American Eel Subpopulation Characteristics In The Potomac River Drainage, Virginia.

by

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AMERICAN EEL SUBPOPULATION CHARACTERISTICS
IN THE POTOMAC RIVER DRAINAGE, VIRGINIA

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(ABSTRACT)

The demographic characteristics of American eels (*Anguilla rostrata*) are believed to vary with latitude and distance inland from the ocean; eels are generally thought to increase in length, age, and the proportion of females in inland and more northerly areas. Understanding this variation is necessary for the sound management of eels, but investigations into characteristics on a broad scale within drainages are scarce. Eels in the Potomac River drainage, Virginia, were sampled over a two-year period in both near-coastal and inland areas to describe characteristics in each area as well as to understand drainage-wide patterns. Inland data resulted from sampling in the Shenandoah River drainage and near-coastal data resulted from sampling tributaries to the lower Potomac River. Movement and growth were also investigated in inland areas.

Eels from the Shenandoah River drainage were significantly longer (median = 763 mm TL) and older (median = 11.5) than those found in the Potomac River tributary sites (median = 142 mm TL; median = 2.0, respectively). Both total length and age increased with increasing distance inland and sex ratio shifted from varying ratios of males:females in Potomac River tributaries to all females in the Shenandoah River drainage. Movements confirmed through mark-recapture over periods ranging up to one year were short, generally <100 m, with the longest detected movement being 1.5 km. Recapture rates were low and may be due either to low sampling efficiency, long-distance movements, or a combination of these factors. Growth and 95% confidence interval from five eels recaptured after approximately one year was 43.0 +/- 29.7 mm/year. CPUE decreased with increasing distance inland, confirming information reported by others for Virginia streams.

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INTRODUCTION

The American eel (*Anguilla rostrata*, LeSueur) is unique among North American freshwater fishes, but many characteristics of this fish remain largely unknown. This highly migratory fish is the only known catadromous species in eastern North America and is broadly adapted to habitats ranging from estuarine and brackish waters to lakes and high-elevation freshwater streams (Helfman et al. 1987; Facey and Van Den Avyle 1987).

Juvenile and adult eels have been harvested in North America for food and bait for hundreds of years. With the decline in European and Asian eel stocks (*Anguilla anguilla* and *Anguilla japonica*, respectively) increasing demand has been placed on the American eel market for the export of all life stages, especially on young eels for export to Japan's aquaculture industry (Facey and Van Den Avyle 1987). Due to this growing use it is important to have good information on population parameters when considering management schemes (Facey and Van Den Avyle 1987).

Numerous published studies of the European eel have examined the dynamics of inland freshwater populations. This type of information is not found extensively in the literature on the American eel. Size distributions, relative densities, non-migratory movement patterns as well as age and sex composition of inland populations have not been explored to a great degree in North America. Most working "knowledge" of *A. rostrata* has been inferred from studies of other anguillid eels, mainly European and Australian species. These theories have been largely untested in North America.

Castonguay et al. (1994) and others have raised concern about the potential decline in abundance of American eels in recent years. This concern, as well as increasing demand for young eels, has prompted the development of a draft Fishery Management Plan (FMP) for American eels by the Atlantic States Marine Fisheries Commission (ASMFC 1999). This document proposes that efforts be taken to increase the understanding of not only commercial and recreational harvest efforts and abundance levels throughout various life stages, but also eel population dynamics and the forces structuring them (ASMFC 1999). A greater understanding of the American eel may result in more enlightened management plans and harvest regulations being established.

This study was designed to investigate inland eels and elucidate demographic patterns related to distance inland. In the first chapter, data on total length (mm), age (years), and sex ratio were used to typify and compare characteristics of inland and coastal freshwater eels in the Potomac River drainage; data were also analyzed to understand trends in these characteristics with increasing distance inland. In Chapter II, relative densities were compared on a drainage-wide scale using catch-per-unit-effort electrofishing data. The third (and final) chapter summarizes a tagging study conducted to better understand non-migratory movement and growth in inland eels. The results of all three chapters were interpreted relative to other published information on the American eel in an attempt to understand theorized population-wide trends along latitudinal and distance-inland gradients. Management implications based on these findings are also discussed.

Chapter I. AMERICAN EEL LENGTH, AGE, AND SEX RATIO CHARACTERISTICS AND INLAND PATTERNS IN THE POTOMAC RIVER DRAINAGE, VIRGINIA

INTRODUCTION

Numerous published studies of the European eel (*Anguilla anguilla*) have examined the dynamics of inland freshwater populations, but this type of information is not found extensively in the literature on the American eel. Size distributions, as well as age and sex composition of inland eel subpopulations have not been explored to a great degree in North America (but see Ogden 1970; Harrell and Loyacano 1980; Facey and LaBar 1981; Levesque and Whitworth 1987). Studies of estuarine subpopulations of *A. rostrata* have led to some insight into their characteristics but most working "knowledge" has been inferred from studies of other anguillid eels, mainly European and Australian species. Investigations into variations in age, length, and sex structure are warranted given the theorized changes in these characteristics depending on latitude and distance inland. Information resulting from these studies in both spatial directions may aid in tailoring the management of this species to local differences.

Many studies have focused on oceanic life stages and on the environmental timing mechanisms of both the adult and juvenile migratory stages of life (Schmidt 1923; McCleave and Kleckner 1985; Sorensen and Bianchini 1986; McCleave and Wippelhauser 1987; Dutil et al. 1989); this focus has left a gap in understanding the longest portion of the eel's life. The few studies of estuarine and inland populations of American and European eels provide evidence for the strong similarity between the two species (Harrell and Loyacano 1980; Hansen and Eversole 1984; Helfman et al. 1984a; Aprahamian 1988; Barak and Mason 1992; Naismith and Knights 1993). The continued inland migration of older eels as well as other population characteristics of riverine fish between immigration to freshwater and emigration back to the sea to spawn have been left largely unstudied. The similarity between *A. rostrata* and *A. anguilla* has led to the extrapolation of life history and population characteristics of European eel to the American species. Much of this supposition is largely untested, leaving questions about the true nature of North American eels.

Haro and Krueger (1991) studied American eels in a coastal Rhode Island stream and found that both their mean length and age increased with distance from the ocean. Helfman et al. (1984a) compared estuarine eels in Georgia with some from a freshwater river and found the riverine fish to be longer on average. Smogor et al. (1995) studied distribution patterns of eels in Virginia and found that small to medium (< 374 mm) eels showed an inverse relationship between density and distance inland. Large (>374 mm) eels did not show a similar relationship and analysis indicated that large eel density and median eel length may increase with increased distance inland (Smogor et al. 1995). These findings agree with information on the European eel showing increases in average length and age with increasing distance upstream (Aprahamian 1988; Barak and Mason 1992; Naismith and Knights 1993; Lobón-Cerviá et al. 1995). Studies have also established a positive correlation between length and age, although there is sizable overlap between year classes (Hurley 1972; Michener and Eversole 1983; Helfman et al. 1984a; Barak and Mason 1992).

Based on these studies, it is generally assumed that American eels are both older and longer the farther inland they occur from the coast. It is not known whether past studies of American eels have adequately defined the full range of variation within their particular drainage or merely defined differences in coastal and near-coastal eels. Patterns of eel movement in inland riverine habitats are poorly understood as is age and length at maturation in these waters. It is necessary to investigate basin-wide trends in demographic characteristics so that management decisions concerning harvest or fish passage can be placed in the context of the entire drainage.

Female eels apparently predominate in inland waters in both Europe and America, although the data for American eels come largely from coastal populations and is variable. The commonly held belief that males prefer an estuarine habitat and females move inland to mature is supported by studies showing low ratios of 0% to 6% males in freshwater (Harrell and Loyacano 1980; Facey and LaBar 1981; Helfman et al. 1984a). Investigations of brackish and estuarine habitats have found males ranging from about 7% to 55% (Winn et al. 1975; Michener and Eversole 1983; Helfman et al. 1984a). By contrast, Facey and Helfman (1985) found that 91% of mature eels from freshwater areas in Georgia were males, and eels in freshwater Rhode Island streams were almost 90%

male (Winn et al. 1975; Krueger and Oliveira 1997). Others in Canada have reported 0% to 5% males in brackish waters (Gray and Andrews 1970; Dolan and Power 1977).

Some variation in sex ratios between studies may be related to the latitude and scale at which investigators looked for differences between freshwater and brackish/estuarine habitats. Rhode Island studies showing high percentages of males in freshwater sites (Winn et al. 1975; Krueger and Oliveira 1997) sampled locations within approximately 10 river kilometers (rkm) of tidal areas, a scale at which differences may not occur.

Variation in sex ratios may not necessarily be driven as much by salinity as by distance inland. Definitive information on variation in sex ratio over distance inland within a drainage is sparse for American eels, but most information suggests that the percentage of females increases inland. Helfman et al. (1984a) studied eels both in brackish waters and up to 80 rkm inland finding a decrease in the proportion of males from 36% to 6%, respectively. This information would be especially pertinent when establishing harvest regulations. Areas with a high proportion of females, lenient regulations, and a heavy harvest may affect recruitment disproportionately. Harvest regulations are particularly critical because the presumed semelparity of eels makes any harvest of any life stage additive to other pre-spawn mortality.

The Shenandoah River drainage, Virginia, provides a unique opportunity to explore patterns of eel characteristics over large inland distances (>500 rkm) because of eel presence throughout the drainage. Research on subpopulation characteristics this far inland is almost completely lacking in the published literature for this latitudinal region of the range of *A. rostrata* (but see Smogor et al. 1995). Research conducted in New Jersey (Ogden 1970) and lakes Champlain (Facey and LaBar 1981; LaBar and Facey 1983) and Ontario (Hurley 1972) provide the most comparable data in terms of distance inland. Results from investigations in this area can be compared to those from other studies throughout the eel's range, increasing the understanding of how these characteristics vary latitudinally.

Because American eels are highly migratory and utilize inland habitats to some extent for growth and maturation, impedance to their normal migration patterns may artificially structure their subpopulations in a drainage. Differences in density and age structure have been noted in other studies and attributed in part to obstructions to the migration of young eels (Smith and Saunders 1955; Levesque and Whitworth 1987). The importance of inland freshwater habitats in the eel life cycle is unknown, as are the effects on eel populations if migration to these areas is reduced or cut off by artificial barriers. Multiple small hydropower dams on both the South Fork Shenandoah and Shenandoah rivers (SFSR and SR, respectively) allow the study of potential effects of partial barriers to migration on the characteristics of these inland eels.

OBJECTIVE

Gather information on the length, age and sex distribution of American eels throughout the Shenandoah River drainage. Relate this information to distance from the coast and dams encountered during migration.

METHODS

Study Area

The SR drains approximately 7870 square kilometers, largely within the state of Virginia. The Shenandoah River drainage lies mostly in the Valley and Ridge physiographic province, with some tributaries flowing out of the Blue Ridge province (Jenkins and Burkhead 1994). The drainage consists primarily of the North and South forks (NFSR and SFSR, respectively), each flowing for over 250 rkm before joining in Front Royal, VA to form the SR, approximately 290 rkm from the Chesapeake Bay (Fig. 1-1). At Harpers Ferry, WV the SR joins the Potomac River which flows into the Chesapeake Bay.

The primary study areas focused on the SR and SFSR. Reaches sampled were typically 50-100 m wide and 1-2 km long with a substrate primarily of bedrock ridges, boulders and cobble. Areas with reduced flow and backwaters are often silt laden. Shorelines are mostly well vegetated with little direct alteration from humans other than cattle watering access areas adjacent to grazing land. The floodplain consists largely of crop and pasture land, forested land, and some single-family homes.

Six tributary sites in the Shenandoah drainage were sampled to investigate eel presence and characteristics in smaller streams. These sites were 3-15 m in width and had a substrate composition mostly of bedrock, cobble and gravel. Two of these sites were in the headwaters of the SFSR, the uppermost samples taken in the drainage, three flowed east out of the Shenandoah National Park into the SFSR, and one flowed into the SR. These latter four tributaries were closely associated with sampling sites on the SFSR and SR.

The fish assemblage in the Shenandoah drainage comprises 40 native species and subspecies and 18 introduced species (Jenkins and Burkhead 1994). Common taxa in the South Fork and Shenandoah rivers include dace (*Rhinichthys spp.*), central stoneroller (*Campostoma anomalum*), river chub (*Nocomis micropogon*), shiners (*Cyprinella spp.* and *Notropis spp.*), common shiner (*Luxilus cornutus)*, bluntnose minnow (*Pimephales notatus*), various sunfishes (*Lepomis spp*.), smallmouth and largemouth bass (*Micropterus dolomieu* and *M. salmoides*), rock bass (*Ambloplites rupestris*), channel catfish (*Ictalurus punctatus*), margined madtom (*Noturus insignis*), shorthead redhorse (*Moxostoma macrolepidotum*), northern hogsucker (*Hypentelium nigricans*), white sucker (*Catostomus commersoni*), common carp (*Cyprinus carpio*), and fantail and tessellated darters (*Etheostoma flabellare* and *E. olmstedi*).

Ten tributaries along the Virginia portion of the lower Potomac River were also used in this study for information from more coastal freshwater eels in the drainage. These Coastal Plain and Piedmont province (Jenkins and Burkhead 1994) streams were small; typically 3-10 m across with a sand, gravel, and cobble bottom.

Numerous anthropogenic and natural barriers exist between the headwaters of the Shenandoah drainage and the Chesapeake Bay. The SR and SFSR have five run-of-river hydropower dams that are owned and operated by Allegheny Power Company (APCo) (Fig. 1-1). These dams range in height from approximately 3 to 7 m and have no or very short headrace areas leading into their powerhouses. All but one of these facilities (Luray Hydro) lack fish passageways, and it is not designed to pass eels. There are also two dams and a large natural falls (Great Falls) on the lower Potomac River below the mouth of the SR. All of these pose a potential impedance to fish movement and migration.

The Shenandoah drainage samples were used to characterize inland eel subpopulations in this latitudinal region. These data were compared to information gathered from sites in the lower Potomac drainage both to test for differences between areas and to attempt to understand trends or gradients throughout the drainage, if they exist.

Sampling and Site Selection

Because the North and South forks extend over 500 rkm inland, this river system provided a unique opportunity to investigate characteristics of inland stocks of resident eels. Sampling sites occurred throughout the Shenandoah drainage, concentrating on the SFSR and SR in particular. Some sites were sampled more intensively (up to 18 times) as part of other objectives (see Chapter 2 and 3) while others were only sampled once. Field data were collected from July, 1996 through October, 1998 with most effort focused in May-November each year.

Information on total length (mm) was recorded from all eels at all sites; age and sex data were collected from a subsample of eels throughout the study. Eleven sites on ten tributaries to the Potomac River below the Shenandoah River confluence were each sampled once to investigate population characteristics on a broader geographic scale (Fig. 1-1). All eels sampled in these tributaries were collected for length, age and sex data.

Sampling sites in the Shenandoah drainage were determined by Virginia Department of Game and Inland Fish (VDGIF), U.S. Forest Service (USFS), and APCo access points, as well as private land access. Lower Potomac tributaries used in this study were determined using data from previous collections as well as input from VDGIF biologists. Sampling sites on these tributaries were located using Virginia Department of Transportation right-of-way access areas (state road crossings), and private land access. Efforts were made to distribute tributary samples throughout the lower Potomac below the confluence of the SR.

Capture Methods

Early efforts using eel pots for eel collection were unsuccessful. This collection method is used in many commercial eel fisheries and has proven useful in a number of published eel studies (e.g. Harrell and Loyacano 1980; Hansen and Eversole 1984; Helfman et al. 1984a). The use of pots, however, has been largely confined to coastal studies where eel densities are likely to be much higher than those encountered in the Shenandoah drainage. Although numerous baited and unbaited pots were set in 1996 and

1997 in areas known to contain eels (N = 166 eel pot-nights), the effort involved and the complete lack of eel capture precluded their use in this study. Eel pots were also unsuccessful in a study on the effectiveness of various sampling methods in the River Thames catchment, England (Naismith and Knights 1990).

The use of trap nets was also examined. This method has been used in some lentic studies (e.g. Vøllestad 1985; Aprahamian 1987; Poole and Reynolds 1996) but was inappropriate in this study due to the lack of eel capture and the difficulty in setting these nets properly in this lotic habitat.

Due to the lack of success by both eel pots and trap nets, boat, barge, and backpack electrofishing were used as the collection method for this study. The use of electrofishing consistently resulted in the capture of eels throughout the drainage. Electrofishing has also been widely utilized in published studies of eels in riverine habitats (e.g. Levesque and Whitworth 1987; Aprahamian 1988; Naismith and Knights 1993; Smogor et al. 1995; Oliveira 1996). Eels were also captured by VDGIF personnel during routine electrofishing sampling for other ongoing studies.

The boat used was an aluminum jon boat with a small (9.9 hp) outboard motor. The sampling setup consisted of a Coffelt VVP-15 electrofishing unit (AC) powered by a 240 V Honda generator. Output from this unit was typically run at 200V between 5-10 amperes (A), with most sampling done using 6-8 A depending on water depth, clarity, and flow. This setting allowed for the almost instantaneous recovery of most small- to mid-sized (<300 mm) fish encountered once the boat (and the electrical field) had passed. Eels were effectively stunned while in this field and once removed typically recovered within one minute. A Smith-Root backpack electrofisher or barge electrofisher (constructed by VDGIF) were used for smaller tributary sampling and isolated low-water conditions in the Shenandoah drainage. All Potomac tributaries (PT) were sampled using the backpack unit.

Sites on the SFSR and SR were sampled by shocking the entire perimeter shoreline areas, running mid-river transects where appropriate (based on depth, flow, and turbidity), and all other potential habitat (snags, leaf packs, root wads etc.). An effort was made to keep sampling protocol constant at sites that were sampled more than once and effort (minutes of actual shocking time) was recorded for each sampling occasion.

A passive collection method used as part of a complimentary study also provided eels for the present study. Upstream migrant samplers (eelevators) were built by Conte Anadromous Fish Lab (Turners Falls, MA) and placed in the tailrace areas of the hydropower dams where eels would likely gather when attempting to pass the structure. A built-in submersible pump provided an attracting flow to draw the positively rheotaxic migrants up an inclined ramp and into a holding basket (Fig. 1-2). Samplers were checked periodically for captured eels and to ensure proper functioning. Three samplers were deployed in both 1996 and 1997; one at each of three dams on the SFSR and SR. Four samplers were placed at one dam on the SR in 1998 in an effort to maximize sample size from the most productive 1997 site and reduce time spent travelling between units. Data resulting from the eelevators were sparse. This information has been analyzed separately from the electrofishing data to distinguish between the two collection methods.

Eel Processing

All eels were measured from the tip of the lower jaw to the most posterior caudal ray (TL) to the nearest millimeter (mm) using a measuring board designed especially for eels (“eelvise”, Conte Anad. Fish Lab.). The 1-m-long board enabled the accurate measurement of eels because of its vise-like design (Fig. 1-3). Eels could be immobilized and straightened without the use of chemical anesthetic, ice, or electricity as has been used in other published studies (e.g. Helfman et al. 1984a; Lobón-Cerviá et al. 1995; Oliveira 1996). This technique reduced the total holding time and allowed for the immediate release of eels once processed. Information on eel length was also provided by VDGIF personnel, using the same technique, as part of sampling effort for other projects in the drainage. Forty one eels were recaptured during the study; only the initial length of each was used in the analysis.

A portion of eels caught in the Shenandoah drainage (N=76) and all caught in the lower Potomac tributaries (N=213) were kept for data on age and sex. These eels were sacrificed using the anesthetic MS-222 and held on ice until dissection (within 24 h). Sagittal otoliths were removed from all eels by cutting the jaw laterally past the gill arches to expose the roof of the mouth. Scissors or wire cutters were used to split the posterio-ventral portion of the skull, visible on the roof of the mouth anterior to the first vertebra, exposing the base of the brain and the otic capsules. Both sagittal otoliths were removed, cleaned of tissue, and stored dry in sealed vials.

A section of tissue from the left and right gonad (ovary or testis) of each eel was clipped and stored in histological Histocettes® (Simport Plastics). These samples were stored in 10% buffered formalin until they could be processed for thin-sectioning and histological staining (described in Sex Ratio Methods).

All eels were examined visually in an attempt to differentiate between immature (yellow) and mature (silver) eels. Silver eels were distinguished by morphological characteristics upon capture. Maturing eels undergo a coloration change from the green/ green-yellow of an immature fish to a silver-gray/bronze dorsal coloration with a white venter (Winn et al. 1975). Lateral line pores of mature eels were typically enlarged and the body thickened dorso-ventrally. Others have noted the enlarging of the eye of silvering eels (Tesch 1977; Facey and Helfman 1985) although this was observed only once during the present study in a PT eel.

Age Estimation

Volumes of literature exist on aging techniques for fish in general and eels specifically. An effort was made to use a technique that was cost and labor effective while obtaining useful data on eel ages. Vøllestad et al. (1988) reviewed the most common techniques for eel otoliths including cracking and burning, grinding/slicing, and whole otolith reading. Whole otolith examination was chosen for this study because of its inexpense, ease of technique, and ability to discern seasonal zones of growth when viewed on a dark background in a liquid medium. There has been some concern over the ability to correctly age older eels in this manner due to the thickening of the otolith and the subsequent loss of clarity (Liew 1974; Vøllestad et al. 1988), but this did not appear to be the case in the present study. In fact, larger (and often older) eels frequently displayed some of the clearest, most ‘readable’ otoliths (Fig. 1-4).

Grinding or sanding the otolith into a thin-section was also used on a subset of eels to compare this technique to the whole otolith reading. One otolith from each of 50 pairs was sanded and polished to obtain a transverse thin-section (T. Gunderson, Chesapeake Bay Biological Lab, personal communication; and similar to Gray and Andrews 1971; Michaud et al. 1988). The otolith was mounted convex side up on a glass microscope slide using a heat-set adhesive. It was then hand-sanded using up to 5 grades of superfine sandpaper (220, 320, 400, 600, 1500 grit) and a final polishing cloth until the nucleus was reached and the outer edge of the otolith clearly discerned. These sectioned otoliths were read under a compound microscope with a transmitted light source.

Burning and cracking was used experimentally and rejected because of the potential of over-heating the otolith. This causes the structure to be extremely brittle, often disintegrating into dust. The loss of usable otoliths was unacceptable given the potentially small number of otoliths obtained in the present study.

All otoliths were placed in a glycerin-filled depression in a watch glass lined with black clay and read whole. The black background provided contrast and reduced glare when the otolith was viewed under reflected light. Ethanol (70%), water, and glycerin were tested as potential immersion mediums; glycerin produced the least glare on the otolith surface and the highest resolution of the three when viewed under a dissecting microscope. The light source used for the whole otolith viewing was a modified Fiber-Lite® (Dolan-Jenner Industries Inc.). The flexible light arm was fitted with a rubber disposable dropper bulb with a small hole in the tip. A single piece of light-transmitting fiber was fitted into this hole so that the light was further focused into a beam approximately 1 mm in diameter. This setup was similar to that used by the VDGIF in aging studies (D. Bowman, VDGIF, personal communication) except that a longer piece of fiber was used to increase the maneuverability of the light source. This method was used because of the increased resolution, decreased glare from the background, and the ability to concentrate light on small portions of the otolith being read.

Zones of differing light transmission are formed on the otolith corresponding to periods of growth. Under reflected light on a dark background, such as was used in the present study, zones are viewed as opaque (white) summer growth or translucent (dark) winter growth (Liew 1974). The first opaque mark out from the nucleus is the transition mark, laid down when glass eels reach coastal waters and begin their transition to brackish or fresh water. This mark is often seen as a tight double-check formed by two opaque bands separated by a thin translucent band. Ages assigned in this study started at this transition mark (counting the double ring as age I) and counted opaque zones out to the margin (Fig. 1-4). This method follows that used by numerous eel aging studies

(Helfman et al. 1984a; Vøllestad 1985; Haro and Krueger 1991; Barak and Mason 1992). Other authors have followed the methodology of Gray and Andrews (1971) and do not count this transitional ring, counting instead only freshwater annuli. Provided that this difference in interpretation is known, comparisons can still be made between studies by adding or subtracting the first year to calibrate the data.

All otoliths were read by two people and age was assigned based on agreement between them. Agreement occurred when the two ages were within 10% of each other. According to this protocol, all eel ages less than 10 years had to agree exactly, and ages between 10 and 20 years could not differ more than a year. When disagreement occurred, a third person read the otolith. If the third read did not agree with either of the first two, the otolith was discarded as unreliable. This methodology follows the suggestion by others that multiple interpretations (preferably by different readers) be obtained for ages that cannot be directly validated so that precision is increased (Beamish and McFarlane 1983; Vøllestad et al. 1988)

Sex Determination

Accurate determination of eel sex requires histological examination of the gonadal tissue (Dolan and Power 1977). Eels >200 mm in length were used to determine sex because gonads of eels smaller than this have been shown to be largely undifferentiated (Gray and Andrews 1970; Dolan and Power 1977) and often have gonadal tissue too small to remove.

The histological process involves dehydrating the preserved gonad samples through a series of baths of increasing ethanol concentration. The dehydrated sample is then embedded in paraffin and a thin-section (7[in this study) is stained with hematoxylin and counterstained with eosin (H&E) (Gray and Andrews 1970; Wenner and Musick 1974). Samples were processed by the Virginia-Maryland Veterinary Medical Hospital's Histopathology Lab using standard H&E procedures for dehydration, staining, and thin-sectioning. The resulting samples were viewed under a compound microscope at 35X and 100X to identify the presence of ova/oocytes (female) or spermatogonia/spermatocytes (male) (Gray and Andrews 1970; Dolan and Power 1977).

Statistical Analysis

Except where noted, length and age data were analyzed using distribution-free non-parametric methods. Multiple comparisons were made using a Kruskal-Wallis test (Gibbons 1993). Pairwise Mann-Whitney comparisons were used to determine relationships between individual tested units. The Jonckheere-Terpstra (Jonk-Terp) test statistic for ordered alternatives was used to analyze potential patterns in length and age structure as they relate to distance inland (Daniel 1978). This distribution-free test investigates the alternative hypothesis that there is an ordered pattern to sample medians.

Alpha (α) levels for all tests were set at 0.05 and all tests were two-tailed except where noted when one-tailed tests were used based on knowledge of median value and hypothesized directional trends in the data. Alpha levels were adjusted as noted for multiple Mann-Whitney comparisons to guard against the increasing likelihood of rejecting a true null due to the additive effect of conducting multiple tests (Daniel 1978). The probability of rejecting a true null hypothesis in this situation can be calculated using the formula

$$1 - (1 - \alpha)^c \qquad \text{(Daniel 1978),}$$

where c is the number of independent comparisons being made overall. In order to determine an overall α of 0.05 for multiple comparisons, the equation was rearranged to solve for α dependent on comparison number (c). The resulting equation used was

$$\alpha = 1 - (\sqrt[c]{0.95}).$$

Alpha levels determined by the above equation were used to determine significance for individual comparisons.

Regression analysis was used to provide a best linear or curvilinear fit to describe patterns in the raw data and determine the ability of distance (defined by rkm or dams passed) to account for the variation in length or age. Simple linear and polynomial regression, and robust local linear regression (rllr; described below) were each used to compare the resulting fit from each method to the data being examined for both length and age. The optimal fit of a line to the data was determined by the variance described by the predictor (measured by r-squared and f-ratio values) and the characteristics of residual plots. Simple and multiple linear regression were used to investigate the ability of either rkm, number of dams passed, or both in predicting eel length. Reported regression models include the total degrees of freedom (d.f.) and residual mean square error (RMSE) for the model.

The rllr method is a nonparametric technique suggested by the Virginia Tech Statistical Consulting Department (S. Wilcox, personal communication) as a more appropriate technique given the lack of normality and unequal variance in the length and age data. Because the data was not normally distributed and lacked a uniform variance, the assumptions of simple least squares regression could not be met. The rllr was used to compare the fit of this distribution-free model to the standard parametric (polynomial) regression model. The non-normality of the data made the rllr method more appropriate to use, but the comparison to a polynomial fit helped to define the patterns in the data.

The rllr is based on a weighting function determined by the choice of a bandwidth, which is a range of data points on the x-axis used as a ‘window’ through which to weight observations around a specific area being studied (in this case sampling locations defined by rkm). The weights given to data points decrease with distance from the center of the ‘window’ to the margins (determined by the bandwidth). These weighting functions decrease in both the x and y axis directions (upstream/downstream as well as above/below the sample median) so that the farther a point is from the center of the data, the less it is weighted in the computation of the predicted median. Wider bandwidths tend to under-fit a trend by including too many points and oversmoothing the function; narrow bandwidths do the opposite and over-fit resulting in a very irregular function. For further description see Altman (1992) and Mays and Birch (1998).

Bandwidths of 65 rkm for the length data and 81 rkm for the age data were chosen based on the criteria of reducing the mean square error (mse) without choosing a bandwidth smaller than the shortest distance between two sampling sites (S. Wilcox, personal communication). A bandwidth smaller than the distance between sites leads to gaps in the data, resulting in a poor estimate (Altman 1992). Once a bandwidth is set, the rllr program calculates a predicted median at each sampling site along the river according to the local weighting scheme of the data points. These calculations are made for the entire data set and result in the fit of a trend line with 95% confidence interval. The fit of the rllr model was assessed by plotting the residuals, as was done for polynomial regression.

Descriptive analysis of the general pattern of the data with increased distance inland was based on rkm because it allowed for the finest resolution in the data and reflected the actual spatial relation between TL and rkm. All data were analyzed using the MINITAB Release 12 statistical program (Minitab Inc. 1997).

RESULTS

Length Characteristics of Electrofished Eels

All eels (561) captured throughout the study were used for length analysis. Sixty percent (348) of measured eels were captured in the Shenandoah drainage; the remaining 40% (213) were from the lower Potomac tributaries.

The length distribution of all captured eels was bimodal, with greatest frequencies around 100 mm and 800 mm (Fig. 1-5). These peaks corresponded to an abundance of small eels seen in the Potomac samples and large eels in the Shenandoah samples. This combined grouping of all eels ranged from about 80 to 1000 mm with one outlier of 1305 mm, a mean of 541 mm, median of 631 mm, and standard deviation of 292 mm.

The lower Potomac eels were positively skewed (Kolmogorov-Smirnov Normality Test, $P < 0.01$) and dominated by small eels (100-200 mm). Lengths ranged from 76 mm (the smallest eel caught in the study) to 820 mm (Fig. 1-5). Eels from the Shenandoah drainage were negatively skewed (Kolmogorov-Smirnov Normality Test, $P < 0.01$). Lengths ranged from 292 mm to 1305 mm, but were predominantly between 700 and 900 mm. Shenandoah drainage eels were significantly longer than Potomac tributary eels (Mann-Whitney, $P < 0.0001$).

Regression analysis was used to describe the pattern between eel length and distance inland. Of interest were the abilities of river kilometer (rkm) and number of dams passed (dams) to explain length. Multiple linear regression revealed that each predictor was significant ($P < 0.001$) and accounted for a combined 68.3% of the variation in eel length ($y = 160 + 0.62rkm + 66.2dams$; d.f. = 553, RMSE = 27305). Simple linear regression showed that each variable explained 65.5% ($y = 31.7 + 1.62x$; $P < 0.001$, d.f. = 553, RMSE = 29602) and 67.1% ($y = 251 + 103x$; $P < 0.001$, d.f. = 559, RMSE = 28012; rkm and dam, respectively) of the variance in eel length.

The variation explained by either rkm or dam was increased using simple polynomial regression. A quadratic model provided the best fit by explaining 78% of the length-by-dam variation ($y = 192.49 + 215.87x – 19.48x^2$; $P < 0.001$, d.f. = 559, RMSE = 18811; Fig. 1-6a). A cubic model only explained an additional 0.4% of the length-by-dam variation ($y = 186.51 + 288.62x – 48.15x^2 + 2.66x^3$; $P < 0.001$, d.f. = 559, RMSE = 18474), not an appreciable increase from the quadratic model. A quadratic model of length-by-rkm explained 65.6% ($P = 0.24$) while a cubic model significantly increased the variance explained to 72.4% ($y = 233.79 – 2.54x + 1.88E\text{-}02x^2 – 2.31E\text{-}05x^3$; $P < 0.001$, d.f. = 553, RMSE = 23752; Fig. 1-6b). Residual plots from each polynomial model suggest a more linear pattern in the data than the models allow by showing an underestimation at shorter TL and overestimation at longer TL.

An rllr model based on the length-by-rkm data resulted in a fit and residual plot (Fig. 1-7a and b) similar to the cubic polynomial (Fig. 1-6b). The primary difference in the rllr fit is the lack of tailing-up at lower rkm and tailing-down at higher rkm as seen in the cubic fit. The tailing is “forced” by model restrictions and illustrates a disadvantage of parametric regression for data such at these (Altman 1992).

Although the rllr technique does not produce an R^2 value, comparisons can be made by studying the properties of the residuals resulting from both models. Residuals resulting from both regression techniques (cubic polynomial and rllr) were used to determine the fit of each model. Boxplots of the distribution of residuals revealed no significant difference between the two techniques (t-test, $P = 0.96$) although the rllr residuals were grouped more tightly and had a smaller standard deviation (Fig. 1-8). There were few other discernible differences between the residual plots of the two methods.

To further investigate the trend of increasing length with increased distance inland, eels were grouped by river sections separated by dams and analyzed for similarity. This grouping was necessary to pool the numerous and often small sample sizes that resulted when data were examined by rkm. Results from a Kruskal-Wallis test indicate that all medians were not similar ($P < 0.001$). A Jonck-Terp test indicated an overall increase in median length with increasing number of dams passed ($P < 0.0001$).

Finally, Mann-Whitney comparisons were run on each pair of dam groupings to determine similarity between specific dam sites. For these comparisons P-values > 0.001 resulted in the failure to reject the null hypothesis of no difference between sample medians. These comparisons confirmed the general trend shown with the Jonk-Terp test but indicated similarity in lengths among the more upstream dam sites, primarily sites 3-7 (Fig. 1-9). Dam sites 2 and 8 were not significantly different from most other sites probably due to their small sample sizes (n=6 and 4, respectively) combined with the small α-level used in the pairwise comparisons.

Length Characteristics of Eelevator Eels

Eelevator catches were very low for the entire study. No eels were captured during the 1996 or 1998 seasons and 16 were caught in the 1997 season. Eleven eels were caught in the sampler located at the Warren, VA dam and 5 at the Millville, WV dam. There was no difference in mean length between these two sites (t-test, $P = 0.27$) and the samples were combined for descriptive purposes and for comparison with other results.

The length data from the eelevators was normally distributed with a mean of 284 mm, median of 282 mm, and standard deviation of 76 mm. Eels caught in the samplers ranged from 163 to 424 mm and were significantly shorter than eels caught by electrofishing in the Shenandoah drainage ($P < 0.0001$) but significantly longer than the PT electrofished eels ($P = 0.0022$).

Length Characteristics by Maturity Level

When eels were analyzed using morphological characteristics to determine stage of sexual maturity, 22 of 348 (6.3%) Shenandoah eels and 6 of 213 (2.8%) Potomac eels were identified as silver (maturing). By classifying all other eels as yellow (immature), length distributions of silver and yellow eels at each site could be studied. Lengths of silver eels from the Shenandoah ranged from 774 to 984 mm compared to yellow eels from the same area whose range was 292 to 1023 mm, with an outlier of 1305 mm (Fig. 1-10). Potomac silver eels were also longer than their yellow counterparts, with ranges of 346 to 820 mm and 76 to 758 mm, respectively (Fig. 1-11).

Mann-Whitney tests ($\alpha = 0.01$) between all pairs of maturity level-by-region data showed Shenandoah silver eels to be significantly longer than all others, Potomac yellow eels to be significantly shorter than all others and Shenandoah yellow and Potomac silver eels to be similar in length.

Age Characteristics of Electrofished Eels

A total of 289 eels were used for age data. Of these, 76 (26.3%) were from the Shenandoah drainage and the remaining 213 (73.7%) were captured in the lower Potomac tributaries. Reader disagreement resulted in the discard of 10 Shenandoah drainage eels

(13.2%) and 20 lower Potomac eels (9.4%) for an overall discard rate of 10.4%. These discards left 66 and 193 eels for analysis from the Shenandoah and lower Potomac sites, respectively.

Data sets including my age interpretation for the discarded eels were analyzed to test for significant changes resulting from their exclusion from the analysis. Comparisons of age and length structure with and without the discards resulted in no significant difference between medians (Mann-Whitney, $P = 0.21$, $P = 0.26$, respectively). A length-at-age plot did not reveal any apparent pattern to the discarded ages relative to the ages that remained (Fig. 1-12).

The initial two otolith readers agreed on 63.3% of the eels read (183 of 289). The third reader aged the 106 otoliths that were disagreed upon, and provided agreement on 76 additional otoliths (a 71.7% agreement rate between the third reader and one of the initial readers).

Ages from the 259 eels used ranged from 1 to 19 years but differences in age structure between the inland Shenandoah sites and the more coastal Potomac sites were apparent (Fig. 1-13). Shenandoah eels (66) ranged from 6 to 19 years; ages were normally distributed (Kolmogorov-Smirnov Normality Test, $P > 0.15$; Fig. 1-13), and the median was significantly different from the Potomac samples (Mann-Whitney, $P < 0.0001$). The Potomac eels (193) ranged in age from 1 to 16 years; ages were positively skewed (Kolmogorov-Smirnov Normality Test, $P < 0.01$) by the high numbers of age 1 and 2 eels (Fig. 1-13).

Linear and polynomial regression of age on rkm revealed that a cubic model explained 55.6% of the variation in age ($y = 4.86 – 0.06x + 3.79e\text{-}04x^2 – 4.45e\text{-}07x^3$; $P < 0.001$, d.f. = 257, RMSE = 9.69; Fig. 1-14a), similar in shape to the fit for the length data (Fig. 1-6b). The cubic model resulted in a better fit to the data versus the linear and quadratic models each explaining approximately 45% of the variation ($P < 0.001$, $P = 0.055$, respectively). Residual plots for the cubic fit revealed that predicted values were underestimates at lower rkm and overestimates at higher rkm (Fig. 1-14b). This pattern was similar to the length data.

The rllr model using the age-by-rkm data resulted in a fit and residual plot similar to the cubic polynomial (Fig. 1-15a and b). As with the length data, the nonparametric regression analysis is more suitable because it is based on the actual data rather than an a priori parametric model (see Length Characteristics of Electrofished Eels for further discussion). Although the rllr technique doesn't produce a specific R^2 value, residuals resulting from both regression techniques (cubic polynomial and rllr) were used to determine the fit of each model. Boxplots revealed no significant difference between the mean residuals of the two techniques (t-test, $P = 0.14$) although the rllr residuals were grouped more tightly and had a smaller standard deviation (Fig. 1-16). There were few other discernible differences between the residual plots of the two methods.

Jonk-Terp analysis revealed a significant ordered increase in ages grouped by dam with increasing distance upstream ($P < 0.0001$). Mann-Whitney comparisons (using a pairwise comparison $\alpha = 0.001$) only showed a significant difference between those ages below dam 1 and those above (Fig. 1-17).

<u>Age-at-Length</u>

A total of 259 eels were used to analyze the relationship between TL and age in the Shenandoah and lower Potomac drainages. Linear regression indicated that length accounted for 89.8% of the variation in age ($P < 0.001$, d.f. = 258, RMSE = 2.2). The regression equation

$$\text{Age (years)} = 0.0159\ \text{TL (mm)} - 0.193$$

was used to estimate ages of migrant eels in the Shenandoah drainage for which we had no age estimates from otoliths (see below). Plots of the data show an increase in age with length, although variability increased as well (Fig. 1-18). That is, increasing age was associated with increasing variation in the length at each age with a slight decrease after approximately age 10 (Fig. 1-19).

<u>Age Characteristics of Eelevator Eels</u>

Eels that were caught in the upstream migrant samplers (eelevators) in the 1997 season could not be aged because they were released. These fish probably represent the youngest immigrants into this reach of the Shenandoah so their ages may provide information on migration rates to this point. Ages of these eels were estimated from the age-at-length regression model described above (see Age-at-Length results).

A number of studies have demonstrated variable growth in eels depending on length and environmental variables (Smith and Saunders 1955; Gray and Andrews 1971;

Helfman et al. 1984b). For this reason ages of eelevator eels were estimated using two models: one based only on Shenandoah eels and one based on all eels in the study (Fig. 1-20). The model using all eels was chosen because it was based on the broadest range of eel lengths, including eels similar to those in question. This model also yielded more probable ages for these inland migrants, given the distances and obstacles that were passed.

Estimated ages range from 2 to 6 years with a mean of 4.3, median of 4.3, and standard deviation of 1.2. Mean age did not differ significantly between the eels captured in the Millville, WV sampler (downstream) and the Warren, VA sampler (t-test, P = 0.28). This age analysis extends the range of eel ages in the Shenandoah drainage to 2 to 19 years, adding 4 year classes to the lower end of the range.

<u>Age Characteristics by Maturity Level</u>

When eel age was analyzed using stage of sexual maturity (yellow vs. silver) 14 of 66 (21.2%) aged Shenandoah eels and 4 of 193 (2.1%) aged Potomac eels were identified as silver (maturing). By classifying all other eels as yellow (immature), age distributions of silver and yellow eels at each site could be studied. Silver eels in the Shenandoah ranged from 10 to 19 years (mean 13.6, median 13.0, standard deviation 2.5) and were older than yellow eels, which ranged from 6 to 16 years (mean 10.6, median 11.0, standard deviation 3.1) (Fig. 1-21). Silver Potomac eels ranged from 5 to 11 years (mean 7.3, median 6.5, standard deviation 2.6) compared to yellow eels in the same area which ranged from 1 to 16 years (mean 3.2, median 2.0, standard deviation 3.0) (Fig. 1-22). Mann-Whitney tests ($\alpha = 0.01$) between all pairs of maturity level-by-region indicated that Shenandoah silver eels were significantly older than all others, Potomac yellow eels were significantly younger than all others, and Shenandoah yellow and Potomac silver eels were similar in age.

<u>Sex Ratio</u>

A total of 69 eels were used for sex ratio analysis from each of the sampling regions (Shenandoah drainage and Potomac tributaries). The male:female ratio for Shenandoah eels was 0:69, whereas the ratio for PT eels examined was 20:49 (29% male). These two ratios were different (2 Proportion Test, Minitab, P < 0.001). PT sex ratios ranged from 0 to 100% males among sites, but sample sizes were often small (Table 1-1).

Sex explained some of the variation in both length and age of PT eels. Potomac males and females differed in length and age at each maturity level (yellow and silver). Males, on average, were younger and shorter than females of similar maturity (Table 1-2). This helps explain the range of silver eel lengths in the Potomac tributaries (Fig. 1-11). The two eels shown in the 350-mm size class are silver males, which are much smaller than the mature females (600-800 mm).

DISCUSSION

It is widely recognized that American eel demographic patterns vary with changes in latitude and distance inland. Knowledge of length, age, and sex structure (among other characteristics) are important for sound management of the species throughout its range. Comparison with other studies' findings is valuable so that hypothesized trends can be further understood and elucidated. The results from the present study are best considered relative to other studies by separating them into Shenandoah drainage and Potomac tributary groupings because of the significant difference in age, length, and sex characteristics between the two.

Eel Length and Age in the Shenandoah River Drainage

A few studies have examined characteristics of eel populations at distances inland similar to the present study (> 300 rkm) (see Gunning and Shoop 1962; Ogden 1970; Hurley 1972; Facey and LaBar 1981; Facey and Helfman 1985; Euston 1997). It is useful to examine this information separately from the more numerous estuarine/brackish/coastal plain investigations to understand the demographic variation present within drainages and throughout the range of *A. rostrata*. Findings from areas that are > 300 rkm inland show some strong similarities, regardless of latitude. Shenandoah drainage eels display length, age, and sex ratio qualities that are comparable to these findings as well, particularly findings from more northerly subpopulations.

Eels in the Shenandoah drainage (281-540 rkm inland) are most similar to eels studied by Hurley (1972) in Lake Ontario (Canada), and Facey and LaBar (1981) in Lake Champlain (Vermont) (Table 1-3). All three areas display a broad range of eel lengths with maxima approximately one meter long. Information on the length and age of both immature and maturing eels in Lake Ontario and the Shenandoah drainage were very similar, as was the range for immature eels in New Jersey streams (Ogden 1970; Hurley 1972). However, the Lake Champlain data lacked the smaller sizes or ages found in the other studies (Facey and LaBar 1981). Facey and LaBar (1981) also found only females in Lake Champlain, similar to the present study.

Both Hurley (1972) and the present study utilized secondary sampling methods to capture young migrants. In both cases migrant eels were generally smaller (< 200 mm TL) than other eels. These small eels provide data on minimum sizes and ages present in these areas as well as highlight the potential sampling bias inherent in certain methods. Facey and LaBar (1981) state that their sampling method (boat electrofishing) was not biased and that the minimum size in Lake Champlain of 43 cm is representative.

The significantly smaller sizes of eelevator eels compared to electrofished eels in the Shenandoah drainage indicates that boat electrofishing as it was used in this study was size-biased for eels in this system. This bias may not be a result of the ability of the gear to stun small eels, but may instead be related to their habitat use. Two small eels seen in cobble-sized substrate during boat electrofishing were not captured due to the inability to net them before they could escape amongst the rocks. It is also possible that smaller eels do not tend to occupy the shoreline areas, particularly during the day, and so did not spatially overlap with areas sampled. Accurate characterization of eel demography may require the use of multiple gear types and sampling of multiple habitat strata to further confirm presence or absence of eels that may be underrepresented by simpler sampling protocols (see Hurley 1972; Michener and Eversole 1983; Helfman et al. 1984a; Hansen and Eversole 1984; Ford and Mercer 1986).

Eel Length and Age in the Potomac River Tributaries

My findings from the Potomac tributaries are more comparable to the bulk of published information on the American eel. Research on both freshwater (within approximately 100 rkm of the ocean) and brackish/tidally-influenced habitat provides the majority of data on eel characteristics in North America (Table 1-4). These coastal areas are typified by smaller, younger eels with males present to varying degrees. Data on immature and maturing eels from South Carolina (Harrell and Loyacano 1980) and

Georgia (Helfman et al. 1984a) are particularly similar in length and age to those from the lower Potomac River tributaries (Table 1-4).

There appears to be a latitudinal trend in coastal data, particularly as it pertains to age range and mean age at maturation. Northerly studies (Gray and Andrews 1970 and 1971; Jessop 1987) report broad ranges in age and older minimum and mean ages at maturation when compared to more southern investigations (Harrell and Loyacano 1980; Helfman et al. 1984a; Facey and Helfman 1985). However, this does not seem to be the case with the length data. Ranges in total length as well as minimum lengths at maturation are similar for studies in Nova Scotia, Maryland, South Carolina, and Georgia (Wenner and Musick 1974; Harrell and Loyacano 1980; Helfman et al. 1984a; Facey and Helfman 1985; Jessop 1987). A difference in minimum age at maturation with a similarity in minimum length suggests that growth rate changes with latitude. The longer growing season and higher temperatures in the southerly latitudes have been cited by several authors as a possible source of variation in length-at-age seen from north to south (Harrell and Loyacano 1980; Hansen and Eversole 1984; Helfman et al. 1984b; Oliveira 1997). However, the relation between growth and latitude is confounded by variation in sex ratio and sex-specific growth rates (Oliveira 1997; see Chapter 3 for further discussion on growth). Discretion should also be used when comparing these types of data due to the potential for sampling bias and variation between studies in the interpretation of annuli for age classification.

The rarity of large and old eels in the Potomac River tributaries (Figs. 1-11 and 1-13) provided the opportunity to estimate the rate of loss of eels to either mortality or emigration. Hoenig (1983) used longevity data from a number of aquatic species to develop a model to estimate mortality rates based on maximum age. The maximum age of 16 years found in the Potomac River tributary eels resulted in an annual loss rate of 27.7% using this method. Another estimate using Baranov’s catch curve (Ricker 1975) produced an estimate of 27.4% over the entire age distribution. An estimate based only on the first seven year classes using Baranov’s catch curve was 35.7%. Estimations using only ages one through seven may be more meaningful because the relation between age and catch is a decreasing, approximately linear, function (Fig. 1-13) for this age range and the oldest eel caught in upstream migrant samplers was estimated to be six years old (see Age Characteristics of Eelevator Eels). Perhaps seven years may be the maximum age that eels are still likely to move inland. Small sample sizes of older/longer eels (> 7 years) also reduce their usefulness in estimating the slope of frequency over time necessary for calculations of mortality. Both methods above, as well as calculations of change in frequency over age classes from the actual data, all estimate mortality/loss rates within <10% of each other. Regardless of the method, data from the Potomac River tributaries suggest that approximately 30% of the eels per year either die or move to other areas. For younger/smaller eels this movement is likely to be a continued inland migration while older/longer eels are more likely to mature and emigrate to spawn.

Defining Subpopulations and Study Scale

A common theme among eel studies is the desire to describe demographic characteristics both to aid local management and to understand patterns throughout their range. Determining a meaningful scale over which eel subpopulation characteristics should be defined is vital to interpreting findings and designing future studies. Existing descriptions of demographic differences between salt- and freshwater habitats focus primarily on near-coast habitats (typically < 100 rkm inland). However, because of their catadromous life history, eels that move inland are vulnerable to harvest when passing through coastal areas as well as being exposed to other sources of mortality such as hydropower turbines during their migratory movements. This potential to contribute to coastal fisheries and eels' exposure to other anthropogenic sources of mortality underscore the need to consider inland eels in management plans.

Drainage-wide studies may be more useful in both management and ecological contexts. The migratory pattern of American eels is typified by their metamorphosis and immigration from the ocean into estuarine and freshwater habitats. The rheotaxic nature of immigrants and their apparent semelparity increases the likelihood that the drainage system they enter as an elver is the same one in which they will spend the majority of their life until emigration for spawning. In fact, studies of immature eels captured and tagged in one drainage and released in a different drainage displayed some homing (Vladykov 1971). Homing is further evidence of the unlikelihood that eels leave a drainage system until ready to spawn.

Genetic studies have demonstrated differences in the allelic frequency at certain enzyme loci in American eels both within and between five study sites ranging from Newfoundland to Puerto Rico (Williams et al. 1973; Koehn and Williams 1976). Patterns in three of these loci have been attributed to natural selection acting on portions of the migratory population either prior to reaching the continental shelf, or after taking up residence in continental waters (Koehn and Williams 1976). Post-oceanic selection acting on migrants illustrates the potential for genetic differences to arise among drainages. However, such differences have not been documented.

The probable lack of mixing between drainages supports their use as logical subunits of the eel population. Management on a drainage-by-drainage basis allows for the consideration of potential demographic variations in each watershed. Because eels are typically harvested in the coastal portions of drainages, either as residents or migrants moving from or back to the sea, management in these areas can impact eels throughout the entire drainage. When making management decisions about these coastal portions of the subpopulation, characteristics of eels throughout the watershed should be considered to effectively manage the subpopulation. It may be useful to manage on a broader scale by combining drainages displaying similar characteristics or feeding into a distinct management area, such as the Potomac and Susquehanna river drainages flowing into the Chesapeake Bay.

A number of studies of *A. rostrata* have attempted to typify and compare characteristics of local freshwater and brackish/estuarine eels (e.g. Gray and Andrews 1970, Winn et al. 1975, Helfman et al. 1984a). While differences found between eels in fresh and saltwater habitats in published studies are often statistically different, they may not truly represent the range of variation in that drainage if the full inland extent occupied by eels was not sampled. Assumptions that information from a limited inland distance accurately describes freshwater eels throughout a drainage may be erroneous.

Information in the present study from the upper range of the Potomac tributaries was significantly different from that farther downstream, and all of the Potomac data was very different from that in the Shenandoah drainage. Had the study been restricted to the 10 tributary sites, which ranged from 19 to 268 rkm inland, it would confirm much of what is reported from other studies throughout the species' range but would have missed an important component of the subpopulation in the large Shenandoah females.

Length and age ranges similar to those in lakes Ontario, Champlain, and the Shenandoah drainage are found in other studies but they tend to only represent the upper tail of negatively skewed distributions rather than the majority (as indicated by measures of central tendency). Recognition that large eels may predominate many inland waters has implications for harvest regulations, habitat loss, and water quality issues. Although eels in these inland areas may be fewer in absolute number compared to more coastal habitats in the same drainage, they constitute a unique and potentially important portion of mature spawners each year.

The large eels found in distant inland portions of their drainages may form a vital portion of the breeding population that migrates to the Sargasso Sea each year to spawn (Barbin and McCleave 1997). Using a fecundity-at-length relationship developed from eels in the Chesapeake Bay, Virginia, the approximate contribution of silver female eels migrating from the Shenandoah drainage can be estimated (Wenner and Musick 1974). The formula used to predict reproductive potential is

$$\text{Log(base 10)} \quad = 3.74418\text{Log(base 10)}x - 4.29514$$

where x is the length of the female eel and is the estimated fecundity in number of eggs. The average total length at emigration is approximately 870 mm in the Shenandoah drainage, as determined by this study and prior work done in the area (Euston et al.1997). This formula predicts that the average mature female eel from the Shenandoah drainage will produce approximately 5.2 million eggs, compared to a mature female of 734 mm from the lower Potomac, which will produce 2.7 million. This relationship, while not developed using eels as large as those found in the Shenandoah drainage, serves to illustrate the potential role that these large inland eels may have in the species' population dynamics. Fecundity models developed for Maine waters generated higher estimates than those seen by Wenner and Musick (1974) and resulted in similar differences in fecundity if used with the present data (10.2 versus 6.2 million eggs for the Shenandoah and lower Potomac tributaries, respectively) (Barbin and McCleave 1997).

Regression modeling, such as that used in this study, can be particularly useful in understanding patterns in demographic characteristics over broad spatial scales. This information can be used for general estimates of fecundity in various portions of a drainage and compared to other areas to understand the relative breeding potential of individual eels throughout their range and the related costs, in terms of time spent inland, of reaching a certain size and fecundity. This may be particularly useful if coupled with density estimates to obtain estimates of total reproductive potential for selected portions of the species' range.

For eels to attain the larger size and higher fecundity in the Shenandoah River drainage there is a cost in terms of delayed maturation and emigration. The regression equation from the length and age data (see Length-at-Age Results) predicts that two additional years are needed to reach the larger size found in the Shenandoah drainage. The two-year delay represents an approximate 15% increase in maturation time in return for a potential 65 to 93% increase in fecundity, depending on model used. While this delay in emigration increases the potential for natural mortality it may also increase the ability to complete the long migration. Larger fish may enjoy enhanced survival and spawning success due to increased energy reserves and stronger swimming ability. While this is conjectural, it cannot be ruled out until the characteristics of successful American eel spawners are understood.

The loss of large inland eels due either to habitat loss or harvest may also represent the loss of unique genetic segments of the supposed panmictic breeding population. A number of studies have found slight intraspecific genetic variation with latitude that is theorized to be a result of post-larval migration selection. Although it has not been studied, variation similar to that found latitudinally may also exist over increasing distance inland. The potential reduction or loss of this type of variation in the breeding population could reduce the species' ability to persist throughout its large geographic range.

Due to the longevity and distance inland that eels like those in the Shenandoah drainage traverse, they may be disproportionately influenced by human impacts. Eels in the present study, for example, passed 3 to 7 dams depending on where in the Shenandoah drainage they were captured. Degradation of habitat, and physical or chemical barriers (complete or partial) to upstream habitat can impact the potential for producing large, long-lived individuals by reducing or eliminating the ability of young eels to migrate upstream.

The longevity of the eels in these areas in itself can be cause for concern where issues of water quality exist. Castonguay et al. (1994) and other Canadian studies have cited toxicity from such pollutants as PCBs, mirex, and DDT as potential problems for inland eel stocks and even as a possible cause for declines seen in eel recruitment in the St. Lawrence River and Gulf. Chemical pollution is also a concern in the Shenandoah drainage because of the presence of DDT and chlordane and high levels of mercury and PCBs (Ator et al. 1998). Although the conditions experienced by eels in the Shenandoah drainage do not appear to be acutely toxic, the potential effects on reproductive tissue, and egg and larvae viability remain a concern (Castonguay et al. 1994).

Conclusions

The extent of inland sampling in this study is unique among eel investigations, particularly in the southern portions of their range. Investigations by others into variation in eel demographics have often found differences between fresh and saltwater habitats, but there is little published material on how these characteristics vary within drainage over distances greater than 200 rkm inland (but see Smogor et al. 1995). Typical comparisons of salt and freshwater data often focus on spatial scales similar to that represented by the information from Potomac River tributaries in the present study. Sampling in the Shenandoah River drainage (500+ rkm inland) allowed for patterns on a drainage-wide scale to be compared. My findings from the Shenandoah drainage indicate that attempts to describe subpopulation characteristics in the Potomac River drainage based solely on information from a limited distance (<200 rkm) inland would miss a potentially important segment of the subpopulation. This information on changes in demographics over a broader scale than is typically considered may be useful in guiding study designs in other large riverine habitats.

The harvest of eels is often focused on the migratory stages, either immigrating young eels (glass eels and elvers) or emigrating adults (silver eels). Because of this, the fishing effort that is focused on bays, estuaries, and the lower portions of rivers has the potential to impact portions of the subpopulation moving into or out of the entire drainage. Management based on the characteristics of coastal or near-coastal eels may not be sound for the protection of inland eels exhibiting very different demographic qualities. Consideration of eel demographics throughout a drainage appears to provide more accurate data on the true range of variation not only present within the drainage, but that should be taken into account when establishing management schemes.

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Table 1-1. Sex ratios of eels, with 95% confidence interval (CI) within each sampling area.

Area	Number Examined	Number Female	Number Male	Percent Male	95% CI of Percent Male
Shenandoah Drainage	69	69	0	0	0.0 - 5.2
All Potomac Tributaries	69	49	20	29.0	18.7 - 41.2
			Potomac Tributaries		
Goose Creek	3	3	0	0	0.0 - 70.8
Broad Run	3	3	0	0	0.0 - 70.8
Difficult Run	20	18	2	10.0	1.2 - 31.7
Pimmit Run	12	6	6	50.0	21.1 – 78.9
Pohick Creek	15	15	0	0	0.0 – 21.8
Austin Run	3	3	0	0	0.0 – 70.8
Nomini-Beales	8	0	8	100.0	63.1 – 100.0
Bush Mill	5	1	4	80.0	28.4 – 99.5

Table 1-2. Total length (TL) and age characteristics of Potomac River tributary eels, analyzed by sex (male: ♂; female: ♀) and stage of sexual maturity (Silver = mature, Yellow = immature) within sex. Sample size = N, standard deviation = S.D.

Sex	Maturity	N (TL)	Mean TL	Median TL	S.D. TL	N (Age)	Mean Age	Median Age	S.D. Age
♀	Silver	4	718.7	733.5	99.0	2	8.0	8.0	4.2
♂	Silver	2	346.5	346.5	0.7	2	6.5	6.5	0.7
♀	Yellow	45	450.4	433.0	133.7	37	7.9	8.0	2.7
♂	Yellow	18	271.4	273.0	37.9	13	5.4	5.0	1.7

Table 1-3. Subpopulation characteristics of inland American eels from published studies. Total length = TL; * signifies approximations from published data; modal distribution shows range (TL) and percentage of eels falling within; ** represents eels caught using methods targeting upstream migrant eels, which were not used in computing measures of central tendency. N/A means no applicable information.

	Lake Ontario (Hurley 1972)	Lake Champlain (Facey and LaBar 1981)	New Jersey Streams (Ogden 1970)	Shenandoah drainage (present study)	Louisiana Streams (Gunning and Shoop 1962)
TL Sample Size	1471	426	196	347	18
TL Range	(196**)480-1060 mm	43.0-90.0 cm	14.5-85.0 cm*	(163**)292-1023 mm	255-915 mm
Mean TL	776 mm	67.0 cm	39.0 cm*	735 mm	434*
TL Modal Distribution	753-832 mm (46%)	55.0-79.0 cm(84%)*	24.5-54.4 cm (82%)	700-899 mm (61%)	N/A
Age Sample Size	195	416	169	66	N/A
Age Range (years)	(2**)4–18	9–24	3–19	(2**)6–19	N/A
Mean Age (years)	11.5*	16.9	10	11.3	N/A
Silver Eel TL Range	832–918 mm	N/A	N/A	774–984 mm	N/A
Silver Eel Age Range	13-14	N/A	N/A	10–19	N/A
Sex Ratio (% males)	N/A	0%	N/A	0%	N/A

Table 1-4. Characteristics of coastal and near-coastal American eels from published studies. Some studies provide data from multiple sites in a similar habitat, if so, data are grouped and a range of values given. Total length denoted by TL. Silver signifies sexual maturity. N/A means no applicable information.

	Potomac Tributaries (present study)	Newfoundland (Gray and Andrews 1970, 1971)	Nova Scotia (Jessop 1987)	Maryland (Wenner and Musick 1974)	South Carolina (Harrell and Loyacano 1980)
Salinity (distance inland)	Fresh (< 270 rkm)	Fresh/Brackish (< 16 rkm)	Fresh (< 20 rkm)	Tidal	Fresh (< 80 rkm)
TL Range	76 – 820 mm	159 – 931 mm	321 – 702 mm	339 – 845 mm	98 – 834 mm
Mean TL	226 mm	382 – 561 mm	465 mm	439 mm	N/A
Age Range (years)	1 – 16	3 - 13	7 – 22	N/A	1 - 16
Mean Age (years)	3.3	6.7 – 9.7	12.9	N/A	6.1
Silver Eel TL Range	346 – 820 mm	N/A	346 – 945 mm	339 – 845 mm	214 – 834 mm
Male Silver TL	346 mm	N/A	346 – 473 mm	339 – 438 mm	214 – 322 mm
Female Silver TL	719 mm	535 – 931 mm	394 – 945 mm	418 – 845 mm	369 – 834 mm
Silver Eel Age Range	5 – 11	N/A	6 - 43	N/A	N/A
Male Silver Age	6.5	N/A	6 – 18 (mean = 12.7)	N/A	4 (mean)
Female Silver Age	8	10 – 19	8 – 43 (mean = 19)	N/A	7 – 8.6 (mean)
Sex Ratio (% males)	29%	0.3%	~1%	N/A	1.3 – 1.6%

Table 1-4 (cont'd). **Inland study located in coastal plain.

	South Carolina (Michener and Eversole 1983)	Georgia (Helfman et al. 1984a)	Georgia (Facey and Helfman 1985)
Salinity (distance inland)	Tidal	Fresh/Tidal (< 80 rkm)	Fresh (< 300 rkm)**
TL Range	213 – 719 mm	79 – 705 mm	287 – 607 mm
Mean TL	438 mm	357 – 403 mm	452 mm
Age Range (years)	2 – 10	1 – 13	N/A
Mean Age (years)	5.4	4.6 – 6.0	N/A
Silver Eel TL Range	N/A	N/A	N/A
Male Silver TL	N/A	353 - 411 mm	282 - 375 mm
Female Silver TL	550 mm	587 mm	413 - 682 mm
Silver Eel Age Range	N/A	N/A	N/A
Male Silver Age	N/A	3 – 6	2 - 8
Female Silver Age	6.8	5	4 - 13
Sex Ratio (% males)	6.6%	6% (fresh), 36% (tidal)	N/A

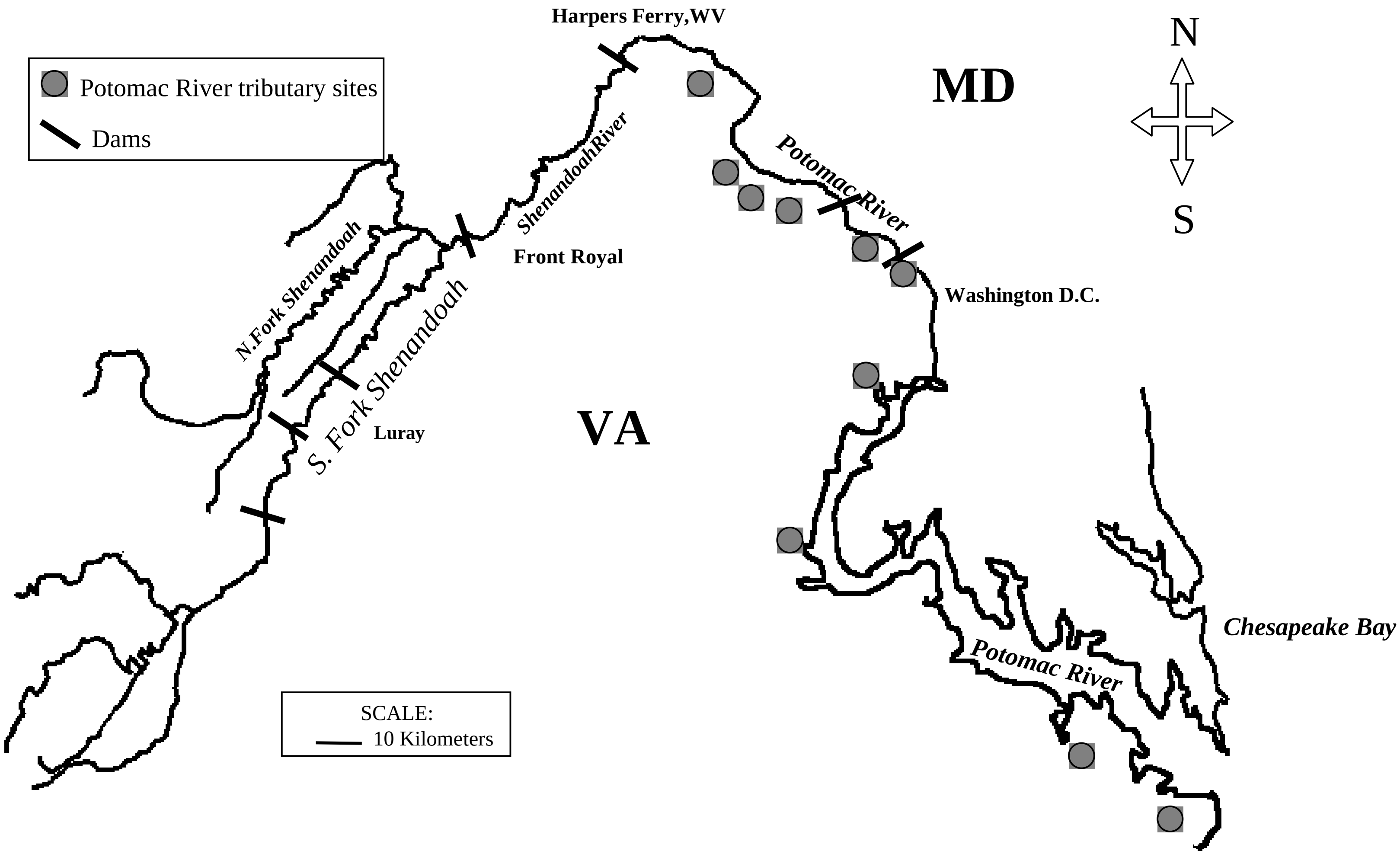


Fig. 1-1. Map of sampling areas showing Shenandoah drainage and Potomac tributary sites.

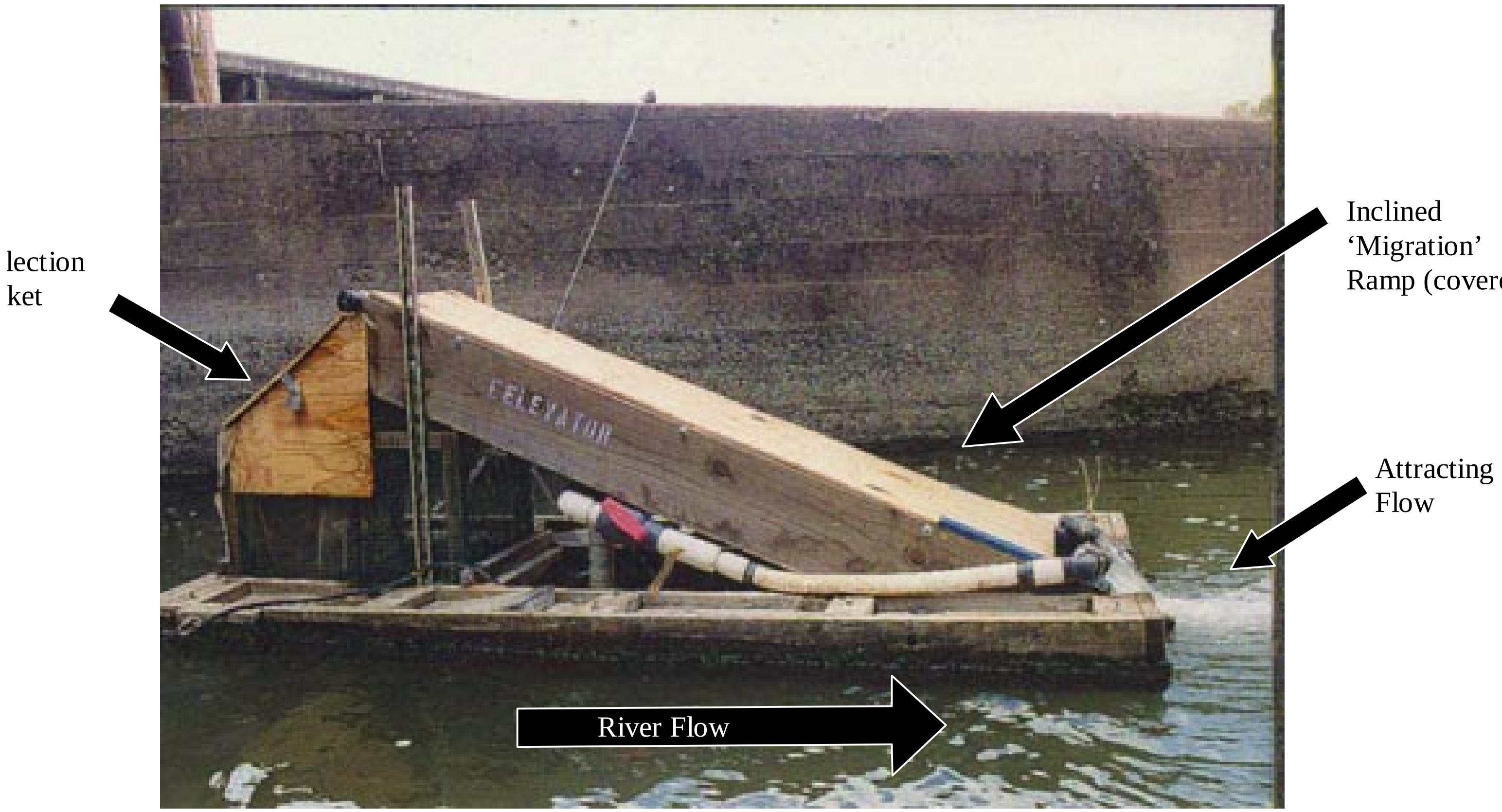


Fig. 1-2. Upstream migrant sampler (eelevator) installed in tailrace below dam powerhouse.

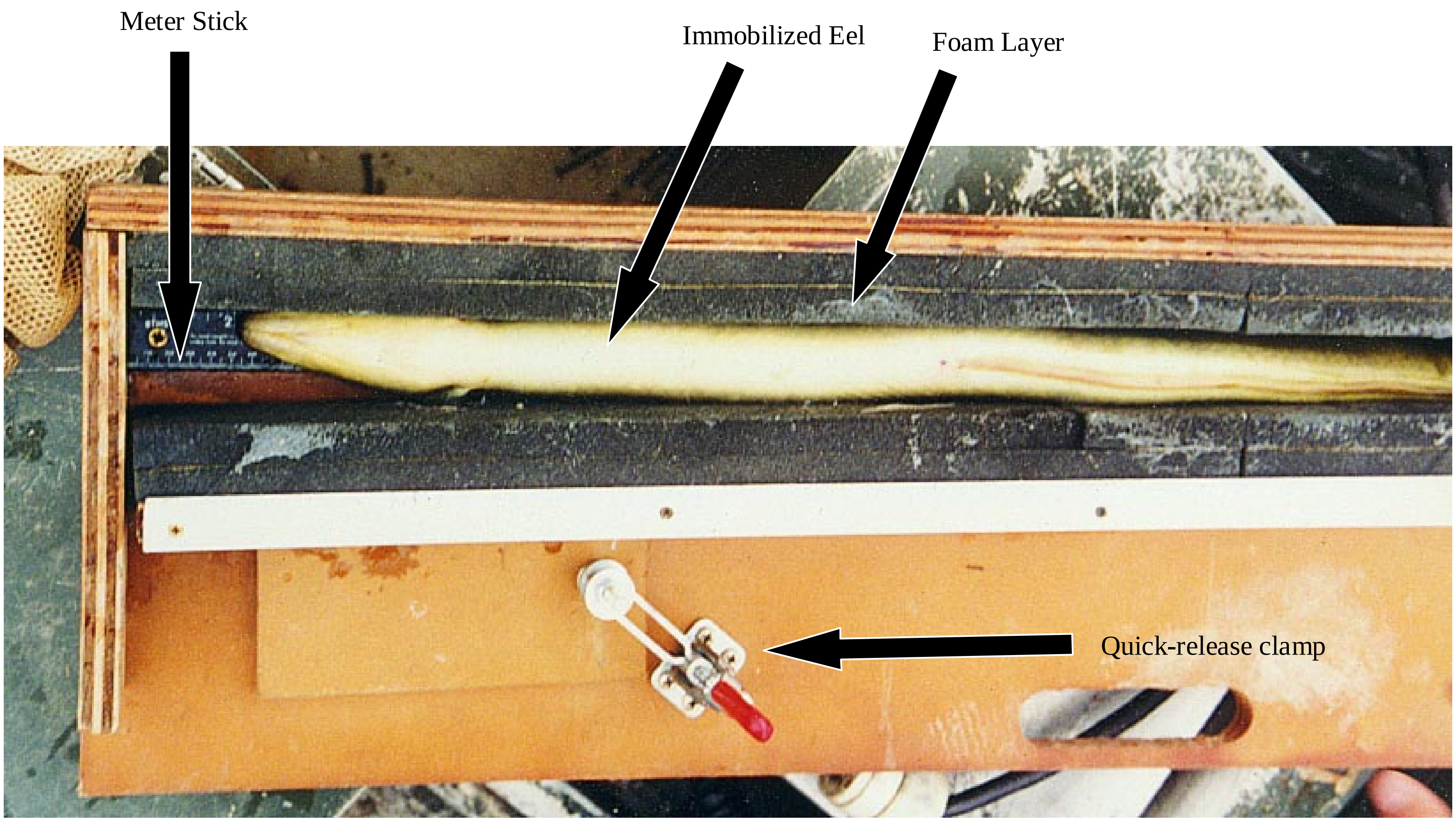


Fig. 1-3. Eel measuring board (eelvise) designed to clamp eel between two foam layers for measuring and tagging.

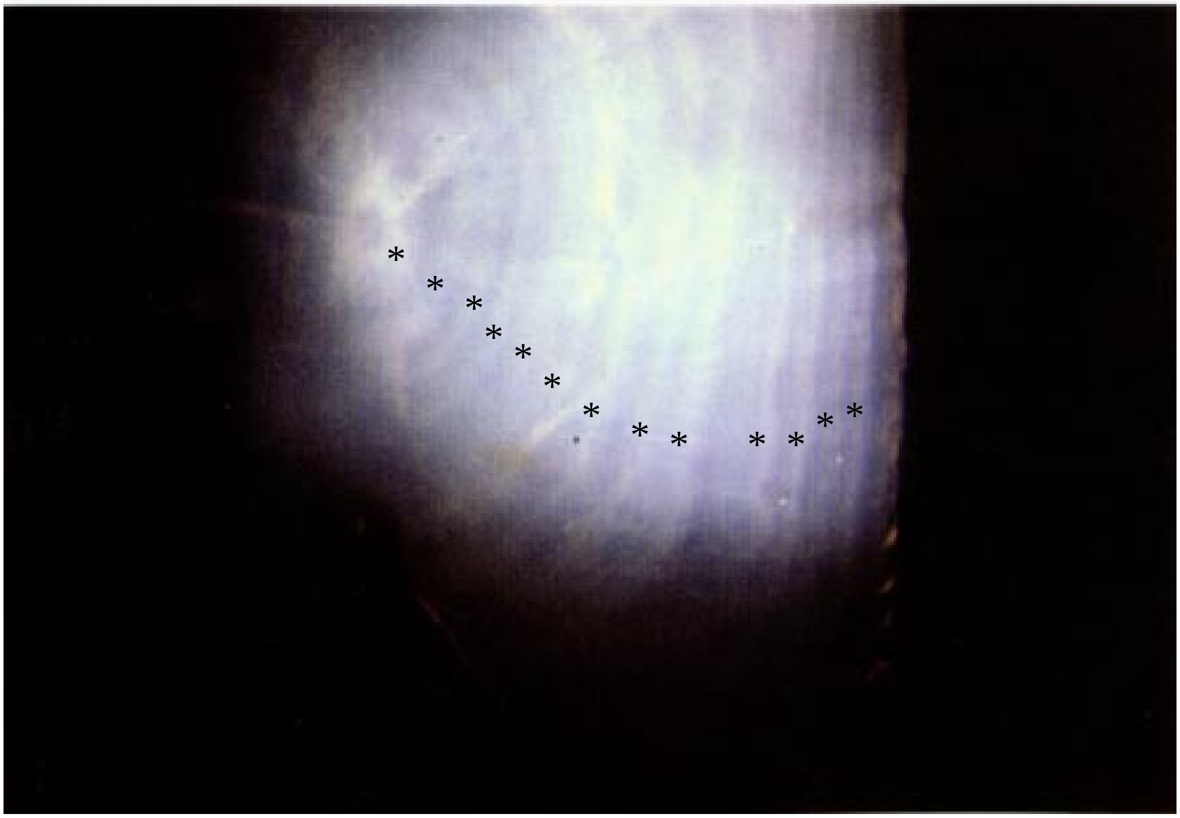


Fig. 1-4. Whole otolith viewed under dissecting microscope on black background in glycerin with reflected light. Opaque annuli (marked with *) represent periods of summer growth. The innermost double-ring represents the transition into freshwater and is counted as the first year.

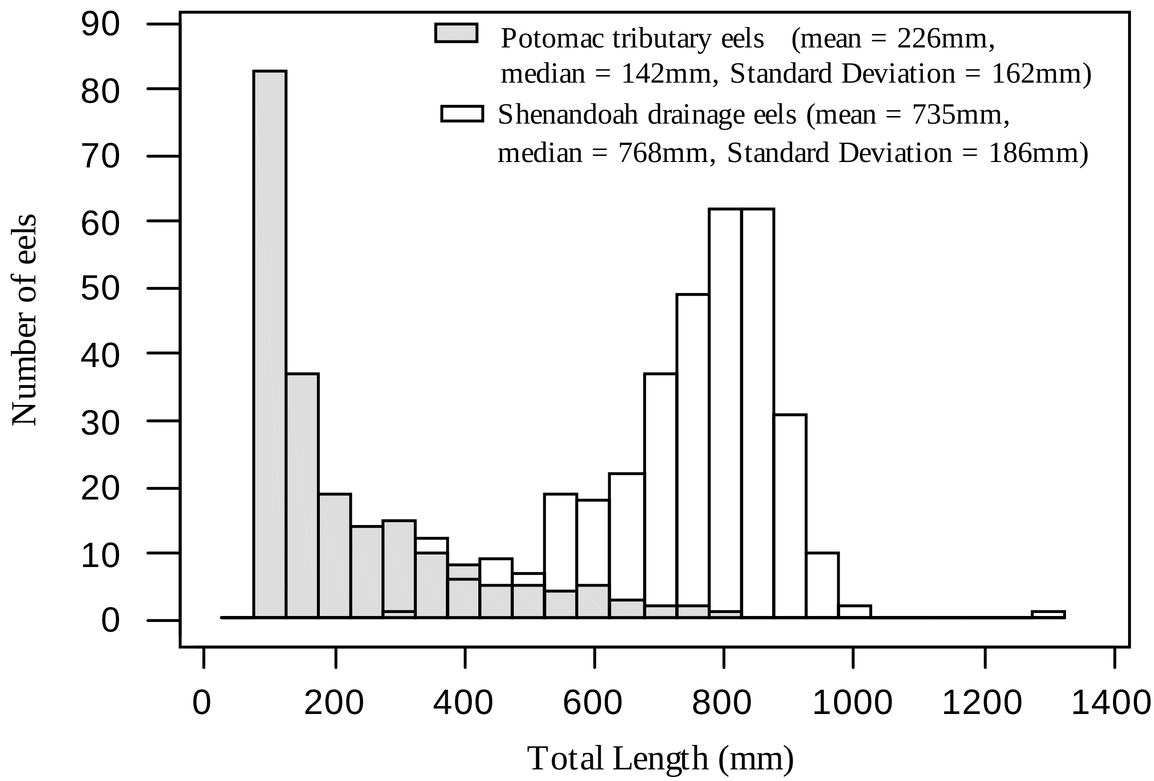
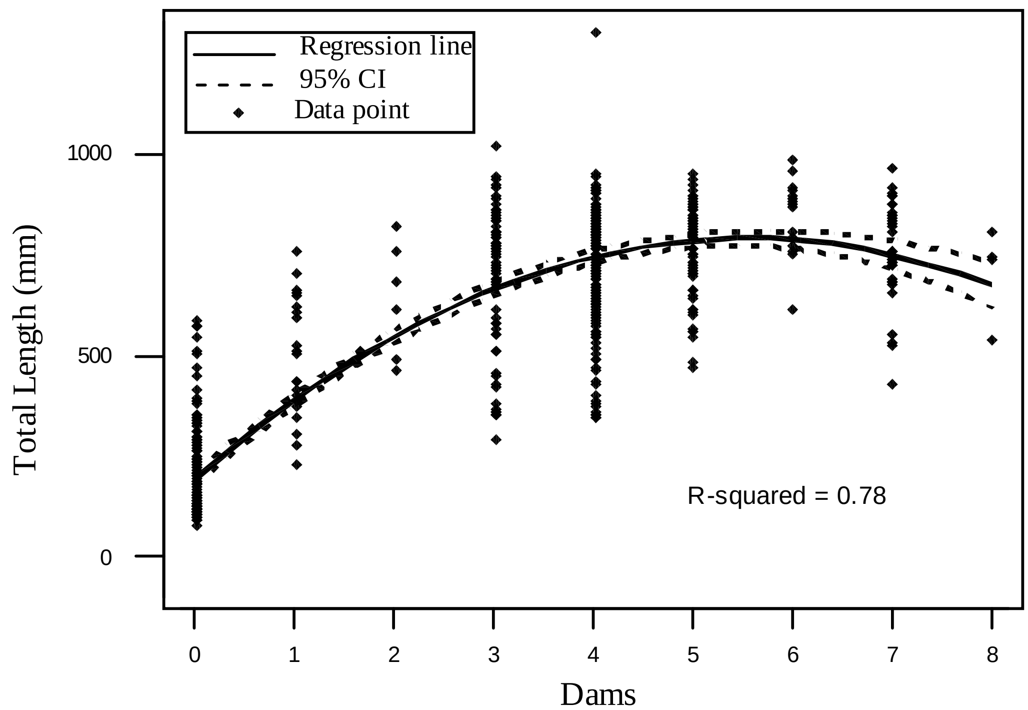


Fig. 1-5. Total length distribution of all eels captured in the Potomac tributaries and Shenandoah drainage (N=561).



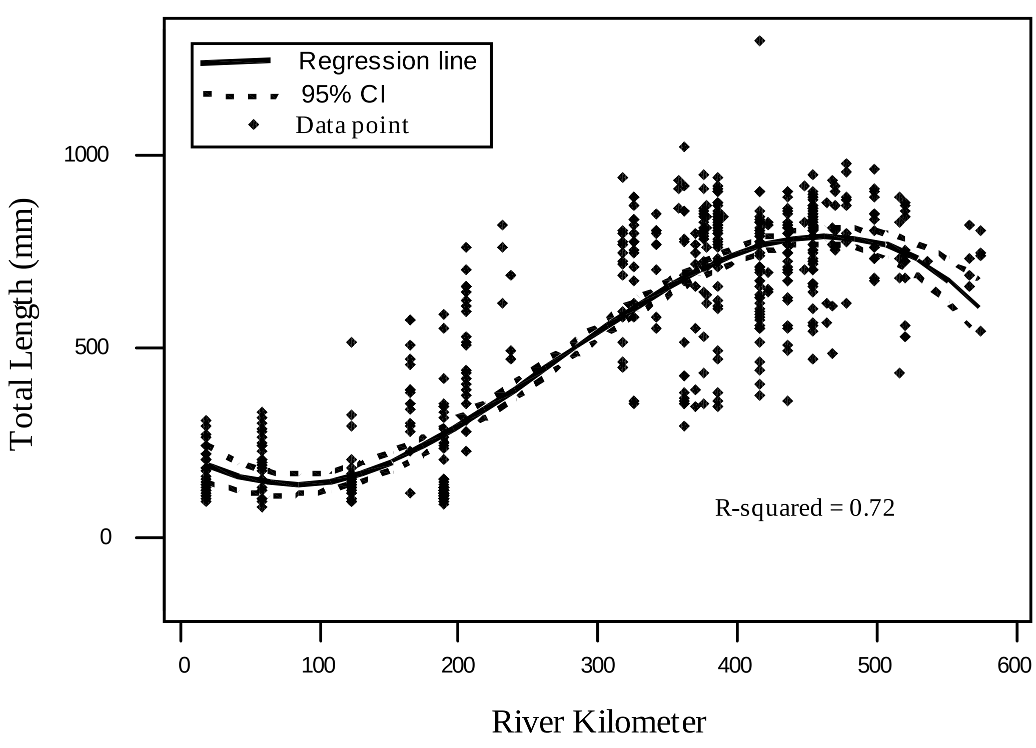


Fig. 1-6a and b. Quadratic polynomial regression (top) of eel total length (N = 560) on number of dams passed, with 95% confidence intervals (CI) around the regression line ($y = 192.49 + 215.87x – 19.48x^2$, d.f. = 559, RMSE = 18811) . Cubic polynomial regression (bottom) of eel total length (N = 554) by river kilometer with 95% confidence intervals (CI) around the regression line ($y = 233.79 – 2.54x + 1.88E\text{-}02x^2 – 2.31E\text{-}05x^3$; d.f. = 553, RMSE = 23752).

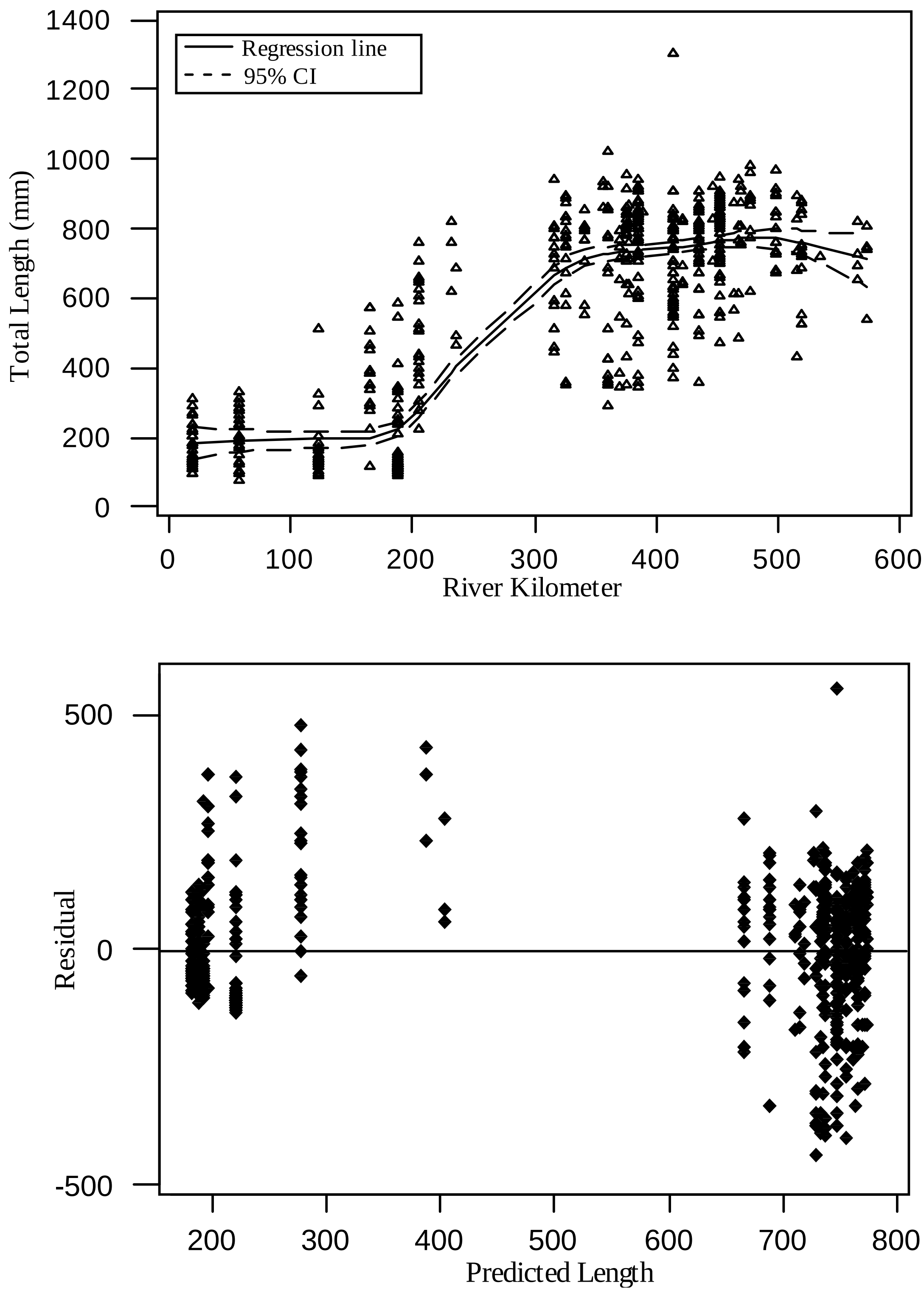


Fig. 1-7a and b. Robust local linear regression of eel total length on river kilometer (top), with 95% confidence interval (CI) around the regression line. Data indicated by open triangles. Plot of residuals (actual length – predicted length) versus predicted length (bottom) from robust local linear regression.

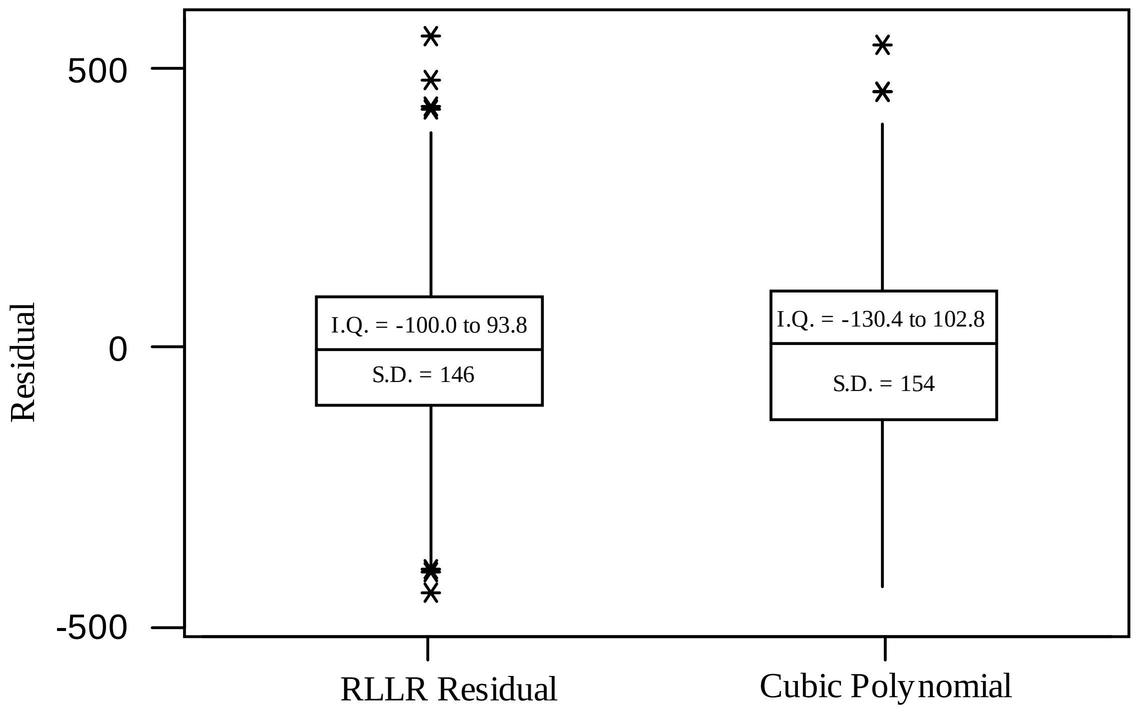


Fig. 1-8. Boxplots of residuals from two methods used to regress eel length on river kilometer (Robust Local Linear Regression (RLLR) and Cubic Polynomial). Boxes represent interquartile (I.Q.) ranges (25^{th} to 75^{th} percentile) of data, middle horizontal lines are the medians, whiskers represent data within +/- 1.5 multiplied by the upper or lower interquartile range, respectively; outliers are represented by asterisks; S.D. represents standard deviation.

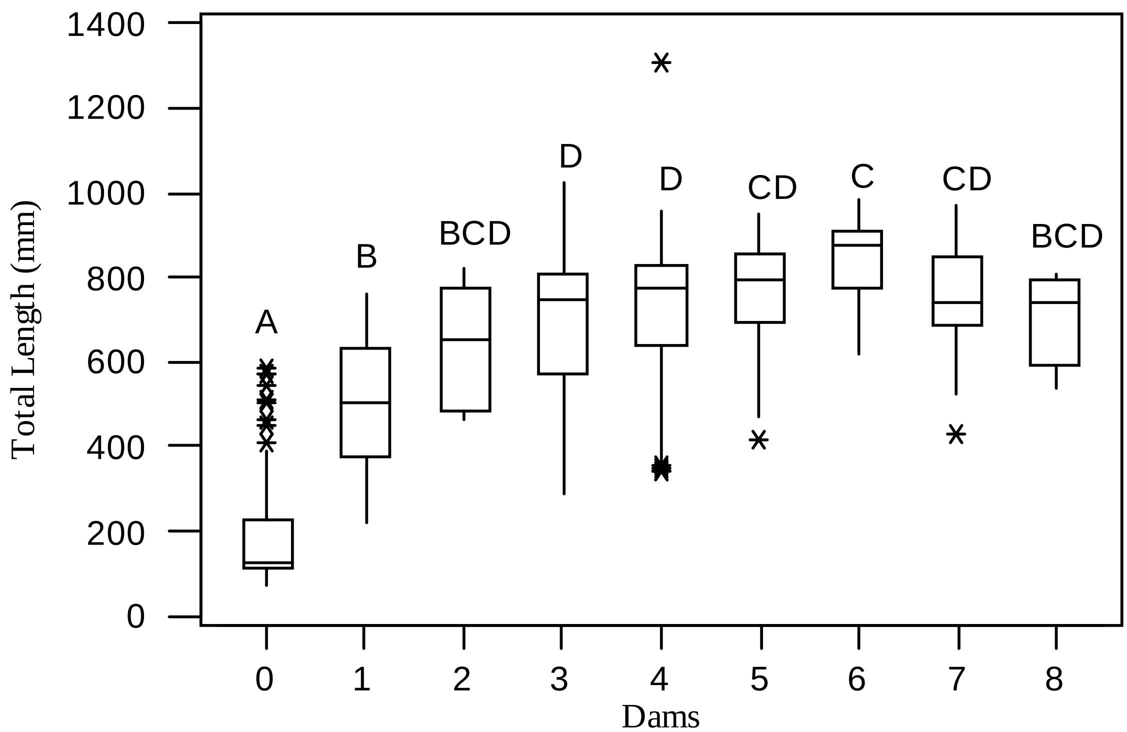


Fig. 1-9. Boxplots of eel total length grouped by dam (number of dams downstream). Similar letters indicate similar medians (One-tailed Mann-Whitney test based on hypothesized increasing length with increasing dams, pairwise $\alpha = 0.001$, overall $\alpha = 0.05$). Boxplot format is the same as in Fig. 1-8.

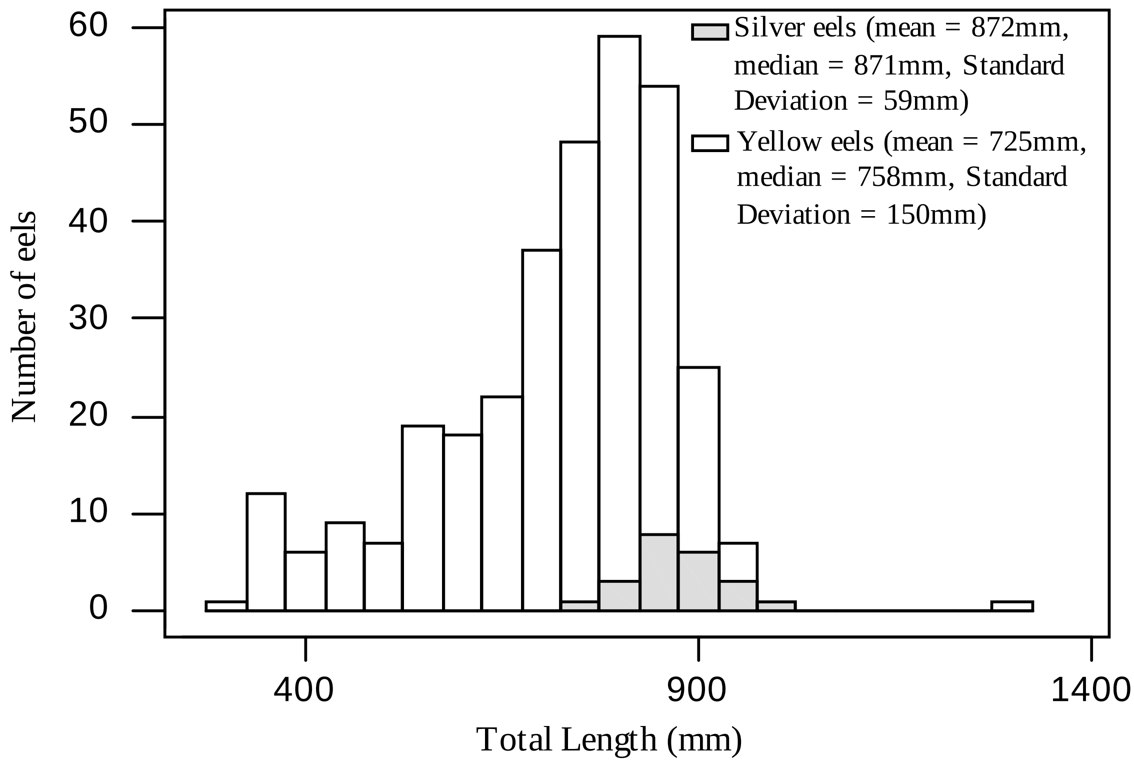


Fig. 1-10. Total length distribution of sexually mature (silver, N = 22) and immature (yellow, N = 326) eels in the Shenandoah drainage, Virginia.

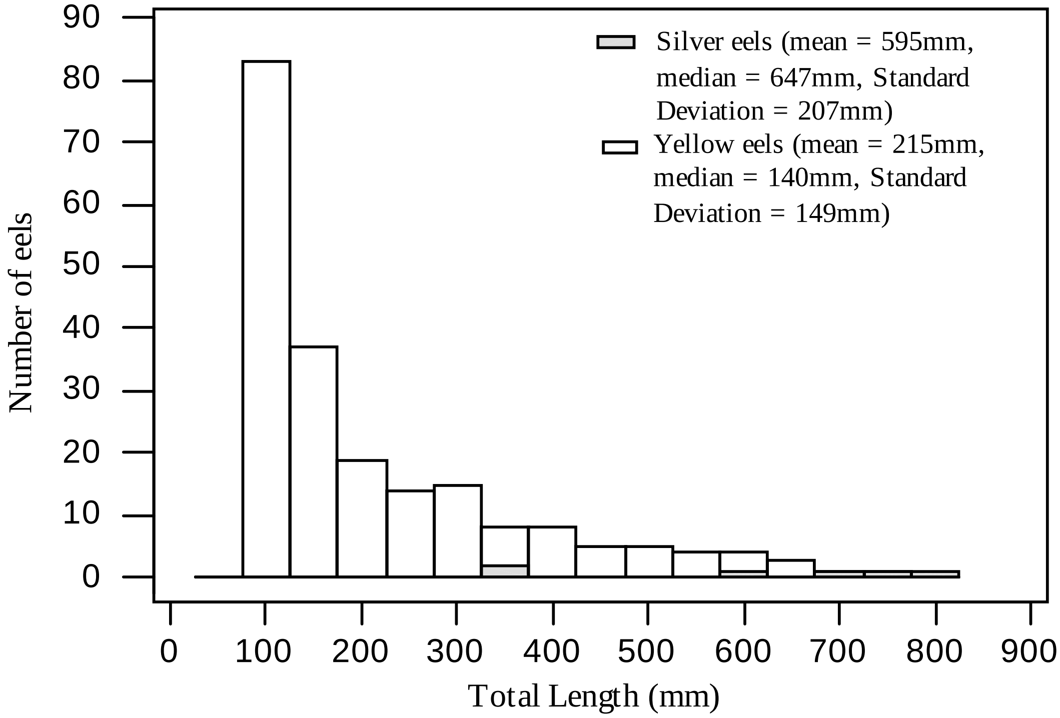


Fig. 1-11. Total length distribution of sexually mature (silver, N = 6) and immature (yellow, N = 207) eels in Potomac River tributaries, Virginia.

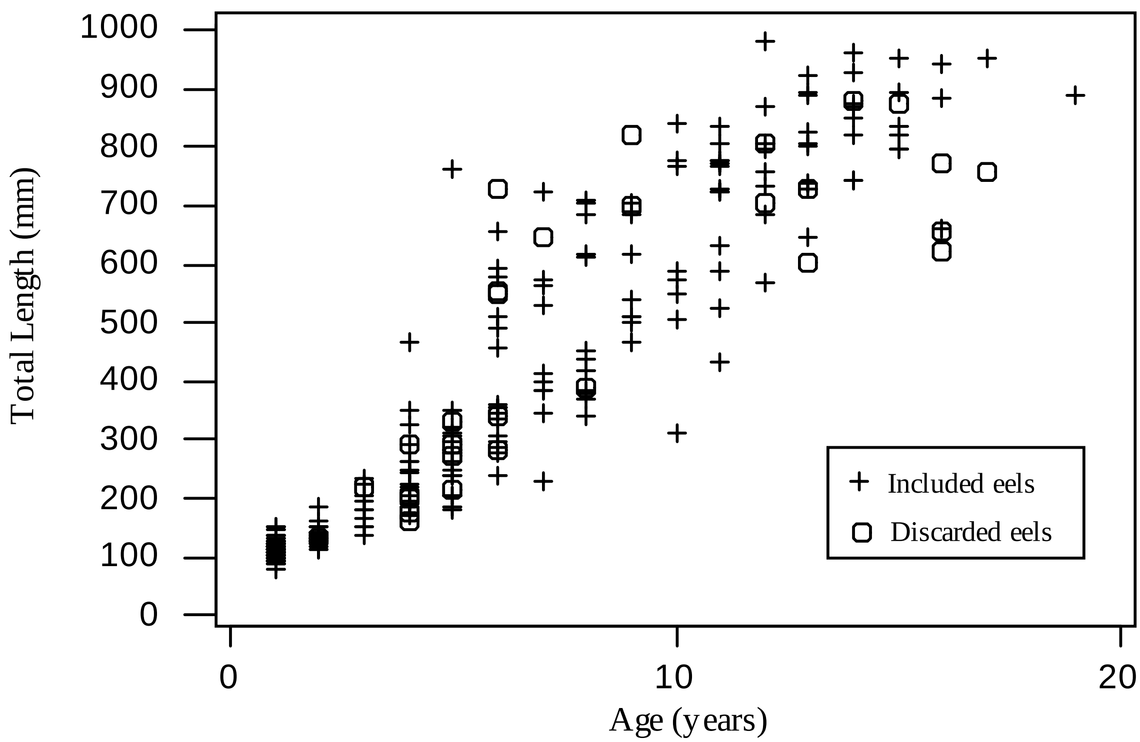


Fig. 1-12. Scatterplot of total length–at-age for eels used in age analysis (plus) and eels discarded due to interpretation disagreement (circle).

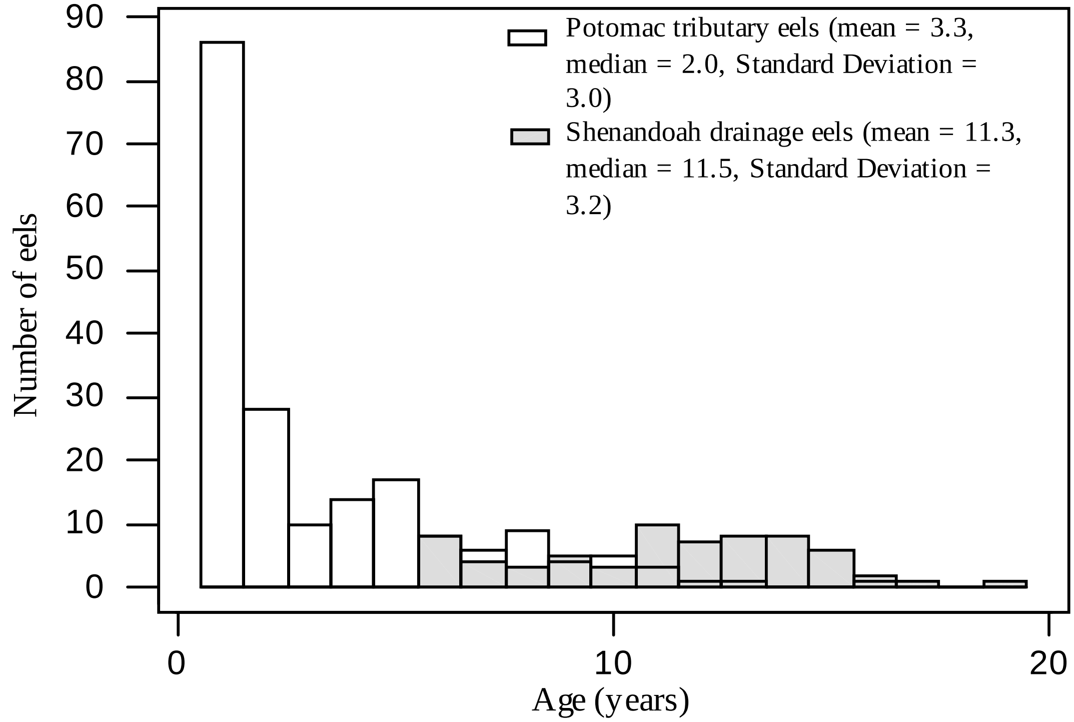


Fig. 1-13. Age distribution of all eels captured in Potomac River tributaries and the Shenandoah drainage, Virginia (N = 259).

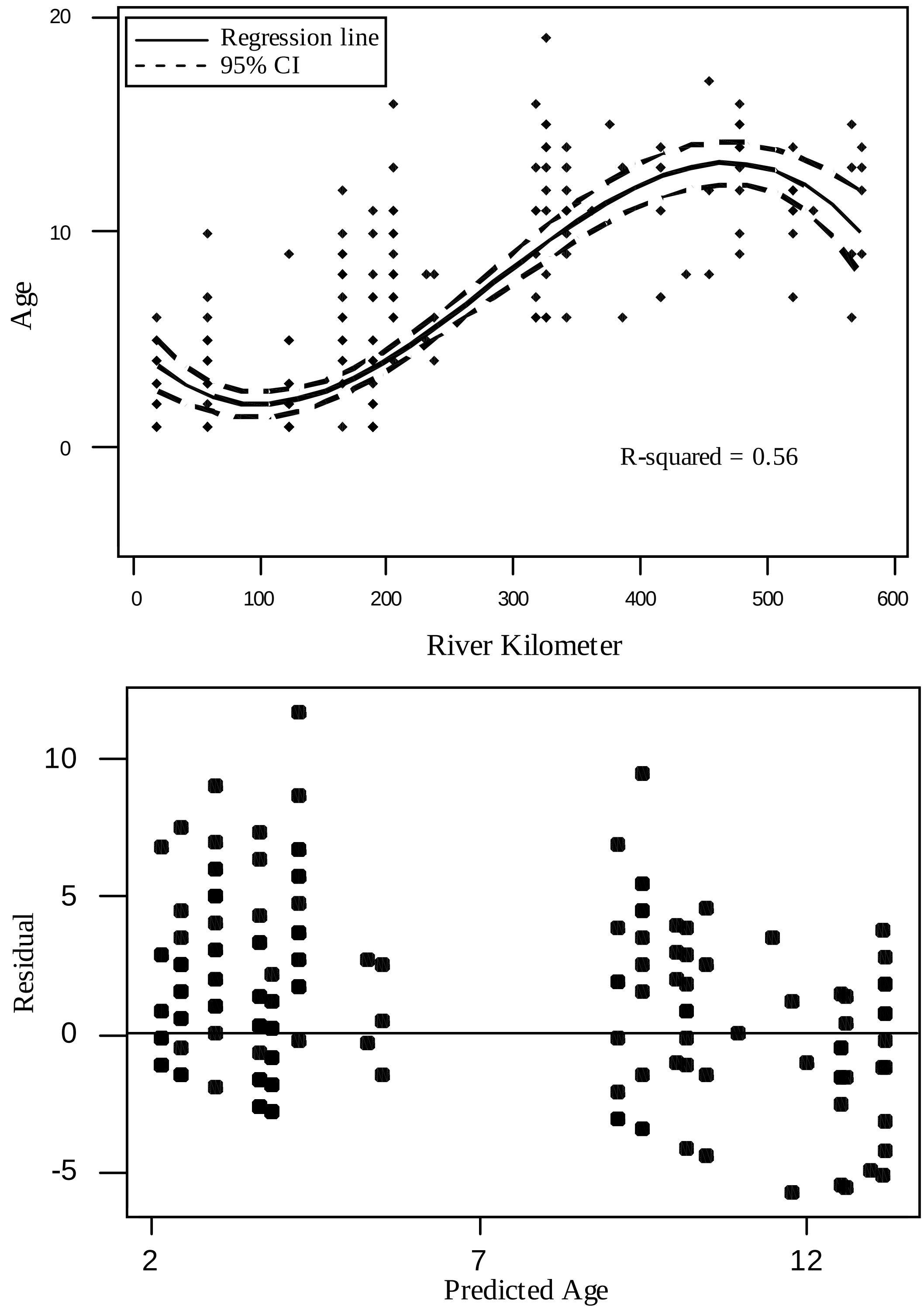


Fig. 1-14a and b. Cubic polynomial regression of eel age on river kilometer (top) with 95% confidence interval (CI) around regression line ($y = 4.86 - 6.19E\text{-}02x + 3.79E\text{-}02x^2 – 4.45E\text{-}07x^3$, d.f. = 257, RMSE = 9.69) for the Shenandoah drainage and lower Potomac tributaries, Virginia. Plot of residuals (actual age – predicted age) versus predicted age from cubic polynomial regression model (bottom) on eel age by river kilometer.

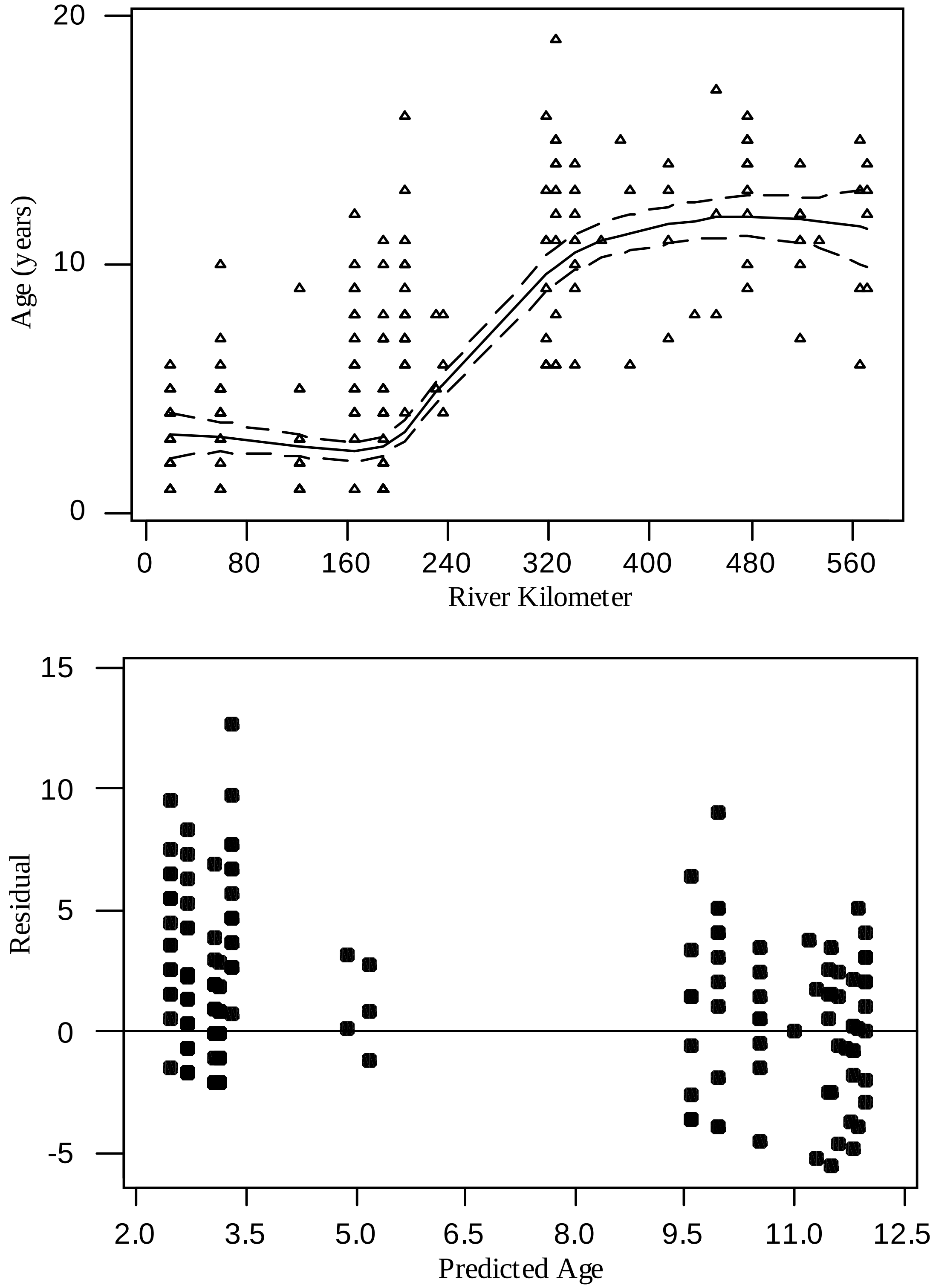


Fig. 1-15a and b. Robust local linear regression (solid line) of eel age on river kilometer (top) with 95% confidence band (dashed line) around model prediction for the Shenandoah drainage and lower Potomac tributaries, Virginia. Triangles represent individual eels. Plot of residuals (actual age – predicted age) versus predicted age from robust local linear regression model (bottom) for eel age on river kilometer.

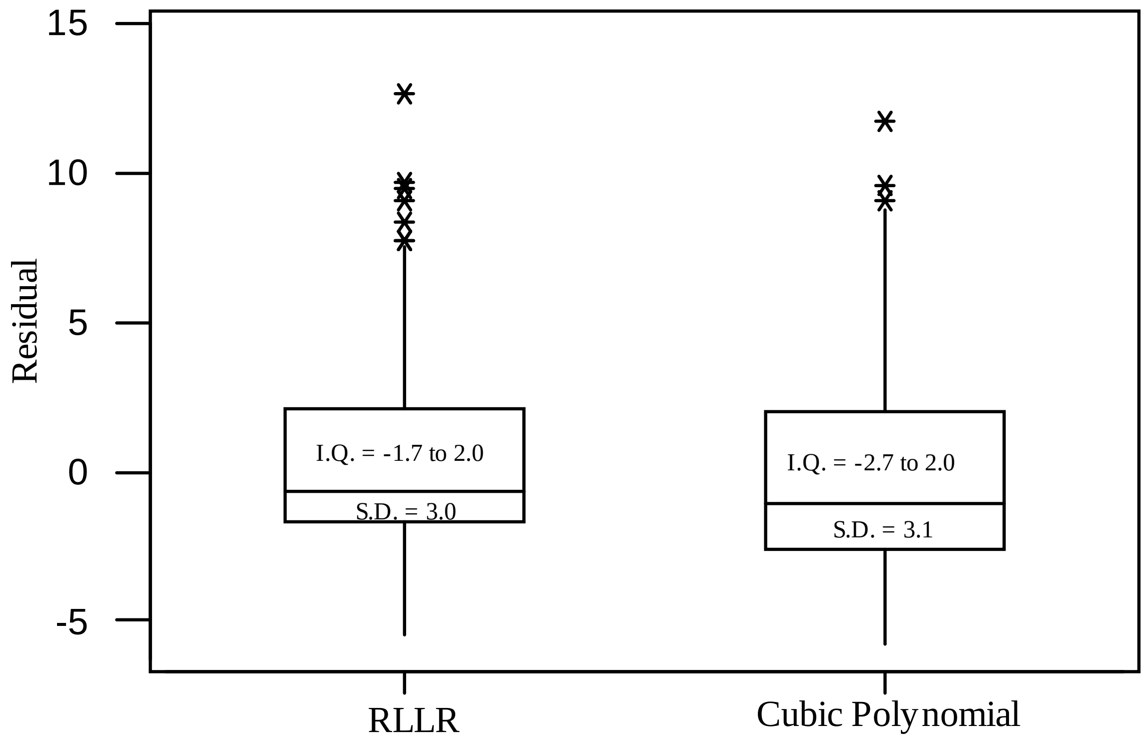


Fig. 1-16. Boxplots of residuals from two methods used to regress eel age on river kilometer (Robust Local Linear Regression (RLLR) and Cubic Polynomial). Boxplot format is the same as in Fig. 1-8. S.D. represents Standard Deviation.

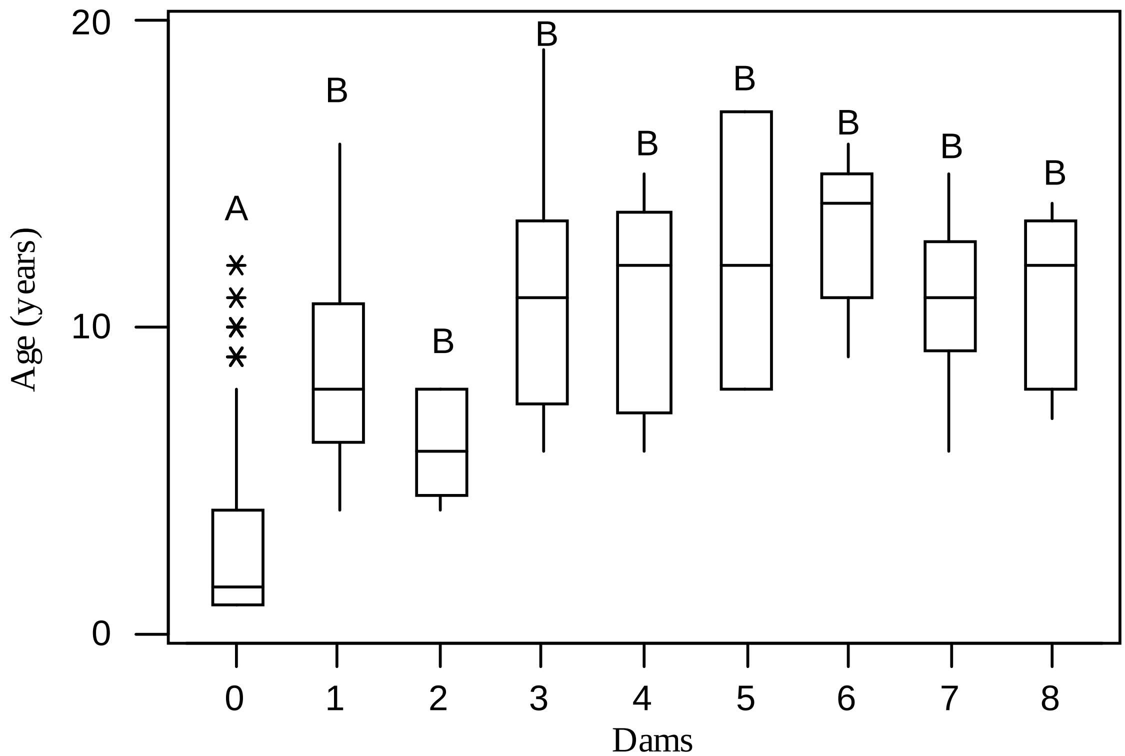


Fig. 1-17. Boxplots of age grouped by dam (number of dams downstream). Similar letters indicate similar medians (One-tailed Mann-Whitney test based on hypothesized increasing age with increasing dams, pairwise $\alpha = 0.001$, overall $\alpha = 0.05$). Boxplot format is the same as in Fig. 1-8.

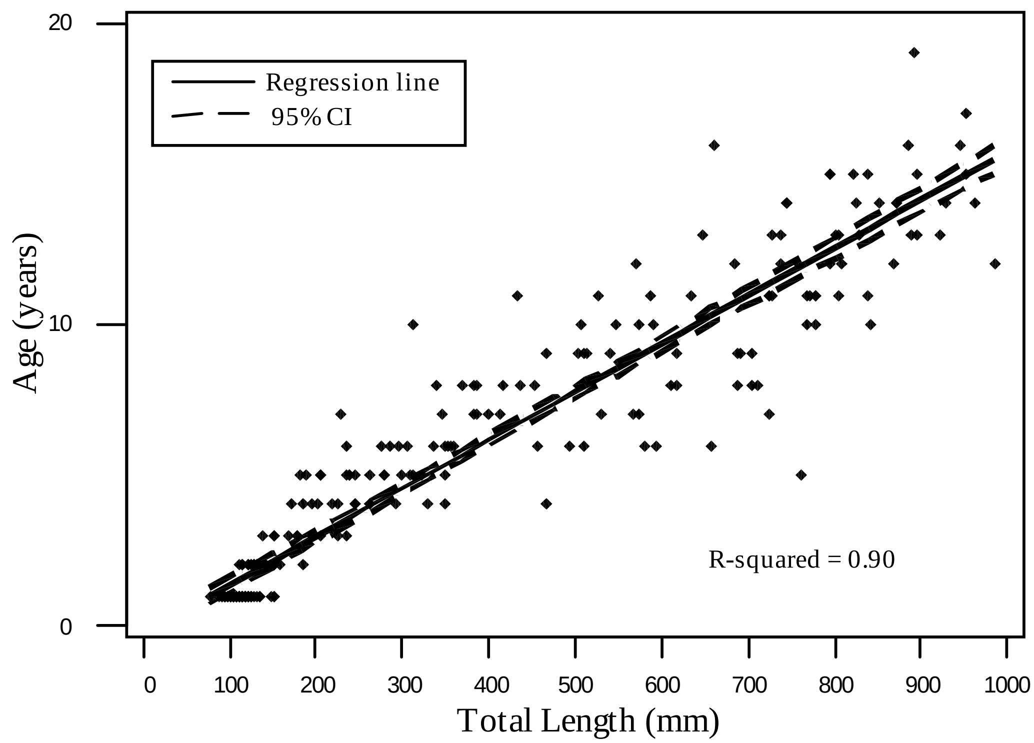


Fig. 1-18. Linear regression of eel total length (TL) on age with 95% confidence interval (CI) around regression line (y = 0.0159x – 0.193, d.f. = 258, RMSE = 2.2).

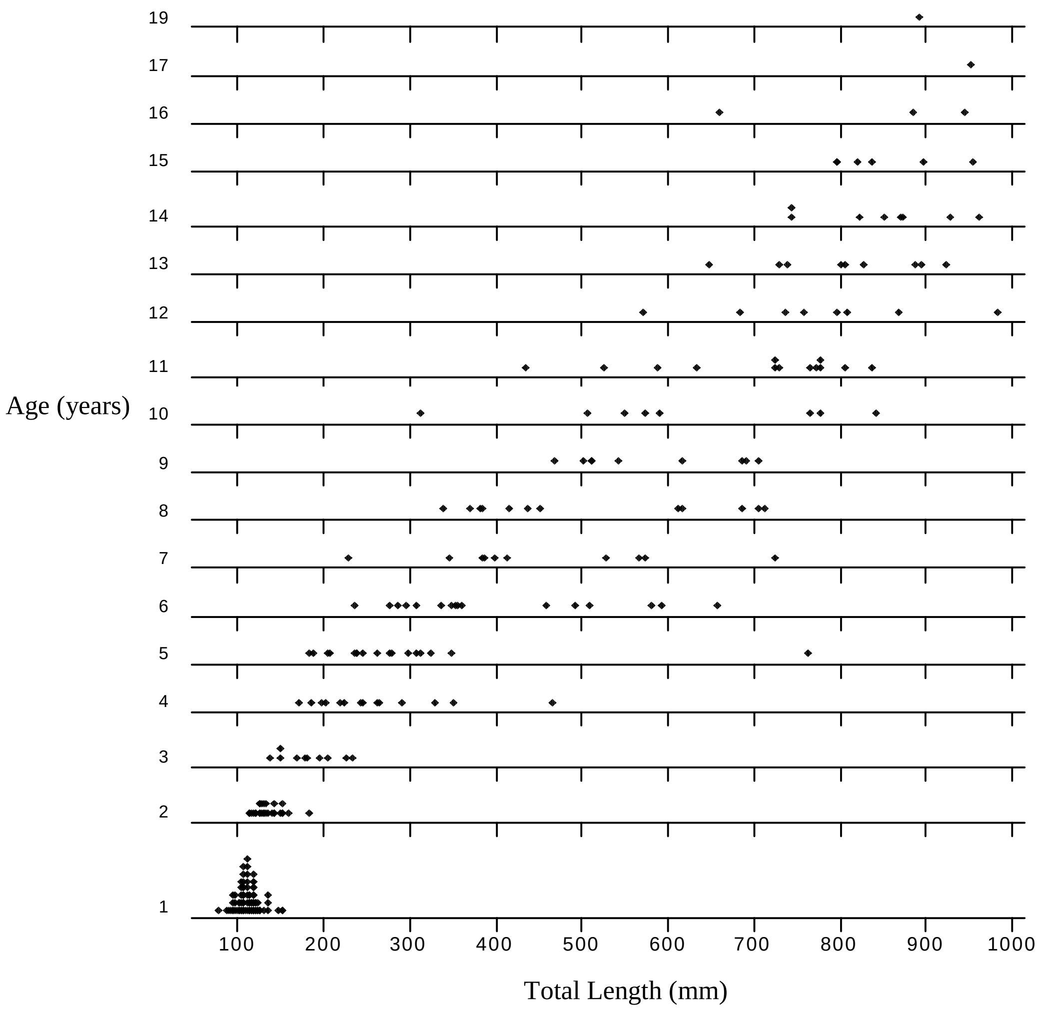


Fig. 1-19. Plot of eel total length (mm) at each age for samples from the Shenandoah drainage and Potomac River tributaries, Virginia.

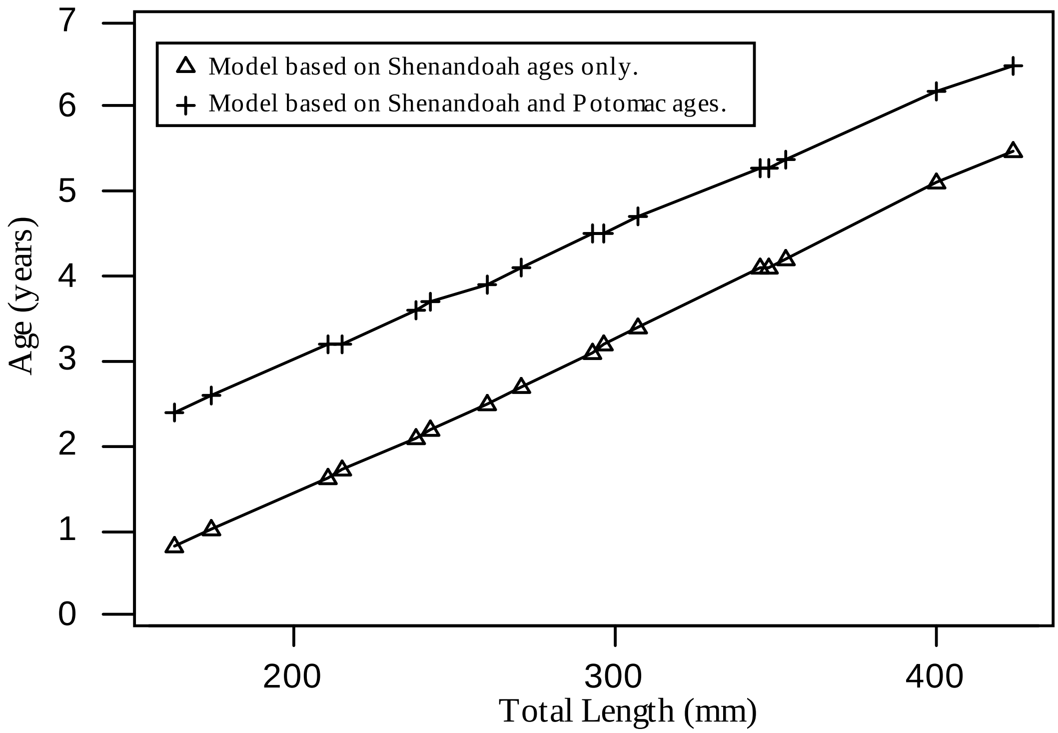


Fig. 1-20. Estimated ages of eels released from upstream migrant samplers. Age-at-length relationship was modeled using aged eels from the Shenandoah drainage only (triangle) and from both the Shenandoah drainage and Potomac River tributaries combined (plus).

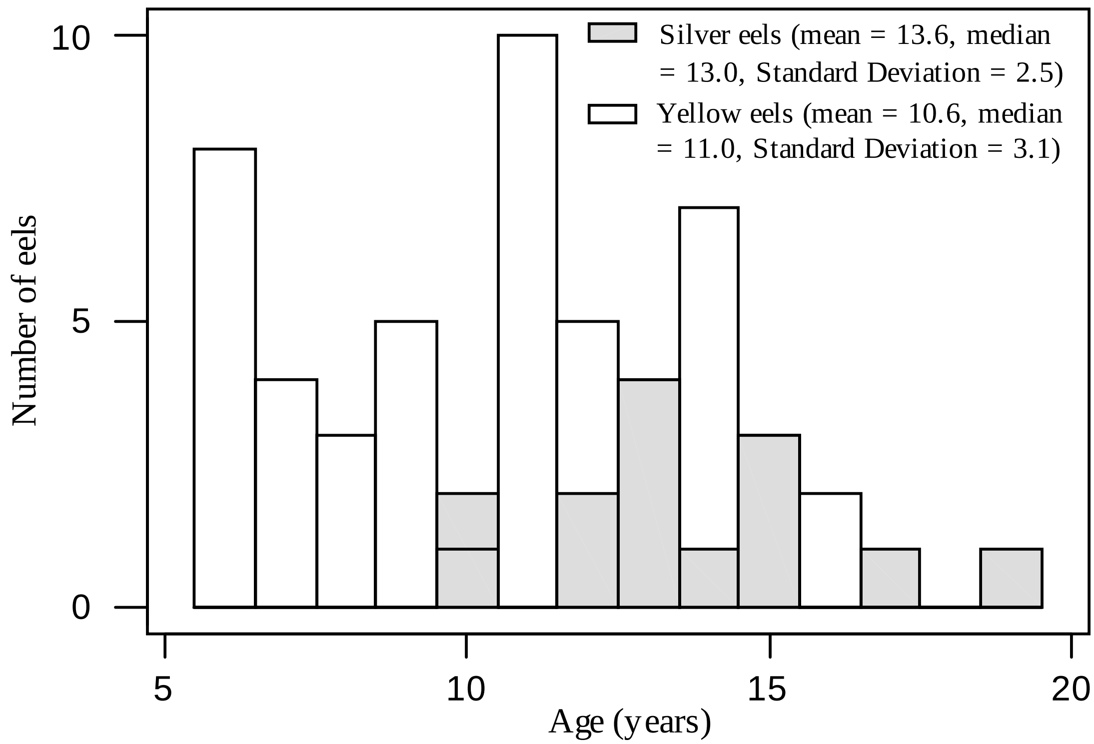


Fig. 1-21. Age distribution of sexually mature (silver, N = 14) and immature (yellow, N = 52) eels in the Shenandoah drainage, Virginia.

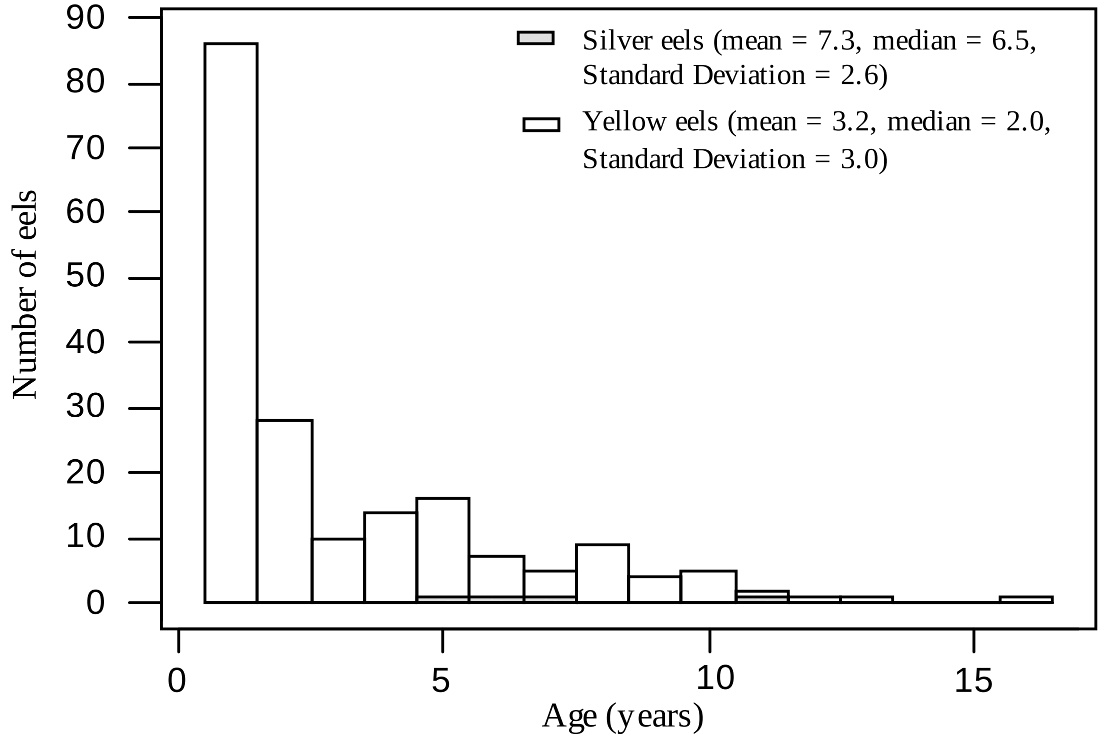


Fig. 1-22. Age distribution of sexually mature (silver, N = 4) and immature (yellow, N = 189) eels in Potomac River tributaries, Virginia.

Chapter II. PATTERNS OF ELECTROFISHING CATCH PER UNIT EFFORT OF AMERICAN EELS IN THE POTOMAC RIVER DRAINAGE, VIRGINIA.

INTRODUCTION

Population densities of European eels have been shown to be negatively correlated with increased distance from the ocean (Barak and Mason 1992; Lobón-Cerviá et al. 1995). A similar relationship has been seen in limited studies in North America but density estimates at multiple sites in the same drainage are rare (but see Smith & Saunders 1955; Smogor et al. 1995). Smogor et al. (1995) demonstrated patterns of decreasing densities of eels in Virginia streams consistent with what would be expected under a model of particle diffusion.

This relationship between population density and inland distance can be influenced by the presence of obstacles (e.g., dams, falls, or lakes) which can impede migration upriver (Smith and Saunders 1955; Reyes-Gavilán et al. 1996). In trapping and poisoning studies of Canadian lakes, Smith and Saunders (1955) found smaller standing stocks of eels in lakes that were farther from the ocean and with obstructions (dams, falls, and lakes). Although many dams are not complete barriers to eel migration, any hindrance remains a concern, and the cumulative effect of multiple dams may be substantial. Thus, eel densities within a drainage are expected to decrease with increasing distance inland, and obstacles such as dams should exaggerate the pattern.

The Shenandoah drainage in northern Virginia has a resident subpopulation of eels that provide an opportunity to investigate abundance patterns in inland freshwater. Eels migrate into headwater areas of the drainage, which are over 500 river kilometers (rkm) inland. The South Fork Shenandoah River (SFSR) has three hydropower dams that potentially impede normal movements of American eel and may exaggerate changes in densities of resident eels. From upstream to downstream we refer to them herein as Shenandoah, Newport, and Luray. Two additional hydropower dams (Warren and Millville) occur downstream on the Shenandoah River (SR) and also may affect the ability of eels to migrate unimpeded.

Information on *A. rostrata* densities at inland distances such as those in the Shenandoah drainage is virtually nonexistent in the published literature (but see Smogor et al. 1995). As well as providing information on dam effects, this knowledge is important for better understanding demographic characteristics on a broad scale for eels in the region.

OBJECTIVE

Obtain density estimates using catch per unit effort (CPUE) and mark-recapture information at intensively sampled sites on the South Fork Shenandoah and Shenandoah rivers. Relate these estimates to distance from the coast.

METHODS

Sampling and Site Selection

A series of sites were chosen on the SFSR and SR to investigate whether there were predictable changes in local stock size along the rivercourse. Seven sites were chosen in 1996 for multiple mark-recapture studies during the 1996 and 1997 sampling seasons (Goodwin et al. 1999; Fig. 2-1). Three of the original sites were not sampled in the 1998 season due to very low capture rates in the 1996 and 1997 seasons (Riverton North and South forks) and lack of access in the 1998 season (Shenandoah Shores). One new site (Front Royal) was sampled in the 1997 and 1998 seasons.

Sites were characterized by slow-flowing wide pools or runs bordered both upstream and downstream by riffle/chute sections not easily negotiated by electrofishing boat. Mark-recapture sites were 1.2 – 2.5 rkm long and 50 - 125 m wide and were sampled 6 to 18 times between 1996 and 1998. The 1996 – 1997 sites were dispersed over approximately 90 river kilometers (rkm) and were chosen to represent this span and in an effort to sample both upstream and downstream of two of the hydropower dams on the Shenandoah and South Fork Shenandoah rivers (Luray and Warren). The 1998 sites spanned approximately 80 rkm and one dam (Luray); the farthest downstream site from 1996-1997 was dropped. Sites were also chosen based on their accessibility to sampling by electrofishing boat.

Electrofishing was the primary means of eel capture due to the lack of success using other methods (see Chapter I Methods). The sampling protocol at each site was kept constant throughout the study and efforts were made to standardize the electrofishing effort (minutes of shocking) at each. The entire shoreline area of a site was shocked as well as mid-river areas with suitable depth, cover, and visibility. Mid-river areas included any root-wads, leaf packs, bedrock ridges and boulders providing fish cover.

Tagging

Eels captured in mark-recapture sites were measured, individually tagged, and released back into the general area of capture. Eels were immobilized in the vise-like measuring board both for measurement and tagging (see Chapter I Methods). Once measured, each fish was given a Passive Integrated Transponder (PIT) tag (Biomark). The PIT tag was injected ventrally, approximately 1 cm lateral to the midline and 3-4 cm anterior to the anus, and carried in the abdominal cavity. Each PIT tag was numbered individually, readable through the skin by a hand-held 'wand'.

Eels were also given a secondary external batch mark to guard against misidentifying recaptured fish that had lost a PIT tag. Tag loss can be problematic with eel studies because of the fish's propensity to burrow into substrate and other tight areas (Nielsen 1988). Published use of PIT tags in eels is sparse and information on tag retention is lacking. Injectable elastomer (Northwest Marine) was used for the external marking. Elastomer was injected into the ventral side of the eel's right pectoral fin, forming 2-3 stripes between the fin rays. All eels captured were inspected for elastomer and scanned for the presence of a PIT tag to reduce the potential for misidentifying recaptures.

Mark-recapture

Information from mark-recapture sites was used in estimating population densities with the Jolly–Seber model. This model is based on the following assumptions, all of which were assumed to be valid at the beginning of this study: a) tagged individuals experience no tag loss and are correctly identified upon recapture, b) tagged individuals are not subject to increased mortality or vulnerability to angling when compared to unmarked individuals, and c) there is equal probability of capturing tagged and untagged eels due to random mixing of the two groups and random sampling (Ricker 1975).

The Jolly–Seber model is defined by the two equations,

$$N_i = ß_i C i \, / \, m_i$$

where N_i is the estimate of the population before the *i*th sample, m_i is the total recaptures of marked fish at time *i*, $ß_i$ is the number of marked fish in the population prior to the *i*th sample (as determined from the equation below) and C_i is the total number of fish captured in the *i*th sample, and

$$ß_i = M_i K_i / R_i + m_i$$

where M_i is the number of newly marked fish at time *i*, K_i is the number of fish caught in samples later than time *i* that were marked before time *i*, and R_i is the number of fish marked at time *i* that are subsequently caught in later samples (Ricker 1975).

Catch Per Unit Effort

Information on eel catch per unit effort (CPUE) was recorded during all sampling effort throughout the study. Boat electrofishing CPUE data was not only taken at mark-recapture sites, but numerous other sites throughout the drainage that were sampled for other objectives (see Chapters I and III). These sites ranged from approximately 350 to 520 river kilometers (rkm) from the mouth of the Potomac River at the Chesapeake Bay. CPUE is expressed as the number of eels caught per hour of electrofishing.

Backpack electrofishing was used for other objectives (see Chapters I and III) and provided CPUE information as well. Backpack electrofishing CPUE data in the Shenandoah River drainage came from three tributaries to the SFSR, 1 site in the SFSR, 1 site in the SR and one tributary to the SR (11 samples total). These data were compared to 11 sites in tributaries to the Potomac River, Virginia, all below the confluence of the SR and Potomac River. The Potomac information was used to examine variation in CPUE over a broader scale than strictly within the Shenandoah River drainage. Backpack electrofishing sites ranged from approximately 19 to 435 rkm from the mouth of the Potomac River.

Statistical Analysis

Variation in CPUE was examined among mark-recapture sites and among river sections between dams (dam reaches). Multiple comparisons were made using Kruskal-Wallis tests ($\alpha = 0.05$; Gibbons 1993). Pairwise Mann-Whitney comparisons were used to determine relationships between individual dam reaches. Alpha levels (α) for pairwise comparisons were adjusted according to the formula in Chapter I (Methods, Statistical Analysis) for a cumulative level of 0.05. CPUE at mark-recapture sites within the same dam reach were first analyzed for differences due to distance-upstream effects then compared to mark-recapture sites above and below the next upstream and downstream dam, respectively. If CPUE at different mark-recapture sites between dams is similar but sites separated by a dam are different, then a dam effect could be inferred. Data from the Riverton North and South forks were combined as one site (Riverton) due to their adjacent location and lack of barrier between.

The Jonckheere-Terpstra (Jonk-Terp) test statistic was used to study patterning in CPUE with increased distance inland (Chapter I, Methods, Statistical Analysis). Both dam reach and mark-recapture sites were tested for hypothesized decrease in abundance (measured by a decrease in CPUE) with increased distance inland.

Simple linear and polynomial regression analyses were used to model patterns in CPUE related to distance inland (rkm). Rkm was used as the dependent variable because it allowed for the finest resolution in the data and reflected the actual spatial relation between CPUE and distance inland. Boat electrofishing CPUE from the Shenandoah River drainage was modeled, as was backpack electrofishing CPUE from there and the lower Potomac tributaries. Regression analysis was used to provide a best linear or curvilinear fit to describe patterns in the raw data and determine the ability of distance (defined by rkm) to account for the variation seen in CPUE.

RESULTS

Mark-recapture

A total of 195 eels were captured and marked in the mark-recapture sites throughout the study. Eel recapture rates in the SFSR were low and sporadic. Although up to 24% of the eels marked in a given site were recaptured over two years, the total for all mark-recapture sites was 15.9% (31 of the 195 marked). Eight of these were recaptured two or more times, resulting in 43 total recaptures (Table 2-1). Five eels (2.6%) in the mark-recapture sites displayed characteristics of mature (silver) eels. These fish were not recaptured and represent a minimum estimate of marked eels that may have migrated out of the drainage to spawn during the study.

Site-specific density estimates could not be obtained as planned due to the infrequent and sporadic recaptures and apparent violations of model assumptions (see

Discussion). However, drainage-wide density estimates were made with the acknowledgment that model assumptions were violated. Two data-pooling methods were used to obtain density estimates. First, capture and recapture data from mark-recapture sites were pooled by sample year (1996 – 1998) and each year was treated as a single marking period or single recapture period (e.g., 1997 was the recapture period for the 1996 marking year and 1998 was the recapture period for the 1997 marking year). The simple Petersen method (Ricker 1975) was used to estimate density using the formula,

$$N = (MC/R)/ha$$

where N is the number of eels per hectare, M is the number of eels caught and marked, C is the number of eels caught in the following year, R is the number of eels caught in the following year that were recaptures, and ha is the total area of all sample sites in hectares. For example, 137 eels were marked in 1997, 43 eels were captured in 1998, six of which were recaptures. The total surface area of mark-recapture sites was approximately 100 ha, resulting in an estimate of 9.8 eels/ha in 1997 (compared to 11.9 eels/ha in 1996 using the same method).

Analysis of pooled total capture and recapture rates at individual sites over the entire study period produced estimates of 3.4, 8.1, 10.1, 16.9, 19.0, 19.7, and 22.3 eels/ha, averaging 14.2 eels/ha, using the formula,

$$N = (M/P)/ha$$

where M is the total number of eels marked, and P is the total recapture rate (total number of recaptures/total number marked). Marked and recaptured eels pooled from all sites for the entire study produced and estimate of 10.5 eels/ha using the same formula. An assumption of the simple Petersen estimate is that recruitment into the catchable population is negligible, violation of which will lead to an increased estimate (Ricker 1975). The potentially high level of mobility (see Chapter III Discussion) and open population in the SFSR and SR raise doubts as to the validity of this assumption in this study. The most probable estimate of eel density in the Shenandoah River drainage based on these estimates and personal observation is closer to the low-end of the individual site range, perhaps 5 eels/ha. When extrapolated over the SFSR and SR, the estimated stock size is approximately 9800 eels (ranging from 6500 to 43600 if the above individual site estimates are used).

Euston et al. (1997) estimated that approximately 393 silver eels passed the Luray hydropower dam during their 1994 study on the SFSR. Using the density estimate of 5 eels/ha, approximately 4900 eels reside upstream of the Luray dam. The estimate from this study of a 6.3% maturity rate among eels in the SFSR and SR annually (see Results: Length Characteristics By Maturity Level) yields an estimated 309 silver eels maturing (and ostensibly passing the Luray dam). Using the same maturation rate, approximately 6.7 eels/ha (6550 eels) would be needed above the Luray dam to agree with the data in Euston et al. (1997). While these estimates are made at the grossest level, their similarity suggests that a density of 5-7 eels/ha may be a reasonable estimate for the SFSR and SR. Inaccuracy in this estimate is likely but it is improbable that densities in the Shenandoah River drainage are above 10 eels/ha.

CPUE was used as a measure of relative abundance in the place of density estimates for further data analysis.

Catch Per Unit Effort

CPUE was low for boat electrofishing in virtually all SFSR and SR sites including those outside of the mark-recapture sites, ranging from 0.0 to 9.0 eels/hour (mean = 1.5, median = 1.1, standard deviation = 1.5; Fig. 2-2). No differences in CPUE occurred among reaches between dams (Kruskal-Wallis, $P = 0.63$; Fig. 2-3). Different CPUE was found between mark-recapture sites (Kruskal-Wallis, $P = 0.004$). Pairwise Mann-Whitney comparisons ($\alpha = 0.0026$) of mark-recapture site CPUE found differences only between one site (Riverton) and the four most upstream sites, all of which were similar to each other (Fig. 2-4).

Simple linear, quadratic, and cubic regression models with rkm as the independent variable did not explain a significant portion of the variation in boat CPUE ($P > 0.05$). Jonk-Terp tests were not significant for patterning of CPUE among dam reaches or mark-recapture sites ($P = 0.490$ and 0.998, respectively).

Four tributary sites were sampled a total of nine times (416 minutes total) without capturing eels. One site on the SFSR (Luray Dam) and one on the SR (Warren Dam) were also sampled with a backpack electrofisher below the dams during low water periods (75 minutes total). No eels were caught or seen during backpack electrofishing.

CPUE from backpack electrofishing in Potomac tributaries ranged from 0.0 to 83.3 eels/hour (mean = 28.4, median = 28.0, standard deviation = 30.9; Fig. 2-5). CPUE decreased with increased distance upstream, with a sharp drop after approximately 200 rkm (Fig. 2-5). CPUE was different among dam reaches (Kruskal-Wallis, $P = 0.001$, Fig. 2-3). Pairwise comparison was not possible due to small sample sizes. Backpack CPUE below 200 rkm was greater than that above 200 rkm (Mann-Whitney, $P < 0.0001$).

A simple linear regression model with rkm as the independent variable explained 56.4% of the variation in backpack CPUE ($y = 57.4 – 0.15x$, d.f. = 21, RMSE = 305.4; Fig. 2-6). Quadratic and cubic polynomial regression did not explain a significantly greater amount of the variation in CPUE ($P > 0.09$). When boat and backpack electrofishing data were pooled, the quadratic polynomial regression model explained 67% of the variation in CPUE ($y = 77.55 – 0.37x + 4.35E\text{-}04x^2$, d.f. = 137, RMSE = 42.34; Fig. 2-6), although it did not appreciably change the shape of the regression model from that found using only the backpack CPUE.

DISCUSSION

Mark-Recapture

Population estimates could not be obtained because of the sporadic nature and low number of the recapture incidents throughout the study. While the overall percentage of recaptured eels at each mark-recapture site was consistent with other studies, they were cumulative over approximately two years. The low or nonexistent recapture rates per sampling event resulted in an inability to obtain any meaningful population estimates.

The low densities of eels, scattered recaptures, and likely violation of assumptions precluded the use of mark-recapture methods in determining densities in the Shenandoah drainage. Although the Jolly-Seber model allows for individuals moving into and out of the study area, the small numbers of eels apparent in study sites and the potential for large proportions of these to move during the study could have been a problem. At least 2.6% of the marked eels probably matured during the study and emigrated. Approximately 10% of eels caught in mark-recapture sites were longer than the average mean length of silver (maturing) eels in the South Fork Shenandoah and Shenandoah rivers (Chapter I) and almost 35% were longer than the mean minus one standard deviation. These estimates illustrate the potential numbers of eels emigrating over the two-year study period. No estimates of immigration of young eels into mark-recapture sites or long-distance movement of juvenile eels (see Chapter III for discussion of movement) could be made.

The inability to sample all habitats in each mark-recapture site violated the assumption that all eels were sampled at random and with equal probability of capture. Because of the large size of the SFSR and SR, the limited sampling field produced by the electrofishing boat, and the need to visually locate stunned eels, deep water and turbidity made thorough sampling of large portions of these sites difficult. Without sampling all habitats, deep pools in particular, all eels in a site could not be subject to random sampling.

The marking techniques used did not appear to violate any of the assumptions of mark-recapture studies. Tag retention in the recaptured eels was 100% for both methods. Elastomer marks remained bright and easily identifiable up to a year post-marking and PIT tags were easily located with the hand-held scanner over a year post-marking. Eels recaptured within 3 weeks of tagging were almost completely healed from the PIT tag injection. Eels caught 4-6 weeks after initial marking often had no discernible scarring from the tagging process. No infection or other abnormality related to the PIT tag entrance wound was seen in this study.

One marked eel was sacrificed at the end of the study as part of the objectives in Chapter 1. This eel had been tagged for over 400 d and provided an opportunity to study the PIT tag location within the body cavity. The tag was difficult to see because it had become encased in the ventral musculature of the abdomen. The site did not appear infected or otherwise irritated.

Catch Per Unit Effort

No pattern in CPUE was seen between mark-recapture sites or dams on the SR and SFSR; eels exhibited low density throughout the Shenandoah River drainage. The highest catch rate for a sample (9 eels/hour) on the SFSR was upstream of Newport dam, the second hydropower dam on the SFSR and fourth from the confluence of the Shenandoah and Potomac rivers. Relatively high catch rates in the SFSR seemed to be more closely associated with site characteristics such as leaf packs, root wads, and woody debris than distance upstream. Close association with current was also apparently important based on the greater capture success in flowing areas versus backwaters and other slack-water areas.

The backpack electrofisher CPUE data represented a broader geographic gradient. Catch rates dropped sharply when distance inland exceeded 200 rkm. This coincides with the location of Great Falls on the Potomac River, which may be a partial natural barrier to eel migration. There are also two dams on the Potomac River within the study area, one downstream and one just upstream of Great Falls. CPUEs upstream of 200 rkm were all low compared to those in the coastal plain tributaries below Great Falls. The potential effects of Great Falls and the two lower Potomac dams are confounded and cannot be sorted out with these data.

Higher catch rates in lower Potomac sites indicate that low densities throughout the Shenandoah drainage are not likely to be a product of sampling bias. The presence of downstream dams in this study may have had a significant 'screening' effect, significantly reducing the abundance of the migratory eels prior to their reaching the study area. If the drop in CPUE after 200 rkm in the present study is a result of impedance at downstream barriers (falls and dams), then the ability to detect a natural pattern or dam effect in the SFSR may be virtually eliminated.

The cubic regression model used to describe the trend in backpack CPUE explained by rkm, although explaining more of the variation in CPUE, makes less sense biologically than the quadratic model (Fig. 2-6). The cubic model shows an increasing CPUE at the greatest rkm, which is apparently an artifact of the model. As discussed in Chapter I, the model restrictions of a cubic polynomial tend to force the tailing up or down of the fitted trendline where it does not appear sensible from a biological standpoint. The quadratic model of CPUE explained by rkm shows a strong decline, eventually leveling off at low rates after approximately 350 rkm, and is biologically reasonable.

Smogor et al. (1995) studied distribution patterns of eels in Virginia streams throughout the state finding an inverse relation between the densities of eels <374 mm and distance inland (km). Plots of their data show apparently significant drops in density at approximately 200 rkm both within drainages and throughout the state. Large eels

(>374 mm) did not show a similar pattern, exhibiting low densities statewide (Smogor et al. 1995). This statewide pattern of declining density suggests that Great Falls may not be a significant barrier to eel migration but, as Smogor et al. (1995) suggested, that large-scale processes may be most influential in determining eel densities throughout the state.

Catch rates for eels in the SFSR and SR, while not directly comparable with other studies, appear to be lower than most published information gained through electrofishing. Many studies using electrofishing have focused on freshwater streams in coastal areas within approximately 60 rkm of the ocean (see Levesque and Whitworth 1987; Haro and Krueger 1991; Oliveira 1997). Catch rates (approximated from reported sample sizes and sampling effort) in these studies were all apparently similar to those found in lower Potomac tributaries in the present study. Electrofishing information from more inland areas indicates greater catch rates than those typical of the SFSR and SR. Ogden (1970) sampled small streams in northern New Jersey and caught between two and approximately 30 eels per sampling occasion. LaBar and Facey (1983) used boat electrofishing in Lake Champlain, Vermont, tagging 369 eels in 19 sampling occasions. In contrast, the 195 eels marked in the SFSR and SR resulted from 86 sampling occasions totaling over 160 hours of electrofishing.

The most common sampling method for eels in published studies has been trapping, usually in eel pots or fyke nets (e.g., Helfman et al. 1984; Hansen and Eversole 1984; Bozeman et al. 1985; Ford and Mercer 1986). The ineffectiveness of these methods in the present study may be partially due to the placement of traps in slower-flowing areas (primarily hydropower pools) and a paucity of information on more useful deployment techniques in a lotic environment. More probably, however, the low density of eels in the SFSR and SR precluded the efficient use of these passive capture methods in this study.

There is no published information on electrofishing American eels in large riverine habitat at great distances inland. Data published from sampling efforts on other large eastern river systems (e.g., Connecticut, Hudson, Delaware, and Susquehanna) by state agencies or other researchers could provide valuable information in similar habitats. Ancillary data on eel CPUE from river surveys using boat electrofishing, such as those done by the VDGIF on the SFSR and SR, could provide useful CPUE data comparable over broad geographic scales. Analyses over spatial and temporal scales may help define trends in the relative densities of eels both throughout their range as well as over time. Recent concerns by Castonguay et al. (1994) and Casselman et al. (1997) over the decreasing numbers of migratory eels in some Canadian waters raise questions as to whether this pattern exists throughout the species' range. This trend has not been investigated to a great extent in the more southerly portions of the range. CPUE information over time and in a number of drainages could aid in corroborating or refuting the presence of these trends on a population scale.

The investigation of abundance estimates, whether through population estimates or relative estimates such as CPUE, can aid managers in understanding broad patterns of distribution within and between drainages. This information may be used to interpret broad patterns and departures that may result from local impacts such as loss of habitat, impedance of migration, or harvest. This type of data can aid in prioritizing restoration efforts and in identifying specific areas where human impacts have occurred. Such data can also be used to justify regulations on harvest and other human activities impacting eel distribution and density.

Conclusions

Recapture rates in the Shenandoah River drainage were low and recaptures were sporadic making population estimates unrealizable. Low recapture rates are common in mark-recapture studies of eel and in this study were likely due to a combination of low eel density in the drainage, potentially high rates of movement by marked eels out of sampling sites, and sampling inefficiency in some habitats. Boat electrofishing, although probably the most appropriate sampling method in this study, was not suitable at sampling deep pools or during periods of turbidity. Mark-recapture studies in smaller streams increase the ability to thoroughly sample all available habitat thereby increasing the likelihood of marking and recapturing a greater proportion of the resident fish. The assumption that marked eels are stationary appears to be inaccurate for sites on the SFSR and SR and should be approached with caution in eel studies in other areas.

The density of eels throughout the SFSR and SR appears to be low, as indicated by low CPUE at all sites within the drainage (mean = 1.5 eels/hour). Analysis of CPUE data from more coastal sites in the lower Potomac River drainage (mean = 28.4 eels/hour) are similar to that found in the literature. The trend in decreasing CPUE with increasing distance inland (rkm) is similar to statewide information on eel distribution by Smogor et al. (1995) suggesting that influences at a broader scale may play an important role in structuring eel subpopulations. Departures from expected patterns based on large-scale trends could assist in focusing regulation and/or mitigation for human-induced impacts. Inland areas, though they may support lower eel densities relative to coastal habitats, may contribute significantly to the spawning success of the species due to the highly fecund females they support. A heavy harvest, loss of habitat, or loss of habitat accessibility in these areas may have a disproportionate impact on the breeding population and subsequent recruitment.

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Table 2-1. Mark-recapture sites on the Shenandoah and South Fork Shenandoah rivers listed downstream (left) to upstream (right). Data are from boat electrofishing.

	Shenandoah Shores	Riverton (North & South)	Front Royal	Gooney	Compton	Hawksbill	Whitehouse
No. of eels caught and marked	16	8	19	38	42	35	37
No. of eels recaptured	1	1	2	6	8	4	9
% eels recaptured	6.3	12.5	10.5	15.8	19.0	11.4	24.3
Effort (hrs.)	13.2	21.4	18.2	25.7	23.2	28.6	30.2

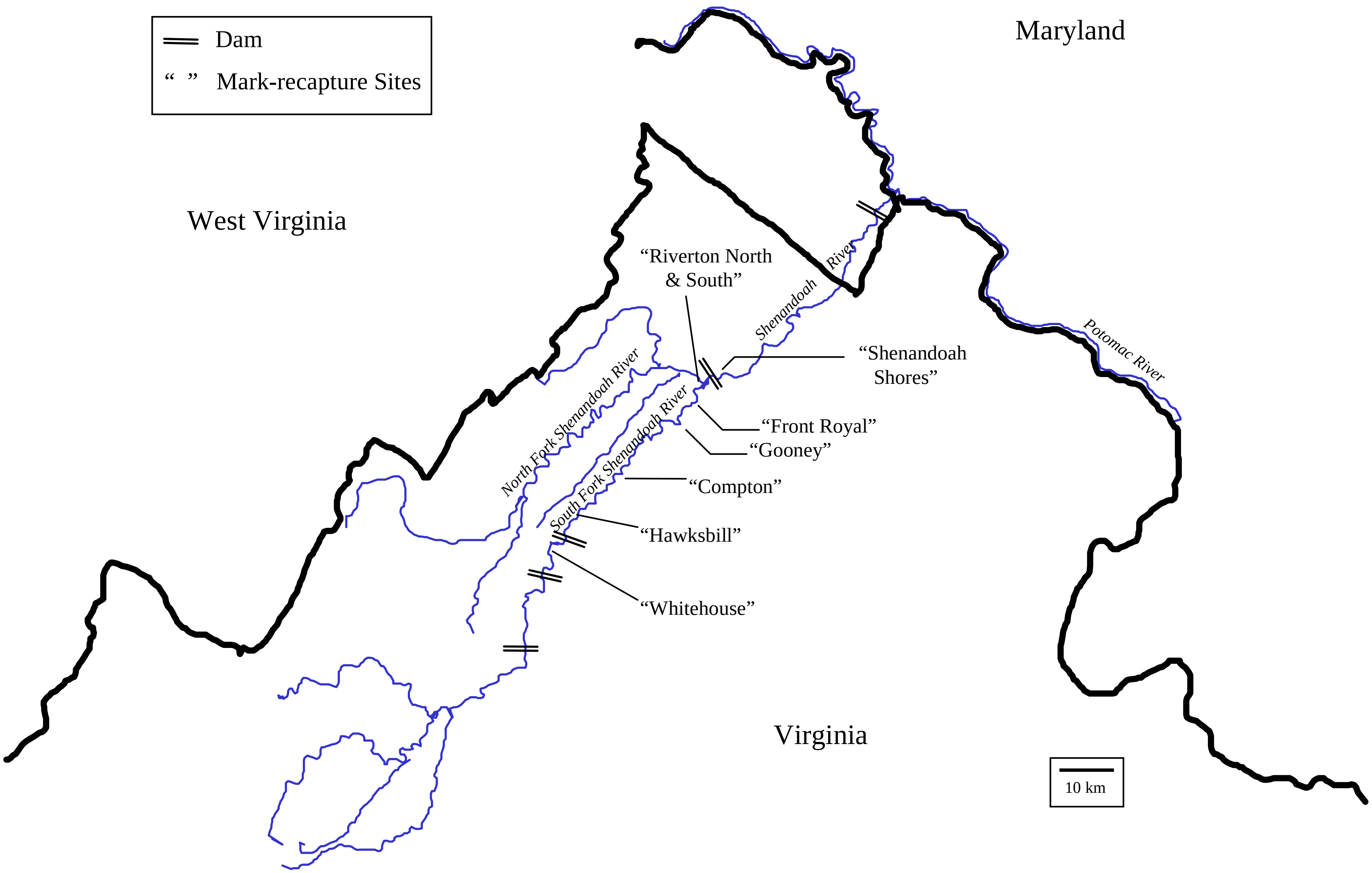

Fig. 2-1. Mark-recapture sites (in quotes) on the South Fork Shenandoah and Shenandoah rivers, Virginia. Locations of hydropower dams are marked with parallel double lines.

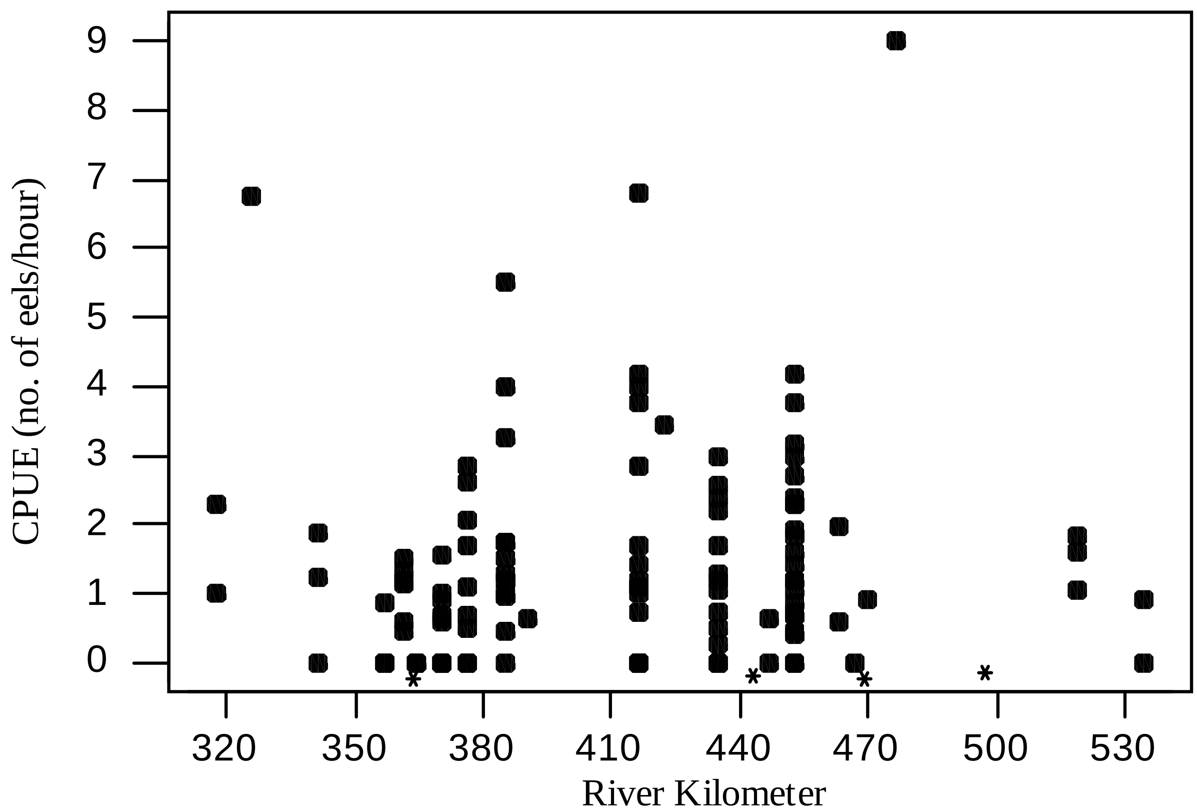

Fig. 2-2. Catch per unit effort (CPUE; number/hour) of eels in individual samples plotted by river kilometer for boat electrofishing on the South Fork Shenandoah and Shenandoah rivers, Virginia. Asterisks represent hydropower dam locations.

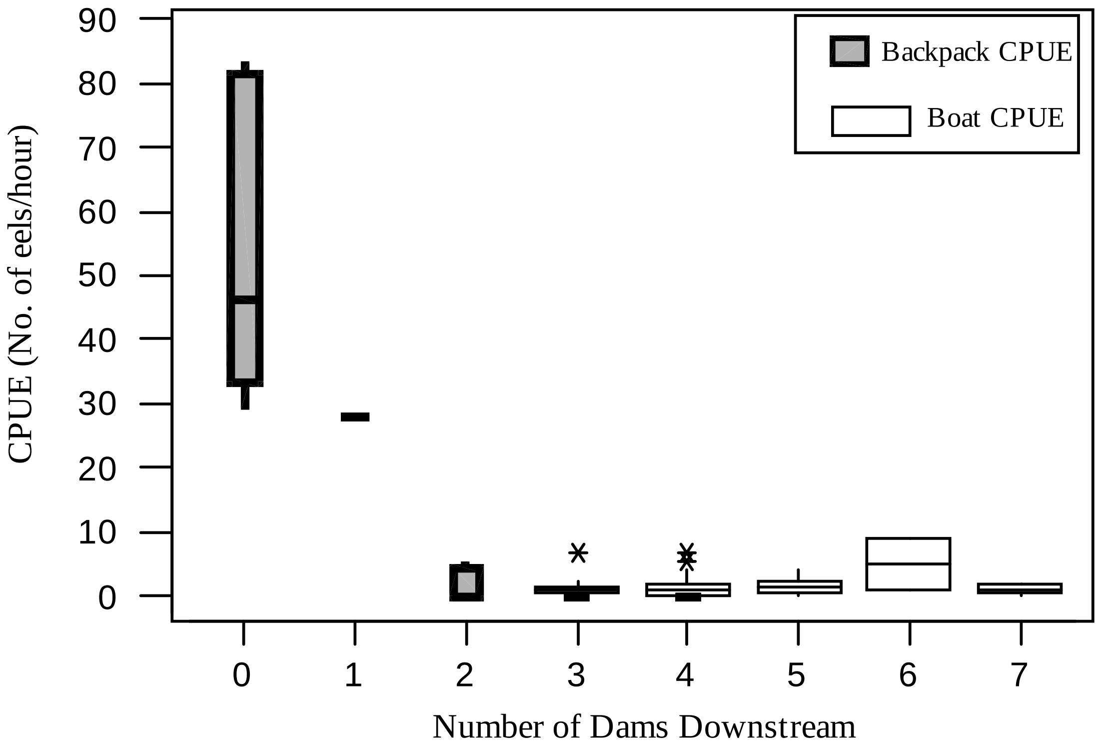

Figure 2-3. Combined boat and backpack electrofishing catch per unit effort (CPUE; number of eels/hour) plotted by dam. Potomac tributary sites are dams 0 to 2, Shenandoah drainage sites are dams 3 to 7. Boxes represent interquartile range (25^{th} to 75^{th} percentile) of data, middle horizontal lines represent the median, whiskers represent data within 1.5 units of the upper or lower interquartile range, and asterisks represent outliers.

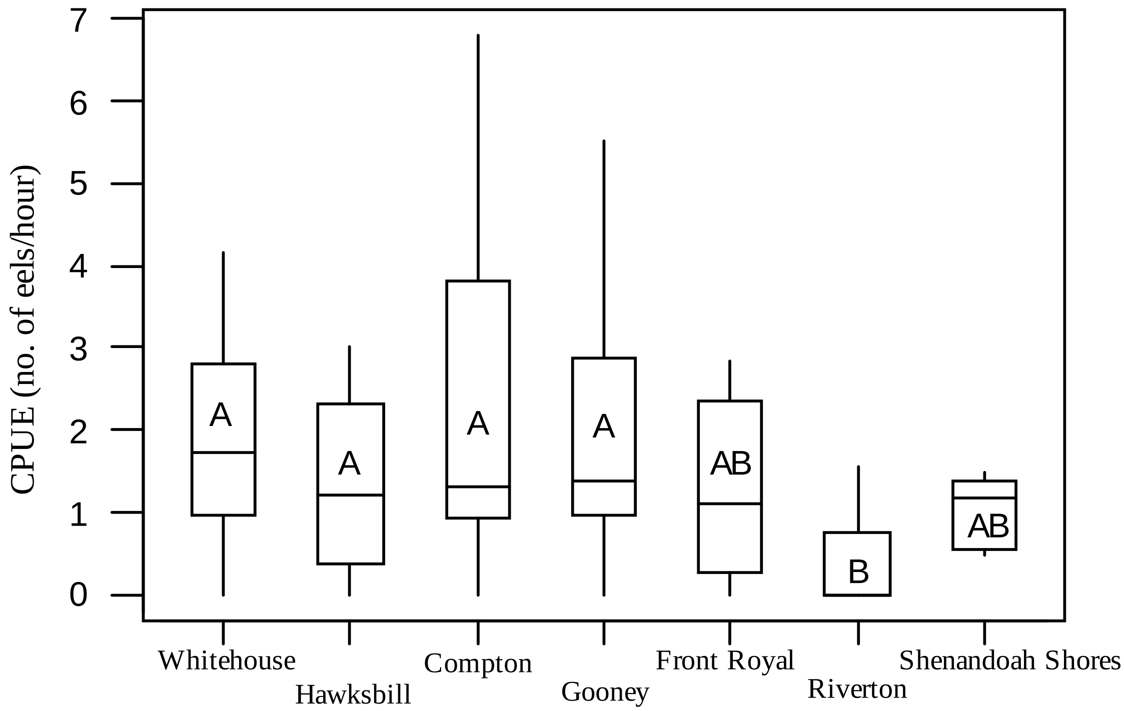

Fig. 2-4. Boat electrofishing catch per unit effort (CPUE; number of eels/hour) plotted by mark-recapture site. Boxes represent interquartile range (25th to 75th percentile) of data, middle horizontal lines represent the median, and whiskers represent data within 1.5 units of the upper or lower interquartile range. Different letter (A, B) indicates different median (Mann-Whitney, pairwise comparison alpha (α) = 0.0026).

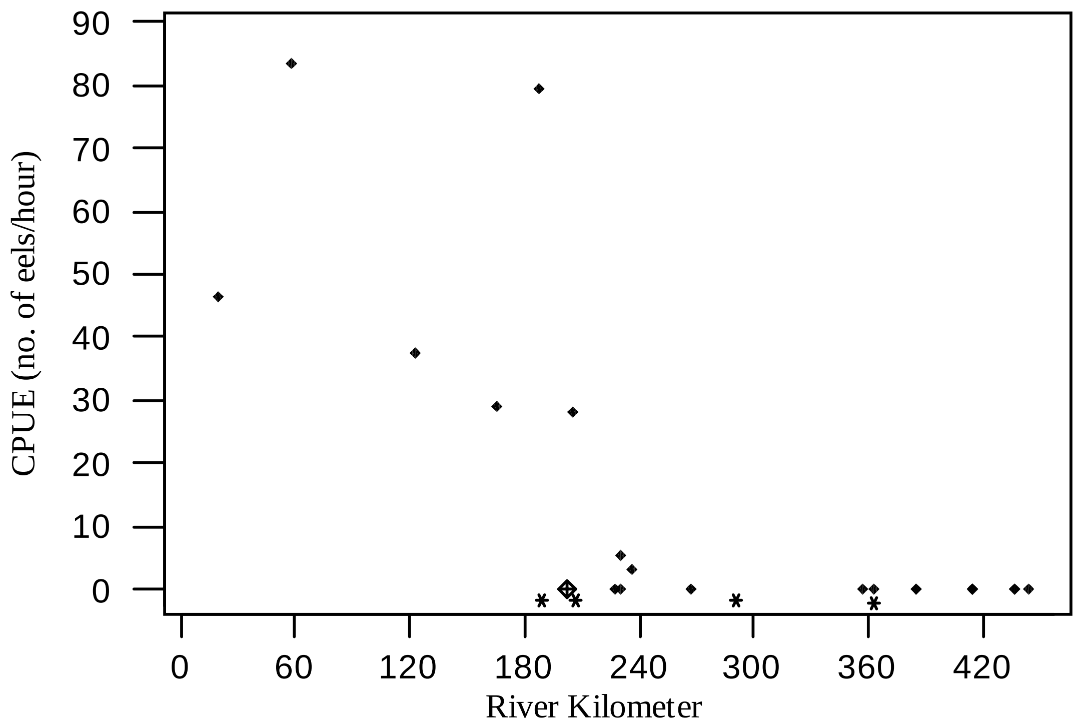

Fig. 2-5. Individual site catch per unit effort (CPUE; number/hour) of eels plotted by river kilometer for backpack electrofishing in lower Potomac River tributary sites and the South Fork Shenandoah and Shenandoah rivers, Virginia. Asterisks represent hydropower dam locations on the Potomac and Shenandoah rivers. The crossed diamond represents Great Falls.

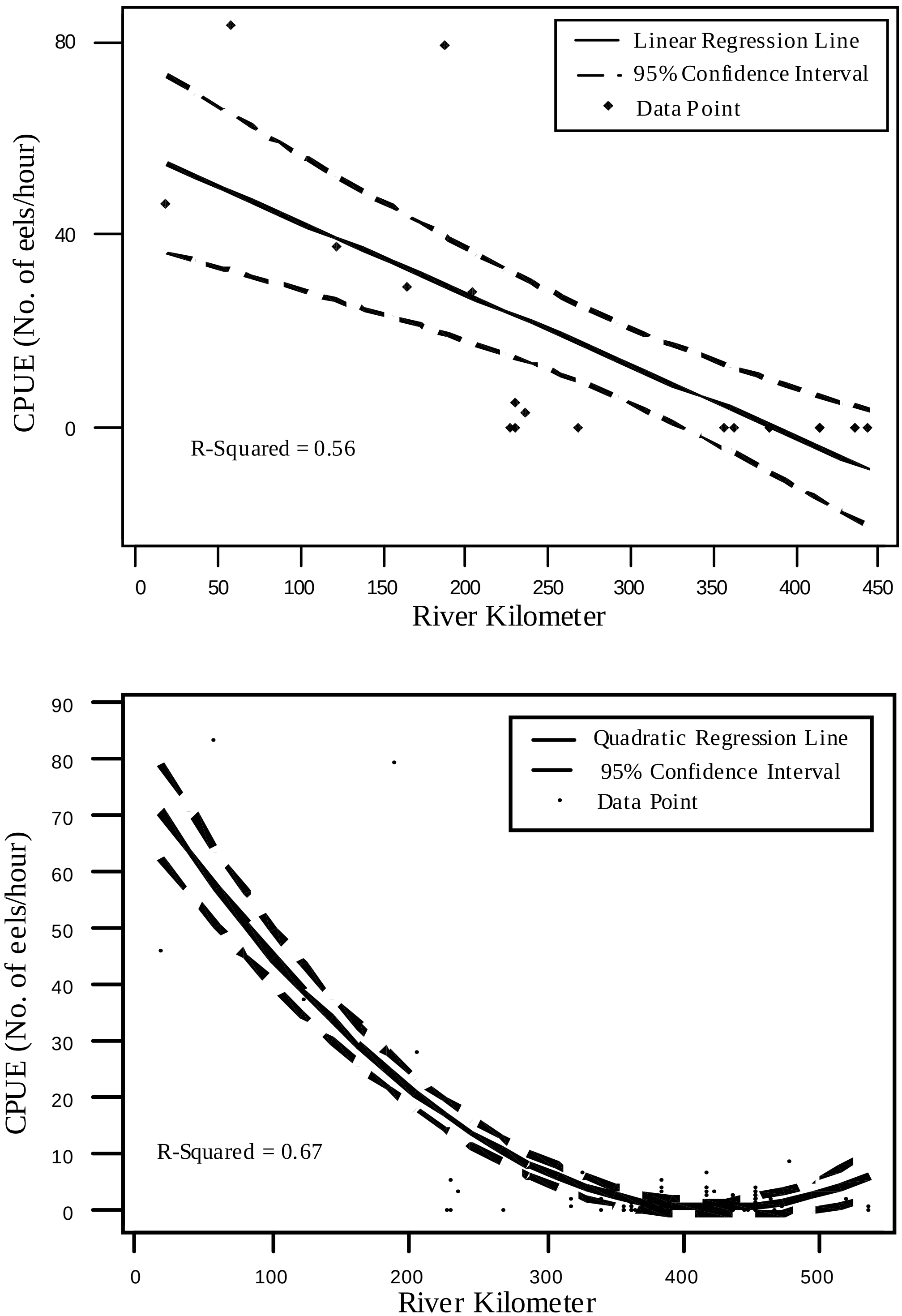

Fig. 2-6. Linear regression analysis ($y = 57.4 - 0.148x$, d.f. = 21, RMSE = 305.4) of backpack electrofishing (top) and quadratic regression analysis ($y = 77.55 - 0.37x + 4.35E\text{-}04x^2$, d.f. = 137, RMSE = 42.34) of backpack and boat electrofishing (bottom) catch per unit effort (CPUE; number/hour) of eels by river kilometer in lower Potomac River tributary sites and the South Fork Shenandoah and Shenandoah rivers, Virginia. Solid lines indicate regression model; dashed lines show 95% confidence interval.

Chapter III. AMERICAN EEL MOVEMENT AND GROWTH IN THE SHENANDOAH RIVER DRAINAGE, VIRGINIA.

INTRODUCTION

Most studies of American eel movement have focused on the inland migration of small/young eels (<300 mm total length/<6 years old) in coastal areas; little is known about non-migratory movement, particularly of larger/older eels further inland. An understanding of the rates of eel migration into inland areas and the patterns of movement once there can aid in the comprehension of their biology, providing insight into habitat use and the life history variability within the species. This behavioral knowledge can also lead to sound management of these potentially distinct demographic portions of subpopulations (see Chapter I). Proper design of eel passage around dams should consider the range of sizes that need to be passed and how often individual eels might encounter dams during both migratory movement and during long-distance or continual non-migratory movements. If inland eels demonstrate long-distance or continual movements during their juvenile stage, efforts to maintain habitat continuity and accessibility must be sought for their sound management.

Non-migratory movements of American eels have been studied in tidal areas (Helfman et al. 1983; Bozeman et al. 1985; Ford and Mercer 1986; Dutil et al. 1988) as well as some freshwater habitats (Gunning and Shoop 1962; LaBar and Facey 1983; Oliveira 1997) and the extent of movement is highly variable. Estimates of non-migratory movement based on telemetry (Helfman et al. 1983) and mark-recapture studies (Bozeman et al. 1985) in tidal creeks in the southeastern U.S. ranged from 0 m to 850 m over 6-d periods. A one-year study in small Louisiana streams found movements under 200 m (Gunning and Shoop 1962). LaBar and Facey (1983) reported movements of from 0.6 to 4.9 km and evidence for home ranges of from 2.4 to 65.4 ha in their two-month telemetry study in Lake Champlain, Vermont. By contrast, estimates of home range in a salt marsh in Massachusetts were approximately 0.02 ha based on a one-month mark-recapture study (Ford and Mercer 1986).

Some information indicates that eels exhibit seasonal as well as migratory and home range movements (Medcof 1969). Eels from estuaries in Canada move up to approximately 5 km into freshwater lakes in the fall then back to the estuaries in the spring (Medcof 1969). Whether such seasonal movement occurs within a river drainage (e.g., between tributaries and main channels) is unknown. Information on seasonal movements is important for understanding habitat requirements on annual time scales.

Another important biological aspect of the juvenile stage of the eel is their rate of growth. Growth rates in eels have been theorized to decrease with increasing latitude and with increasing distance inland (Helfman et al 1984a; Helfman et al. 1987). Because attaining a larger size appears to be more important for the fitness and reproductive potential of female eels (Helfman et al. 1987), the rate of growth will, in part, determine residence time in inland waters. Insight into growth rates not only can corroborate age information but can also provide an understanding of the cost, in terms of the time, of migrating at a certain size, relative to that seen in other portions of a subpopulation.

Growth by eels in inland areas has not been investigated to a great degree and information on a latitudinal relationship is scant and confounded by sex-dependent variations and inconsistency in estimation methods. The compilation of data from multiple studies over a range of habitats can help ascertain relations between growth rate and upstream distance and latitude on a broad geographic scale, provided that an effort is made to compare results from similar techniques and habitats when possible. The Shenandoah River drainage in northern Virginia has resident eels that provide an opportunity to investigate both movement and growth patterns in inland freshwater habitat.

OBJECTIVE

1. Document the movement of tagged eels over seasonal and annual time scales within the South Fork Shenandoah and Shenandoah rivers and associated tributaries.
2. Estimate rate of growth for eels in the South Fork Shenandoah and Shenandoah rivers based on recaptured eels and length-age regression analysis.

METHODS

Sampling and Site Selection

Temporal and spatial movements of eels in the SFSR were investigated with a mark-recapture procedure from August 1996 through August 1998. Eels used for this study were captured using the same boat electrofishing methods as described in Chapter II (Methods) for the mark-recapture study. Sites were characterized by slow-flowing wide pools or runs bordered both upstream and downstream by riffle/chute sections not easily negotiated by electrofishing boat. Mark-recapture sites were 1.2 – 2.5 rkm long and 50 - 125 m wide and were sampled 6 to 18 times between 1996 and 1998. Eels captured in the mark-recapture sites were used to analyze movement, as were eels sampled in approximately 15 other sites throughout the drainage. Samples outside mark-recapture sites were an attempt to distribute effort throughout the Shenandoah drainage but also depended on access to the river by electrofishing boat (typically VDGIF launch sites).

To acquire information on movement, sampling focused on the mark-recapture sites during the 1996 and 1997 seasons. This effort was shifted in the 1998 season to a more extensive sampling regime due to low recapture rates in prior seasons. Sites adjacent to the mark-recapture sites as well as other sites throughout the SFSR and SR were sampled in an effort to both recapture moving fish and to mark a broader segment of the stock. Eels were also marked by VDGIF personnel during sampling for other projects in the drainage.

All captured eels were given both PIT and elastomer tags, as described in Chapter II (Methods). Eels caught after the first marking trip in 1996 were inspected visually for elastomer marks and scanned for the presence of a PIT tag. Both forms of inspection were carried out to ensure that neither type of tag was lost.

Some studies have shown that eels move seasonally into larger water bodies to overwinter (Medcof 1969). Three tributaries to the SFSR and one to the SR were sampled with backpack electrofishing in an effort to quantify movement between the main river and these smaller streams. The confluences of all three SFSR tributaries were within mark-recapture sites, increasing the likelihood of capturing marked eels moving from one habitat to the other.

Movement Estimation

Capture and tagging records were used to determine encounter points for individual eels for movement analysis. Location was recorded only by mark-recapture site in 1996 and early 1997. During the 1997 sampling season efforts were made to record the specific location of captured eels within the sample site. This increased resolution was necessary to monitor movement on smaller spatial scales (within sample site) for fish recaptured in the same site in which they were released.

Movement was measured using linear distance between capture locations plotted on United States Geological Survey topographic maps (1:24000 scale); movements were classified as upstream, downstream, round-trip, or none. This designation was determined by the distance and direction moved relative to the initial capture point. Lateral or directional moves less than or equal to the width of the river were termed 'none' while longer directional moves were either upstream or downstream. Round-trip moves included at least two individual moves, with an ultimate return to the approximate area of initial capture.

The area of activity for eels that moved was estimated using the longitudinal movement (downstream or upstream) multiplied by the average river width in that reach (Bozeman et al. 1985; Ford and Mercer 1986). This method assumes that the entire river channel is within the range of movements demarcated by capture locations; this is plausible given the lateral movement recorded for many of the eels that showed no directional movement. Numerous eels were also seen during electrofishing as they fled the electric field by moving across the channel. They were often followed and subsequently captured on the opposite shore.

Growth Estimation

Growth was estimated using total length measurements from recaptures as well as length-age regression models. Regression models were derived from eel age and length data from the Shenandoah River drainage (see Chapter I). Helfman et al. (1984) cautioned against the strict use of length-age data in defining eel growth because of the high variability often found in length at a given age. Information from recaptured eels can help to validate or refute estimates of growth derived from length-age regression models by providing actual data on growth over a given period of time between marking and recapture.

A number of authors have reported a growing season encompassing the spring to fall months for eels in their study areas (Harrell and Loyacano 1980; Helfman et al. 1984b; Oliveira 1997). Walsh et al. (1983) found that eels in a laboratory setting became torpid below 10^{o} C. Oliveira (1997) used this information on temperature regime and metabolic rate to define a 214-d growing season in his Rhode Island study site, from April through October. Helfman et al. (1984) used similar methods in defining a 'fast growth' period from March through October in Georgia creeks.

Using temperature data taken while electrofishing, a period from March through October (245 d) was used in the present study as the growing season for eels in the SFSR and SR based on the approximate 10^{o} C cutoff. Annual growth was calculated using a modification of the equation in Oliveira (1997),

Annual Growth = 245(change in length (mm)/ time at liberty (d)),

where time at liberty is the number of days between captures within the 245-d growing season. Growth was also analyzed using a standard 365-d growing season for comparison with other published studies using similar methods. Both season lengths (245 d and 365 d) were analyzed after removing length data from eels recaptured within 30 d of initial marking and not subsequently recaptured. Oliveira (1997) and Helfman et al. (1984) discarded data from eels caught within 30 d and 20 d, respectively, because of lack of growth and to guard against measurement error.

Statistical Analysis

Eel movement type (upstream, downstream, round-trip, or none) was analyzed for differences attributable to total length and time between captures using parametric (one-way ANOVA) and non-parametric (Kruskal-Wallis) methods depending on the result of Kolmogorov-Smirnov normality testing; alpha for all tests was set at the 0.05 level. Multiple pairwise comparisons were made using the non-parametric Mann-Whitney test. Growth rates obtained using various season lengths were compared using two-sample t-tests with alpha = 0.05.

RESULTS

Movement

A total of 279 eels were marked throughout the study, 195 of which were captured in the mark-recapture sites. Thirty-one eels (11.1%) were recaptured; eight were recaptured two or more times, resulting in 43 total recaptures. Forty-two of the 43 recaptures (97.7%) occurred within the same site where that eel was originally marked. One eel was recaptured in an adjacent site directly downstream of the pool in which it was marked. This eel made the longest single direction movement (1.5 km) recorded.

Movements were analyzed for 21 of the 31 recaptured eels; ten recaptures could not be analyzed for movement because of a lack of data on precise capture location. The majority (57%) of these analyzed recaptures indicated very little movement (< 100 m) upstream or downstream but often involved lateral movement. Upstream movements occurred in 19% of the recaptures, downstream movements in 14%, and 10% made round-trip movements (Table 3-1). One eel that made a round-trip movement first moved upstream, then downstream, then upstream again (within approximately 50 m of the original capture site). The other round trip-eel was caught several times on various sides of an island in the river channel. Area of activity ranged from 1.88 ha to 11.25 ha (mean = 6.15 ha, median = 5.25 ha, standard deviation = 2.69 ha).

Total length of eels analyzed for movement ranged from 470 to 906 mm and showed no significant difference by movement type (upstream, downstream, round-trip, and none; one-way ANOVA, P = 0.499; Fig. 3-1).

Four tributary sites were sampled a total of nine times (416 minutes total) without capturing eels. One site on the SFSR (Luray Dam) and one on the SR (Warren Dam) were also sampled with a backpack electrofisher below the dams during low water periods (75 minutes total). This was an effort to capture eels at the base of the dams attempting to move upstream. No eels were caught or seen during the backpack electrofishing.

The elapsed time between marking, recapture, and successive recaptures ranged from 6 to 405 d (mean = 90 d, median = 44 d, standard deviation = 103 d) and did not differ between mark-recapture sites (Kruskal-Wallis, P = 0.33). Time between sampling at mark-recapture sites ranged from 4 to 318 d (mean = 42 d, median = 21 d, standard deviation = 66 d), roughly half the time interval between recaptures.

Total time between marking and final recapture ranged from 6 to 411 d (mean = 125 d, median = 67 d, standard deviation = 129 d). Total time between marking and final recapture analyzed by movement type was different between types (Kruskal-Wallis, $P = 0.03$); round-trip moves ($n = 2$) had a median of 350.5 d, downstream moves ($n = 3$) a median of 108.0 d, and upstream moves ($n = 4$) and no move ($n = 12$) had medians of 34.5 d and 45.0 d, respectively. None of these movement types were found to be different from any other using pairwise comparison techniques (Mann-Whitney, $P > 0.05$, Fig. 3-2). Discrepancy between the Kruskal-Wallis and Mann-Whitney tests appears related to small sample sizes. Although round-trips tended to have longer times between marking and final recapture, this was expected due to the multiple recaptures needed to define this type of movement. When round-trips were divided into their upstream and downstream components and reanalyzed, no differences were found either among all three movement types (none, upstream, downstream; Kruskal-Wallis, $P > 0.05$) or between pairs of types (Mann-Whitney, $P > 0.05$).

Growth

The linear model of eel length versus age from the Shenandoah River drainage (Chapter I),

$$\text{Total Length} = 37.7\text{Age} + 322,$$

accounted for 67.7% of the variation in length for ages 6 to 19 (d.f. = 65, RMSE = 7058). Annual growth, following this model, is approximately 38 mm per year averaged over these ages and all sampling locations. This model omits Potomac River tributary length and age data to isolate growth patterns more characteristic of the longer, older, predominantly female eels in the Shenandoah River drainage (Chapter I Results). Other authors have noted apparent changes in eel growth rate with variation in sex ratio, total length, and salinity levels (Gray and Andrews 1971; Helfman et al. 1984b; Oliveira 1997).

Thirty-one eels were recaptured, seven of which were not used because they were recaptured less than 30 d after their initial marking. Growth estimates were based on the remaining 24 recaptured eels, which ranged in length from 436 to 908 mm (mean = 755 mm, median = 795 mm, standard deviation = 123 mm) and were recaptured 32 to 411 d (mean = 158 d, median = 109 d, standard deviation = 130 d) after marking. Daily growth was estimated using the change in length (mm) divided by the number of days between marking and subsequent recapture. A linear regression indicated that total length explained 2.4% of variation in daily growth (P = 0.47; Fig 3-3.) and that growth rate was not size dependent. Linear regressions of distance upstream (rkm) and movement distance (m) explained 0.4 and 1.4% of variation in daily growth, respectively (P = 0.77 and 0.66, respectively); all 24 eels remained pooled for growth analysis.

The 245-d growing season resulted in mean growth estimates of 0.28 mm/d (median = 0.25 mm/d, standard deviation = 0.22 mm/d) and 69.7 mm/year (95% CI = +/- 23.2 mm, median = 62.4 mm/year, standard deviation = 54.9 mm/year). A 365-d season resulted in estimates of 0.26 mm/d (median = 0.22 mm/d, standard deviation = 0.23 mm/d) and 95.7 mm/year (95% CI = +/- 34.9 mm, median = 78.5 mm/year, standard deviation = 82.5 mm/year). Neither daily nor annual estimates were different between different season length (t-test, P = 0.73 and 0.21, respectively).

Five eels were recaptured after approximately one year (322 to 411 d) and were analyzed for direct information on annual growth. Annual growth (AG) for these fish was calculated by the formula

$$AG = (365/d)g,$$

where d was the number of days between captures and g was the growth in mm between captures. Mean annual increase in length for this group was 43.2 mm (95% CI = +/- 29.7 mm, range 18.6 to 74.7 mm/year).

DISCUSSION

Movement

Eel recapture rates in the SFSR were low and sporadic, making definitive statements on movement difficult. Although up to 24% of the eels marked in a given site were recaptured over two years, the average for all mark-recapture sites was 15.9%, and the average for all eels marked in the study was 11.1%. While information from these recaptures can be used to infer some types of movement within this system, the majority of marked eels were never caught again leaving both their spatial and temporal movements a mystery. Emigration probably contributed to low recapture rates. Five eels (2.6%) in the mark-recapture sites displayed characteristics of mature (silver) eels. These fish were not recaptured and represent a minimum estimate of marked eels that may have migrated out of the drainage to spawn during the study.

Higher recapture rates at some sites, while not statistically different, suggest that some pools support local eel concentrations or that certain habitat qualities facilitate more efficient sampling. Deep water and turbidity made sampling large portions of some sites difficult. Pools with relatively high recapture rates had less extensive deep areas and often contained habitat such as leaf packs, root wads, and woody debris associated with current that were accessible to electrofishing. However, eels were captured in virtually all habitat types at some point during the study.

Variable recapture rates are common among studies of American eels. Helfman et al. (1984b) recaptured 15% of their marked eels in a Georgia tidal creek over a two-year study, although a recapture rate of 41% in the same system was reported during a later study over a 6-d period (Bozeman et al. 1985). Oliveira (1997) recaptured 24% of the eels released in a small coastal Rhode Island stream over a two-year study, similar to a Massachusetts tidal stream with a recapture rate of almost 28% over five weeks (Ford and Mercer 1986). Coastal studies are often conducted in relatively small estuaries and streams, thereby providing a more constrained area in which to carry out mark-recapture studies. Studies of eels further inland have resulted in lower recapture rates. LaBar and Facey (1983) found 8.6% of 369 eels released over a four-month period in Lake Champlain, Vermont and Hurley (1972) had recapture rates of <9% over approximately four years in a Lake Ontario mark-recapture study.

Distances of directional movements in this study are similar to what is known for immature eels in other areas. Gunning and Shoop (1962) saw movements over one year in inland Louisiana streams between 0 and 150 m. Eels in a Massachusetts salt marsh moved <100 m in one month; the modal movement was <20 m (Ford and Mercer 1986). The extent of movement in some tidally influenced areas was similar to these freshwater studies (Dutil et al. 1988).

Other studies have demonstrated more significant movement by immature eels. A telemetry study in a Maine tidal estuary showed movements averaging 6.7 km in less than 80 hours (Parker 1995). Radio-tracked eels in Lake Champlain, Vermont moved 0.6 to 4.9 km in 20 to 67 d (LaBar and Facey 1983). These moves are not particularly surprising given the highly migratory life history of this species.

Mark-recapture studies often focus on spatial scales that limit the ability to recapture eels that have moved long distances. Because the design of many mark-recapture studies has been biased against detection of long-distance movement, they may be inadequate to describe eel movement. My study was also biased against detecting movements of eels outside the study sites.

Radio-telemetry (e.g., LaBar and Facey 1983; Parker 1995) allows eels to be followed over a greater area, hindered only by transmitter battery life and the ability of the researcher to follow eels while tracking. Telemetry studies can provide a more accurate picture of short-term eel movement through almost continuous monitoring. This information must be used with caution however because of the limited sample sizes and the stress incurred by the tagging process, including undergoing anesthesia, the surgery to implant internal or attach external tags, and the presence of the tag itself inside or outside the eel's body. Periods of exaggerated movement apparently associated with tagging have been noted in some studies (Helfman et al. 1983; LaBar and Facey 1983).

Because the majority of marked eels are never recaptured, extensive and/or continuous movements cannot be discounted, but some individuals do establish a home 'area' for at least some portion of their life cycle. Multiple recaptures (up to 5 times in the present study) demonstrate stationary individuals and the ability of electrofishing to successfully locate eels in sampled areas. Given the longevity of the American eel in inland waters, this localized presence, even if for a few years, represents only a portion of an otherwise unknown inland movement pattern.

Gowan et al. (1994) cautioned against the design of most mark-recapture studies because the conclusions drawn are typically based on the small number of recaptures rather than the potentially more mobile individuals not recaptured. This concept is relevant in the present study when attempts to describe movement are based on 21 eels, roughly 11% of the eels caught in mark-recapture sites. These eels show a modal movement of <100 m, with all moves <2 km. However, the majority of eels were not captured again, raising questions as to the movement patterns of the missing marked eels.

If the typical movement in the Shenandoah drainage consists of long or continual movement, then the effect of impedance is compounded. The ability of inland eels to move freely would be more affected by dams or other barriers if movements are long and/or frequent throughout their residency.

Low recapture numbers in the Shenandoah drainage also raise questions about the ability of the methods used to effectively sample eels. Because of the large size of the SFSR and SR and the limited sampling field produced by the electrofishing boat, the lack of recaptures may reflect the inability to sample thoroughly. Without sampling all habitats, deep pools in particular, inferences about movement by eels not recaptured remain speculative. Unfortunately, other sampling methods are probably even less effective for capturing eels than electrofishing.

Growth

Depending on the method used (tag-return analysis or length-age regression model) growth of eels in the Shenandoah River drainage was estimated to be between 38 and 96 mm per year. The growth of five eels recaptured after approximately one year provide the most accurate information on annual length increases (43 mm/year) because their direct measurement does not rely on an estimated growing season or regression model (Fig. 3-3). The variation in growth estimates illustrates the difficulty in using different methods for comparison. My regression model, based on eel TL and age in the Shenandoah drainage, resulted in an estimation of growth similar to the actual growth measured in the five tag-returned eels.

Seasonal growth estimates resulting from tag-returns may also be fraught with inaccurate assumptions of growth periods. The growing season used in the present study assumed constant growth for all 214 d and did not allow for variation in growth within the season or growth during the non-growing season. If the determination of growing season length is inaccurate, this will also affect the accuracy of estimates. Estimates of growth for the SFSR and SR can not be extrapolated to other portions of the drainage due to the likelihood of differential growth rates dependent on sex (Oliveira 1997).

Comparison of the present data with growth estimates in published studies is difficult due to methodological differences. However, data from the SFSR and SR displayed many similarities to other published findings. Eels in a brackish creek in

Georgia were analyzed using both tag-return data with a March - October growing season and length-age regression, resulting in growth estimates of 57 and 44 mm/year, respectively (Helfman et al. 1984b). Analogous growth rates in the present study were 70 and 38 mm/year, respectively. Tag-return information from a Rhode Island stream indicated an overall growth rate of 30 mm/year based on a 214-d growing season. However, eels greater than 400 mm TL grew approximately 62 mm/year (Oliveira 1997), 11% less than the estimate from the Shenandoah River drainage using a 245-d season.

Data from inland freshwater studies are scarce. A length-age regression model explaining 27% of the variation in data from Lake Champlain estimated growth to be 18.8 mm/year, 50% of that found in the Shenandoah River drainage (Facey and LaBar 1981). Hurley (1972) reported a growth rate of 54.9 mm/year for eels aged 4 to 14 in Lake Ontario based on length-age regression modeling, 45% greater than that observed using similar methods in the Shenandoah River drainage.

Growth rates calculated from all methods are highly variable. Comparing the results of similar growth estimation methods appears to be most instructive. Direct measure of changes in total length from eels recaptured after approximately one year seem to intuitively provide the most accurate data on annual growth because their growth accounts for any seasonal variations. Investigations in Louisiana, Georgia, Virginia (present study), and Lake Ontario, Canada estimated growth to be 232, 62, 43, and 34 mm/year, respectively, and show an apparent decline in growth rate with increased latitude, based on information from eels recaptured between 6 months and 4 years (Gunning and Shoop 1962; Hurley 1972; Helfman et al. 1984b). However, sample sizes were small for all of these studies, ranging from 2 to 13, making definitive statements on growth rates untenable.

Theorized changes in growth rate with latitude are difficult to investigate given the varying methodological techniques used to estimate growth. Tag-return data are subject to low recapture rates and small sample sizes, making definitive conclusions and comparison between studies difficult. Linking estimates of growth to specific latitude, habitat, and demographic composition might increase the clarity of data interpretations across studies. The difficulty of isolating effects of these individual variables makes comparisons between existing published studies useful at only the grossest level.

Conclusions

Movement estimates based on recaptured eels in the Shenandoah River drainage were low, with a modal value of <100m, similar to results from other American eel studies. A number of recaptured eels were caught three or more times, indicating a degree of permanence for some eels during portions of their juvenile period. However, movement estimates in this and most other mark-recapture studies of eels are based on low recapture rates and may be biased against detecting longer movements. The potential for long-distance or even continual movements by a portion of the subpopulation cannot be ruled out because of the inability to thoroughly sample all habitats and the inability to detect movements outside sampling sites. I found no other published data on the movement of eels in a large riverine habitat at an inland distance similar to the Shenandoah River drainage.

Radio-tracking studies may be better suited for detecting long-distance movements in habitats such as the SFSR and SR, while mark-recapture techniques may be more efficient in smaller streams that can be sampled thoroughly. A study by Oliveira (1997) in a small Rhode Island stream involved block-netting and multiple-pass electrofishing for a higher probability of capturing eels at ten sites, but recapture rates were only 24% over the approximately two-year study, suggesting movement out of the sampling sites and perhaps out of the study reach. In general, higher proportions of eel recaptures have been associated with shorter-duration studies, supporting this notion of potentially high mobility among inland eels. The use of directional weirs might facilitate understanding patterns in movement as well as detecting movement on a larger scale out of study reaches. Because long-distance non-migratory movements cannot be discounted, obstructions may impact fish movement throughout their life and not just during migratory periods.

Tagged eels recaptured after approximately one year showed an average growth of 43 mm/year, although growth rates for all eels ranged from 38 to 96 mm/year, depending on the method used. These data, when compared with similar data from other studies, support the hypothesis of decreasing growth with increasing latitude. Slower growth in more northerly portions of the eel population may help explain trends in increased age in these areas. Some researchers suggest that there may be minimum sizes that eels must attain, depending on sex and distance from spawning grounds, in order to migrate and spawn successfully (Helfman et al. 1987; Krueger and Oliveira 1997). If this it true, eels with slower growth rates would need to remain in coastal or inland habitats for a longer period of time until such a size is attained. Longer inland residence times translate into an increased susceptibility to harvest or other sources of mortality. Management efforts should reflect the long-term exposure to harvest that inland eels face so that the ability of these fecund females to successfully spawn is not unduly affected by human activities including angling and mortality due to passing through hydropower turbines.

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Table 3-1. Individual movement direction and distance of recaptured eels from mark-recapture sites in the Shenandoah River drainage, Virginia. Asterisk (*) indicates eel recaptured outside of pool in which it was originally marked. Number of recaptures (Recaps) and total length are also given for each eel.

Site	Direction	No. Recaps	Movement (m)	Total Length (mm)
Whitehouse	Upstream	1	700	890
Whitehouse	Round-trip	5	500	790
Whitehouse	Round-trip	3	1800	803
Whitehouse	Downstream	1	700	645
Whitehouse*	Downstream	1	1500	866
Whitehouse	None	1	< 100	873
Whitehouse	None	2	< 100	603
Hawksbill	None	2	< 100	850
Hawksbill	None	1	< 100	555
Hawksbill	None	1	< 100	726
Compton	Downstream	1	700	436
Compton	None	1	< 100	800
Compton	None	1	< 100	830
Compton	None	2	< 100	594
Gooney	None	1	< 100	659
Gooney	None	1	< 100	723
Gooney	None	1	< 100	839
Gooney	None	1	< 100	854
Gooney	Upstream	1	1000	832
Riverton	Upstream	1	500	545
Shenandoah Shores	Upstream	1	500	855

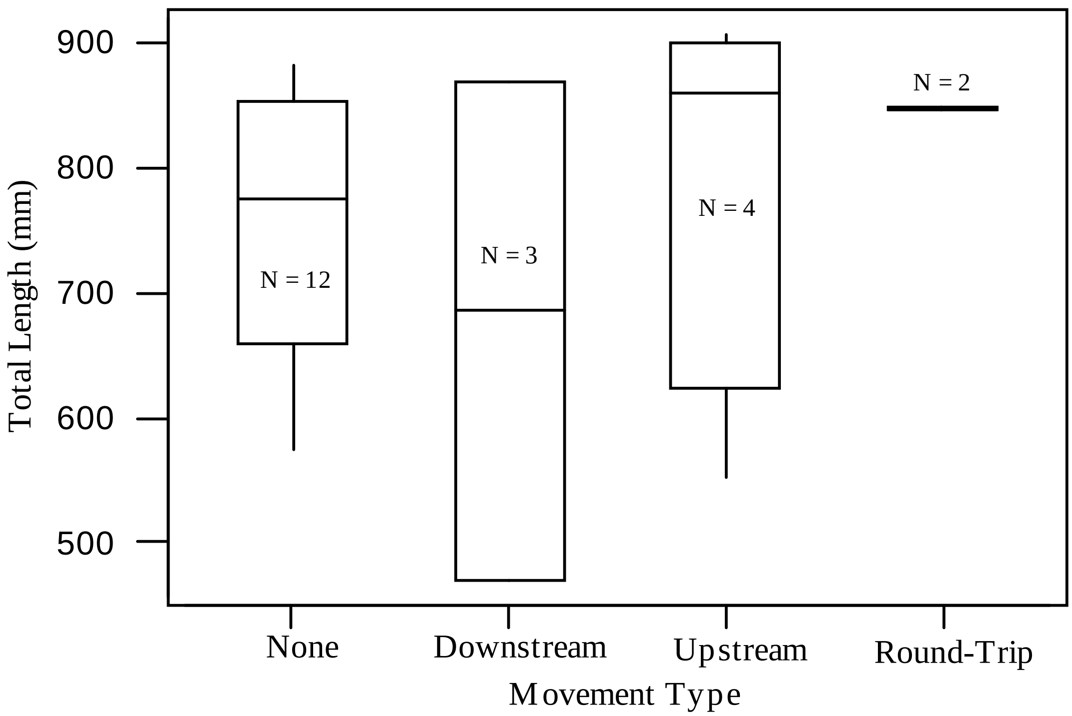

Fig. 3-1. Boxplots of eel total length grouped by movement type (none, downstream, upstream, round-trip). Mean total length was similar among movement type (ANOVA, P = 0.499). Box circumscribe interquartile ranges (25th to 75th percentile), middle horizontal line is the median, whiskers represent data within +/- 1.5 multiplied by the upper or lower interquartile range, respectively.

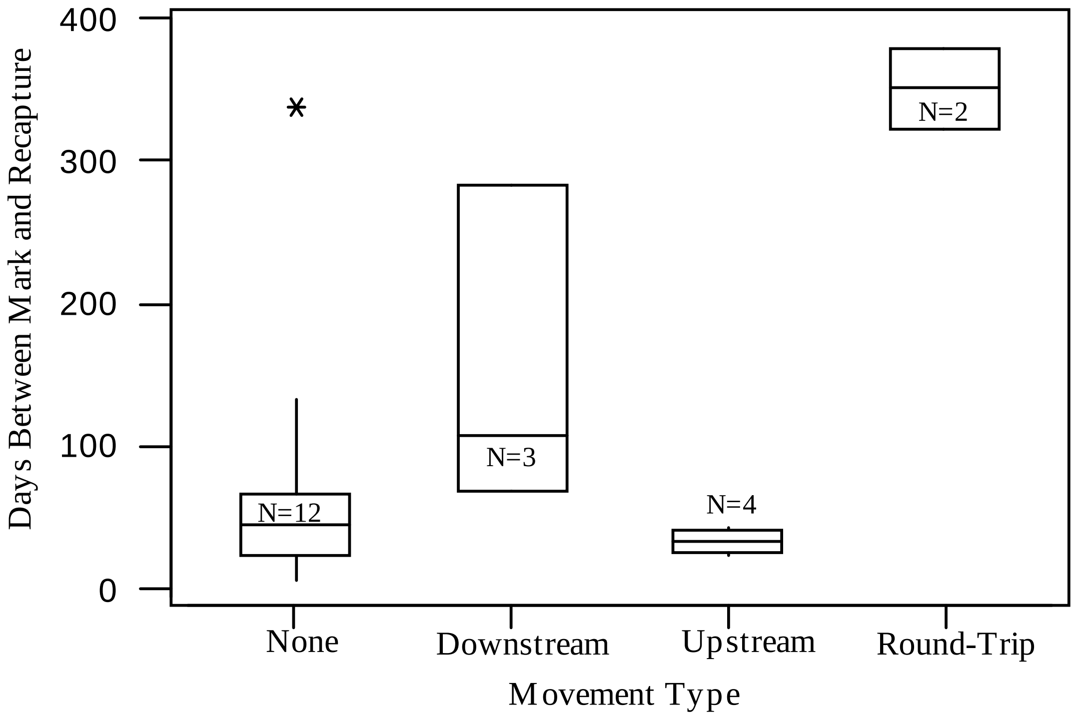

Fig. 3-2. Boxplots of total days between marking and recapturing eels grouped by movement type (none, downstream, upstream, round-trip). Medians were similar between movement type (Mann-Whitney pairwise comparison, $P > 0.05$). Boxplot format is the same as in Fig. 3-1. Asterisk represents an outlier.

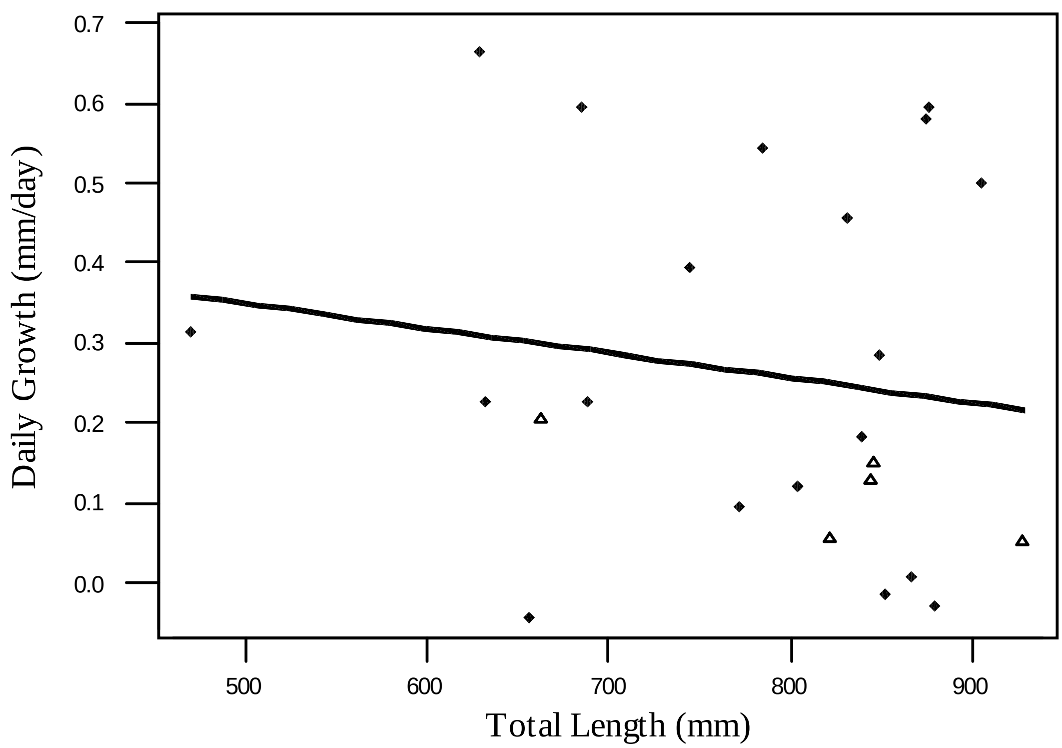

Fig. 3-3. Linear regression fit of eel growth (mm/day) on total length (TL). Length explains 2.4% of the variation in growth and is not significant (P = 0.47). Triangles represent daily growth of eels recaptured after approximately one year.

CONCLUSION

The American eel is a highly migratory species occurring in diverse habitats over a broad geographic range. Because demographic characteristics and densities vary throughout its range it is necessary to understand broad patterns in these characteristics so that management can be tailored to regional differences. The design of studies should take into account the potential mobility of this fish and sample at appropriate temporal and spatial scales.

This study provides data from distances over 500 rkm inland, apparently the most intensive inland data of its kind in the southern portion of the eel's range. Eels in the Shenandoah River drainage were, on average, larger, older females, relative to those found in more coastal portions of the drainage. Coastal characteristics were represented by samples from tributaries to the lower Potomac River and are more typical of the demographics found in other coastal studies throughout their range. Potomac River tributaries are typified, on average, by smaller, younger eels and varying sex ratios.

The harvest of eels is often focused on the migratory stages, either immigrating young eels (glass eels and elvers) or emigrating adults (silver eels). Because of this, the fishing effort that is focused on bays, estuaries, and the lower portions of rivers has the potential to impact portions of the subpopulation moving into or out of the entire drainage. Management based on the characteristics of coastal or near-coastal eels may not be sound for the protection of inland eels exhibiting very different demographic qualities. Consideration of eel demographics throughout a drainage appears to provide more accurate data on the true range of variation not only present within the drainage, but that should be taken into account when establishing management schemes. Management efforts in areas like the Shenandoah River drainage should reflect the long-term exposure to harvest that inland eels face so that the ability of these fecund females to successfully spawn is not unduly affected by human activities including angling and mortality due to passing through hydropower dams.

Although not confirmed in this study, long distance or continual non-migratory movements by inland eels can not be discounted. Movements detected were small, suggesting that at least some eels are stationary for a portion of their inland life. Low recapture rates in this study may also be the result of sampling inefficiency by electrofishing in this riverine habitat. Because long-distance non-migratory movements cannot be discounted, management plans should consider that obstructions may impact fish movement throughout their life and not just during migratory periods.

Trends in increasing size and age inland were coupled with apparent decreases in densities, as indicated by declines in CPUE between coastal and Shenandoah River drainage sample sites. Although lower in density, the higher fecundity of these inland females, relative to those in coastal habitats, may still contribute significantly to the breeding population. Smogor et al. (1995) found a similar pattern of decreasing densities inland in a statewide study in Virginia, suggesting that large-scale processes (such as dispersal and habitat selection) may structure eel populations. If a pattern such as this is predictable, it may enable management to be focused on areas displaying departures in that pattern due to human impacts such as harvest or damming.

Vita

Kevin Robert Goodwin was born Thanksgiving morning, 1968 in Gettysburg, Pennsylvania. He spent his formative years in New Jersey, graduating from Sparta High School in 1987. During his circuitous journey in search of a B.S. he attended Allegheny College, Morris County Community College, and the University of Massachusetts at Amherst, as well as working for a couple of years. He earned a degree with honors in Wildlife and Fisheries Biology with a minor in Zoology from UMASS in 1994. The next two years were spent working as a technician for the Illinois Natural History Survey at the Kaskaskia and Ridge Lake biological stations. He began graduate work toward a Master of Science degree in the Department of Fisheries and Wildlife Sciences at Virginia Polytechnic Institute and State University in 1996, ultimately earning his degree in July 1999.