

Age, growth, and condition of European eel (*Anguilla anguilla*) from six lakes in the River Havel system (Germany)

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A total of 199 female yellow European eels (*Anguilla anguilla*), 21.6–66.2 cm long and 3–14 years old, was collected by electro-fishing from six lakes in the River Havel system (Germany) in spring 2001. The condition and the growth rate, estimated by otolith increments, varied between eels within single lakes and between lakes. Fulton's condition factor ranged from 0.10 to 0.24 and the gross energy content varied between 4.3 and 15.3 MJ kg⁻¹. There were no significant differences in mean condition factor (0.16–0.18) or gross energy content (6.5–9.3 MJ kg⁻¹) between lakes. Fastest growth was in Lake Blankensee (mean 5.3 cm year⁻¹), and the slowest in Lake Sacrow (mean 4.0 cm year⁻¹). For all lakes combined, the overall mean annual increment was estimated to be 4.5 cm year⁻¹. The biggest annual increment on the otoliths was generally laid down during the first and second years in fresh water, when the growth rate was 6.1–8.5 cm year⁻¹. Then, in the subsequent 12 years, the annual increment remained almost constant or decreased slightly (with lake-dependent values of between 1.6 and 6.8 cm year⁻¹). In the River Havel system, the time between stocking of the lakes with glass eels and the recapture of eels at 45 cm body length was 7–10 years. The physiologically possible maximum length (L_{∞} values) of eels lay in the range 50–130 cm. In comparison with previous investigations (between the 1950s and the 1970s), the only difference observed was a trend towards slower growth.

Keywords: age, *Anguilla anguilla*, condition, European eel, gross energy, growth.

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Introduction

Since the early 1990s, there has been a huge decrease in European eel (*Anguilla anguilla*) stocks and yields (Moriarty and Dekker, 1997; Dekker, 2004). ICES has adjudged the situation of eel stocks as being no longer within biologically safe limits, and that the fisheries in recent years have not been operating sustainably. Moreover, secure natural recruitment and commercial use has not been guaranteed (ICES, 2002, 2003).

Different possible global and regional influences have been advanced to account for this situation (e.g. Moriarty and Dekker, 1997; Dekker, 2000; ICES, 2001, 2002; Feunteun, 2002; Kirk, 2003; Knights, 2003; Knösche *et al.*, 2004). Examples of proposed influential factors are changes in oceanographic conditions (possibly linked to climate change), declined glass eel recruitment, barriers to migration in rivers, habitat loss, infestation with the swim bladder nematode *Anguillicola crassus*, pollution, re-oligotrophization of fresh-water habitats and reduction in available prey, and predation by cormorants (*Phalacrocorax* spp.). The contributions of these different potential influences have not been evaluated or clarified.

To analyse some of these problems (e.g. re-oligotrophization of fresh-water habitats and reduction in available prey), determination of the age of eels is important. It can be used in calculating growth rates, the age at onset of sexual maturity, longevity, rates of

mortality, and the yields of eel populations. Age determination additionally shows the success and profitability of stocking with eels, which in turn can be used as a means of promoting eel stocks and fishing. Further, as data become available for different water bodies (lakes and other fresh-water habitats) and from historical stock analyses, these can be compared with modern data to indicate trends and developments.

In Germany, European eel stocks and yields in the most productive fresh-water eel habitats of the River Havel system have declined drastically (Knösche *et al.*, 2004). The River Havel is one of the main tributaries of the River Elbe and has a catchment area of 24 096 km² and an annual yield per ha of eels twice as high as in the River Elbe and its other tributaries (Anwand, 1980). In the tributaries of the River Havel, more than 3000 lakes covering an area of roughly 1000 km² and ca. 35 000 ha of water surface drain via the Elbe River into the North Sea. Some 73% of the catchment is in the Federal State of Brandenburg around the city of Berlin in northeast Germany. Commercial fishing is still the main form of fish production in the lakes and rivers of the system, and eels are the dominant species in the catch (Brämick, 2005) with, for example, >50% of sales (Brämick and Fladung, 2006). However, annual landings of eels have declined significantly, from 6.0 kg ha⁻¹ in 1980 to 2.2 kg ha⁻¹ in 2002 (Knösche *et al.*, 2004). Reasons for the decline in yield can

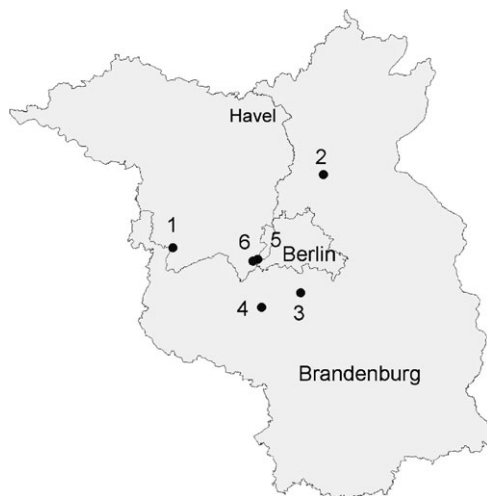


Figure 1. Location of the six study lakes in the River Havel system: 1, Lake Pritzerbe; 2, Lake Eiserbude; 3, Lake Rangsdorf; 4, Lake Blankensee; 5, Lake Sacrow; and 6, Lake Jungfernsee.

include a slowing of growth rate or reduced survival. The aim of the present study, therefore, was to examine the age, growth, and condition of eels in six lakes of the River Havel system, and to compare this with previous studies to show whether a decrease in the growth rate of eels is the main factor behind the declining yield.

Methods

Eels were sampled from six lakes of the River Havel system in the Federal State of Brandenburg (Figure 1) in May 2001. The limnological parameters of the lakes are taken from the lake register of the Federal State of Brandenburg and from the Institute of Applied Water Ecology Seddin GmbH (Table 1). Information on stocking of the lakes with eels is given in the fishery statistics provided by fishers operating in the lakes over the past 10 years.

A sample of ~50 eels per lake was caught by electro-fishing (EFGI 4000, Fa. Bretschneider Spezialelektronik, Germany; 4 kW direct current, voltage series 210–610 V), along the borders of reed areas. All eels were killed by freezing and stored under vacuum at -20°C .

The total lengths (L_T) of each eel (to the nearest 0.5 cm) and the associated total weight (± 1 g) were recorded after thawing. As the freezing procedure leads to a reduction in weight and length, the values were corrected by assuming a reduction of 2.8% in

weight and 2.5% in length (Wickström, 1986). Eel sex was determined by gross morphological examination by eye (Frost, 1945; Tesch, 1999), using a binocular microscope for smaller eels. Fulton's condition factor (K) was calculated from the gross weight and total length of the eels using the formula of Fulton (1904):

$$K = \frac{(\text{weight}[\text{g}] \times 100)}{\text{length}^3[\text{cm}]} \quad (1)$$

The energy content (gross energy) of the eels was estimated by the dry matter content of 20 g of muscle fillet according to the method outlined by Schreckenbach *et al.* (2001).

To investigate eel age in each lake, 199 female yellow eels were selected (25 from Blankensee; 35 from Eiserbude; 34 from Jungfernsee; 46 from Pritzerbe; 22 from Rangsdorf, and 37 from Sacrow), because 94% of the eels in the sample were females, and the growth rates of males and females tend to differ (Penáz and Tesch, 1970; Poole and Reynolds, 1996; Holmgren *et al.*, 1997). Also, in most previous studies, only female age and growth were analysed (e.g. Moriarty, 1983; Kangur, 1998; Matthews *et al.*, 2003) because of their greater economic importance. Sagittal otoliths were extracted and stored in 96% ethanol, then prepared according to the method of Secor *et al.* (1992). The otoliths were burnt over a candle, broken transversely through the centre, embedded broken side down in wax (Mounting Wax Crystalbond 590 Amber, Fa. Buehler®) on a microscope slide, and ground with a series of grinding papers (600, 800, and 1200 grade) down to 0.1–0.2 mm. Finally, each otolith was smoothed by polishing for 1 min in alumina powder (0.3 μm), then cleaned with a wet fibre polish (Microcloth with adhesive, Fa. Buehler). To back-calculate growth, the distance between the winter rings of the otoliths was measured under a light microscope with the help of an eyepiece micrometer (Fa. Ernst Leitz Wetzlar GmbH, Germany) at 125-fold magnification (measuring accuracy $\pm 11.11\mu\text{m}$). Measurements were taken from the centre of the nucleus to the “transition zone”, which represents the start of fresh-water growth (Michaud *et al.*, 1988), for calculating glass eel size, and from winter ring to winter ring for calculating annual growth. I read each set of otoliths twice, 2 months apart. When first and second readings differed, I read the set a third time.

Back-calculation of growth and determination of the physiologically possible maximum length (L_{∞}) of eels were undertaken using a Ford–Walford Plot (Walford, 1946) and a von Bertalanffy

Table 1. Characteristics of the six lakes of the River Havel system.

Parameter	Blankensee	Eiserbude	Jungfernsee	Pritzerbe	Rangsdorf	Sacrow
Longitude	13°07'W	13°35'W	13°05'W	12°29'W	13°25'W	13°05'W
Latitude	52°14'N	52°49'N	52°25'N	52°30'N	52°30'N	52°26'N
Fishing area (ha)	290.5	30.7	233.0	193.6	244.8	107.2
Maximum depth (m)	3.9	6.2	6.0	4.0	2.0	36.0
Average depth (m)	0.7	4.2	5.3	2.1	2.0	10.5
Stratified	No	No	No	No	No	Yes
Total phosphorus concentration (TP) ($\mu\text{g l}^{-1}$)	73	55	–	130	179	–
Depth of view in summer (m)	0.2	0.4	–	1.3	0.57	–
Trophic status	Hypertrophic	Polytrophic	Polytrophic	Polytrophic	Polytrophic	Eutrophic

growth curve (von Bertalanffy, 1957), adapted according to Berg (1988). Growth was described using the von Bertalanffy (1957) growth equation $L_t = L_\infty(1 - e^{-k(t-t_0)})$, where L_t is the length at time t , L_∞ the maximum theoretical length 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. To minimize the natural spread of the data in each sample, the back-calculated growth data are shown graphically only for the age group in which a mean value of a minimum of eight eels from one lake was available.

The statistical analyses, e.g. two-way ANOVA and Mann–Whitney U -test, were performed with the statistical program SPSS (Statistical Package for the Social Sciences) version 9.0. A Kruskal–Wallis H -test was used to test for significant differences between mean characteristics (e.g. L_T and gross energy) of the eels in each lake, using a significance level of 0.05 and following rank analysis (rank transformation) with a Nemenyi test.

Results

Stocking rates of eels in the lakes has differed in the past 10 years (Table 2). It was more or less continuous in Lakes Eiserbude, Jungfernsee, and Pritzerbe. However, in Lakes Blankensee and Rangsdorf, stocking started again in 1999 after being stopped in 1990. In Lake Sacrow, the natural immigration of elvers was deemed to be sufficient (fishers Ebel and Zienert, pers. comm.), so no stocking took place there.

The L_T of female yellow eels ranged from 21.6 to 66.2 cm (Table 3). For each lake, eels of roughly the same length range were investigated, although eels sampled from Lake Eiserbude were clearly longer (Table 3) and older ($p < 0.05$) (results not shown) than those in the other five lakes. Fulton's condition factor for yellow eels in the various lakes varied between 0.10 and 0.24, and the gross energy content ranged between 4.3 and 15.3 MJ kg⁻¹. There were no significant differences in mean condition factor ($p > 0.05$) or mean gross energy content between eel samples in the different lakes (Table 3).

The ages of eels ranged from 3 to 14 years. With increasing age, the length of female yellow eels increased, but there was a wide scatter between and within lakes (Figure 2a). Growth in the first few years was mainly in length, but thereafter (after the 7th or 8th year) more obvious in weight (Figure 2b). Summaries of the

annual minimum, mean, and maximum increase in length, and the mean values of L_∞ are presented in Table 4. The biggest annual increment on the otoliths in all six lakes was generally in the first, but often also in the second, year of growth in fresh water, ranging from 6.1 to 8.5 cm year⁻¹. In the subsequent 12 years, the annual increment remained stable or decreased, and ranged from 6.8 to 1.6 cm year⁻¹.

The mean back-calculated growth rates of the eels from the six lakes in the River Havel system are shown in Figure 3a. The intersection point of the growth curve with the y -axis corresponds to the length of the eels when they enter European waters, i.e. as glass eels. The length of glass eels calculated by back-calculation ranged from 5.8 to 8.7 cm (mean for all lakes 6.7 cm). Further analyses (two-way ANOVA) revealed significant differences in the mean total length and mean growth rate between the six lakes for the first seven continental years (Table 5).

Representing the growth by von Bertalanffy growth curves (Figure 3b) shows that growth rate decreases with increasing age of eel, and allows prediction of an optimal catching time. In the lakes of the River Havel system, the minimum time between stocking of the lakes with glass eels and the recapture of the eels at a length of 45 cm was 7 years. However, the size was attained by female eels mainly after 8–9 years, and at the latest after 10 years (Figure 3a and b). The 45 cm body length corresponds to the legal minimum capture size in Germany and with an eel body weight of 130–180 g.

Table 3. Total length, Fulton's condition factor (K), and gross energy content (\pm s.d.) of female yellow eels from the six lakes in the River Havel system.

Lake	Total length (cm)			Mean condition factor K (\pm s.d.)	Mean gross energy (\pm s.d.) (MJ kg ⁻¹)
	Minimum	Mean	Maximum		
Blankensee	24.6	45.1	66.2	0.17 (0.028)	6.53 (1.99)
Eiserbude	41.1	48.8	62.6	0.17 (0.021)	9.30 (3.15)
Jungfernsee	21.6	41.6	65.8	0.16 (0.026)	7.14 (2.37)
Pritzerbe	23.6	43.6	61.1	0.18 (0.025)	8.21 (2.78)
Rangsdorf	31.8	44.1	57.0	0.17 (0.021)	8.47 (3.10)
Sacrow	23.1	40.3	59.0	0.18 (0.024)	7.22 (2.81)

Table 2. Stocking of eels (kg) over the past 10 years at the six lakes investigated in the River Havel system.

Year	Blankensee	Eiserbude	Jungfernsee	Pritzerbe	Rangsdorf	Sacrow
1990	0	5 A ₀	0	60 A ₀	0	0
1991	0	5 A ₀	123 A _V	13 A ₀	0	0
1992	0	0	0	20 A ₀	0	0
1993	0	15 A ₀	98 A _V	25 A ₀	0	0
1994	0	5 A ₀	98 A _V	26 A ₀	0	0
1995	0	15 A ₀	54 A _V	7 A ₀	0	0
1996	0	70 A ₀	98 A _V	0	0	0
1997	0	0	74 A _V	903 A _S	0	0
1998	0	36 A ₀	110 A _V	185 A _S	0	0
1999	140 A _V	10 A ₀	74 A _V	57 A _V	230 A _S	0
2000	170 A _V	12.12 A _S	98 A _V	78 A _V	275 A _S	0
2001	500 A _S	12.12 A _S	88 A _V	195 A _S	200 A _S	29 A _S

A₀, glass eels; A_V, farm eels; A_S, bootlace eels.

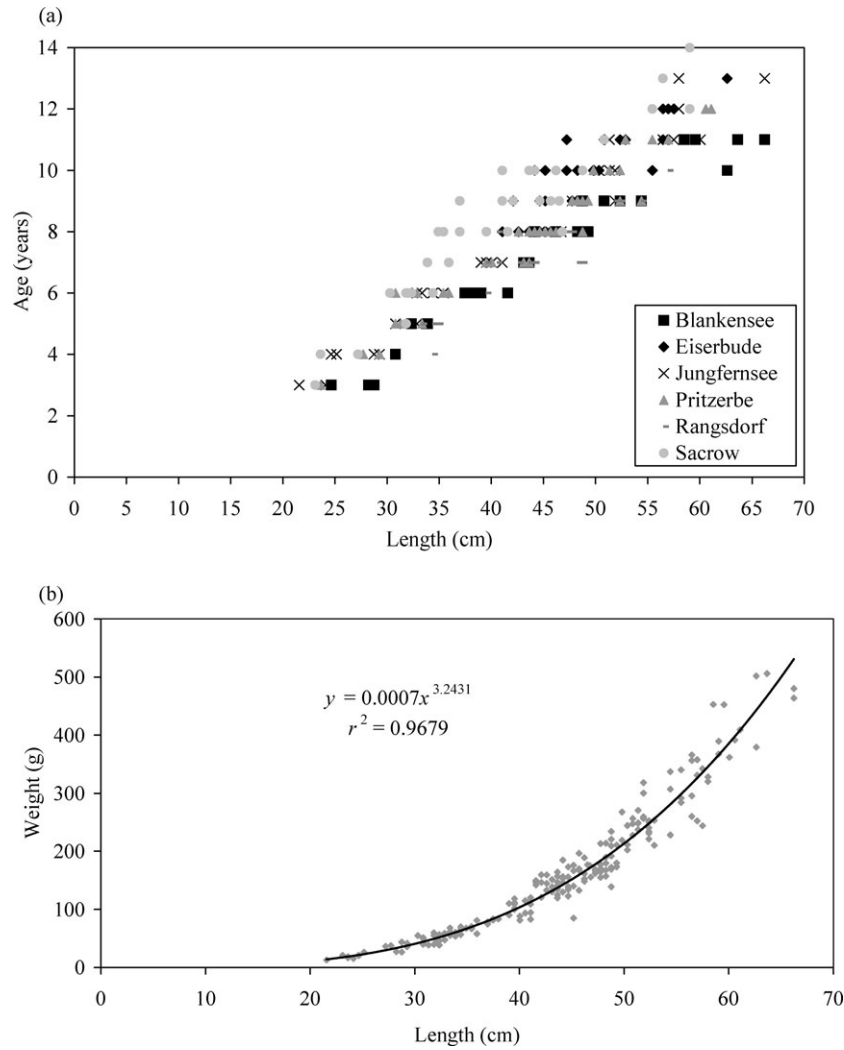


Figure 2. Correlation between (a) age and length, and (b) length and weight of female yellow eels ($n = 199$).

Discussion

In all six lakes, the condition factors of female yellow eels lay in the normal range for eels in lakes in northeastern Germany (Schreckenbach, 1996, 1998). The mean values were similar between the lakes, 0.16–0.18, but there was a wide spread of individual values. My mean values of condition factors are consistent with the values observed in eels in Lake Võrtsjärv (Estonia), 0.16–0.24 (Kangur and Kangur, 1998), and my range of condition factors, 0.10–0.24, with that of yellow eels in the upper River Havel, 0.149–0.212 (Jørgensen, 1988). The spread of condition factors determined here is greater than in eels found in Dutch coastal waters at the same time of year (0.08–0.12; Tesch, 1928). The fact that mean condition factors in this study and also in eels from the upper River Havel were higher than in Dutch coastal waters probably indicates a worse dietary state in the latter area, and supports similar differences found in growth rate (see below).

No eel had a critical gross energy content $< 4 \text{ MJ kg}^{-1}$ which, according to Schreckenbach *et al.* (2001), would reflect poor condition or an energy deficiency. The mean values of gross energy content in the eels analysed here were in the range $6.5\text{--}9.3 \text{ MJ kg}^{-1}$, less than the average value of 11.5 MJ kg^{-1} for eels

in lakes in northeastern Germany (Schreckenbach *et al.*, 2001). This may possibly be a consequence of a different time of capture (mid-May in this study), when the eels may not have completely compensated for a decrease in energy resources during winter. In Lake Eiserbude, the greater mean gross energy content was possibly partly the result of the larger average body size of eels there and the absence of bream (*Abramis brama*) in the lake

Table 4. Growth data for female yellow eels from the six lakes in the River Havel system.

Lake	Age classes represented	Increase in length per year (cm)			Mean L_{∞} (cm)
		Minimum	Mean	Maximum	
Blankensee	3–11	2.5	5.3	8.5	90
Eiserbude	8–13	2.0	4.1	7.6	83
Jungferensee	3–13	2.3	4.5	8.1	80
Pritzerbe	3–12	2.2	4.3	7.0	83
Rangsdorf	4–10	2.6	5.0	8.4	84
Sacrow	4–14	1.6	4.0	7.2	73
All lakes			4.5		82

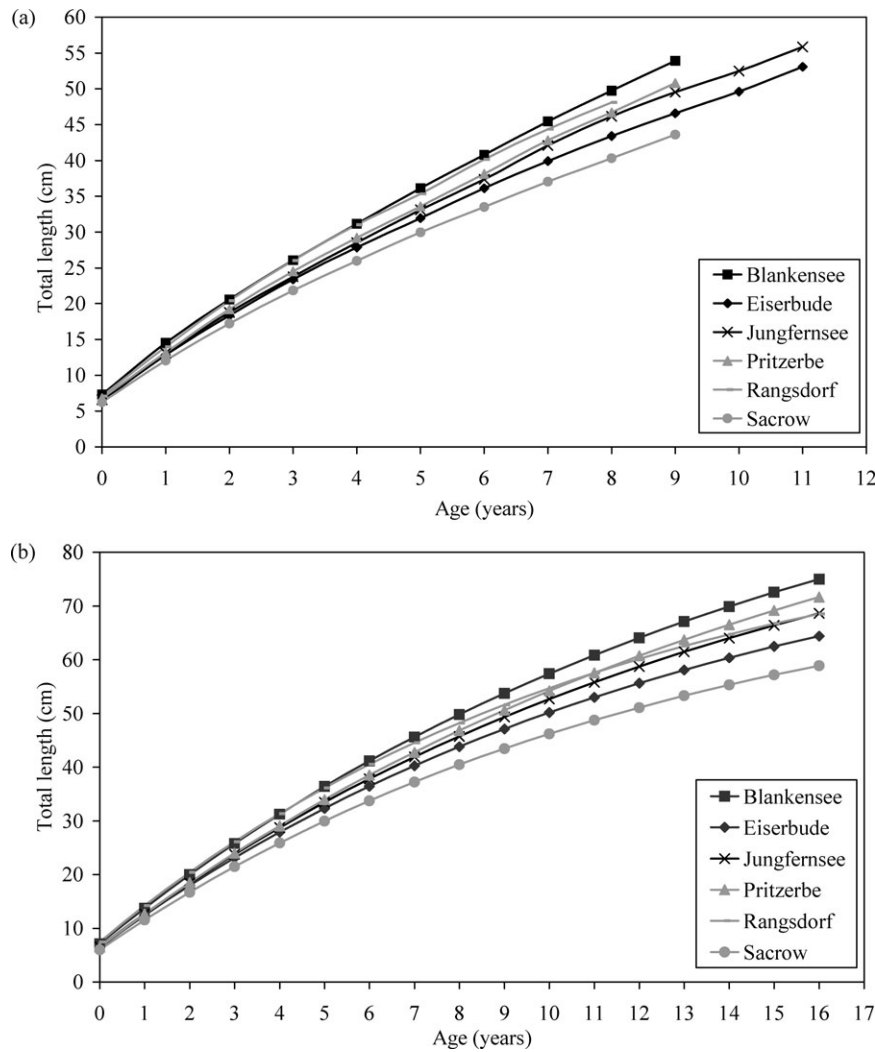


Figure 3. (a) Back-calculated growth, and (b) von Bertalanffy growth curves of female yellow eels from the six lakes in the River Havel system.

(an important competitor for food resources; Lammens *et al.*, 1985; Kangur and Kangur, 1998).

Growth

The wide range in size of eels of the same age (Figure 2a) is consistent with the results from other studies (Berg, 1990; Panfili

et al., 1994). Because of the local geography, the catches from the six River Havel system lakes were a mixture of immigrant, stocked, and migrating eels, which resulted in some heterogeneity of eel stocks throughout the lakes. Holmgren (1996) and Holmgren and Wickström (1996) showed that the relationship between body length increase and otolith increment is not

Table 5. Comparison of eel mean total length and mean growth rate between the six lakes of the River Havel system for the first seven years of continental life (two-way ANOVA, Tukey-test type B, d.f. = 5, $p < 0.05$).

Parameter	Blankensee	Eiserbude	Jungfernsee	Pritzerbe	Rangsdorf
Total length	Eiserbude*				
	Jungfernsee*	Jungfernsee*			
	Pritzerbe*	Pritzerbe*	Pritzerbe*		
	Rangsdorf*	Rangsdorf*	Rangsdorf	Rangsdorf	
	Sacrow*	Sacrow*	Sacrow*	Sacrow*	Sacrow*
Growth rate	Eiserbude*				
	Jungfernsee*	Jungfernsee*			
	Pritzerbe*	Pritzerbe*	Pritzerbe*		
	Rangsdorf	Rangsdorf*	Rangsdorf	Rangsdorf*	
	Sacrow*	Sacrow*	Sacrow*	Sacrow*	Sacrow*

*Significant.

always linear for the European eel, potentially causing errors when back-calculating growth. However, the deviation of back-calculated length from observed body length is, with few exceptions, usually within $\pm 15\%$ (Holmgren, 1996).

The eel growth rates estimated by otolith increments varied within and between lakes (Figure 2a), as reported in other studies (e.g. Anwand and Valentin, 1981; Moriarty, 1987; Vøllestad, 1992). Faster growth has been recorded in Lake Võrtsjärv (Estonia) by Kangur (1998), similar rates in the rivers of Ireland by Moriarty (1983), and relatively slower growth in Erne Lakes, Ireland, by Matthews *et al.* (2001, 2003), in the upper River Thames, England, by Naismith and Knights (1993), in Dutch coastal waters by Tesch (1928), and in the Burrishoole system, Ireland, by Poole and Reynolds (1996, 1998). However, the growth rate of eels in lakes without natural stocks can reach 8–10 cm year⁻¹ in the first 4 years after stocking with bootlace eels (Wickström, 1986).

The wide range in annual growth seen here is likely a result of the variable growth rates of eels generally, and fastest growth can be linked with the rapid growth of eels in their first year after arriving in Europe. During the first year (and often also in the second year), the eels grew considerably faster than in subsequent years, and at a rate of 6.1–8.5 cm year⁻¹, eels double their size at the glass eel stage within no more than 2 years. Such rapid increases in body size in the first year in Europe have been described before (Moriarty, 1983; Poole *et al.*, 1992; Matthews *et al.*, 2001). However, from the results of this study, the rapid growth rate can also extend to the second continental year, as reported previously by Sinha and Jones (1967). In contrast, some authors have recorded the fastest increases in body length of eels during the third (Schneider, 1909), fourth (Jørgensen, 1988), or even sixth (Thurrow, 1959) continental year. The decreases in mean annual growth with increasing age reported here are similar to previous results (Pedersen, 1998, 2000).

The back-calculated length of eels when they entered European waters as glass eels (5.8–8.7 cm) corresponds with the length of glass eels observed in the wild, i.e. 5.6–9.2 cm (Heermans and Van Willigen, 1982, cited in Deelder, 1984).

The mean values of L_{∞} for eels in lakes of the River Havel system were between 73 cm (Lake Sacrow) and 90 cm (Lake Blankensee). All values seem to be realistic, with reported mean values of L_{∞} ranging from 59.83 cm for eels in a Danish stream (Rasmussen and Therkildsen, 1979) to 145.90 cm for eels in Lake Neusiedler, Germany (Paulovitz and Biro, 1986).

Comparison with earlier studies of eel growth

In the 1950s in Lake Sacrow, growth of female yellow eels was reported to be somewhat faster than reported here for 2001 (Rahn, 1955) (Figure 4a). The mean length of female yellow eels aged 5–9 years in the 1950s was significantly higher than nowadays (U -test, d.f. = 1, $p < 0.05$). There have been no significant changes in hydrochemical or hydrophysical parameters (cf. Möller, 1932; Rahn, 1955), in the morphology of the lakes (cf. Wundsch and Meseck, 1939), or in the number or lengths of eels being stocked (fishers Ebel and Zienert, pers. comm., Table 2) between the 1950 and 2001. However, one possible factor underpinning the faster growth of eels in earlier years, as reported by Rahn (1955), was the intensity of the eel fishery just before his investigation, with annual yields of >200–400 kg. By comparison, the yield was <100 kg year⁻¹ in the 10 years before this investigation. Perhaps, the more intensive

fishing activity in the 1950s resulted in thinning-out of the eel stock and less intraspecific competition. Moreover, the number of small prey fish was much higher in the 1950s than today (fisher Ebel, pers. comm.). This fact is also reflected in the head ratio of eels: during the 1950s, it was 64% broadhead to 36% narrowhead, but in 2001, the ratio had almost reversed, to 17% broadhead to 83% narrowhead. The diet of eels influences the shape of the head (Lammens and Visser, 1989; Proman and Reynolds, 2000). Broadhead eels consume large and/or hard-bodied organisms (e.g. fish, molluscs, and beetles), whereas narrowhead eels prefer small/soft-bodied prey (e.g. chironomids and amphipods) (Lammens and Visser, 1989; Proman and Reynolds, 2000).

In the 1970s in Lake Blankensee, the growth rate of female eels was greater than that of eels sampled in 2001 (Anwand and Valentin, 1981) (Figure 4b). The hydrochemical and hydrophysical parameters and morphology of that lake have not changed to any great extent in the past 20 years. However, the faster growth of eels in the 1970s may have been partly the consequence of the more-intensive bream fishery then (fisher Wildemann, pers. comm.), because as stated above, bream are competitors of eels for food. Therefore, the greater density of prey for eels (chironomid larvae in the sediment) and a lesser stocking density (unpublished statistics for Lake Blankensee) in the past 10 years could have resulted in lower inter- and intraspecific competition for food in the lake than today.

Jørgensen (1988) investigated two parts of the River Havel system not far from Lake Jungfernsee during 1987. Both were comparable with Lake Jungfernsee because they were lake-like expansions of the river a few kilometres higher up the River Havel than the open-tube Lake Jungfernsee itself. The growth of female eels in both parts of the River Havel and in Lake Jungfernsee does not differ significantly despite an interval between the studies of almost 20 years (Figure 4c). The mean length of female yellow eels in 1987 (age 4–6 years) is not much different from today's values (U -test, d.f. = 1, $p > 0.05$).

In addition to the lake-specific changes discussed above, there has been a general decrease in the direct and diffuse introduction of nutrients (primarily nitrogen and phosphorus) into German fresh waters since the 1990s, as a consequence of the modernization of industry, new regulations and conditions, and the inauguration of cleaning stations with a third cleaning step (of phosphorus elimination). This has resulted in a slight decrease in the trophic status of the lakes in the Federal State of Brandenburg (Institute for Inland Fisheries e.V. Potsdam–Sacrow, unpublished data). This is evident, e.g. in Lake Jungfernsee, in the lesser development of algae and increased transparency during a long clear-water period in summer (fisher Weber, pers. comm.). With decreasing nutrient concentration, there is less food available for predatory fish, which results in slower growth and subsequently in declining fish stocks.

In the lakes of the Federal State of Brandenburg, the intensity of fishing for eels has not dropped over the past 10 years (Brämick and Fladung, 2006), because eels remain the most sought species by the commercial fishery (Brämick, 2005). However, yields have been dropping continuously in the lakes (pers. obs.).

To conclude, the slower growth of eels in 2001 compared with the situation 50 years earlier cannot alone explain the huge drop in yield in the River Havel system. Other factors clearly play at least as important a role.

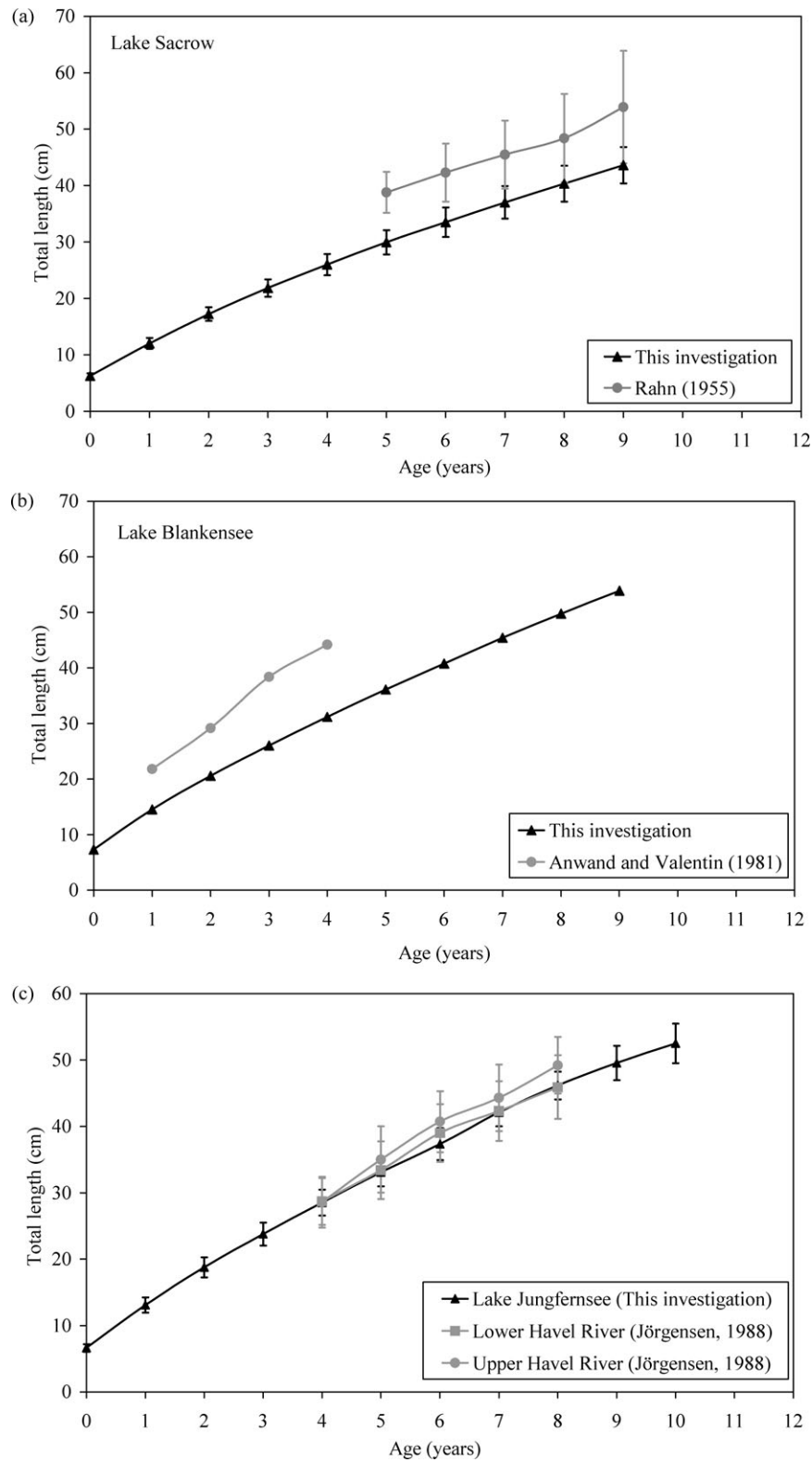


Figure 4. Mean age and growth (\pm s.d.) of female yellow eels in (a) Lake Sacrow according to Rahn (1955), (b) Lake Blankensee according to Anwand and Valentin (1981) and in the current investigation, and (c) in the River Havel according to Jørgensen (1988) and in Lake Jungfersee in the current investigation. The differences between total length data examined were significant (U -test, $d.f. = 1$, $p < 0.05$) in (a) and (b), but not in (c).

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