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Annual and Seasonal Variability in the Size and Biological Characteristics of the Runs of American Eel Elvers to Two Nova Scotia Rivers

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Abstract.—The recruitment of American eel *Anguilla rostrata* elvers to the East River, Sheet Harbor, Nova Scotia, Canada annually varied from 101,500 to 467,400 during the years 1990–1999, with no temporal trend. In the more southerly and smaller East River, Chester, recruitment annually varied from 432,400 to 1,419,000 elvers between 1996 and 2000. Annual elver counts in each river were highly correlated ($r = 0.998$, $P = 0.002$, $N = 4$), perhaps due to the effects on coastal distribution of elvers of the southwestward flowing Nova Scotia Current. Upstream migration typically occurred between early May and mid-July, beginning about 13 days earlier in the East River, Chester, than in the East River, Sheet Harbor. Two to six, usually three or four, waves or modes of daily abundance occurred over the elver run with an interval between waves of five to eight days, reflecting the tidal cycle and effects of river discharge. Sample sizes of about 1,500 elvers collected systematically throughout the run provided estimates of the seasonal population mean elver length and weight that generally differed little from estimates that were adjusted by the weekly count frequency. Annual mean length, weight, and condition index varied significantly among years and rivers. Annual variability in mean length was small relative to that for weight and condition and possibly of less biological importance. Elver mean length declined during the first six to nine weeks of the run in 13 of 16 annual observations, weight declined in all years, and the residual index of elver condition declined in 15 of 16 cases. The biological meaning should be carefully considered of statistically significant effects with small effect sizes (degree to which an effect exists) and of insignificant effects with moderate or large effect sizes.

Introduction

Large numbers of elvers of the catadromous American eel *Anguilla rostrata* enter the estuaries of eastern North American rivers during late winter and spring (Tesch 1977; Helfman et al. 1987; ASMFC 2000). Most elvers are believed to migrate into and up streams and rivers where they reside until the onset of sexual maturation and their return to the sea to spawn.

Variability in abundance and biological characteristics, whether geographic, annual or seasonal, is typical of diadromous fishes but has been minimally described for the catadromous American eel, particularly the elver phase. Vladykov (1966, 1970) and Haro and Krueger (1988) examined the latitudinal cline of increasing elver mean length along the Atlantic coast of North America and seasonal changes in size and pigmentation. Groom (1975), Hutchison (1981), Dutil et al. (1989), Jessop (1998a, b) and EPRI (1999) document various aspects of the geographic, seasonal, and occasionally annual, trends and/or changes in one or more aspects of elver length, weight, condition, and pigmentation stage. Dutil et al. (1989) also examined annual variability in elver relative abundance while Able and Fahay (1998) reported the seasonal timing and relative abundance of an elver run. Jessop (1997) provided annual estimates of elver run size based on trap catches, Jessop (1998b) examined seasonal timing and relative abundance on a regional basis and Jessop (2000a) estimated run size and seasonal mortality rate. Recent Canadian (Peterson 1997) and American (EPRI 1999) surveys of eel stock status and biology and the U.S. Interstate Fishery Management Plan for American Eel (ASMFC 2000) have noted the limited information available on the elver phase and have recommended additional research to address knowledge gaps so as to assist development of appropriate management decisions.

This study examines the annual variability in run size and timing and seasonal (May–July) mean lengths, weights, and condition indices of the elver runs to the East River, Sheet Harbor, Nova Scotia for the years 1989–1999, and to the East River, Chester, for the years 1996–2000. European eels *A. anguilla* have declined in elver recruitment and mean length since the 1970s (Desaunay and Guerault 1997). A similar relation might be hypothesized for North American elvers given the concern about the status of the eel population (EPRI 1999; ASMFC 2000).

The geographic pattern in elver catch and catch-per-unit-fishing effort (CPUE) by the commercial fishery suggests that the pattern and relative abundance of elvers distributed to different geographic areas may be annually consistent (Jessop 1998b). Thus, it can be hypothesized that annual elver counts in the two East Rivers will vary synchronously in relative abundance. Any synchrony in annual elver abundance between rivers in adjacent geographic areas might be influenced by environmental factors such as the Nova Scotia Current that runs from north-east to south-west along the Atlantic coast of Nova Scotia and is largely driven by the discharge from the St. Lawrence River (Smith 1989; Jessop 1998b). Further, annual river discharge, as modified by monthly mean precipitation during the January–June period when elvers are moving shoreward and into rivers, might have an influence on elver run size (Jellyman and Ryan 1983). Hvidsten (1985) observed a correlation between the annual size of the run of European eel elvers in the Imsa River and the cumulative number of degree-days exceeding 11°C as did Vøllestad and Jonsson (1988) with mean June–July water temperatures. Similar hypotheses were examined by correlation of the annual counts in the East River, Sheet Harbor with annual discharge from the St. Lawrence River, monthly mean precipitation, and seasonal river water temperatures.

Study Area

The East River, Sheet Harbor, (ERSH) is located on the Atlantic coast of Nova Scotia; the East River, Chester, (ERC) is located about 130 km to the southwest. Both rivers have low pH (range 4.7–5.0) and are moderately colored by organic acids (40–130 relative units) (Watt 1986; Farmer et al. 1988; Watt et al. 2000). Water temperatures increase from about 8–10°C in late April to 20–24°C in mid-July in both rivers. The ERSH drains an area of 526 km^2 and mean discharge ranges from about 23.5 m^3/s in May to 8.6 m^3/s in July (Environment Canada 1991). A 3-m high, vertical face, concrete barrier dam is located at the head of tide. The ERC drains 134 km^2 with discharge ranging from 0.5 to 4.8 m^3/s between 28 May and 20 September 1999 (Jessop 2000b). The stream mouth drops about 1.1 m over a distance of 10.6 m (slope 0.11) between the small falls (0.6 m) at the outlet and the high tide mark. Additional details about the ERSH and ERC sites may be found in Jessop (1995, 2000a, c).

Methods

Elvers were collected by Irish-type elver traps (O'Leary 1971) set up just at or upstream of the head of tide (Jessop 1998b, 2000a). In the ERSH, one elver trap was set at each side of the low head dam at the head of tide. In the ERC, two elver traps were set at each side of the river just downstream of the low falls at the river mouth. The elver traps were annually operated between about the beginning of May and mid-July. The objective was to enumerate and obtain representative life history data on a subsample of all elvers migrating upstream in each river as part of an annual elver-index monitoring program. The run was declared over when catches had declined to about 100 elvers per week. Elver trap catches were estimated daily. All elvers were counted in 1989 and 1990. Catches exceeding about 1,000 elvers were estimated with a calibrated 500-mL measuring cup between 1991 and 1993. After 1993, total catch was estimated volumetrically with a calibrated graduate cylinder with a 1 mm^2 mesh bottom for water drainage. Beginning in 1996, the calibration was repeated midway through the run so as to account for the decline in elver length and weight during the run (Jessop 1998a). Catch estimation procedures followed Jessop (2000b, c) with the exception that the total daily elver trap catch for each calibration period (k = 1,2) was estimated as $Y = \Sigma \cancel{S}_i N_i \bar{y}_i + count$ where Y is the total daily trap catch, N_i is the number of aliquots at the ith volume (50, 75, 100 mL), $\bar{y}_k$ is the mean calibration count at that volume, and *count* is the count of individual elvers (Cochran 1977). The daily trap counts for each calibration period were summed to estimate the total trap catch. The variance of the estimated trap catch for each calibration period (C_k) was estimated as

$$S_C^2 = \sum_i \frac{N_i^2 S_i^2}{n_i}$$

where N_i is the number of aliquots at the ith calibration volume, S_i^2 is the variance of the calibration for that volume, and n_i is the number of counts for that volume (Cochran 1977). The standard error and 95% confidence interval for the estimated total trap catch was estimated as in Jessop (2000c).

In four of five years, an analysis of covariance (ANCOVA) of the regressions of calibration count on volume for the ERC data indicated a significant difference ($P < 0.0001$) between the adjusted mean counts for each calibration period. In 1996, there was no significant difference ($P = 0.37$) between calibration counts at 50 mL (the only measurement volume used that year) because the time between calibrations (seven days) was short relative to the three to four weeks in other years.

Dip net fisheries for commercial or aquacultural purposes occurred in each river during the years 1996–1998 (the market collapsed in 1999 and 2000). Daily commercial fisheries catches (kg), reported by logbook for each river, were converted on a weekly basis to numbers of elvers, weekly catches were summed to give the season total commercial catch, and a 95% confidence interval for the total catch was estimated following the procedures in Jessop (2000c).

When commercial fisheries occurred, the total count = fishery count + trap count. Except for 1989, the annual total or run count is believed to be a close underestimate of the true run size. A single trap that was not fully effective was used during 1989, the first year of operation at ERSH, and the run was probably largely underestimated. The low head dam in the ERSH is believed, based on observation, to be an effective barrier to upstream elver movement. In the ERC, the effectiveness as a barrier to elver movement of the low falls at the river mouth was enhanced by active measures at the stream edge to prevent their upstream movement and the accuracy of the run estimates is believed to be high (Jessop 2000~~b~~c). Confidence intervals for the total run (fishery plus trap catch) were estimated in the standard manner after estimating the standard error of the total run as:

$$S_{Tot} = \sqrt{S_F^2 + S_T^2 + 2rS_F S_T}\,,$$

where S_T^2 and S_F^2 are the variances of the fishery and trap catches and the final term adjusts for the covariance (r often about 0.6) between weekly fishery and trap catches.

Samples of elvers were collected systematically throughout the runs in each river but sampling protocols varied over time and between rivers. In the ERSH from 1989 to 1991, nonselective samples of up to 50 elvers per day, as available, were collected five to seven days per week. During 1992, up to 60 elvers per day were collected three days per week every second day, Monday to Friday. From 1993–1996, up to 30 elvers per day were collected three days per week and from 1997 to 1999, up to 30 elvers per day were collected five days per week. For the years 1989–1994, the elver samples were killed in 5% formalin and remained in the formalin for up to two hours before processing for biological data; from 1995 onwards, elvers were killed in 5% formalin and immediately processed. Elvers shrink in length and gain in weight when preserved in formalin (Jessop 1998a, 2001); consequently, the years in which elvers were preserved (1989–1994) were analyzed separately from those in which they were measured fresh (1995–1999). Elver condition was reported only for those years in which elvers were unpreserved. In the ERC, samples of up to 50 elvers per day were collected three days per week and were measured fresh immediately after killing in 4% formalin. Elvers were measured for total length (TL, to 0.1 mm with calipers), weight (to 0.01 g) after blotting dry, and classified as to pigment stage following Jessop (1998a).

Annual discharge (1990–1998) from the St. Lawrence River was obtained from the Ocean Circulation Division, Fisheries and Oceans Canada, Dartmouth, Nova Scotia and monthly mean precipitation (no discharge data are available) for the ERSH at Malay Falls was obtained for 1990–1999 from the Environment Canada Weather Service, Bedford, Nova Scotia. Water temperatures for the ERSH were recorded by thermograph (to 0.1°C) on a one or two hour frequency in 1990, 1992, 1996, and 1997 and in other years were taken daily in mid-morning with a mercury or digital thermometer.

Although the importance of a treatment effect is often evaluated by the degree of statistical significance at a chosen probability level, typically $\alpha = 0.05$, statistical significance does not necessarily imply biological importance (Kirk 1996; Johnson 1999). The potential biological importance of an observed effect can be evaluated by estimates of effect magnitude (degree to which a phenomenon is present or to which the null hypothesis is believed false), including measures of strength of association (e.g., correlation coefficient and coefficient of determination) and effect size (standardized mean difference) (Cohen 1988; Kirk 1996). Effect size can also be conceptually defined as the significance-test statistic divided by the sample size (Tatsuoka 1993). Differences in annual run lengths and weights of an elver run to a river, as estimated from weekly systematic samples, and from those samples adjusted by the weekly count (theoretically more accurate) and among annual means in elver length, weight, and condition were evaluated by measures of effect magnitude. Other statistical relations were also evaluated for effect magnitude. Effect size analyses are uncommon in fisheries studies but Myers (1997) used effect size in the meta-analysis of recruitment variation in fish populations.

Annual population mean lengths and weights for the ERSH were estimated first from weekly sample values then were estimated by adjusting the weekly sample frequency distributions by the weekly counts. The magnitude of the difference between sample-based and count-adjusted means was evaluated by Glass's g' measure of effect size, the standardized mean difference between treatment groups, where $g' = (\bar{Y}_c - \bar{Y}_s)/S_c$ and $\bar{Y}_c$ is the count-adjusted mean value, $\bar{Y}_s$ is the sample-based mean, and S_c is the standard deviation of the count-adjusted mean (Kirk 1996). The effect size of the difference between annual estimates of elver condition was estimated by Hedge's g, where $g = (\bar{Y}_{\max} - \bar{Y}_{\min})/S_{\text{pooled}}$ and the $\bar{Y}$ values are the maximum and minimum condition values to be compared and S_{pooled} is the error mean square from the ANCOVA of the annual weight-length regressions. Cohen (1988) provides guidelines for the interpretation of the magnitude of the experimental effect size g' and g values, where 0.2 is a small effect, 0.5 is a medium effect, and 0.8 is a large effect.

Annual and seasonal variability in mean elver length and weight, for each river and for formalin-preserved and fresh measurement groups, was evaluated by analysis of variance (ANOVA) and the Tukey-Kramer multiple comparison test. The effect magnitude of the differences among annual means in elver length and weight was evaluated by the correlation coefficient (r), which is a measure of the strength of association (Cohen 1988; Kirk 1996). Effect magnitude values for r of 0.1 are defined as small, 0.3 as medium and 0.5 as large (Cohen 1988).

Seasonal variability in weekly mean lengths and weights was examined visually by box and whisker plots and statistically by ANOVA. The magnitude of change in mean weekly length and weight over the period of the run characterized by decline (typically weeks 1 to 7–9, after which growth became evident) was evaluated by the correlation coefficient (r).

Annual and weekly sample length distributions typically showed slight nonnormality (positive skewness, occasional extended tails) as assessed by normal probability plots while weight distributions showed moderate positive skewness. Annual length and weight samples showed significant ($P < 0.01$; statistical significance was set at $\alpha = 0.05$) heterogeneity of variances ($F_{\max}$ test; Sokal and Rohlf 1981), mainly as a consequence of large ($N = 450$-$2{,}821$) sample sizes, and a slight tendency for variances to increase with the mean. Weekly lengths and weights, within a given year, typically had homogeneous variances. Elver lengths and weights were logarithmically (base 10) transformed to meet the assumptions of normality of distribution and homogeneity of variances that underlie linear regression, ANOVA, and ANCOVA. Independence within and among annual sample lengths and weights was assumed. An index of mean elver condition (a measure of weight relative to length, indicative of well-being) was estimated by the mean weights adjusted to a common (the overall mean) length by ANCOVA (Sokal and Rohlf 1981) of annual weight-length regressions (Cone 1989; Springer et al. 1990). Comparisons of mean elver condition among years were evaluated by Tukey-Kramer multiple comparison tests. An index of individual elver condition was estimated by the residuals from the annual weight-length regression and plotted by week to examine the seasonal pattern in the condition of individual elvers (Jakob et al. 1996; Sutton et al. 2000).

The large number and ovoid distribution of elver weight-length data points in each annual data set presents three problems during analysis. At large sample sizes (median $N = 1{,}020$, range 450–2,821 for ERSH; median = 1,374, range 1,181–1,549 for ERC) statistical significance may not imply biological significance because very small effect sizes become statistically significant.

Unequal numbers of observations among the range of observed sizes tends to bias regression parameters (Ricker 1975) and may lead to heterogeneity of variances at each length (Sokal and Rohlf 1981). Consequently, representative annual weight-length regressions for elvers, for comparing seasonal elver condition among years, were based upon random subsamples of up to 60 elvers per 5 mm length interval, e.g., 50.0–54.9 mm, selected from the total sample. Annual weight-length regressions were thus based on sample sizes ranging from 158 to 247 elvers for the ERSH and 246–268 elvers for the ERC. Where the requirement for homogeneity of slopes among annual data was not met, the data were subdivided into groups of years having homogeneous slopes before further analysis. The homogeneity among years of weight-length regression slopes was evaluated by ANCOVA *F*-test of the interaction between treatment (year) and covariate (total length) (Wilkinson et al. 1996). Estimates of weight at a given length from the weight-length regressions were back-transformed from logarithmic values following Ricker (1975, page 275).

Results

Elver Abundance and Run Timing

Between 1989 and 1999, the annual estimate of American eel elvers migrating to the ERSH ranged from 10,700 elvers in 1989, 467,400 elvers in 1997 (Table 1; Figure 1). If the 1989 elver abundance estimate is omitted as a large underestimate, the annual abundance over 10 years varied 4.6-fold, ranging from 101,500 elvers in 1995, to 467,400 elvers in 1997. No temporal trend in abundance is evident ($F = 0.19$, df = 1,9, $P = 0.67$). In the ERC, annual abundance varied threefold over the five years from 1996 to 2000, ranging from 432,400 elvers in 1998, to 1,419,000 elvers in 1997. The elver run in the ERSH annually began (daily count exceeding 50 elvers) between 15 May and 1 June while in the ERC it began between 4 May and 22 May, about 13 days earlier (range 4–28 days). Once the elver run began, it developed rapidly (Figure 2). In the ERSH, the dates by which 5% of the run had entered the river ranged among years from May 6–28 while 95% of the run had entered by 22 June to 15 July. The modal duration between the fifth and 95th percentiles of the run was 42 days. In the ERC, the dates at which 5% of the run had entered the river ranged among years from 7 to 23 May while 95% of the run had entered by 8–23 June. Between the 5th and 95th percentiles of the run, the modal duration was 29.5 days. In both rivers, the elver run essentially ended (daily count less than 50 elvers) between 6 July and 30 July, most often between 10 July and 19 July.

In the ERSH and the ERC, the annual elver run consisted of two to six, usually three or four, waves or modes of elver abundance. The first run mode occurred from two to 15 days (median five days) after the start of the run. Indications of the wave pattern can be seen in Figure 2 where a reduced slope indicates a trough

Table 1. Annual estimates, with 95% confidence intervals (CI), of the run of American eel elvers to the East River, Sheet Harbour, and the East River, Chester, Nova Scotia.

	East River, Sheet Harbour		East River, Chester	
Year	Estimate	95% CI	Estimate	95% CI
1989	10,700[a]			
1990	218,300			
1991	376,000			
1992	219,200			
1993	134,100			
1994	309,900	± 10,900		
1995	101,500	± 1,600		
1996	336,500	± 11,800	1,138,100	± 28,100
1997	467,400	± 8,500	1,419,000	± 58,900
1998	109,200	± 2,500	432,400	± 9,900
1999	134,600	± 600	441,800	± 9,800
2000			791,200	± 17,300

[a] The run size was greatly underestimated due to operational problems.

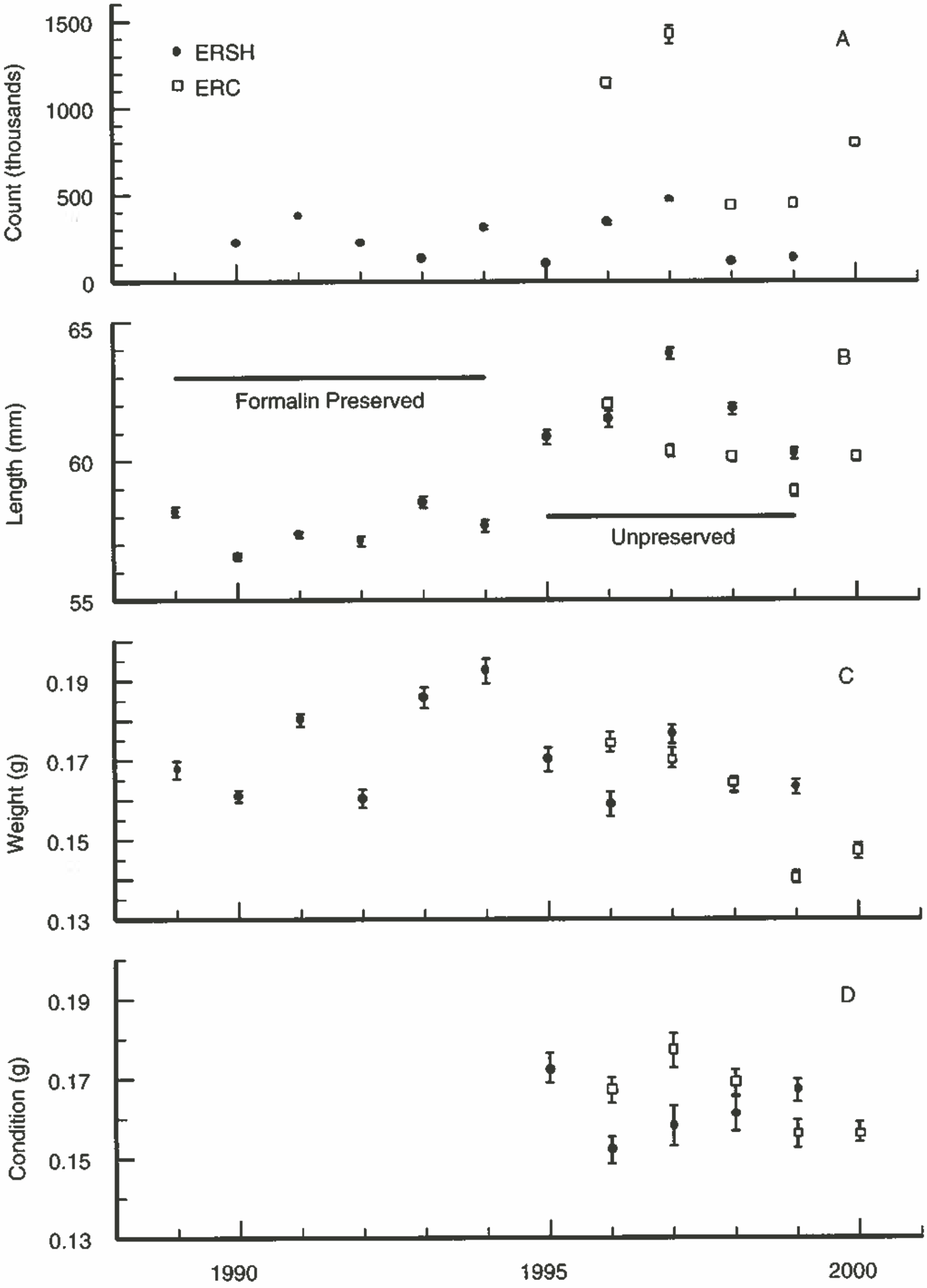

Figure 1. Annual run size (A), mean length (B), mean weight (C), and index of condition (D), with 95% confidence intervals, for American eel elvers from the East Rivers, Chester and Sheet Harbor, 1990–2000 (the 1989 run size was excluded as an underestimate). Elvers from the East River, Sheet Harbor, were preserved in formalin prior to measurement during 1989–1994. Condition was estimated as the mean weight, adjusted to the overall mean length of 60.97 mm, from weight-length regressions of the logarithmically (base 10) transformed data then back-transformed for presentation.

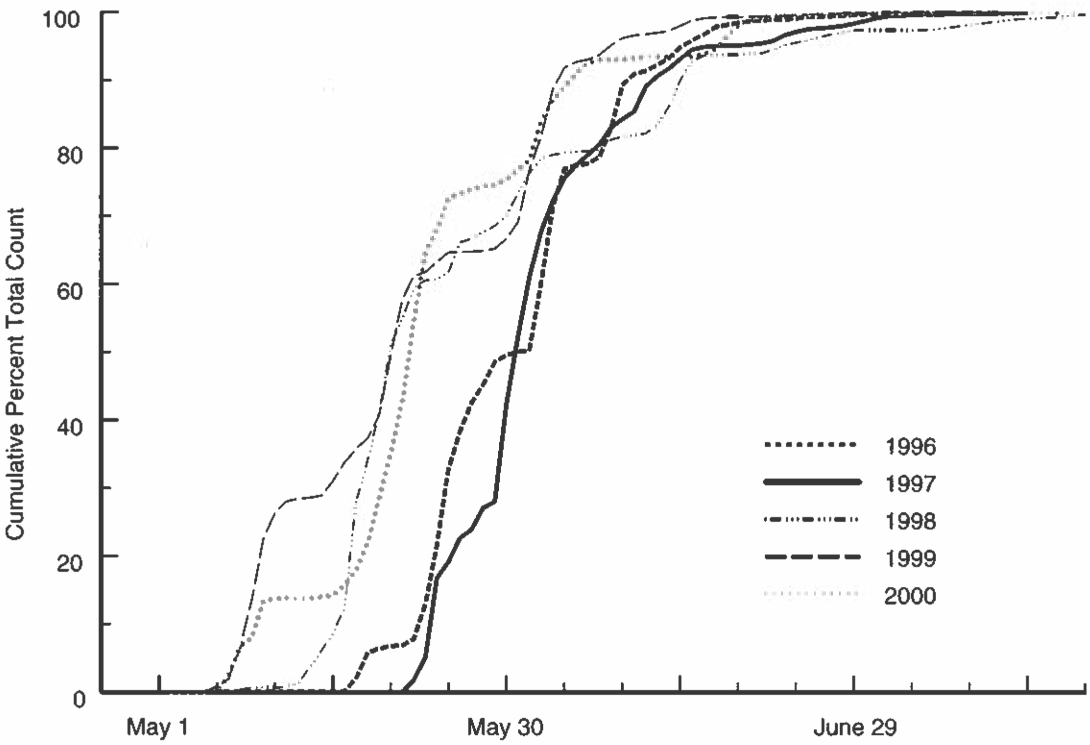

Figure 2. Seasonal progression of the annual run of American eel elvers to the East River, Chester, as indicated by the cumulative percentage of the daily count for the years 1996–2000.

between waves. The largest daily mode of elvers typically entered with the first wave of elvers (eight of eleven years in ERSH, two of five years in ERC), less frequently with the second wave. The interval between the first and second waves of elvers entering the river ranged from 5 to 25 days in the ERSH. Seven of 11 years had an interval between waves of five to eight days, and 3 of 11 years had an interval of 13–15 days. In the ERC, the period between the first two waves of elvers ranged from four to 11 days.

Annual elver counts in the two rivers were highly correlated (r = 0.998, P = 0.002, N = 4). Annual elver counts in the ERSH were not significantly correlated with annual (r = 0.34, P = 0.33, N = 10) or with January–June (r = 0.21, P = 0.55, N = 10) discharge from the St. Lawrence River. Nor were they correlated with January–June precipitation in the local area (r = 0.04, P = 0.91, N = 10) or with the number of degree-days above 11°C (r = 0.17, P = 0.63, N = 10,) or with mean June water temperatures (r = 0.13, P = 0.73, N = 10). No significant autocorrelations or cross-correlations were found at any lag in the time series of annual elver counts and environmental variables. Annual elver counts were not significantly correlated with mean elver length for either the ERSH (r = 0.80, P = 0.11, N = 5) or the ERC (r = 0.61, P = 0.28, N = 5).

Elver Length, Weight, and Condition

Estimates of the mean annual elver length and weight generally differed little whether based on systematic samples or on samples adjusted by count frequency. The effect size g' of the comparison of the two estimation methods was typically smaller for length than for weight, ranging from less than 0.01–0.41 (N = 15, median = 0.08) for elver length and from 0.02 to 0.57 (median = 0.13) for weight. For elver length, only one of 15 cases had a g' value exceeding 0.20 while for weight, 5 of 15 cases had a g' value exceeding 0.20, with one case exceeding 0.5. Seasonal sample sizes larger than about 1,500 elvers produced effect sizes less than 0.3 (small) for both mean length and weight. Sample sizes less than 1,500 elvers may produce effect sizes less than 0.3 but may also reach about 0.6 (large).

Annual weight distributions of elvers were often more skewed than were length distributions. For the ERSH, the median was typically about 60–65 mm for elver length (unpreserved) and 0.13–0.20 g for elver weight (Figure 3) while for the ERC, the respective values were 59–62 mm and 0.14–0.17 g (Figure 4). Outliers of the length and weight frequency distributions were more frequent at the higher side. Annual mean lengths of elvers from the ERSH were all significantly shorter for the years (1989–1994) during which they were measured after preservation than when they were measured fresh (1995–1999) (Table 2; Figures 1B, 3A). The annual mean weights of preserved elvers were higher (0.175 g) than for unpreserved elvers (0.166 g) but there was much overlap in mean weights between groups (Table 2; Figures 1C, 3B). In the ERSH and ERC, annual sample mean elver lengths and weights varied significantly ($P < 0.0001$) among years whether they were preserved or measured fresh (Table 3). The effect magnitude of the difference in mean lengths and weights among years, as measured by r, ranged from 0.17 to 0.35 (Table 3).

Annual mean elver lengths, measured fresh, were significantly smaller in the ERC than in the ERSH in three of four years (1997–1999) but were larger in 1996 (Figure 1B). Mean annual elver weights were smaller in the ERC than in the ERSH in two of four years, larger in one year and similar in one year (Figure 1C). The annual pattern of change in elver lengths and weights varied between rivers but both rivers experienced a decline in length and weight during the years 1997–1999 (Figures 1B, 1C).

Elver condition (weight adjusted to the overall mean elver length of 60.97 mm) varied significantly among years for each river (Figure 1D), as can be roughly judged by the degree of no overlap of the 95% confidence intervals. The comparison of condition among years and between rivers could not be made by ANCOVA and multiple-comparison test where the assumption of homogeneous regression slopes was not met. For the ERC the annual weight-length regression slopes (Table 4) were homogeneous ($F = 1.66$, df = 3,1007, $P = 0.17$) for the years 1996–1999 but were heterogeneous when the year 2000 was included ($F = 3.06$, df = 4, 1249, $P = 0.016$). Elver condition in the ERC varied among the years 1996–1999 ($F = 24.4$, df = 3,1010, $P < 0.0001$), such that years without a letter in common were significantly different (1997, 0.177z; 1998, 0.169zy; 1996, 0.167y; 1999, 0.156x). For the ERSH the annual (1995–1999) weight-length regression slopes were heterogeneous ($F = 15.6$, df = 4,1037, $P < 0.0001$) except among the pairs of years 1995 and 1996 ($F = 0.87$, df = 1,375, $P = 0.35$) and 1997 and 1999 ($F = 0.72$, df = 1,462, $P = 0.40$), which had homogeneous slopes. The mean condition of elvers from ERSH was significantly higher in 1995 (0.172 g) than in 1996 (0.152 g) and higher in 1999 (0.167 g) than in 1997 (0.158 g). The interaction of elver condition at various lengths when annual weight-length regression slopes are nonhomogeneous is illustrated in Figure 5 by the crossing of the lines connecting annual condition values at the lengths examined. Elver mean condition was higher in the ERC than in the ERSH for the years 1996–1998 and lower in 1999 (Figure 1D).

In the ERSH elver mean lengths varied significantly ($P < 0.01$) among weeks in 9 of 11 years (probability of annual variability in weekly mean lengths = 0.82) and weights varied significantly ($P < 0.004$) in all years (Table 5). Specifically, elver mean lengths declined significantly ($P < 0.01$) over the first six to nine weeks of the run in seven of 11 years (probability of decline in weekly mean lengths = 0.64), declined after an initial increase in length in 1 year, and varied with no trend in three years. In the ERSH, elver weights declined in all years although minimally so in two years. Elver weight increased late in the run in some years. The weekly variation in mean length was of generally small, occasionally medium, effect with r values ranging from 0.12 to 0.35, and of small to large effect for weight, with r values from 0.13 to 0.55 (Table 5). In the ERC, elver mean lengths and weights declined seasonally in all years with r values ranging from 0.21 to 0.42 for length (small to medium effect) and from 0.45 to 0.56 for weight (medium to large effect).

Individual elver condition, as represented by the residual from the annual weight-length regression, declined significantly through the first five to nine weeks of the run in 15 of 16 years of data (probability of annual decline = 0.94) from the ERSH and ERC (Table 5). For those years in which the elver run continued beyond the decline-in-condition phase, elver mean condition leveled out or increased while the variability

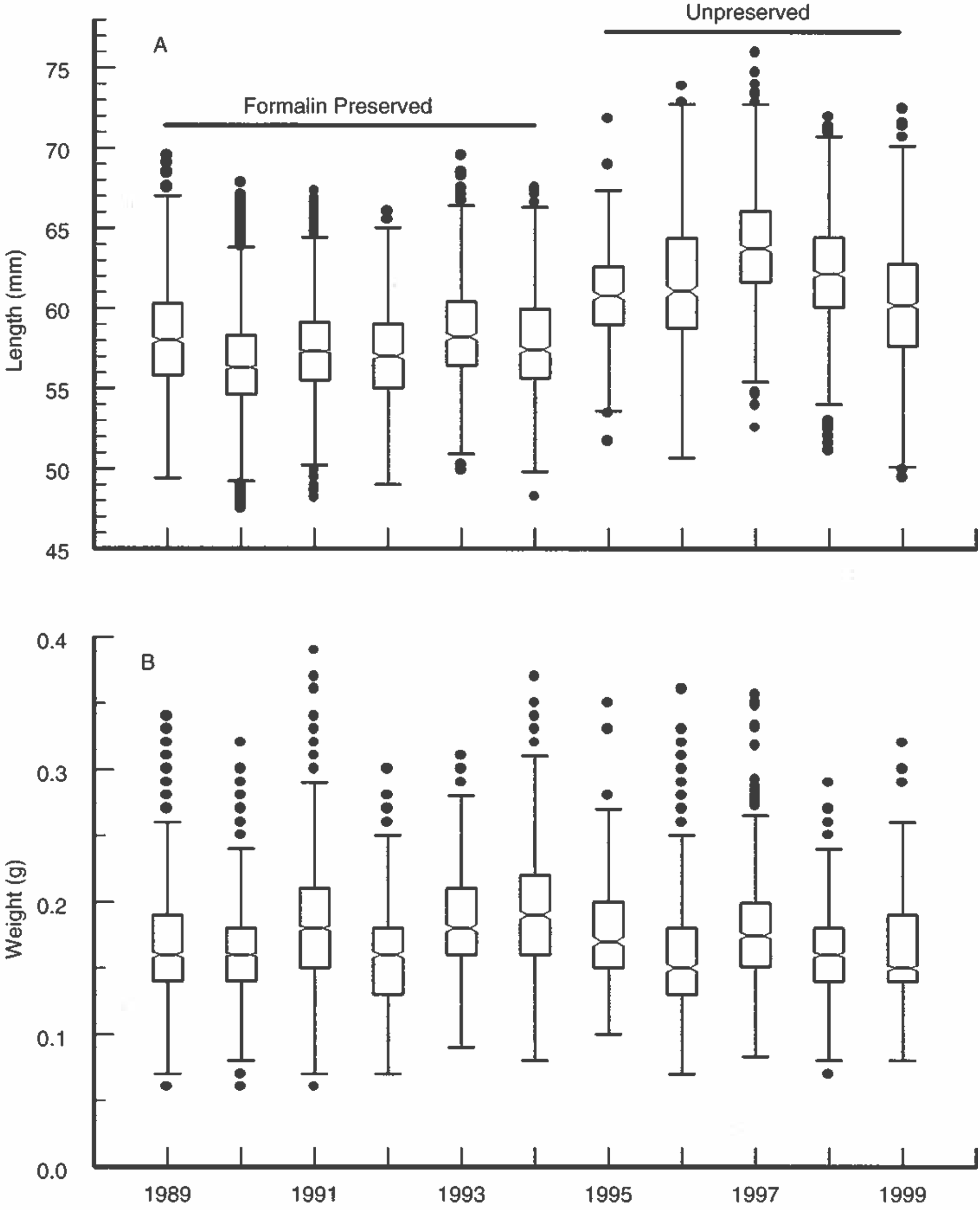

Figure 3. Box plots of the annual length and weight frequency distributions of American eel elvers from the East River, Sheet Harbor, 1989–1999. Annual sample sizes ranged from 450 elvers in 1995, to 2,821 elvers in 1991 (median 1,020 elvers). Notches indicate the 95% confidence interval about the median; the box encloses the middle 50% of the data; whiskers indicate the data range except where outliers (solid dot) occur. Length and weight data were from preserved samples during 1989–1994.

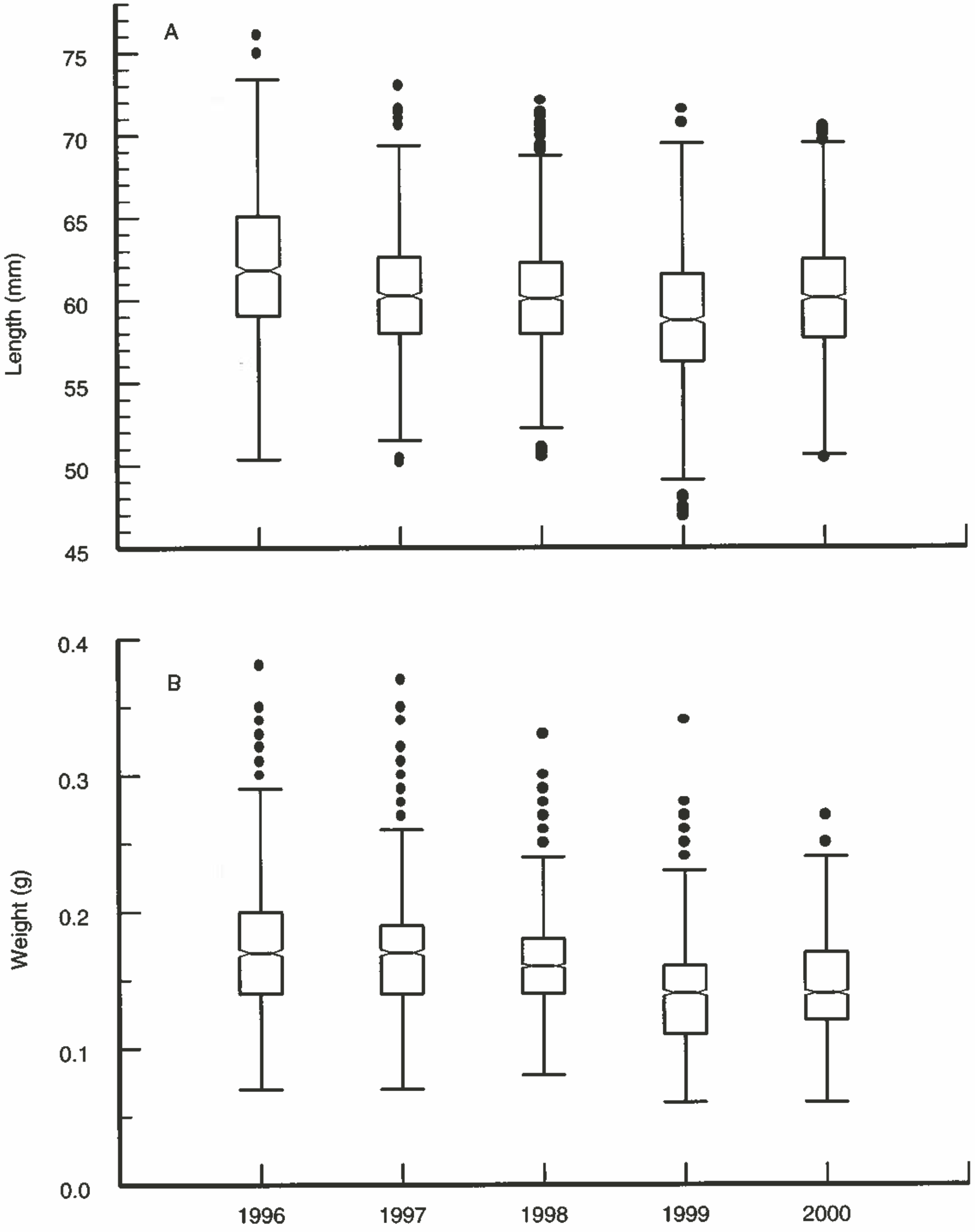

Figure 4. Box plots of the annual length and weight frequency distributions of American eel elvers from the East River, Chester, 1996–2000. Annual sample sizes ranged from 1,181 elvers in 1997, to 1,641 elvers in 2000 (median 1,446 elvers). Notches indicate the 95% confidence interval about the median; the box encloses the middle 50% of the data; whiskers indicate the data range except where outliers (solid dot) occur.

Table 2. Annual mean lengths (mm) and weights (g) of American eel elvers from the East Rivers, Sheet Harbour and Chester. Means from each river have been arranged in ascending order; those without a letter in common are significantly different at $\alpha = 0.05$. The annual sample sizes (*N*) apply to both length and weight for the year indicated.

	East River, Sheet Harbour										
Length	56.57z	57.12y	57.36y	57.66y	58.20x	58.52x	60.25w	60.84v	61.49vu	61.84u	63.84t
Year	1990	1992	1991	1994	1989	1993	1999	1995	1996	1998	1997
Weight	0.159z	0.160z	0.161z	0.163zy	0.164zy	0.168yx	0.170yx	0.176xw	0.180w	0.186v	0.192v
Year	1996	1992	1990	1999	1998	1989	1995	1997	1991	1993	1994
N	2,156	1,004	2,821	868	1,316	819	1,320	450	694	1,106	1,020
	East River, Chester										
Length	58.90z	60.13y	60.14y	60.34y	62.02x						
Year	1999	1998	2000	1997	1996						
Weight	0.140z	0.147y	0.164x	0.170v	0.174v						
Year	1999	2000	1998	1997	1996						
N	1,446	1,549	1,614	1,181	1,301						

Table 3. Analysis of variance *F*, degrees of freedom (df), *P*, and correlation coefficient (*r*) values with associated scale of effect magnitude from the comparison of annual mean American eel elver lengths and weights (base 10 logarithm transformed) measured either fresh or after preservation in 5% formalin. Data from the East River, Sheet Harbour (ESHS) are for the years 1989–1994 (preserved) and 1995–1999 (fresh) and from the East River, Chester (ERC) are for 1996–2000.

River	Year-group	ANOVA	*F*	df	*P*	*r*	Effect size
ERSH	preserved	length x year	80.0	5, 8,978	< 0.0001	0.20	small
	fresh	length x year	158.8	4, 4,585	< 0.0001	0.35	medium
	preserved	weight x year	133.6	5, 8,978	< 0.0001	0.26	small
	fresh	weight x year	36.2	4, 4,585	< 0.0001	0.17	small
ERC	fresh	length x year	124.3	4, 7,086	< 0.0001	0.26	small
	fresh	weight x year	209.4	4, 7,086	< 0.0001	0.33	medium

Table 4. Annual parameter values for weight-length regressions (base 10 logarithm transformed) for American eel elvers (measured fresh) from the East Rivers, Sheet Harbour and Chester. The data were random subsamples of up to 60 elvers per 5-mm length interval, e.g., 50.0–54.9 mm, selected from the total annual sample.

Year	N	r^2	Slope	95% CI	Intercept	95% CI
			East River, Sheet Harbour			
1995	158	0.63	3.0533	2.6846–3.4221	–6.2200	–6.8784 to –5.5616
1996	221	0.73	3.2794	3.0164–3.5425	–6.6793	–7.1502 to –6.2084
1997	219	0.43	2.3462	1.9855–2.7068	–4.9978	–5.6845 to –4.3470
1998	202	0.33	1.7512	1.4089–2.0936	–3.9283	–4.5409 to –3.3157
1999	247	0.74	2.5126	2.3233–2.7018	–5.2665	–5.6030 to –4.9300
			East River, Chester			
1996	268	0.74	2.7833	2.5828–2.9838	–5.7520	–6.1110 to –5.3930
1997	246	0.63	2.8372	2.5604–3.1140	–5.8257	–6.3182 to –5.3332
1998	246	0.67	2.5162	2.2952–2.7372	–5.2695	–5.6627 to –4.8763
1999	255	0.71	2.8665	2.6402–3.0928	–5.9313	–6.3325 to –5.5301
2000	244	0.82	3.1084	2.9241–3.2927	–6.3582	–6.6861 to –6.0304

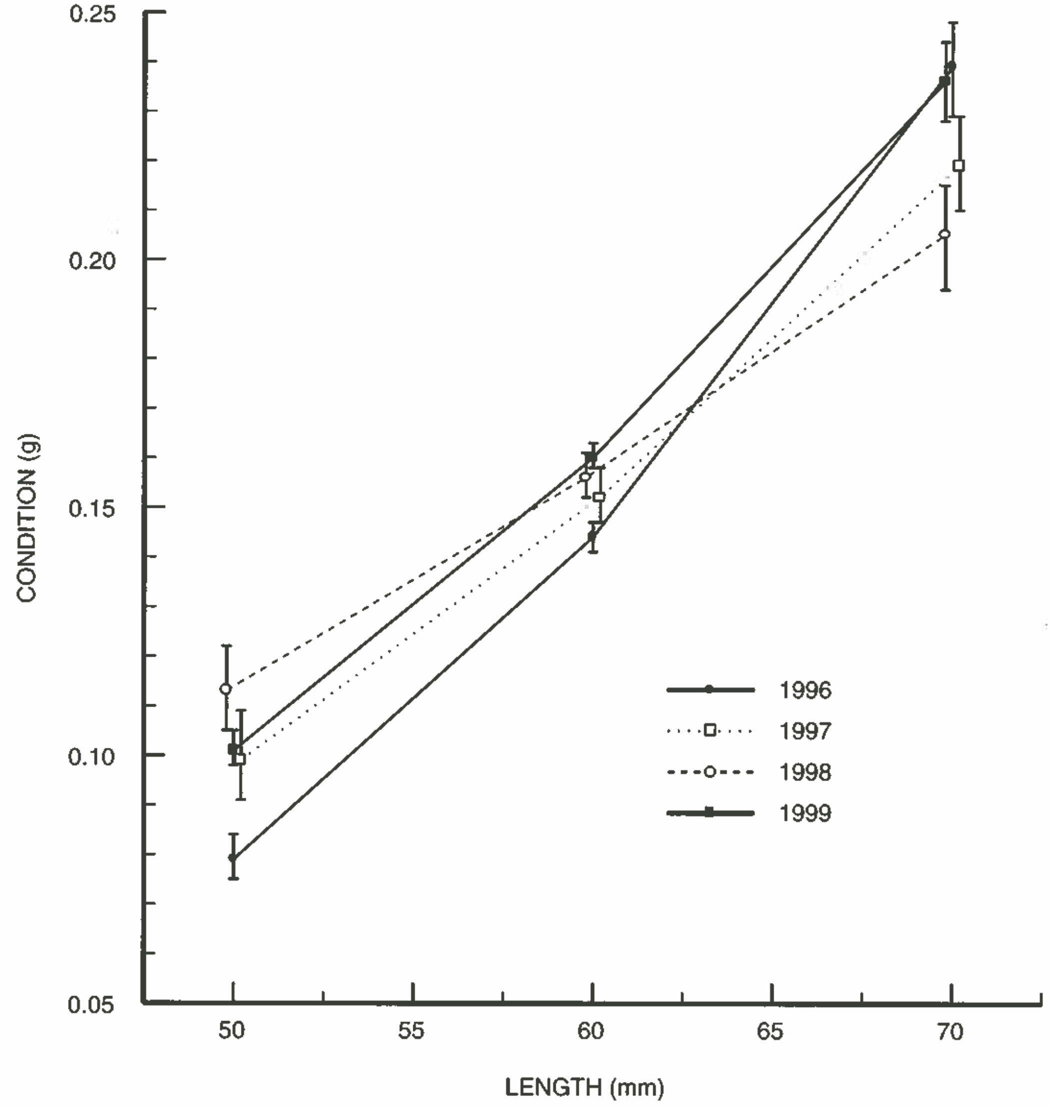

Figure 5. Index of condition, with 95% confidence intervals, at different lengths (50, 60, 70 mm) for American eel elvers from the East River, Sheet Harbor, 1996–1999. Condition was estimated as the mean weight at a given length from annual weight-length regressions of the logarithmically (base 10) transformed data and back-transformed for presentation. For each year, condition indices at different lengths were connected to illustrate the interaction effect of nonhomogeneous weight-length regression slopes.

about the mean increased. Thus, for example, during 1999 in the ERC the decline in the residual index of individual condition during the first 6 weeks of the run ($F = 28.8$, df = 1, 137, $P < 0.0001$, $r = 0.41$) was followed by a net leveling of mean condition and by an increased variance in condition (Figure 6).

Discussion

Elver Abundance and Run Timing

Annual estimates of the run of American eel elvers to the ERSH showed no temporal trend between 1990 and 1999. The cause of the decline in

Table 5. Analysis of variance results, by year, from the examination of weekly variability and trend in mean length and weight (base 10 logarithm transformed) of American eel elvers from the East Rivers, Sheet Harbour and Chester. The correlation coefficient *r* indicates the strength of association between mean length or weight and week. Samples at the end of the run showing a change in trend have been omitted.

		Length (mm)							Weight (g)				
Year	Weeks	Trend	*N*	df	*F*	*P*	*r*	Effect size	Trend	*F*	*P*	*r*	Effect size
						East River, Sheet Harbour							
1989	1–9	None[a]	1,192	7, 1,184	5.0	< 0.0001	0.17	small	decline	21.9	< 0.0001	0.34	medium
1990	1–7	decline	1,954	6, 1,947	12.6	< 0.0001	0.19	small	decline	34.8	< 0.0001	0.31	medium
1991	1–7	decline	2,180	6, 2,173	13.1	< 0.0001	0.19	small	decline	76.1	< 0.0001	0.42	medium
1992	1–6	decline	1,004	5, 998	3.1	0.009	0.12	small	decline	63.5	< 0.0001	0.49	medium
1993	1–7	decline	529	6, 522	8.3	< 0.0001	0.29	small	decline	9.6	< 0.0001	0.31	medium
1994	1–8	decline	718	7, 710	13.6	< 0.0001	0.34	medium	decline	43.0	< 0.0001	0.55	large
1995	1–7	decline	450	6, 443	4.3	< 0.0001	0.23	small	decline	11.9	< 0.0001	0.37	medium
1996	1–7	none	619	6, 612	1.2	0.31	0.11	small	decline	9.2	< 0.0001	0.29	small
1997	3–8	decline	763	5, 757	11.1	< 0.0001	0.26	small	decline	10.1	< 0.0001	0.25	small
1998	3–8	none	660	5, 654	2.0	0.07	0.12	small	decline	12.1	< 0.0001	0.29	small
1999	1–8	decline	1,170	7, 1,162	3.4	0.001	0.14	small	decline	3.0	0.004	0.13	small
						East River, Chester							
1996	1–9	decline	1,201	8, 1,192	7.8	< 0.0001	0.22	small	decline	39.5	< 0.0001	0.46	medium
1997	1–9	decline	1,181	8, 1,172	31.6	< 0.0001	0.42	medium	decline	66.5	< 0.0001	0.56	large
1998	1–8	decline	1,112	7, 1,114	7.2	< 0.0001	0.21	small	decline	41.6	< 0.0001	0.45	medium
1999	1–7	decline	1,000	6, 993	7.3	< 0.0001	0.20	small	decline	48.0	< 0.0001	0.47	medium
2000	1–9	decline	1,200	8, 1,191	19.8	< 0.0001	0.34	medium	decline	51.0	<0.0001	0.50	large

a. No trend although length varied significantly among weeks.

commercial eel fishery catches in many parts of eastern North America, and in some juvenile abundance indices, is uncertain (Peterson 1997; ASMFC 2000; EPRI 1999). It may reflect a decline in elver recruitment induced by marine environmental effects or human activity such as growth or recruitment overfishing or obstructed upstream access or a combination of these factors.

Whether the presently observed level of recruitment is low or high relative to historic levels is unknown. Few, and short (less than 12 years), elver time series exist for North America. There are several juvenile eel indices (EPRI 1999) but their relation to elver recruitment is uncertain. Elver recruitment to the Atlantic coast of Nova Scotia and New Jersey may have been relatively stable during the 1990s (Jessop 1997; EPRI 1999). The constant, predominantly male sex ratio for silver eels in Rhode Island since the 1980s implies that elver recruitment may also have been stable, or at least high, relative to the available habitat, because high elver densities produce male-dominated sex ratios (Krueger and Oliveira 1999). The relatively stable recruitment of European eel elvers during the 1990s in some index rivers was low relative to abundances during the 1960s–1980s but comparable to abundances in the 1930s and 1940s (Moriarty 1990; ICES 2000). Any decline in elver recruitment in North America since the 1980s may have been restricted to the Gulf of St. Lawrence (Castonguay et al. 1994a, b). More specifically, decline may have been largely restricted to the lower Gulf of St. Lawrence (Nova Scotia, New Brunswick, Prince Edward Island; Chaput et al. 1997) and the upper Gulf of St. Lawrence (Quebec; Castonguay et al. 1994a, b). The northern Gulf of St. Lawrence (north shore of Quebec east of the Saguenay River) may have been less affected (Caron and Verreault 1997). The strong correlation between the juvenile eel index at the Moses-Saunders Dam and the total annual flow through the locks at the downstream Beauharnois Dam may compromise the

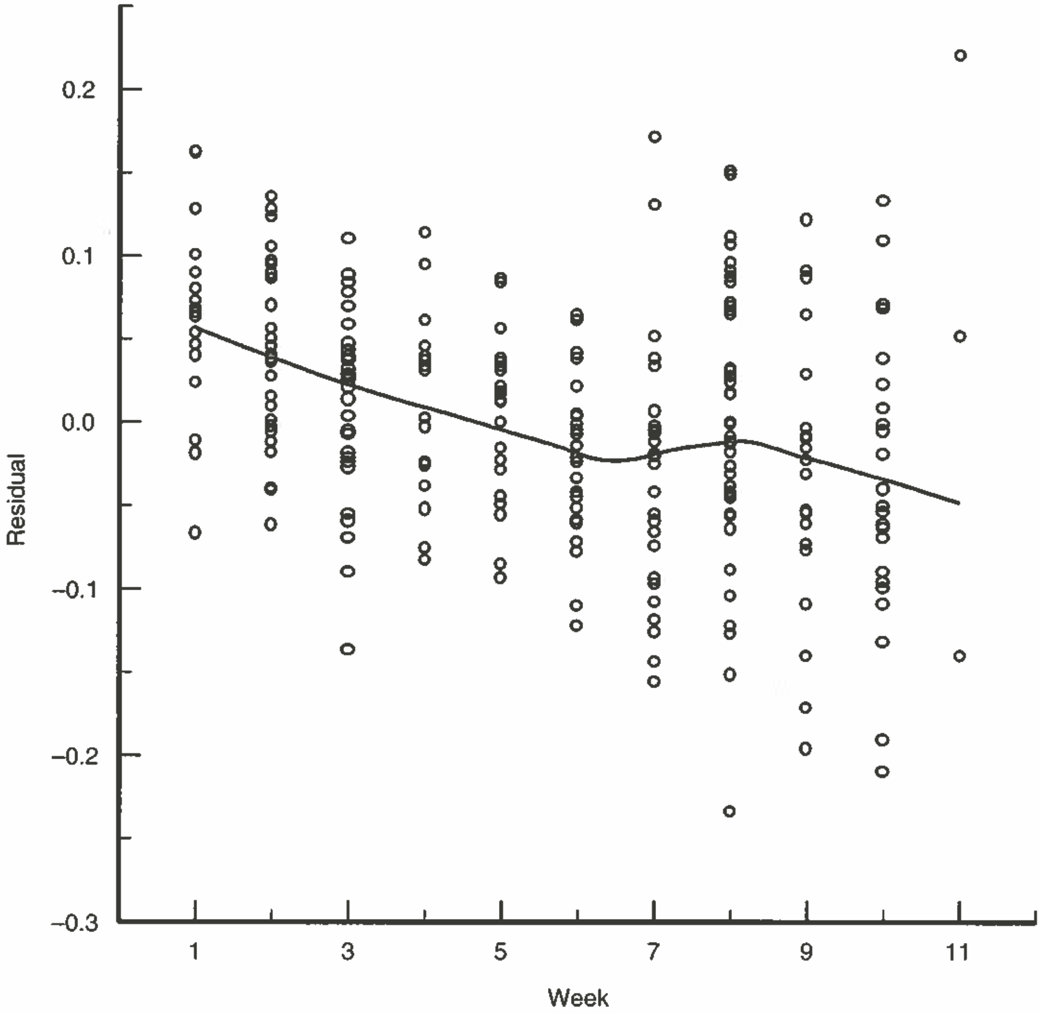

Figure 6. Seasonal pattern in the index of condition of American eel elvers from the East River, Chester, 1999. The index of individual elver condition was estimated as the residual from the weight-length regression of the logarithmically (base 10) transformed data. The line is loess smoothed.

reliability of the index as an indicator of natural juvenile eel recruitment to the upper St. Lawrence River, but not to Lake Ontario (EPRI 1999; Desrochers and Fleury 1999).

Despite the reduced elver recruitment to Europe since the 1980s, there is no evidence that the level of recruitment is insufficient to minimally stock the available habitat although the availability of recruitment and habitat may be geographically mismatched (Moriarty and Dekker 1997). Elver abundances vary geographically along the Atlantic coast of Nova Scotia and in the Bay of Fundy (Jessop 1998b). The geographic variability in oceanographic conditions provides reason to expect geographic variability in elver recruitment to other regions of the Atlantic coast of North America (Smith 1989; Castonguay et al. 1994b) as occurs along the European coast (Moriarty and Dekker 1997). The high acidity, low productivity and relatively small size of most Atlantic coastal Nova Scotia streams (Watt 1986; Watt et al. 2000) and high

(> 0.99; Jessop 2000b), possibly density-dependent, elver mortality rates (Vøllestad and Jonsson 1988) may be such that the present elver recruitment exceeds habitat carrying capacity. The high proportion (65%) of male silver eels in the ERC also implies a high elver density relative to the available habitat (Oliveira et al. 2001).

Annual elver recruitment to the ERC exceeded that to the ERSH and began earlier in the year. The high correlation between recruitment to the two rivers implies a consistent, environmentally mediated, pattern in geographic distribution. The distance between rivers with correlated run sizes has practical implications in the number and location of the index rivers required to monitor North American elver recruitment (e.g., ASMFC 2000).

Synchrony in annual elver abundance and run timing may result from the combined effects of several factors. The southwest flow of the Nova Scotia Current may affect the coastal distribution of elvers, the mid-shelf location of channels and basins in the Scotian Shelf may allow earlier shoreward access to the ERC by elvers utilizing the deep shoreward current flow in these channels, and consistent geographic and temporal differences in coastal and stream water temperature patterns may influence run timing (Smith 1989; Jessop 1998b). Although the correlation between annual discharge from the St. Lawrence River, which contributes greatly to the Nova Scotia Current, and elver run size to the ERSH was not significant, the correlation coefficient r of 0.34 indicated a medium effect size and possible biological importance. The absence over 10 years of any significant correlation between elver run size and seasonal total precipitation and a negligible effect size ($r = 0.04$) implies that stream discharge had little impact on run size. This contrasts with the conclusion by Jellyman and Ryan (1983), based on four years of data, that higher rainfall during the migratory period produced a larger elver run to a New Zealand stream. A significant correlation between the elver run and the number of degree-days greater than 11°C was noted by Hvidsten (1985) and with mean June–July water temperatures by Vøllestad and Jonsson (1988) for the Imsa River, Norway. The absence of such correlations for the ERSH may indicate a difference among regions in such a temperature effect given the similarity in temperature response by European and American eel elvers (Tesch 1977; Helfman et al. 1984; Sorensen and Bianchini 1986). The Imsa is one of the warmest streams in Norway, which may partially account for its relative success in elver recruitment (Hvidsten 1985) while the ERSH is typical of streams along the Eastern Shore of Nova Scotia. Although no significant relation was found between elver run size and mean length for either river, perhaps because of the short available time series, a simultaneous decrease was found for European elvers between the 1970s and 1990s (Desaunay and Guerault 1997).

Environmental conditions offshore and across the continental shelf may substantially control the abundance and general timing of the elver run to a river (Jessop 1998a, b, this study). However, the daily abundance and rate of movement of elvers into freshwater is controlled by environmental conditions inshore and at the river mouth (Sorensen and Bianchini 1986; Haro and Krueger 1988; Martin 1995). Waves of elver abundance with periods of 5–11 and 13–15 days during stream ascent are consistent with the interactions of selective tidal stream transport and tidal phase (McCleave and Kleckner 1982; Jessop this volume) and stream discharge and temperature (Haro and Krueger 1988; Martin 1995; Jessop 1998a). Waves of elver abundance are typical of European (Cantrelle 1984; Böetius and Böetius 1989; Ciccotti et al. 1995), Pacific (Jellyman 1979; Tzeng 1984) and American eels (Martin 1995; Jessop 1997; 1998a).

The estimation of mean population lengths and weights for the run of elvers to a stream by systematic samples was biased little by daily abundance that varied greatly over the run rather than being relatively uniform. The generally small effect size g' less than about 0.2) or small-to-medium (less than 0.3) effect size of the difference in run mean elver lengths and weights, as estimated by sample means and sample means adjusted by the elver count, implies that sample means provide an acceptable estimate of population mean values. Seasonal sample sizes of at least 1,500 elvers will generally ensure an effect size for differences between means sufficiently small to be of little biological concern. Small differences in mean lengths and weights between estimation methods may be statistically significant at $\alpha = 0.05$ because of the large sample (over one thousand elvers) sizes involved. The relative abundance of outliers in the upper range of the frequency distributions of length and weight may result from the natural occurrence of unusually large elvers and from the difficulty of readily distinguishing large elvers, when highly pigmented, from small juvenile eels in this size range (Jessop 1998a).

Some consistencies occurred between rivers (larger lengths and weights in the East River, Sheet Harbor) and among years (declining in three of four years) in the pattern of annual differences in population mean elver lengths and weights in the East Rivers, Chester and Sheet Harbor. Mean elver condition was higher in the ERC than in the ERSH in three of four years. Such consistencies may reflect the geographic and temporal consistency of local oceanographic conditions. The pattern of increasing elver size with increasing latitude over the 140 km separating the two rivers matches the geographic cline of increasing elver length, and presumably weight, from south to north along the Atlantic coast of North America (Vladykov 1966; Haro and Krueger 1988). However, it more likely results from regional effects of the Nova Scotia Current on the coastal distribution of elvers rather than continental-scale effects by the Gulf Stream (Jessop 1998a, b). Annual variability in elver mean lengths and weights for each river, while statistically significant, was generally of small effect magnitude (*r* values ranged from 0.17 to 0.35), suggesting that such variability is of little biological importance. A low effect magnitude (*r*) may be influenced by the interaction of high annual variability in individual elver length and weight and in the magnitude of their seasonal decline, thereby masking the degree to which both factors may be of biological importance. European elvers show similar geographic and temporal differences in biometrics (Desaunay and Guerault 1997).

Elver Length, Weight, and Condition

The declines in elver mean length, weight and condition during the elver run documented for single years (Haro and Krueger 1988; Jessop 1998a) can be expected to occur in almost all years and to varying degree. Seasonal effects accounted for more of the decline in elver weight (21–31% of variance accounted for) than of length (4–18%). This difference may be due to the wider variability of elver weights (*CV*% range = 19.5–26.5) than of lengths (*CV*% range = 4.6–6.6) throughout the annual run and the greater physiological effects on weight (e.g., starvation, energetic cost of swimming) during the estuarine adjustment period (Tesch 1977; Cantrelle 1984; Jessop 1998a). Statistically significant declines in seasonal mean length had low to medium effect size *f* values and may be of less biological importance than the declines in weight. The effect size *f* values for weight were often (nine of sixteen years) large (exceeding 0.4) and are probably of biological significance since biological significance for large effect sizes has been reported in other studies (Kirk 1996; Arft et al. 1999). Note that weighing a sample of 50 elvers to the nearest 0.01 g provides a potential 5% measurement difference (effect size *g'* of about 0.3 or small-to-medium effect) on an elver of 0.20 g with very little change in true weight. Measuring elvers to the nearest 0.1 mm provides a potential 0.2% measurement difference (effect size *g'* of less than 0.01) and is clearly trivial in effect.

The seasonal decline in elver length, weight, and condition during stream entrance has been linked to changes in physiology and behavior interacting with oceanic, estuarine and stream environmental conditions (Callamand 1943; Cantrelle 1984; Haro and Krueger 1988; Böetius and Böetius 1989; Jessop 1998a, b). The consequences of seasonal declines in length, weight, and condition on subsequent elver growth and mortality are poorly understood (Jessop 1998b, 2000b). Reliable estimates of seasonal parameters require sampling throughout the run. The increased elver mean weight sometimes observed at the end of the run may arise from the resumption of growth or the recent arrival of elvers with high condition although their advanced pigmentation suggests the former.

The use of an index of weight adjusted to a common length by ANCOVA to describe elver condition among different rivers, years, or even weeks within a year is problematic because of the requirement for equal regression slopes (Bolger and Connolly 1989; Cone 1989; Springer et al. 1990; Jakob et al. 1996). American eel elvers from different rivers and years have a common genetic basis for their weight-length relationship (Helfman et al. 1987) but the effects of sampling variability, seasonal decline in length and weight, and local environmental conditions may create differences among empirical weight-length relations. At 60.7 mm, the mean annual length over 10 years of data (unpreserved) from both East

Rivers (range 58.9–63.8 mm), the effect size *g* of the maximum difference in 1996–1999 annual mean elver condition for the East River, Sheet Harbor, was 0.65. This medium-large effect size indicates probable biological importance for the variability in annual mean condition. A comparison of elver condition at the overall mean length is biased, but minimally so, to the degree that the weight-length slopes differ, with the bias increasing at the extremes of the length distribution. The resulting interaction (change in relative magnitude or order) in weight at different lengths requires caution when interpreting differences in elver condition among stocks (Bolger and Connolly 1989). The comparison of elver condition from rivers in different geographic regions will be further biased to the extent that the latitudinal increase in mean elver length (Haro and Krueger 1988) increases the difference in mean length of elvers from the regions of interest. Also, the assumption that changes in wet body weight relative to length reflect changes in physiological condition, particularly fat content, may be weak for elvers as it is for Atlantic salmon *Salmo salar* parr (Sutton et al. 2000).

The use of a residual index of condition proved useful for examining the seasonal change in individual elver condition. Elvers that may have resumed growth following the transitional period of stream entrance and elvers that may be showing signs of starvation and potential mortality could be identified by the increased variance in the residual index of condition and the positive or negative residual value. Residual variation may be interpreted as environmentally induced variation in condition given that the genetic variation in body shape is assumed to be small between individuals, as is plausible for the American eel (Helfman et al. 1987; Sutton et al. 2000). A residual index is not appropriate for comparing condition among populations unless a common weight-length regression can be estimated (Jakob et al. 1996; Sutton et al. 2000).

Further evaluation is required of the meaning of effect sizes in relation to various aspects of elver biology. The meaning of statistically significant results should be evaluated because not all will be of probable biological importance. The biological relevance of an effect size may ultimately be determined by the nature of the study and the researcher's judgment (Cohen 1988).

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