Life history characteristics and strategies of the American eel, *Anguilla rostrata*

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Abstract: Several life history hypotheses for the American eel, *Anguilla rostrata*, were examined using seaward-migrating silver-phase eels collected in the Annaquatucket River, Rhode Island, U.S.A. Female eels were significantly larger and older than males. Female eels also had a significantly higher mean growth rate. The addition of life history data from Annaquatucket River eels to published silver eel data from locations throughout the eels' range shows that female size at migration is positively correlated with latitude ($r = 0.56$, $p = 0.05$) but male size is not ($r = 0.54$, $p = 0.17$). Female age was not related to latitude ($r = 0.57$, $p = 0.27$) but male age showed a positive relationship ($r = 0.87$, $p = 0.05$). Growth rates for females and males were inversely related to latitude ($r = -0.98$, $p = 0.02$ and $r = -0.95$, $p = 0.05$, respectively). Differences between the latitudinal relationships and life history traits of the sexes may be due to differences in life history strategies.

Résumé : On a examiné plusieurs hypothèses concernant le cycle vital de l'anguille d'Amérique, *Anguilla rostrata*, en étudiant des anguilles en phase argentée migrant vers la mer recueillies dans la rivière Annaquatucket, dans le Rhode Island (É.-U.). Les anguilles femelles étaient significativement plus grosses et plus âgées que les mâles. Leur taux de croissance moyen était également significativement plus élevé. En considérant à la fois les données sur le cycle vital des anguilles de l'Annaquatucket et les données publiées sur les anguilles argentées de divers endroits dans leur aire de répartition, on s'aperçoit que la taille des femelles au moment de la migration est corrélée positivement avec la latitude (r = 0,56, p = 0,05), mais que la taille des mâles ne l'est pas (r = 0,54, p = 0,17). L'âge des femelles n'était pas corrélé avec la latitude (r = 0,57, p = 0,27), mais celui des mâles y était corrélé positivement (r = 0,87, p = 0,05). Les taux de croissance des femelles et des mâles variaient en raison inverse de la latitude (respectivement, r = –0,98, p = 0,02 et r = –0,95, p = 0,05). Les différences entre les corrélations avec la latitude et les caractéristiques du cycle vital chez les deux sexes pourraient être dues à des différences dans les stratégies utilisées dans leur cycle vital.

[Traduit par la Rédaction]

Introduction

The extent to which environmental variations modulate the life history traits of a population is of importance to both the ecologist and the fisheries scientist. A population's ecological significance in a particular community or a strategy for management and conservation may vary according to the responses of the population to changes in the environment.

The unusual life cycle of the American eel, *Anguilla rostrata*, makes the species a useful model for examining environmentally induced variations in life history strategies. All American eels comprise a single panmictic (randomly breeding) population, and the recruitment of juveniles to a particular area of the species' range is reportedly stochastic (Avise et al. 1986). Each new year class entering a particular habitat is likely to be the offspring of eels that developed in completely different habitat types. This prevents local selection pressure in individual environments from having a long-term effect on life history strategies. Any effects of differential mortality of growing eels (yellow phase) do not accumulate between generations.

The American eel is a catadromous species spending the growth phase (yellow eel) of its life in continental waters (Tesch 1977). The growth phase ends with metamorphosis to the maturing phase (silver eel) and subsequent migration to the spawning area. Several life history traits associated with this metamorphosis have been studied through some of the species range: age (Gray and Andrews 1971; Hurley 1972; Harrell and Loyacano 1982; Facey and Helfman 1985; Jessop 1987), length (Hurley 1972; Winn et al. 1975; Jessop 1987; Krueger and Oliveira 1997), and growth rate (Gray and Andrews 1971; Jessop 1987). These traits are essential to understanding the eel's life history strategies because each trait is the result of the eel's entire freshwater existence.

Helfman et al. (1987) proposed a life history scenario for both sexes of the American eel in freshwater. They hypothesized that length and age at metamorphosis from the yellow to silver phase are directly related to latitude for female eels. In addition, they proposed that male eels use a time minimizing strategy and migrate at the earliest possible age, while females are size maximizers and migrate when an optimal body size has been achieved. They further hypothesized that these strategies would result in females being the dominant sex in upstream habitats, which produce older and larger female eels, while male eels would be found in habitats that favor rapid growth.

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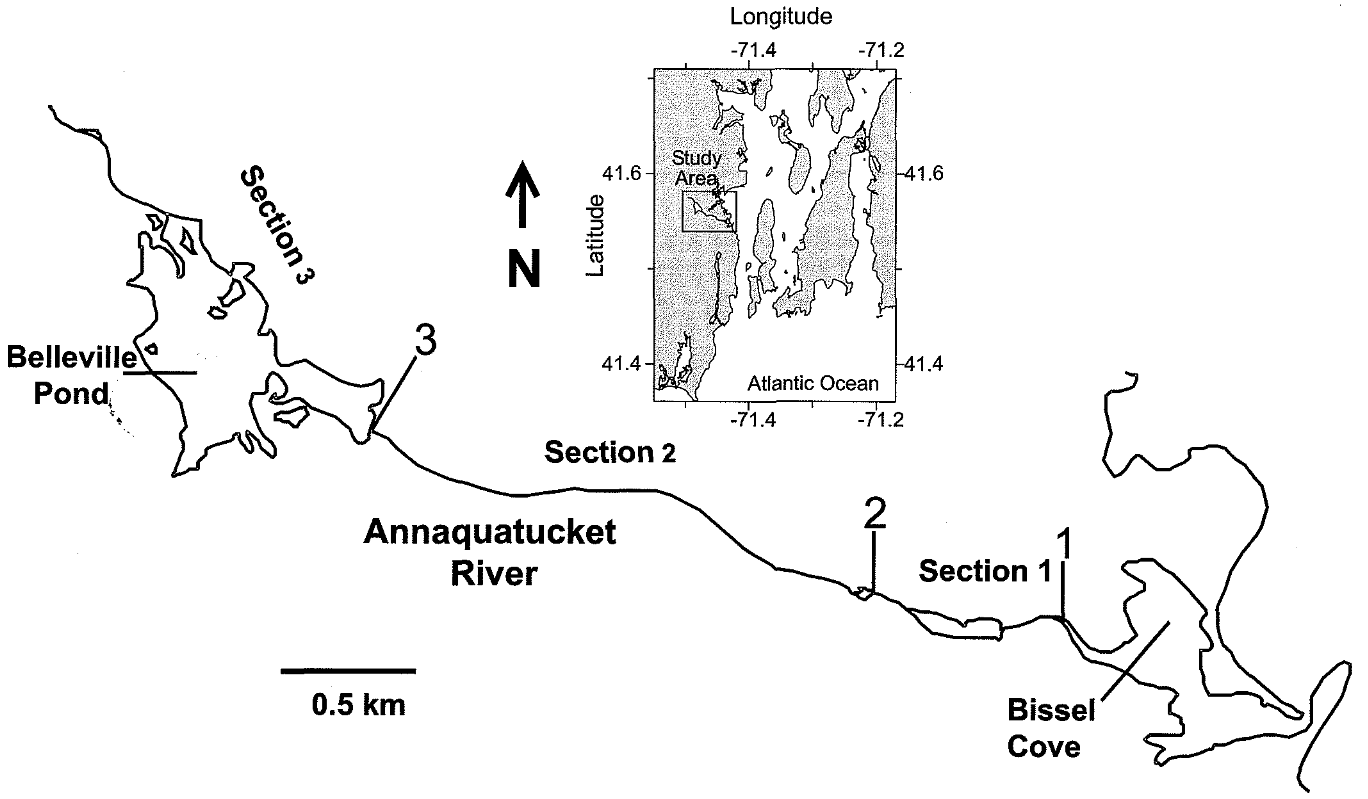
Fig. 1. Map of collection sites in the Annaquatucket River, Rhode Island. The section of river between stations 1 and 2 is section 1, between stations 2 and 3 is section 2, and above station 3 is section 3.



There is a lack of data for many life history traits for the mid-Atlantic area of the eel's range (Helfman et al. 1987) that could be used to test these hypotheses. Gray and Andrews (1971) compared age and growth of silver eels migrating from a pond with those of yellow eels from brackish and freshwater locations in Newfoundland. Jessop (1987) also examined age, length, and growth of silver eels from Nova Scotia but only used a single collection site per river. Comparisons of size and age (Helfman et al. 1984) and growth (Oliveira 1997) of yellow eels have been made from different locations on the same river, but no study has examined silver eels from different areas of the same river. Such a study could test the life history predictions of Helfman et al. (1987) by supplying data on the distribution of life history traits of silver eels within a river and on the possible modulation of life history strategies associated with different habitats.

The present study investigates age and size at migration, sex distribution, and growth rate of silver eels migrating from a Rhode Island, U.S.A., river. The data from Rhode Island eels were combined with data from studies conducted at different latitudes and used to test hypotheses regarding the influence of latitude on life history traits. These combined data also provided the opportunity to examine differences in male and female life history strategies. The final objective was to determine if life history traits vary within a river. Significant differences in traits due to habitat variability within a river could mask the influence of sexual differences and latitudinal effects. This objective was achieved by collecting eels migrating from three river sections that have different habitat characteristics.

Methods

Study area

The Annaquatucket River (Fig. 1), North Kingstown, Rhode Island (41°30'N, 71°22'W), is a small tributary of Narragansett Bay with a length of about 8 km from the head waters to the head of tide. Although the Annaquatucket River is relatively small, it possesses attributes of larger rivers that make it a useful model for comparing life history traits from different river sections. The shifts in habitat that usually occur over extensive upstream distances in larger rivers are present in the Annaquatucket River, but in smaller well-demarcated regions. Different habitat types dominate each of the three river sections examined in this study. Section 1 consists of the transition zone from estuarine to freshwater habitat that is separated from a small mud-bottom pond by the first dam on the river. Section 2 is primarily riverine habitat, faster water flow dominated by riffle, with substrate varying from boulder and cobble to gravel and sand. Section 3 is sand and mud substrate and has Belleville Pond (0.7 km^2), which receives water from a small river section draining swampland.

Sampling

Silver eels were collected during two seasons while making their downstream migration in the Annaquatucket River. In 1990 (24 October – 28 December), migrating silver eels were collected at station 1 (Fig. 1) using a 12 × 1.2 m fyke net (6 mm square mesh) that spanned the width of the river and extended from the river substrate to the surface. This mesh size was assumed to be adequate to retain all size classes of silver eels. To gain a perspective of the overall collection efficiency of each net in this study, a second net with similar mesh size was set on the downstream side of each. These second nets were in place for a total of five nights that had more than 20 eels migrating in a night. All primary nets collected more than 99% of the total catch.

Nets were checked daily and all captured eels measured to the nearest millimetre (total length, TL). Daily, random subsamples (maximum of 20%, range 1–72·day^{-1}) of eels <400 mm TL were taken for age and sex determination. All eels >400 mm TL were kept to enhance the data collected for females, which comprise <10% of the population (Winn et al. 1975; Krueger and Oliveira 1997). Krueger and Oliveira (1997) found that 400 mm was the size to distinguish the sexes in 99.7% of eels in the Annaquatucket River. This 400-mm cutoff was confirmed for subsampled eels by the squash method of Guerrero and Shelton (1974).

Collections were repeated in 1991 (6 August – 18 December) using nets placed at stations 1, 2, and 3. These methods allowed the collection of TL, age, and sex data for two migratory seasons and the comparison of TL, age, sex ratio, and growth rate of three sections of the river for 1991. River sections and their lengths were section 1 (0.84 km), section 2 (2.56 km), and section 3 (all river area above station 3) (Fig. 1). A dam with a Denil-type fish passage separates each river section. Yellow eels are capable of ascending Denil-type fish passages without any size selection (Baras et al. 1994), so these dams should not influence the characteristics of the eels within each section.

Age was determined by counting annuli on sagittal otoliths prepared using methods described in Oliveira (1996), who showed that ring formation in this river is annular. Otoliths that did not produce repeatable counts were omitted from analysis. Repeatable counts were obtained from 853 of 915 otoliths taken from male eels and 110 of 137 otoliths from female eels. Although impossible to age, rejected otoliths were from eels that had sizes distributed over the entire range of each sex. Mean annular growth rates were determined for eels collected in 1991. These was calculated by dividing the TL of individuals minus 57.9 mm, the mean size of Annaquatucket River elvers (Haro and Krueger 1988) at the onset of annular ring formation, by the number of annuli present on the otolith. In order to compare growth rates from this study with published data from other locations, a mean growth rate was calculated for each location based on mean TL divided by mean age without a correction for eel size at the onset of annular ring formation. Comparisons were restricted to studies that collected silver eels in the process of migrating.

Analysis

Data presented are means ± SE. All data were log transformed to meet the assumptions of parametric analysis. An unpaired *t* test was used to test for differences in variables (TL, age, and growth rate) between the sexes and sampling year and in cases when data were available from only two river sections. Statistical differences between river sections were analyzed using one-way analysis of variance and the Bonferroni test.

To examine the relationship between latitude and life history traits (mean TL and age at maturity), data from this study and the Nova Scotian Rivers LeHarve and Medway (Jessop 1987) were added to the multilatitudinal data set used by Helfman et al. (1987). Latitude for rivers not given in Helfman et al. (1987) or in the primary sources was estimated to the nearest minute of latitude using the original descriptions of the collection sites. All relationships between latitude and life history traits were analyzed using Pearson correlations.

Results

Length

In 1990 and 1991, 1486 and 1649 migrating silver eels were collected, respectively. Mean TL of females was significantly larger ($p < 0.01$) than that of males. Females also had a greater range of TL and coefficient of variation (CV) (Table 1). There was little overlap in the TL distribution of the sexes (only two of 3117) (Fig. 2), and neither sex had significant differences between years (Table 1). No significant differences in TL of males were found between river sections ($p = 0.61$) (Table 2). No female eels were captured in section 1, so comparisons were limited to sections 2 and 3, with no significant difference observed ($p = 0.70$).

Helfman et al. (1987) found a positive correlation ($r = 0.64$, $p < 0.05$, $n = 9$) between female size at migration and latitude. The same analysis for their male eels produced no significant correlation ($p > 0.50$, $n = 6$). The addition of the mean female TL of Annaquatucket River eels and the Nova Scotian eels reduced the correlation ($r = 0.56$, $p = 0.04$) but maintained a significant relationship between female size and latitude. The size relationship for male eels ($r = 0.54$, $p = 0.17$) was not significantly correlated with latitude.

Age

A total of 962 silver eels were subsampled for age analysis, 485 from 1990 and 477 from 1991 (Fig. 3). Mean age of females (12.8 ± 0.2 years) was significantly greater ($p < 0.001$) than that of males (10.9 ± 0.1 years). Age at migration was highly variable, with ranges encompassing 14 years (CV = 14.8%) for females and 11 years (CV = 15.8%) for males (Table 1). Mean ages at migration differed significantly between years for both males ($p < 0.01$) and females ($p < 0.01$).

Significant age differences were found for male eels collected in 1991 migrating from different sections ($p < 0.01$), with mean age increasing upstream (Table 2). Male eels collected from section 1 were significantly older than males from section 3 (Bonferroni, $p = 0.02$), but no significant differences were found between male eels from sections 1 and 2 or sections 2 and 3 (Bonferroni, $p = 0.35$ and $p = 0.08$, respectively). Female age at migration did not differ significantly ($p = 0.33$) between river sections.

Helfman et al. (1987) found a correlation ($r = 0.63$, $p < 0.20$, $n = 5$) between female age at migration and latitude. They did not perform a similar analysis for male eels because of the scarcity of male age data. The correlation between female age and latitude decreased after the addition of the mean ages of eels from Rhode Island and Nova Scotia ($r = 0.57$, $p = 0.27$), while the relationship for male eels was $r = 0.87$, $p = 0.05$.

Growth rate

Annaquatucket River female eels grew significantly faster ($p < 0.01$) than males. Differences in growth rates were found between male eels from different river sections ($p = 0.02$) (Table 2). Eels from section 1 had a higher mean annual growth rate than eels from section 3 (Bonferroni, $p < 0.01$), but eels from sections 2 and 3 and sections 1 and 2 were not different (Bonferroni, $p = 0.08$ and $p = 0.20$, respectively). Growth rates for female eels were not different between stations 2 and 3 ($p = 0.67$).

Mean annular growth rate estimates based on mean TL divided by mean age for Annaquatucket River eels were 39.8 mm·year^{-1} for females and 30.9 mm·year^{-1} for male eels. The female growth rate estimate for the Georgia site was based on a single specimen (Table 3). This estimate was used in the correlation analysis because of its similarity to yellow female eel estimates from a Louisiana study mea-

Table 1. Lengths and ages of silver-phase American eels migrating from the Annaquatucket River, Rhode Island, in 1990 and 1991.

	1990	1991	Years pooled
TL (mm)			
Males			
Mean ± SE	337.5±0.5	337.1±0.5	337.3±0.4
n	1428	1570	2998
Range	228–397	275–398	228–398
CV (%)	6.0	5.6	5.8
Females			
Mean ± SE	513.3±12.4	507.6±10.5	510.0±7.9
n	58	79	137
Range	400–793	400–867	400–867
CV (%)	18.4	18.3	18.3
Age (years)			
Males			
Mean ± SE	10.5±0.1	11.8±0.1	10.9±0.1
n	441	412	853
Range	4–16	6–15	4–15
CV (%)	15.0	14.8	15.8
Females			
Mean ± SE	12.2±0.2	13.1±0.2	12.8±0.2
n	44	66	110
Range	8–16	6–20	6–20
CV (%)	14.3	14.3	14.8

Note: Age at migration for both sexes differed significantly between years (*t* test, $p < 0.01$).

Table 2. Lengths, age, and growth rates of silver-phase American eels migrating from three sections of the Annaquatucket River, Rhode Island, in 1991.

	Section 1	Section 2	Section 3
TL (mm)			
Males			
Mean ± SE	336.0±1.3	337.4±0.5	336.6±1.6
n	219	1299	122
Range	294–389	275–398	278–378
Females			
Mean ± SE	—	510.4±11.2	497.8±30.7
n	—	69	9
Range	—	400–867	402–716
Age (years)			
Males			
Mean ± SE	10.6±0.1^{3}	11.4±0.1	12.0±0.3^{1}
n	535	255	63
Range	7–15	7–15	6–15
Females			
Mean ± SE	—	13.1±0.21	14.0±0.77
n	—	67	6
Range	—	6–20	12–16
Growth rate (mm·year^{-1})			
Males			
Mean ± SE	25.8±0.6^{3}	24.9±0.3	23.9±0.6^{1}
n	93	249	63
Range	22.4–47.8	21.5–49.1	21.4–54.9
Females			
Mean ± SE	—	33.4±1.0	32.5±2.2
n	0	67	6
Range	0	28.2–88.2	29.4–44.8

Note: Significant differences between sections are indicated by the superscripted number of the section from which the section differs. Significance was determined by the Bonferroni or by a *t* test when data from only two groups were available. All significance levels were at least $p < 0.01$.

sured at similar latitude (Gunning and Shoop 1962). Analysis of these data in Table 3 shows that growth rate is inversely correlated with latitude for female ($r = -0.98$, $p = 0.02$) and male silver eels ($r = -0.97$, $p = 0.02$).

Sex ratio

Collections for 1990 and 1991 yielded 58 and 79 female eels, respectively. Males comprised 96.1% ($n = 1428$) of the 1990 and 95.2% ($n = 1570$) of the 1991 silver population. The 1991 collections showed an increase in the proportion of female eels progressing upstream, 0, 4, and 7% for sections 1, 2, and 3, respectively.

Discussion

The hypothesis that size is the primary factor inducing migration in anguillid eels (Frost 1945; Rossi and Colombo 1979) is supported by the lack of variation in TL at migration between years. However, the difference in the variability between the sexes (CV: males 5.8%, females 18.3%) indicates that males have a more constrained size at migration. The importance of size for both sexes is emphasized further by the within-year variability and the significant differences between years for age at migration. The variability in age at migration does not allow age to be a reliable cue for stimulating the onset of silver eel migration in this river.

The Annaquatucket River is a numerically male-dominated river, where females average 173 mm longer than males. Krueger and Oliveira (1997) showed that the size difference, distribution, and sex ratio are consistent over time in this river using data collected from silver eels migrating during 1977, 1978, 1981, and 1991. Annaquatucket River females averaged smaller than silver-phase females from any studied geographical region, but were similar to eels from other rivers in the region (Bianchini et al. 1984), indicating that the life history traits of eels in the Annaquatucket River are not unique for this region.

The placement and characteristics of the fyke nets and the length of the collecting period should have allowed the collection of all but a few migrating silver eels during the course of this study. Therefore the data are representative of migrating silver eels in the Annaquatucket River.

Female eels grew 33 mm·year^{-1}, an average of 8 mm·year^{-1} faster than male eels. Therefore, the larger size of female eels is the result of both more time spent growing and a higher growth rate. The differences in growth rates between the sexes are in agreement with yellow eel growth data obtained from the same river. Oliveira (1997) calculated rates of 28 ± 5 mm·year^{-1} for eels < 399 mm (presumed males and small females; see Krueger and Oliveira 1997) and 62 ± 15 mm·year^{-1} for eels >400 mm (presumed females) using mark–recapture methods. The differences in magnitude may

Fig. 2. Distribution of TL for 3135 silver-phase American eels collected while migrating from the Annaquatucket River, Rhode Island, in 1990 and 1991. Open bars represent male eels (n = 2998) and solid bars represent female eels (n = 137). Six eels >600 mm were omitted for ease of graphing. Their lengths were 682, 716, 733, 890, 911, and 935 mm.

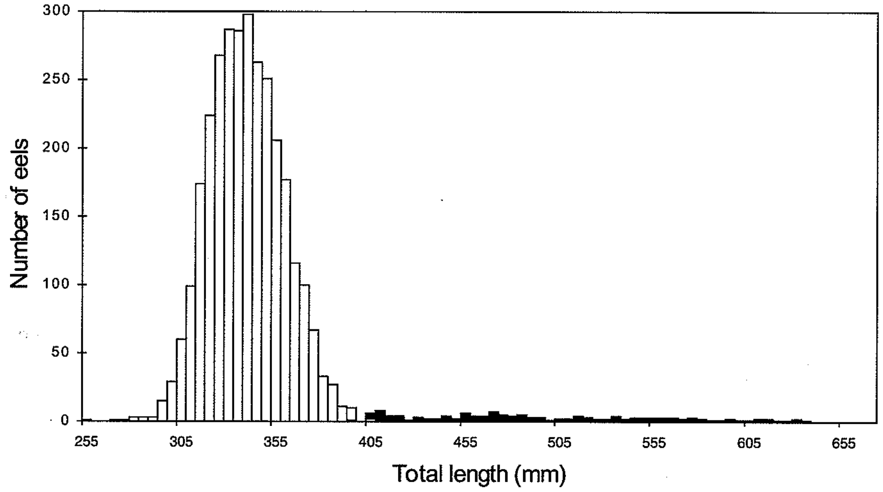
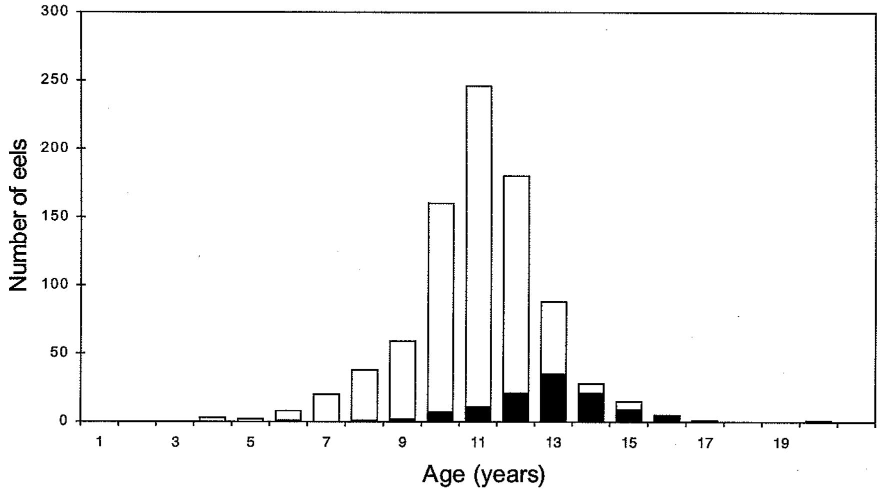


Fig. 3. Age distribution for 963 silver-phase American eels migrating from the Annaquatucket River, Rhode Island, during 1990 and 1991. Open bars represent male eels (n = 853) and solid bars represent female eels (n = 110).



be attributed to the relatively small monitoring period of that study (31 days to 2 years) compared with the total time that an eel spends as a yellow eel. The smaller sample size (n = 16) for yellow females may have also contributed to the observed differences. Differences in annual growth rates over the entire yellow phase, which may be considerable, could not be considered in that study. The estimates of growth rate presented in this study for silver eels are more indicative of the eels' complete freshwater phase.

Section comparisons: river location and life history traits

The 1991 data comparing river sections are in agreement with the general life history predictions for both sexes. Although 95.2% of silver eels were male, the proportion of female eels increased upstream (above station 3) and females were absent downstream (below station 2). Male eels collected above station 3 were the oldest and had the slowest growth rates, indicating that this area is not as conducive to male growth as downstream areas. Significant differences between male and female growth rates were found between eels collected from common river sections (both sections 2 and 3). The low proportion of females in these river sections reduces the likelihood of male–female competition being a plausible explanation for these differences. However, female eels appear to make better use of habitat resources than males, suggesting growth rate to be a trait that is not only sexually different but also modulated by environmental factors.

These sexually different growth rates may vary throughout the yellow phase because both sexes begin this phase as sexually undifferentiated. In addition, environmental factors may influence the timing as well as the outcome of sexual differentiation during the yellow phase. The relationship between pre- and post-differentiation growth rates is unknown, and therefore the extent of sexual growth differences is difficult to evaluate.

The presence of male eels upstream may be due to density-avoiding movements during the early yellow phase (Moriarty 1986). K. Oliveira (personal observation) in an electrofishing survey found mean densities of yellow eels below station 3 to be 2.5 times greater than in the areas above.

Table 3. Mean annual growth rate based on mean TL divided by mean age of American eels from different locations.

Location	Latitude	Mean growth of males (mm·year^{-1}) (*n*)	Mean growth of females (mm·year^{-1}) (*n*)	Reference
Topsail Pond, Newfoundland	47°32′	— (0)	5.6 (92)	Gray and Andrews 1971
Holyrood Pond, Newfoundland	46°52′	— (0)	5.9 (90)	Bouillon and Haedrich 1985
LeHarve River, Nova Scotia	44°18′	30.8 (352)	— (0)	Jessop 1987
Medway River, Nova Scotia	44°08′	28.9 (7)	31.4 (276)	Jessop 1987
Annaquatucket River, Rhode Island	41°32′	30.9 (2998, 853)[a]	39.8 (137, 116)[a]	This study
Altamaha River, Georgia	32°47′	94.4 (8)	117.4 (1)	Helfman et al. 1984

Note: These data do not account for eel size at the onset of annular ring formation.

[a] The sample sizes for mean TL and mean age for the Annaquatucket River eels were not equal; the first *n* is for length and the second *n* is for age.

Oliveira (1997) has concluded that most upstream movements in the Annaquatucket River are conducted by small yellow eels <200 mm, and this agrees with the conclusions of Haro and Krueger (1991). Therefore the observed changes in age and growth rate as distance upstream increases are due to changing growth conditions and not the constant upstream migration of larger and older individuals.

Two assumptions must be made when comparing life history parameters from different areas of a river using the sampling methodology employed in this study. First, eels collected in a net are assumed to come from a site upstream of the net. This presumption is plausible because, once the migration begins, the dominant behavior of silver eels in freshwater is to move downstream (Hain 1975). Since the nets spanned the entire river and net efficiency was shown to be high, the chances of an eel being collected in a river section other than the one in which its migration originated are small. Second, an eel must have spent the majority of its yellow phase in the river section where it was collected. Restricted movements have been shown for yellow-phase American eels (Gunning and Shoop 1962), and Oliveira (1997) demonstrated high site fidelity for yellow eels ≥180 mm within this river with few exceptions involving long-range movements.

Latitude and life history traits

The addition of data from mid-Atlantic regions to the Helfman et al. (1987) data did not improve the correlation between female size and latitude, but it does not allow the rejection of the latitude–size at migration hypothesis for American eels. Size at migration of female silver-phase American eels is correlated with latitude. Although longitude and distance were complicating factors, Vøllestad (1992) demonstrated a similar relationship for the European eel, *Anguilla anguilla*.

The additional mean size data from silver eels presented here (Jessop 1987; this study) for male eels maintain the lack of a relationship between latitude and TL noted by Helfman et al. (1987). Size at migration of male eels does not appear to be correlated with latitude. However, it should be noted that Krueger and Oliveira (1997) reported evidence for significantly larger male eels in rivers north of Rhode Island. Thus, further sampling may demonstrate a positive relationship between size and latitude for males.

The data suggest that growth rate of both sexes decreases with increasing latitude, although the effect of different ageing methods on the estimated growth rates must be considered (Panfili et al. 1990). Conover and Present (1990) have shown that growth rate can be genetically selected and may allow for compensation for different growth conditions at a given location. The American eel's panmictic life cycle prevents long-term selection from acting on growth rates in this way. The growth potentials of all eels are equal and are the result of the habitat's growth conditions.

Male and female strategies

The differences in latitudinal relationships between male and female eels may be explained by the life history strategy used by each sex. Data collected from male eels (TL, age, and growth rate) support a time-minimizing life history strategy for male eels. Size at metamorphosis may be a fixed requirement that is less dependent on environmental influences and is more closely constrained by the minimal size requirements of the sex. This is supported by the lack of a latitudinal cline in size at migration. Size at migration was also consistent in Annaquatucket River males collected from river sections with different growth conditions. In addition, male eels have a size range that is about 20% of the average of male sizes from all locations, whereas females have a range encompassing 58% of the average from all locations.

Size at migration of male eels was not affected by latitude, although both age at migration and growth rate were, indicating independence of size from the other traits. In the Annaquatucket River, age and growth rate did not affect the size of male eels migrating from river sections, further supporting a constrained male size. Age at metamorphosis is most likely the result of the time required to reach a critical size. The significant correlation between latitude and age at migration, growth rate, and the lack of a relationship between size and latitude for male eels are further evidence that growth conditions do not influence male size at migration.

Because a male eel's fitness is presumed to be dependent solely on the ability to reach the spawning area, a simple life history strategy is possible: a time-minimizing strategy that allows males to reduce the growth period by migrating at the minimum size necessary to survive the spawning migration. However, without knowledge of possible selection for size during the marine phase of the migration or of the spawning grounds, it is difficult to surmise testable hypotheses to explore further the importance of male size.

Unlike male eels, females are confronted with a classic trade-off. Increased size increases fecundity (Wenner and Musick 1974; Barbin and McCleave 1997), but the time spent growing also increases the chance of prespawning mortality. Helfman et al. (1987) hypothesized that females have a life history strategy that maximizes size at metamorphosis. The greater variability in TL for females as compared with males within the Annaquatucket River, as well as throughout the eels' distribution, may be the result of a more complex set of requirements, which create greater sensitivity to environmentally influenced factors. The lack of a significant relationship between latitude and age at migration, while growth rate was highly correlated with latitude, indicates that factors other than growth may play a role in determining the size of a female at migration. This is consistent with Vøllestad's (1992) conclusion that European eels may use different developmental pathways, which are expressed in response to localized environmental pressures. However, this is contrary to Svedäng et al. (1996), who concluded that the negative relationship between age and growth rate for European female eels, which is also evident in Annaquatucket River females, is indicative of the same time-minimizing strategy as for males. Females may actually use a trade-off between the two strategies. The panmictic life history of eels precludes adaptation to a single environment, and therefore, a female may have to develop in any of a wide range of habitats. Female fitness would be most enhanced by a strategy that prolongs the yellow phase in habitats that have favorable characteristics. Likewise, a male-like strategy would benefit females that enter areas with less favorable conditions. It would be beneficial to reach the optimal size for a specific habitat as rapidly as possible. It is probable that habitat conditions act as cues to modulate female size accordingly. Svedäng et al. (1996) hypothesized that female size variations were related to the opportunity for nutrient accumulation presented by a habitat. Therefore, the female size requirement may change according to the maximum growth rate that a habitat can sustain.

The hypothesis of an environmentally modulated size requirement needs to be tested by further study in a river system with a higher proportion of female eels and a greater range of growth conditions. Presently, this hypothesis may explain the variation in size between female eels collected from different habitats where growth rates were similar (Svedäng et al. 1996).

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