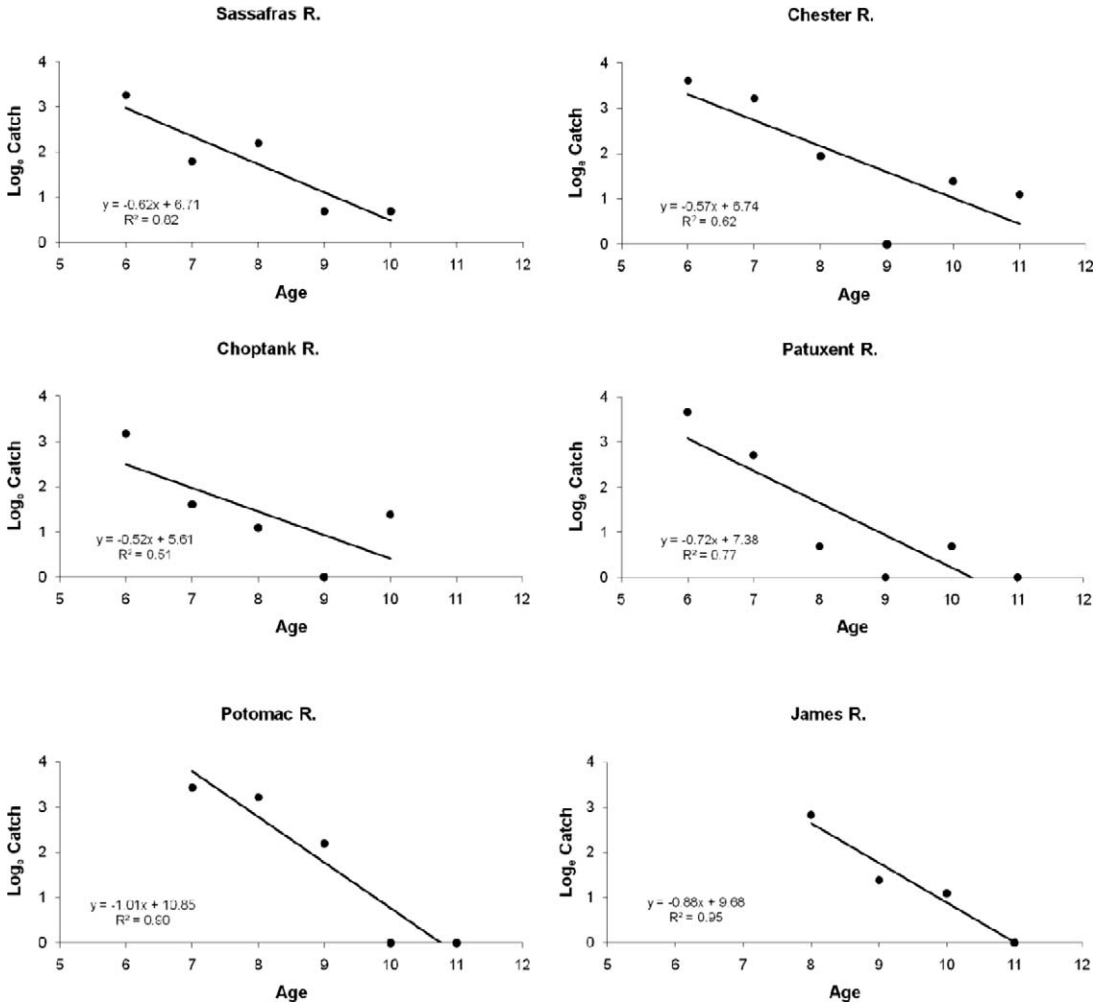


FIGURE 4.—Catch curves for yellow-stage American eels from each Chesapeake Bay subestuary. Age-classes used in catch curve analysis are indicated for each subestuary. Instantaneous mortality rates are indicated by the slope of the regression line.

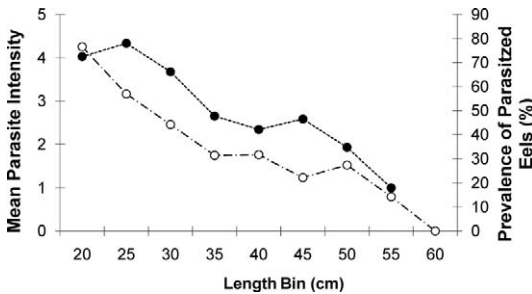


FIGURE 5.—Mean *Anguillicola crassus* intensity (number of parasites per infected American eel; black shaded circles) and prevalence (percentage of American eels infected; open circles) versus American eel size-class (total length) for all sampled Chesapeake Bay subestuaries combined.

TABLE 3.—*Anguillicola crassus* prevalence (percentage of American eels infected) and mean (SE) intensity (number of parasites per infected individual) in American eels from six subestuaries of the Chesapeake Bay. Parasite range is the number of parasites per swim bladder in all sampled individuals. Mean parasite intensity was adjusted for length and subestuary effects by use of analysis of variance with American eel size-class and subestuary as class variables.

River	Parasite prevalence (%)	Parasite intensity	Parasite range
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

for a brackish system in South Carolina was 27–69 mm/year (Hansen and Eversole 1984). Growth estimates for the freshwater Hudson River ranged from 13 to 114 mm/year (mean = 33 mm/year; Machut et al. 2007); estimated growth in brackish water was 58.4 mm/year (Morrison and Secor 2003). The mean growth rate of migrating female silver American eels in Rhode Island was 39.8 mm/year; the mean for migrating male silver American eels was 30.9 mm/year (Oliveira 1999). Two rivers in western Newfoundland had mean growth rates of 31.8 and 65.0 mm/year (Jessop et al. 2009).

Estimates of growth rate were biased by size-grading in this study. Although efforts were made to subsample without bias, samples represented harvested American eels taken over limited temporal and spatial scales from each subestuary, and some of the subestuary samples were known to be size-graded. In particular, this practice limits inferences that can be drawn specific to the Potomac and James rivers. Inferences were also constrained by gear type, which selected a size range similar to those in other studies that used eel pots (26–69 cm: Hansen and Eversole 1984; 15–65 cm: Ford and Mercer 1986; ~26–70 cm: Morrison and Secor 2003). 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 of approximately 6–78 cm (study years: 1997–2000; $n = 594$). The use of pots could have led to underrepresentation of male, intersexual, and undifferentiated American eels in our study.

We observed a fairly narrow age distribution for Chesapeake Bay American eels (90% were between 4 and 8 years old), which could be explained by exploitation effects (age truncation and growth compensation), high underlying habitat productivity, or both. The age range of American eels in the Chesapeake Bay was substantially younger than that from a study in the Hudson River, which used similar sampling and aging procedures (3–38 years: Morrison and Secor 2003). Growth rates were moderately lower in the Hudson River study (mean = 54.8 mm/year for Hudson River brackish-water sites). Exploitation in the Chesapeake Bay could result in higher growth rates if growth is density dependent. Density-dependent growth in American eels has been suggested as the cause of decreased growth rates below dams or other barriers where densities are high (Machut et al. 2007).

The age range in the Chesapeake Bay was similar to those reported for American eels in South Carolina rivers (0–15 years: Harrell and Loycano 1982; 1–12 years: Hansen and Eversole 1984); the South Carolina populations are exploited but probably do not receive

the same amount of directed fishing as those in the Chesapeake Bay (National Oceanic and Atmospheric Administration [NOAA], unpublished harvest data). Owens and Geer (2003) found a few substantially older American eels (range = 1–18 years) in the Virginia portion of the bay than we found in the present study, although as in our study, most were between 3 and 6 years old.

Gender Differences

Differences that we observed between genders have been well documented elsewhere; females grew faster and to larger sizes than males (Table 2; Helfman et al. 1984; Oliveira 1999; Oliveira and McCleave 2002). Oliveira and McCleave (2002) suggested that male and female anguillid eels have different life history strategies. Females benefit from maturing at larger sizes because fecundity increases with size and increased size may confer greater diet breadth and survival advantages; males, however, mature at smaller sizes so they can reproduce as rapidly as possible. The present study supports this view. The prevalence of male and intersexual American eels in upper Chesapeake Bay subestuaries was higher than has been reported for many other estuaries. Female American eels dominated (>95%) in the Hudson River estuary (Morrison and Secor 2003); the Cooper River, South Carolina (Harrell and Loycano 1982; Hansen and Eversole 1984); and the Matamek River, 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 to be about 36% in Georgia and about 90% in Rhode Island. Helfman et al. (1987) suggested that male American eels should predominate in brackish waters, but this was not supported by our results. For instance, only 12% of the American eels sampled in the brackish portion of the Patuxent River were male. Inferences should be robust to biases due to size-grading since the inferences held for systems other than the Potomac and James rivers.

Mortality

Loss rate estimates combine mortality from natural causes, maturation, and fishing. Therefore, any differences in estimated loss rates between subestuary systems may indicate differences in (1) natural mortality rates between rivers, (2) fishing mortality, or (3) the number of American eels that are maturing and emigrating to the Sargasso Sea. Some subestuaries also contained fall samples (Potomac and Chester rivers), which could have biased age distributions because of the influence of new recruits growing into the fishery. Further, catch curve estimates of mortality

assume that recruitment is not trending over time. This assumption probably oversimplifies the recruitment patterns in the Chesapeake Bay, especially given that recent recruitment indices have indicated a decline during the past two decades (Fenske 2009). The narrow age range of American eels present in the Chesapeake Bay limits the range of ages available for catch curve analysis; typically, catch curves in this study were based on 4–6 age-classes. The limited range added uncertainty to the loss rate estimates, contributing to high variances and lack of statistical sensitivity to tests of subestuary differences.

Despite the limiting assumptions inherent in using loss rate as a measure of overall mortality, such estimates can be useful in supporting fishery assessments and reference points for American eels. Very few such estimates are available for American eels. Morrison and Secor (2003) estimated annual loss rates of 9–24% for American eels in the Hudson River and cited an anonymous source with annual natural mortality estimates of 22% for American eels from Prince Edward Island and 12–55% for 10-year-old American eels from a portion of the Gulf of St. Lawrence. By comparison, the average 34–59% loss rate estimated from our catch curve analysis was not unrealistic for a productive population that is experiencing both natural mortality and fishing mortality.

Parasitism

Prevalence of *Anguillicola crassus* among American eels in the Chesapeake Bay has increased since the first report of this parasite in the bay (Barse and Secor 1999). Initial reported estimates of 10–24% prevalence in the Patuxent and Sassafras rivers (Barse and Secor 1999) were substantially lower than the current mean Chesapeake Bay prevalence and lower than current estimates for the two rivers (Table 3). Seasonal patterns in parasite prevalence may explain some of the difference in prevalence between the present study and the Barse and Secor (1999) study, but increasing parasite prevalence and intensity over time have also been noted in the Hudson River, where prevalence increased from less than 20% in 1997 to more than 60% in 2000 (Morrison and Secor 2003). The tripling of parasite prevalence in the Hudson River over 3 years was similar to the three- to fourfold increase observed in the Sassafras and Patuxent River subestuaries during the past decade. Studies have also indicated that the range of *Anguillicola crassus* is increasing northward (Aieta and Oliveira 2009).

Mean parasite intensity in female Chesapeake Bay American eels had a significant negative correlation with female size-class (Figure 5), which is opposite the trend observed by Moser et al. (2001) in North

Carolina. A negative association between size and parasite infection might occur if *Anguillicola crassus* diminished the growth or increased the mortality of infected American eels. Thus, survivors or fast-growing American eels would be those that had avoided parasitism. However, we found that among subestuaries, parasitism was unrelated to growth or mortality. In addition, American eels with swim bladder damage (based on SBtt score) did not differ in age or growth rate relative to individuals that lacked swim bladder damage. Although the strong correlation between parasite intensity and SBtt supports a cause-and-effect relationship, little is known about how rapidly swim bladder damage occurs in response to repeated infections or whether swim bladders can recover to a healthy condition. A controlled laboratory study of parasitism would be beneficial in our understanding of *Anguillicola crassus* parasitism effects on swim bladder histology and function in American eels.

Between summer and fall, we observed that parasite intensity and swim bladder damage decreased for two Chesapeake Bay tributaries, a trend that was also detected in European eels by Lefebvre et al. (2002). Those authors hypothesized that the observed decrease in swim bladder damage might be the result of mortality of infected European eels. However, the current study did not support this inference, which would have been evident through either differences in loss rates among subestuaries or a truncated age distribution of those individuals exhibiting heavily damaged swim bladders. Duration of the *Anguillicola crassus* life cycle is influenced by temperature; cooler water reduces hatching of the juvenile parasite and thus reduces recruitment of the parasite to intermediate hosts (De Charleroy et al. 1990; 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 swim bladder condition during fall is that swim bladder damage in individuals is reversible within a span of several months.

Conclusions and Implications

American eels in the Chesapeake Bay subestuaries and bay regions exhibited different growth, gender, parasitism, and condition levels. 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. 2009). The presence of male and female American eels in the Chesapeake Bay subestuaries suggests that the Chesapeake Bay is contributing to male and female spawner

escapement. High growth rates relative to other estuaries and the mix of male and female American eels among subestuaries point to the Chesapeake Bay as a central growth habitat that is critical for sustained escapement of American eel spawners.

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