



The disappearance of the European eel from the western Wadden Sea

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ABSTRACT

A cohort model for the European eel is presented, which enables the interpretation of observed catches of yellow eel and silver eel in the western Wadden Sea in terms of recruitment data of glasseel. The model builds on various assumptions on length-dependent mortality and silvering rates and on the standard Dynamic Energy Budget (DEB) model which predicts length growth. DEB parameter values are estimated on the basis of literature data. The model predictions are generally in good agreement with the data, though the final decline in numbers in the 1980s occurs earlier than predicted. This suggests that the decrease in eel stock is not just a consequence of lower glasseel immigration but that local conditions must have impoverished, a phenomenon earlier observed in fresh water.

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1. Introduction

Reconstructed long-term series on landings of the European eel *Anguilla anguilla* (L.) in Northern European countries show a steady decline since the mid 1960s (Dekker, 2004a). The immigration of glasseel, as indicated by long-term monitoring programmes in Sweden, Germany, the Netherlands and France, only started to decline in the early 1980s (Dekker, 2003). This difference in the onset of the decline, points to a decreasing yield per recruit, i.e. yield per immigrating glasseel, starting in the 1960s. In theory, a declining yield per recruit may be due to a severely increasing fisheries mortality resulting in growth overfishing. Long-term records on fishery effort and mortality are lacking for most of Europe, but the few series that are available, such as those for the IJsselmeer (sometimes translated as Lake Yssel), indeed point to a strong increase in the number of fykes used (Dekker, 2004b). A fyke is a fish trap consisting of a net suspended over a series of hoops, laid horizontally in the water, and is routinely used for catching eel. However, research surveys from the IJsselmeer, one of the largest fresh-water lakes of western Europe, show that undersized eel in the range between 10 and 25 cm, also started to decline in the 1960s, whereas the smallest size class, that is smaller than 10 cm, more or less followed the recruitment signal and only started to decline in the early 1980s. Recall that the arriving glasseel are around 7 cm long and that the minimum landing size is 28 cm. Hence, overexploitation can be ruled out as the main cause of the decline. In an extensive analysis, Dekker (2004a) also rejected other explanations for the observed declining trend, such as habitat loss, barriers to

migration, introduced parasites and changes in ocean climate. He concludes that the decline of the IJsselmeer stock is still a mystery.

Not all glasseel arriving along the European shores migrate into fresh water, and a minor part remains in the coastal waters and estuaries during the entire yellow eel stage (Daverat et al., 2006; Cairns et al., 2009). At the end of this period, which may last up to 20 years, the animals mature, metamorphose and return as silver eels to their breeding grounds in the Sargasso Sea, without ever having entered fresh water. Here we present so far unpublished data on eel catches in a research fyke for the period 1960–2009 from such a coastal water, namely the shallow areas around the island of Texel in the western Wadden Sea. Apart from describing the temporal trend in abundance of this local population, we examine by using a quantitative model approach whether the fyke catches can be linked to the recruitment data of the neighboring monitoring site at the Den Oever sluices by simply assuming constant mortality and growth conditions during the observation period. If a similar decline in yield per recruit has occurred in the coastal waters as in the fresh water, such simple linkage would not be possible. This way the analysis aims to shed more light on the mystery of the declining yield per recruit in the fresh water habitat since the mid 1960s. Recently, Henderson et al. (in press) reported a population collapse over the last 30 years in Bristol Channel, another estuarine stock.

Linking recruitment to catch is merely a matter of good book-keeping of growth, size-related natural and fisheries mortality, and size-related escapement from the local population as silver eel. Eels caught in the research fyke were not aged, so we had to estimate growth in an indirect way. Basis of the growth model applied here is the standard Dynamic Energy Budget (DEB) model as developed by Kooijman (2010), and see also Van der Meer (2006). Under constant food conditions the DEB model simplifies to the well known

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Bertalanffy growth model, but where the ultimate size depends upon the food conditions. All basic DEB model parameters are estimated using independent datasets from the literature, generalizing our results. This only leaves the food condition and the mortality to be estimated from the catch data. Strong evidence exists that the European eel is a panmictic species (Als et al., 2010), and for this reason we have refrained from building a closed population model. Such model would be of little use to describe the local Wadden Sea situation. Hence, recruitment data are model input and no stock-recruitment relationship was involved.

2. Material and methods

2.1. DEB model parameter estimation

Using a variety of datasets on various life-history parameters, on growth in the field (Tesch, 2003), growth in the laboratory (Angelidis et al., 2005), and on length–mass relationship (Tesch, 2003), a total of 10 DEB model parameters are estimated according to a procedure described in this volume by Lika et al. (2011). Parameters on natural mortality, net selection, and escapement are taken from the literature, but two parameters, that is the scaled functional response *f*, describing the food conditions, and the instantaneous fishery mortality rate *F* are estimated by maximizing the likelihood of these parameters given the observed catch data. The DEB parameter estimation procedure as advocated by Lika et al. (2011) starts with 10 so-called zero-variate data points and 7 pseudo-data points (Table 1).

These pseudo-data are in fact standard values for a selection of DEB parameters and these values are taken from Kooijman (2010), Table 8.1. Zero-variate data on age, length and mass at birth and at puberty, on maximum reproductive rate and on maximum length, mass and age are all taken from Tesch (2003), and references therein. Growth and development are probably rather similar in *A. anguilla* and the related North-American species *A. rostrata* and Asian species *A. japonica*. Hence, if no or only few data are available for *A. anguilla*, data from one of the related species are also presented. Tesch (2003) refers to work of Bezdenyehnykh et al. (1983) on the European eel, who obtained 3 mm long larvae 50–60 h after fertilization. Unfortunately no temperature at which the larvae were reared is

given. Pedersen (2004) observed hatching of the European eel 48–52 h after fertilization at 20–21 °C. Larvae were 2.35 mm long. Yamamoto et al. (1974), who worked with *A. japonica* observed hatching 38–45 h after fertilization at 23 °C at a length of 4.8 mm. American eel larvae hatched 32–43 h after fertilization at 20 °C, and larval size at hatching was 2.7 mm (Oliveira and Hable, 2010). We have chosen an age at birth of 50 h and a length at birth of 2.7 mm. In order to arrive at the dry mass of the newly hatched larva, we use a wet mass–cubic length conversion factor of 0.0014 g/cm³, which has been reported for glasseel (Tesch, 2003). We have not been able to find a specific conversion factor for the youngest larval stage. We use a single conversion factor dry mass–wet mass of 0.4 (Tesch, 2003), though some evidence exists that this factor changes during lifetime (Boëtius and Boëtius, 1985). Puberty is defined as the stage when fully differentiated immature testes and ovaries appear, which happens at a length of 30 cm (Colombo and Grandi, 1996). In northern European waters, this length is reached around 5 years after immigration. The animals weigh then around 44 g (Tesch, 2003). Maximum length and age are taken from Tesch (2003) and Dekker (2004b). Tesch (2003) reports that eels as long as 130 cm were caught in a Swiss lake and Dekker (2004b) mentions a maximum length of 133 cm for the IJsselmeer. Tesch (2003) further reports an average wet mass of 1622 g (range from 1360 to 1884 g) for eel within the size class 98–103 cm. This points to a wet mass–cubic length conversion factor of 0.0016 g/cm³. Using the same factor implies a maximum wet mass of around 3500 g for the Swiss eels. Tesch (2003) refers to the work of Edel (1975) who counted 1.3–1.5 million eggs in mature *A. rostrata* weighing 560 g. However, Barbin and McCleave (1997) report a much higher fecundity for American eel of that mass, namely between 4 and 5 million eggs. Boëtius and Boëtius (1980) report that European eels of 560 g produce slightly less than one million eggs. We have chosen a maximum of 2 million eggs for an eel of 560 g, resulting in a maximum reproductive rate of slightly more than 900 eggs/day. This mass corresponds to a length of 66 cm, which in northern European waters is reached about 11 years after immigration, and thus 6 years after reaching puberty. Eel can become very old, and in Denmark a specimen was held for 55 years (Walter, 1910), which we took as the maximum lifespan.

The standard DEB model provides predictions for all zero-variate data. We do not repeat the relevant equations, but refer the reader to Kooijman (2010). Detailed references to the equations are given in Table 1. For completeness, several conversion coefficients should be mentioned here: volume–wet mass 1 g/cm³, volume–dry mass 0.4 g/cm³ (Tesch, 2003), energy per C-mol in the reserves 550 kJ/C-mol (Kooijman, 2010), and dry mass 23.9 g/C-mol (Kooijman, 2010). Combined these coefficients reveal an energy content within the reserves of 9.2 kJ/g wet mass.

The procedure of Lika et al. (2011) further allows for the use of any kind of so-called univariate data, such as length data obtained at a various ages. Age–length data from the field are taken from Tesch (2003), who reports in his Table 3.10 last row, average Northern European data. We set the average temperature for these waters at 10 °C. Data of glasseel growth in the laboratory in the form of age–wet mass data, which were obtained at ad-libitum food conditions and at a much higher temperature of 21.5 °C, were taken from Angelidis et al. (2005). These growth data are only concerned with animals that have already entered the glasseel stage. Food conditions and temperature may be very different for the earlier oceanic life stage, but because duration of the oceanic stage is still unknown (Tesch, 1998) and relevant information on the environmental conditions that the leptocephali larvae experience is lacking, growth during this stage was not explicitly modeled. Instead an additional time-lag parameter τ was used, resulting in the growth equation

$$L = fL_i - (fL_i - L_b)e^{\dot{g}_B(t+\tau)} \tag{1}$$

Table 1

Data used to fit the standard Dynamic Energy Budget model. Data in the upper part of the table are true zero-dimensional data, the middle part gives pseudo-data. These pseudo-data are a-priori estimates of the parameters and are needed to avoid overfitting. The lower part gives true univariate data. The last column gives the model equations that link the data to the model parameters; L_i^{ref} is a reference length and equals 1 cm, z is the zoom factor, δ_M the shape coefficient. Equation and section numbers refer to Kooijman (2010).

Variable	Explanation	Model
a_b	Age at birth	Eq. 2.39
a_p	Age at puberty	Eq. 2.53
a_m	Maximum life span	Sn 6.1.1
L_b	Physical length at birth	Eq. 2.46
L_p	Physical length at puberty	Eq. 2.54
L_i	Ultimate physical length	$L_i^{ref} z / \delta_M$
W_b	Dry mass at birth	Sn 1.2.3; Eq. 3.3
W_p	Dry mass at puberty	Sn 1.2.3; Eq. 3.3
W_i	Ultimate dry mass	Sn 1.2.3; Eq. 3.3
\dot{R}_i	Maximum reproductive rate	Eq. 2.58
\dot{v}	Energy conductance	
κ	Allocation fraction to soma	
κ_R	Reproduction efficiency	
$[\dot{p}_M]$	Volume-specific somatic maintenance rate	
$\{\dot{p}_T\}$	Area-specific somatic maintenance rate	
\dot{k}_T	Maturity maintenance rate coefficient	
κ_G	Growth efficiency	
L, a	Physical length versus age	See text
$W_{w, a}$	Wet mass versus age	See text
$W_{w, L}$	Wet mass versus physical length	Sn 1.2.3; Eq. 3.2

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