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Heather Hildebrand
West Virginia University

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Size, age composition, and upstream migration of American eels at the
Millville Dam eel ladder, Shenandoah River, West Virginia

Heather Hildebrand

Thesis submitted to the
Davis College of Agriculture, Forestry, and Consumer Sciences
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in partial fulfillment of the requirements
for the degree of

Master of Science
in
Wildlife and Fisheries Resources

Stuart A. Welsh, Ph.D., Chair
Patricia Mazik, Ph.D.
Kyle J. Hartman, Ph.D.
Kerry Bledsoe, M.S.

Division of Forestry

Morgantown, WV
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ABSTRACT

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Heather Hildebrand

Abundances of American eel (*Anguilla rostrata*) are declining along the east coast of the United States and Canada, possibly due to habitat loss and barriers to migration. In Atlantic coast watersheds, dams detain upstream migration of juveniles, and little is known about age class composition, age-length relationships, or environmental cues to upstream migration of yellow-phase eels. An eel ladder was installed on the Millville hydroelectric dam, lower Shenandoah River, WV, to facilitate and monitor the upstream movement of yellow phase eels. Daily length measurements (TL cm) and weights (g) were taken on eels using the ladder during three sampling periods; spring/summer 2004 (May 14 - July 23), fall 2004 (Sept 10 - 30), and spring/summer 2005 (June 1 - July 31). Additionally, otolith-based ages were estimated from a subsample of eels. To examine environmental variables associated with upstream migration, candidate models were fit to daily count data and included combinations of four environmental covariates (barometric pressure, local precipitation, lunar illumination, and river flow) and a year effect. A total of 4,847 eels used the ladder during the three sampling periods. Eel sizes were similar among sampling periods (range 19 - 75 cm TL), and age estimates from 74 eels (21.4 - 55 cm TL) ranged from 3 to 10 years. Estimates of mean length at age of eels from Shenandoah River were low relative to published estimates from southern and northern latitudes. Peaks in eel counts coincided primarily with low levels of lunar illumination or with rise in river flow, and the data supported an additive model of lunar illumination and river flow. The data did not support single-variable or additive models with covariates of barometric pressure or local precipitation, or models with a year effect. Management strategies for American eels will benefit from short and long-term studies of eel ladders, including additional focus on eel counts, size and age composition, and upstream migration.

DEDICATION

To Zach, thank you for listening and laughing with me when I needed it.

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CHAPTER 1: Literature Review

This thesis includes two chapters; a literature review of American eels (*Anguilla rostrata*) and a manuscript from a study of yellow-phase American eels at the Millville Dam eel ladder, lower Shenandoah River, West Virginia. In the first chapter, I review the literature of American eel ecology, cues to upstream eel migration, and dam related influences on eel movements. A manuscript (Chapter 2) documents numbers of eels, age/length of eels, and environmental variables associated with upstream eel movements at the Millville Dam eel ladder.

Ecology

The American eel (*Anguilla rostrata*), a catadromous fish distributed widely as a panmictic population from Greenland to Venezuela (Barbin and McCleave 1997, Krueger and Oliveira 1999, and Oliveira 1999), develops into five life stages: leptocephalus, glass, elver, yellow, and silver eel. American eels spawn in late winter-early spring in the Sargasso Sea (Tsukamoto and Aoyama 1998, Oliveira 1999, Powles and Warlen 2002). Leptocephali (7-10 mm TL) drift in the upper 300 m of the water column (Kleckner et al. 1983) and transform into glass eels during transport northwest along the east coast of the United States (Helfman et al. 1987, Dutil et al. 1989, Haro and Krueger 1990). The elver stage occurs in estuaries and is characterized by an elongate shape and long-based dorsal and anal fins merging with the caudal (Able and Fahay 1998, Powles and Warlen 2002). Elvers adjust physiologically to freshwater during upstream migration from tidal to nontidal habitats (Haro and Krueger 1988, Dutil et al. 1989). Eels are characterized as yellow phase once complete pigmentation has occurred and after TL exceeds (approximately) 100mm (Able and Fahay 1998, ASMFC 1999, BEAK 2001). The yellow phase (a feeding and growth phase) is the transition before the sexually-mature

silver phase (Able and Fahay 1998, Oliveira 1999, BEAK 2001), and can last 9 to 30 years for females and 7 to 12 years for males (Helfman et al. 1987, Able and Fahay 1998, Cottrill et al. 2002, Goodwin and Angermeier 2003).

Most somatic growth occurs in the yellow phase and gender differences are evident. Females grow larger in the more northern regions of their freshwater distribution (Ford and Mercer 1986, Barbin and McCleave 1997), while males tend to occur in brackish water (Helfman et al. 1987, Wang and Tzeng 1998, Goodwin and Angermeier 2003) and exhibit lower growth rates compared to the females (Helfman et al. 1984, Oliveira 1997, Powles and Warlen 2002). Growth rates of males and females diverged at age 4; however, they did not become statistically different until age 6 (Helfman et al. 1984, Oliveira and McCleave 2002). Male eels begin metamorphosis into the silver phase at smaller sizes ($< 400\text{mm}$) and younger ages, which suggests that they switch resources away from somatic growth to gonadal development earlier (Krueger and Oliveira 1997, Krueger and Oliveira 1999, Oliveira and McCleave 2002). This explains the sharper decline in male growth after age 3 (Helfman et al. 1984, Oliveira 1997, Oliveira and McCleave 2000).

At maturity both sexes undergo a fall migration downstream to the sea (Barbin and McCleave 1997, Able and Fahay 1998, Krueger and Oliveira 1999). Metamorphosis to a silver eel stage accompanies this migration; during which the eye diameter enlarges (ASMFC 1999, Cottrill et al. 2002), the internal organs atrophy, and the lateral surface assumes a silver sheen (Hain 1975, Winn and Winn 1975, Krueger and Oliveira 1999). Movement within the ocean to the Sargasso Sea is not well understood. After spawning, adults are presumed to die (Able and Fahay 1998, Krueger and Oliveira 1999, Tsukamoto et al. 2002).

Environmental Cues to Upstream Migration

Although the majority of the eel's life is spent in the yellow phase and in freshwater systems, little is known about environmental influences on movement and upstream migration. Environmental cues initiating migration are difficult to ascertain with respect to yellow phase eels (Barbin 1998) due to collection techniques of juveniles at the interface of a stream and an estuary (Sorensen et al. 1986, McCleave and Wipplehauser 1987). Decreasing abundance with increased distance from the ocean, contributes to the difficulty in assessing the impacts of environmental variables on upstream migration (Wiley et al. 2004, Laffaille et al. 2005). Most data of environmental influences on upstream migration are from estuaries, the interface of estuaries and freshwater, and tidally-influenced freshwaters (Martin 1995, White and Knights 1997, Laffaille et al. 2003).

Water chemistry, sunlight, barometric pressure, air temperature, and water temperature potentially cue upstream migration of eels in freshwaters (Walsh et al. 1983, Parker and McCleave 1997, Wipplehauser and McCleave 1988). Although Miles (1968) found an association with water pH and movement of elvers, Sorensen (1984) was unable to verify this finding. Sunlight, barometric pressure, air and water temperature correlated positively with the onset of upstream migration (Sorensen and Bianchini 1986, Baras et al. 1998, Euston et al. 1998). Upstream migration coincided with water temperatures from 12°C to 19°C in a Rhode Island brook (Sorensen and Bianchini 1986) with peak migration around 20°C in the rivers Severn and Avon in England (White and Knights 1997), which was lower than the 20-25°C peak range reported by Verdon and Desrochers in the St. Lawrence River in Canada (2003). Water temperatures exceeding this

threshold (20°C) at the estuarine-riverine interface had little (if any) influence on movements (Sorensen et al. 1986, Haro and Krueger 1988, Haro and Krueger 1991). However, Sorensen and Bianchini (1986) stated that their study failed to discern any environmental variable with a strong influence of upstream migration of elvers in freshwater systems.

Olfactory, river flow, and lunar phase potentially cue upstream migration of yellow phase eels. Olfactory cues are likely important, although the odorant is unidentified (Sorensen 1986, McCleave and Wippelhauser 1987, Barbin 1998). Sorensen (1984) found streambed gravel and stones, dead alewife (*Alosa pseudoharengus*) eggs, leaf detritus, and riverbank mud to be possible chemoattractants. River flow and lunar phase coincide with yellow-phase movements (Durif et al. 2003, Hammond 2003). Eel activity increases nocturnally with peak activity around midnight (Dutil et al. 1987, 1988, Parker 1995), often beginning with the waning third quarter moon (Lamothe et al. 2000, Hain 1975).

Migration Concerns

The abundance of American eel (based on catch data) has declined dramatically over the past two decades from 816,466 kg in 1985 to 294,881 kg in 2002 along the east coast of the United States (ASMFC 2004). Researchers speculate population declines are due to habitat loss (Wiley 1999, Casselman 2003, Tremblay 2005), over harvest (Appelbaum et al. 1998, Haro et al. 2000, Patrick et al. 2000, Casselman 2003), pollution and/or barriers to migration (Wiley 1999, Neraas and Spruell 2001, Wiley et al. 2004). The recent awareness of population fluctuations caused the Atlantic States Marine Fisheries Commission to draft an eel management plan (Euston et al. 1998, ASMFC 1999, Patrick et al. 2000). The management plan recommends research of both up and downstream eel

passage at hydroelectric dams (ASMFC 1999, Patrick et al. 2000). However, more than 90% of dams on the eastern seaboard are not hydroelectric facilities, and are therefore not subject to continual re-licensing and fish passage analysis (ASMFC 1999, FERC 2003). Not all dams impede eel movements; however, few studies have examined the magnitude of impacts of dams or management practices associated with dams (Goodwin et al. 1999, ASMFC 1999).

Habitat fragmentation by dams, navigation weirs and hydroelectric plants have reduced ranges and increased extinction risks of numerous migratory fishes (Agostinho et al. 2002, Ovidio and Philippart 2002). Dams screen and reduce abundances of eels in upper watersheds (Wells 1999, McCleave 2001, Goodwin and Angermeier 2003). Turbine mortality for downstream migrants can exceed 25% (EPRI 1999) with some estimates exceeding 50% (Ritter et al. 1997, Verreault and Dumont 2000). In the St. Lawrence River watershed, a total of 8,411 dams (at least 2.5 m high) prevent, hinder, or delay access to 12,140 km² of freshwater habitat (10 m or less deep)(Verreault et al. 2004). Based on data analysis from three tributaries in the St. Lawrence River watershed and historic distributions, annual productivity loss was estimated at 836,500 eels (Verreault et al. 2004). Based on historical recruitment, re-opening access upstream of dams to migrant yellow eels could potentially contribute 737,000 spawners a year (Verreault et al. 2004).

Ladders

Structures and mechanisms such as ladders, elevators and floodgates are constructed worldwide to transport fishes up and downstream of dams (Cada 2001, Agostinho et al. 2002, FERC 2004). Upstream passage technologies are well developed for certain anadromous species, mainly salmonids and clupeids, in North America and Europe

(Larinier 2000). Passes for young eels are used in Europe, Canada, the United States and New Zealand (Larinier 2000, Verdon et al. 2003, FERC 2004).

Eel ladder monitoring provides information about upstream migration and recruitment of yellow phase eels. Based on an eel ladder study at Arzal dam (Vilaine, France), eel odor (from conspecifics on the ladder) increased eel use of the ladder (Briand et al. 2002). The mean catch of glass and yellow eel was about 1.4 times higher with the presence of conspecific odor (Briand et al. 2002). Possible sources of attraction are the skin, mucus, bile salts, or other amino acids (Saglio 1982, Sorensen 1986, Briand et al. 2002). Briand et al. (2002) concluded that odor assists migrant eels in location of passes, and eel ladder designs would benefit from water diversion from holding bins.

Passage of juveniles decreased (118-fold) at the eel ladder of the R.H. Saunders hydroelectric dam at Cornwall, Ontario from 1982-1983 and has progressively declined since the mid 1980's (Casselman et al. 1997, McGrath et al. 2003). At this ladder, larger eels pre-dominated initial migrations with smaller eels being more abundant during peak migration, but decreasing in number as the season progressed and water temperatures decreased (Liew 1978, McGrath et al. 2003). Before ladder installation, eels remained downstream and grew in size, as a result, the first two years of ladder operation yielded larger eels with a gradual decrease in eel size by the third and fourth years (Liew 1978, McGrath et al. 2003). The primarily nocturnal use of this ladder corroborates findings of studies on the Richelieu River and a tidal tributary of the St. Lawrence River (McGrath et al. 2003).

A study of the upstream movement of yellow phase eels between the Beauharnois (Quebec) and the Moses-Saunders (Ontario/New York) hydroelectric dams on the St. Lawrence River investigated both the movement between the two dams and the effects of

commercial harvest on eel movements (Verdon and Desrochers 2003). Peak migration occurred between 16 July and 15 August, corresponding with temperatures above 20°C, which agreed with other studies on the Sud-Ouest and Rimouski rivers (two tributaries of the lower St. Lawrence River) (Verdon and Desrochers 2003). The number of eels from the Moses-Saunders to the Beauharnois dam was reduced, possibly due to the presence of the locks on both dams having a compounding effect on the upstream movement of eels (Verdon and Desrochers 2003).

In 1997, an eel ladder was installed at the Chambly dam on the Richelieu River (115 km between Lake Champlain and the St. Lawrence River) for the purpose of monitoring upstream migration of yellow phase eels (Verdon et al. 2003). Results of movement and water temperature agreed with past research, where the onset of upstream migration in the Richelieu River occurred about a month earlier than in the upper St. Lawrence (Verdon et al. 2003). Further, yellow eels were active nocturnally, and migrations peaked between 18:00 and 24:00 hours, and were disrupted by artificial light (Verreault 1995, Verdon et al. 2003). Eels released at the dam base (on both banks) were recaptured in equal proportion in the ladder; a finding that supports active eel movements along the dam (McGrath et al. 2003, Verdon et al. 2003). Knights and White (1998) found European eels in quieter water near the bottom and sidewalls of a dam, and suggested the entrance location to eel passes should be located near the base of walls. Knights and White (1998) also concluded that strong flows near ladder entrances attract eels, a finding consistent with observations at the Chambly Dam (Verdon et al. 2003).

An eight year study on the Fremur River, France, examined temporal changes in density, biomass, and length of eels following construction of eel passes (Laffaille et al. 2005). The Fremur, a small river of northern Brittany (France), represents many small

coastal catchments in the Biscay region. Barriers on the Fremur, however, have disturbed natural connectivity, including three high dams (14 m) that inhibit eel upstream migration and reduce recruitment of elvers and yellow eels (Laffaille et al. 2005). No significant decreases in eel densities were observed in the Fremur river, except in the most upstream part of the catchment, despite a general decline elsewhere in Europe. The presence of eels before the installation of the passes suggests elvers could bypass the dams, however, passes greatly improve access to upstream habitat and are indispensable for assisting upstream movements of larger eels (>120mm) (Laffaille et al. 2005). During 1997-2003 following eel pass installation, over 100,000 eels were counted from passes on the Fremur River.

Given apparent declines in American eel abundance over portions of the species' range, knowledge of freshwater migration may be increasingly important for effective management and conservation (Oliveira and McCleave 2000, Wiley et al. 2004). Eel ladders provide an opportunity for study of freshwater migration, and increase access to upper watersheds.

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CHAPTER 2: Environmental variables associated with upstream migration and length and age of American eels at the Millville Dam eel ladder, Shenandoah River, West Virginia.

Introduction

Abundances of American eel (*Anguilla rostrata*) have declined along the east coast of the United States and Canada (ASMFC 2004). Population declines possibly result from human influences such as habitat loss (Wiley 1999, Casselman 2003, Tremblay 2005), over harvesting (Appelbaum et al. 1998, Haro et al. 2000, Patrick et al. 2000, Casselman 2003), pollution (Castonguay et al. 1994) or barriers to migration, such as dams (Wiley 1999, Neraas and Spruell 2001, Wiley et al. 2004). In response to recent population fluctuations, the Atlantic States Marine Fisheries Commission (ASMFC) drafted an eel management plan (Euston et al. 1998, ASMFC 1999, Patrick et al. 2000) and recommended research of both up and downstream eel passage at hydroelectric dams (ASMFC 1999, Patrick et al. 2000).

Population declines possibly result from multiple causes of mortality within all American eel life phases (leptocephalus, glass, elver, yellow, and silver); however, the yellow phase encompasses most of the lifespan (7-30 years in freshwater systems, Able and Fahay 1998). Since many yellow-phase eels migrate long distances upstream within river systems (Laffaille et al. 2005) and ultimately become large fecund females in silver-phase (Helfman et al. 1987), range reductions of yellow eels owing to upstream migration barriers possibly contribute to population declines (White and Knights 1997, Agostinho et al. 2002, Laffaille et al. 2005). Dams fragment habitat and detain upstream migration of eels (Haro et al. 2000), and are distributed widely within and among Atlantic coast river drainages (Casselman 2003). Specifically, in the St. Lawrence River watershed, a

total of 8,411 dams (at least 2.5 m high) limit eel access to 12,140 km² of freshwater habitats of 10m or less in depth (Castonguay et al. 1994). Eel abundances within watersheds decrease naturally with increased distance from the ocean; hence, longitudinal patterns of eel distributions within river drainages with dams are equivocal indicators of population status (Wiley et al. 2004, Laffaille et al. 2005).

Dams also detain upstream movement of juveniles (Levesque 1978, Goodwin and Angermier 2003, Haro et al. 2000). In Canada and Europe, eel ladders on hydroelectric dams have allowed access to upstream habitat (a management goal), but also have promoted eel research and provided data on upstream migration and recruitment of yellow phase eels (i.e., a source of data useful for management). Studies of eel ladders have focused on conspecific detection (Briand et al. 2002), upstream movement (Casselman et al. 1997, McGrath et al. 2003, Verdon et al. 2003), ladder design requirements (Verreault et al. 1994, Knights and White 1998, Verdon et al. 2003), harvest impacts on movement (Verdon and Desrochers 2003), and temporal variations in size structure (Laffaille et al. 2005). A lack of information on upstream movement of yellow eels in upper tributary reaches of Atlantic coast drainages results partly from an absence of eel ladders.

Few studies exist on age class composition and age-length relationships of migrant yellow-phase American eels or on environmental cues to upstream migration of yellow eels in upper reaches of Atlantic coast watersheds. Studies from estuaries, estuary/freshwater interfaces, and tidally-influenced freshwaters have documented a wide range of lengths within age-classes of American eels (Ogden 1970, Helfman et al. 1984, Owens and Geer 2003), and have reported abiotic correlates to eel movements (Martin 1995, White and Knights 1997, Laffaille et al. 2003). Environmental correlates of eel

movements include barometric pressure (Sorensen and Bianchini 1986, Baras et al. 1998, Euston et al. 1998), water temperature (Sorensen et al. 1986, Haro and Krueger 1988 and 1991, Verdon et al. 2003), river flow (Hammond 2003, Laffaille et al. 2003), and lunar phase (Hammond 2003, Lamothe et al. 2000).

This study examined upstream migration of yellow-phase American eels at an eel ladder on Millville Dam, a hydroelectric facility on the lower Shenandoah River, West Virginia. Study objectives were to: (1) document numbers of eels entering the Shenandoah River drainage, (2) examine size and age structure of upstream migrants, and (3) examine relationships among environmental variables and upstream migration of American eels. The first two objectives were not hypothesis-driven, but rather focused on estimation of parameters associated with the number, size, and age of upstream migrants. For the third objective, we examined alternative hypotheses of environmental cues to upstream migration of yellow-phase eels. Although similar studies exist for estuaries and lower reaches of rivers, few studies have examined size and age composition, and upstream migration in upper watersheds. Due to the absence of dams downstream (of the Millville Dam) to detain upstream migrants, this study allowed us to assess the number of eels using the Shenandoah River.

Methods

Study site

The Shenandoah River drainage encompasses approximately 7,870 km², and lies mostly in Virginia within the Valley and Ridge physiographic province, with some tributaries flowing out of the Blue Ridge province (Jenkins and Burkhead 1994). The drainage consists primarily of the North Fork and South Fork of the Shenandoah River, each flowing for over 250 rkm before forming the Shenandoah River at Front Royal, VA.

At Harper's Ferry, WV, the Shenandoah converges with the Potomac River (a large Chesapeake Bay drainage). The Millville dam (owned and operated by Allegheny Energy) is a low head dam located 7.24 km from the confluence of the Potomac and Shenandoah Rivers at Harper's Ferry, WV, and 249 rkm from the mouth of the Potomac River at the head of tide. The 700-m wide Millville Dam has a head of 5m, and a total generating capacity of approximately 1.8 MW.

Ladder Design and Placement

The eel ladder, a covered metal sluice, slopes 50° and extends 11m on the western end of the dam (Appendix 1). An attraction flow (>10 l/s) adjacent to the ladder base gravitates through a PVC pipe from the top of the dam (Appendix 2). A pool at the base of the ladder results from flashboards on the face of the dam and enables eels to distinguish between spillway and attraction flows (Appendix 2). An internal facilitation flow (0.5 l/s) pumps from the top of the ladder and provides a constant “upstream current” and to facilitate eel use of the ladder (Appendix 2). In addition, three rows of vertically-placed PVC pipe act as a “peg board” substrate to further facilitate movement (Appendix 2). A pipe at the top of the ladder passes through the dam and enters into a collection tank (Appendix 2). Within the collection tank, the PVC pipe connects to a double net system, including a 2.13m long (60.96cm diameter with 6.35mm mesh) net, inserted into a 2.74m long (60.96cm diameter with 9.53mm mesh) net. This double net design separates small and large eels thereby easing removal of eels from the tank and reducing possibility of predation.

Data Collection

Eels within the collection tank were counted daily during three sampling periods; late spring/summer 2004 (May 14-July 23), fall 2004 (Aug-Sept 24), and late

spring/summer 2005 (June 1-July 31). A total count of eels was recorded from an initial study of ladder efficacy during late summer/fall 2003 (Aug 28-Sept 17); however, numbers of eels were not always counted daily during this efficacy study. The three sampling periods (after the efficacy study) were not selected by study design, but rather were determined by discretion of the hydroelectric power company (based on weather and flow conditions) and on periods of dam construction. Ladder installations during the spring of 2004 (May 14) and 2005 (June 1) were delayed until after a decrease in spring flows (allowing workers access to the dam spillway). Dam construction ended the late spring/summer sampling periods of 2004 and 2005, because dewatered tailwaters prevented eel access to the ladder. The fall 2004 sampling period began when river flows allowed access to the ladder, and included several high hurricane-induced flow events (the latter event removed the ladder and ended the fall sampling period).

Eels were collected daily during the three primary sampling periods, and calmed in an ice slurry for weights (g) and measures (TL cm). Eels collected during the 2003 efficacy study were also counted and measured (TL cm). After collection of length and weight data, eels were acclimated to ambient water temperatures and released 0.40 km upstream of the dam.

Ages were estimated from a subsample of eels by sagittal otolith analysis. Sagittal otoliths were extracted following methods of Oliveira (1996). Before cross sectional analysis, otoliths were fixed in epoxy to prevent fragmentation of thin sections and to stabilize the otolith while cutting. Sections of otoliths were obtained by saw (Buehler Isomet 1000, Germany), and prepared, set, and stained following procedures of Secor et al. (1992) and Oliveira (1996). Estimates of age included one year for

leptocephalus and glass eel phases (Helfman et al. 1984). All counts were triple checked before a subsample was double checked by a blind count.

We collected daily measures of five environmental variables: river flow, lunar phase, water temperature, local precipitation, and barometric pressure. River discharge (cubic meters per second, cms) was obtained from the U.S. Geological Survey gage at Millville Dam (<http://waterdata.usgs.gov>), and is hereafter referred to as river flow. We quantified percent lunar illumination as a range from 0 to 1; new moon (0.00), first and last quarter (0.50), and full moon (1.00);

<http://aa.usno.navy.mil/data/docs/MoonFraction.html>). Onset temperature loggers recorded daily water temperatures both inside the collection tank and at the hydroelectric facility. Local precipitation was recorded daily at the hydroelectric facility with a Hobo event rain gage (model number 1001-056). Daily measures of barometric pressure were downloaded from (<http://www.wunderground.com/weatherstation/WXDailyHistory>).

Data Analyses

Parameter estimates of length, weight, and age described the size and age composition of eels, and those of environmental variables summarized means and variation of site and sampling conditions. We estimated mean length at age, and regressed and plotted age-length relationships. Length-weight relationships were calculated with data from all individuals using the equation $w = aL^b$ where parameters a and b were estimated given data of weight (g) and total length (cm) (Murphy and Willis 1996). Differences in environmental conditions among sampling periods were depicted with estimates of within-sample means of environmental variables (and associated variation).

A total of 22 biologically-reasonable candidate models were fit to daily count data from the spring/summer sampling periods of 2004 and 2005. Candidate models included combinations of four environmental covariates and a year effect (Table 1). The 22 candidate models (selected before analysis and representing multiple hypotheses, Chamberlin 1965) were ranked by an overdispersion-corrected second-order adjustment to Akaike's information criterion (QAIC_c). The QAIC_c and other model selection statistics were derived from calculations from the DIST = NEGBIN option in PROC GENMOD of the Statistical Analysis System (SAS; Littell et al. 2002). This information-theoretic approach, where QAIC_c estimates Kullback-Leibler distance, selects the best model (or suite of competing models) through a parsimonious tradeoff among bias, variance, and the number of estimable model parameters (Burnham and Anderson 2003).

Results

A total of 4,847 eels used the ladder during the three sampling periods; 1,384 during late spring/summer 2004 (May 14-July 23), 2,816 during fall 2004 (Sept 10-Sept 30), and 647 during summer 2005 (June 1-July 31). A total of 409 eels used the ladder in an initial study of ladder efficacy in late summer and fall 2003; however, these counts were not recorded daily and we included these data only in the frequency histograms. Daily eel counts fluctuated within and among the three sampling periods with peaks in 2004 on June 17 (n=236), June 18 (n=117), July 6 (n=219), Sept 12 (n=2072), and Sept 13 (n=550), and in 2005 on July 10 (n=96), July 11 (n=92), and July 19 (n=160). The fall 2004 sampling period was also excluded from environmental covariate analysis; large numbers of eels were associated with an atypical hurricane-induced flow event after a 48-d period of dewatered tailwaters and ladder closure.

The spring/summer sampling periods of 2004 and 2005 were relatively similar in environmental conditions, although a higher mean river flow occurred in 2004 (Table 2). The fall 2004 sampling period, however, experienced highest flows owing to hurricane-induced storm events (Table 2). The spring/summer sampling period of 2004 included two full moons and three new moons, and that of 2005 encompassed two full moons and two new moons. Daily water temperatures were not used as an analysis covariate because daily values were relatively constant within each sampling period (Table 2). Barometric pressure varied among days within sampling periods, but variation occurred within a narrow range (Table 2). Local precipitation varied widely within sampling periods, although mean values were similar among sampling periods (Table 2). In general, high river flows resulted from rain events within upstream sections of the Shenandoah River watershed, and were not associated with local precipitation.

Eel size was similar among sampling periods; summer/fall 2003 (range 19.7-51 cm TL, $\mu = 30.4$ cm TL; Figure 1A), spring/summer 2004 (range 20-69 cm TL, $\mu = 29.4$ cm TL; Figure 1B), fall 2004 (range 20.6-70 cm TL, $\mu = 33.5$ cm TL; Figure 1C), and summer 2005 (range 19-53 cm TL, $\mu = 30.1$ cm TL; Figure 1D). The length-weight relationships were also similar among sampling periods; spring/summer 2004 ($w = 0.0011L^{3.0719}$, $R^2 = 0.8436$), fall 2004 ($w = 0.001L^{3.0873}$, $R^2 = 0.9194$), and summer 2005 ($w = 0.0008L^{3.1527}$, $R^2 = 0.8961$; Figure 2). Age estimates from 74 eels (21.4 - 55 cm TL) ranged from 3 to 10 (Table 3, Figure 3A). Mean weights g (N and standard error) for ages 3 through 9 were 26.7 (4, 14.3), 42 (16, 7.1), 33.9(18, 6.7), 48.2(17, 6.9), 73(13, 7.9), 68(3, 16.5), and 223.0(2, 20.2), respectively (Figure 3B). Age-length and age-weight regressions revealed R^2 values of 0.329 and 0.308, respectively (Figures 3A, 3B).

During the two spring/summer sampling periods of 2004 and 2005, peaks in eel counts coincided primarily with low levels of lunar illumination (near new moon) or with rise in river flow (Figures 4A, 4B). The additive model of lunar illumination and river flow was the best approximating model with QAIC_c weight of 0.99 (Table 4). The other 21 models (i.e. hypotheses) were not supported by the data, and only one other model received weight (the river flow model with weight of 0.01; Table 4). The data did not support single-variable or additive models with covariates of barometric pressure or local precipitation, or models with a year effect.

Discussion

In this study, the size composition, age structure, and migratory cues of upstream migrant yellow-phase American eels were examined through daily collections of eels from an eel ladder. This sampling approach led to several important results. First, we documented large numbers of yellow-phase American eels migrating upstream during summer and fall in an upper watershed (Shenandoah River) of the Potomac River drainage. Second, estimates of mean length at age of eels from Shenandoah River were low relative to published estimates from southern and northern latitudes. Third, low levels of lunar illumination and rises in river flow were important environmental changes associated with upstream migration of yellow-phase eels in the lower Shenandoah River. Data did not support local precipitation, barometric pressure, or water temperature as environmental variables associated with upstream migration during the late spring/summer sampling periods.

Length and Age

Based on averages of mean length at age data for ages 3-9, eels from the lower Shenandoah River grew slower than those from Newfoundland, Canada (4.1 cm, Gray

and Andrews 1971), tributaries (James, York, and Rappahannock rivers) of Chesapeake Bay, VA (8.7 cm, Owens and Geer 2003) and Cooper River, SC (16.0 cm, Hansen and Eversole 1984). Literature supports a latitudinal difference in growth rates of eels on the Atlantic coast, where northern populations grow slower than those of southern populations (see review in Owens and Geer 2003); hence, the large difference was expected between Shenandoah and Cooper river estimates of mean length at age. Given latitudinal differences, however, one would expect growth rates of eels from Shenandoah River to be relatively similar to those of Chesapeake Bay tributaries, VA, and greatly exceed those from Newfoundland. Although Shenandoah River and Virginia tributaries drain to Chesapeake Bay (i.e., share latitudinal similarity), study locations differ by distance to the estuary. Data from VA tributaries were collected from the river mouths to approximately river km 72 (Owens and Geer 2003), and those from the Shenandoah River were collected at approximately river km 249 (upstream of head of tide). Yellow-phase eels in upper reaches of watersheds likely budget more energy for migration (and less for growth) than those closer to the estuary. The longitudinal difference (i.e., distance from estuary) in study location and energy trade-offs between migration and growth, possibly explain differences among mean length at age between eel samples from Shenandoah River and tributaries of Chesapeake Bay, VA. Although an average of mean lengths at age for ages 3-9 differed between data from Shenandoah River and Newfoundland, the difference was not consistent among individual age classes. Mean length at age for ages 3 and 4 from the Shenandoah River exceeded those from Newfoundland by 4.9 and 3.4 cm, respectively. However, mean length at age for ages 5-9 from Newfoundland exceeded those from the Shenandoah River by 3.0, 2.5, 12.6, 14.1, 4.8 cm, respectively. This possibly results from combined effects of latitude and

longitude (distance from estuary), where the latitude effect dominates the early age classes, and older ages are influenced by the energy trade-off of growth and migration.

The wide range of lengths within each age class of Shenandoah River eels corroborates findings from a wide latitudinal geographic range; Altamaha River, GA (Helfman et al. 1984), Cooper River, SC (Harrell and Loyacano 1976), Chesapeake Bay tributaries, VA (Owens and Geer 2003), Atlantic coast tributaries, NJ (Ogden 1970), Hudson River, NY (Morrison and Secor 2003), Lake Champlain, VT (Facey and LaBar 1981), and eastern Lake Ontario, Canada (Hurley 1972). Owens and Geer (2003) generalize two possible explanations for the wide range of lengths within an age class; variable growth rates among individual yellow eels or problems with aging. My study does not provide an explanation of the wide range of lengths within age classes of American eels, but does document its occurrence in an upper watershed of the Potomac River drainage.

Environmental Variables

The data supported lunar illumination and river flow as environmental variables associated with upstream migration of yellow-phase eels in the lower Shenandoah River. Previous research on eel movements has concentrated primarily on lunar phase (Hain 1975, Winn et al. 1975, Dutil et al. 1989, Parker 1995, Baras et al. 1998, Lamothe et al. 2000, and McGrath et al. 2003) as opposed to river flow (Laffaille et al. 2003), and few studies have emphasized the importance of both variables (Verdon et al. 2003).

The use of covariates within models precludes strong inference from analysis of observational data, because relationships are only correlative (White 2002). Researchers have suggested that low light availability (due to increased turbidity and river flow) and low levels of lunar illumination synergistically cue upstream migration of eels (Dutil et

al. 1988). Lunar influences on eel migration may result from light rather than a periodic effect (Hain 1975). The effect of lunar illumination and river flow on eel movements in the Shenandoah River may also be unmeasured variables related to light such as cloud cover and turbidity. We speculate that lunar illumination and river flow (or unmeasured correlates of these two variables) would also be associated with eel movements elsewhere in the Potomac River drainage, as well as within other Atlantic coast watersheds.

Our data did not support a relationship between upstream movement and barometric pressure, local precipitation or water temperature, although numerous studies have reported a relationship of these three variables either separately or synergistically (Liew 1978, Sorensen and Bianchini 1986, Baras et al. 1988, Dutil et al. 1988, Haro and Krueger 1991, White and Knights 1997, and Verdon and Desrochers 2003). We collected data primarily during late spring, summer, and fall; hence, our results are not transferable to winter and spring periods during which barometric pressure, local precipitation, or water temperature may be important. Yellow-phase eels are torpid during water temperatures below 10°C (Walsh et al. 1983), and the onset of upstream migration during spring coincides with a 10-16°C range of water temperatures (EPRI 1999). We did not examine the influence of spring water temperatures on eel movement given the dates of ladder installation. Other studies have documented sunlight, barometric pressure, local precipitation, or air and water temperatures as correlates with the onset of upstream migration (Winn et al. 1975, Sorensen and Bianchini 1986, Baras et al. 1998, Euston et al. 1998).

Implications for management and research

This study of an eel ladder documented large numbers of migrant yellow-phase eels in the lower Shenandoah River, a finding that supports important implications for

management and research. First, results support the efficacy of eel ladders and promote a management strategy for allowing eels access to additional habitat in upper watersheds. Second, eel ladders (when used as a passive collection gear) provide managers with valuable data on eel numbers and migration. With long-term deployment, an eel ladder will provide time-series data for examination of seasonal or annual trends, a current management need given population declines.

Managers cannot decouple ladder-induced upstream migration of yellow eels from downstream migration of silver eels. Increasing numbers of yellow eels upstream of hydroelectric dams via ladders require further consideration of turbine mortality of outmigrant silver eels. Turbine mortality can exceed 25% (EPRI 1999) with some estimates exceeding 50% (Ritter et al. 1997, Verreault and Dumont 2000). Some hydroelectric facilities schedule turbine shutdowns to reduce turbine mortality; Allegheny Energy provides night-time shutdown of turbines during fall downstream migration (Chuck Simons, personal communication). Management strategies for American eels will benefit from short and long-term studies of eel ladders, including additional focus on eel counts, size and age composition, and upstream migration, as well as further research of silver outmigrants.

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Table 1. List of models with corresponding hypotheses. Each of the 11 models was repeated with a year effect for a total set of 22 candidate models.

Model	Hypothesis
Lunar illumination	Lunar illumination associated with upstream migration
River flow	River flow associated with upstream migration
Local precipitation	Local precipitation associated with upstream migration
Barometric pressure	Barometric pressure associated with upstream migration
Lunar illumination + river flow	Lunar illumination and river flow associated with upstream migration
Lunar illumination + local precipitation	Lunar illumination and local precipitation associated with upstream migration
Lunar illumination + barometric pressure	Lunar illumination and barometric pressure associated with upstream migration
River flow + local precipitation	River flow and local precipitation associated with upstream migration
River flow + barometric pressure	River flow and barometric pressure associated with upstream migration
Local precipitation + barometric pressure	Local precipitation and barometric pressure associated with upstream migration
Local precipitation + barometric pressure + River flow + lunar illumination	All environmental variables associated with upstream migration

Table 2. Mean, standard error (SE) and range of environmental variables depicted for three sampling periods of a study of upstream migration of American eels at the Millville Dam eel ladder, Shenandoah River, West Virginia.

Variable	Spring/summer 2004 (n = 71)			Fall 2004 (n = 21)			Spring/summer 2005 (n = 61)		
	Mean	SE	Range	Mean	SE	Range	Mean	SE	Range
River flow (cms)	65.64	2.35	37.6-108.4	222.79	53.50	51.2-1030.1	48.07	2.59	27.2-115.2
Barometric pressure	30.02	0.02	29.68-30.39	30.18	0.17	29.64-30.49	30.03	0.02	29.65-30.27
Local precipitation	9.28	3.64	0-226	10.52	6.38	0-124	10.16	4.69	0-255
Water temperature (C)	23.17	0.18	21-25	17.24	0.32	15-19	26.70	0.32	18-30

Table 3. Mean total length (cm) and standard error (SE) at age of American eels from a latitudinal range of Atlantic slope drainages.

Age	Shenandoah River, Millville Dam, WV			Chesapeake Bay tributaries, VA (Owens and Geer 2003)			Cooper River, SC (Hansen and Eversole 1984)			Newfoundland, Canada (Gray and Andrews 1971)	
	N	Mean TL	SE	N	Mean TL	SE	N	Mean TL	SE	N	Mean TL
1				7	17.6	2.9	2	29.2			
2				42	20.4	0.9	33	36.1	0.9	2	17.4
3	4	26.9	2.6	162	27.4	0.8	97	41.1	0.7	6	22.0
4	16	30.2	1.3	151	34.6	1.0	126	45.5	0.6	18	26.8
5	18	28.8	1.2	124	45.1	1.2	108	48.2	0.7	27	31.8
6	17	35.6	1.4	55	47.6	1.6	57	51.1	0.7	46	38.1
7	13	32.2	1.2	18	49.3	3.7	9	58.0	2.1	42	44.8
8	3	37.3	3.0	5	47.6	2.2	6	51.4	1.1	57	51.4
9	2	53.3	3.6	6	53.6	4.3	3	61.1		66	58.1
10	1	40.2		1	62.4					35	66.3

Table 4. Model selection statistics, sample size (n), number of parameters (K), log likelihood values (Log L), Akaike Information Criterion (QAIC_c) values adjusted for small sample size and overdispersion, distance from lowest QAIC_c (Δ_i), and Akaike weights (w_i) from a set of 22 candidate models. Variables include a year effect (year) and environmental covariates: lunar illumination (lunar), river flow (flow), local precipitation (precip), and barometric pressure (bp).

Model	n	K	Log (L)	QAIC _c	Δ_i	w_i
Lunar + flow	131	5	4896.7	-9782.9	0	0.99
Flow	131	4	4890.74	-9773.2	9.76	0.01
Lunar	131	4	4881.67	-9755	27.89	0
Bp	131	4	4878.71	-9749.1	33.82	0
Flow + year	131	5	4878.69	-9746.9	36.01	0
Precip	131	4	4878.06	-9747.8	35.1	0
Lunar + flow + year	131	6	4864.85	-9717	65.9	0
Precip + flow	131	5	4854.33	-9698.2	84.74	0
Flow + bp	131	5	4852.45	-9694.4	88.49	0
Lunar + precip	131	5	4843.84	-9677.2	105.71	0
Lunar + year	131	5	4843.65	-9676.8	106.1	0
Lunar + bp	131	5	4843.57	-9676.7	106.27	0
Bp + year	131	5	4842.32	-9674.2	108.76	0
Precip + flow + year	131	6	4842.02	-9671.4	111.55	0
Precip + year	131	5	4841.22	-9672	110.95	0
Precip + bp	131	5	4840.88	-9671.3	111.64	0
Flow + bp + year	131	6	4839.7	-9666.7	116.2	0
Lunar + precip + year	131	6	4805.83	-9599	183.94	0
Lunar + bp + year	131	6	4805.46	-9598.2	184.67	0
Precip + bp + year	131	6	4804.53	-9596.4	186.53	0
Lunar + precip + flow + bp + year	131	8	4790.94	-9564.7	218.21	0

Figure 1. Length-frequency histograms of eels collected from the Millville Dam eel ladder during (A) Aug 28-Sept 17, 2003 ($N = 409$; $\mu = 30.4$ cm TL; range 19.7-51 cm), (B) May 14-July 23, 2004 ($N = 1,384$; $\mu = 29.4$ cm TL; range 20-69 cm), and (C) Sept 10-30, 2004 ($N = 2,542$; $\mu = 33.5$ cm TL; range 20-73 cm), and (D) June 1-July 31, 2005 ($N = 647$; $\mu = 30.1$ cm TL; range 19-53 cm).

Figure 2. The length-weight relationship of eels (N = 4,847) pooled from three sampling periods at the Millville Dam eel ladder, Shenandoah River, West Virginia.

A)

B)

Figure 3. Age-length (A) and age-weight (B) relationships of American eels from the Millville Dam eel ladder, Shenandoah River, West Virginia.

A)

B)

Figure 4. Daily counts of eels (bars) at the Millville Dam eel ladder and associated environmental variables lunar illumination (solid line) and river flow(dashed line) during two sampling periods; (A) May 14-July 23, 2004 and (B) June 1-July 31, 2005.

APPENDIX

Appendix 1. Millville Dam eel ladder (design by Milieu, Inc. Canada).

Appendix 2. Design specifications (A) flashboard placement and attraction flow, (B) internal design, (C) source of facilitation flow, and (D) upstream collection tank (housing the net system).