Assessment of Reintroduction of American Eel into Buffalo Creek (Susquehanna River, Pennsylvania)

Joshua J. Newhard,* Julie Devers, Steve Minkkinen, Mike Mangold

U.S. Fish and Wildlife Service, Maryland Fish and Wildlife Conservation Office, 177 Admiral Cochrane Drive, Annapolis, Maryland 21401

Current address of J. Devers: U.S. Department of Agriculture, Natural Resources Conservation Service, 339 Busch’s Frontage Road, Suite 301, Annapolis, Maryland 21409

Abstract

American Eel *Anguilla rostrata* populations along the Atlantic coast of the United States have been in decline over the past several decades. One suggested cause of the decline is construction of barriers that block access to upstream tributaries where they can spend a significant portion of their lives. Success of reintroduction efforts above barriers has rarely been evaluated. Within the Susquehanna River (Chesapeake Bay watershed), over 1 million eels were released above four major downstream barriers in the past decade. We used backpack electrofishing and tagging to monitor growth, sexual differentiation, and population density of reintroduced eels in Buffalo Creek, a tributary to the Susquehanna River (Pennsylvania). From 2012 to 2019, we caught over 2,000 individuals, tagged more than 1,800, and recaptured 229. Recaptured eels provided insight into growth, sexual differentiation, and movement. Nearly 99% of recaptures remained near stocking locations. The average growth rate was 47.8 mm/y and ranged between −5.8 and 116.0 mm/y. Females generally grew significantly faster than males, and growth rates of several females exceeded 100 mm/y, a rate typically associated with estuarine residents. The population density within stocking sites was over 2,300 eels/km, roughly four times higher than Susquehanna River tributaries below the most downstream dam, and exceeded the target stocking goal of 529 eels/km. While we caught most eels in areas sampled near stocking locations, we captured some eels in smaller upstream tributaries away from stocking locations. Our study is the first to examine how reintroduced eels grow following stocking above four major dams on the Susquehanna River. We suggest that managers considering moving eels above blockages account for release location and density to achieve desired benefits to the overall population.

Keywords: American Eel; PIT tagging; fish passage

Introduction

In the 20th century, American Eel *Anguilla rostrata* populations declined along the Atlantic coast and remain depleted (ASMFC 2017). Before the decline, American Eel (hereafter, eel) comprised more than 25% of fish biomass in streams of the Mid-Atlantic region (Smith and Saunders 1955; Ogden 1970). Factors that contributed to their decline include overharvest, poor water quality, habitat loss from fragmentation by blockages, and turbine mortality in hydroelectric power stations during downstream migration (ASMFC 2017). The Chesapeake Bay and its tributaries support a large portion of the coastwide eel population. The Susquehanna River constitutes 43% of the Chesapeake Bay watershed, but Conowingo Dam, a large (>28 m)
hydropower dam at river kilometer 16, blocks upstream passage to most of the river. Fish passage facilities at Conowingo (and three additional upstream hydropower dams) were designed to pass migrating alosine adults (Alosa spp.) but are unable to pass eels (Sheldon 1974). To remedy this, eels are captured at Conowingo Dam and moved upstream above blockages. Over 17 million eels were intermittently released from 1936 to 1980 (Miller et al. 2010), with a renewed annual effort beginning in 2007 (Reily and Minkkinen 2016).

In large rivers where eel movement is not blocked by barriers, growth, density, and sex ratio can vary between upstream and downstream areas (Goodwin and Angermeier 2003). In upstream areas, population densities are lower, females predominate, and individuals have slower annual growth depending on latitude (Goodwin and Angermeier 2003; Morrison and Secor 2003; Jessop 2010; Jessop et al. 2004). Where movement is prohibited, demographic differences between upstream and downstream areas of a barrier can be dramatic. Population densities downstream of barriers can be artificially high, thereby causing slow growth and low survival (Machut et al. 2007). Currently, many upstream eel passage operations occur along the Atlantic coast. However, few studies have assessed upstream relocation into previously occupied watersheds, and the studies that do exist have been at latitudes north of the Susquehanna River Basin (St. Lawrence River and Lake Ontario, Canada). Results of those studies suggest that growth rates were high after stocking into lakes but not rivers (Verreault et al. 2009; Pratt and Threader 2011). Relocating eels in upstream watersheds above blockages was assumed to increase the female population, because females were prevalent in other nearby watersheds without barriers. However, some relocated eels developed into males (Verreault et al. 2009; Côté et al. 2015). Targeted relocation in the Susquehanna River has occurred for over a decade. However, growth and sexual differentiation is unknown because elvers (juvenile eels) are likely not sexually differentiated before their release (Krueger and Oliveira 1999). Information on such demographics is necessary to guide efforts that are underway, including transport of elvers above barriers, which is assumed to increase female abundance (Sweka et al. 2014).

The preclusion of eels from upstream habitats likely had a profound effect on ecosystem function, as they are a host fish to the freshwater mussel Eastern Elliptio Elliptio complanata (Lellis et al. 2013). In many Atlantic draining watersheds, Eastern Elliptio comprise the most abundant biomass of any fauna in the watershed and can provide great filtration capacity (Kreeger et al. 2018). However, Eastern Elliptio is less abundant in the Susquehanna River than in nearby watersheds (Blakeslee et al. 2018), presumably in part due to the lack of eels. From 2008 to 2019, a long-term study evaluated eel as a host fish to Eastern Elliptio in the Susquehanna River watershed (Lellis et al. 2013; Galbraith et al. 2018). One objective of that study was to determine if increasing eel abundance would increase recruitment of Eastern Elliptio. Localized abundance was increased by relocating eels into Buffalo Creek (Union County, Pennsylvania) and Pine Creek (Tioga County, Pennsylvania), which are both upstream of the four mainstem dams in the Susquehanna River.

Before 2010, post-relocation assessment was relatively difficult due to the width and depth of stocking locations in the Susquehanna River. Beginning in 2010, eels were released into Buffalo Creek for the freshwater mussel study, with the assumption that they would disperse throughout the watershed, reaching a target density of 529 individuals per stream kilometer, similar to Susquehanna River tributaries below Conowingo Dam (Galbraith et al. 2018). Relocation of eels into wadable reaches of Buffalo Creek provided an opportunity to examine movement, sexual differentiation, growth, and population density of reintroduced eels. Our objectives were to quantify growth rates, sexual differentiation of individuals, and population density following reintroduction into Buffalo Creek. We hypothesized that most individuals would be female and growth rates would be high, given the presumed absence of eels in Buffalo Creek before stocking.

**Methods**

**Near stocking site assessment**

From 2010 to 2013, we released over 118,000 eels into Buffalo Creek. There were two stocking locations within Buffalo Creek, Swinging Bridge and Prison (SB and P, respectively; Figure 1). Between 2010 and 2012, we released all eels downstream of site SB but upstream of site P (2010: 24,874 eels; 2011: 46,538 eels; 2012: 16,716 eels). In 2013, we released all fish at site P (N = 30,614). Most eels were pigmented elvers (total length [TL], 80–130 mm) except for 9,000 glass-stage (nonpigmented)
eels (\~56 mm) released in 2010 at SB (Minkkinen et al. 2020).

We conducted annual assessments between 2012 and 2019. We sampled in late August or early September of each year, except for in 2014 when we sampled in late October. We chose sites near release locations (Figure 1) to maximize capture potential and determine if eels remained in the immediate area after their release. We conducted a single pass using two backpack electrofishers (Smith-Root, Seattle, WA) over a defined area at each site for a total area sampled of 1.88 ha (SB: 0.64 ha; P: 1.24 ha). Sample sites were the same between years except in 2014, when we could only sample a downstream portion of SB. We recorded shock seconds and backpack settings to standardize electrofishing efforts across years.

Following capture, we placed fish in a bucket with water or in an aerated livewell placed in situ. After sampling, we anesthetized eels with Aqui-S 20E (Aquatactics, Kirkland, WA), a clove oil derivative (used under Investigational New Animal Drug permit 11-741). We measured all individuals for TL (mm), and we tagged those greater than 200 mm using a passive integrated transponder (PIT) tag (Biomark, Boise, ID). We only tagged eels longer than 200 mm to minimize potential sublethal effects of tagging. We tagged individuals ranging between 200 and 300 mm in TL with an 8-mm tag to reduce the potential for injury, and we used a 12-mm tag for those longer than 300 mm. We inserted all tags into the musculature near the insertion of the dorsal fin. After tagging, we scanned eels to confirm PIT tag presence, and PIT tag number was recorded. We then put tagged fish into an aerated recovery tank until they resumed activity. We released all individuals at their capture site and noted and removed any mortalities from the population of tagged eels. After our first survey year, we scanned all captured eels for PIT tags before measurement. If a PIT tag was present, we recorded the individual as a recapture and no new tag was inserted. We assumed all captured fish had been previously stocked into Buffalo Creek and had not immigrated from other Susquehanna River stockings.

When possible, we externally identified sex for each individual. We assumed that silver-phase (i.e., sexually mature adult) eels that were less than 400 mm in TL were male, while we assumed that those that were in yellow phase (i.e., sexually immature adult) and greater than 450 mm were female (Krueger and Oliveira 1997). We did not assign sex for individuals that did not meet either of these criteria. We distinguished silver-phase males from other yellow-phase individuals by their enlarged eye, lighter-colored ventral side, pronounced golden band along the lateral line (Figure 2), and thicker skin (noted at the time of needle insertion during PIT tagging).

Beginning in 2015 (when silver males were first

Figure 2. Photographs of American Eel Anguilla rostrata collected during backpack electrofishing surveys from 2012 to 2019 to assess reintroduction in Buffalo Creek (Susquehanna River, Pennsylvania). Both individuals are similar in length (less than 400 mm) with the top photo of a silver male (sexually mature adult). Note the enlarged eye and lighter-colored ventral side of the silver-phase compared with the yellow phase (sexually immature adult) photo on bottom. The sex of the yellow-phase American Eel was not assigned.
identified), we sacrificed and dissected a subsample of eels to determine accuracy of external sex identification.

We measured growth rates by subtracting initial TL from recapture TL and dividing by the number of days between encounters. We then standardized daily growth rates to 1 y and reported rates as mm/y. For eels recaptured multiple times, we calculated the average growth rate per individual for analysis. Growth rates were not normally distributed, and various transformations did not fit normal distributions (examined via Shapiro–Wilk tests; all tests resulted in P < 0.05). Therefore, we compared growth rates between sexed (male, female) and unsexed (unknown) individuals using a Kruskal–Wallis test. We conducted Conover–Iman tests post hoc to test for significant differences between groups. Additionally, to account for potential growth differences due to length, we compared growth rates of similarly sized eels using four length groups. We grouped individuals by TL at initial tagging into four categories: 1) less than 250 mm, 2) 250–299 mm, 3) 300–349 mm, and 4) 350–399 mm. We did not compare fish longer than 400 mm because we assumed they were all females or the sex was unknown. For comparison among size groups, we also used Kruskal–Wallis tests and post hoc Conover–Iman tests. We conducted analyses in Systat (version 13.0).

We estimated the abundance and survival of eels by fitting Jolly–Seber mark–recapture models (Jolly 1965; Seber 1965) to our data. Assumptions of Jolly–Seber mark–recapture models include that 1) capture probability and survival rate are the same for marked and unmarked individuals, 2) marked eels retain their mark throughout the experiment, 3) tags are read properly, and 4) the study area is constant over time. Because Jolly–Seber models cannot distinguish true death from emigration, we considered survival (\( N \)) and apparent survival (\( \phi N \)), not true survival. Abundance (\( N \)) is the estimated abundance at the start of the study (2012). Additional parameters of the model we estimated include capture probability (\( p \)) and population growth (\( \lambda \)). We compared a suite of models ranging from those that calculated year-specific estimates of survival, capture probability, and population growth with those that had constant rates over all years. We used Akaike’s information criteria corrected for small sample size (AIC\(_c\)) to identify the best-fit model (Burnham and Anderson 1998). We then used abundance estimates from mark–recapture models to estimate two measures of population density. We divided population size by total area (1.88 ha) or stream length (1.4 km) sampled to compare densities with other published studies. We conducted all mark–recapture analyses in program MARK (White and Burnham 1999).

**Upstream assessment**

Between 2017 and 2019, we sampled 12 sites in upstream areas of Buffalo Creek (Figure 1). We selected these sites based on accessibility and representation of a range of stream orders and distances from stocking locations. At each site, we used one or two backpack electrofishers depending on stream width. We sampled each site in an upstream direction for approximately 20 min. We followed the same procedures for eel handling and tagging as the assessments of near-stocking locations.

**Results**

**Near stocking site assessment**

At sites sampled near stocking locations, we captured 2,339 eels between 2012 and 2019. We tagged 1,838 of those eels and did not tag the remaining 501. TL of all individuals ranged from 101 to 805 mm. Relative abundance at both sites generally increased each year until 2017, after which catch per unit effort (CPUE) markedly decreased (Table 1). In 2019, we recorded our lowest CPUE. The average and range of TL generally increased over time (Figure 3). In 2019, the median TL

### Table 1. Yearly catch, effort, and relative abundance data (catch-per-unit effort; CPUE, eels/h) for American Eel *Anguilla rostrata* captured during backpack electrofishing surveys to assess reintroduction of American Eel in Buffalo Creek (Susquehanna River, Pennsylvania) from 2012 to 2019.

| Year | Eels caught | CPUE |
|------|-------------|------|
| 2012 | 233         | 34.8 |
| 2013 | 295         | 44.4 |
| 2014 | 313         | 57.5 |
| 2015 | 432         | 64.6 |
| 2016 | 457         | 54.1 |
| 2017 | 515         | 55.5 |
| 2018 | 217         | 29.8 |
| 2019 | 141         | 19.8 |

**Figure 3.** Box plot of total lengths of all American Eel *Anguilla rostrata* captured during backpack electrofishing surveys to assess reintroduction in Buffalo Creek (Susquehanna River, Pennsylvania) from 2012 to 2019. The line inside the box represents median total length (mm), while the lower and upper bounds of the box represent the 25th and 75th percentiles, respectively. Extended lines represent the 10th and 90th percentiles.
was highest at 434 mm. In 2017, we captured the largest individual (805 mm). We caught smaller individuals less frequently over time (Figure 4). Between 2012 and 2014, 90% of fish were shorter than 350 mm, whereas by 2019, 90% were longer than 350 mm (Figure 4).

Of the 1,755 individuals that we tagged from 2012 to 2018, we recaptured 229 unique fish (13.0% unique recapture rate). Of those recaptured multiple times, we recaptured 30 individuals two times, 4 individuals three times, and 1 individual four times. Most recaptures occurred 1 y following release (Table 2). The maximum time at large was 7 y, the full period of our study. We recaptured three eels (1.1%) away from their initial tagging site. Each of these moved upstream from site P to site SB.

We were able to identify the sex of some stocked eels as early as 2012, when sampling began. The first individuals were all large (>495 mm in TL) females. We did not identify any silver males until 2015 (Table 3). We could only assign sex to 10% or less of annual catches until 2017. In 2019, we assigned sex to more than half of all eels. Over time, females were more abundant (Table 3) and constituted 32% of total catch in 2019 (~20%). Assignment of sex based on external criteria was 100% correct based on dissections of 43 sacrificed eels.

The average growth rate was 47.8 mm/y (SD = 23.1). Growth rates ranged from –5.8 to 116.7 mm/y. Only one individual had negative growth, which could be due to measurement error. The lowest nonnegative growth rate was 2.1 mm/y (N = 2). Growth rate significantly differed among sexes for all pooled data (Kruskal–Wallis H = 74.773, P < 0.001; Conover–Iman tests P < 0.001). Sex-specific growth rates overlapped (Figures 5 and 6), but females grew significantly faster than males and unsexed individuals. Females grew at an average rate of 69.7 mm/y (SD = 20.5), while males grew the slowest at an average rate of 32.0 mm/y (SD = 9.6). Unsexed eels grew at an average rate of 43.9 mm/y (SD = 20.9).

Females grew significantly faster than males for all length groups except for the smallest one (shorter than 250 mm; Kruskal–Wallis H = 5.028, P = 0.072; Figure 5). Notably, the sample size was lower for males in this group (N = 2) than for females (N = 9) and unsexed eels (N = 33). For fish 250–299 mm in TL, females grew significantly faster than males and unsexed individuals (Kruskal–Wallis H = 12.209, Conover–Iman tests P < 0.010). For eels 300–349 mm in TL, females also grew significantly faster than males and unsexed eels (Kruskal–Wallis H = 20.947, Conover–Iman tests P < 0.001). Females grew significantly faster than males but not unsexed eels for eels that were 350–399 mm in TL (Kruskal–Wallis H = 7.018, male–female Conover–Iman test P = 0.006). As males approached our assumed asymptotic length of 400 mm, their growth rates declined (Figure 6). Eels that we initially

**Table 2.** Yearly number of releases and recaptures for American Eel *Anguilla rostrata* tagged at two sites to assess reintroduction of American Eel in Buffalo Creek (Susquehanna River, Pennsylvania) from 2012 to 2019.

| Release year | Tags released | 2013 | 2014 | 2015 | 2016 | 2017 | 2018 | 2019 | Recapture rate* |
|--------------|---------------|------|------|------|------|------|------|------|----------------|
| 2012         | 174           | 11   | 6    | 4    | 3    | 2    | 2    | 3    | 17.8           |
| 2013         | 168           | —    | 6    | 3    | 3    | 3    | 1    | 4    | 14.0           |
| 2014         | 171           | —    | —    | 9    | 4    | 1    | —    | —    | 7.9            |
| 2015         | 320           | —    | —    | 11   | 9    | 4    | 2    | 3    | 18.1           |
| 2016         | 324           | —    | —    | —    | 31   | 21   | 4    | 2    | 13.0           |
| 2017         | 434           | —    | —    | —    | —    | 42   | 13   | 11   | 20.4           |
| 2018         | 162           | —    | —    | —    | —    | —    | 10   | 14   | 11.3           |

*Recapture rate (%) is specific to each release year.

**Figure 4.** Percentage of American Eel *Anguilla rostrata* captured near release locations from backpack electrofishing surveys to assess reintroduction in Buffalo Creek (Susquehanna River, Pennsylvania) from 2012 to 2019 by length frequency category (in mm).

**Table 3.** Proportion of total catch of American Eel *Anguilla rostrata* by sex captured via backpack electrofishing to assess reintroduction of American Eel in Buffalo Creek (Susquehanna River, Pennsylvania) from 2012 to 2019.

| Year   | Female | Male |
|--------|--------|------|
| 2012   | 0.017  | 0.000|
| 2013   | 0.017  | 0.000|
| 2014   | 0.019  | 0.000|
| 2015   | 0.039  | 0.090|
| 2016   | 0.035  | 0.070|
| 2017   | 0.101  | 0.082|
| 2018   | 0.198  | 0.101|
| 2019   | 0.319  | 0.199|
tagged near 400 mm in TL and later identified as female typically had growth rates higher than 40 mm/y. We had one large female tagged at a length of 576 mm, and it had one of the slowest growth rates for females (24.0 mm/y; Figure 6).

Only two mark–recapture models successfully converged. The best fit model (AICc weight = 0.86; ΔAICc = 3.68) was over six times more supported than the second model (AICc weight = 0.14). The best-fit model included time-varying capture probability and constant survival and population growth. Apparent survival was 0.52 (SE, 0.03; 95% CI, 0.46–0.58), and we estimated abundance (in 2012) as 3,259 (SE, 700; 95% CI, 2,163–4,960). Population density across both tagging sites was 1,734 eels/ha (95% CI, 1,150–2,638) or 2,328 eels/km (95% CI, 1,545–3,543), exceeding the management goal of 529 eels/km. The population growth rate between 2012 and 2019 was 0.88 (SE, 0.04; 95% CI, 0.82–0.96). Capture probabilities generally increased over time from a minimum of 0.05 in 2012 to 0.13 in 2019, with peak capture probability in 2017 (0.29; Table 4).

**Upstream assessment**

Between 2017 and 2019, we captured 61 eels at 10 of 12 sites in upper Buffalo Creek. Relative abundance ranged from 1.5 to 14.0 eels/h (mean = 4.7, SD = 3.3; Table 5), which is lower than sites sampled near release locations (see Table 1). Relative abundance increased over time at sites 2, 5, 8, and 11. We did not capture eels at sites 1 and 10. Relative abundance varied over time at other sites (Table 5).

We tagged all captured eels as TLs ranged from 232 to 700 mm (mean = 473.1 mm, SD = 121.1; Figure 7). We recaptured two eels at upstream sites (one at site 5 and one at site 4, both in 2019). One recaptured eel escaped before being measured. The other recaptured eel, a 575-mm female when recaptured in 2019, grew at a rate of 112.5 mm/y. We did not assign sex when it was tagged in 2017 at 340 mm. Females comprised a larger portion of the catch at upstream sites than at downstream sites. The annual proportion of females was 45% in 2017, 59% in 2018, and 63% in 2019. We only captured one silver male, which was at site 12 in 2019.

**Discussion**

**Near stocking site assessment**

Eels stocked into Buffalo Creek grew and survived for years following their reintroduction. Relative abundance

| Parameter | Estimate | SE   | 95% CI          |
|-----------|----------|------|-----------------|
| $\phi$    | 0.52     | 0.03 | 0.46–0.58       |
| $P_{2012}$| 0.05     | 0.01 | 0.03–0.08       |
| $P_{2013}$| 0.06     | 0.01 | 0.04–0.09       |
| $P_{2014}$| 0.15     | 0.02 | 0.12–0.19       |
| $P_{2015}$| 0.18     | 0.02 | 0.15–0.23       |
| $P_{2016}$| 0.29     | 0.03 | 0.23–0.35       |
| $P_{2017}$| 0.14     | 0.02 | 0.11–0.18       |
| $P_{2018}$| 0.13     | 0.02 | 0.10–0.18       |
| $\lambda$ | 0.88     | 0.04 | 0.82–0.96       |
| $N$       | 3,259    | 700  | 2,163–4,960     |

* Parameter estimates include apparent survival ($\phi$), year-specific capture probability ($P$), population growth rate ($\lambda$), abundance in 2012 ($N$), and their associated standard error (SE) and 95% confidence interval (CI).
and length of individuals increased over time, suggesting that eels resided and grew near release locations. Abundances were highest near release locations, suggesting that eels may not distribute evenly throughout a watershed after being released. The total catch increased between 2012 and 2017. Although we stocked eels in Buffalo Creek in 2013 and in the mainstem Susquehanna River from 2013 to 2019, the increase in catch between 2012 and 2017 may not have been due to increasing abundance within Buffalo Creek. Instead, the increase may be due to recruitment of larger fish (>200 mm) to electrofishing gear (Price and Peterson 2010). Estimated capture probabilities reflect a similar pattern, increasing each year until 2017, after which they declined (Table 5). Additionally, if increased catch rate was due to increasing abundance from other stockings, smaller eels (shorter than 350 mm) would likely be abundant. However, after 2014, the abundance of smaller eels declined (Figure 4), while catch rates increased. This further suggests that larger eels may be more easily captured than smaller eels. Regardless, increased catch rates suggest that eels stayed near stocking locations and continued to grow in those areas.

Catch rates began to decline in 2018. Lower CPUE in 2018 could have been due to substantially higher than normal flows that made sampling difficult. Stream flow data are not available for Buffalo Creek, but a stream gauge from nearby Penns Creek, Pennsylvania, suggests that 2018 flows were at least four times higher than normal (USGS 2020). However, CPUE was also low in 2019, which cannot be attributed to high flows. Flow at the nearby gauge in Penns Creek was similar to all other sampling years, except for 2018 (USGS 2020). Likewise, flows in Buffalo Creek in 2019 were near their lowest of any sampling years. It is likely that the reduction in catch rate is because adult eels are beginning to leave Buffalo Creek to migrate back to the Atlantic Ocean. Population growth rate was below one during the study period, which means the reduction in catch could mirror that of a diminishing population. Silver males observed since 2015 as well as large females may have left Buffalo Creek to migrate to the Sargasso Sea. Additionally, a new study that began in 2020 to remotely monitor downstream migration of PIT-tagged eels at the mouth of Buffalo Creek recorded 12 adults leaving the creek (J. Newhard, unpublished data). Reduced abundance in recent years suggests that some individuals are leaving the watershed, likely to migrate downstream to the Atlantic Ocean.

The growth rates that we observed in Buffalo Creek were relatively high compared with nonstocked eel populations in freshwater streams (Oliveira and McCleave 2002; Jessop et al. 2004). Faster growth rates of stocked eels may lead to migrations at younger ages, because growth rate is inversely related to age at spawning migration (Jessop et al. 2004). If fish were 1 y old or less at the time of stocking, they would have been more than 10 y old by 2019, which is an age when spawning migration may begin (Jessop et al. 2008). Elvers captured at Conowingo Dam in 2019 ranged between 1 and 4 y old (86% were 1 to 2 y old) and had similar lengths to elvers stocked into Buffalo Creek (Normandeau 2019). More importantly, size may be a greater factor than age for determining when downstream migration begins (Oli-

| Sample site | Catch 2017 | CPUE 2017 | Catch 2018 | CPUE 2018 | Catch 2019 | CPUE 2019 |
|-------------|------------|-----------|------------|-----------|------------|-----------|
| 2           | 1          | 1.5       | 1          | 2.4       | 1          | 2.4       |
| 3           | 5          | 3.1       | 2          | 3.1       | 4          | 5.7       |
| 4           | 3          | 9.3       | —          | —         | 1          | 3.4       |
| 5           | 2          | 3.2       | 8          | 11.9      | 8          | 14.0      |
| 6           | 1          | 3.1       | —          | —         | —          | —         |
| 7           | 1          | 1.5       | —          | —         | 1          | 1.5       |
| 8           | 3          | 3.0       | 3          | 4.3       | 4          | 5.1       |
| 9           | 1          | 1.6       | —          | —         | —          | —         |
| 11          | 1          | 1.7       | 1          | 5.1       | 2          | 5.7       |
| 12          | 5          | 6.8       | 2          | 2.9       | 3          | 4.1       |

* No eels were captured at sites 1 or 10, and those sites are not listed.

Figure 7. Length–frequency histogram for all American Eel Anguilla rostrata captured during upper watershed backpack electrofishing surveys to assess reintroduction in Buffalo Creek (Susquehanna River, Pennsylvania) from 2017 to 2019.
The fast growth recorded in Buffalo Creek may have a significant impact on eel management in dammed watersheds. An egg-per-recruit model for evaluating the benefits of relocating eels in the upper Susquehanna River against their possible downstream mortality at hydroelectric dams assumed that growth rate in the upper basin was significantly lower than downstream of Conowingo Dam (Sweka et al. 2014). This follows a general assumption that eels in downstream freshwater watersheds or in brackish estuaries have faster growth than those found in small upstream freshwater tributaries (Morrison and Secor 2003; Jessop et al. 2009). However, growth rates of many females and the average growth rate of all eels in Buffalo Creek were similar to those of other Chesapeake Bay tributaries (Fenske et al. 2010). The model also assumed that maximum size and associated eggs per recruit were larger for eels in the upper Susquehanna River and that individuals in upstream areas would take longer to mature than those downstream (Sweka et al. 2014). However, growth rates that we observed in Buffalo Creek suggest the time to maturation may be less than assumed in the model for the Susquehanna River, which would subsequently reduce assumed natural mortality (Sweka et al. 2014). Further, faster than expected growth may result in higher than expected eggs per recruit for reintroduced eels and thereby increase the overall benefit of reintroduction to upstream areas of the Susquehanna River.

Limited studies of eel reintroductions have found elevated growth rates like those in Buffalo Creek. For example, growth rates of eels released into the St. Lawrence watershed ranged between 60 and 120 mm/yr (Verreault et al. 2009; Pratt and Threader 2011), higher than previously published studies (Helfman et al. 1987; Oliveira and McCleave 2002; Morrison and Secor 2003). Reintroduced eels likely grow faster than expected at low density (compared with high density below blockages) as an expected density-dependent response. For example, introduced populations of other aquatic species often grow faster than populations in the native range (Sakaris et al. 2006; Pintor and Sih 2011). Additionally, eel growth is faster above barriers where density is low (Machut et al. 2007). Density near release locations in Buffalo Creek is at least three times higher than some other watersheds along the Atlantic coast (Morrison and Secor 2004; Hightower and Nesnow 2006), and therefore reduced density alone may not explain fast growth in Buffalo Creek (although densities at Conowingo Dam are unknown). The Buffalo Creek density is likely artificially high due to the large number of eels released directly into two locations, and thus we cannot make comparisons to more natural low-density habitats. Moreover, site selection was not random, as sites were chosen to maximize potential eel capture by sampling near release locations.

The peak in silver male proportion in 2019 (20%) is higher than is generally assumed for freshwater tributaries, where lower densities typically favor the development of females (Davey and Jellyman 2005), although this remains contested (Côté et al. 2015). If sex is genetically determined at earlier life stages, sex of elvers may have been determined before stocking into Buffalo Creek. However, if sex determination occurs after the elver stage and is determined by population density, as has been suggested (Krueger and Oliveira 1999), we would need to carefully consider stocking density on a broader scale within the Susquehanna if relocation above blockages is used as a management tool to increase female abundance. Density near Buffalo Creek stocking locations may be unexpectedly high given that 99% of recaptures were at the same site as original tagging. To achieve a more natural density, we may need to spatially spread out future stockings into small tributaries, following similar stockings of eels elsewhere (Verrault et al. 2009; Pratt and Threader 2011). It is likely that as emigration occurs from release locations in the mainstem Susquehanna to smaller tributaries, we may observe lower densities similar to other undammed rivers.

The proportion of eels that become female is an important parameter of egg-per-recruit models, especially if the model assumes all relocated eels become female (e.g., Sweka et al. [2014]), which did not occur in Buffalo Creek. Increased sexual diversity would reduce the number of eggs per recruit estimated in such models, which would subsequently impact management decisions related to moving eels upstream of barriers. As in our study, other studies that examined the sex of relocated eels also found males to be more prevalent than expected (Pratt and Threader 2011). Such results could help refine existing (e.g., Sweka et al. [2014]) and future models to better estimate the effects of reintroduction on the coastwide population.

In addition to silver males, large females were present over time. Nearly one-third of eels were female in 2019, which was similar to an earlier estimate (35%) of relocated eels (Côté et al. 2015). As males emigrate from Buffalo Creek, the proportion of females remaining may increase if no new male migrants enter the population and females do not leave the sampling area. Silver-phase females have not been found in Buffalo Creek, although many of the largest individuals are large enough for downstream migration (Oliveira 1999; Jessop et al. 2004). Many eels remain in Buffalo Creek that are unable to be externally sexed (nearly 50% in 2019). As these continue to grow, they will be large enough to be externally sexed. Additionally, as mature adults leave Buffalo Creek, sex ratio may change if emigration rates differ between sexes. Of the 12 eels recorded migrating downstream (see above), 7 are female, 1 is male, and 4 are not known (J. Newhard, unpublished data). Future sampling will reveal how sex ratio changes as the remaining eels grow and downstream migration is monitored.
Females grew faster than males at all sizes except those shorter than 250 mm, as has generally been found in other studies (Oliveira 1999; Fenske et al. 2010). For example, females grew faster than males as females became larger (Oliveira and McCleave 2002). Further, females are typically older and larger at maturation than males (Helfman et al. 1987). Therefore, the risk-prone approach of growing fast may be more appropriate for females, because they outgrow the most vulnerable size classes at a younger age. Trade-offs associated with faster growth include increased vulnerability to predation during more frequent or longer duration feeding times and slower developmental rate (Arendt and Wilson 1997). Because females take longer to reach sexual maturity, they may be able to survive these trade-offs. Within relatively small streams, large eels are unlikely to be consumed by piscivores, which are likely not as abundant as in larger waterbodies. Additionally, growing to a larger size may allow them to avoid competition for resources with similar or smaller-sized individuals. Larger eels may become partly piscivorous after reaching lengths of at least 400 mm, a size that most males do not achieve (Oliveira and McCleave 2002). Conversely, males mature at a younger age and smaller size and therefore may take the risk-averse strategy of slower growth. The contrast in growth rates between sexes may change over time because we have not yet found silver-phase females in Buffalo Creek. As females grow and sexually mature, their growth rate would likely slow (Oliveira and McCleave 2002; Fenske et al. 2010), which would influence differences in sex-specific growth rates. Furthermore, males may have grown more slowly as they approached their asymptotic length and prepared for downstream migration, when feeding typically ceases (Oliveira and McCleave 2002). However, as expected, of the individuals that we first tagged when we could not identify sex (i.e., most eels less than 350 mm), females grew significantly faster than males (Figure 5).

**Upstream assessment**

Eels colonized many areas upstream of release locations in Buffalo Creek. On average, individuals captured at upstream locations were larger than those captured near release sites. In addition, the proportion of females was higher at upstream sites (up to 63%) than at downstream sites, which supports a hypothesis that smaller, freshwater tributaries are dominated by females (Helfman et al. 1987). Upstream movement may be driven by reduced competition, perhaps leading to higher growth rates in those habitats. The only silver male that we observed at an upstream site was at the site closest to release locations, where males were common. The one recaptured female grew at a similar high growth rate (>100 mm/y) as those near release locations.

Relative abundance at upstream sites was much lower than release locations, which suggests that relocated eels rarely migrated upstream. Eels relocated to a Canadian lake also did not migrate far (<3 km over 4 y) from release locations (Verreault et al. 2009). Stocking density may influence how far eels move, as for European Eels Anguilla anguilla where high downstream density caused juveniles to migrate upstream (Berg and Jørgensen 1994). Within Buffalo Creek, stocking density (minimum = 350 eels/ha; maximum = 2,100 eels/ha; J. Newhard, unpublished data) was much higher than another study where eels were stocked into a lake (100 eels/ha; Verreault et al. 2009). Although population density within Buffalo Creek appears to be high, perhaps the stocking density of eels into Buffalo Creek was not high enough to cause eels to move far from release areas. If areas near stocking locations are highly productive, they may support a higher than expected density of eels (Wiley et al. 2004). While unknown, if productivity of Buffalo Creek was high, upstream movement may not be favored given enough resources to support the observed high densities. Additionally, we assumed movement was upstream only, so we did not monitor areas downstream of release locations, but we recognize that eels may have moved downstream.

**Management implications**

We were apparently successful in reintroducing eels into Buffalo Creek, given that eels are surviving and growing in the watershed. Additionally, some silver males and large females likely migrated downstream to reproduce. We have not yet observed mature, silver-phase females, but they are likely to be caught in the coming years as females approach their asymptotic length. Relocating eels has also been successful in increasing the recruitment of freshwater mussels, the primary goal of stocking into Buffalo Creek (Galbraith et al. 2018). Ultimately, the goal of relocating eels above barriers is to increase production of the coastwide population. Assessment of female size at maturity, fecundity, and downstream migration success is needed to determine if reintroduced eels contribute to the overall population. Many studies demonstrate how barriers restrict eel movement (Goodwin and Angermeier 2003; Machut et al. 2007; Hitt et al. 2012), and efforts are encouraged to increase upstream and downstream passage of eels where barriers exist (ASMFC 2017). Our study sheds light on how reintroduced eels may fare in freshwater tributaries upstream of barriers. Stocking density may influence sex ratios and growth rates, and research is underway that may offer insight to that effect. Additional research is needed to examine the proportion of relocated eels in other areas that become female and attempt to migrate back to the Atlantic Ocean. Furthermore, efficiency of downstream passage at hydrofacilities will need to be assessed to increase and ensure the survival of mature adults returning to spawn in the Atlantic Ocean.

**Supplemental Material**

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supplemental material. Queries should be directed to the corresponding author for the article.

Data S1. All individual tagging and length data collected during electrofishing surveys to assess reintroduction of American Eel Anguilla rostrata in Buffalo Creek (Susquehanna River, Pennsylvania) from 2012 to 2019.

Data S2. All site survey data from backpack electrofishing surveys conducted to assess American Eel Anguilla rostrata reintroduction in Buffalo Creek (Susquehanna River, Pennsylvania) from 2012 to 2019.

Data S3. Encounter history file used for Jolly–Seber mark–recapture analysis to assess American Eel Anguilla rostrata reintroduction in Buffalo Creek (Susquehanna River, Pennsylvania) from 2012 to 2019.

Reference S1. Minkkinen SP, Devers JL, Newhard J, Galbraith HS. 2020. Experimental stocking of American eels in the Susquehanna River watershed. Final report for mitigation project for city of Sunbury, Riverbank Stabilization Project.

Reference S2. Normandeau Associates. 2019. Muddy Run pumped storage project Conowingo Eel Collection Facility. Washington, D.C.: Federal Energy Regulatory Commission, Project 2355.

Reference S3. Reily C, Minkkinen S. 2016. American Eel: collection and relocation Conowingo Dam, Susquehanna River, Maryland 2016. Annapolis, Maryland: U.S. Fish and Wildlife Service report.

Reference S4. [USGS] U.S. Geological Survey. 2020. National water information system data available on the world wide web (USGS Water Data for the Nation). Available: https://waterdata.usgs.gov/pa/nwis/uv?site_no=01555000 (March 2021).

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