

## Pigmentation, size, and migration of elvers (*Anguilla rostrata* (Lesueur)) in a coastal Rhode Island stream

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Progressive pigmentation of *Anguilla rostrata* elvers was very similar to that described for *A. anguilla*. Pigmentation increased rapidly with the advancing season, while total length decreased. The increase in pigmentation was independent of the decrease in length and may have been influenced by increased contact with the substrate. Mean lengths showed significant differences within seasons and between years, and the range of variation was greater than that described by V. D. Vladykov (1966. *Verh. Int. Ver. Theor. Angew. Limnol.* **16**: 1007–1017) for elvers collected from Maryland to Quebec. We substantiate Vladykov's finding that elver size tends to increase with increasing distance from the spawning area, but reject his size/sex hypothesis. The main migration occurred in April and May and was related to decreasing water depth and rising stream temperature. Elvers took about 4 weeks to ascend 180 m above the tidal zone, probably because of a high stream gradient and the absence of tidal influence.

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L'apparition progressive de la pigmentation chez les civelles d'*Anguilla rostrata* se rapproche beaucoup de celle qui se produit chez *A. anguilla*. La pigmentation augmente rapidement au cours de la saison, alors que la longueur totale diminue. L'augmentation de la pigmentation se fait indépendamment de la diminution de longueur et est sans doute influencée par les contacts de plus en plus fréquents avec le substrat. La longueur moyenne varie significativement d'une saison à l'autre et d'une année à l'autre et l'amplitude des variations obtenue ici s'est avérée supérieure à celle qui a été décrite par V. D. Vladykov (1966. *Verh. Int. Ver. Theor. Angew. Limnol.* **16** : 1007–1017) pour des civelles récoltées du Maryland au Québec. Nous sommes d'accord avec la conclusion de Vladykov, à savoir que la taille des civelles tend à augmenter en fonction de la distance d'éloignement de l'aire de fraye, mais nous rejetons son hypothèse taille/sex. La migration principale a lieu en avril et en mai et est reliée à la profondeur décroissante de l'eau et à la température croissante du cours d'eau. Les civelles mettent environ 4 semaines à remonter jusqu'à 180 m au-delà de la zone de marée, probablement à cause du gradient assez fort du ruisseau et de l'absence de l'influence des marées.

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### Introduction

Unpigmented elvers (glass eels) of the American eel, *Anguilla rostrata*, appear in estuaries in winter and spring (Jeffries 1960; Vladykov 1966; Eldred 1968). Sorensen and Bianchini (1986) studied the influence of environmental factors on freshwater migration, but gave little information on pigmentation or size. Hickman (1981) and Sykes (1981) included data on size and (or) pigmentation, but did not quantify the relationship between the two. Neither addressed variation from year to year.

Our study focuses on the following: (i) pigmentation in comparison with that of the closely related European eel, *A. anguilla*; (ii) spatial and temporal variation in pigmentation and total length; and (iii) the upstream migration in relation to environmental factors. We also reexamine Vladykov's (1966) geographic size/sex hypothesis in the light of additional information on both elvers and adult eels.

### Materials and methods

Elvers were collected from the Annaquatucket River, a small coastal freshwater stream in Rhode Island, U.S.A. (41°33'N, 76°26'W). Samples were taken at three stations between Mill Pond and Bissel Cove (Fig. 1) from 30 March to 28 May 1983, and from 27 January to 19 June 1984. Data on elvers dipnetted at the same stations in 1982 were provided by James DiCanzio. Stream depth was

0.2–0.5 m; stream width was 5–10 m. Gradient averaged 2.2%. All collections were made at or near low tide, when even the tidal station was completely fresh, with the water shallow and flowing rapidly. In 1984, stream level was recorded to the nearest centimetre at a gauge above the Mill Pond dam and water temperature was recorded to the nearest 0.5°C just below the dam.

In 1983 elvers were collected from the upper 5–10 cm of substrate (sand, gravel, and cobble) with a reinforced dip net of 0.5-mm mesh. Approximately 50% of the catch was placed in 95% ethanol; the remaining elvers were fixed in 10% buffered formalin and transferred to 70% ethanol after 72 h. Total lengths were measured to 0.1 mm with dial calipers; length data are expressed as mean  $\pm$  SE. Mean lengths of elvers preserved in 70% ethanol ( $56.82 \pm 0.11$  mm,  $n = 764$ ) were significantly greater than those preserved in 95% ethanol ( $56.38 \pm 0.11$  mm,  $n = 610$ ) ( $P < 0.05$ ); however, we consider the 0.44-mm difference unimportant for reasons that will become obvious.

In 1984 elvers were collected with a Smith-Root type VII electrofisher. Sections of stream ca.  $1 \times 8$  m were electrofished downstream into a  $0.6 \times 1.8$  m bag seine constructed of 1.5-mm mesh. All 1984 fish were anesthetized with MS-222, fixed in 10% buffered formalin, and transferred to 70% ethanol after 72 h. All 1983 elvers were used in the analyses, but large 1984 collections were subsampled by removing 100 specimens at random. To evaluate the validity of this methodology, a subsample of 100 fish was taken from a sample of 227. No significant difference was found between the mean length of the subsample and that of the entire sample ( $P > 0.05$ ).

Epidermal pigmentation was examined under a binocular dissecting microscope at  $15\times$  and a pigmentation sequence was derived based on classifications by Strubberg (1913), Boëtius (1976), and Charlon and Blanc (1982) (Table 1). We recognized seven stages (Fig. 2). Stage 1: no pigment on any part of body between dorsal and anal fin origins. Stage 2: pigment along base of dorsal fin, but not extending

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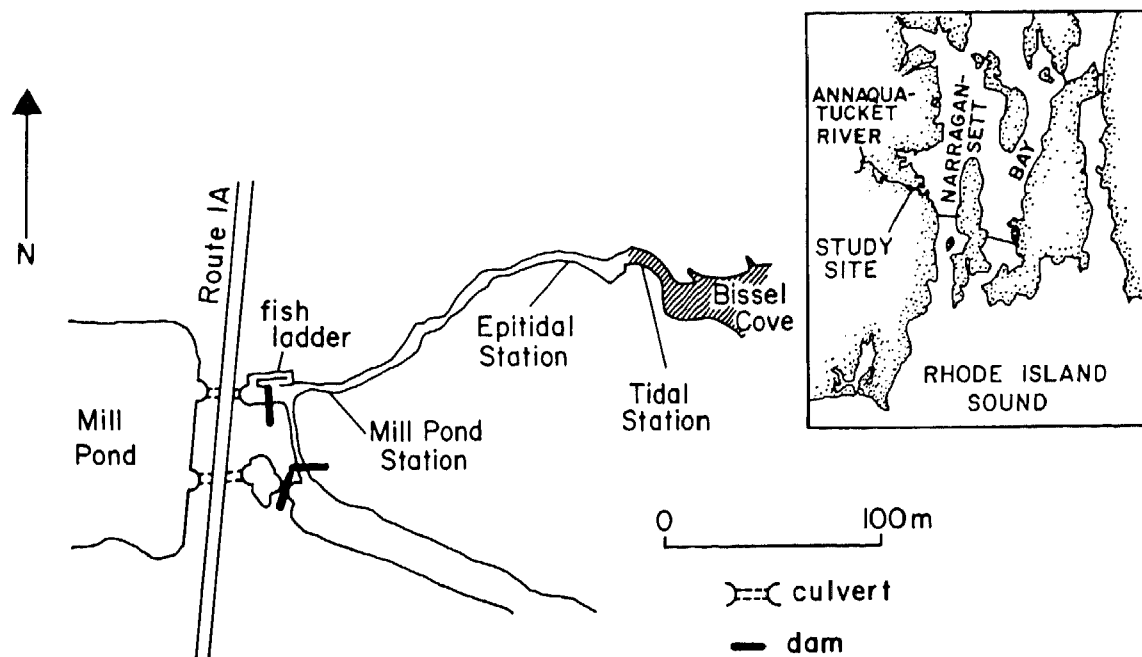


FIG. 1. Elver sampling areas on the lower Annaquatucket River. Shading indicates areas of tidal influence.

below apices of dorsal posterior cone myosepta. Stage 3: pigment extends ventrally along myosepta ca. halfway to lateral line; intermyoseptal pigment present or absent. Stage 4: pigment extends to lateral line, which is now distinctly pigmented; intermyoseptal pigment usually present dorsolaterally. Stage 5: pigment extends ventrally to midway between lateral line and apices of ventral posterior cone myosepta; intermyoseptal pigment always present dorsolaterally, but pigment more intense along myosepta. Stage 6: pigment extends further ventrally along myosepta, forming irregular ventral margin; dorsolateral surfaces uniformly pigmented; intermyoseptal pigment usually present below lateral line, but myosepta more distinctly pigmented; pigment on base of dorsal fin present or absent. Stage 7: previously pigmented areas now uniformly pigmented, obscuring myoseptal pigmentation; ventral margin or pigment a distinct line; base of dorsal fin usually pigmented; base of anal fin pigmented or not.

Mean lengths were compared with *t*-tests and mean pigmentation stages with Duncan's multiple range test. Because of wide variation of sample sizes (Fig. 3), two-way analyses of variance were based on means for each date and station rather than on the raw data.

## Results

### Pigmentation

Elvers became progressively more pigmented with the advancing season at all three stations in both years (Figs. 3, 4). Mean pigmentation stage (stations pooled) increased from 2.82 on 8 April to 5.57 on 28 May in 1983 and from 1.53 on 14 March to 6.21 on 19 June in 1984. Two-way analysis of variance of the means for 16 April to 28 May 1983 indicated significant differences in pigmentation with time ( $F_{[5,18]} = 56.02$ ;  $P < 0.0001$ ) and significant differences among stations ( $F_{[2,18]} = 8.35$ ;  $P < 0.01$ ). Means for the tidal (4.26) and epitidal (4.43) stations were not significantly different, but the mean for the Mill Pond station (4.76) was significantly greater ( $P < 0.05$ ).

### Total length

Elver length decreased over time at all three stations in both years (Fig. 5). Mean lengths (stations pooled) decreased from

TABLE 1. Comparison of pigmentation stages recognized in this study with those of European authors

This study	Strubberg 1913	Boëtius 1976	Charlon and Blanc 1982
1	VB	A	1
2	VI AI, 1	B	2
3	VI AII, 1-4	C	3
4	VI AIII, 1-3	C	3, 4
5	VI AVI, 1-3	D	4
6	VI AVI, 4	D	5, 6
7	VI B, 1	E	7

$57.79 \pm 0.31$  mm on 8 April to  $55.82 \pm 0.26$  mm on 28 May in 1983 and from  $60.93 \pm 0.26$  mm on 14 March to  $57.96 \pm 0.23$  mm on 19 May in 1984. Two-way analysis of variance of the means for 16 April to 28 May 1983 revealed significant differences in length with time ( $F_{[5,18]} = 8.37$ ;  $P < 0.01$ ), but no significant differences among stations ( $F_{[2,18]} = 1.81$ ;  $P = 0.21$ ).

Mean lengths and 95% confidence intervals of Annaquatucket elvers collected in 1982-1984 were compared with lengths of elvers from other localities in North America (Fig. 6). Although mean lengths for 1982 ( $56.44 \pm 0.10$  mm) and 1983 ( $56.63 \pm 0.08$  mm) were not significantly different, the mean for 1984 ( $59.35 \pm 0.08$  mm) was significantly greater ( $P < 0.0001$ ) and is the largest mean shown.

### Upstream migration

In 1984, when sampling began on 27 January, elvers first appeared at the tidal station ( $n = 2$ ) on 30 January, at the epitidal station ( $n = 1$ ) on 14 March, and at the Mill Pond station ( $n = 7$ ) on 23 April. Elvers first became abundant ( $n \geq 100$ ) at these stations on 14 March, 9 April, and 20 May, respectively (Fig. 4). Elver abundance peaked on 23 April at the tidal and epitidal stations and on 20 May at the Mill Pond station (Fig. 7). This time period showed the greatest increase in

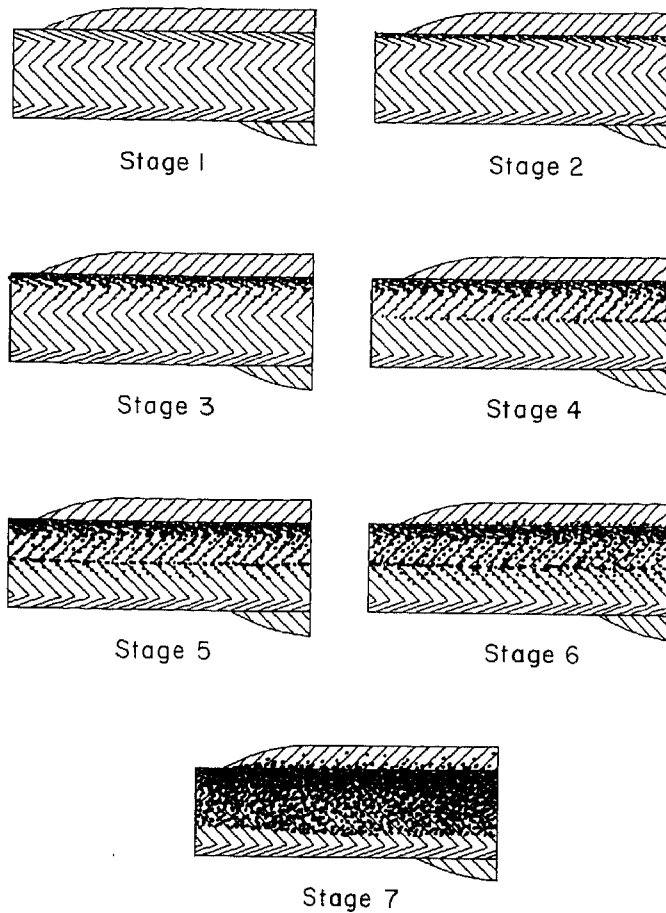


FIG. 2. Pigmentation stages recognized in this study.

stream temperature (from 10.5 to 21.5°C) and the lowest water levels (5 or more cm below the baseline) for the sampling period (Fig. 7).

### Discussion

#### Pigmentation

Progressive pigmentation in Annaquatucket River elvers was similar to that described for *A. anguilla* elvers. Boëtius (1976) assigned pigmentation stages to elvers of both *A. anguilla* and *A. rostrata* in Denmark and made no mention of differences between the species. The only difference we noted was that *A. rostrata* tends to develop pigment on the base of the dorsal fin somewhat later than *A. anguilla*. None of our elvers were completely unpigmented, which indicates that *A. rostrata* elvers develop cerebral and caudal pigment before entering freshwater, as in *A. anguilla* (Bertin 1956).

Elvers became significantly more pigmented as the season progressed, possibly in response to rising temperature. Struberg's (1913) experiments with *A. anguilla* showed that the rate of pigmentation increases with increasing temperature and Charlton and Blanc (1982) observed increased pigmentation in elvers entering warmer fresh water versus delayed pigmentation in those from colder coastal waters. Our later arriving elvers were more pigmented, which suggests that pigmentation proceeds rapidly offshore as the season progresses and the temperature of coastal waters increases.

By the time elvers reached the Mill Pond station they were significantly more pigmented than those collected at the down-

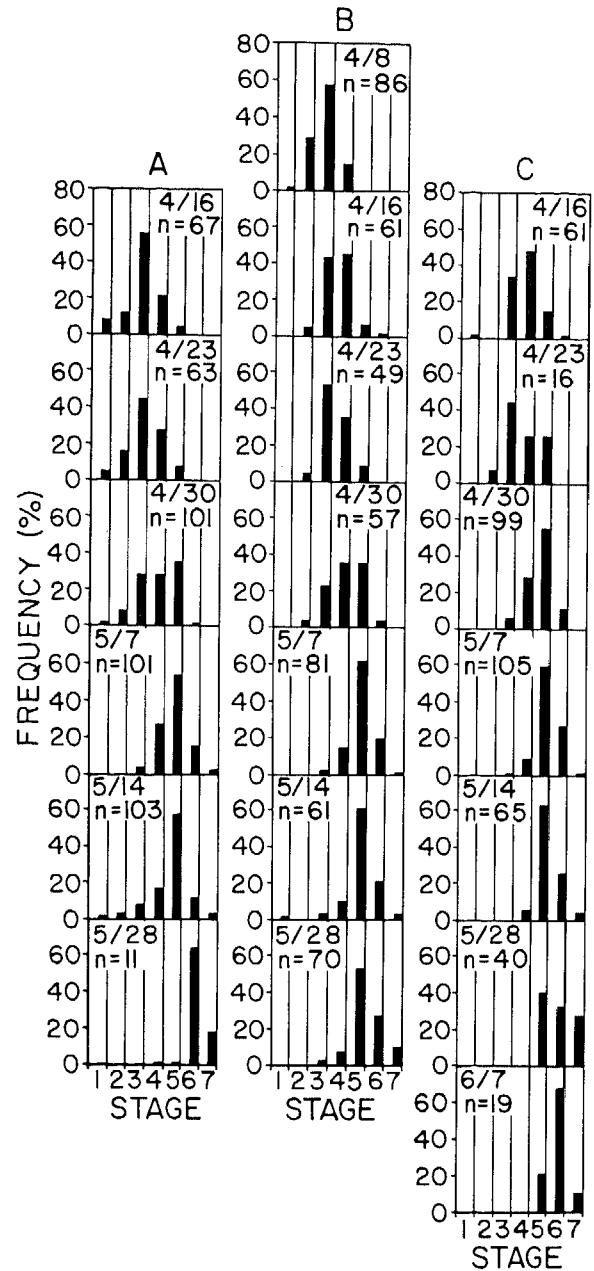


FIG. 3. Frequency distribution of pigmentation stages at each sampling station in 1983. Column A, tidal station; column B, epitidal station; column C, Mill Pond station. Only samples with  $n > 10$  are included. Dates are given as month/day.

stream stations, despite the lack of significant interstation differences in elver length. Thus the increase in pigmentation is independent of the decrease in length and may be influenced by some factor(s) in addition to temperature. Travel time between the tidal and epitidal stations and between the epitidal and Mill Pond stations was about the same (see below); thus time alone does not explain the increase. Because the development of pigment adapts the pelagic glass eel to a benthic existence, the increase in pigmentation between the epitidal and Mill Pond stations may reflect increased contact with the substrate.

#### Total length

Reduction in length over time (Fig. 5) has also been shown

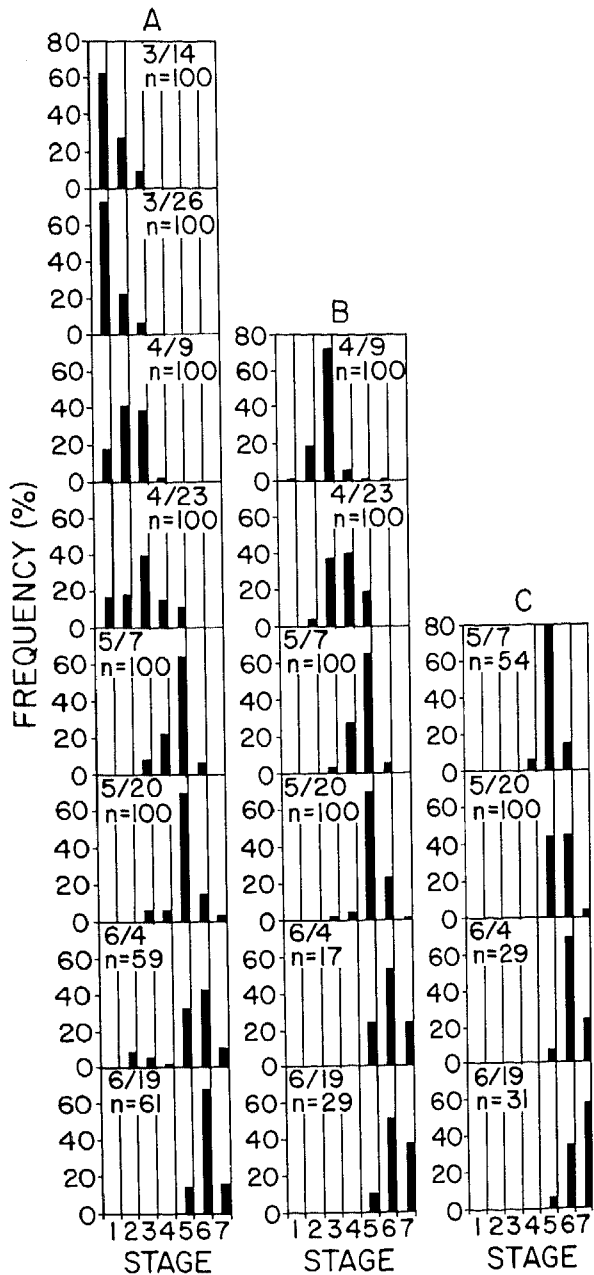


FIG. 4. Frequency distribution of pigmentation stages at each sampling station in 1984. Column A, tidal station; column B, epitidal station; column C, Mill Pond station. Only samples with  $n > 10$  are included. Dates are given as month/day.

for elvers in Maine (Hickman 1981: Fig. 1d) and mirrors studies of *A. anguilla* (Strubberg 1923; Boëtius 1976; Charlon and Blanc 1982). Seasonal decreases in length have been attributed to two mechanisms; our data support only one. Strubberg's (1913) experiments suggested that elvers shrink as they develop pigment in response to increasing temperature. In contrast, Strubberg (1923), Boëtius (1976), and Charlon and Blanc (1982) attributed seasonal decreases in length to later arriving elvers averaging progressively shorter. Because elver length decreased with the advancing season at all three stations in both years of our study (Fig. 5), but showed no significant change among stations, the decrease in length must be due to later arriving elvers averaging smaller. If length con-

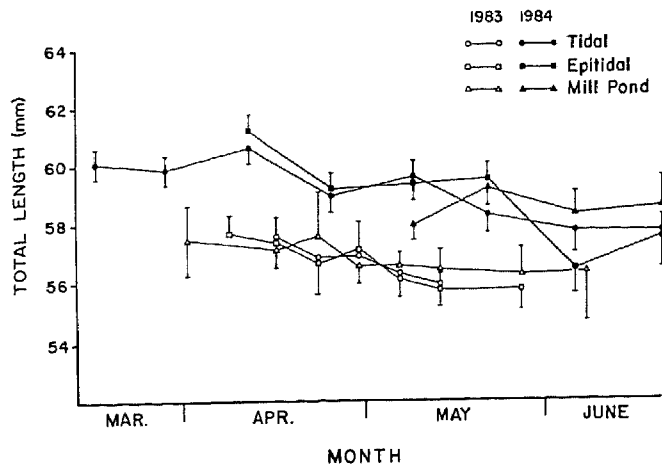


FIG. 5. Seasonal changes in total lengths of elvers in 1983 and 1984. Only samples with  $n > 10$  are included. Vertical bars indicate 95% confidence intervals.

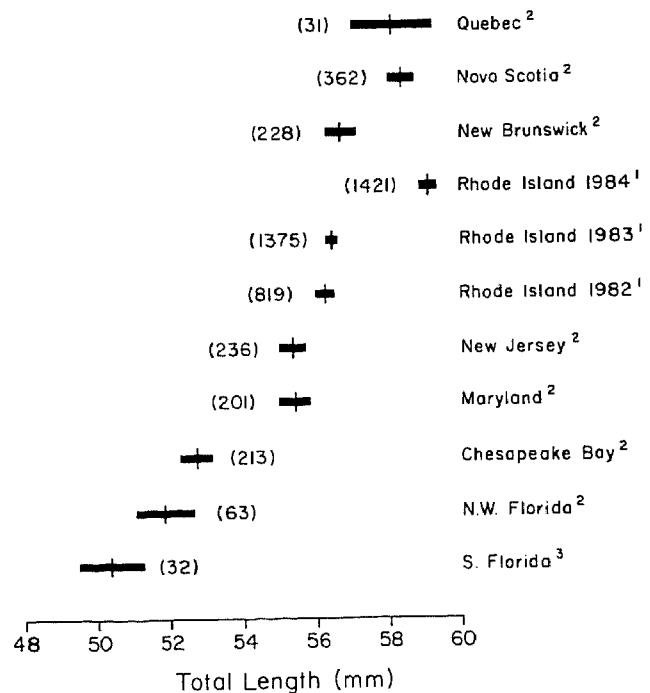


FIG. 6. Mean total lengths (vertical bars) and 95% confidence intervals (rectangles) for North American collections of elvers, arranged in order of increasing distance from the spawning area. Numbers in parentheses indicate sample sizes. Superscript numbers indicate sources: 1, present study; 2, Vladykov 1966; 3, Smith 1968. We converted Smith's standard lengths to total lengths by multiplying by 1.02, a conversion factor derived from our elvers.

tinues to decrease as elvers ascend the Annaquatucket, the shrinkage is too gradual to be detected within our 180-m study area.

McCord (1977) found no correlation between weight of glass eels and collection date in South Carolina and Sykes (1981) found a net increase in length with the advancing season for elvers in North Carolina. Both study sites were much further inland than ours, suggesting that the size-time relationship may change with distance from the sea.

Vladykov (1966) described a progressive increase in the

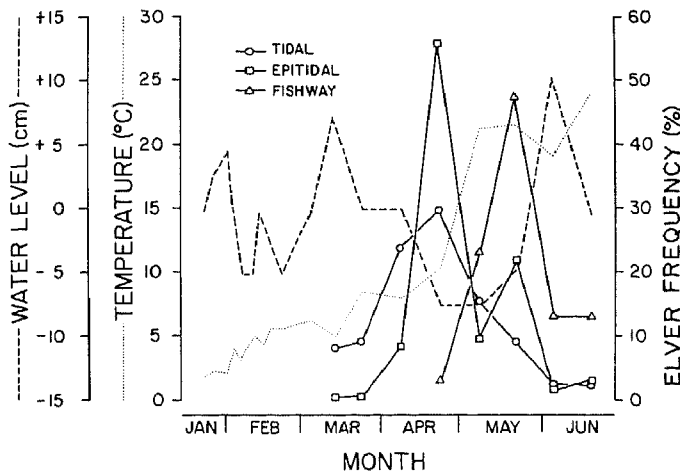


FIG. 7. Relative abundance of elvers (—) collected at each sampling station in 1984, with corresponding temperature (.....) and water levels (---). Water levels were measured from an arbitrary base line.

length of *A. rostrata* elvers with increasing distance from the spawning area and our 1982 and 1983 collections fit his model quite well (Fig. 6). However, our 1984 elvers averaged considerably longer than Vladykov's specimens from Nova Scotia, which were the largest in his series. Because our elvers were dipnetted in 1982 and 1983 and electrofished in 1984, we suspected a sampling effect. To test this, we resampled the tidal station on 24 March 1985, using both techniques. Mean lengths of elvers electrofished ( $60.07 \pm 0.25$  mm,  $n = 146$ ) and dipnetted ( $59.47 \pm 0.32$  mm,  $n = 97$ ) were not significantly different ( $P > 0.05$ ). Furthermore, there is no significant size difference between these elvers and those collected at the tidal station on 26 March 1984 (mean length  $59.86 \pm 0.27$  mm,  $n = 100$ ;  $P > 0.05$ ). In contrast, elvers collected at all three stations averaged nearly 3 mm longer on 7 May 1984 than on 7 May 1983 ( $59.20 \pm 0.17$  mm vs.  $56.28 \pm 0.15$  mm). Therefore, we attribute the size increase between 1983 and 1984 to year class variation and note that significant size differences may persist for at least 2 years.

Even larger elvers were collected in Maine by Hickman (1981), whose Fig. 1d shows mean lengths as great as 62 mm. Shrinkage during preservation may be a factor, for Hickman used no preservative while Vladykov's specimens were stored in formalin for up to 8 years prior to measurement. However, we have demonstrated significant length changes in Annaquatucket River elvers both between years and within sampling periods of 6–8 weeks. The increase in mean length from 1983 to 1984 is 2.7 mm and the range of means among large samples ( $n \geq 100$ ) is 55.8–60.9 mm, a difference of 5.1 mm. In contrast, the difference in mean lengths reported by Vladykov (1966) for elvers collected from Maryland to Quebec is only 3.1 mm. Clearly day and year of capture are important determinants of size in *A. rostrata* elvers.

Despite the complication of capture time, the trend for elver length to increase with increasing distance from the spawning area (Vladykov 1966) appears to be real. Elvers collected from the panhandle in northwestern Florida on 2–7 April, when lengths should be relatively small, averaged larger than elvers taken at the southern tip of Florida on 19 January (Fig. 6). The panhandle locality represents a much longer migration from the spawning area, particularly if these elvers

reached Florida via the Caribbean Current and Yucatan Channel, the route that Kleckner and McCleave (1985) proposed for eels that populate the Gulf coast. At the other end of the range, Boëtius (1976) reported 20 *A. rostrata* elvers of the 0-group from Denmark. Their mean length of  $69.65 \pm 0.83$  mm is much greater than any mean reported for North America.

The geographic trend in elver length may be explained by variation in the timing of metamorphosis of leptocephali to the glass eel stage. Early metamorphosis may thus yield glass eels that average smaller and tend to come ashore closer to the spawning area, e.g., the southeastern United States, while late metamorphosis produces larger glass eels that tend to populate more distant areas such as the maritime provinces of Canada. The few *A. rostrata* elvers that reach Europe may represent leptocephali whose metamorphosis is exceptionally late.

Vladykov's (1966) data on adult eels suggested that males predominate in the southern portion of the range and females in the north. Because males average much smaller than females, Vladykov proposed that most southern elvers develop into males and most northern elvers become females. However, recent studies of adult eels in South Carolina (Harrell and Loyacano 1982; Hansen and Eversole 1984) and Georgia (Helfman et al. 1984) indicate that southern U.S. populations are dominated by females, which also outnumber males in Bermuda (Boëtius and Boëtius 1967). Furthermore, despite the large average size of elvers in the Annaquatucket, almost 90% of the adults are males (Winn et al. 1975; W. H. Krueger and R. C. Kleckner, unpublished data), although estuaries only a few kilometres away are populated mainly by females (Bieder 1971; Winn et al. 1975). Therefore, we reject Vladykov's (1966) size/sex hypothesis. Vladykov noted that a similar hypothesis for *A. anguilla* was criticized by European authors. Helfman et al. (1987) have proposed that sex of anguillids may be determined during the oceanic larval stage, where short planktonic periods and rapid initial growth favor maleness and long larval periods and slow growth favor femaleness, thus producing the latitudinal distribution of the sexes. However, the karyological data from larvae or glass eels arriving along the coast that are necessary to test this theory are lacking.

#### Upstream migration

Our earliest date of capture, 30 January, is in close agreement with Jeffries' (1960) report of elvers collected in Rhode Island estuaries on 3 and 12 January. Elvers first became abundant at the epitidal station nearly 4 weeks after they became abundant at the tidal station. Because these stations are only 30 m apart, this time lag probably represents a period of physiological adjustment to freshwater. Similar periods of adjustment have been described for elvers of *A. anguilla* (Deelder 1958), *A. australis* and *A. dieffenbachii* (Jellyman 1979), and *A. japonica* (Tzeng 1984), as well as for *A. rostrata* (Sorensen and Bianchini 1986).

The shift in peak abundance from the downstream stations to the Mill Pond station (Fig. 7) suggests that elvers ascended this 180-m section of the Annaquatucket in about 4 weeks, at an average rate of little more than 6 m per day. Much more rapid rates of migration have been documented for European elvers (Tesch 1977). However, those studies were conducted on large river systems, where selective tidal transport (Deelder 1952; Creutzberg 1958) may enhance elver migrations. Selective tidal transport has also been demonstrated for

*A. rostrata* elvers (McCleave and Kleckner 1982). However, tide is not a factor in the Annaquatucket and elvers must negotiate a swift current.

The main migration occurred while water temperature was rising and water level was decreasing. Increasing temperature has long been thought to initiate upstream migration. Sorensen and Bianchini (1986) reviewed the evidence and found it equivocal, noting that the onset of migration in Gilbert Stuart Brook coincided with rising barometric pressure and increased sunlight as well as increasing temperature. They suggested that the relative importance of the environmental variables influencing upstream migrations may depend on local hydrographic conditions. We suggest that in a high gradient stream such as the Annaquatucket, rising temperature reflects a more important parameter, namely the reduction in stream velocity that accompanies a decrease in water depth. McCleave (1980) determined that *A. anguilla* elvers could not progress against currents  $> 50 \text{ cm} \cdot \text{s}^{-1}$  and suggested that they move upstream by alternating between burst swimming and resting in the substrate or by seeking out slower currents. In our study, significant areas of slow current were seen only before the main migration, when the stream was in flood stage and overflowing its normal channel. We suspect that Annaquatucket River elvers spend much time in the substrate and that their slow upstream migration is due to stream gradient and the absence of tidal influence.

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- BERTIN, L. 1956. Eels, a biological study. Cleaver-Hume Press, London.
- BIEDER, R. C. 1971. Age and growth in the American eel, *Anguilla rostrata* (LeSueur), in Rhode Island. M.Sc. thesis, University of Rhode Island, Kingston, RI.
- BOËTIUS, I., and BOËTIUS, J. 1967. Eels, *Anguilla rostrata*, LeSueur, in Bermuda. Vidensk. Medd. Dan. Naturhist. Foren. **130**: 63–84.
- BOËTIUS, J. 1976. Elvers, *Anguilla anguilla* and *Anguilla rostrata* from two Danish localities. I. Size, body weight, developmental stage and number of vertebrae related to time of ascent. Medd. Dan. Fisk. Havunders. **7**: 199–220.
- CHARLON, N., and BLANC, J. M. 1982. Étude des civelles d'*Anguilla anguilla* L. dans la région du bassin de l'Adour. 1. Caractéristiques biométriques de longueur et de poids en fonction de la pigmentation. Arch. Hydrobiol. **93**: 238–255.
- CREUTZBERG, F. 1958. Use of tidal streams by migrating elvers (*Anguilla vulgaris*, Turt.). Nature (London), **181**: 857–858.
- DEELDER, C. L. 1952. On the migration of the elver (*Anguilla vulgaris* Turt.) at sea. J. Cons. Cons. Perm. Int. Explor. Mer, **18**: 187–218.
- . 1958. On the behaviour of elvers (*Anguilla vulgaris* Turt.) migrating from the sea into fresh water. J. Cons. Cons. Perm. Int. Explor. Mer, **24**: 135–146.
- ELDRED, B. 1968. Larvae and glass eels of the American freshwater eel, *Anguilla rostrata* (LeSueur, 1817), in Florida waters. Fla. Board Conserv. Mar. Res. Lab. Leaflet Ser. 4(Pt. 1, No. 9): 1–4.
- HANSEN, R. A., and EVERSOLE, A. G. 1984. Age, growth and sex ratio of American eels in brackish-water portions of a South Carolina river. Trans. Am. Fish. Soc. **113**: 744–749.
- HARRELL, R. M., and LOYACANO, H. A., JR. 1982. Age, growth and sex ratio of the American eel in the Cooper River, South Carolina. Proc. Annu. Conf. Southeast. Assoc. Fish Wildl. Agencies, **34**: 349–359.
- HELFFMAN, G. S., BOZEMAN, E. L., and BROTHERS, E. B. 1984. Size, age, and sex of American eels in a Georgia river. Trans. Am. Fish. Soc. **113**: 132–141.
- HELFFMAN, G. S., FACEY, D. E., HALES, L. S., JR., and BOZEMAN, E. L., JR. 1987. Reproductive ecology of the American eel. Am. Fish. Soc. Symp. **1**: 42–56.
- HICKMAN, R. A. 1981. Densities and swimbladder development of juvenile American eels, *Anguilla rostrata* (LeSueur) as related to energetics of migration. J. Fish Biol. **18**: 507–517.
- JEFFRIES, H. P. 1960. Winter occurrences of *Anguilla rostrata* elvers in New England and middle Atlantic estuaries. Limnol. Oceanogr. **5**: 338–340.
- JELLYMAN, D. J. 1979. Upstream migration of glass-eels (*Anguilla* spp.) in the Waikato River. N.Z. J. Mar. Freshwater Res. **13**: 13–22.
- KLECKNER, R. C., and MCCLEAVE, J. D. 1985. Spatial and temporal distribution of American eel larvae in relation to North Atlantic Ocean current systems. Dana, **4**: 67–92.
- MCCLEAVE, J. D. 1980. Swimming performance of European eel (*Anguilla anguilla* (L.)) elvers. J. Fish Biol. **16**: 445–452.
- MCCLEAVE, J. D., and KLECKNER, R. C. 1982. Selective tidal stream transport in the estuarine migration of glass eels of the American eel (*Anguilla rostrata*). J. Cons. Cons. Perm. Int. Explor. Mer, **40**: 262–271.
- MCCORD, J. W. 1977. Food habits and elver migration of American eel, *Anguilla rostrata* (LeSueur), in Cooper River, South Carolina. M.Sc. thesis, Clemson University, Clemson, SC.
- SMITH, D. G. 1968. The occurrence of larvae of the American eel, *Anguilla rostrata*, in the Straits of Florida and nearby areas. Bull. Mar. Sci. **18**: 280–293.
- SORENSEN, P. W., and BIANCHINI, M. L. 1986. Environmental correlates of the freshwater migration of elvers of the American eel in a Rhode Island brook. Trans. Am. Fish. Soc. **115**: 258–268.
- STRUBBERG, A. C. 1913. The metamorphosis of elvers as influenced by outward conditions. Medd. Komm. Havunders. Ser. Fisk. **4**: 1–11.
- . 1923. Elvers from north and south Europe. Rep. Dan. Oceanogr. Exped. Mediterr. **3**: 1–28.
- SYKES, D. P. 1981. Migration and development of young American eels, *Anguilla rostrata* in coastal North Carolina. UNC Sea Grant College Program Working Paper 81-5. University of North Carolina Sea Grant College Publication, North Carolina State University, Raleigh, NC.
- TESCH, F.-W. 1977. The eel. Biology and management of anguillid eels. Chapman and Hall, London.
- TZENG, W.-N. 1984. Dispersal and upstream migration of marked anguillid eel, *Anguilla japonica*, elvers in the estuary of the Shuang River, Taiwan. Bull. Jpn. Soc. Fish. Oceanogr. **45**: 10–20.
- VLADYKOV, V. D. 1966. Remarks on the American eel (*Anguilla rostrata* LeSueur). Sizes of elvers entering streams; the relative abundance of adult males and females; and the present economic importance of eels in North America. Verh. Int. Ver. Theor. Angew. Limnol. **16**: 1007–1017.
- WINN, H. E., RICHKUS, W. A., and WINN, L. K. 1975. Sexual dimorphism and natural movements of the American eel (*Anguilla rostrata*) in Rhode Island streams and estuaries. Helgol. Wiss. Meeresunters. **27**: 156–166.