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Diel periodicity and chronology of upstream migration in yellowphase American Eels (Anguilla rostrata)

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Diel periodicity and chronology of upstream migration in yellow-phase American Eels (*Anguilla rostrata*)

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ABSTRACT

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This thesis examined 24-h diel periodicity of upstream migration of yellow-phase American Eels (*Anguilla rostrata*), and the chronology of upstream movements within diel periods (day, night, and twilight). Further, relationships were examined for total lengths of upstream migrants and diel movements (vespertine, nocturnal, matutinal, and diurnal), as well as for total lengths and season of year. The thesis is comprised of two chapters: (1) an introduction and literature review on American Eel life history, migration and movement, and population concerns, and (2) a research study of diel periodicity and movement chronology of upstream migrant yellow-phase American Eels at an eel ladder. Study objectives were to (1) examine diel periodicity of upstream migrants using time-series spectral analysis, (2) describe the distribution of passage counts during diel periods (day, twilight, and night) among seasons (spring, summer, and fall), and (3) examine size of upstream migrants relative to diel and seasonal periods. Data were collected at the Millville Dam eel ladder on the lower Shenandoah River, West Virginia, from 2011–2014. Six multi-day passage events with a high number of passage counts were selected for analysis and categorized by season (spring, summer, late summer/early fall, fall) and diel periods of movement (vespertine, nocturnal, matutinal, and diurnal). To examine diel periodicity of movements, I graphically-depicted passage count data as time-series histograms (10-min bins) and used time-series spectral analysis (Fast Fourier Transformation, FFT) to identify cyclical patterns and periodicity of upstream migration. I also pooled histogram data into 14-h periods (18:00–08:00 hours) using 10-min bins for each multi-day passage event (representing vespertine, nocturnal, and matutinal movements). Using pooled 14-h histograms, I examined patterns of movements for each passage event and described multiple peaks of passage counts for vespertine, nocturnal, and matutinal movements by fitting a normal model and eight normal mixture models (2–9 mixtures). The Bayesian information criterion (BIC) was used to select the best approximating model. A mixed-model methodology was used to examine relationships among total length (TL), diel period, and season. Periodicity of movements closely followed a 24-h cycle of activity with most movement being nocturnal. Based on mixture model analysis, multimodal models were supported by the data, but distribution patterns and timing of upstream migration were complex and variable across the six passage events. An additive-effects model of diel period + season was selected as the best approximating model for the mixed-model analysis of TL. Also, the mean TL of individuals using the eel ladder decreased as the night progressed (i.e., from vespertine to diurnal periods of movement) and was the highest during fall (330.3 mm ± 1.9 SE, n = 472) relative to similar mean values of TL for spring (304.1 mm ± 1.0 SE, n = 1700), summer (301.2 mm ± 1.1 SE, n = 1548) and late summer/early fall (303.4 mm ± 0.87 SE, n = 2269). This study provided new insights into the upstream migration ecology of yellow-phase American Eels and an increased understanding of dam passage at the Millville Dam eel ladder.

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Chapter 1: Literature Review

This thesis focuses on the diel periodicity, timing, and lengths of upstream migrant yellow-phase American Eels (*Anguilla rostrata*) and includes two chapters. The first chapter reviews American Eel ecology and consists of information on life history, upstream migration, population concerns, and dams and eel ladders. The second chapter is a research study on the diel periodicity of upstream migration of yellow-phase American Eels at the Millville Dam eel ladder on the Shenandoah River, WV.

Ecology

Life History

The American Eel (*Anguilla rostrata*) is a catadromous species with a complex life history. It has a vast geographical distribution, ranging from Greenland to Venezuela (Tesch 1977; Facey and Van Den Avyle 1987; Oliveira 1999). The species occupies a variety of habitat types, including ponds, lakes, streams, rivers, marshes and estuaries (Tesch 1977; Fahay 1978; Helfman et al. 1984; Van Den Avyle 1984; Facey & Van Den Avyle 1987; Jessop 2010). It has also been observed in a variety of microhabitats, such as leafy, mud bottoms and undercut banks, coarse gravel and cobble, and sandy substrates (Tesch 1977; Meffe and Sheldon 1988; Strickland 2002). Given its large geographic range and ability to thrive in freshwater and saltwater habitats, the American Eel is considered a highly adaptive species.

There are five major life stages of the American Eel during which biological changes occur: leptocephalus, glass, elver, yellow and silver (Oliveira 1999). American Eels spawn in the Sargasso Sea primarily from February to April (Schmidt 1923; Helfman et al. 1987; Oliveira 1999; Powles and Warlen 2002), relative to European Eels that spawn there from March into June (McCleave and Kleckner 1987; McCleave et al. 1987). After hatching, ribbon-shaped leptocephalus larvae are carried by Gulf Stream ocean currents for up to a year and dispersed along the North American continental shelf (Kleckner and McCleave 1985; Castonguay and McCleave 1987). Upon entering coastal areas, they metamorphose into "glass eels," characterized by transparent, snake-like bodies (Kleckner and McCleave 1985; Castonguay and McCleave 1987; McCleave et al. 1987). During winter and spring, glass eels move into estuaries where they become pigmented and transition to elvers (Facey and Van Den Avyle 1987; McCleave and Wippelhauser 1987; Dutil et al. 2009). Elvers may migrate to freshwater or remain in tidal rivers and estuaries (Facey and Van Den Avyle 1987; Helfman et al. 1987). As the elvers make their way upstream and grow larger (>150mm), their pigment changes to a yellow-green, and they transition to the yellow phase, the dominant growth phase and longest life stage (Fahay 1978; Facey and Van Den Avyle 1987; ASMFC 2000; Beak 2001).

Yellow-phase eels are considered sexually immature adults. Gender differences are present although not externally evident (ASMFC 2000). Sex can be determined by examining gonadal tissues (Dolan and Power 1977; Facey and LaBar 1981). Sex determination may be influenced by environmental factors, such as population densities (Helfman et al. 1987; Krueger and Oliveira 1999). High density areas are mainly occupied by males while low-density areas are predominantly female (Krueger and Oliveira 1999). During the yellow phase, eels inhabit estuaries or migrate long distances upstream where they spend as many as 30 years feeding and growing to maturity before migrating downstream (Tesch 1977; Helfman et al. 1987; Jessop 1987; McCleave et al. 1987; Smogor et al. 1995). Males are typically found in estuaries and lower river systems while females tend to occupy the upper portions of watersheds (Helfman et al. 1987). The growth rate, size, and life span of males are typically less than that of females (Helfman et al. 1984; Krueger and Oliveira 1997; Oliveira 1997; Powles and Warlen 2002).

Males mature and migrate downstream at a smaller size and earlier age than females. The lengthy, slow growth of females maximizes size and increases fecundity (Helfman et al. 1987). Several studies have found that growth rates of males and females vary depending on latitude (Helfman et al. 1987; Oliveira 1999; Oliveira and McCleave 2002; Jessop 2010). Eels in the northern region of their range remain in freshwater systems longer and reach larger sizes before migrating back to the Sargasso Sea than do eels in the southern region (Helfman et al. 1987). In some cases, yellow-phase eels begin downstream migration before transitioning to the silver phase (Kleckner et al. 1983).

During the final stage, the silver phase, American Eels reach sexual maturity and undergo morphological and physiological changes that equip them for their seaward migration (McCleave et al. 1987; Oliveira 1999; ASMFC 2000). These changes include the silver pigment that gives the phase its name (Krueger and Oliveira 1999), increased eye diameter which may enhance vision in deep water (ASMFC 2000; Cottrill et al. 2002), enlarged pectoral fins which may increase swimming capacity (Durif et al. 2003; McGrath et al. 2003), an increased number of swim bladder blood vessels that may enhance buoyancy control (ASMFC 2000), and lateral line development (Zacchei and Tavolaro 1988). The eels also stop feeding, and the digestive tract degenerates (Pankhurst and Sorensen 1984; Durif et al. 2003). Downstream migration to the Sargasso Sea typically occurs from September to December (Able and Fahay 1998; Krueger and Oliveira 1999). Several studies have found downstream migration to be associated with environmental factors including water temperature, stream flow, precipitation, turbidity, lunar phase, and incident light (Lowe 1952; Winn et al. 1975; Tesch 1977; Vøllestad et al. 1986; Bergersen and Klemetsen 1988; Euston et al. 1997; Hammond and Welsh 2009; Eyler 2014). Olfaction has also been associated with downstream migration from estuary to ocean (Barbin et al. 1998; Haro 2003). Spawning occurs during late winter through early spring in the Sargasso Sea (Oliveira 1999; Powles and Warlen 2002). Although spawning behavior has not been observed, American Eels are presumed to spawn panmictically before dying (McCleave et al. 1987; Oliveira 1999; ASMFC 2000). The exact spawning location is unknown; however, based on the collection of leptocephalus larvae, researchers hypothesize that spawning occurs in the southern region of the Sargasso Sea, on the warm side of thermal fronts, in the upper 500-m section of the water column (Kleckner et al. 1983; Kleckner and McCleave 1985; McCleave et al. 1987). While the ages of silver-phase American Eels vary, length ranges are similar among sexes, with males being smaller than females (Helfman et al. 1987; Oliveira 1999). Studies have also found the size of mature females and the age of mature males to be positively correlated with latitude (Helfman et al. 1987; Oliveira 1999; Jessop 2010).

Migration and Movement

A key component of the American Eel's yellow phase is migration and movement, which is influenced by several variables, including time of year and night as well as water temperature (Walsh et al. 1983; ASMFC 2000; Hammond and Welsh 2009). Migration occurs primarily during night and twilight, but movements have been observed during the day (McGrath et al. 2003; Verdon et al. 2003; Welsh and Aldinger 2014). In many freshwater systems including the Potomac River drainage, yellow-phase eels migrate upstream from spring through fall (Richkus and Whalen 2000; Hammond and Welsh 2009; Welsh & Liller 2013). The start and termination of annual upstream migration is controlled partly by seasonal water temperature changes. In the spring, upstream movements of immature eels are associated with water temperatures between 10 and 16°C (Smith and Saunders 1955; Sorensen and Bianchini 1986; EPRI 1999; Jessop 2003; Schmidt et al. 2009; Welsh et al. 2015). Hammond & Welsh (2009) determined that upstream migration during spring was associated with water temperature and stream flow, and spring temperatures exceeding 15°C necessitate upstream eel passage at hydroelectric facilities. They also found that downstream movements during fall coincided with decreasing water temperatures (Hammond and Welsh 2009). When water temperatures fall below 10 °C, juvenile American Eels become torpid (Walsh et al. 1983). In the lower Shenandoah River drainage of the Potomac River system, eels overwintered near tributary mouths in thermal refuge areas (Hammond and Welsh 2009).

Other environmental cues can influence migration including olfaction, lunar phase, stream flow, and precipitation (Lowe 1952; Walsh et al. 1983; Sorensen and Bianchini 1986; Barbin 1998; Cairns and Hooley 2003; McGrath et al. 2003; Hammond & Welsh 2009; Welsh & Liller 2013). Olfactory cues may be used for orientation, especially to locate home sites and identify appropriate transport tides in estuaries (McCleave and Wippelhauser 1987; Barbin 1998). American Eel migration and localized movements seem to be influenced by lunar phase as well. Eels tend to avoid ambient light, and movements increase during new moon phases when lunar illumination is minimal and nights are darkest (Lowe 1952; Winn et al. 1975; Lamothe et al. 2000; Cairns and Hooley 2003; Hammond & Welsh 2009; Welsh and Liller 2013; Welsh et al. 2015). Fluctuations in stream flow and sudden changes caused by precipitation may cue upstream migration (Durif et al. 2003; Verdon et al. 2003; Hammond and Welsh 2009; Welsh and Liller 2013). Water temperature, stream flow, and lunar phase have been correlated with migration in the Shenandoah River drainage of the upper watershed of the Potomac River system, and similar results have been found along the east coast (Lowe 1952; Tesch 1977; Cairns and Hooley 2003; Hammond and Welsh 2009; Schmidt et al. 2009; Welsh and Liller 2013). Welsh and Liller (2013) and Welsh et al. (2015) found that upstream migration of yellow-phase eels in the lower Shenandoah River was associated with increased river discharge as well as low-light new moon phases. Welsh and Liller (2013) considered that an increase in water volume may offer less constrained travel and provide access to additional migration routes and habitat or, possibly, that increased turbidity associated with high river discharge provides reduced-light conditions favorable for migration. Also, considering the American Eel's nocturnal behavior and avoidance of ambient light, cloud cover may influence upstream migration (Lowe 1952; Cairns and Hooley 2003; Schmidt et al. 2009; Welsh and Liller 2013).

Evaluating the impacts of environmental factors on upstream migration in freshwater systems is difficult, because the abundance of eels decreases as the distance upstream increases (Wiley et al. 2004; Laffaille et al. 2005). Much of the research investigating environmental influences of migration was conducted in estuarine systems (Dutil et al. 1988; Martin 1995; Parker and McCleave 1997; Jessop 2003). In addition to the variables previously discussed, water chemistry, barometric pressure, air temperature, and sunlight may affect upstream migration (Miles 1968; Sorensen and Bianchini 1986; Euston et al. 1997). Migration can also be affected directly and indirectly by obstacles such as dams, which may prevent eels from reaching habitat upstream or cause mortality by turbines as they migrate downstream (McCleave 2001; Verdon and Desrochers 2003; Verreault et al. 2004).

In addition to long-range migration, yellow-phase eels have displayed homing behavior and established home ranges (Bianchini et al. 1982; Parker 1995; Oliveira 1997; Lamothe et al. 2000). In estuaries, tidal stages affect localized movements (Dutil et al. 1988; Parker 1995). Short-range movements upstream and downstream have been observed during summer months at dusk and dawn (Gunning and Shoop 1962; Ford and Mercer 1986; Oliveira 1997; Hammond and Welsh 2009). American Eels often use cover during daylight and move near dusk and dawn and throughout the night, suggesting crepuscular or nocturnal foraging (Sorensen et al. 1986; Meffe and Sheldon 1988; Hammond and Welsh 2009). These local movements may be affected by food and habitat availability as well as eel abundance and intraspecific competition (Ford and Mercer 1986; Helfman 1986; Wiley et al. 2004).

American Eels tend to avoid ambient light, and several studies have observed movement peaks occurring near dusk and dawn and around midnight, suggesting a pattern of nocturnal movement rather than migration occurring during all hours of the night (Helfman 1986; Sorensen et al. 1986; Dutil et al.1988; Parker 1995; McGrath et al. 2003; Verdon et al. 2003; Hammond and Welsh 2009; Schmidt et al. 2009; Welsh and Aldinger 2014). Behavioral diel periodicity has been documented in other fishes, especially in the spawning behaviors of reef fishes and sciaenids (Lobel 1978; Locascio and Mann 2008). Lobel (1978) repeatedly observed reef fishes courting and spawning one hour before sunset during the evenings of the week prior to a full moon throughout their spawning seasons. These species include angelfish (*Centropyge potteri*), butterflyfishes (*Chaetodon fremblii*, *C. multicinctus*, and *C. unimaculatus*), goatfish (*Parupeneus multifasciatus*), and surgeonfishes (*Acanthurus nigroris*, *Ctenochaetus strigosus*, *Zebrasoma flavescens*). Several studies have also found that spawning-related choruses produced by sciaenid species occur from dusk to several hours after nightfall, usually ceasing or dramatically declining by 0000–0300 hours (Fish and Cummings 1972; Takemura et al. 1978; Mok and Gilmore 1983; Holt et al. 1985; Saucier and Baltz 1993; Connaughton and Taylor 1995; Locascio and Mann 2008). Few studies, however, have researched diel periodicity of movement in fishes, and while several studies have examined different aspects of the American Eel's yellow phase including migration and diel activity, few have considered a temporal component, necessitating future research to examine the relationship between movement and time of night.

Population Status

American Eel abundance has decreased considerably throughout its range since the early 1980s (ASMFC 2000; COSEWIC 2006; MacGregor et al. 2008). Because of its vast distribution, the extent of global population decline is unknown, but regional declines in numbers and juvenile recruitment, like those documented in the St. Lawrence River, have been used as indicators (Oliveira 1999; Richkus and Whalen 2000; COSEWIC 2006; Cairns et al. 2008; de Lafontaine 2009). Studies on the Upper St. Lawrence River have indicated that while the number of eels using ladders has declined in recent decades, the size of eels migrating upstream has increased significantly, possibly due to decreased recruitment (Casselman 2003; McGrath et al. 2003; de LaFontaine et al. 2009; Marcogliese & Casselman 2009). Harvest data from the Atlantic coastal states also indicates a dramatic decline in recent decades (ASMFC 2013). Harvest landings peaked at 1,792,568 kg in 1979 and hit a low of 290,854 kg in 2002. Several environmental and anthropogenic factors may be contributing to declines (Castonguay et al. 1994a; 1994b; Haro et al. 2000; McCleave 2001; Neraas and Spruell 2001; Casselman 2003; Verreault et al. 2004; Wiley et al. 2004; COSEWIC 2006; Clark 2009; ASMFC 2013).

Concern for the American Eel is increasing as the population continues to decline. In response to the decline, the Atlantic States Marine Fisheries Commission (ASMFC) created an interstate fishery management plan in 2000 to conserve and protect the species while providing sustainable fisheries (ASMFC 2000). In April 2006, the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) designated the American Eel as a species of “special concern” due to its population decline, especially in the upper St. Lawrence River (COSEWIC 2006). Declines in harvest landings have prompted two petitions to list the American Eel as “threatened” or “endangered” under the Endangered Species Act (ESA). Upon completing a 12-

month status review, the U.S. Fish and Wildlife Service (USFWS) and the National Marine Fisheries Service (NMFS) determined in 2007 that listing the species was not warranted at that time, finding that declines in some areas had not put the total population in danger of extinction (50 CFR 17 2007). The review considered the eel's vast range, adaptability of different habitat types and aquatic systems, habitat availability, stable recruitment, and also that the population still contained millions of individuals. In April 2010, the American Eel was petitioned again for listing under the ESA by the Center for Environmental Science, Accuracy, and Reliability (CESAR, formerly the Council for Endangered Species Act Reliability), resulting in another status review (50 CFR 17 2011). The USFWS is currently conducting the status review and must submit a finding to the Federal Register by September 30, 2015.

Population Concerns

While the exact cause of decline remains unknown, potential factors include oceanic and climatic changes (Castonguay et al. 1994b; Haro et al. 2000), chemical contamination and pollution (Castonguay et al. 1994a), overharvest (Casselman 2003; Clark 2009; ASMFC 2013), and habitat loss (Wiley et al. 2004), as well as migration barriers and hydroelectric impacts (McCleave 2001; Neraas and Spruell 2001; Verreault et al. 2004; COSEWIC 2006). The parasite *Anguillacoloides crassus* also may contribute to the species' population decline (Haro et al. 2000). The nematode damages the eel's swim bladder, reducing swimming performance and potentially reducing growth, which can impact a yellow-phase eel's ability to migrate upstream or prevent a silver-phase eel from completing its spawning migration to the Sargasso Sea (Barse et al. 2001; Kirk 2003; Kennedy 2007; Palstra et al. 2007; Zimmerman and Welsh 2012).

Climatic changes and chemical contamination are environmental factors that could greatly impact the American Eel population and should be considered in conservation. Oceanic changes, including changes in currents and temperature, could impact the development and success of leptocephalus larvae (Knights 2003). Currents slowing oceanic migration can increase starvation and predation of larvae. Unfavorable currents may affect the passive drifting of larvae and reduce their dispersal along the Atlantic coast and also influence glass eel recruitment along the continental shelf. Knights (2003) suggested that warming of the Sargasso Sea/Sub-Tropical Gyre spawning area may also increase starvation of leptocephalus larvae by inhibiting spring mixing of the thermocline, which impedes nutrient circulation and decreases productivity. Water contamination and chemical pollution could also potentially affect the eel's migratory and breeding success by disrupting migratory behavior, reducing reproductive ability, and increasing mortality (Robinet and Feunteun 2002). The American Eel's long lifespan and high fat content put it at a greater risk of exposure to and bioaccumulation of contaminants and xenobiotics including polychlorinated biphenyl (PCBs), mirex, and mercury. As the eel migrates seaward and stops feeding, lipid stores that contain the contaminants are used for energy. This problematically releases the pollutants back into circulation, concentrating in the eel's gonads during the critical time of gametogenesis. Robinet and Feunteun (2002) suggest that, based on toxicological analysis, the condition of individuals migrating to spawn is a limiting factor of spawning success. Because of the high levels of contaminant absorption, some states have issued consumption advisories for the American Eel.

Overfishing of eels at different phases of their life cycle may also be significantly affecting population decline (ASMFC 2013). Although today's American Eel fisheries are only a fraction of what they have been historically, they are still a valuable resource commercially and recreationally. Glass eels, considered a delicacy in Asia, are in high demand, but most coastal states have restricted or banned glass eel harvest (ASMFC 2013). In 2012, only Maine and South

Carolina permitted commercial harvest of glass eels. The landings totaled 10,077 kg and were valued at almost $40 million, which is 20 times greater than the past 11 years' average value, according to the ASMFC (ASMFC 2012, 2013). Yellow- and silver-phase eels are also commonly harvested. The ASMFC fishery management plan created in 2000 suggested that heavy harvest may contribute to population decline because of the American Eel's slow maturation rate, glass eels' tendency to aggregate during migration, the effect of multiple-year yellow-phase harvest on the same year class, and all harvests occurring before spawning (ASMFC 2000). As a result of the 2012 stock assessment, two addenda were added to the interstate fishery management plan to reduce American Eel mortality and increase conservation of stocks (ASMFC 2013). These addenda include new management for recreational and commercial glass eel, yellow-phase, and silver-phase fisheries.

Another potential contributor to the American Eel's population decline is its drastic habitat loss and extirpation from historic freshwater habitat in the last century (Verreault et al. 2004; USFWS 2007). Some habitat degradation is the result of dredging and filling channels as well as the loss of wetlands. Most loss of habitat and migration passageways is a result of dams. Some dams do not impede eel migration, but over 15,000 dams exist along Atlantic coastal streams, which have obstructed access to 84% of the eel's historical habitat (Busch et al. 1998; Eyler 2014). Although few studies have examined the degree of impact that dams and their management practices have on migrating eels (Goodwin et al. 1999; ASMFC 2000), habitat fragmentation attributed to dams, hydroelectric facilities, and navigation weirs have reduced distribution ranges and increased extinction risks for migratory fishes including trout, pike, and minnow species (Agostinho et al. 2002; Ovidio and Philippart 2002). Over 90% of the Atlantic coastal dams do not require re-licensing or fish passage analysis, because they are not considered hydroelectric facilities (ASMFC 2000; FERC 2004). Dams act as barriers that reduce the range and abundance of upstream migrating elvers as well as yellow-phase eels in the upper portions of watersheds (EPRI 2001; McCleave 2001; Goodwin and Angermeier 2003). Also, considering that eels in upper watershed regions typically differentiate as females, dams may affect sex ratios (Krueger and Oliveira 1999). Turbines at hydropower facilities can disrupt downstream migration and cause significant mortality rates of pre-spawning yellow- and silver-phase eels (Ritter et al. 1997; EPRI 1999; Haro et al. 2000; USFWS 2007). Turbine-induced mortality rates have ranged from 5% to 100% at different hydropower stations (ASMFC 2000; Jansen et al. 2007; Carr and Whoriskey 2008; Bruijs et al. 2009; Calles et al. 2010; Pedersen et al. 2012; Buysse et al. 2014). To combat the threats that dams pose to eels, researchers and fisheries managers have installed bypass structures and altered operation times at hydroelectric plants, turning off turbines at night when downstream migration is occurring. Eel ladders are also installed to aid in upstream migration (Whitfield and Kolenosky 1978; ASMFC 2000; Welsh and Liller 2013). Eels at different life stages require different ladder substrates in order to climb (EPRI 1999). While elvers are capable of ascending simple passageways comprised of gravel or mesh, yellow-phase eels often use vertical cylinders protruding from the bottom of the ladder for traction.

Justification

While the American Eel has gained attention in recent decades, little is understood about the species, especially young yellow-phase eels, and many unanswered questions remain. There is a growing need to study the species due to its economic and ecological importance as well as its population decline (Castonguay et al. 1994a; Haro et al. 2000; Casselman 2003; Verreault et al. 2004; COSEWIC 2006; Clark 2009). Historically, the species was an important food source for Native Americans and early settlers (Casselman 2003). The American Eel continues to be a valuable resource, playing an important role in today's international food market as well as supporting a commercial and domestic bait fishery (Castonguay et al. 1994a; Haro et al. 2000; Casselman 2003; ASMFC 2007). Ecologically, American Eels play an important role in aquatic ecosystems as a predator and prey species, being preyed upon by a variety of piscivorous fishes, mammals, and birds (Sinha and Jones 1967; Ogden 1970; Seymour 1974; Casselman 2003; Thompson et al. 2005; ASMFC 2007). They are also an important glochidia host in the Chesapeake Bay drainage for the freshwater mussel *Elliptio complanata* (Lellis et al. 2013). Given regional declines in abundance throughout its range, gaining a better understanding of the American Eel, especially knowledge of upstream migration, may be crucial for successful management and conservation (Oliveira and McCleave 2000; Wiley et al. 2004). This study examined the diel periodicity and chronology of upstream migration of yellow-phase American Eels and relationships between movement and total length in order to better understand upstream migration ecology and dam passage of yellow-phase American Eels at the Millville Dam eel ladder.

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Chapter 2: Diel periodicity and chronology of upstream migration in yellow-phase American Eels (*Anguilla rostrata*)

ABSTRACT

This study examined the diel periodicity and chronology of upstream migration of yellow-phase American Eels (*Anguilla rostrata*) and relationships between movement and total length. Passage count data were collected during 2011–2014 at the Millville Dam eel ladder on the lower Shenandoah River, West Virginia. Six multi-day passage events with a high number of passage counts were selected for analysis and categorized by diel periods of movement (vespertine, nocturnal, matutinal, and diurnal) and season (spring, summer, late summer/early fall, fall). To examine periodicity of movements, I graphically-depicted these data as time-series histograms and used time-series spectral analysis (Fast Fourier Transformation, FFT) to identify cyclical patterns and diel periodicity of upstream migration. I also created histograms to examine movement patterns within diel periods for each passage event and described multiple peaks of passage counts for vespertine, nocturnal, and matutinal movements by fitting normal mixture models (2–9 mixtures). A mixed-model methodology was used to examine relationships among total length (TL), diel period, and season. Periodicity of movements closely followed a 24-h cycle of activity for each multi-day passage event with most movement occurring nocturnally. To my knowledge, this is the first study to quantify the pattern of diel periodicity of upstream migration using spectral analysis. Based on mixture model analysis, distribution patterns and timing of upstream migration were relatively complex and variable across seasons, although there were some similarities across the six passage events. Multimodal models were supported by the data, where most modes represented nocturnal movements, but modes at or near the transition between periods of twilight and night were also common. For the mixed-model analysis of TL, the additive-effects model of diel period + season was selected as the best approximating model. Based on values of mean TL, a decreasing trend occurred across diel movement periods (vespertine = 311.5 mm ± 1.7 SE, nocturnal = 305.8 mm ± 0.59 SE, matutinal = 298.3 mm ± 1.9 SE, and diurnal = 282.8 mm ± 5.5 SE, n = 58). Also, mean TL was highest during fall (330.3 mm ± 1.9 SE) relative to similar mean values of TL for spring (304.1 mm ± 1.0 SE), summer (301.2 mm ± 1.1 SE) and late summer/early fall (303.4 mm ± 0.87 SE). This study increased our understanding of upstream migration ecology of yellow-phase American Eels and dam passage at the Millville Dam eel ladder.

INTRODUCTION

The American Eel (*Anguilla rostrata*) is a catadromous species with a complex life history, including larval, glass, elver, yellow, and silver phases (Tesch 1977; Facey and Van Den Avyle 1987; Oliveira 1999). The species spends a large portion of its life in the yellow phase, the dominant growth phase, during which many individuals migrate long distances upstream, often facing migration barriers, such as dams (Tesch 1977; Facey and Van Den Avyle 1987; ASMFC

2000). The upstream migration ecology of the American Eel is not well understood, particularly little is known about the periodicity and timing chronology of upstream movements. In the last few decades, eel ladders have been installed on some Atlantic Coast rivers, providing opportunities to study and monitor upstream movements of American Eels (McGrath et al. 2003; Verdon et al. 2003; Schmidt et al. 2009; Welsh and Liller 2013; Welsh et al. 2015). Further studies on the upstream migration ecology of the yellow-phase American Eel, however, are relevant to management and conservation efforts, given migration barriers on upstream movements and recent concerns of population decline (Haro et al. 2000; Richkus & Whalen 2000; Casselman 2003).

Bianchini et al. (1982), as cited in Oliveira (1997) hypothesized a punctuated pattern of upstream migration, where short-term home ranges of American Eels alternate with long-range movements. Interestingly, punctuated patterns of upstream migration may occur at several temporal and spatial scales. Annually, punctuated upstream movements are due, in part, to seasonal changes in water temperature. Walsh et al. (1983) and Renaud and Moon (1980) reported torpor and reduced feeding at 10°C in juvenile American Eels. Yellow-phase American Eels cease upstream movements during fall when water temperatures reach 10°C (McGrath et al. 2003; Hammond and Welsh 2009) and resume upstream movements the following spring during water temperatures of ~15–20°C (K. McGrath, pers. comm.; Welsh et al. 2015). In addition to water temperature, other environmental variables have been associated with punctuated upstream movements, including periods of dark lunar phases and periods of increased river discharge (Welsh and Liller 2013; Welsh et al. 2015).

Diel periodicity of upstream migration is expected for American Eels, because upstream movements are punctuated by nocturnal or crepuscular behavior, as American Eels primarily move at night or twilight, although some movements have been observed during the day (Helfman 1986; Sorensen et al. 1986; Dutil et al.1988; McGrath et al. 2003; Verdon et al. 2003; Welsh and Aldinger 2014). Few studies, however, have examined the timing of upstream migration within diel periods (day, twilight, and night). McGrath et al. (2003) and Verdon et al. (2003) documented the timing (30-min increments) of upstream migrants at eel ladders on the St. Lawrence and Richelieu Rivers, respectively. From these studies, McGrath et al. (2003) and Verdon et al. (2003) emphasized the predominance of nocturnal movements, but did not separate movements for twilight and night periods.

This study examined diel periodicity, passage timing, and lengths of upstream migrant yellow-phase American Eels at the Millville Dam eel ladder on the lower Shenandoah River, West Virginia from 2011–2014. Study objectives were to (1) examine diel periodicity of upstream migrants using time-series spectral analysis, (2) describe the distribution of passage counts during diel periods (day, twilight, and night) among seasons (spring, summer, and fall), and (3) examine size of upstream migrants relative to diel and seasonal periods.

METHODS

Study site

The 296-m-wide Millville hydroelectric dam (owned and operated by PE Hydro Generation, LLC) stands five meters tall and is located on the lower Shenandoah River, approximately nine rkm upstream of the confluence of the Shenandoah and Potomac rivers, 100 rkm upstream of the Potomac River at the head of tide, and 285 rkm upstream from the mouth of the Potomac River estuary (Welsh and Liller 2013; Welsh et al. 2015). An 11-m eel ladder with a 50° slope (Milieu Inc, Quebec, Canada) is installed annually on the western end of the dam. The eel ladder, a stainless steel-covered sluice that contains a peg board climbing substrate, is typically in operation from spring or summer through fall to aid upstream migration (Welsh and Liller 2013; Welsh et al. 2015).

Data collection

Data on passage counts from digital photographs, including date and time of passage, were downloaded from an infrared-triggered digital camera located near the apex of the eel ladder (Welsh 2014). The digital photographs were also used to obtain photogrammetric measurements of American Eel lengths as described by Welsh and Aldinger (2014). River flow, lunar phase, and astronomical data were also collected for the passage events. Daily estimates of river discharge (m^3/s) of the Shenandoah River were obtained from the U.S. Geological Survey gage located approximately 400 m downstream of the Millville Dam (http://waterdata.usgs.gov). I calculated the illuminated fraction of the moon for each passage event in package *oce* (version 0.9–14, Kelley 2014) in program R (version 3.1.3 R Development Core Team 2015), where the fraction ranged from 0.00 (new moon) to 1.00 (full moon). I collected daily astronomical data for Millville Dam using the package *maptools* (version 0.8–36, Bivand et al. 2015) in program R (version 3.1.3 R Development Core Team 2015) and classified activity periods for a 24-h cycle based on the rising and setting of the sun. Because eels exhibit crepuscular and nocturnal behavior (Sorensen et al. 1986; Meffe and Sheldon 1988; Hammond and Welsh 2009), I separated upstream movements by periods of twilight, night, and day:

- Vespertine = movements during dusk period between sunset and evening astronomical twilight (i.e., when the sun is 0–18º below the horizon);
- Matutinal = movements during dawn period between sunrise and morning astronomical twilight (i.e., when the sun is 0–18º below the horizon);
- Diurnal = movements during the daytime period between sunrise and sunset; or

- Nocturnal = movements during the nighttime period after astronomical twilight ends in the evening and before astronomical twilight begins the next morning.

Data analysis

I analyzed six multi-day passage events, which ranged in length from 7 to 18 days. The six passage events were selected based on time periods that had high passage counts within a short time frame, which reduced variation associated with temporal (i.e., seasonal) changes in lengths of twilight, nighttime, and daylight periods. These six passage events were categorized as four seasonal periods: spring (17–28 May 2012, n=1,848), summer (12–21 July 2013, n=1,617, and 22 July–3 August 2014, n=285), late summer/early fall (13 September–1 October 2011, n=666, and 18–27 September 2012, n=1,868), and fall (14–21 October 2014, n=519).

To examine periodicity of movements, I aggregated counts of individuals passing through the ladder into 10-min bins for each multi-day passage event starting at 12:00 noon on the first day and ending at 12:00 noon on the last day. I graphically-depicted these data as time-series histograms, including a secondary y-axis for river discharge (m^3/s) to emphasize the relationship between upstream movements and river discharge as previously reported by Welsh et al. (2015). I examined the histogram data with time-series spectral analysis (Fast Fourier Transformation, FFT) to identify cyclical patterns and diel periodicity of American Eel upstream migration (JMP, version 12.0.1 SAS Institute Inc. 2015). An FFT classifies data by component frequencies using an algorithm to convert time to frequency while finding sinusoidal patterns (Chatfield 1996). Frequencies of dominant patterns are represented as peaks in periodograms and can be graphically depicted as time (x-axis) by spectral density (y-axis) (Meyer et al. 2007; Baluev 2013). I applied FFTs to count data for each of the six passage events and added a reference line to the time axis to indicate the dominant frequency.

To examine patterns of vespertine, nocturnal, and matutinal movements for each passage event, I created histograms of the number of individuals passing through the ladder pooled into a 14-h period (18:00–08:00 hours) using 10-min bins. As a descriptive approach, I fit a normal model to the histogram data for each passage event representing a hypothesis of a unimodal peak. Additionally, I fit eight normal mixture models (2–9 mixtures) representing hypotheses of multimodal distributions (JMP, version 12.0.1 SAS Institute Inc. 2015). Using these nine candidate models, I used Bayesian information criterion (BIC, Schwarz 1978) to select the best approximating model (Steele and Raftery 2010). This analysis approach allowed for the description of multiple modes or peaks of passage counts for vespertine, nocturnal, and matutinal movements.

A mixed-model methodology was used to examine relationships among total length (TL), diel period, and season (SAS 9.4, PROC MIXED). Given that the TL of individuals passing within a 24-h diel period may not be independent, this approach adjusted covariance structure of the models through a random block effect on TL within each 24-h period (12:00 to 12:00 hours). I fit the following four models to TL data: (1) an intercept model, (2) a diel period model, (3) a season model, and (4) an additive–effects model of diel period + season. I used BIC as a model selection criterion. To aid interpretation of model selection, I plotted descriptive statistics of mean ± SE of TL for categories of movements during diel periods (vespertine, nocturnal, matutinal, diurnal) and seasons (spring, summer, late summer/early fall, fall). I did not have data for every season of every year. Therefore, I modeled seasons separately and could not test for a year effect. Also, given that passage events were selected from time periods of high counts associated with increased river discharge and often with new moon periods (Welsh et al. 2015), I did not expect to find relationships between TL, river discharge, and lunar illumination.

Therefore, I did not fit models with covariates of river discharge and lunar illumination. However, as a separate analysis, I did depict these relationships by plotting the log TL and log river discharge and log TL and lunar illumination.

RESULTS

A total passage count of 9,042 individuals was recorded at the Millville eel ladder during 2011–2014, including annual counts of 1255 (6 May–9 November 2011), 4263 (28 June–7 November 2012), 2470 (1 July–12 October 2013), and 1054 (22 July–5 November 2014). I reduced variation associated with temporal changes in lengths of twilight, night, and day periods by analyzing six short-term passage events representing 75.2% (n=6,803) of the total number of individuals that used the eel ladder during 2011–2014. Total lengths were photogrammetrically measured for 5,989 of the 6,803 individuals, with a mean TL of 305.2 mm ± 0.55 SE, range = 185–609 mm.

Time series data of passage events separated into 10-min intervals depicted diel periodicity of upstream movements, where most individuals moved during periods of twilight and night, and few individuals moved during the day (Figures 2.1, 2.2). Peaks in movement for the multi-day passage events were associated with an increase in river discharge (Figure 2.1). For diel periods, the counts of vespertine, nocturnal, matutinal, and diurnal movements were 506 (7.4%), 5,625 (82.7%), 588 (8.6%), and 84 (1.2 %), respectively. For each passage event, time-series spectral analysis using FFT recovered dominant frequencies representing 24-h cycles (Figure 2.1).

Based on mixture model analysis, multimodal models were supported by the data. Multimodal patterns of movement differed across the six passage events, but there were some similarities in timing of modal peaks (Table 2.1, Appendix 2.1). Most movement peaks occurred during the nighttime period, although three of the six periods had peaks for vespertine or matutinal movements. All passage events had peaks during the middle of the nighttime period (0:00–02:00, Figure 2.2), which is likely the darkest part of the night. Also, peaks in movement occurred at or near the transitions of evening twilight/night, and night/morning twilight in 4 of 6 and 5 of 6 passage events, respectively (Figure 2.2). For the spring passage event, a four-mixture model was supported, with a modal movement peak during each twilight period, and two peaks during the night period (Figure 2.2A). For the first summer passage event, a six-mixture model was supported by the data, with single modal peaks for vespertine and matutinal movements and four peaks of nocturnal movements (Figure 2.2B). For the second summer passage event, however, data supported only three movement peaks, including two for nocturnal movements and one at the transition of night and early morning twilight (Figure 2.2C). The first and second passage events of late summer/early fall contained eight and six peaks, respectively, where all peaks were during the nighttime period, except for a single peak of matutinal movement (Figures 2.2D, 2.2E). The fall passage event included four peaks of nocturnal movements and no peaks during twilight periods (Figure 2.2F).

For the mixed-model analysis of TL, the additive-effects model of diel period + season was selected as the best approximating model (BIC = -7686.0), where BIC values for the intercept, diel period, and season models were -7676.1, -7650.5, and -7679.1, respectively. The additive-effects model was visually supported and interpreted with use of descriptive statistics, where mean TL depicted a decreasing trend across diel periods (vespertine = 311.5 mm ± 1.7 SE, n = 235; nocturnal = 305.8 mm ± 0.59 SE, n = 5182; matutinal = 298.3 mm ± 1.9 SE, n = 514; and day = 282.8 mm ± 5.5 SE, n = 58; Figure 2.3). Also, mean TL was highest during fall (330.3 mm ± 1.9 SE, n = 472) relative to similar mean values of TL for spring (304.1 mm ± 1.0 SE, n =

1700), summer (301.2 mm ± 1.1 SE, n = 1548) and late summer/early fall (303.4 mm ± 0.87 SE, n = 2269; Figures 2.4, 2.5). The higher mean TL of individuals undergoing vespertine movements did not influence the higher mean TL during fall passage (14–21 October 2014), as vespertine movements were not observed during the fall passage event. Separate correlation analyses of log TL and log river discharge and log TL and lunar illumination supported weak relationships (r=0.1, Figure 2.6; r=0.05, Figure 2.7; respectively).

DISCUSSION

While studies have suggested that American Eels exhibit nocturnal or crepuscular behavior (Sorensen et al. 1986; Meffe and Sheldon 1988; Hammond and Welsh 2009), to my knowledge, this is the first study to quantify diel periodicity of upstream migration of yellow-phase American Eels. It is well established that American Eels are primarily nocturnal (Helfman et al. 1983; Helfman 1986; Sorensen et al. 1986; Dutil et al.1988, 1989; Meffe and Sheldon 1988; Parker 1995), thus diel periodicity of movements would be expected to closely follow a 24-h cycle of activity. Based on six multi-day passage events during this study, time-series spectral analysis found a dominant frequency at 24 h. While studies have examined the periodicity of movement (Bohun and Winn 1966; Helfman et al. 1983; Sorensen and Bianchini 1986), I am unaware of other studies using spectral and FFT analysis for American Eel upstream migration; however, FFT has been used in several recent studies to identify periodicity in movements of various fish species (Graham et al. 2006; Shepard et al. 2006; Meyer et al. 2007; Afonso et al. 2009; Brunnschweiler and Sims 2011).

Few studies have addressed diel chronology and timing of upstream movements of yellow-phase American Eels during periods of twilight and night. The majority of movements in this study were nocturnal, and all six events had peaks of movement occurring during the middle of the nighttime period. Dutil et al. (1989) observed movements of glass and elver American Eels in the Gulf of St. Lawrence occurring primarily between 21:00 and 23:00. In a study of upstream migrant yellow-phase eels at an eel pass on the Moses-Saunders Power Dam, St. Lawrence River, McGrath et al. (2003) reported nocturnal movements where most individuals (94%) used the ladder between 19:30 and 05:30 hours. During a three-year study (1997–1999) of the Chambly Dam eel ladder, Richelou River, Verdon et al. (2003) reported the diel timing of eel use as mostly nocturnal, from 21:00 hours to dawn, with a peak near 1:00 hours. My results support that upstream migrants primarily undergo nocturnal movements, which is consistent, in part, with McGrath et al. (2003) and Verdon et al. (2003). However, McGrath et al. (2003) and Verdon et al. (2003) used passage data of eel counts for 30-min periods and did not separate periods of day, twilight, and night, whereas my data represented 10-min time periods, and separated day, twilight, and night based on time periods of astronomical twilight. Also, it is interesting to note that all passage events had peaks during the middle of the nighttime period (0:00–02:00, Figure 2.1), likely the darkest part of the night. It is possible that some American Eels select darker conditions when migrating to avoid the risk of predation.

Although the distribution patterns and timing of upstream migration in this study were complex and variable across seasons, there were some similarities. The majority of peaks in movement were nocturnal, and five of the passage events had movement peaks occurring near the interfaces of twilight (vespertine and matutinal movements) and night, which supports previous studies finding that eels exhibit nocturnal and crepuscular behavior. There are several simple biologically reasonable hypotheses for diel chronology and timing of upstream movements. One hypothesis, which would represent a unimodal distribution, is where upstream migrants initiate vespertine movements at dusk, depict a modal peak of nocturnal movements during the night, and continue with matutinal movements at a decreasing rate until dawn. However, my data did not support a unimodal distribution. Additionally, bimodal distributions, which were not supported by the data, could result from peaks of vespertine and nocturnal movements, or peaks of nocturnal and matutinal movements. Another hypothesis, which would represent three distributions, would involve modal peaks of vespertine, nocturnal, and matutinal movements, but this distribution pattern was also not supported by the data. Based on my observational data, I was not able to explain why distribution patterns of diel chronology and timing of upstream migration were relatively complex (three to eight modal peaks). I was also not able to explain why the most complex distribution patterns occurred during the two passage events of late summer/early fall. Peaks in movement, however, occurred at or near the interfaces of evening twilight and night, and night and morning twilight in 4 of 6 and 5 of 6 passage events, respectively. This finding is consistent with experimental studies by Bohun and Winn (1966), who reported that locomotor activity in 203–305 mm American Eels was highest at times of light change, corresponding to dusk and dawn periods, and by Edel (1976), who found bursts in activity during times of light change. Helfman (1986) also observed that changes in the movements of American Eels in a Florida cave-spring occurred around dusk and dawn.

The diel chronology of upstream migrants using the eel ladder may be linked to the longitudinal distribution of individuals downstream of the dam, the initial distance downstream of the dam prior to starting vespertine or nocturnal movements, and the speed of upstream migration. Assuming a constant rate of upstream migration, individuals closest to the dam may find the eel ladder sooner than those farther from the dam. Another consideration is the variation in search time among individuals in finding the ladder entrance. Presumably, there is a time delay from when an upstream migrant reaches the dam and when it finds the eel ladder entrance.

This may explain why peaks in vespertine movements were only observed during two of six passage events.

The mean TL of individuals passing the dam followed a time trend where the longest individuals used the ladder during evening twilight (vespertine movements) and the shortest individuals used the ladder during the day (diurnal movements). Our finding of larger individuals moving during the vespertine period is not influenced by the fall period (14–21 October 2014), because we did not have TL data for any vespertine movement of that period (Figure 2.5D). To my knowledge, no other studies have documented a difference in TL of upstream migrants among diel periods of day, twilight, and night. Although the eel ladder is expected to pass upstream migrants, it is also possible that American Eels with established home ranges just downstream of the dam may also use the ladder. American Eels with established home ranges will likely have higher mean TL than upstream migrants, and if proximately located downstream of the dam would have a relatively short distance of travel to reach the dam during vespertine movements. Ford and Mercer (1986) found in Great Sippewissett Marsh, Falmouth, Massachusetts, that the average size of individuals decreased as their home range distance upstream increased; however, they found no relationship between size of individuals and distance of diel movement. It is also unclear why smaller individuals moved during the daytime period.

The mean TL of individuals passing during the fall exceeded that of individuals migrating upstream during the spring, summer, and late summer/early fall periods. Similarly, Welsh and Liller (2013) reported mean TL of upstream migrants during 2004–2005 at Millville Dam as 29.3 cm ± 0.13 SE (during a spring/summer period), 30.2 cm ± 0.23 SE (late spring/summer period), and 33.6 cm ± 0.12 SE (late summer/early fall period). Dutil et al. (1989)

also found a decrease in the proportion of smaller sized eels in the Gulf of St. Lawrence as the migration season progressed. Although I found no studies examining the effect of water temperature on different size eels, I speculate that the influence of colder water temperatures on the activity of larger individuals may be less than that of smaller individuals, particularly during fall when water temperatures are between 10 and 15°C, but I was not able to test this hypothesis with observational data. Hammond and Welsh (2009) found that larger yellow-phase eels (518–810 mm TL) were active during fall time periods with mean water temperatures as low as 9.3°C.

This study examined the timing chronology of upstream migration of yellow-phase American Eels among and within 24-h (diel) periods. In summary, it quantified the pattern of diel periodicity of upstream migration. Based on the time-series spectral analysis of six multi-day passage events, periodicity of movements closely followed a 24-h cycle of activity with the majority of movements were nocturnal with a few peaks occurring near the interfaces of twilight (vespertine and matutinal periods) and night, which supports previous studies finding that eels exhibit nocturnal and crepuscular behavior (Sorensen et al. 1986; Meffe and Sheldon 1988; McGrath et al. 2003; Verdon et al. 2003; Hammond and Welsh 2009). The distribution patterns and timing of upstream migration were complex and variable. The TL of individuals passing the dam followed a chronological trend with time, where the longest individuals passed through the ladder during the vespertine period and the shortest individuals used the ladder during the day (diurnal movements). The mean TL of individuals passing was greater during the fall period than that of individuals using the ladder during the spring, summer, and late summer/early fall periods, which supports the results found by Dutil et al. (1989), Hammond and Welsh (2009), and Welsh and Liller (2013).

While this study provides insight into the patterns of upstream migration of yellow-phase American Eels in the Shenandoah River, I realize that correlative effects associated with observational data limit strong inference. Also, inference is restricted to the lower Shenandoah River, as I do not know if these results are representative of other watersheds within the geographic range of American Eels. Future studies of similar design including multiple watersheds could offer a better understanding of upstream migration throughout the American Eel's geographic distribution. This could be especially useful in areas where the number of individuals passing during the upstream migration season is much greater and there is a larger TL range. This study did not consider the presence of artificial light and did not measure the amount of ambient light at the Millville Dam, which would be an interesting variable to include in future, similar studies. Based on the 24-h cycle and the range of time for movement peaks, our study suggests that the monitoring counts of individuals migrating upstream should occur on a nightly basis and throughout the entire night (i.e., from sunset to sunrise) to ensure inclusion of most upstream migrants.

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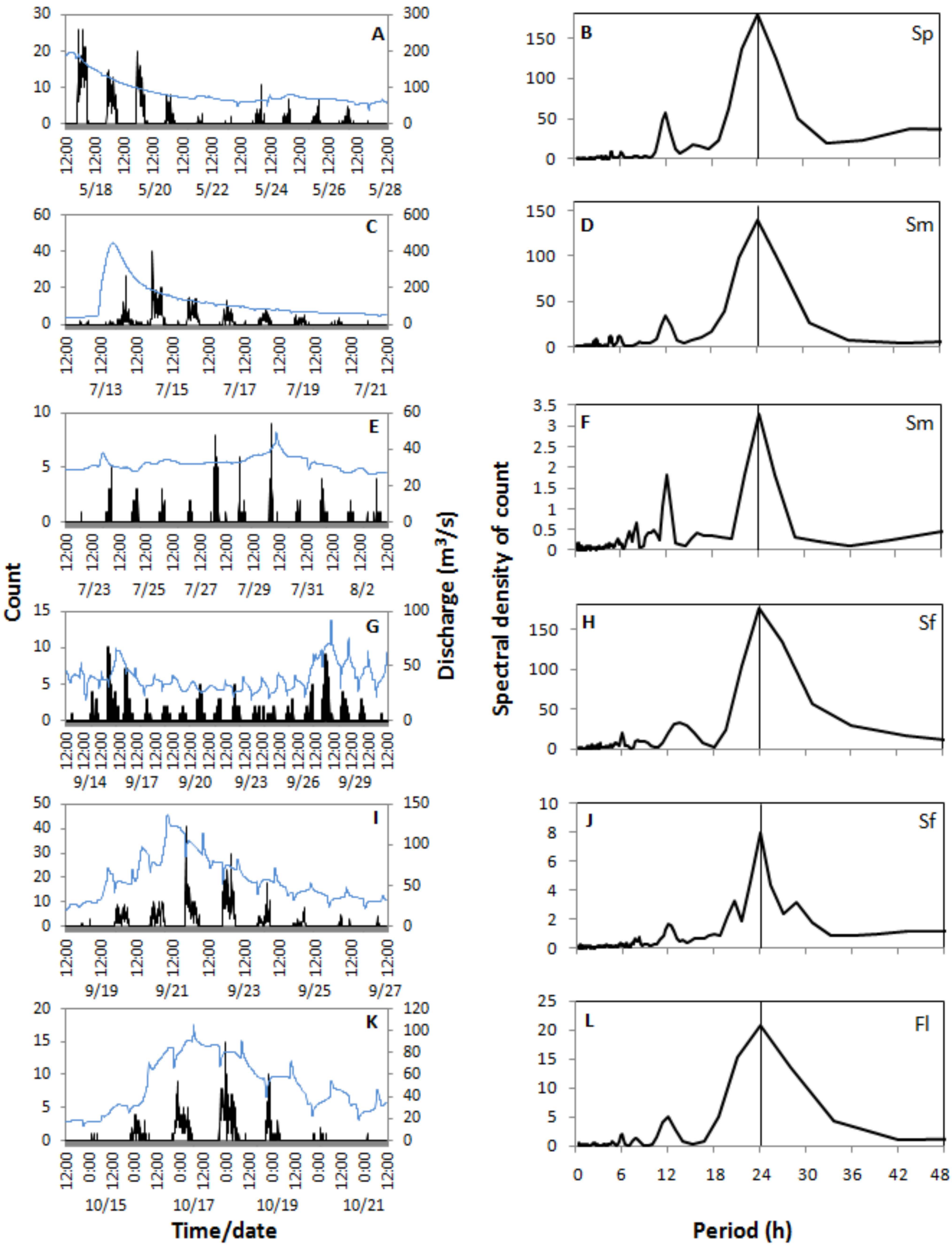

Figure 2.1. Frequency of counts of American Eels passing through the eel ladder and river discharge (m^3/s) at the Millville Dam using 10-min bins (starting at 12:00 on the first day of the period) for six periods: 17–28 May 2012 (A, B), 12–21 July 2013 (C, D), 22 July–3 August 2014 (E, F), 13 September–1 October 2011 (G, H), 18–27 September 2012 (I, J), and 14–21 October 2014 (K, L). Seasons are labeled as spring (SP), summer (SM), late summer/early fall (SF), and fall (FL). A reference line indicates the dominant frequency

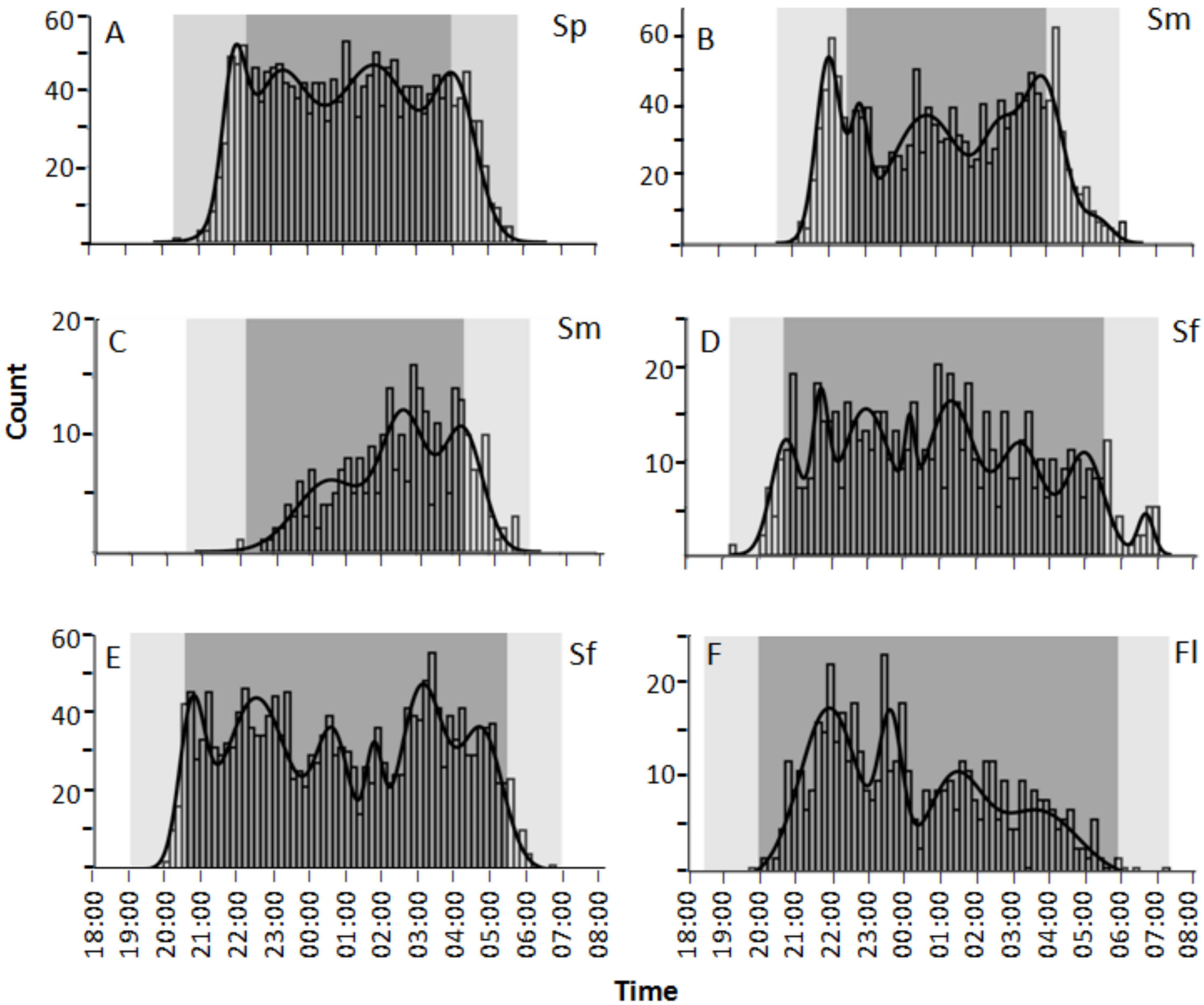

Figure 2.2. Frequency of counts of American Eels passing through the Millville Dam eel ladder on the Shenandoah River pooled into a 14 h period (starting at 18:00) using 10-min bins for six periods: 17–28 May 2012 (A), 12–21 July 2013 (B), 22 July–3 August 2014 (C), 13 September–1 October 2011 (D), 18–27 September 2012 (E), and 14–21 October 2014 (F). The lighter shaded areas represent twilight periods (vespertine and matutinal movements) and the dark shaded area represents night (nocturnal movements). Seasons are labeled as spring (SP), summer (SM), late summer/early fall (SF), and fall (FL).

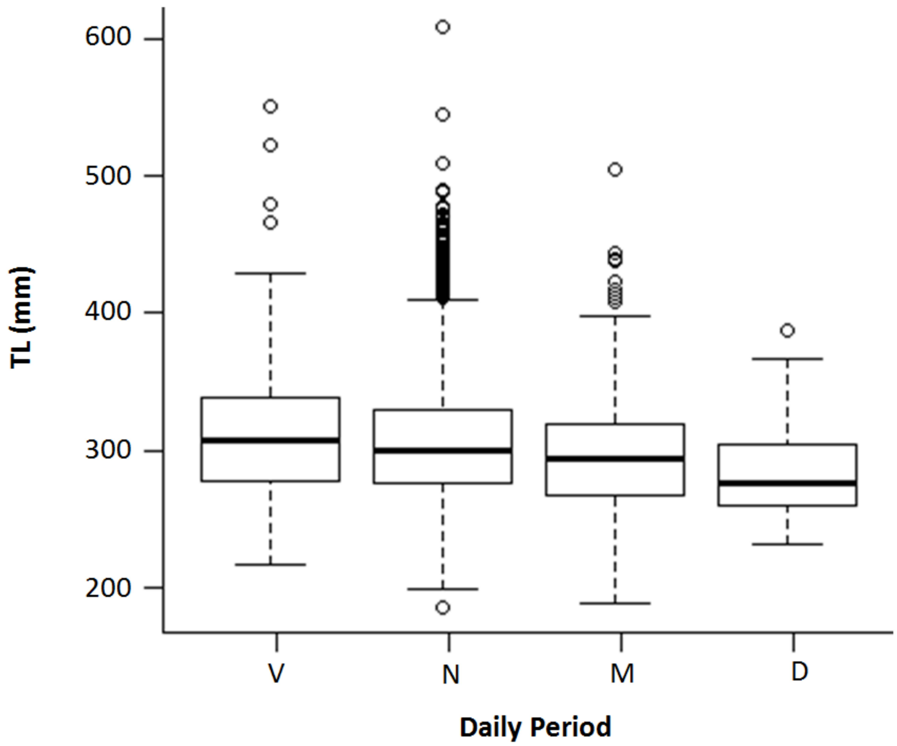

Figure 2.3. Descriptive statistics of TL (mm) of American Eels using the Millville Dam eel ladder during four diel periods of movement (vespertine=V, nocturnal=N, matutinal=M, and diurnal=D). Means for each period are represented with a bolded line, boxes indicate 25% and 75% quantiles, and tails indicate 95% confidence intervals. Points indicate outliers.

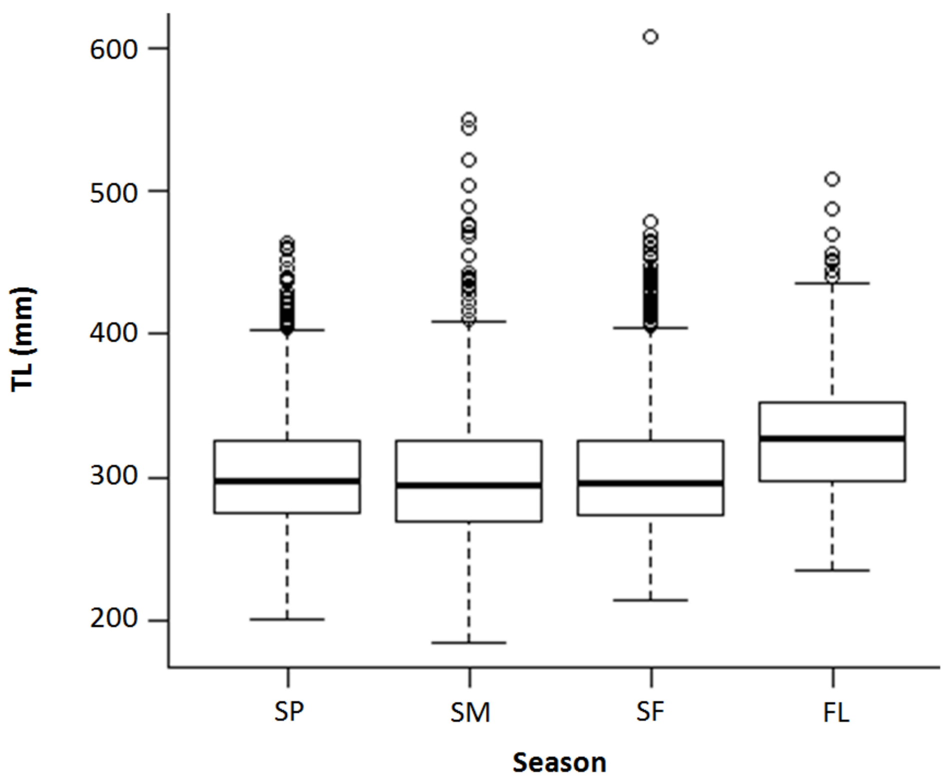

Figure 2.4. Descriptive statistics of TL (mm) of American Eels using the Millville Dam eel ladder during four seasonal periods (spring=SP, summer=SM, late summer/early fall=SF, and fall=FL). Means for each season are represented with a bolded line, boxes indicate 25% and 75% quantiles, and tails indicate 95% confidence intervals. Points indicate outliers.

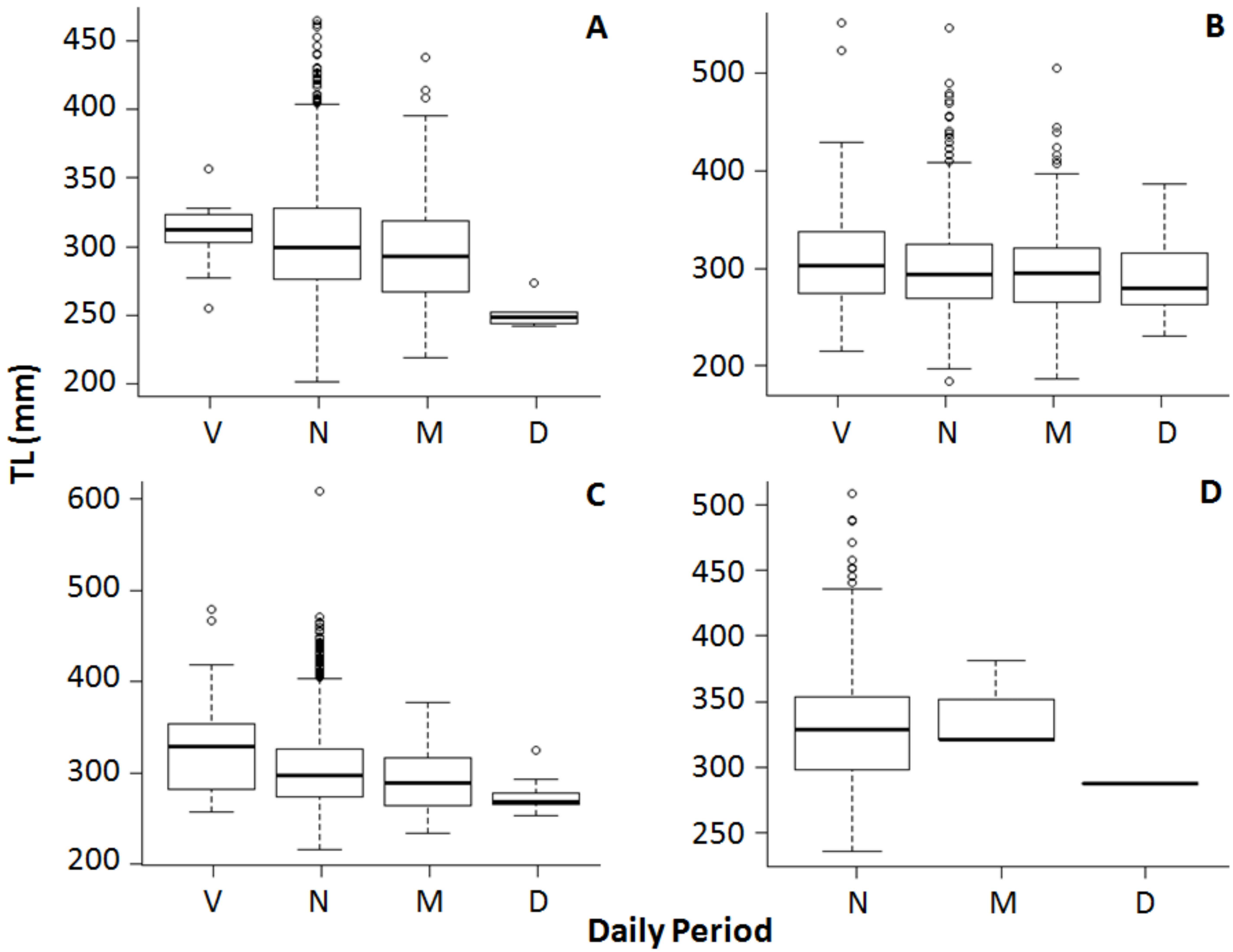

Figure 2.5. Descriptive statistics of TL (mm) of American Eels using the Millville Dam eel ladder during four diel periods of movement (vespertine=V, nocturnal=N, matutinal=M, and diurnal=D) for spring (A), summer (B), late summer/early fall (C), and fall (D). Means for each season are represented with a bolded line, boxes indicate 25% and 75% quantiles, and tails indicate 95% confidence intervals. Points indicate outliers.

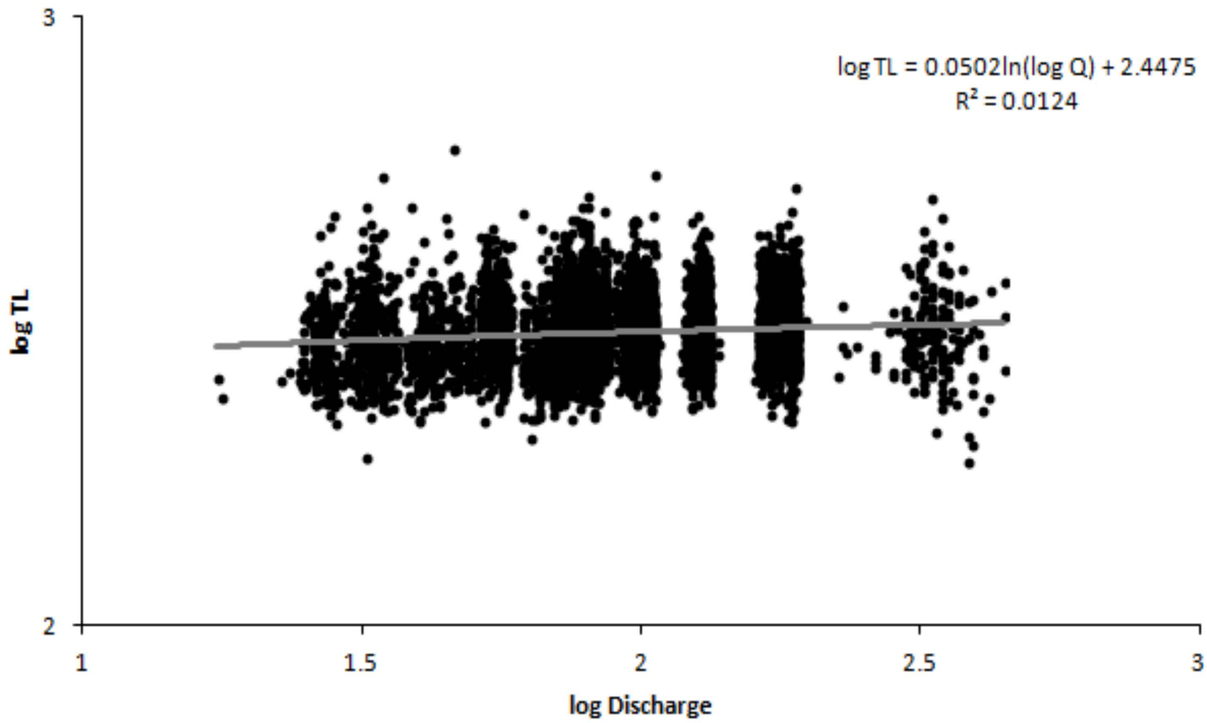

Figure 2.6. Relationship between log TL of American Eels passing through the eel ladder and log river discharge (m^3/s) at the Millville Dam on the Shenandoah River.

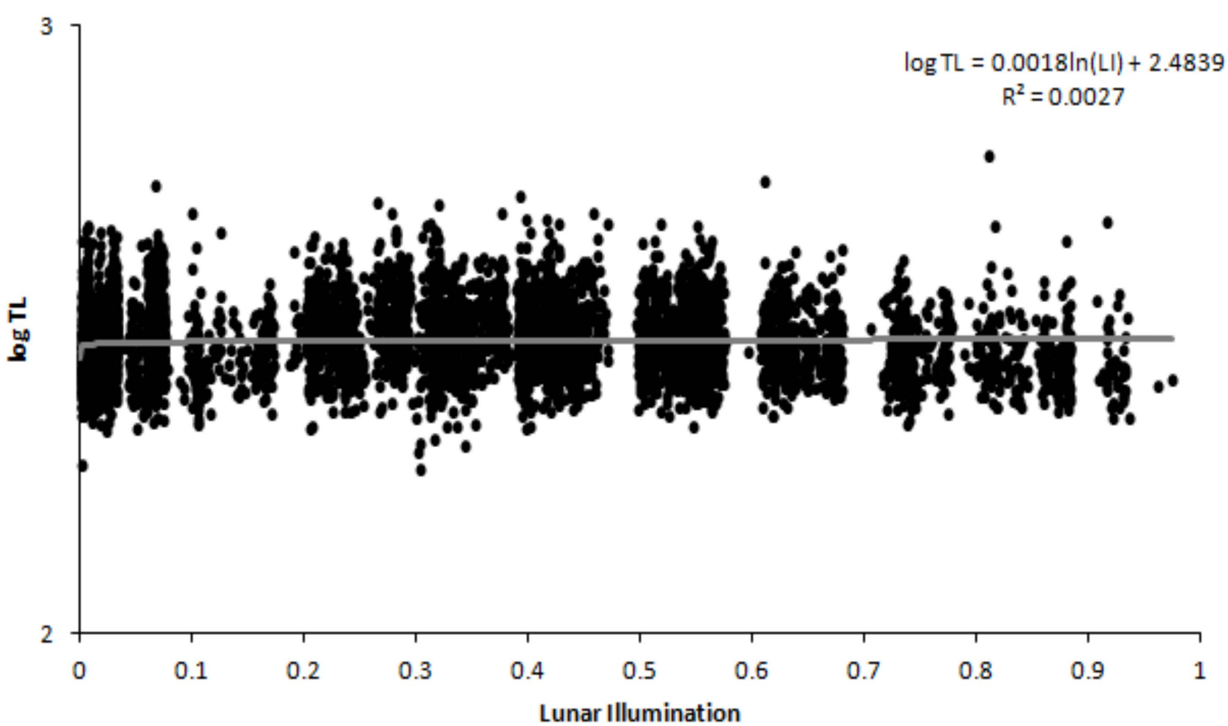

Figure 2.7. Relationship between log TL of American Eels passing through the eel ladder and lunar illumination at the Millville Dam on the Shenandoah River.

Table 2.1. Model selection statistics (BIC values) for mixture models used to describe the number of modal peaks of American Eel passage at the Millville Dam eel ladder during periods of twilight and night. Models were fit to histograms of the number of individuals passing through the eel ladder pooled into a 14 h period (starting at 18:00 hours, with 10-min bins) for each multi-day passage event. The BIC values in bold print represent the best approximating model for each passage event.

	BIC values for nine candidate models								
Passage event	Normal	2-mixture	3-mixture	4-mixture	5-mixture	6-mixture	7-mixture	8-mixture	9-mixture
17–28 May 2012	23159.8	22887.8	22781.1	**22754.5**	22763.6	22770.6	22773.8	22780.4	22781.8
12–21 July 2013	19863.9	19523.9	19391.6	19400.7	19404.6	**19384.6**	19391.3	19388.8	19390.4
22 July–3 Aug 2014	3379.1	3363.5	**3361.4**	3364.9	3363.6	3369.3	3372.9	3378.2	3380.6
13 Sept–1 Oct 2011	8610.2	8543.2	8528.0	8529.0	8532.0	8536.7	8536.3	**8525.0**	8535.0
18–27 Sept 2012	24388.0	23979.5	23871.8	23839.4	23800.4	**23796.5**	23801.0	23798.8	23801.4
14–21 Oct 2014	6656.9	6571.5	6577.3	**6563.2**	6569.0	6574.6	6577.9	6585.9	6574.0

Model	k	-2log(*L*)	BIC	ΔBIC
17–28 May 2012				
4-mixture	6	22709.4	22754.5	0
5-mixture	7	22711	22763.6	9.2
6-mixture	8	22710.4	22770.6	16.1
7-mixture	9	22706.2	22773.8	19.4
8-mixture	10	22705.2	22780.4	25.9
3-mixture	5	22743.6	22781.1	26.7
9-mixture	11	22699.1	22781.8	27.4
2-mixture	4	22857.8	22887.8	133.4
Normal	3	23137.2	23159.8	405.3
22 Jul–3 Aug 2014				
3-mixture	5	3333.2	3361.4	0
2-mixture	4	3341	3363.5	2.1
5-mixture	7	3324.1	3363.6	2.2
4-mixture	6	3331.1	3364.9	3.6
6-mixture	8	3324.2	3369.3	7.9
7-mixture	9	3322.2	3372.9	11.5
8-mixture	10	3321.9	3378.2	16.8
Normal	3	3362.2	3379.1	17.7
9-mixture	11	3318.7	3380.6	19.3
18–27 Sept 2012				
6-mixture	8	23736.2	23796.5	0
8-mixture	10	23723.5	23798.8	2.3
5-mixture	7	23747.6	23800.4	3.9
7-mixture	9	23733.2	23801	4.5
9-mixture	11	23718.6	23801.4	4.9
4-mixture	6	23794.2	23839.4	42.9
3-mixture	5	23834.2	23871.8	75.4
2-mixture	4	23949.4	23979.5	183
Normal	3	24365.4	24388	591.6

Model	k	-2log(*L*)	BIC	ΔBIC
12–21 July 2013				
6-mixture	8	19325.8	19384.6	0
8-mixture	10	19315.2	19388.8	4.2
9-mixture	11	19309.5	19390.4	5.8
7-mixture	9	19325.1	19391.3	6.7
3-mixture	5	19354.9	19391.6	7
4-mixture	6	19356.6	19400.7	16.1
5-mixture	7	19353.2	19404.6	20
2-mixture	4	19494.5	19523.9	139.3
Normal	3	19841.9	19863.9	479.3
13 Sept–1 Oct 2011				
8-mixture	10	8460.1	8525	0
3-mixture	5	8495.5	8528	3
4-mixture	6	8490.1	8529	4
5-mixture	7	8486.5	8532	7
9-mixture	11	8463.6	8535	10
7-mixture	9	8477.9	8536.3	11.3
6-mixture	8	8484.8	8536.7	11.7
2-mixture	4	8517.2	8543.2	18.2
Normal	3	8590.7	8610.2	85.2
14–21 Oct 2014				
4-mixture	6	6525.7	6563.2	0
5-mixture	7	6525.2	6569	5.7
2-mixture	4	6546.5	6571.5	8.3
9-mixture	11	6505.2	6574	10.7
6-mixture	8	6524.6	6574.6	11.4
3-mixture	5	6546	6577.3	14.1
7-mixture	9	6521.7	6577.9	14.7
8-mixture	10	6523.4	6585.9	22.6
Normal	3	6638.2	6656.9	93.7

Appendix 2.1. Model selection statistics (model name, number of parameters (k), BIC and ΔBIC values) for mixture models used to describe the number of modal peaks of American Eel passage at the Millville Dam eel ladder during periods of twilight and night for each passage event.