Geographic and seasonal variation in biological characteristics of American eel elvers in the Bay of Fundy area and on the Atlantic coast of Nova Scotia

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Abstract: Seasonal (April–July) patterns in the decline of length, mass, and condition and an increase in pigmentation stage of American eel (*Anguilla rostrata*) elvers collected during the estuarine commercial fishery and during entrance into fresh water varied among rivers in the Bay of Fundy and on the Atlantic coast of Nova Scotia. Elver mean length, adjusted to a mean collection date, varied among commercially fished rivers by up to 9%; mean mass varied by up to 27%. Within commercially fished rivers, mean length declined seasonally by 2–5%, mass by 0–60%, and condition by 0–44%. Elver condition declined 7–9% by the time 50% of the run (number of elvers) had entered the East River, Chester, and East River, Sheet Harbour, and by 21% at 95% of the run, while the mean pigmentation stage increased to 4.1–4.8 and 5.7–6.5, respectively, on a scale of 1–7. Such geographic variability in biological traits may result from the effect of varying annual and seasonal environmental conditions on the coastal distribution of elvers and on their run timing and physiological development in estuarine and stream habitats. The biological importance of the seasonal decline in elver length, mass, and condition is uncertain, but a seasonal decline in mass of 35% may be commercially important when elvers are sold by weight rather than count.

Résumé : Les tendances saisonnières (avril–juillet) à une diminution de la longueur, de la masse et de la condition physique et à une augmentation de la pigmentation chez des civelles (*Anguilla rostrata*) capturées dans les pêches commerciales, en estuaire ou lors de leur entrée en eau douce, variaient d'un cours d'eau à l'autre dans la baie de Fundy et le long de la côte atlantique de la Nouvelle-Écosse. La longueur moyenne des civelles, ajustée à une date de récolte moyenne, différait parfois de 9% dans les différents cours d'eau exploités par les pêches commerciales; la variation de la masse moyenne pouvait atteindre 27%. Dans les cours d'eau exploités commercialement, la longueur moyenne subissait une diminution de 2–5% au cours d'une saison, la masse, de 0 à 60%, et la condition physique, de 0 à 44%. La condition physique des civelles avait diminué de 7 à 9% au moment où 50% d'entre elles avaient déjà pénétré dans les branches de les rivières East, à Chester et à Sheet Harbour, et de 21% quand 95% des civelles étaient déjà dans les cours d'eau, alors que la pigmentation avait augmenté de 4,1-4,8 et de 5,7-6,5 (sur une échelle de 1 à 7) dans les mêmes cours d'eau. Une telle variabilité géographique des caractéristiques biologiques peut être attribuable à l'effet des conditions environnementales saisonnières et annuelles sur la répartition des civelles le long de la côte et à leur développement physiologique ainsi qu'au synchronisme de la formation de leurs bancs dans l'estuaire et dans les cours d'eau. L'importance biologique de la diminution saisonnière de la longueur, de la masse et de la condition physique des civelles reste à déterminer, mais le déclin saisonnier de 35% de la masse peut avoir une importance économique lorsque les civelles sont vendues en fonction de leur masse plutôt que de leur nombre.

[Traduit par la Rédaction]

Introduction

The rapid development since the late 1980s of commercial fisheries for the elvers of American eels, *Anguilla rostrata*, in Canada and the United States has increased interest by fishery managers and culturists in the biology of this life stage and of the species (Atlantic States Marine Fisheries Commission (ASMFC) 1997; Jessop 1998*a*; Peterson 1998). American eels occur in coastal rivers between Greenland and Venezuela (Tesch 1977; Helfman et al. 1987). Sexually maturing eels migrate from rivers in eastern North America to the Atlantic Ocean, where they travel to the Sargasso Sea to spawn. After hatching, eel leptocephali are transported via the Gulf Stream and other ocean currents along the eastern coast of North America, where they metamorphose into unpigmented (glass) elvers and move shoreward by means of active swimming and various modes of current transport such as Gulf Stream eddy intrusions, long-shore currents, and selective tidal stream transport (McCleave and Kleckner 1982; McCleave 1993). Glass eels develop into pigmented elvers as they traverse estuaries and enter coastal streams, moving upstream in response to a rheotactic tendency and distributing themselves throughout the available habitat over a period of years. Elvers enter streams progressively later from south to north, entering Atlantic coast streams of the Maritime Provinces primarily during May and June.

The American eel and the closely related European eel (*Anguilla anguilla*) are ecological generalists with highly plastic life histories, as might be expected of species with

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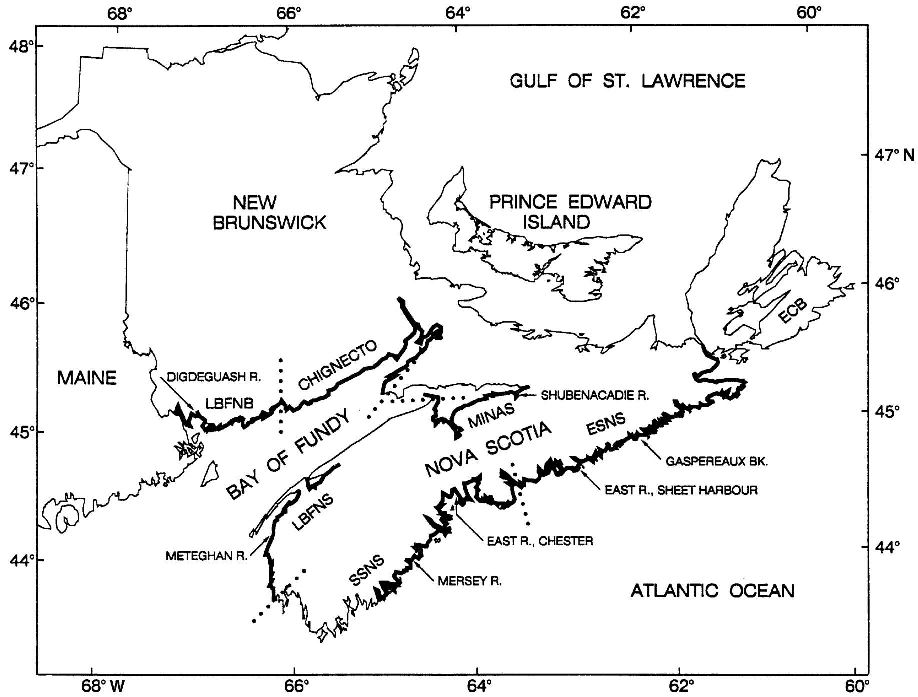
Fig. 1. Map of the Maritime Provinces with survey rivers and geographic regions indicated. The thickened coastal line demarcates the areas in which the elver fishery occurs. LBFNB, lower Bay of Fundy, N.B.; UBFNS, upper Bay of Fundy, N.S.; LBFNS, lower Bay of Fundy, N.S.; SSNS, South Shore, N.S.; ESNS, Eastern Shore, N.S.; ECB, eastern Cape Breton Island.



such wide geographic ranges and panmictic breeding (Tesch 1977; Helfman et al. 1987). The variability in expressed biological characteristics of the eel is poorly documented for many traits, which hinders understanding of the role of such variability in the success of these species (Vøllestad 1992). Knowledge of the rate and degree of seasonal and geographic variability in length, mass, condition, and pigmentation stage can be of economic value to fishers, for whom the number of elvers per kilogram and degree of pigmentation are market factors, to culturists, for whom elver size may affect rearing success, and to fishery managers, for whom better knowledge may improve fishery management.

Elver lengths increase clinally from south to north along the Atlantic coast of North America (Vladykov 1966, 1970; Haro and Krueger 1988), but the expected clinal variation in mass is poorly documented (Vladykov 1970; Dutil et al. 1989). Haro and Krueger (1988) examined seasonal changes in elver length and pigmentation stage within a New England stream, while Dutil et al. (1989) reported seasonal changes in pigmentation stage and annual variability in length and mass of elvers from the northern Gulf of St. Lawrence. Within the Maritime Provinces, length and some mass data for elvers from several rivers in New Brunswick (N.B.) and Nova Scotia (N.S.) have been provided by Vladykov (1966, 1970) and Hutchison (1981), who also examined seasonal migration in relation to environmental factors. Qualitative observations on relative abundance and run timing, in relation to environmental factors, of elver runs to streams in N.B. have been made by Leblanc (1973) and Groom (1975). Jessop (1998*c*) concluded that elver abundance, as indicated by the commercial fishery catch, varies geographically in the Bay of Fundy and along the Atlantic coast of N.S. in relation to environmental factors such as ocean currents. Seasonal changes in elver condition and the regional variability in seasonal changes in length, mass, condition, and pigmentation stage are undocumented for the American eel.

This study examines the seasonal (April–July) and geographic (among rivers) variation in length, mass, condition, and pigmentation stage of elvers from seven rivers distributed throughout the Bay of Fundy area of N.B. and N.S. and the Atlantic coast of N.S. (hereafter termed the Scotia–Fundy area). The importance of such variability to elver biology and the commercial fishery is discussed.

Materials and methods

Elvers were collected in the estuarine zone near or at the head of tide by commercial fishers throughout the 1997 commercial fishery (mid-April to early July, depending upon the area) in the Digdeguash River, N.B., and the Shubenacadie, Meteghan, Mersey, and Gaspereaux rivers in N.S. (Fig. 1). Elvers were caught primarily by dip net except in the Digdeguash River, where pots were also used, and the Shubenacadie River, where fyke nets were used. All gear types used a mesh of 1.0 mm^2 and were fully capable of capturing elvers of the existing range of sizes. Fishers deploy various gears according to preference and suitability for local river conditions and fish opportunistically in relation to perceived elver abundance (Jessop 1998*c*). High elver value ensures diligent fishing throughout the elver run. Elvers were also collected by Irish-type elver traps (O'Leary 1971) set just upstream of the head of tide in the East River, Chester, and the East River, Sheet Harbour, N.S. Daily monitoring of the research traps permitted evaluation of the representativeness of the more irregular commercial fishery sampling. Run size (excluding fishery catch) was estimated at 1.02 million elvers for the East River, Chester (Jessop 1998*b*), and 0.52 million elvers for the East River, Sheet Harbour (Jessop 1998*b*; B.M. Jessop, unpublished data).

The rivers sampled can be conveniently classified by geographic area: 1, Digdeguash – lower Bay of Fundy, N.B. (LBFNB); 2, Shubenacadie – upper Bay of Fundy, N.S. (UBFNS); 3, Meteghan –

lower Bay of Fundy, N.S. (LBFNS); 4, Mersey and East River, Chester – South Shore of N.S. (SSNS); 5, East River, Sheet Harbour, and Gaspereaux River – Eastern Shore of N.S. (ESNS). The rivers are typical of their geographic area in most respects. They vary from 82 to 2604 km^2 in drainage area and from 0.5 to 6.6 $m \cdot km^{-1}$ in gradient, as follows: Digdeguash River, 451 km^2, 2.0 $m \cdot km^{-1}$; Shubenacadie River, 2604 km^2, 0.5 $m \cdot km^{-1}$; Meteghan River, 214 km^2, 1.7 $m \cdot km^{-1}$; Mersey River, 1944 km^2, 1.2 $m \cdot km^{-1}$; Gaspereaux River, 82 km^2, 1.7 $m \cdot km^{-1}$; East River, Chester, 134 km^2, 6.6 $m \cdot km^{-1}$; East River, Sheet Harbour, 526 km^2, 3.8 $m \cdot km^{-1}$. River pH varies geographically, from about 4.7–5.0 in the Mersey and East rivers, Chester and Sheet Harbour, to 5.1–5.4 in the Gaspereaux River, to more than 6.0 in the Digdeguash, Meteghan, and Shubenacadie rivers (Watt 1986). All possess features attractive to elvers (resident eel stock, decaying leaf detritus, and, except for the two East rivers, an alewife (*Alosa pseudoharengus*) run; Sorensen 1986) and support productive elver fisheries.

The commercial fishers collected samples of, usually, 60 elvers and associated surface water temperatures (°C) approximately every week between late April and early June. Between late May and mid July, elver catches were recorded daily and samples of 50 elvers were collected three times weekly from the elver traps at East River, Chester, while samples of 30 elvers were taken five times weekly at the East River, Sheet Harbour, from the elver traps located just upstream of the head of tide (Jessop 1998*a*, 1998*b*; B.M. Jessop, unpublished data). Elver samples from the commercial fishery were preserved in 4% formalin for 1–6 weeks (a few samples were held for about 4 months) while trap-caught elvers were processed immediately after killing in 4% formalin. Elvers were measured for total length (TL, to 0.1 mm with calipers), mass (to 0.01 g) after being carefully blotted dry, with particular attention being paid to the buccal and gill areas, and classified as to pigment stage (1–7 following Haro and Krueger 1988) by means of a binocular microscope at 15×

Young eels with a wide range of lengths, masses, and pigment phases may be captured between April and July in the Scotia–Fundy area. The possibility exists that large elvers of the current year (age 0) could be confused with small, late-arriving (into August) elvers of the previous year (now age 1). After mid-May, elvers of advanced pigment stage 7 of the current year may be difficult to distinguish from pigment stage 8 juvenile eels (stage VII of Elie et al. 1982) of the previous year, particularly when their sizes are similar and atypical individuals occur that are well developed in one characteristic and less so in another. Analysis of length and mass frequency plots (Petersen's method) and pigmentation stage patterns in 8 years of data from the East River, Sheet Harbour (B.M. Jessop, unpublished data), has produced the following criteria for classification, in the absence of age data, as elver (age 0), and therefore for inclusion in this analysis: (*i*) ≤ pigment stage 5 at any size; (*ii*) ≤ 70 mm and (or) 0.30 g, and ≤ pigment stage 7 before June 1; and (*iii*) ≤ 75 mm and (or) 0.35 g, and ≤ pigment stage 7 after June 1 and before July 15. Only elvers occurred in the commercial fishery samples, but the elver traps in the two East rivers caught both elvers and older juvenile eels. In the East River, Chester, a total of 21, or 1.4%, of putative elvers were classified as older juveniles. No classification ambiguities occurred in the East River, Sheet Harbour.

Seasonal changes in elver mean length and mass within a river and among rivers were examined visually by box and whisker plots and statistically examined by analysis of variance (ANOVA) and multiple comparisons of sample means by the Tukey–Kramer test (Wilkinson et al. 1996). Elver condition (a measure of mass relative to length, indicative of well-being) among rivers and seasonally during the run period for each river was evaluated by Tukey–Kramer multiple comparison tests of mean masses adjusted to a common (the overall mean) length by analysis of covariance (ANCOVA; Sokal and Rohlf 1981) of sample mass–length regressions (Cone 1989; Jackson et al. 1990). Seasonal changes in elver pigmentation stages for the different rivers were compared by box and whisker plots, while ANOVA and Tukey–Kramer multiple comparison tests were used to evaluate changes in mean elver length and mass with increasing pigmentation stage. Daily samples from each of the East rivers were pooled on a weekly basis for all analyses.

Daily sample lengths and masses of elvers showed slight to moderate heterogeneity of variances for several rivers. Variance increased ($0.02 < P < 0.05$) with the mean for one of five commercially fished rivers and the F_{max} test (Sokol and Rohlf 1981) was significant (statistical significance was accepted at $\alpha \leq 0.05$) for either length or mass in three of the commercially fished rivers. For the larger weekly (pooled) samples from the trap-fished rivers, only elver masses in the East River, Chester, had a significant ($P < 0.01$) F_{max} test. Consequently, elver lengths and masses were logarithmically (base 10) transformed before ANOVA and multiple comparison tests and for mass–length regression. Estimates of mass at a given length from these regressions were back-transformed from logarithmic values following Ricker (1975, p. 275). There was no requirement to logarithmically transform elver lengths or masses for the pigmentation stage analysis. The adjusted r^2 (coefficient of determination) was used to assess and compare the goodness of fit of the regressions.

Representative mass–length regressions for elvers from each river, for comparing seasonal elver condition among rivers, were based upon random subsamples of up to 60 elvers per 5 mm length interval selected from the total sample. Analyses of elver condition within the run period were stratified by sampling period for each commercially fished river and by week for the East rivers, Chester and Sheet Harbour. Where the requirement for homogeneity of slopes was not met, samples were subdivided into groups having homogeneous slopes before further analysis. Homogeneity of mass–length regression slopes among sites/dates was evaluated by ANCOVA *F* test of the interaction between treatment (site/date) and covariate (total length) (Wilkinson et al. 1996).

Preservation effects

A sample of 60 elvers was measured fresh then preserved in 4% formalin and remeasured 2, 4, 10, and 15 d later to estimate preservation effects. Elvers preserved in 4% formalin for 15 d shrank a significant ($F_{[1,118]} = 39.6$, $P < 0.0001$) 5.6%, or 3.5 mm, in mean length. The associated 4.7%, or 0.007 g, gain in mean mass was nonsignificant ($F_{[1,118]} = 1.7$, $P > 0.10$) because of the high variability (CV = 0.18) in masses. Most (91%) of the shrinkage in mean length occurred during the first 2 d of preservation, after which no significant ($P > 0.50$) change in length occurred. Mean masses of preserved elvers increased a significant ($P < 0.0001$) 18.8% by day 4, then decreased significantly ($P < 0.001$) until day 15, leaving masses essentially unchanged from their fresh mass. Condition (adjusted mean mass) increased a significant 22% ($F_{[1,117]} = 39.7$, $P < 0.0001$), from 0.137 to 0.167 g. Biological data from preserved elvers obtained from the relatively short commercial fishery were analyzed separately from those measured fresh during the longer elver run period. Most (87%) preserved samples were processed for biological data after more than 15 d of preservation; none had been preserved for less than 5 d. Of the three samples preserved for between 5 and 9 d, none exhibited atypical patterns in the means or variances of length or mass. Length and mass changes during preservation tend to stabilize over time (Shields and Carlson 1996), and elver samples processed more than 15 d after preservation were expected to undergo little, if any, further change.

Table 1. Mean lengths and masses with 95% confidence intervals (CI), adjusted to the overall mean sampling date of May 19, of American eel elvers from rivers in the Bay of Fundy and Atlantic coast areas of New Brunswick and Nova Scotia, 1997.

River	Area*	Length (mm)	95% CI	Mass (g)	95% CI
Digdeguash	LBFNB	61.51*b*	61.10–61.93	0.224*c*	0.218–0.231
Shubenacadie	UBFNB	58.88*c*	58.58–59.19	0.211*d*	0.206–0.216
Meteghan	LBFNS	57.66*d*	57.32–58.01	0.205*d*	0.200–0.210
Mersey	SSNS	61.02*b*	60.71–61.34	0.226*c*	0.219–0.232
Gaspereaux	ESNS	63.50*a*	63.07–63.93	0.280*b*	0.274–0.285

Note: Lengths and masses were logarithmically transformed for analysis then back-transformed for presentation. Values followed by a different letter are significantly different at $\alpha = 0.05$.

*LBFNB, lower Bay of Fundy, N.B.; UBFNS, upper Bay of Fundy, N.S.; LBFNS, lower Bay of Fundy, N.S.; SSNS, South Shore, N.S.; ESNS, Eastern Shore, N.S.

Results

Elver fishery and trap sampling

In 1997, the earliest elver catches were made during late April in the Meteghan River (lower Bay of Fundy, N.S.) and by early May in the other rivers (Table 1, Figs. 1 and 2). Estuarine surface water temperatures at the time when elvers were first caught in quantity varied from 7°C on April 20 in the Meteghan River to 7.5°C on May 1 in the Shubenacadie River, 6.5°C on May 13 in the Digdeguash River, and 8°C on May 1 in the Gaspereaux River. The elver fishery ceased between early and late June in all areas.

The commercial fisheries in the estuaries of the East rivers, Chester and Sheet Harbour, began catching elvers 11–14 d before they began entering the river traps. Elvers first entered fresh water beyond the head of tide in the East River, Chester, on May 22, when the water temperature was 11.9°C. Although elvers were present earlier in the upper estuary, river entry was prevented by high water levels (Jessop 1998*b*). In the East River, Sheet Harbour, elvers first entered the freshwater traps on May 26, when the water temperature was 10.7°C. By mid-July, elver catches had declined to about 100/d in the East River, Chester, compared with over 50 000/d at the peak of the run (Jessop 1998*b*) and to 700/d in the East River, Sheet Harbour, compared with over 44 000/d at the peak of the run (B.M. Jessop, unpublished data), and the runs were considered essentially over.

Variability in length and mass seasonally and among rivers

Mean elver lengths and masses varied significantly ($P < 0.0003$ in all cases), tending to decline, throughout the commercial fishing season (late April – early June) in the Digdeguash, Shubenacadie, Meteghan, Mersey, and Gaspereaux rivers (Fig. 2) and during the elver run (late May – mid-July) in the East rivers, Chester and Sheet Harbour (Fig. 3). In each river, the relative variability (coefficient of variation) in sample masses exceeded that for lengths by three to five times. Elver lengths were approximately normally distributed, but masses tended to be positively skewed; occasional extreme values occurred in all rivers.

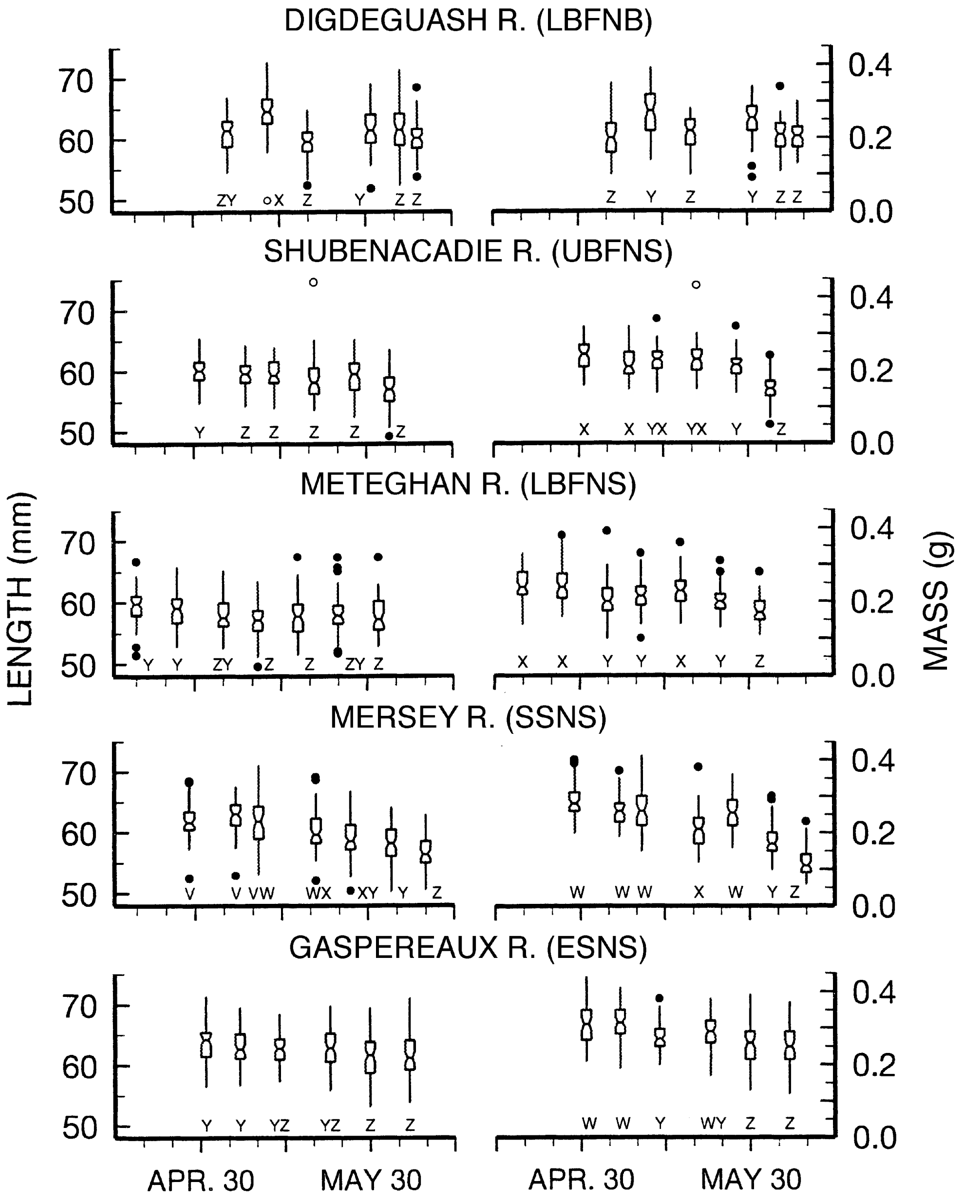
Regressions of elver length declined significantly ($P < 0.02$) with collection date for each commercially fished river, while masses declined significantly ($P < 0.001$) in four of five rivers, with no significant change ($P = 0.09$) in mass in the Digdeguash River (LBFNB; Fig. 4). If the first sample with low mass is ignored (Fig. 2), the seasonal decline in mass in the Digdeguash River is also significant. Observed declines in mean length during the fishing season ranged from 2% in the Digdeguash River to 5% in the Shubenacadie River. Declines in mean mass during the fishing season averaged 31% (35% if the early season low mass in the Digdeguash River is ignored) and ranged from 0% (or 25% if the maximum observed mean mass is used) in the Digdeguash River to 60% in the Mersey River. The minor seasonal decline in elver mean length and absence of decline in elver mass in the Digdeguash River derive from a significant increase in length and mass between the first (May 6: 61.14 mm, 0.202 g) and second (May 13: 64.44 mm, 0.270 g) samples, followed by a significant decline (May 20: 59.45 mm, 0.211 g) with no significant change in length or mass between the May 6 and May 20 samples or between the May 6 and June 8 (59.96 mm, 0.203 g) samples.

Mean elver lengths and masses, adjusted to the overall mean collection date of May 19 to account for their seasonal decline, differed significantly (as indicated by the non-overlap of the 95% confidence intervals) among elver fishing rivers (Table 1). Mean lengths and masses varied geographically, being highest in the Gaspereaux River, intermediate in the Mersey and Digdeguash rivers, and lowest in the Meteghan and Shubenacadie rivers. The maximum difference in adjusted mean lengths among the commercially fished rivers was about 9%, while mean masses differed by 27%.

Elver lengths and masses decreased irregularly throughout the elver run to the East River, Chester (Fig. 3), declining by 8 and 40%, respectively. Elver lengths were similar for the first 2 weeks of the run to the East River, Sheet Harbour, then increased significantly (6%) before declining (4%) until the end of the run for no net decline, while elver masses decreased (24%) throughout the run.

Elver length ($F_{[1,1179]} = 150.8$, $P < 0.0001$) and mass ($F_{[1,1179]} = 477.4$, $P < 0.0001$) both declined significantly throughout the run in the East River, Chester, but in the East River, Sheet Harbour, length increased slightly ($F_{[1,1018]} = 4.3$, $P = 0.038$), while mass declined ($F_{[1,1018]} = 223.4$, $P < 0.0001$) (Fig. 4). For the East River, Sheet Harbour, exclusion of the low length samples present prior to June 7 results

Fig. 2. Box plots, by river, of seasonal change in lengths and masses of preserved (4% formalin) American eel elvers from the commercial fishery in the Scotia–Fundy area of New Brunswick and Nova Scotia, 1997. Notches indicate the 95% confidence interval about the median, whiskers indicate the data range except where outliers (solid dot) and far outliers (open dot) occur. Sample mean lengths (means usually differed little from medians) and masses accompanied by a different letter are significantly different at $\alpha \leq 0.05$, based on ANOVAs and the Tukey–Kramer multiple comparison test. Data were logarithmically transformed (base 10) before analysis. N = 50–60 elvers for each commercial fishery sample except N = 46 for May 1, Shubenacadie River. LBFNB, lower Bay of Fundy, N.B.; UBFNS, upper Bay of Fundy, N.S.; LBFNS, lower Bay of Fundy, N.S.; SSNS, South Shore, N.S.; ESNS, Eastern Shore, N.S.

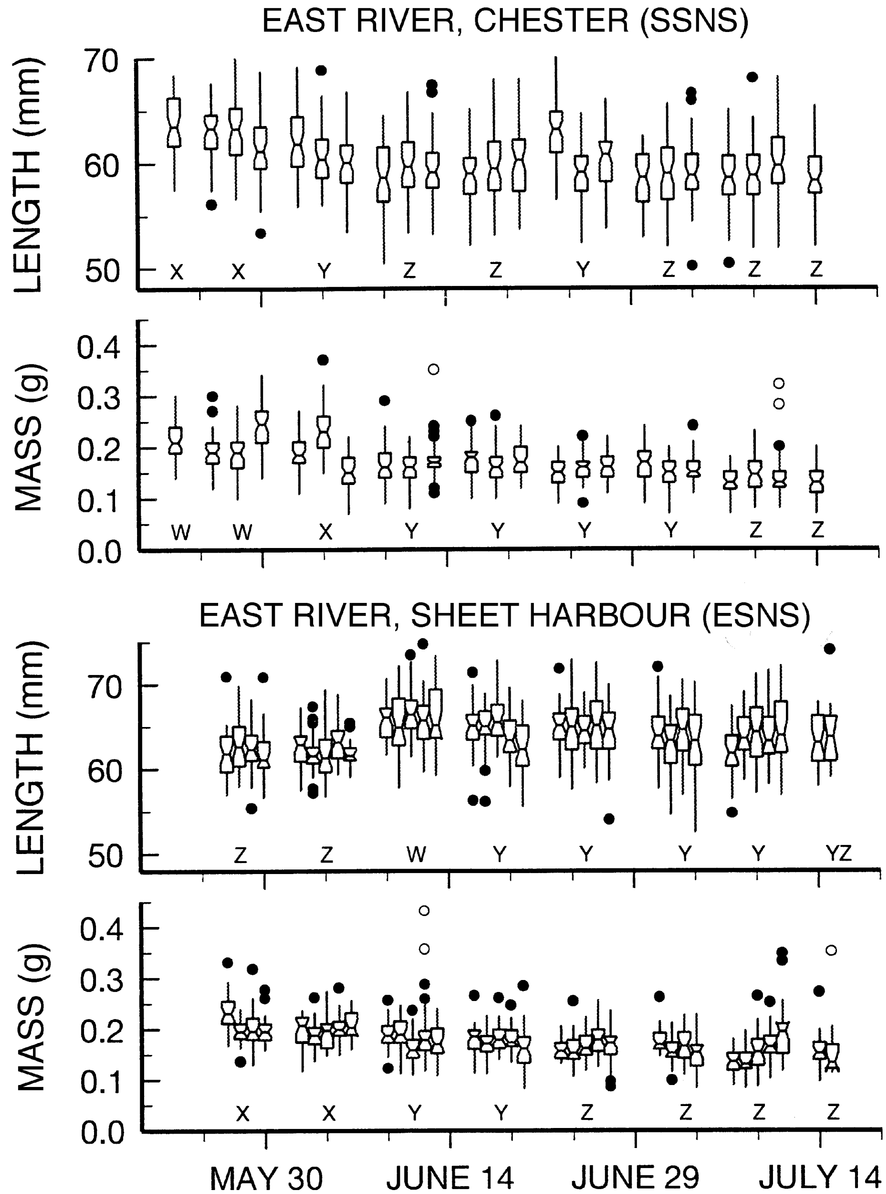


in a significant seasonal decline in length ($F_{[1,1731]} = 37.5$, $P < 0.001$). Mean lengths, adjusted to the overall mean sampling date (excluding the East River, Sheet Harbour, samples prior to June 7), were 64.7 mm in the East River, Chester, and 60.1 mm in the East River, Sheet Harbour, an 8% difference ($F_{[1,1912]} = 798.3$, $P < 0.0001$; homogeneity of slopes, $F_{[1,1911]} = 0.10$, $P = 0.76$). Mean masses differed by about 5% ($P < 0.0001$), with heavier elvers in the East River, Sheet Harbour, than in the East River, Chester (0.174 vs. 0.166 g), although heterogeneous slopes ($F_{[1,1911]} = 33.45$, $P < 0.0001$) make the comparison problematic.

Variability in condition seasonally and among rivers

Elver mass–length regressions varied among rivers (Table 2), with significant differences in regression slopes ($F_{[4,912]} = 7.9$, $P < 0.0001$) and in elver mean masses adjusted to the overall mean length (condition) among the commercially fished rivers ($F_{[4,916]} = 44.8$, $P < 0.0001$). Two groupings occurred, each with a common slope but with significantly different intercepts (equivalent to adjusted mean masses when slopes are equal) within each group. Thus, within the Digdeguash–Meteghan–Gaspereaux river group (slopes: $F_{[2,553]} = 1.5$, $P = 0.23$; intercepts: $F_{[2,555]} = 68.2$,

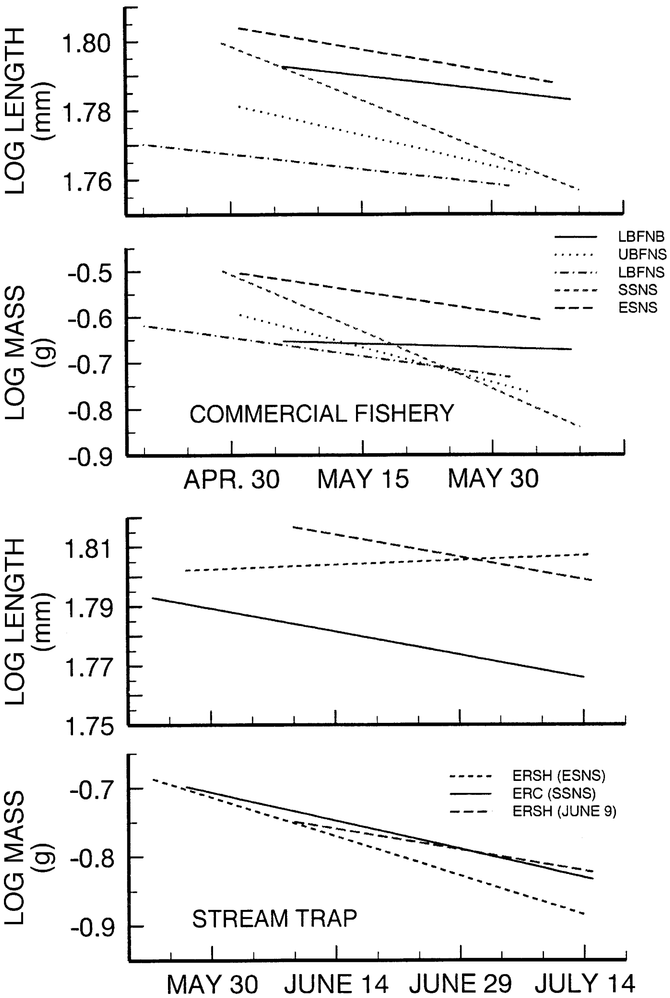
Fig. 3. Box plots of seasonal change in fresh lengths and masses of American eel elvers collected by trap in two rivers on the Atlantic coast of Nova Scotia, 1997. Notches indicate the 95% confidence interval about the median, whiskers indicate the data range except where outliers (solid dot) and far outliers (open dot) occur. Sample mean lengths (means usually differed little from medians) and masses accompanied by a different letter are significantly different at $\alpha \leq 0.05$, based on ANOVAs and the Tukey–Kramer multiple comparison test. Data were logarithmically transformed before analysis. Samples (N = 50) were taken three times weekly in the East River, Chester, and five times weekly (N = 30) in the East River, Sheet Harbour. SSNS, South Shore, N.S.; ESNS, Eastern Shore, N.S.



P < 0.0001), the adjusted mean masses were similar for the Meteghan and Gaspereaux rivers, which differed significantly from that for the Digdeguash River. For the Shubenacadie–Mersey river group, the adjusted mean masses differed significantly (slopes: $F_{[1,359]}$ = 0.5, P = 0.47; intercepts: $F_{[1,360]}$ = 18.6, P < 0.0001). Adjusted mean masses and regression slopes for elvers caught by trap in the East rivers, Chester and Sheet Harbour, also differed (adjusted means: $F_{[1,463]}$ = 16.0, P = 0.0001; slopes: $F_{[1,462]}$ = 5.1, P = 0.025). Within each river, elver mass varied moderately with length, as indicated by the r^2_{adj} values (0.47–0.67) of the mass–length regressions.

Elver condition varied significantly, typically declining, during the commercial fishing season for each river (Fig. 5A). Comparison of condition, within and among rivers, was complicated by non-homogeneity of mass–length regression slopes in some samples. Thus, the mean mass at 60 mm TL (a value close to the mean length of each sample; Table 1) was used to estimate elver condition for each sample. Mass–length regressions for samples collected throughout the commercial fishery did not differ in slope in the Digdeguash ($F_{[5,343]}$ = 0.09, P = 0.99) and Gaspereaux ($F_{[5,341]}$ = 2.06, P = 0.07) rivers, although a single sample had a different slope in each of the Meteghan (7 samples) and Shubenacadie (6 samples) rivers. In the Mersey River, 8 samples were arranged in four groups (3, 2, 1, 1 samples) with similar slopes. Declines in elver condition during the fishery ranged from 12% in the Gaspereaux River to 44% in

Fig. 4. Linear regressions of the seasonal change in lengths and masses, by river, of American eel elvers during the estuarine commercial fishery (preserved in 4% formalin) and the migration (fresh) into fresh water from rivers in the Scotia–Fundy area of New Brunswick and Nova Scotia, 1997. LBFNB, lower Bay of Fundy, N.B.; UBFNS, upper Bay of Fundy, N.S.; LBFNS, lower Bay of Fundy, N.S.; SSNS, South Shore, N.S.; ESNS, Eastern Shore, N.S.; ERC, East River, Chester; ERSH, East River, Sheet Harbour. In the regressions marked June 9 for East River, Sheet Harbour, the samples of low elver length and mass to that date have been deleted.



the Mersey River, but no change occurred in the Digdeguash River.

Elver condition (adjusted to 60 mm elver length) declined significantly (29–30%) through the run in both East rivers (Fig. 5B). Heterogeneity of sample mass–length regression slopes was minor. For the East River, Chester, two groups of samples with homogeneous slopes occurred ($F_{[6,851]} = 0.88$, $P = 0.51$; $F_{[1,312]} = 0.53$, $P = 0.47$), while for the East River, Sheet Harbour, all sample mass–length regressions had homogeneous slopes ($F_{[7,1004]} = 1.50$, $P = 0.16$).

Mean elver masses (condition), estimated at lengths of 50, 60, and 70 mm to permit comparison in the absence of common slopes, varied substantially among rivers (Table 3). Elver condition increased with increasing elver length in all rivers. The pattern and number of significant differences in elver condition among rivers varied with increasing length, owing to heterogeneous mass–length regression slopes.

Pigmentation stage

Elver pigmentation increased progressively through the spring during the fishery and the run into fresh water (Fig. 6). The degree of elver pigmentation varied by date among rivers, being significantly (based on a comparison of median 95% confidence intervals) more advanced during the fishing season in the Meteghan River (lower Bay of Fundy, N.S.) than in other rivers (geographic areas). By the end of the fishery, median elver pigmentation stages were 1–2 in the Shubenacadie (upper Bay of Fundy, N.S.) and Gaspereaux (Eastern Shore, N.S.) rivers and 3–6 in the other rivers.

The rivers of the South Shore (Mersey; East River, Chester) and Eastern Shore (Gaspereaux; East River, Sheet Harbour) illustrate the seasonal increase in pigmentation as elvers pass through the estuarine fishery and enter the river fresh waters. Elver pigmentation advanced more quickly during the early part of the run to the East River, Chester, than to the East River, Sheet Harbour, but by late June most elvers were of pigment stage 6–7.

Although elver length decreased with increasing pigmentation stage in the East River, Chester, it increased slightly with pigmentation stage in the East River, Sheet Harbour (Table 4). In both rivers, elver mass decreased with increasing pigmentation stage. Elver condition varied with increasing pigmentation stage in the East River, Chester, but developed no trend (declined if the small samples of pigmentation stages 1–2 occurring early in the run are ignored). In the East River, Sheet Harbour, elver condition decreased with increasing pigmentation stage.

Seasonal declines in condition and increase in pigmentation stage varied almost linearly with run progression, except in the East River, Chester, where a rapid decline in condition and increase in pigmentation stage occurred over the final 5% of the run (Fig. 7). By the time that 50% of the elver run (number of elvers) had entered the river, elver condition had declined about 7% in the East River, Chester, and about 9% in the East River, Sheet Harbour, and pigmentation stage averaged 4.1–4.8. By the 95th percentile of the runs, elver condition had declined about 21% in each river, and pigmentation stage averaged 5.7–6.5.

Discussion

Preservation effects

Preservation effects on fish length and mass can be substantial and highly variable, depending upon the preservative, time spent in preservation, and species involved (Shields and Carlson 1996). Although relatively small changes in length or mass may be statistically significant, particularly when samples are large, they may not be considered biologically important (Haro and Krueger 1988; Shields and Carlson 1996). However, given the small absolute size of elvers, even small changes in length or mass may become moderate (20%) changes in relative mass and condition and be perceived as of potential biological significance. Estima-

Table 2. Coefficients and their confidence intervals for the regression of mass (g) on total length (mm) ($\log_{10}$ mass = $\log_{10} a + b \log_{10}$ length, where $\log_{10} a$ is the intercept and b is the slope) for American eel elvers from rivers in New Brunswick and Nova Scotia,

River	Area*	N	r^2_{adj}	Intercept	95% CI	Slope†	95% CI	Adj. mean‡
Commercial fishery								
Digdeguash	LBFNB	188	0.59	–6.1718	–6.8328 to –5.5109	3.0801*d*	2.7110–3.4492	0.211*d* A
Shubenacadie	UBFNS	186	0.67	–7.2749	–8.1314 to –6.4183	3.7207*c*	3.2365–4.2049	0.210*c* D
Meteghan	LBFNS	185	0.52	–5.3597	–6.0191 to –4.7003	2.6601*d*	2.2862–3.0340	0.246*d* B
Mersey	SSNS	209	0.57	–7.8184	–8.6584 to –6.9784	4.0006*c*	3.5269–4.4742	0.188*c* E
Gaspereaux	ESNS	154	0.60	–5.7810	–6.3106 to –5.2515	2.9072*d*	2.6122–3.2022	0.254*d* B
Stream trap								
East, Chester	SSNS	246	0.62	–5.9473	–6.4554 to –5.4391	2.8998*a*	2.6143–3.1853	
East, Sheet Harbour	ESNS	220	0.47	–5.0756	–5.6798 to –4.4713	2.3955*b*	2.0608–2.7301	

Note: The regressions are based on random subsamples of up to 60 elvers per 5 mm length interval selected from the total sample. Regressions for each river followed by a different letter are significantly different at $\alpha = 0.05$ (ANCOVA; intercept comparisons reflect adjusted means).

*LBFNB, lower Bay of Fundy, N.B.; UBFNS, upper Bay of Fundy, N.S.; LBFNS, lower Bay of Fundy, N.S.; SSNS, South Shore, N.S.; ESNS, Eastern Shore, N.S.

†Pooled regression coefficients for the Digdeguash–Meteghan–Gaspereaux rivers: 2.7893, SE = 0.1033, $r^2_{adj} = 0.57$; for the Shubenacadie–Mersey rivers: 3.8678, SE = 0.1797, $r^2_{adj} = 0.56$.

‡Mean masses, adjusted for length and corrected for logarithmic transformation, followed by a different letter are significantly different at $\alpha = 0.05$. Letter pairs A and B and D and E denote significant differences in adjusted means within the *d* and *c* groups of nonsignificantly different slopes, respectively. Commercial fishery and stream trap catch values are not compared.

tion of condition is particularly affected by the reduction in length and gain in mass during preservation. Comparison of preserved with unpreserved elvers may be inadvisable even if conversion equations to adjust for preservation effects are available (Shields and Carlson 1996). I have not made such comparisons. If preserved samples are to be used, sufficient time should be allowed for preservation effects on fish length and mass to stabilize. In this study, preservation should not have greatly affected comparison, within or among rivers sampled by the fishery, of seasonal trends in elver length, mass, or condition because preservation effects had stabilized.

Elver fishery and trap sampling

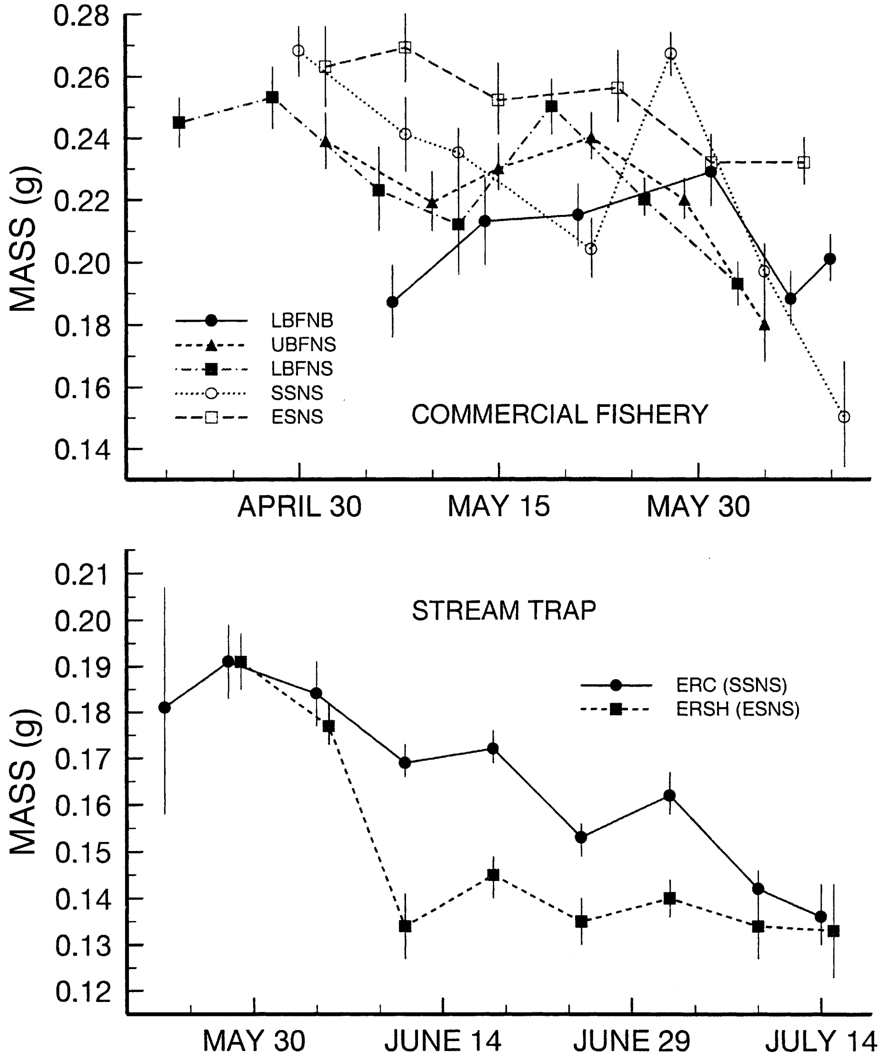
Throughout the Scotia–Fundy area, the 1997 elver fishery began when surface water temperatures in the upper estuary reached 6–8°C and elver densities became economically fishable (test fishing occurred earlier) and ceased when elver densities declined to uneconomic levels or, in some rivers, when catch quotas were reached (Jessop 1998*c*). Movement into rivers upstream of the head of tide began at 11–12°C, but such movement is also much influenced by stream water levels (Martin 1995; Jessop 1997, 1998*b*). Although over 90% of the elver run may enter a river in several waves during the first 4–5 weeks of the run, small quantities of elvers may continue to enter the river until late July or later (Jessop 1997, 1998*b*; B.M. Jessop, unpublished data). The daily pattern of catch by research traps mirrored, though with a lag of several days, the catch in the estuarine commercial fishery in the East rivers, Chester and Sheet Harbour, implying that the commercial fisheries of the other rivers reflected their elver runs.

Variability in length, mass, and condition seasonally and among rivers

The seasonal decline in elver mean length, mass, and condition that typically occurred in both the commercial fishery and in the migration upstream is well known for European eels (Cantrelle 1981; Elie and Rochard 1994) but incompletely documented for American eels (Vladykov 1970; Haro and Krueger 1988). Studying such a seasonal decline, which may vary in pattern among rivers and years (B.M. Jessop, unpublished data), requires data collection throughout the run to permit unbiased interpretation of differences in elver length, mass, and condition among rivers and years. The degree of seasonal decline in mean length observed for elvers from the Scotia–Fundy area (2–8%) compares well with that observed for elvers from Rhode Island (3–5%; Haro and Krueger 1988). European elvers from France can decline about 6–9% in mean length and 25–35% in mean mass during a 7-month migratory period (Cantrelle 1981) or even show a 52% decline in mass over 9 months (Elie and Rochard 1994), compared with a 5% decline in mean length and a 35% decline in mean mass in the Scotia–Fundy area. The decline in mass is not simply proportional to decreasing length, but rather reflects a decline in condition also. During the estuarine migratory period, elver mean condition declined up to 44% in the Scotia–Fundy area and 12–16% for European elvers (Cantrelle 1981). The difference in the seasonal decline in condition is substantial between species despite the use of different methods to estimate condition (ANCOVA for American elvers and Fulton's K for European elvers). The total seasonal decline in condition of American eel elvers is the sum of the declines occurring during the estuarine and river-entrance phases of migration, which can be roughly approximated (different rivers are involved) as 49% for each of the South Shore and Eastern Shore areas by combining the data for each migratory phase.

The reduction in length is less readily explained than the reduction in mass (Cantrelle 1981). The decrease in length during the run results from smaller elvers arriving later in the run (Boëtius 1976; Cantrelle 1981; Haro and Krueger 1988), perhaps because larger elvers have superior swimming ability to assist their initial movement inshore and later movement upstream against the higher water velocities occurring early in the run (Martin 1995; Jessop 1997, 1998*b*). Further reduction in elver length results from a rearrangement of the vertebral column in the caudal region during the

Fig. 5. Mean condition (mass adjusted to 60 mm TL) and 95% confidence intervals, by river and date, for American eel elvers during the estuarine commercial fishery (preserved in 4% formalin) and the migration into fresh water (fresh) from rivers in the Scotia–Fundy area of New Brunswick and Nova Scotia, 1997. Commercial fishery samples are 50–60 elvers; stream trap samples are pooled by calendar week and are typically 120–160 elvers, except at the start and end of each series, when some samples are 44–56 elvers. Stream-trap results for weeks 2 and 3 are shifted to avoid overlap. LBFNB, lower Bay of Fundy, N.B.; UBFNS, upper Bay of Fundy, N.S.; LBFNS, lower Bay of Fundy, N.S.; SSNS, South Shore, N.S.; ESNS, Eastern Shore, N.S.; ERC, East River, Chester; ERSH, East River, Sheet Harbour.



elver phase (Lecomte-Finiger 1977; Cantrelle 1981). No information is available on the seasonal size composition of leptocephali or glass eels sufficiently offshore that size selection offshore due to coastal current effects or inshore due to river discharge effects can be discounted.

Elver mass declines as a result of metabolic use of body energy reserves prior to initiation of feeding, which is linked to the degree of pigmentation (elvers of pigment stage 3 or 4 have usually begun feeding), which, in turn, is influenced by the seasonal increase in water temperature (Tesch 1977; Cantrelle 1981; Dutil et al. 1989). The duration of the period of inanition determines the degree of mass loss. Elver water content also increases via rehydration during the estuarine period, following the dehydration due to metamorphosis from leptocephalus to elver (Callamand 1943), which implies a greater decrease in body energy reserves than would be indicated solely by the decline in condition. After feeding resumes, energy content increases as elvers increase in mass and condition, while decreasing in water content, before growing in length (Peterson and Martin-Robichaud 1994). The few elvers of high length and mass and low pigmentation stage at the start of the elver run may derive from unusually large leptocephali or unusually rapid movement inshore (Elie and Rochard 1994). Conversely, the few eels of high pigmentation stage and typical elver mass may be juveniles that arrived in the estuary late in the previous year and did not enter the stream at that time, or may be elvers with unusually rapid pigmentation. Only ageing by otolith analysis will allow a correct determination.

The time elapsed between the first arrival of glass eels in an estuary and their movement upstream, which may vary from several weeks to months among rivers (Tesch 1977; Haro and Krueger 1988; Sorensen and Bianchini 1986; Dutil et al. 1989), may contribute to differences among rivers in

Table 3. Condition, represented by the mean mass (g) at various total lengths (mm), and associated 95% confidence intervals (in parentheses) of American elvers from rivers in the Bay of Fundy and Atlantic coast areas of New Brunswick and Nova Scotia, 1997.

		Length		
River	Area*	50 mm	60 mm	70 mm
Commercial fishery				
Digdeguash	LBFNB	0.117*d* (0.108–0.127)	0.205*d* (0.200–0.211)	0.330*d* (0.313–0.348)
Shubenacadie	UBFNS	0.113*d* (0.104–0.123)	0.223*c* (0.216–0.230)	0.396*c* (0.362–0.433)
Meteghan	LBFNS	0.147*c* (0.108–0.138)	0.238*b* (0.232–0.245)	0.359*cd* (0.333–0.387)
Mersey	SSNS	0.099*d* (0.090–0.108)	0.205*d* (0.197–0.213)	0.380*c* (0.348–0.415)
Gaspereaux	ESNS	0.145*c* (0.136–0.155)	0.245*b* (0.241–0.252)	0.384*c* (0.371–0.401)
Stream trap				
East, Chester	SSNS	0.097*d* (0.092–0.103)	0.165*d* (0.156–0.175)	0.258*c* (0.245–0.271)
East, Sheet Harbour	ESNS	0.100*d* (0.092–0.109)	0.156*d* (0.151–0.161)	0.225*d* (0.216–0.234)

Note: Adjusted mean masses were estimated from mass–length regressions and corrected for logarithmic transformation. Mass–length regressions are based on random subsamples of up to 60 elvers per 5 mm length interval drawn from the total sample for each river. Values followed by a different letter are significantly different at $\alpha \leq 0.05$.

*LBFNB, lower Bay of Fundy, N.B.; UBFNS, upper Bay of Fundy, N.S.; LBFNS, lower Bay of Fundy, N.S.; SSNS, South Shore, N.S.; ESNS, Eastern Shore, N.S.

Fig. 6. Box plots, by river, of seasonal change in pigmentation stage of American eel elvers from the commercial fishery (A) and trap surveys (B) in the Scotia–Fundy area of New Brunswick and Nova Scotia, 1997. Notches indicate the 95% confidence interval about the median; whiskers indicate the data range except where outliers (solid dot) and far outliers (open dot) occur. In the A panels, samples are 50–60 elvers; in the B panels, samples are pooled by calendar week and are typically 120–160 elvers, except at the start and end of each series, when some samples are 44–56 elvers. LBFNB, lower Bay of Fundy, N.B.; UBFNS, upper Bay of Fundy, N.S.; LBFNS, lower Bay of Fundy, N.S.; SSNS, South Shore, N.S.; ESNS, Eastern Shore, N.S.

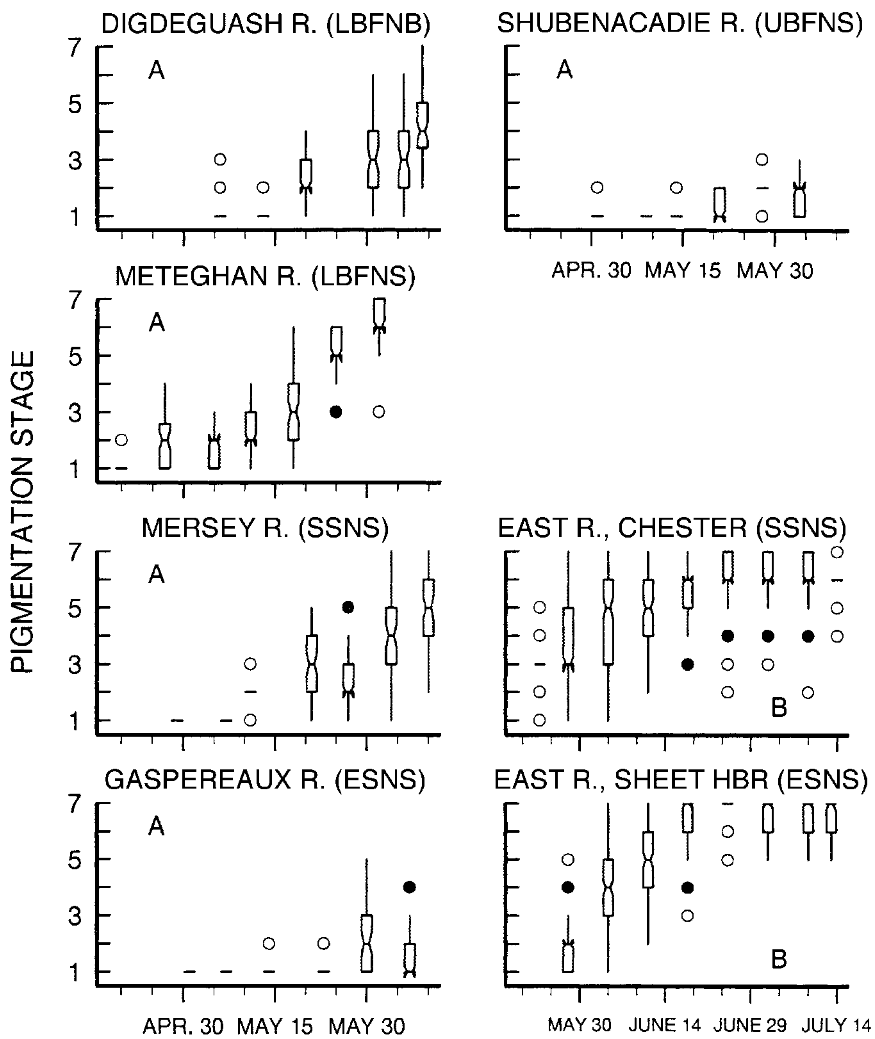


Table 4. Mean total lengths (mm), masses (g), and condition (g) with 95% confidence intervals (CI), by pigmentation stage, of American eel elvers from two Nova Scotia rivers, 1997.

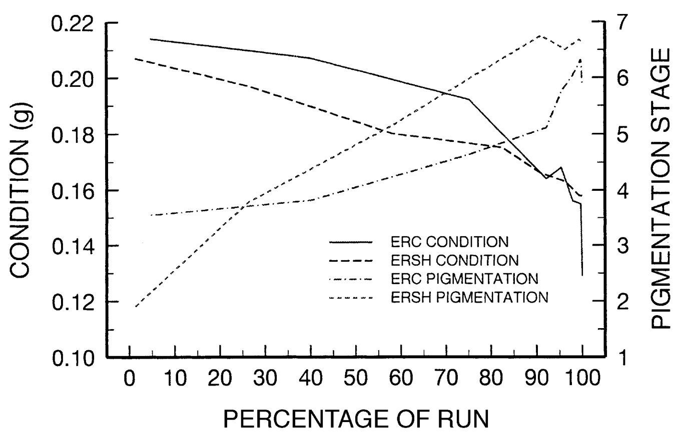
	Pigmentation stage						
	1	2	3	4	5	6	7
				East River, Chester			
N	4	44	137	134	194	424	222
Length	62.7*cd*	62.0*d*	62.3*d*	61.2*c*	59.8*c*	59.5*c*	59.7*c*
CI	60.0–65.4	60.9–63.1	61.8–62.9	60.6–61.8	59.3–60.2	59.2–59.8	59.2–60.1
Mass	0.185*bd*	0.184*d*	0.198*d*	0.186*d*	0.170*cd*	0.157*bc*	0.158*b*
CI	0.155–0.216	0.171–0.197	0.191–0.205	0.178–0.194	0.164–0.176	0.153–0.160	0.154–0.163
Condition	0.168*bcd*	0.169*cd*	0.180*b*	0.176*b*	0.171*c*	0.160*d*	0.161*d*
CI	0.139–0.203	0.159–0.179	0.175–0.187	0.170–0.182	0.160–0.175	0.157–0.163	0.157–0.165
				East River, Sheet Harbour			
N	48	81	63	74	105	211	438
Length	62.5*c*	62.7*c*	62.9*c*	63.3*cd*	63.7*d*	63.8*d*	64.5*d*
CI	61.6–63.4	62.0–63.3	62.2–63.6	62.5–64.1	63.1–64.7	64.3–63.4	64.2–64.8
Mass	0.211*d*	0.202*d*	0.192*cd*	0.185*c*	0.177*bc*	0.166*b*	0.169*b*
CI	0.201–0.211	0.194–0.209	0.185–0.198	0.177–0.193	0.170–0.184	0.161–0.171	0.166–0.173
Condition	0.222*a*	0.210*ab*	0.199*bc*	0.188*bc*	0.176*c*	0.165*d*	0.163*d*
CI	0.213–0.233	0.203–0.218	0.191–0.207	0.181–0.195	0.171–0.181	0.161–0.168	0.161–0.166

Note: Values followed by a different letter are significantly different at $\alpha = 0.05$. "Condition" is mean mass adjusted to 60.2 mm for the East River, Chester, and 63.8 mm for the East River, Sheet Harbour.

elver mass and condition. Differences among rivers in this delay could increase the variability of differences in elver mass and condition among rivers via increased mass gain by rehydration or more rapid resumption of feeding for later arriving elvers (Callamand 1943; Cantrelle 1981). A relatively short delay between estuary arrival and upstream migration may minimize the potential variability in elver mass and condition. Elver arrival in the estuary in advance of conditions (stream water temperature, discharge) suitable for stream entrance and upstream migration may have survival advantages over late arrival, particularly when the delay is short. In the East River, Chester, elvers were first caught (test fishing began 11 d before first capture) in the fishery 11 d before their first entrance to the river, yet once upstream migration was established, only 1–3 d passed between catch peaks in the fishery and in the stream traps (Jessop 1998*b*, 1998*c*). In the East River, Sheet Harbour, elvers were first caught 14 d after the start of the fishery and, after upstream migration was established, a lag of 8–9 d occurred between catch peaks in the fishery and in the traps.

Seasonal declines in elver length, mass, and condition may influence rates of upstream movement and survival, but there is little evidence for such effects. The tendency to migrate varies among individual eels (Naismith and Knights 1988), and larger eels may migrate upstream over a longer period than smaller eels (Moriarty 1986). It is plausible that the larger, better conditioned elvers arriving early in the run may migrate more quickly and farther upstream during their first summer in fresh water (Fontaine 1976), but it is not known if they do so (Elie and Rochard 1994). Eel densities tend to decrease in upriver reaches (Smith and Saunders 1955; Smogor et al. 1995) and there may be survival benefits at the individual and stock level for dispersal through the river system. Whether elver or juvenile eel mortality depends on size or age is uncertain (De Leo and Gatto 1995). Size-dependent mortality of marine organisms, with decreased vulnerability to starvation and predation with in-

Fig. 7. Mean condition and pigmentation stage, in relation to cumulative run proportion (number of elvers), of American eel elvers from the East River, Chester (ERC), and East River, Sheet Harbour (ERSH), Nova Scotia, 1997. Condition is the mean mass of weekly elver samples adjusted by mass–length regression to an overall mean length of 60.2 mm for the East River, Chester, and 63.8 mm for the East River, Sheet Harbour. Masses and lengths were logarithmically transformed for analysis, then back-transformed for presentation.



creasing size, has been widely accepted (Pepin 1991, 1993). However, larval mortality rates, relative to fish size, may be constant for some marine species (Pepin 1993). The decline in elver length, mass, and condition during their migration into fresh water and increase in size of larval/juvenile marine fishes during these life stages might imply that elver mortality rates increase seasonally as elver size declines. Such a conclusion is premature. The greater lengths and masses of early elver migrants may compensate, through higher body energy reserves (Brett and Groves 1979), for the higher probability of seasonally adverse environmental conditions (low water temperatures, high stream discharge, and low prey availability) early in the run and consequent delay in the initiation of feeding and in upstream migration (Cantrelle 1981; Martin 1995; Jessop 1997, 1998*b*). The low pigmentation stage of early arrivals also reflects a less developed digestive tract and dentition (Cantrelle 1981). The smaller size of later migrants may be balanced by their greater pigmentation stage (physiological development) and better environmental conditions (higher water temperatures, lower stream discharge, greater prey availability), with consequently less effect on the initiation of feeding, upstream migration, and mortality rate.

The biological importance of seasonal declines in elver length, mass, and condition during spring migration may be determined largely by the degree of decline and the proportion of the run so affected. Elver runs typically exhibit several waves or peaks of abundance, influenced by environmental factors such as tidal phase, river discharge, and water temperature (Tesch 1977; Martin 1995; Jessop 1997, 1998*b*). Consequently, the number of elvers in any specific developmental state might also vary with their abundance. However, the roughly linear interactions of declining elver condition and increasing physiological development, as indicated by pigmentation stage, with run progression produced through the migration period roughly equal numbers of elvers in each elver condition/pigmentation state. Presumably, the seasonal pattern of variability in elver state reflects the developmental and ecological plasticity of eels (Helfman et al. 1987) encountering the high environmental variability during spring in the Scotia–Fundy area. A uniform distribution of the number of elvers of various developmental stages during a run, rather than pulses of particular states, could indicate an efficient bet-hedging strategy, while higher proportions of better conditioned elvers could reflect the survival value of higher condition.

The mortality rate of wild elvers during their first year in fresh water is unknown but likely high and variable. Knowledge of factors, such as seasonal and geographic variability in elver condition, that might influence first-year mortality may assist our understanding and management of this critical life stage. For example, is it practical or desirable to more highly exploit a portion of the run where natural mortality may be higher? Overall exploitation by an elver fishery might, amongst other considerations, be set relative to the first-year elver mortality rate.

The geographic pattern in elver mean lengths and masses (highest in the Gaspereaux River, intermediate in the Mersey and Digdeguash rivers, and lowest in the Meteghan and Shubenacadie rivers) may be linked with ocean currents (Jessop 1998*c*). Elver mean lengths tend to increase northward along the Atlantic coast (Vladykov 1966; Haro and Krueger 1988), perhaps reflecting leptocephali / glass eel length distributions in the offshore, northeast-flowing Gulf Stream. After elvers depart the Gulf Stream for the continental shelf, their lengths may decrease, via differential loss of the larger elvers, the farther they are carried by coastal currents such as the Nova Scotia Current, which flows southwestward along the Scotian Shelf offshore of the Atlantic coast of N.S., moves around the southeastern tip of N.S. into the lower Bay of Fundy and subsequently merges with a northward current from the Gulf of Maine gyre, then continues counterclockwise around the Bay of Fundy (Hachey et al. 1954). The larger, rather than smaller, mean size of elvers from the Digdeguash River on the N.B. side of the lower Bay of Fundy than from the Meteghan River on the N.S. side may arise from slope water intrusions into the upper Gulf of Maine and lower Bay of Fundy bringing in elvers from the continental shelf via the Northeast Channel rather than via the Nova Scotia Current and counterclockwise progression around the Bay of Fundy (Sutcliffe et al. 1976; Smith 1983).

A seasonal increase then decline in mean elver length in the East River, Sheet Harbour, may indicate the arrival of different waves of elvers to the estuary. Two modes occurred 6 d apart during elver migration into fresh water (B.M. Jessop, unpublished data), but whether these modes indicate waves of elver arrival in the upper estuary or the gating effects of environmental factors such as stream discharge or tidal phase (Martin 1995; Jessop 1997) is uncertain. Oceanographic conditions (currents, water temperatures) over the Scotian Shelf are complex and may well distribute different groups of eel larvae / glass eels among different geographic regions (Jessop 1998*c*). Although heterogeneity of regression slopes adds complexity to the analysis of seasonal changes in elver lengths, masses, and condition, such complexity seems to be inherent in the high variability of elver mass at a given length and the existence of seasonal changes and geographic variability in elver lengths and masses. Comparisons of lengths and masses among rivers will be substantially biased if seasonal effects are not considered and may be detrimental to future comparative or meta analysis, e.g., Vøllestad (1992).

Seasonal declines in mean length may be unimportant to the elver fishery, but declines in mass have an economic impact because elvers may be sold either by mass or by piece count. A seasonal decline of 35% in elver mass substantially reduces income when the market value is about CAN$500/kg (Statistics Branch, Department of Fisheries and Oceans, P.O. Box 550, Halifax, NS B3J 2S7, Canada). When piece count is used to determine value, a 35% reduction in mass increases the count from 3660 elvers/kg at the start of the fishery to 5580 elvers/kg at the end of the fishery, given the overall observed mean elver masses at the respective times. Whether fisher income is enhanced by selling by the piece rather than by mass is determined by buyer preference and the price for each sales method.

The seasonal decrease, or slight increase, in elver length with increasing pigmentation stage reflects the variability among streams in the specific pattern of interaction between seasonally declining elver length and increasing pigmentation stage. At a given pigmentation stage, elver mass may decrease seasonally in a more consistent manner than does length because of the greater relative decline in mass than in length. Variability in the nature of seasonal trends in length and mass with increasing pigmentation stage determines the presence or absence of a seasonal decline in condition. The decline (or moderate increase) in elver length and decline in elver mass with increasing pigmentation stage observed in this study occurred also in elvers from the north shore of the Gulf of St. Lawrence in the early stages of pigmentation but not in the later stages, when the elvers had begun to feed (Dutil et al. 1989). Elver runs in the Scotia–Fundy area are of shorter duration, and progression through the range of pigmentation stages is more rapid than in European elver runs (Cantrelle 1981; Elie and Rochard 1994). Consequently, the seasonal decrease in European elver length and mass, within a given pigmentation stage, has no equivalent in the elver runs of the Scotia–Fundy region. The conclusion that a higher degree of pigmentation of European elvers indicates earlier entrance to the estuary because of the interaction of the phenomena of seasonally decreasing elver length and mass within a given pigmentation stage and the more general seasonal decline in elver length and mass (Cantrelle 1981; Elie and Rochard 1994) may not usefully apply to American elvers in the Scotia–Fundy area. The increasing pigmentation of later running elvers may simply reflect an increased rate of pigmentation in response to rapidly rising water temperatures and the stimulus to pigmentation provided by entrance into estuarine and fresh waters (Cantrelle 1981) rather than a longer residence. This conclusion is consistent with the relatively short time between appearance in the upper estuary and catch in the fishery and entrance into fresh water and movement upstream. Increased pigmentation increases, via protective coloration, the adaptation of elvers to a stream-bottom existence.

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