VARIABILITY IN GROWTH RATE IN EUROPEAN EEL *ANGUILLA ANGUILLA* (L.) IN A WESTERN IRISH CATCHMENT

W. Russell Poole and Julian D. Reynolds

ABSTRACT

The length, age and growth rate of female silver eels trapped in the Burrishoole system, western Ireland, were investigated in 1987 and 1988. Length ranged from 40cm to 100cm, and age from 8 to 57 years. Of the total sample of 8612 eels measured, 0.7% were larger than 62cm: 0.6% in 1987 and 0.7% in 1988. Annual growth rates were generally faster for the larger eels (>62cm). The growth curve for eels ≤62cm decreased annually, approaching an L_∞ of 99.9cm, and the curve for eels >62cm was almost linear over the entire period of growth. This study has shown that eels of exceptional size regularly reach the mature silver stage and migrate, even at ages as great as 57 years.

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Received 17 July 1998. Read 1 October 1998. Published 30 December 1998.

INTRODUCTION

The European eel successfully inhabits a wide range of habitats and consequently shows considerable variation in growth rate and size for a given age (Vøllestad 1992). While many of the studies of eel growth and population characteristics have been carried out on exploited populations, few have examined the natural growth of unexploited populations (Poole *et al.* 1992; Poole and Reynolds 1996a).

In many eel populations a small number of individuals are exceptionally large (e.g. Frost 1945; Poole 1994), and to date these have never been studied in detail. Observations of both the yellow eel catches and the silver eel migrations in the Burrishoole catchment, Co. Mayo, have indicated the presence of such large individuals (Poole *et al.* 1990; Poole 1994; Poole and Reynolds 1996a). Information on eel age and growth rate from different catchments is important for the effective management of eel populations. This study in the Burrishoole catchment examines the age and growth of large female silver eels, longer than 62cm, and compares them with female silver eels from 40cm to 62cm long.

METHODS

The Burrishoole system, Co. Mayo, (9°55′W 53°55′N), an oligotrophic and poorly buffered system, has a catchment area of 8949ha and consists of three main lakes (the brackish L. Furnace (141ha) and the freshwater lakes Feeagh (410ha) and Bunaveela (46ha)) and some 45km of shallow stream area (Poole *et al.* 1990; Poole 1994). Upstream and downstream Wolf-type fish traps, employing horizontal grids with 12mm gaps, were placed in two short outflow rivers joining L. Feeagh to L. Furnace. Full trapping of migrating silver eels commenced at these traps in 1970 (Poole *et al.* 1990).

Samples of silver eels were measured ($n =$ 8612) between 1986 and 1994. In 1987 and 1988 an intensive study of the downstream migrating silver eels was undertaken, and in 1988 all eels between 40cm and 50cm were sexed internally in order to establish the size overlap between the sexes (Poole *et al.* 1990; Poole 1994; Poole and Reynolds 1996a). In total 72 eels between 40cm and 62cm and nine eels larger than 62cm were sacrificed, measured and the sagittal otoliths were extracted. Otoliths were prepared by burning and cracking (Christensen 1964; Moriarty 1973a), mounted against a glass slide in silicone rubber (Hu and Todd 1981) and measured under ×100 magnification with an eye-piece graticule (Poole *et al.* 1992; Poole 1994).

The first clearly marked annulus was taken to be equivalent to 7.2cm, the mean total length of local estuarine glass eel in the winter of 1987/8 (Poole 1994). Assuming linear growth, values for the annual increments were calculated according to the formula (Moriarty 1983)

$$a = i(L - 7.2)/I$$

where i = distance between the annular rings measured on otoliths, $I = \Sigma i$ for the individual, L = total length of the individual and a = calculated annual length increment. Growth was described using the von Bertalanffy (1957) growth equation:

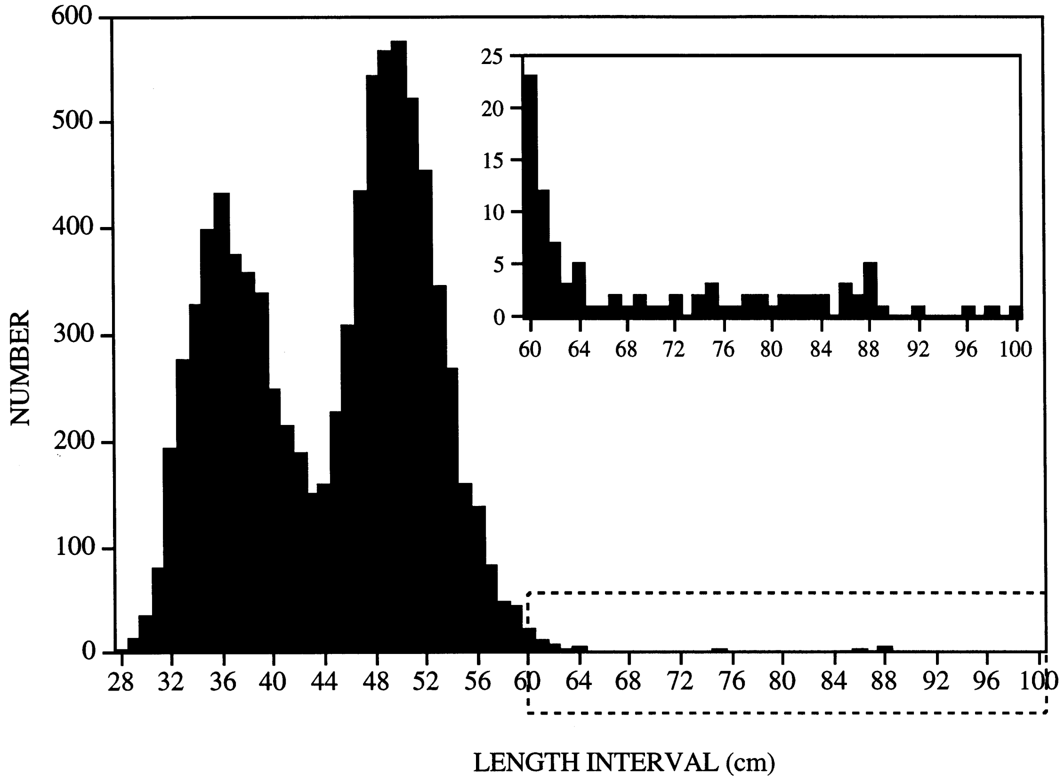

Fig. 1—Silver eels trapped in the Burrishoole system between 1986 and 1994 ($n = 8612$). Inset shows the 60–100cm portion of the graph with an expanded scale.

$$l_t = L_\infty(1 - e^{-K(t - t_0)})$$

where l_t = length at time t, L_∞ = maximum size towards which the length of the fish tends, K = the rate at which the length approaches L_∞, and t_0 = the (hypothetical) time at which the fish would have been zero size if it had always grown according to the von Bertalanffy equation.

RESULTS

The length distribution for male and female silver eels was bimodal, with the lower mode comprised of males and the upper mode females (Fig. 1). Of the total sample of 8612 eels measured over the nine-year period, 0.7% were larger than 62cm. The proportion of these large eels in 1987 was 0.6%, and in 1988 it was 0.7%. In 1988 all eels were sexed internally, and the females ranged in length from 40.5cm to 92.9cm with a mean of 50.5cm (S.D. = 4.56). However, there was a small number of females larger than 62cm. The length frequency for female eels (Fig. 1) has a strong positive skew, with the 99% confidence limit of the normal distribution at 62cm, therefore eels greater than 62cm were designated 'large' as opposed to 'normal'.

Variation in mean length between age groups was considerable (Fig. 2). The age–length plot for female silver eels sampled in 1987 and 1988 can be divided into two sections. The silver eels can be grouped into large (>62cm) eels ranging in age from 32 to 57 years and normal length (≤62cm) eels ranging from 8 to 42 years of age. The von Bertalanffy growth curves calculated from back-calculations were fitted to the age–length scatter-plots (Fig. 2).

Annual growth rates were calculated separately for normal and large female eels (Table 1). There was an irregular pattern of fast and slow annual growth increments. Generally the fastest back-calculated growth occurred in the first year, although years of relatively fast growth (i.e. more than 3cm) occurred throughout the first 17 years in the normal eels and the first 34 years in the large eels. The greatest annual increment of 7.3cm occurred in the 13th year in a 61.5-cm eel. The mean annual increment was 1.42cm for normal eels and 1.6cm for large eels, whereas the modes were between 0.5cm and 1.0cm and 1.0cm and 1.5cm, respectively.

The back-calculated incremental growth (Fig. 3) of the large eels was faster, but not significantly, in all but 7 of the first 24 years of growth. From 25 years onwards the large eels grew significantly faster (comparison of 95% Confidence Limits: $P < 0.05$) in each year (Fig. 3).

The von Bertalanffy values of L_∞, K and t_0 (Table 2) were calculated and were used to fit

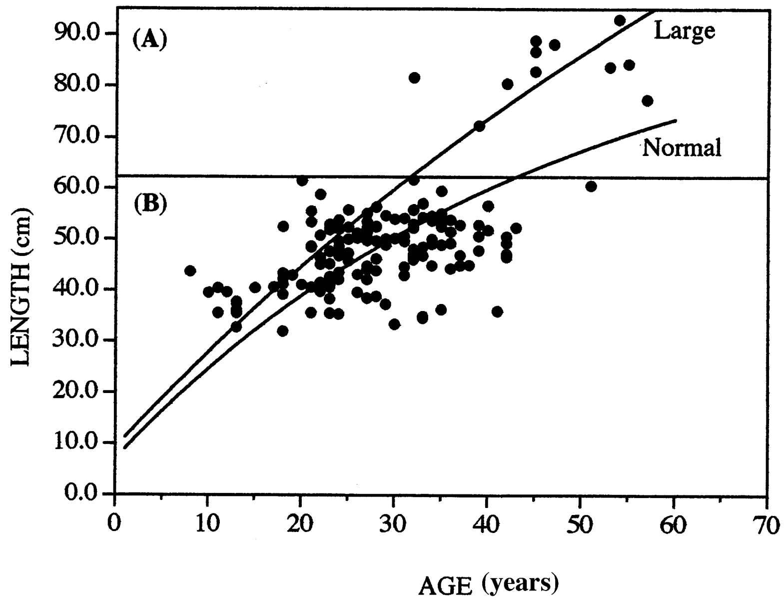

Fig. 2—The mean length at age of female silver eels taken in Burrishoole, 1987 and 1988: (A) large eels (>62cm) and (B) normal-sized eels (≤62cm); curves are back-calculated von Bertalanffy growth curves.

theoretical growth curves to the length at age data (Fig. 2). The normal eels had an L_∞ of 99.9cm with a growth curve decreasing with age, while large eels grew at an almost constant rate, faster than normal eels, with a growth curve approximating to an unrealistic L_∞ of 204.5cm. While the L_∞ for large eels was calculated using a small sample size ($n = 9$), and the variance of this data set is likely to be greater than for the normal eels, the pattern of annual growth increments shows the difference between the two L_∞ values to be real. Silver eels clearly mature and migrate at considerably less than their potential maximum size.

DISCUSSION

Length, age and growth rate of eels have received much attention in the literature, but only passing mention has been made of the occurrences of very large eels in many populations (Moriarty 1973b; 1986; Poole *et al.* 1990; Poole and Reynolds 1996a). Reference has also been made to large eels occurring in landlocked water bodies (e.g. Moriarty and Hackett 1976).

The Burrishoole silver eels display a typical bimodal length distribution, with the females being considerably larger than the males, a phenomenon not unusual among the fishes (Parker 1992). The Burrishoole eel population has not been commercially exploited, and both large eels and extremely old eels have been recorded in this system (Poole and Reynolds 1996a). Age and length at maturity appear to be independent of growth rate as observed in silver eels trapped in other Irish waters (Moriarty 1987) and by Vøllestad (1992). It appears that size, rather than age, is a determining factor in maturation and that a few eels grow on to mature at longer lengths and older ages than the majority. Growth of eels in the Burrishoole is known to be slow (Vollestad and Jonsson 1986; Poole and Reynolds 1996a), with mean annual increments of *c.* 1.5cm (Poole 1994), although much higher individual annual increments were recorded. These growth rates have been validated by long-term mark–recapture methods (Poole and Reynolds 1996b).

Eels longer than 62cm at migration tended to grow at a greater rate, although not significantly, than normal-sized eels during the first 7 years in fresh water, and after 25 years they maintained a significantly faster growth through to maturation. While the growth curve of the normal eels flattened out towards an L_∞ of 99.9cm, the curve for the large eels was almost linear, tending towards an unrealistic L_∞ of 205cm. It would appear that a small number of eels grow relatively rapidly early on and continue to grow at a steady rate achieving a large size before maturing, irrespective of their age, compared to the normal-sized eels, which experienced a decrease in growth with age. Similar types of growth pattern have been observed in Irish 'specimen weight' brown trout

Table 1—Summary of calculated growth increments (cm) for normal-sized (≤62.0cm) and large (>62.0cm) silver eels, 1987 and 1988, giving mean, modal annual increment, mean increment in the first year, and the greatest annual increment and the year in which it occurred. Year 1=year after the first winter in the estuary as a glass eel. Standard error and number of increments measured are given in parentheses (S.E.; *n*); *n*=number of eels.

Group	*Mean annual increment*	*Modal annual increment*	*Mean increment in first year*	*Greatest annual increment*		
				cm	*years*	*n*
Normal	1.42 (0.02; 2203)	0.5–1.0	2.96 (0.13; 72)	7.3	13	72
Large	1.60 (0.04; 445)	1.0–1.5	3.86 (0.44; 9)	7.08	1	9

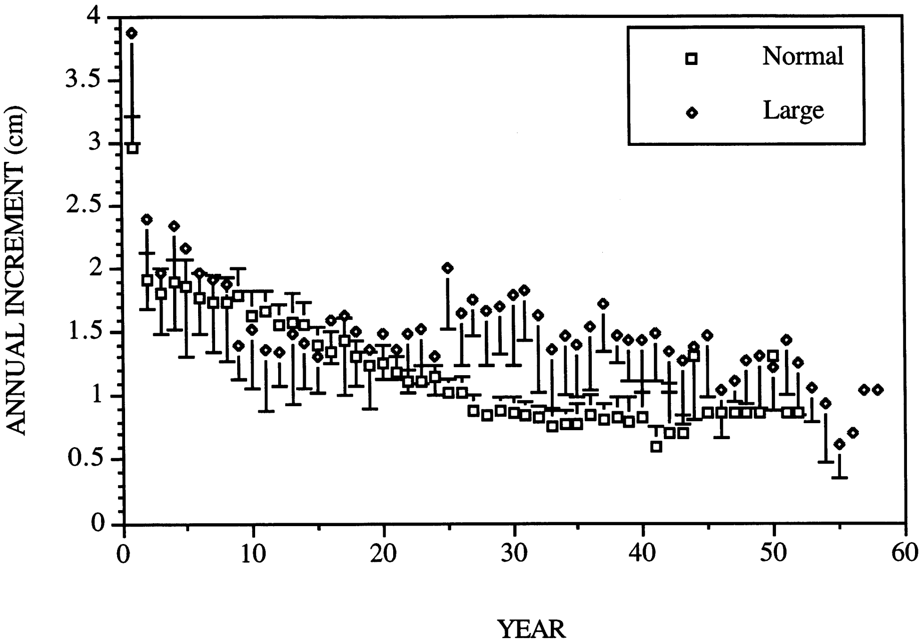

Fig. 3—Annual growth increments for female silver eels, 1987 and 1988, separated by length (normal-sized ≤ 62.0cm > large). Bars indicate 95% confidence intervals.

(Went 1968). Such extended periods of faster growth have been attributed to a change in diet from an invertebrate to a piscivorous one, enabling the trout to survive and grow without undue expenditure of energy in catching their food. Similar changes in diet from invertebrates to fish have been observed in the larger eels (Moriarty 1973b; Ezzat and El-Seraffy 1977; Poole 1994). In situations where invertebrate food is scarce, a diet predominantly of fish is adopted by eels (Tesch 1977; Moriarty 1988). However, a fish diet will allow a large eel to maintain growth long after it becomes unprofitable to hunt for small, scarce invertebrates. Eels that are able, or inclined, to make this change will probably grow to a large size. What governs the change is unknown, although factors such as the competition for food, sex and the shape of the eels head may be influential.

The factors that determine the onset of sexual maturation in eels are still unknown. Maturity depends to some extent on size. Tesch (1977) quotes maximum and minimum lengths for mature males of 48cm and 31cm (as low as 25.6cm in Burrishoole) and minimum lengths of 37cm for females. Females up to a maximum of 100.3cm were recorded in this study, although the majority of females mature between 40cm and 62cm. There must be a trade-off between optimum size for ova production and longevity. The triggers for metamorphosis and the onset of maturation remain unknown, although the accumulation of sufficient energy reserves, such as lipids, may be important (Boëtius and Boëtius 1985). Energy is required for migration and formation of eggs, which may constitute up to 50% of the females body weight (Boëtius and Boëtius 1980). There may be a relationship between growth rate, available food resources and the partitioning of energy that determines the point at which an eel reaches the optimum size and energy reserves for ova production and extended migration. Vøllestad and Jonsson (1986) proposed that for female eels there may be a compromise between the postponement of reproduction and the increased risk of mortality while waiting to mature. They also contend that the increase in fecundity as a result of body-size increases may not be balanced by decreased survival rates caused by waiting another year.

This study has shown that eels of exceptional size regularly reach the mature silver stage and migrate, even at ages as great as 57 years. The growth rate of these large eels is almost linear, unlike the normal-sized eels, which exhibit decreasing growth with age.

Table 2—von Bertalanffy values for L_∞ (cm), K and t_0 for normal-sized and large female silver eels, 1987 and 1988.

Group	L_∞	K	t_0
Normal	99.9	0.021	−3.51
Large	204.5	0.010	−4.68

ACKNOWLEDGEMENTS

We are indebted to Dr Christopher Moriarty for his involvement with this study and to the field and technical staff of the Zoology Department, Trinity College Dublin, and the Salmon Research Agency for monitoring traps and general assistance. This research was supported by grants made available by the Irish Departments of the Marine and Education.

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The subvention granted by Trinity College Dublin towards the cost of publication of papers by members of its staff is gratefully acknowledged by the Royal Irish Academy.