Fisheries Research 164 (2015) 278–285

Contents lists available at ScienceDirect

Fisheries Research

journal homepage: www.elsevier.com/locate/fishres

Age and growth of European eels (*Anguilla anguilla*) in the Elbe River system in Germany

Janek Simon*

Institute for Inland Fisheries e.V. Potsdam-Sacrow, Im Königswald 2, D-14469 Potsdam, Germany

ARTICLE INFO

Article history:
Received 15 July 2014
Received in revised form
15 December 2014
Accepted 18 December 2014
Handling Editor B. Morales-Nin
Available online 13 January 2015

Keywords:
Otolith increments
Silver eel
von Bertalanffy
Sex related growth
Size classes
Eel management

ABSTRACT

Models to describe the stock dynamics of the endangered European eel, *Anguilla anguilla*, are needed on river system level to develop conservation management strategies. For these models, estimations of age and growth of local eel stocks are important prerequisites. To investigate the variation of these two parameters I collected 160 European silver eels grouped by 100 mm size classes at capture from the lower part of the Elbe River in Germany during fall 2011. Length of collected eels ranged from 360 mm to 957 mm and age from 7 years to 23 years. Mean age and growth, estimated by otolith increments, were higher for females (14 years, growth 52 mm year^{-1}) than for males (13 years, 35 mm year^{-1}). Larger females were older and grew faster as compared to smaller females. Across all size classes at capture, the weighted mean age and annual length increment based on the percentage of eels per size class of the migrating silver eels were 13 years and 50 mm year^{-1}, respectively. The parameters of the von Bertalanffy growth model L_∞, k and t_0 for silver eels are given, which can be used to model the dynamics of the eel stock of the Elbe River system.

1. Introduction

Management plans are basic tools for sustainable use of commercially important fish species. They exist for several marine and freshwater fishes, such as Atlantic cod (*Gadus morhua*) and walleye (*Sander vitreus*) (EU, 2007a; Berry, 1995; Locke et al., 2005). Furthermore, for endangered fish species management plans are helpful tools to assist conservation action (EU, 2007b). To develop sound management plans detailed knowledge on the biology and population structure (age structure, growth rates, rates of survival, age at onset of sexual maturity, and longevity) of the fish species of interest is needed. In many cases, however, comprehensive population data are rarely available. In such cases models of the population dynamics may be helpful.

The European eel (*Anguilla anguilla*) is an example of a commercially important and endangered species with limited knowledge on its biology and population structure. All three life stages of this eel species: glass eel, yellow eel and silver eel are of commercial interest for human consumption and stocking (Tesch, 2003). On the red list of the International Union for Conservation of Nature (IUCN), this species is currently listed as critically endangered (IUCN, 2014). Since 1999, the European eel population is considered to be outside of safe biological limits (ICES, 1999). In 2007 the Council of the European Union (EU) adopted a regulation (EU, 2007b) establishing recovery measures for the European eel population. This regulation forces the EU member states to develop and implement eel management plans at river system level (EU, 2007b). To develop local management plans, estimates of age and growth of eels are important prerequisites for describing eel stock dynamics in a river system (Oeberst and Fladung, 2012).

Having a catadromous life cycle, this fish species enters the European continent in the glass eel stage and some of them start an upstream migration to colonise inland waters (Tesch, 2003). Within the different inland waters eels grow up until they metamorphose from the pre-pubescent yellow eel stage into the maturing silver eel stage to start their spawning migration back downstream to the sea. Depending on environmental factors and sex it can take up to 57 years until eels start maturing to silver eels (Poole and Reynolds, 1996a). Furthermore, the European eel exhibits strong sexual dimorphism in terms of growth and maturation (e.g. Penàz and Tesch, 1970; Holmgren et al., 1997). Male silver eels reach a size of only 290–540 mm whereas female silver eels can grow up to a size of 1330 mm (Dekker, 2004).

Age determination of eels has been conducted by different methods for more than a century (e.g. Gemzøe, 1906; Ehrenbaum and Marukawa, 1914; ICES, 2009). However, accurate ageing of European eels is very difficult (Svedäng et al., 1998; ICES, 2009). Growth of eels varies substantially not only between, but also

* Tel.: +49 33201 40620; fax: +49 33201 40640.
E-mail address: janek.simon@ifb-potsdam.de

http://dx.doi.org/10.1016/j.fishres.2014.12.005
0165-7836/

within local stocks (e.g. Sinha and Jones, 1967; Vøllestad, 1992; Moriarty, 1987). This variability results into a potentially broad size variation of sexually mature eels (silver eels) of the same age (e.g. Frost, 1945; Poole and Reynolds, 1996a; Matthews et al., 2003). In consequence, age estimation by length-frequency analyses (Petersen method: Petersen, 1895) may lead to erroneous results (Ehrenbaum and Marukawa, 1914).

According to studies conducted during recent decades, otoliths are the most suitable structure for eel age determination (ICES, 2009). A wide variety of otolith preparation and staining techniques has been developed for age examination (reviewed in Vøllestad et al., 1988; ICES, 2009). As silver eels represent the fully mature and migrating stage (Tesch, 2003) silver eel otoliths provide a complete growth history of the individual eel such that variations in growth may be observed both between and within the sexes at the two continental life history stages (Poole and Reynolds, 1996a). Additionally, growth and age of eels in the catchment area of a river can vary greatly (e.g. Sinha and Jones, 1967; Barak and Mason, 1992; Aprahamian, 2000) because of different environmental conditions from the spring to the estuary.

To obtain a representative view on age composition and mean growth of eels from the entire catchment area, a random sample of yellow eels representing the entire river has to be investigated. Such comprehensive sampling, which is very expensive and time consuming, was conducted by Matthews et al. (2003) for the lakes of the Erne catchment in Ireland and by Simon et al. (2013) for the German coastal areas of the southern Baltic Sea. An alternative method of sampling migrating semelparous species like the eel is to investigate a random sample of mature migrating individuals based on the assumption that they reflect the complete variation in age and growth of silver eels of a specific river system. The sampling location, however, should not be located too close to the mouth of the river (in the area of tidal influence) to minimise the risk of having also eels in the sample that did not grow up in the river system. Some eels during their growth phase migrate several times between fresh and sea water habitats (inter-habitat shifter according to Shiao et al., 2006).

The aim of my study was to examine age of silver eels and previous growth during their continental phase in a German river system to obtain a representative view of age composition and mean growth. I hypothesised that the size at capture of female eels, in particular, is not an unequivocal indicator of eel age, because growth of eel can differ between the tributaries, and may furthermore depend, for example, on stocking history and habitat characteristics.

2. Materials and methods

2.1. Study area

The Elbe River (Fig. 1) is one of the largest rivers in Germany with a catchment area of about 148.000 km^2 and a mean discharge 861 m^3 s^{-1} at the water mouth (Simon et al., 2005). The river spring is located in the southern part of the Giant Mountains (Czech Republic) from where it flows 1094 km through Czech Republic and Germany into the North Sea at the German city of Cuxhaven (Simon et al., 2005). Besides the weir near the city of Geesthacht, no further migration obstacles (e.g. dams, weirs, sluices, water power stations) and hydropower stations exist in the German part of the main stream of the Elbe River. In contrast, the tributaries to the Elbe River are extensively obstructed with about 4900 obstacles in Germany and more than 120 in the Czech Republic (Simon et al., 2005; Brämick et al., 2008). Most of the main current of the Elbe River is channelised and regulated with an extensive riverbank reinforcement of 6900 groyne fields and 327 km training walls to improve navigation up to the city of Praha (Czech Republic) (Simon et al., 2005). The fish community of the Elbe River from spring to the estuary comprises 94 species (43 limnic, 17 euryhaline and 34 marine species) (Gaumert, 2000). Due to the large catchment area of the river, a high variability of connected water bodies ranging from oligotrophic to polytrophic and shallow to more than 60 m deep lakes, respectively, exist which all drain into the Elbe River. Moreover, both cool and slowly flowing mountain streams as well as slowly running lowland rivers with summerly water temperatures of over 20 °C are part of the Elbe River system.

European eels are found in all waters bodies of the Elbe River system up to the low mountain range where the fish community is typical of the trout zone (Huet, 1949, 1964; Kammerad et al., 2012) and play an important role in commercial and recreational fisheries (Fladung et al., 2012b). Between 2000 and 2010, about 400 commercial fishing companies and 330,000 recreational fishermen captured about 300 t of eels per year within the German part of the Elbe River system alone (Brämick et al., 2008; Fladung et al., 2012b). Intensity of eel fishing and yield, however, vary considerably in the system. Eels are caught by fyke netting, electrofishing, stow nets and with stationary eel traps. Annual yield of commercial eel catch in the Elbe River system is approximately 1.0 kg ha^{-1} which is only half the yield of its nutrient-rich lowland tributary river Havel, where, on average, 2.2 kg ha^{-1} are captured (Fladung et al., 2012b). A limited but not marginal natural immigration of glass eels and elvers exists in the main current of the Elbe River and in some of its tributaries (Beckedorf and Schubert, 1995; Simon et al., 2006). Stocked eels, however, numerically dominate in the eel stock of the Elbe River system. In the 1980s, eel stocking was high with in average 16.0 Mio. glass eels and 0.3 Mio. small yellow eels per year. After the German reunification until 2006, annual stocking intensity decreased to in average 2.6 Mio. glass eels, 1.0 Mio. farm eels, and 0.6 Mio. small yellow eels (Brämick et al., 2008).

2.2. Sampling programme

For the Elbe River a location of commercial eel catch as close as possible to the mouth of the river was chosen to sample silver eels. The sampling location was situated near the village of Gorleben (53°054′ N, 11°348′ W). Three otter-board stow nets with wings of 20 m, an opening of three times 12 m and a mesh size of 15 mm in the cod-end were operated by commercial fishermen in response to expected eel catches at four spots about 269–277 km upstream the mouth of the Elbe River. The estimated age and growth data therefore describe the eel stock from the catchment area upstream the sampling location which represents 85% (without estuary) of the total catchment area of the Elbe River system (Fladung et al., 2012a). Downstream the sampling location, however, only some small tributaries drain into the main current of the Elbe River (Fig. 1).

The stow nets were operated in the main current of the river and, therefore, the power of the water current stretched the mesh openings to small grooves. In combination with the used mesh size of 15 mm in the cod-end, eels of ≥250 mm total length (L_T) were captured ensuring a representative sampling of male silver eels (Gemzøe, 1906; Tesch, 2003). Silver eels were measured from 25 daily catches with 11–147 captured eels per sampling throughout the silver eel fishing period (5 August to 29 November 2011). These 25 sampling events were needed as size and sex ratios of migrating silver eels can vary during downstream migration (Durif and Elie, 2008; Reckordt et al., 2014). In addition, the proportions of both the smallest and the largest silver eels can lie below 1% of the total catch (Poole and Reynolds, 1998), but the values of these eels predominantly influence the trend of the von Bertalanffy

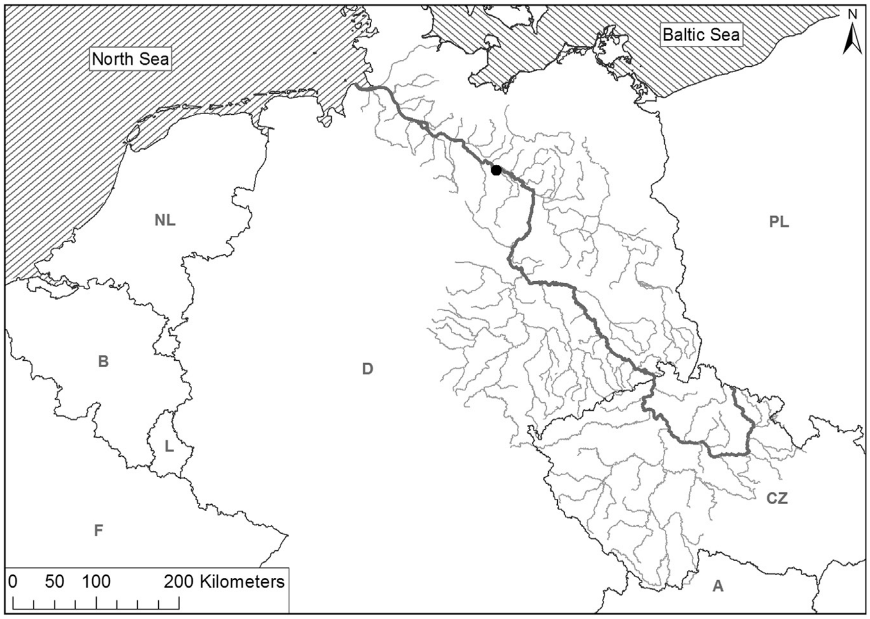

Fig. 1. Map of the Elbe River system with the sampling location (●) for silver eels in the north-eastern part of Germany. Map based on dataset of the Federal State of Brandenburg and of the German Federal Institute of Hydrology (BfG).

growth function. For this reason, a minimum number of eels per size class (L_T) were sampled: <400 mm: 20 eels, 400–499 mm: 50 eels, 500–599 mm: 20 eels, 600–699 mm: 20 eels, 700–799 mm: 20 eels, ≥800 mm: 20 eels, to minimise over- or underestimation of growth and to also include a representative number of males in the sample (Table 1).

For measuring all eels were anaesthetised with tricaine methanesulphonate (MS-222, 0.012% aqueous solution). The L_T of each eel (±1 mm) and the associated weight (±1 g) were recorded along with the eye diameter and length of the pectoral fin to assess the silvering degree (Durif et al., 2009). Studies in the Elbe River system and Warnow River system have shown that also female eels at premigrant stage (FIII) migrate successfully (Simon et al., 2012; Reckordt et al., 2014). Therefore, beside eels classified as migrating stage FIV, FV, and MII, respectively (Durif et al., 2009), also eels at the premigrant stage (FIII) were classified as silver eels and were included in the study if they clearly showed typical external characteristics of silver eels (large eyes and silvering body). Silver eels were assigned to the correct size class by L_T and from each catch about one or two eels per size class were randomly separated for investigation of sex, age and growth. If the desired number of eels per size class was not achieved after about 20 samplings, the catch of the last five samplings was searched for silver eels of appropriate length to fill the gaps in numbers.

All eels to be used for further analyses were killed with MS-222 (0.015% aqueous solution). Dead eels were individually marked and stored in a plastic bag at −20 °C. The L_T and weight after capture were assigned from the capture protocol by means of the individual markings. A total of 160 silver eels was sampled (Table 1). All other eels were released to shallow areas of the Elbe River after complete recovery.

After thawing, all eels were sexed visually by gross morphological examination in the laboratory (Frost, 1945). Crenulated, ribbon-like gonads were classified as female and narrow, lobed (scalloped) gonads, as male (Frost, 1945). For age determination, the sagittal otoliths of eels were extracted and stored in 96% ethanol. Otoliths were prepared after the cutting and burning method as recommended by ICES (2009). Age estimation was based on counting of the annuli as described by Simon (2007) and ICES (2009).

2.3. Data analyses

To calculate the proportion of males and females in the sample the sex of measured only silver eels was visually determined based on strong sexual dimorphism in growth and maturation (e.g. Penàz and Tesch, 1970; Holmgren et al., 1997), as well as on length frequency distribution of the silver eels (Fig. 2).

Age and growth of males and females were analysed separately. Growth back calculation was done as described by Simon et al. (2013). Briefly, the distance between the opaque rings of the otoliths was measured under a light microscope. Back-calculation of eel growth was done using the Dahl-Lea equation (Francis, 1990) and mean growth was calculated as the mean length increment in L_T of eels per year determined over the first seven and 14 years of continental life.

Eel growth was further described by von Bertalanffy growth curves by fitting the back-calculated lengths-at-age of individual eels to L_∞, k and t_0 of the von Bertalanffy growth equation (von Bertalanffy, 1938) after Beverton and Holt (1956):

$$L_t = L_\infty(1 - e^{-k(t-t_0)}), \quad (1)$$

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 is the (hypothetical) time at which the fish would have been zero size if it had always grown according to the von Bertalanffy equation. The von Bertalanffy growth model is the most popular model for describing the growth of fishes. Furthermore, compared to other models, the von Bertalanffy growth model was the best model for fitting the L_T-at-age data for female eels and has been used in most studies of eels (Tesch, 2003; Lin and Tzeng, 2009).

The number of migrating silver eels per size class at capture normally differs greatly. Furthermore, when the size at capture of eels is not an unequivocal indicator of eel age (as hypothesised), mean growth per size class can further be weighted by the number of eels per size class of the migrating silver eels to increase the

Table 1
Mean total lengths (L_T) ± S.D., mean age ± S.D., mean length increment in L_T from years 1 to 7 ± S.D. and mean and 95% CI from the von Bertalanffy values L_∞, k and t_0 for silver eels from the Elbe River system in Germany. Means with common letters are not significantly different (Mann–Whitney test and Kruskal–Wallis test, respectively, $p > 0.05$); y, z: comparison between sexes; a, b, c: comparison between size classes within sexes. Note that statistical tests were performed only for samples of ≥20 individuals.

Size classes within sexes	n	L_T (mm)	Age classes	Age (years)	Growth year 1–7 (mm)	von Bertalanffy values					
						L_∞ (mm)	95% CI	k	95% CI	t_0	95% CI
Male – overall mean	75	413 ± 27^y	7–23	13 ± 3^y	35 ± 8^y	498^y	486–511	0.123^y	0.109–0.140	−1.303^y	−1.162 to −1.437
Size class <400 mm	23	383 ± 10^a	10–19	14 ± 3^a	31 ± 5^a	491^a	471–511	0.112^a	0.094–0.129	−1.328^a	−1.548 to −1.108
Size class 400–499 mm	52	427 ± 19^b	7–23	12 ± 4^a	39 ± 8^b	504^a	487–520	0.134^a	0.110–0.158	−1.278^a	−1.470 to −1.087
Female – overall mean	85	695 ± 119^z	9–19	14 ± 3^z	52 ± 6^z	961^z	944–1047	0.087^z	0.079–0.095	−1.036^z	−1.068 to −0.920
Size class 400–499 mm	3	479 ± 21	13–16	15 ± 2	38 ± 2	620	554–686	0.095	0.092–0.099	−1.353	−2.106 to −0.599
Size class 500–599 mm	21	558 ± 25^a	9–17	12 ± 2^a	48 ± 8^a	926^a	821–1032	0.085^a	0.067–0.103	−1.099^a	−1.237 to −0.960
Size class 600–699 mm	20	662 ± 23^{ab}	9–16	13 ± 2^a	52 ± 8^b	992^{ab}	911–1073	0.095^a	0.077–0.113	−0.931^a	−1.052 to −0.811
Size class 700–799 mm	21	744 ± 29^{bc}	10–19	15 ± 2^b	57 ± 8^{bc}	1059^{bc}	985–1133	0.085^a	0.070–0.100	−0.925^a	−1.075 to −0.775
Size class ≥800 mm	20	855 ± 44^c	12–19	17 ± 2^b	59 ± 8^c	1206^c	1103–1309	0.076^a	0.062–0.090	−0.873^a	−1.175 to −0.571
Overall mean for all size classes (male and female)	160	605 ± 167	7–23	14 ± 3	48 ± 13	863	760–876	0.098	0.092–0.109	−1.072	−1.176 to −1.030

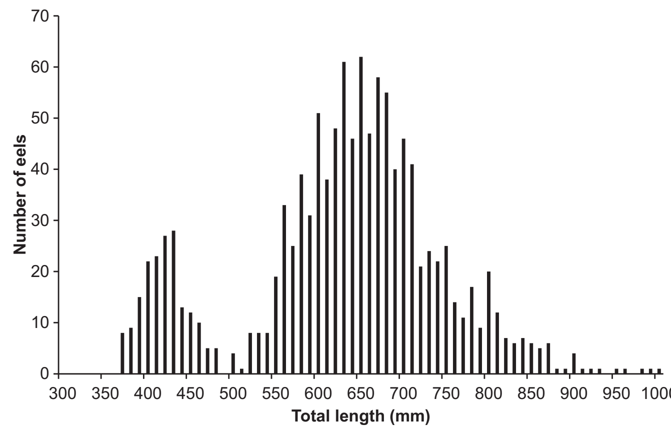

Fig. 2. Length frequency distribution for captured silver eels ($N = 1172$) from the Elbe River system in Germany in autumn 2011. Note: the x-axis starts at 300 mm.

precision of calculation. In a final step, therefore, the average age, the average length increment in L_T from years 1 to 7, and the mean parameters of the von Bertalanffy growth curves were weighted by the number of eels per size class within the eel stock separately for both sexes, and for the total stock. I assume that the length frequency distribution of silver eels in the catch of the fisherman was comparable with the length frequency distribution of all silver eels that passed the sampling location in fall of 2011.

The statistical analyses were performed with the statistical programme SPSS 9.0 (SPSS Inc., Chicago, IL, U.S.A.). The assumptions of normality and homogeneity of variances of the residuals were not met for many analyses. Therefore, to test for significant differences of variables characterising individual fish (L_T, age, average length increment in L_T, and parameters of the von Bertalanffy growth curves) between both sexes or between both size classes at capture of males, the Mann–Whitney-test (U-test) was applied. Comparison of variables between the four size classes at capture of females with a minimum of six fish in each class was conducted by using the Kruskal–Wallis-test (H-test) followed by Nemenyi tests. The significance level was set at $p < 0.05$. To correct for multiple comparisons, the false discovery rate controlling procedure (Benjamini and Hochberg, 1995) was applied.

3. Results

During the 25 sampling events the fraction of silver eels in the catch increased from 57–98% in summer to 88–100% in autumn. In total 1172 silver eels were measured, ranging from 360 mm to 995 mm in L_T. The length frequency distribution of the migrating silver eels was bimodal and approximately 15% of the migrating silver eels were males (Fig. 2). The largest amount of downstream migrating silver eels (43.5%) measured 600–699 mm at capture. Percentages of the other size classes at capture were as follows: 18.3% (700–799 mm), 16.6% (500–599 mm), 11.9% (400–499 mm), 6.1% (>800 mm), and 3.4% (<400 mm).

The L_T of silver eels examined in the laboratory ranged from 360 mm to 474 mm for males and from 457 mm to 957 mm for females. The age of these eels ranged from 7 to 23 years for males and 9 to 19 years for females.

The overall mean age was significantly higher (U-test, d.f. 1, $p < 0.01$) for females (14 years) as compared to males (13 years) across all size classes at capture (Table 1). The overall mean annual length increment during first seven and 14 years of continental life, respectively, were significantly higher in females (52 mm year^{-1} and 45 mm year^{-1}, respectively) as compared to males (35 mm year^{-1} and 23 mm year^{-1}, respectively) (U-test, d.f. 1, $p < 0.001$).

Table 2
Mean total lengths (L_T) ± S.D., mean age ± S.D. and mean length increment in L_T from years 1 to 14 ± S.D. for silver eels ≥14 years old from the Elbe River system in Germany. Means with common letters are not significantly different (Mann–Whitney test and Kruskal–Wallis test, respectively, $p > 0.05$); y, z: comparison between sexes; a, b, c: comparison between size classes within sexes. Note that statistical tests were performed only for samples of ≥6 individuals.

Size classes within sexes	n	L_T (mm)	Age classes	Age (years)	Growth year 1–14 (mm)
Male – overall mean	27	403 ± 19^{y}	14–23	16 ± 2^{z}	23 ± 2^{y}
Size class <400 mm	11	385 ± 10^{a}	14–19	16 ± 2^{a}	22 ± 2^{a}
Size class 400–499 mm	16	416 ± 12^{b}	14–23	17 ± 3^{a}	23 ± 2^{b}
Female – overall mean	51	746 ± 112^{z}	14–19	16 ± 2^{z}	45 ± 7^{z}
Size class 400–499 mm	2	490 ± 13	14–16	16 ± 1	29 ± 2
Size class 500–599 mm	6	568 ± 35^{a}	14–17	12 ± 1^{ab}	35 ± 3^{a}
Size class 600–699 mm	6	677 ± 18^{a}	14–16	15 ± 1^{bc}	43 ± 1^{ab}
Size class 700–799 mm	18	741 ± 28^{a}	14–19	16 ± 1^{bc}	45 ± 2^{b}
Size class ≥800 mm	19	855 ± 45^{b}	14–19	17 ± 1^{c}	51 ± 4^{c}
Overall mean for all size classes (male and female)	78	607 ± 188	14–23	16 ± 2	37 ± 12

The mean age of both size classes at capture of male silver eels was not significantly different (*U*-test, d.f. 1, $p = 0.053$). However, mean growth of male silver eels measuring 400–499 mm was significantly higher as compared to those measuring less than 400 mm during first seven years of continental life (*U*-test, d.f. 1, $p < 0.001$), and during first 14 years of continental life (*U*-test, d.f. 1, $p = 0.020$) (Tables 1 and 2). Females of the size classes 700–799 and >800 mm were significantly older (*H*-test, d.f. 3, $p < 0.001$) and grew faster (*H*-test, d.f. 3, $p < 0.001$) during first seven years of continental life compared to the females of the size classes 500–599 and 600–699 mm (Table 1). During first 14 years of continental life females of the size class >800 mm grew faster compared to the females of the other size classes (*H*-test, d.f. 3, $p < 0.001$), and females of the size class 700–799 mm grew faster compared to the females of the size class 500–599 mm (*H*-test, d.f. 3, $p < 0.001$) (Table 2).

The overall L_∞ of the von Bertalanffy length-at-age curve was significantly higher (*U*-tests, d.f. 1, $p < 0.001$) for females (961 mm) than for males (498 mm), whereas the parameter *k* was significantly lower (*U*-tests, d.f. 1, $p < 0.001$) in females (0.087) than in males (0.123) (Table 1). No significant differences in the parameters of the von Bertalanffy length-at-age curves were found between the size classes at capture within sexes, except that the L_∞ of females were significantly higher in the size classes 700–799 mm and >800 mm than in the size classes 400–499 mm and 500–599 mm (*H*-test, d.f. 3, $p = 0.005$).

Across all size classes at capture, the weighted mean age and annual length increment were 13 years and 50 mm year^{-1}, respectively (Table 3). The current growth of eels in the Elbe River system in Germany is reflected by the weighted von Bertalanffy growth formula with $L_t = 931(1 - e^{-0.096(t+1.009)})$.

4. Discussion

The aim of my study was to determine age and growth of silver eels in the Elbe River system. A procedure was described to representatively investigate growth of eels from a river system by sampling only one location. According to my results, age structure and growth differed between the sexes. Furthermore, remarkable differences in length-at-age and growth increments between eels of different size classes at capture were detected. Overall, growths of eels were intermediate between that observed in brackish and other freshwater habitats in Germany (Simon, 2007; Simon et al., 2013).

For the Elbe River system it was shown that both mean age and growth were higher in females than in males which is in agreement with other studies (e.g. Penàz and Tesch, 1970; Poole and Reynolds, 1996a). In contrast, Holmgren et al. (1997) and Holmgren and Mosegaard (1996) found higher growth in males than in females. The back-calculated length at age growth curves for male and female silver eels showed a divergence in growth between the sexes immediately after the first years of continental life. In contrast, Poole and Reynolds (1996a) observed such divergences first after approximately ten years of continental life by silver eels of the Burrishoole system (Ireland). This may be a result of the comparably very low growth of eels in the Burrishoole system with 13.9 mm year^{-1} for males and 14.6 mm year^{-1} for females.

Higher male silver eel proportion of 28–45% than in this study was observed in the nearby small lowland Warnow River system (Reckordt et al., 2014), which presumably is attributable to the distance of the river system to the sea. Generally, proportion of males in an eel stock decreases with increasing distance of the freshwater body from the sea (Penàz and Tesch, 1970). In terms of sex ratio under natural conditions, in the present study the proportion of male eels in the Elbe River system was overestimated. Male eels are hardly affected by fishing mortality because of the actual minimum legal catch size-limit of 500 mm in the German federal states upstream the sampling area. As a result, nearly all male eels become silver and start their migration. Additionally, the sampled male silver eels in the present study showed a larger range in age (7–23 years) by smaller range in length (360–474 mm) compared to the females which were 9–19 years old and 457–957 mm long. The lower mean age and mean growth of males compared to the females are important reasons why eel stock models should include separate calculations for both sexes and not just for females as used by Oeberst and Fladung (2012) whenever the proportion of male silver eels is not negligible.

Females of the two largest size classes had higher L_∞ values and higher mean annual length increment compared to females of the two smallest size classes. This suggests that fast growing eels can reach a larger theoretical size. In contrast, Poole and Reynolds (1996b) found that faster growth tends to produce lower L_∞ values than in the slower growing eels in the Burrishoole system (Ireland).

Large silver females were not only older but their annual growth was higher than that of small silver females. Therefore, larger size of the biggest eels is not exclusively a result of longer lifetime spent in European continental waters, as could be expected. Instead, faster growth and longer lifetime before maturation, in combination, result into larger size of female silver eels as compared to their smaller counterparts. Therefore, it is necessary to sort eels by size classes at capture to obtain an unbiased reflection of the age structure and growth of an eel stock. Mean growth of the stock can subsequently be calculated accurately based on the amount of eels per size class.

In fall 2011 migrating silver eels in the Elbe River system were numerically dominated by younger and fast growing eels. In consequence, the weighted mean age and annual length increment of the eel stock calculated by the amount of eels per size class was one year lower and 20 mm higher, respectively, compared to the

Table 3
Weighted average age, length increment in total length from years 1 to 7 and from the von Bertalanffy values L_∞, k and t_0 for silver eels from the Elbe River system in Germany. Please note age and growth were determined only from a sub sample of 160 eels from the 1172 measured silver eels.

Size classes	Number	Relative frequency (%)	Age (years)	Growth year 1–7 (mm)	von Bertalanffy values		
					L_∞ (mm)	k	t_0
<400 mm	40	3.2	14	31	491	0.112	−1.328
400–499 mm	140	11.9	12	39	504	0.134	−1.278
500–599 mm	195	16.6	12	48	926	0.085	−1.099
600–699 mm	510	43.5	13	52	992	0.095	−0.931
700–799 mm	215	18.3	15	57	1059	0.083	−0.929
≥800 mm	72	6.1	17	59	1206	0.076	−0.873
Weighted average for males			12	37	501	0.129	−1.289
Weighted average for females			14	53	1009	0.089	−0.959
Weighted average overall			13	50	931	0.096	−1.009

un-weighted mean age and annual length increment across all size classes at capture (Tables 1 and 3). Using the un-weighted mean age and annual length increment across all size classes at capture to model an eel stock would thus result in a significant underestimation of both stock parameters (age and growth) and, for example, underestimate point in time when eels achieve the minimum legal catch size-limit which, in turn, may affect fishing mortality and amount of migrating silver eels.

Compared to previous studies from the Elbe River, back calculated growth of female eels captured at the weir of Geesthacht (i.e. 132 km downstream of my sampling location) was lower than in my study while that of males was higher than reported herein (Penàz and Tesch, 1970). The observed mean length per age class of female eels in the lower part of the Elbe River downstream the City of Hamburg (beginning 171 km downstream of my sampling location) was lower and for males higher compared to female and male eels in the present study (Ehrenbaum and Marukawa, 1914). Together these findings suggest that environmental conditions and/or habitat structure of the river as well as stock density of eels may have changed (Simon et al., 2005; Adams et al., 2008).

In comparison to other waters in northern Germany, the average length increment in L_T from years 1 to 7 of female eels in the Elbe River system was higher than in female eels from the North Sea at Helgoland island, as well as from various freshwater lakes in the tributaries of the Elbe River, where values of 40 mm year^{-1} (Penàz and Tesch, 1970), 45 mm year^{-1} (Simon, 2007), and 49 mm year^{-1} (Simon et al., 2011) were measured. In contrast, the observed growth of female eels in this study was lower compared to eels from the Baltic coast where the average length increment was 59 mm year^{-1} (Simon et al., 2013). Eels generally grow faster in coastal waters than in nearby freshwater habitats (e.g. Daverat and Tomás, 2006; Melià et al., 2006), however, the causes are still unknown. Salinity gradient can influence the growth of eels as observed in the American eel (Fenske et al., 2010) and coastal waters, therefore, may be more productive growth habitats than nearby freshwater environments.

According to back-calculated growth female eels in the Elbe River system tend to achieve the minimum legal catch size-limit in the German federal states upstream of the sampling area (500 mm), on average, after 7 years. In contrast, slower growing females from nearby freshwater habitats have a longer yellow eel growth phase, taking about 9–10 years to reach this size (Simon, 2007; Simon et al., 2011). Assuming a similar annual recruitment in both the Elbe River system and nearby inland waters, the Elbe River system might make a relatively greater contribution to overall number of migrating silver eels.

In addition to environmental variables, growth of eels is furthermore influenced by their early life history as they can either naturally immigrate into a certain water body or were stocked (Pedersen, 2000; Simon and Dörner, 2014; Couillard et al., 2014). Due to the stocking history of the region, catches of silver eels from the Elbe River system were a mixture of both originally immigrated and stocked eels (Beckedorf and Schubert, 1995; Simon et al., 2006; Brämick et al., 2008), resulting in a heterogenic eel stock in the river system. Until the 1990s' stocking intensity was higher and stocked eels were almost exclusively at glass eel stage (Brämick et al., 2008). Since the 1990s' stocking intensity got reduced and use of farm sourced eels for stocking purposes increased. As shown in previous studies, growth of eels can differ depending on size at stocking (glass eel, farm sourced eel, yellow eel) (e.g. Pedersen, 2000; Simon and Dörner, 2014), and between stocked and naturally immigrated individuals (Couillard et al., 2014). Accordingly, it cannot be excluded that the observed heterogeneity in age and growth is partly caused by the origin of the eels and quality of the stocking material.

Finally, not all water bodies in the catchment area of the Elbe River system are continuously connected with the main river system. Such water bodies, like back waters and other dam-regulated parts of the river, are only temporarily connected with the current river depending on weather conditions. Therefore, silver eels from such water bodies may have access to the main river in selected years only, which may not coincide with the point in time when they reached migration stage which subsequently contributes to the observed variability in age and growth.

To conclude, the wide variations of habitats, origin of eel stocks and the temporary connection of selected parts of the water bodies to the main river may all contribute to the observed variation in growth and length of silver eels of the same age found in this study. This divergence in size-at-age corresponds to results of other eel studies (e.g. Frost, 1945; Poole and Reynolds, 1996a; Matthews et al., 2003). To determine the specific influence of these different factors, investigations on yellow eels having different early life histories, collected from different habitats (which may or may not be permanently connected to the current river), along with investigations of eel otolith microchemistry were needed.

The described great variation in growth and age of eels in a catchment area of a river was the reason why I collected silver eels only in one year and not over several years. However, it can be assumed that differences in growth and age of silver eels between years in response to varying densities are too small to be found by sampling eels only during one year. This assumption is supported by Poole and Reynolds (1996a) who found no differences in growth and age of silver eels in the Burrishoole system (Ireland) between two years.

Furthermore, I recommend sampling silver eels by 5 cm size classes (L_T), to account for the significant faster growth of large females compared to small ones (as found in the present study) and the great variability in the number of migrating eels per size class. Dividing an eel stock into weighed 5 cm size classes and sample ten silver eels per size class for age and growth investigations seems to be the optimum in terms of time, sample size and precision of the results (comparison not shown).

Some methodical limitations need to be mentioned that are associated with the ageing and back calculation of growth of the silver eels. The metamorphosis of eels from the pre-pubescent stage into the maturing silver eel stage is coupled with a decrease in growth (ICES, 2009). The subsequent growth of the otolith is characterised by reduced widths of opaque zones and closely spaced winter rings such that counting of rings and age estimation become problematic. Furthermore, additional check marks on the otoliths do not represent winter growth periods but may be indicative of physiological or environmental stressors such as silvering metamorphosis or unsuccessful migration attempts (Vøllestad, 1992; ICES, 2009). Age and growth of silver eels are, therefore, difficult to estimate. Furthermore, Holmgren (1996) reported that the increase in body length does not linearly correspond to otolith increment in European eel, which can result in errors when using the growth back-calculation method. However, under normal conditions, the deviation of back-calculated from observed body length is, with few exceptions, within ±15% range (Holmgren, 1996).

In conclusion, my results show a high variability and significant differences in age and growth of silver eels, not only between sexes but also between size classes at capture within sexes. Calculation of a mean growth of an eel stock weighted by size classes at capture and the numbers of eels per size class results in valuable data which can subsequently be used to model the dynamics of an eel stock. Using weighted age and growth data when modelling eel stock dynamics should, therefore, result in higher precision compared to models based on unweighted mean values. I, therefore, recommend use of weighted age and growth data for future stock modelling.

Acknowledgements

I would like to thank N. Hannemann, J. Kolew and C. Stögner for technical assistance and support, and R. Wolf for preparation of Fig. 1. The fisherman C. Köthke is gratefully acknowledged for providing silver eels and help. I thank R. Oeberst from the Thünen-Institute of Baltic Sea Fisheries, Rostock, for assistance with analyses of the von Bertalanffy growth equations. I also thank T. Mehner and the participants of the workshop “Scientific Writing” at the Leibniz-Institute of Freshwater Ecology and Inland Fisheries for helpful discussions on an earlier draft of the manuscript. Constructive comments from two anonymous referees and M. Dorow are gratefully acknowledged as is the assistance of M. Pietrock who kindly improved the English. Financial support came from the Lower Saxony State Office for Consumer Protection and Food Safety.

References

Adams, M.S., Hale, B.W., Gaumert, T., Bergemann, M., Ohm, B., D’Elia, C.F., 2008. Environmental history of the German Elbe river: interactions among the ecological, economic, and political environments. In: Proceedings of the 2008 Trans-Atlantic Institutional Environmental Policy in Relation to Environmental Education (TIES) Workshop, Madison, Wisconsin, USA, www.wioc.wisc.edu/events/2008-Water/readings/elbe-river-history.pdf (accessed 03.11.14).

Aprahamian, M.W., 2000. The growth rate of eel in tributaries of the lower River Severn, England, and its relationship with stock size. J. Fish Biol. 56, 223–227.

Barak, N.A.-E., Mason, C.F., 1992. Population density, growth and diet of eels, *Anguilla anguilla* L., in two rivers in eastern England. Aquac. Fish. Manage. 23, 59–70.

Beckedorf, R., Schubert, H.-J., 1995. Funktionsüberprüfung der Fischaufstiegsanlagen an der Staustufe Geesthacht. Binnenfischerei in Niedersachsen 4, 49 pp.

Benjamini, Y., Hochberg, Y., 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. J. R. Stat. Soc. B 57, 289–300.

Berry, D.K., 1995. Alberta’s Walleye Management and Recovery Plan. Alberta Environment Protection, Natural Resources Service, Number T/310, Edmonton, Alberta, Canada, 32 pp.

Beverton, R.J.H., Holt, S.J., 1956. The theory of fishing. In: Graham, M. (Hrsg.), Sea Fisheries. London, pp. 372–441.

Brämick, U., Fladung, E., Doering-Arjes, P., 2008. Aalmanagementplan–Flussgebietsgemeinschaft Elbe. Institut für Binnenfischerei e.V. Potsdam-Sacrow. Bericht im Auftrag der Bundesländer Berlin, Brandenburg, Hamburg, Mecklenburg-Vorpommern, Niedersachsen, Sachsen, Sachsen-Anhalt, Schleswig-Holstein u. Thüringen. Report of the Institute for Inland Fisheries e.V. Potsdam-Sacrow, Potsdam, 46 pp.

Couillard, C.M., Verreault, G., Dumont, P., Stanley, D., Threader, R.W., 2014. Assessment of fat reserves adequacy in the first migrant silver American Eels of a large-scale stocking experiment. N. Am. J. Fish. Manage. 34, 802–813.

Daverat, F., Tomás, J., 2006. Tactics and demographic attributes in the European eel, *Anguilla anguilla* in the Gironde watershed, SW France. Mar. Ecol. Prog. Ser. 307, 247–257.

Dekker, W., (PhD thesis) 2004. Slipping Through Our Hands. Population Dynamics of the European Eel. University of Amsterdam, Amsterdam, 186 pp.

Durif, C., Elie, P., 2008. Predicting downstream migration of silver eels in a large river catchment based on commercial fishery data. Fish. Manag. Ecol. 15, 127–137.

Durif, C., Guibert, A., Elie, P., 2009. Morphological discrimination of the silvering stages of the European eel. Am. Fish. Soc. 58, 103–111.

Ehrenbaum, E., Marukawa, H., 1914. Über Altersbestimmung und Wachstum beim Aal. Z. Fischerei 14, 89–127.

EU, 2007a. Council Regulation (EC) No 1098/2007 of 18 September 2007 establishing a multiannual plan for the cod stocks in the Baltic Sea and the fisheries exploiting those stocks, amending Regulation (EEC) No 2847/93 and repealing Regulation (EC) No 779/97. Off. J. Eur. Union L 248, 1–10.

EU, 2007b. Council Regulation (EC) No 1100/2007 of 18 September 2007 establishing measures for the recovery of the stock of European eel. Off. J. Eur. Union L 248, 17–23.

Fenske, K.H., Secor, D.H., Wilberg, M.J., 2010. Demographics and parasitism of American eels in the Chesapeake Bay, USA. Trans. Am. Fish. Soc. 139, 1699–1710.

Fladung, E., Simon, J., Hannemann, N., Kolew, J., 2012a. Untersuchung der Blankaalabwanderung in der niedersächsischen Mittelelbe bei Gorleben. Report of the Institute for Inland Fisheries e.V. Potsdam-Sacrow, Potsdam, 21 pp.

Fladung, E., Simon, J., Brämick, U., 2012b. Umsetzungsbericht 2012 zu den Aalbewirtschaftungsplänen der deutschen Länder 2008. Report of the Institute for Inland Fisheries e.V. Potsdam-Sacrow, Potsdam, 53 pp.

Francis, R.I.C.C., 1990. Back-calculation of fish length: a critical review. J. Fish Biol. 36, 883–902.

Frost, W.E., 1945. The age and growth of eels (*Anguilla anguilla*) from the Windermere catchment area. Part I and II. J. Anim. Ecol. 14, 26–36, 106–124.

Gaumert, T., 2000. Die Entwicklung des Fischartenspektrums der Elbe mit Berücksichtigung der Neozoen-Problematik. Arbeitsgemeinschaft für die Reinhaltung der Elbe, Hamburg, 11 pp.

Gemzøe, K.J., 1906. Age and rate of growth of the eel. Rep. Dan. Biol. St. 14, 10–39.

Holmgren, K., 1996. Otolith growth scaling of eel, *Anguilla anguilla* (L.), and back calculation errors revealed from alizarin labelled otoliths. Nord. J. Freshw. Res. 72, 71–79.

Holmgren, K., Mosegaard, H., 1996. Plasticity in growth of indoor reared European eel. J. Freshw. Res. 72, 63–70.

Holmgren, K., Wickström, H., Clevestam, P., 1997. Sex-related growth of European eel, *Anguilla anguilla*, with focus on median silver eel age. Can. J. Fish. Aquat. Sci. 54, 2775–2781.

Huet, M., 1949. Apercu dés relations entre la pente et les populations des eaux courantes. Schweiz. Z. Hydrol. 11, 333–351.

Huet, M., 1964. The evaluation of the fish productivity in fresh waters. The coefficient of productivity. Verh. Int. Ver. Theor. Angew. Limnol. 15, 524–528.

ICES, 1999. ICES Cooperative Research Report No. 229. Report of the ICES Advisory Committee on Fisheries Management 1998. Part 2, 446 pp.

ICES, 2009. Workshop on Age Reading of European and American Eel (WKAREA), 20–24 April 2009, Bordeaux, France. ICES CM 2009\ACOM 48, 66 pp.

IUCN, 2014. IUCN Red List of Threatened Species. Version 2014.2, http://www.iucnredlist.org (accessed 03.11.14).

Kammerad, B., Scharf, J., Zahn, S., Borkmann, I., 2012. Fischarten und Fischgewässer in Sachsen-Anhalt Teil 1 Die Fischarten. Ministerium für Landwirtschaft und Umwelt des Landes Sachsen-Anhalt, Magdeburg, 240 pp.

Lin, Y.J., Tzeng, W.N., 2009. Modelling the growth of Japanese eel *Anguilla japonica* in the lower reach of the Kao-Ping River, southern Taiwan: an information theory approach. J. Fish Biol. 75, 100–112.

Locke, B., Belore, M., Cook, A., Einhouse, D., Kenyon, R., Knight, R., Newman, K., Ryan, P., Wright, E., 2005. Lake Erie Walleye Management Plan. Lake Erie Committee, Great Lakes Fishery Commission, 45 pp.

Matthews, M.A., Evans, D.W., McClintock, C.A., Moriarty, C., 2003. Age, growth, and catch-related data of yellow eel *Anguilla anguilla* (L.) from lakes of the Erne catchment, Ireland. Am. Fish. Soc. Symp. 33, 207–215.

Melià, P., Bevacqua, D., Crivelli, A.J., Panfili, J., De Leo, G.A., Gatto, M., 2006. Sex differentiation of the European eel in brackish and freshwater environments: a comparative analysis. J. Fish Biol. 69, 1228–1235.

Moriarty, C., 1987. Factors influencing recruitment of the Atlantic species of *Anguillid* eels. Am. Fish. Soc. Symp. 1, 483–491.

Oeberst, R., Fladung, E., 2012. German Eel Model (GEM II) for describing eel, *Anguilla anguilla* (L.), stock dynamics in the river Elbe system. Inf. Fischereiforsch. 59, 9–17.

Pedersen, M.I., 2000. Long-term survival and growth of stocked eel, *Anguilla anguilla* (L.), in a small eutrophic lake. Dana 12, 71–76.

Penàz, M., Tesch, F.-W., 1970. Geschlechtsverhältnis und Wachstum beim Aal (*Anguilla anguilla*) an verschiedenen Lokalitäten von Nordsee und Elbe. Ber. Dt. wiss. Komm. für Meeresforsch. N.F. 21, 290–310.

Petersen, C.G.J., 1895. Eine Methode zur Bestimmung des Alters und Wuchses der Fische. Mitt. Dtsch. Seefischereivereins 11, 226–235.

Poole, W.R., Reynolds, J.D., 1996a. Growth rate and age at migration of *Anguilla anguilla*. J. Fish Biol. 48, 633–642.

Poole, W.R., Reynolds, J.D., 1996b. Age and growth of yellow eel *Anguilla anguilla* (L.), determined by two different methods. Ecol. Freshw. Fish 5, 86–95.

Poole, W.R., Reynolds, J.D., 1998. Variability in growth rate in European eel *Anguilla anguilla* (L.) in a western Irish catchment. Biol. Environ.: Proc. R. Ir. Acad. 98B, 141–145.

Reckordt, M., Ubl, C., Wagner, C., Frankowski, J., Dorow, M., 2014. Downstream migration dynamics of female and male silver eels (*Anguilla anguilla* L.) in the regulated German lowland Warnow River. Ecol. Freshw. Fish 23, 7–20.

Shiao, J.C., Lozys, L., Iizuka, Y., Tzeng, W.N., 2006. Migratory patterns and contribution of stocking to the population of European eel in Lithuanian waters as indicated by otolith Sr/Ca ratios. J. Fish Biol. 69, 749–769.

Simon, J., 2007. Age, growth, and condition of European eel (*Anguilla anguilla*) from six lakes in the River Havel system (Germany). ICES J. Mar. Sci. 64, 1414–1422.

Simon, J., Dörner, H., 2014. Survival and growth of European eels stocked as glass and farm sourced eels in five lakes in the first years after stocking. Ecol. Freshw. Fish 23, 40–48.

Simon, M., Bekele, V., Kulasová, B., Maul, C., Oppermann, R., Řehák, P., 2005. Die Elbe und ihr Einzugsgebiet – Ein geographisch-hydrologischer und wasserwirtschaftlicher Überblick. Internationale Kommission zum Schutz der Elbe, Magdeburg, 258 pp.

Simon, J., Fladung, E., Schaarschmidt, T., 2006. Steigaalmonitoring in Brandenburg und Mecklenburg-Vorpommern im Jahr 2005. Fischer Teichwirt 57, 452–455.

Simon, J., Dorow, M., Ubl, C., 2011. Wachstum von Aalen (*Anguilla anguilla*) in den Binnen- und Küstengewässern Mecklenburg-Vorpommerns. Fischer Teichwirt 62, 449–451.

Simon, J., Berends, K., Dörner, H., Jepsen, N., Fladung, E., 2012. European silver eel migration and fisheries induced mortality in the Havel River system (Germany). River Res. Appl. 28, 1510–1518.

Simon, J., Ubl, C., Dorow, M., 2013. Growth of European eel *Anguilla anguilla* along the southern Baltic coast of Germany and implication for the eel management. Environ. Biol. Fish. 96, 1073–1086.

Sinha, V.R.P., Jones, J.W., 1967. On the age and growth of the freshwater eel (*Anguilla anguilla*). J. Zool. Lond. 153, 99–117.

Svedäng, H., Wickström, H., Reizenstein, M., Holmgren, K., Florenius, P., 1998. Accuracy and precision in eel age estimation, using otoliths of known and unknown age. J. Fish Biol. 53, 456–464.

Tesch, F.-W., 2003. The Eel, 3rd ed. Blackwell Science Ltd, Oxford.

Vøllestad, L.A., 1992. The geographic variation in age and length at metamorphosis of maturing European eel: environmental effects and phenotypic plasticity. J. Anim. Ecol. 61, 41–48.

Vøllestad, L.A., Lecomte-Finiger, R., Steinmetz, B., 1988. Age determination of *Anguilla anguilla* (L.) and related species. EIFAC Tech. Pap. 21 (Suppl. 1), 1–27.

von Bertalanffy, L., 1938. A quantitative theory of organic growth. Hum. Biol. 10, 181–213.