2003

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**Seasonal movements of yellow-phase American eels (*Anguilla rostrata*) in the
Shenandoah River, West Virginia**

Stephen D. Hammond

**Thesis submitted to the
Davis College of Agriculture, Forestry, and Consumer Sciences
at West Virginia University
in partial fulfillment of the requirements
for the degree of**

**Master of Science
in
Wildlife and Fisheries Resources**

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Division of Forestry

**Morgantown, WV
2003**

**Keywords: American eel (*Anguilla rostrata*), seasonal movements, radio telemetry,
eel passage, hydroelectric dam effects, catadromous, Shenandoah River**

ABSTRACT

Seasonal movements of yellow-phase American eels (*Anguilla rostrata*) in the Shenandoah River, West Virginia.

Stephen D. Hammond

Yellow-phase American eels undergo extensive upstream migration in Atlantic coastal river systems. Few studies, however, have focused on movements of large yellow-phase American eels near dams in upper watersheds of Atlantic coastal rivers. We examined relationships between environmental variables (stream flow, water temperature, and lunar phase) and movements of radio-tagged yellow-phase American eels (518 – 810 mm TL) near Millville hydroelectric dam in the lower Shenandoah River drainage, West Virginia (an upper watershed of the Potomac River system). Movements of yellow-phase American eels differed among seasons. Increased water temperature and stream flow were associated with upstream migration during spring. Downstream movements during fall corresponded with decreasing water temperatures and darker nights near the new moon, where eels located and overwintered in thermal refuge areas near tributary mouths. Localized wandering (upstream and downstream movements) during summer occurred near dusk and dawn, and possibly reflected nocturnal foraging. In relation to hydroelectric facilities and eel passage within the Potomac River drainage, our data support a need for upstream passage during spring when water temperatures exceed 15°C.

DEDICATION

To my parents, and Rebecca

ACKNOWLEDGEMENTS

I would like to extend thanks to the members of my graduate committee, especially Dr. Stuart Welsh for his guidance, Dr. Douglas Dixon, Kerry Bledsoe, Dr. Kyle Hartman, and Dr. Pat Mazik, for their contributions during this project.

Funding was provided through EPRI (Electric Power Research Institute) of Palo Alto, California, Allegheny Energy, and West Virginia Division of Natural Resources.

Special thanks and appreciation to Terry Euston, Ben Lenz, Lara Hedrick, Jessica Smith, and Dave Wellman for their assistance with fieldwork and data collection, and Melody Danley, Barbara Douglas, Larry Earnest, Terry Euston, Gary Harbaugh, Alex Hoar, Mike Mangold, Charles Simons, and Julie Weeder for their contributions to the project.

Thank you Linda Tolka for accommodating many last minute requests, and Becky Nestor for radio-telemetry headgear design.

A final thanks to John Gill, Rudy Lukacovic, and Julie Weeder for their letters of recommendation.

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CHAPTER 1: LITERATURE REVIEW

INTRODUCTION

The complex life history of the catadromous American eel, *Anguilla rostrata* (LeSueur), is not clearly understood. Many unanswered questions remain for all life stages of the American eel (larval, glass eel, elver, yellow, and silver). Although reproductive biology is probably least understood (Fontaine et al. 1982, Tsukamoto et al. 1998, EPRI 1999), information on estuarine and freshwater life stages is needed for management and protection of declining eel populations. Studies have shown dramatic declines in numbers and juvenile recruitment since the early 1980s in American and European eel (*Anguilla anguilla*) populations (Castonguay et al. 1994a, De Leo and Gatto 1996, Dekker 2000, Haro et al. 2000, Ing 2000, Richkus and Whalen 2000, Feunteun 2002). American and European eels use a wide range of habitats, which allows many opportunities for detrimental effects on the populations. Although exact causes of decline are unknown, Castonguay et al. (1994b) and Knights (2003) proposed several possible factors, including oceanic and climatic changes, chemical contamination, major habitat modifications, hydroelectric impacts, and over-fishing. Below I review scientific summaries of eel biology and behavior, with emphasis on migration and movements of yellow-phase eels, and potential impacts of dams.

Life history

American eels are distributed widely along the North American Atlantic coast and Gulf of Mexico (Helfman et al. 1987), but occur as far south as the Virgin Islands (Boëtius 1980) and Venezuela, to northern areas near Greenland (Tesch 1977, Jenkins and Burkhead 1993). American eels begin and end life in areas of the Sargasso Sea (Schmidt 1925, Vladykov 1964). After hatching, the larvae (leptocephali) drift westward and northward with the ocean currents of the Gulf Stream for up to a year (Kleckner and McCleave 1985) and metamorphose into “glass eels” before entry into estuaries. Glass eels begin to develop pigmentation as they mature into “elvers” (Haro and Krueger 1988), and become “yellow-phase eels” after exceeding approximately 100 mm total length.

The yellow-phase predominates the life cycle, where eels inhabit estuaries or undergo extensive migration up rivers (Tesch 1977, Moriarty 1978). Yellow-phase eels occur throughout river systems including upper watersheds with high gradients (Jenkins and Burkhead 1993). Higher percentages of males in lower river systems and estuaries, and higher percentages of females in upper watersheds may be associated with density-dependent factors (Helfman et al. 1987). Many factors, including environmental factors, especially eel population densities, may be significantly involved in sex determination, with areas of high density dominated by males, and areas of lower density dominated by females (Krueger and Oliveira 1999). The gender of adult eels is not externally apparent, and histological examination of tissues is necessary for sex determination (Dolan and Power 1977, Facey and LaBar 1981). Males have slower growth, shorter life span, and attain smaller sizes than females (Tesch 1977, Helfman et al 1987, Krueger and Oliveira 1997, Oliveira 1997). Female yellow-phase eels have attained ages of at least 30 years (Jessop 1987) before reaching reproductive maturity, and have been shown to mature at greater ages and sizes in the northern range of their distribution (Helfman et al. 1987).

Spawning migration

Yellow-phase eels transform into a “silver-phase” during or before spawning migration to the Sargasso Sea (Vladykov 1973, Wenner and Musick 1974, Winn et al. 1975, Kleckner et al. 1983). Seaward migration occurs generally from September through December (Vøllestad et al. 1986, Helfman et al. 1987), where eels undergo a number of physiological changes as they metamorphose into the “silver-phase.” External changes include pigmentation change from olive-yellow into a bright silvery color, and a substantial increase in eye diameter (Vladykov 1973, Werner and Musick 1974, Boëtius and Boëtius 1980), as well as development of the lateral line (Zacchei and Tavolaro 1988). Internally, functional morphology and physiology of the swim bladder may change (Kleckner and Krueger 1981), and degeneration of the alimentary tract and feeding cessation may occur (Pankhurst and Sorensen 1984). Spawning migration culminates in areas of the Sargasso Sea, although spawning behavior is undocumented (EPRI 1999).

Research on American eels and European eels, which share similar behavioral, ecological, and life history characteristics (EPRI 1999), indicate environmental influences on upstream and downstream migration, as well as localized movements. Researchers have reported downstream migration of silver-phase eels in association with water temperature, precipitation, stream flow, turbidity, incident light, and lunar phase (Lowe 1952, Smith and Saunders 1955, Winn et al. 1975, Tesch 1977, Haraldstad et al. 1985, Vøllestad et al. 1986, Bergersen and Klemetsen 1988, Euston et al. 1997, EPRI 2001). Migration of silver eels from estuary to ocean may involve olfaction (Barbin et al. 1998).

Freshwater movement studies

Upstream migration and localized movements of juvenile and yellow-phase American eels are also correlated with environmental factors. Water temperature influences upstream movement of elvers (Sorensen and Bianchini 1986; Haro and Krueger 1988; Martin 1995). Sorensen and Bianchini (1986) showed initial upstream movement of elvers between 12 and 19°C, and Haro and Krueger (1988) showed movement between 10.5 and 21.5°C. Daily eel catch data from 1990-1992 from a fish lift at the Conowingo Dam on the Susquehanna River, Maryland, showed first catches occurred between 12 and 15°C (SRAFR 1991, 1992, 1993).

River flow and lunar phase also influence eel movements. Fluctuations or sudden changes in water temperature or stream flow within short time intervals may elicit eel movements (Durif et al. 2003, Verdon et al. 2003). Eel activity (both local and long distance migratory movements) increase during periods of reduced moon illumination of the new moon phases (Lowe 1952, Winn et al. 1975, Lamothe et al. 2000, Cairns and Hooley 2003).

Local and seasonal movements of yellow-phase eels

Few studies have focused on seasonal movements of yellow-phase American eels in freshwater systems. Researchers have reported punctuated periods of upstream migration, where large yellow-phase eels generally migrate upstream during spring, but exhibit local movements during other seasons (Bianchini et al. 1982, Oliveira 1997). Yellow-phase eels, however, migrate upstream during summer and fall in the St.

Lawrence River (McGrath et al. 2003). Strickland (2002) found that yellow-phase eels in the James River, Virginia, were most active during warmer months (May-October), and moved little during winter. At winter water temperatures below 10°C, movements are reduced when eels become torpid (Walsh et al. 1983).

Within seasons, non-migratory, localized and wandering movements of yellow-phase eels in rivers and estuaries are probably associated with food density, habitat type, eel abundance, and interactions with conspecifics (Ford and Mercer 1986, Helfman 1986). Movements in estuarine areas are influenced by tidal stages (Dutil et al. 1988). Eels may establish home ranges (Gunning and Shoop 1962, Hurley 1972, Helfman 1986, Dutil et al. 1988, Oliveira 1997), and some studies support homing behavior (LaBar and Facey 1983, Parker 1995, Lemothe et al. 2002). Although American eels have diverse diets (Ogden 1970, Werner and Musick 1975, Wilson and Turner 1982, Lookabaugh and Angermeier 1992), and foraging modes (Helfman and Clark 1986, Helfman and Winkelman 1991), the distribution and availability of forage likely influences local movements (Helfman 1986). Eels are nocturnal and use cover during daylight hours (Baras et al. 1998), so availability and abundance of cover habitat in relation to food availability also likely influences localized movements. Additionally, intraspecific competition for cover and food in densely populated areas may influence movements at a local scale (Helfman 1986).

Effects of dams on upstream and downstream migration

Dams may directly or indirectly impact eel populations, and contribute to the apparent overall population decline (EPRI 1999). Dams may detain upstream movements of elvers and yellow eels, and disrupt downstream migration of sexually mature silver eels. Passage through hydroelectric turbines is a conservation concern for downstream migrants (EPRI 1999, EPRI 2001, Coutant and Whitney 2000, Haro and Castro-Santos 2000), but is not reviewed herein, given the thesis focus of yellow-phase eels. Dams may indirectly impact eels by fragmenting habitat, changing the amount of habitat types, and altering eel movement and migration through habitat changes from natural riverine conditions to slow-moving lacustrine habitats (EPRI 1999). Additionally, dams may

influence sex ratios, given that eels in upstream river sections typically differentiate as females (Krueger and Oliveira 1999).

Fisheries managers and researchers have implemented and studied several methods to mitigate or reduce effects of dams on upstream migration (EPRI 1999). Eel ladders, specifically designed for eel passage, effectively facilitate upstream movement of eels (Whitfield and Kolenosky 1978, Eckersley 1982, Liew 1982). EPRI (1999) describes specific details of eel-passage requirements for upstream migrating eels. Small eels (<100 mm) are able to ascend simple wetted passageways and pipes with adequate substrate to provide friction for climbing, such as gravel or mesh material. Larger yellow-phase eels require different substrates than smaller eels. Small vertical rods and tubes placed in the bottom of passageways have worked successfully for larger eels (EPRI 1999).

This thesis documents studies of seasonal and nocturnal movements of large (518 – 810 mm TL) yellow-phase American eels in the Shenandoah River below Millville Dam, West Virginia. The results have implications for operational management of hydroelectric facilities, given few studies on movements of large yellow-phase American eels near dams in upper watersheds of Atlantic coastal rivers.

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CHAPTER 2: SEASONAL MOVEMENTS OF YELLOW-PHASE AMERICAN EELS (*ANGUILLA ROSTRATA*) IN THE SHENANDOAH RIVER, WEST VIRGINIA.

INTRODUCTION

Upstream migration is an important part of the yellow-phase life stage of American eels (ASMFC 2000). Dams undoubtedly detain upstream migration and may contribute to the apparent population decline of American eels (Richkus and Whalen 2000, Haro et al. 2000). However, populations persist upstream of dams in upper watersheds of Atlantic coastal rivers (Menhinick 1991, Jenkins and Burkhead 1994, Goodwin and Angermeier 2003). Eel ladders, often installed as a hydroelectric license condition, have assisted upstream passage in some Atlantic coastal rivers, but movements of yellow-phase eels near dams (with or without eel ladders) are not fully understood (EPRI 1999). A better understanding of eel behavior within and downstream of dam tailwaters, and evaluations of environmental cues for upstream migration are needed for management and protection of yellow-phase American eels.

Data are available on movements of American eels in large rivers (Levesque and Whitworth 1987, Oliveira 1997, Verdon and Desrochers 2003, McGrath et al. 2003), streams (Gunning and Shoop 1962), lakes (Hurley 1972, LeBar and Facey 1983, Lamothe et al. 2000), and estuaries (Helfman et al. 1983, Bozeman et al 1985, Ford and Mercer 1986, Dutil et al. 1989, Barbin et al. 1998). Eel movements differ among seasons (Richkus and Dixon 2003) and are possibly triggered by environmental cues, such as water temperature (McGrath et al. 2003, Verdon et al. 2003), precipitation (Tesch 1977, Winn et al. 1975), flow (Euston et al. 1998), and lunar phase (Lowe 1952, Winn et al. 1975, Cairns and Hooley 2003). Movements may be associated with specific environmental thresholds; water temperatures between 10 and 16°C cue upstream movements during spring (Smith and Saunders 1955, Groom 1975, Sorensen and Bianchini 1986, Jessop 2003). Fluctuations or sudden changes in water temperature or stream flow within short time intervals may also elicit eel movements (Durif et al. 2003, Verdon et al. 2003). Most studies of American eel movements have focused on small juveniles within or near estuaries (Sorensen and Bianchini 1986, Haro and Krueger 1987, Dutil et al. 1989), or on larger eels (> 300 mm TL) in lower sections of coastal

watersheds (Jessop 1987, Dutil et al. 1988). Little information, however, exists on seasonal movements of relatively large (>500 mm TL) yellow-phase eels in upper watersheds, or on seasonal movements of yellow-phase eels near dams. Data on eel movements are needed to increase our understanding of eel behavior in upper river sections, and to assist operational management of hydroelectric facilities in relation to eel passage.

The primary objective of this study was to examine potential environmental cues (stream flow, water temperature, and lunar phase) associated with upstream and downstream seasonal movements of yellow-phase eels near the Millville hydroelectric dam in the lower Shenandoah River drainage, West Virginia (an upper watershed of the Potomac River system). Secondary objectives were to estimate average seasonal distances traveled by eels from Millville Dam, and examine nocturnal movements of yellow-phase eels within the tailwater of the dam during summer.

METHODS

The study occurred within a 9 km section (average width 150 m) of the lower Shenandoah River downstream of Millville Dam, West Virginia (Fig. 1). The 5 m high Millville Dam diverts water to a bypass canal for hydroelectric production. The bottom substrate of the 700 m tailwater section (immediately below the dam) is predominantly slanted bedrock, with some areas of small boulders, large cobble, and gravel. During low stream flows, exposed bedrock creates small pools and braided channels in several areas of the tailwater and lower kilometer of the study area. The middle section of the study area contains pool and run habitats with unexposed bedrock, boulder, cobble, and gravel substrates. A road parallels the upper 4 km section of the study area, whereas a footpath provides access to the lower 5 km section.

To obtain data on seasonal and nocturnal movements, 20 yellow-phase American eels were captured with a backpack electrofisher from the tailwater of Millville Dam. We anesthetized eels using a clove oil solution (Anderson et al. 1997) and surgically implanted radio transmitters (Lotek MBFT-5, 11mm x 43mm, 366-day battery life; Lotek Wireless Inc., Ontario, Canada) into the abdominal cavity (Ross and Kleiner 1982). Radio tags were implanted into 13 eels (range 518-810 mm) during 8-23 September 2001, and seven eels (range 599-781mm) during 11-27 June 2002. Eels were monitored

for several hours post-surgery, and released near the collection area. Locations of radio-tagged eels (tracked manually with a Lotek SRX_400 receiver and Yagi antenna) were triangulated using compass bearings and DeLorme 3-D TopoQuads® mapping software Delorme, Yarmouth, Maine, USA. Error of triangulated locations was < 5 m based on electrofishing recaptures of radio-tagged eels. We measured straight-line distances (i.e. minimum distances) between consecutive relocation coordinates of each individual eel. In cases where river sinuosity prevented straight-line distances, we measured the within-river minimum distance between relocations.

Seasonal movements

For analysis of seasonal movements, we tracked eels during daylight hours from 10 fixed stations within a 4 km section of shoreline below the dam. When eels were not relocated from fixed stations, we tracked eels within the lower study area from non-fixed positions. Tracking dates were generally within one to two week intervals from 14 June 2001 to 28 May 2003, but several intervals between 15 to 33 days occurred during winter months because of severe weather conditions. Minimum distances during each time interval between relocations were expressed as m/day.

We used PROC MIXED (SAS 1990) to model covariance associated with repeated measures on individual eels, and analyzed upstream and downstream movements separately. Given unequal time intervals between relocations, we used the spatial power structure (a generalization of the autoregressive first-order covariance structure for equally spaced data) to address within-subject covariance (Littell et al. 1996), where “eel nested within season” was the experimental unit. Relocation times between eels were temporally aligned to account for missing values (Littell et al. 1996). Mixed models included season as a fixed effect, where seasons were partitioned as spring (16 March-15 June), summer (16 June-15 Sept), fall (16 Sept-15 Dec), and winter (16 Dec-15 March). Using the spatial power structure of covariance, least-square means in PROC MIXED (Littell et al. 1996) estimated means of upstream and downstream movements by season.

Seasonal movements were modeled with seven covariates derived from water temperature, stream flow, and lunar phase. Onset® temperature loggers (Onset

Computer Corporation, Pocasset, Massachusetts, USA) recorded daily water temperatures within the study area from the main channel Shenandoah River and one small tributary (Fig. 1). River flows (cubic meters per second, cms) were obtained from the U.S. Geological Survey gage at Millville Dam (<http://waterdata.usgs.gov>). We used the fraction of the moon's visible disc to quantify lunar illumination, where fractions range from new moon (0.00), first and last quarter (0.50), and full moon (1.00; <http://aa.usno.navy.mil/data/docs/MoonFraction.html>). For each time interval between relocations, covariates were determined as (1) maximum values of lunar illumination, stream flow, and water temperature, and (2) mean values of stream flow and water temperature. Covariates of maximum values were used to model the importance of extreme conditions, whereas those of mean values were used to represent general conditions within relocation intervals. Covariates derived from differences in mean water temperatures and stream flows between consecutive relocation intervals were used to model fluctuations or sudden changes within short time periods.

Although a large number of models could be fit to the data, given all potential combinations and interactions between season and covariates, we selected 24 models based on published literature of fish movements. Given the limits of our effective sample size, we avoided models with higher than 10 estimable parameters (Burnham and Anderson 2003). The 24 biologically-reasonable candidate models (selected before analysis and representing multiple hypotheses, Chamberlin 1965) were ranked by the second-order adjustment to Akaike's information criterion (AIC_c). This information-theoretic approach, where AIC_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, and avoids the use of arbitrary significance (alpha) levels for inference from observational data (Burnham and Anderson 2003).

Distances from dam

We calculated distances between coordinates of eel relocations and Millville Dam to determine seasonal locations of eels relative to the dam. Using the spatial power structure to model within-subject covariance, least-square means in PROC MIXED

(Littell et al. 1996) estimated mean distances from the dam by season. The mixed model included season as a fixed effect, with “eel nested within season” as the experimental unit. We accounted for missing values and unequal time intervals between locations with methods described above.

Nocturnal movements

We estimated nocturnal movements of eight eels (518 – 781 mm TL) within the 700 m tailwater of Millville Dam during six nights (25-26, 29-30, and 30-31 July 2002 and 1-2, 6-7, and 8-9 August 2002). Movements (m/hr) were estimated within four 2-hour time periods (2100-2300, 2300-0100, 0100-0300, and 0300-0500 hours) on each night. Lunar illumination (as described above), stream flow, and water temperature were recorded for each 2-hour relocation interval, but water temperature and stream flow were not used as environmental covariates given little variation among nights. To address covariance, we fit the full model (Date x Time) with unstructured, compound symmetry, and first-order autoregressive covariance models using PROC MIXED (Littell et al. 1996), and selected the best model based on the lowest AIC_c value. Using the best covariate model, a set of five candidate models were fit to the nocturnal movement data and represented alternative hypotheses of eel movements associated with dusk (2100-2300 hours), dawn (0300-0500 hours), dusk and dawn combined, and lunar illumination. For statistical inference, we used AIC_c to select the best model or models supported by the data.

RESULTS

Sixteen of the 20 radio-tagged American eels were positioned 471 times during the 617-day study period, with only one location recorded per each tagged eel on each tracking day. Not all tagged eels were relocated on each tracking day, and four eels were not relocated after release (possibly due to transmitter failure or movement from the study area). To reduce bias from tag-induced movements, we removed the first 30 days of relocation data, because eels moved erratically upstream and downstream during the first three weeks after surgery.

Seasonal movements

Movements differed among seasons with highest rates of upstream movement during spring and highest rates of downstream movement during fall. Models without a seasonal effect were unsupported by the data (Table 1). For analysis of upstream movements, AIC_c selected Season $\times$ Maximum Flow as the best model, but two additive models (with temperature fluctuation and/or flow fluctuation) and two interaction models (with average flow and flow fluctuation) were close competitors (Table 1). Based on the five competing “best” models, our data supported an association of higher flows and increasing temperatures with upstream movements during spring. During spring, upstream movements ($O = 33.8$ m/day, $SE = 4.1$) exceeded downstream movements ($O = 11.0$ m/day, $SE = 2.5$), and co-occurred with water temperatures above 15°C and increased stream flows. Models with a lunar illumination covariate received little weight for the analysis of upstream movements (Table 1).

Lunar illumination was associated with downstream movements, where the two best models (supported by lowest AIC_c values) were Season $\times$ Lunar Illumination and Season + Lunar Illumination + Average Water Temperature (Table 1). These models reflected the importance of a lower illuminated fraction of the moon’s visible surface (i.e., darker nights) and decreasing water temperatures on downstream movements during fall ($O = 18.4$ m/day, $SE = 2.9$). During fall, the longest downstream movements (> 50 m) within relocation intervals occurred within a narrow range of mean water temperatures ($11.0 - 11.6^\circ\text{C}$). Upstream movements of eight individuals (range 32 - 363 m) during a 7-day relocation interval (2 Nov 2001 to 9 Nov 2001) influenced the relatively high mean rate of upstream movement during fall ($O = 12.4$ m/day, $SE = 5.3$). These large upstream movements during 2 Nov 2001 to 9 Nov 2001 occurred on a waning full moon with flow ($O = 12.2$ cms, maximum = 12.7 cms) and water temperature ($O = 9.1^\circ\text{C}$, maximum = 9.3°C) relatively unchanged from the previous time interval.

Movements during summer exceeded those of winter, but were less than upstream movements in spring and downstream movements during fall. During summer, localized movements occurred within mean water temperatures of $24.1 - 29.9^\circ\text{C}$, where eels wandered upstream ($O = 10.5$ m/day, $SE = 4.1$) and downstream ($O = 11.5$ m/day, $SE = 1.7$). Winter movements were lowest of all seasons (upstream, $O = 2.1$ m/day, $SE = 6.6$;

downstream, $O = 3.5$ m/day, $SE = 2.4$), and were observed within a mainstem water temperature range of $0.8 - 9.4^{\circ}\text{C}$. Most of the tagged eels overwintered in thermal refuge areas near tributary mouths. Winter water temperatures at one tributary mouth (Fig. 1) averaged 7.2°C , whereas main channel temperatures averaged 3.7°C .

Nocturnal movements

The compound symmetry covariance model was supported by the data (based on lowest AIC_c) and was used to estimate means of nocturnal movements. Eels moved erratically (upstream and downstream) during 2100 – 0500 hrs on six summer nights, with an overall mean movement estimate of 10.2 m/hr ($SE = 0.48$). Data supported the combined dusk and dawn model (Table 2), where nocturnal movements were greatest during dusk (2100-2300 hrs, ($O = 10.1$ m/hr, $SE = 0.75$) and dawn (0300-0500 hrs, ($O = 11.4$ m/hr, $SE = 0.75$), and slightly less during 2300-0100 ($O = 9.7$ m/hr, $SE = 0.75$) and 0100-0300 hrs ($O = 9.6$ m/hr, $SE = 0.75$). Despite a wide range of lunar illumination among the six nights ($0.0 - 0.97$), data did not support an association between movements and lunar illumination (Table 2). Water temperature and stream flow were not modeled as covariates in the analysis of nocturnal movements, given low variation in water temperature (range $26.4 - 30.4^{\circ}\text{C}$) and stream flow (range $11.8 - 18.7$ cms) among the six summer nights, with less variation among time intervals during each night.

Seasonal downstream distances from the dam

Distances of eels downstream from Millville Dam corroborated seasonal movements. Eels were farthest from the dam during fall ($O = 1347$ m, $SE = 287$) and winter ($O = 1954$ m, $SE = 307$), and closest during spring ($O = 1014$ m, $SE = 293$) and summer ($O = 831$ m, $SE = 295$; Figure 2). Radio-tagged eels were closest to the dam ($O = 615$ m, $SE = 102$) after water temperatures exceeded 15°C during late spring (26 April – 10 June). Several eels were located at the base of the dam during spring and summer, but were re-located downstream on subsequent visits. During early fall (18 September – 25 October) eels were also relatively close to the dam ($O = 1200$ m, $SE = 220$) when water temperatures exceeded 12°C . The large effect sizes in mean distances from the dam, between early fall and winter (1200 vs. 1954 m) and winter and late spring (1954 vs.

615 m), reflect downstream movements during fall and upstream movements during spring.

DISCUSSION

Our data supported an association between upstream migration of large (range 518 – 810 mm TL) yellow-phase American eels and two abiotic variables (water temperature and stream flow) during spring. Given relatively warm spring rains, stream flow and water temperature increase concurrently during spring, and may synergistically influence upstream migration. In this study, sudden changes in stream flow and water temperature influenced upstream migration of large yellow-phase eels during spring. Water temperature of 15°C cued upstream migration in the lower Shenandoah River, and is bracketed by the range of temperature cues (10 - 16 °C) from eel studies summarized by EPRI (1999). Upstream migration during spring was expected, based on similar findings by Sorensen and Bianchini (1986), Haro and Krueger (1988), and Jessop (2003). Studies of eel movements, however, have largely focused on elvers or small yellow-phase eels in lower sections of coastal rivers, and less information is available on movements of large yellow-phase eels in upper sections of rivers.

The general pattern of downstream movements of large yellow-phase eels during fall (with some periods of upstream movement) probably reflects downstream and upstream searches for overwintering areas. Downstream movements during fall occurred on darker nights (near new moons) and during decreasing water temperatures, with largest movements during relocation intervals with mean water temperatures of 11.0 – 11.6°C. Although nocturnal movements of eels are well documented (Lowe 1952; Tecsh 1977; Dutil et al. 1988), contrasted results exist for movements associated with lunar phase (see review by Cairns and Hooley 2003). Our data support an association between low levels of lunar illumination and downstream movements of yellow-phase eels during fall. Upstream movements during fall may represent upstream migration instead of searches for suitable winter habitats, where retreat to overwintering areas below the dam possibly occurred after unsuccessful attempts at upstream migration. A period of upstream migration occurs during fall on the St. Lawrence River (Dutil et al. 1989, McGrath et al. 2003). Smaller yellow-phase eels move upstream during late summer in the lower Shenandoah River; an eel ladder installed at Millville Dam on 31 July 2003

passed 408 eels ($O = 304$ mm TL, range 197-510 mm TL) during 22 August 2003 – 17 September 2003 (unpublished data).

Eel locations determined at 1- to 2-week intervals did not indicate directional upstream or downstream migration during summer, but supported erratic wandering movements in upstream or downstream directions. Movement data from night tracking at 2-hr intervals also supported localized movements. Eels may establish small home ranges during summer (Gunning and Shoop 1962, Ford and Mercer 1986, Bozeman et al. 1985), and eels in this study remained within relatively short river sections in the lower Shenandoah River during summer. We did not estimate home range sizes from summer movement data, given dam-induced bias on upstream movements. In our study, nocturnal wandering during summer probably reflects active foraging, because yellow-phase eels feed primarily at night (Sorensen et al. 1986). Although food availability may influence movements (Helfman 1986), large foraging areas were unlikely in our study area, given large populations of crayfish and cyprinids. Crayfish are common diet items of eels in this region (Lookabaugh and Angermeier 1992), and were consumed by eels within this study area, based on crayfish parts excreted during surgical-implantation of radio tags.

Yellow-phase American eels become torpid at water temperatures below 10°C (Walsh et al. 1983); hence, we expected no movements during winter seasons of our study, where water temperatures ranged from 0.8-9.4°C. Nyman (1972) and Barila and Stauffer (1980) reported reduced feeding of eels at water temperatures below 14°C, whereas Renaud and Moon (1980) reported feeding cessation and reduced activity of eels below 8°C. Euston et al. (1998), however, reported downstream movements of silver-phase eels at water temperatures as low as 6°C. In our study, estimates of small upstream ($O = 2.1$ m/day) and downstream ($O = 3.5$ m/day) movements during winter probably represent errors in triangulation of relocation coordinates. Most individuals moved less than 5 m between relocations during winter. During the time interval from 1 - 18 Dec 2001 ($O = 5.1^\circ\text{C}$), relatively large downstream movements (11 and 20 m) of two individuals possibly represent displacement, given that maximum stream flow increased from 15 to 22 cms during this time period. Movement data, however, did not support downstream displacement of torpid eels during larger fluctuations in stream flow. We

believe that larger mean distances from the dam during winter months reflect the location and use of thermal refugia near tributary mouths. Silver-phase European eels used areas of elevated water temperatures near thermal power plants during winter (Nyman 1975), and other riverine fishes use thermal refuge areas during winter (Raibley et al. 1997, Knights et al. 1995, Gent et al. 1995).

Management implications

Movements of yellow-phase American eels differed among seasons in the lower Shenandoah River, owing largely to upstream movements in spring, downstream movements during fall, wandering (upstream and downstream movements) during summer, and minimal movements during winter. Oliveira (1997) citing Bianchini et al. (1982) hypothesized that yellow-phase eels likely move long distances between periods of relatively little movement. Our data are consistent with this punctuated-movement hypothesis, where upstream movements occur during spring followed by localized movements during summer, and relatively little movement during winter. Our data are inconclusive concerning upstream migration of large yellow-phase eels during fall. Movement data from the lower Shenandoah River likely represent behavior of large yellow-phase eels within upper watersheds of other Atlantic coastal streams. From a management perspective, however, we restrict inference to movements of large yellow-phase eels near dams.

Water temperature was important to overall seasonal eel movements, particularly as an environmental cue to upstream movement in spring (combined with increased stream flows). For large yellow-phase eels, our data support spring as the critical period for provision of upstream passage at hydroelectric dams. Data did not support other seasons (fall, winter, and summer) as important for upstream passage of large yellow-phase eels (with the possible exception of fall). Water temperature (combined with darker nights near the new moon) cued downstream movement during fall. We believe that downstream movements during fall and larger distances from the dam during winter reflect locations and use of thermal refuge areas. Although direction of fall movements was generally downstream, a short period of upstream movements also occurred during fall. Possibly, eels settled for thermal refuge areas downstream of the dam after

unsuccessful attempts of upstream migration. We did not find evidence of upstream migration of large yellow-phase eels during summer, where data from 1- to 2-week intervals and nocturnal data within 2-hour time intervals supported localized upstream and downstream movements.

Data from this study provide natural resource managers with a better understanding of the behavior of large yellow-phase American eels in upper watersheds of Atlantic coastal rivers. Additionally, the data are relevant to the operational management of hydroelectric facilities in relation to eel passage. Additional studies on relations between eel movements and dams in upper watersheds, however, are needed to further address seasonal upstream and downstream movements of small and large yellow-phase American eels. Also, given a recent push for provision of upstream passage via eel ladders, further research is needed for dam passage of downstream migrant silver-phase American eels.

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Figure 1. Study area within a 9 km section of the lower Shenandoah River, West Virginia, from Millville Dam to the mouth of the Shenandoah River.

Figure 2. Seasonal distance of radio-tagged American eels from Millville Dam (all relocations plotted for each eel).

Table 1. Selection statistics for 24 alternative models from separate analyses of upstream and downstream movements; second order adjustment of Akaike's Information Criterion (AIC_c), distance from lowest AIC_c (Δ_i), and Akaike weights (w_i). Bold weights represent competing models within each analysis; statistics between upstream and downstream analyses are not comparable. Model variables include season (movements partitioned by spring, summer, fall, and winter), and six covariates determined from each relocation interval: maximum and mean stream flow, maximum and mean water temperature, maximum lunar illumination, and fluctuations of stream flow and water temperature.

Model	Upstream movements			Downstream movements		
	AIC_c	Δ_i	w_i	AIC_c	Δ_i	w_i
Season x Lunar Illumination	570.6	10.0	0.00	408.9	0.0	0.43
Season + Mean Flow + Lunar Illumination	567.5	6.9	0.01	412.5	3.6	0.07
Season + Maximum Flow + Lunar Illumination	568.1	7.5	0.01	412.1	3.2	0.09
Season + Mean Temperature + Lunar Illumination	566.0	5.4	0.02	410.2	1.3	0.23
Season + Lunar Illumination	566.5	5.9	0.01	410.8	1.9	0.17
Season x Mean Flow	561.6	1.0	0.17	423.9	15.0	0.00
Season + Mean Flow	568.9	8.3	0.00	422.4	13.5	0.00
Season x Maximum Flow	560.6	0.0	0.27	423.6	14.7	0.00
Season + Maximum Flow	569.1	8.5	0.00	422.0	13.1	0.00
Season x Mean Temperature	571.6	11.0	0.00	417.1	8.2	0.01
Season + Mean Temperature	567.4	6.8	0.01	422.7	13.8	0.00
Season + Mean Temperature + Mean Flow	569.5	8.9	0.00	422.7	13.8	0.00
Season x Flow Fluctuation	563.5	2.9	0.06	426.2	17.3	0.00
Season + Flow Fluctuation	564.8	4.2	0.03	422.7	13.8	0.00
Season x Temperature Fluctuation	565.4	4.8	0.02	426.8	17.9	0.00
Season + Temperature Fluctuation	561.5	0.9	0.17	423.7	14.8	0.00
Season + Temperature Fluctuation + Flow Fluctuation	561.4	0.8	0.18	423.8	14.9	0.00
Season	567.1	6.5	0.01	422.0	13.1	0.00
Lunar Illumination	597.0	36.4	0.00	428.1	19.2	0.00
Mean Flow	601.0	40.4	0.00	441.7	32.8	0.00
Maximum Flow	602.1	41.5	0.00	440.8	31.9	0.00
Mean Temperature	597.9	37.3	0.00	439.0	30.1	0.00
Flow Fluctuation	597.2	36.6	0.00	441.5	32.6	0.00
Temperature Fluctuation	599.4	38.8	0.00	444.8	35.9	0.00

Table 2. Selection statistics for 5 alternative models of nocturnal movements during six summer nights; second order adjustment of Akaike's Information Criterion (AIC_c), distance from lowest AIC_c (Δ_i), and Akaike weights (w_i). Movements (m/hr) were estimated within four 2-hour time periods (2100-2300, 2300-0100, 0100-0300, and 0300-0500 hours), where models represent movements associated with dusk (2100-2300 hours), dawn (0300-0500 hours), dusk and dawn, and lunar illumination.

Model	Nocturnal movements		
	AIC_c	Δ_i	w_i
Dusk/dawn	371.9	0.0	0.54
Dawn	373.1	1.2	0.29
Lunar Illumination	375.7	3.8	0.08
Dusk	375.8	3.9	0.08
Date	379.2	7.3	0.01