

# Decreasing eel stocks: survival of the fattest?

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**Abstract** – Since the 1980s, the European eel *Anguilla anguilla* stock is in steep decline. Lipid reserves are essential to cover energetic requirements for silver eel migration and reproduction. Two large and independent data sets from Belgium and The Netherlands show an average one-third decrease in fat contents of yellow eels over the past 15 years. Also Le Cren's relative condition factor decreased. On the basis of the somatic energy reserves, reproductive potential of eels from various latitudes over Europe was estimated, assuming fat levels in yellow eel are indicative of those in silver eels. Only large individuals, females as well as males, with high lipid content seem to be able to contribute to the spawning stock. The decrease in fat content in yellow eels may be a key element in the stock decline and raises serious concerns about the chances of the stock to recover.

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**Key words:** *Anguilla anguilla*; fat reserve; stock decline; contamination; migration; reproduction

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## Introduction

Stocks of the Atlantic eel species are in decline. Since the 1980s, the population of the European eel *Anguilla anguilla* (L.) has waned throughout almost its entire habitat. The stock is considered outside safe biological limits and current fisheries are not sustainable (ICES 2001, 2007). From the spawning area in the Sargasso Sea, the eel larvae reach continental waters where they grow up in fresh water and coastal habitats during their sedentary yellow eel phase. Adults leave as mature silver eels for the spawning grounds in the Sargasso Sea. Since the early 1980s, glass eel recruitment has dropped over the whole distribution area to about 1% of the levels encountered in the 1970s (Dekker 2003a) and fisheries yields have decreased in most European countries (Dekker 2003b). In June 2007, the European eel was included to the UN CITES Appendix II list. Several countries (Germany, Sweden and Norway) have listed the eel on their national Red List as Critically Endangered. The Council of the European Union established a framework and measures for the recovery and sustainable use of the stock of European eel and requires the preparation of national eel

management plans in September 2007 (European Commission 2007). The collapse of the stock happened over the whole European continent without a single, obvious cause (Dekker 2003a). Important fluctuations in the presence of eel over Europe have occurred much earlier (in historic and prehistoric times) and were believed to be influenced by oceanic and climatic factors (Kettle et al. 2008a). The recent stock decline has been related to both, natural and anthropogenic factors. Climate and oceanic changes may have influenced reproduction success and larval development, growth and migration (Knights 2003; Friedland et al. 2007). Anthropogenic factors include exploitation, habitat loss, migration barriers (turbines and pumps), pollution, reduced eutrophication and transfer of parasites and diseases) (ICES 2006). Detrimental effects of pollution on fitness and fecundity have been suggested earlier on (Larsson et al. 1990), but recently, there are indications that poor quality of the spawners, namely the silver eels migrating to the oceanic spawning grounds, might be a key factor in explaining the decline. Palstra et al. (2006a) argued that gonadal levels of dioxin-like contaminants, including PCBs, in eels from most

European locations impair embryonic development. Pollution might also impact reproductive success through effects on genotype: a significant negative correlation between heavy metal pollution and eel genetic variability was reported by Maes et al. (2005). Insufficient fitness [condition and energy resources (Svedäng & Wickström 1997)], high bioaccumulation of persistent organic pollutants (especially polychlorinated biphenyls – PCBs) (Larsson et al. 1990; Robinet & Feunteun 2002; Palstra et al. 2006a) and pathological agents (Palstra et al. 2007) have been reported as potential restrictive factors, disabling long distance migration and successful reproduction with prime quality gametes. It has been proposed by several authors that the lipid content of silver eel is crucial for reproduction. Under a critical fat mass in their yellow stage (28%), silvering may not even be initiated (Thurow 1959; Larsson et al. 1990). Quite diverging data upon minimum energy requirements (in lipid weight % of muscle) for the completion of their migration and successful reproduction have been proposed (Böetius 1980: 20%; Palstra et al. 2007: 13.5% fat; van den Thillart et al. 2007: 20.7%). Where spawner quality is poor and lipid content low, silver eels may not contribute to the overall spawning and recruitment of the European stock. Assuming the

hypothesis of a relationship between lipid content in yellow and in emigrant silver eel, poor lipid content in yellow eel would indicate low energy reserves in silver eel. In order to trace changes in lipid contents in eel over time, we analysed two independent data sets of muscle lipid content in yellow eel.

### Methods and study area

#### Samples and sampling

In Belgium and The Netherlands, networks are functioning to monitor the quality of the European eel in its yellow sedentary phase. They monitor hazardous substances, such as PCBs, organochlorine pesticides and heavy metals in eel muscle and provide evidence of their presence in the aquatic environment and the risks for human consumption (de Boer & Hagel 1994; Bilau et al. 2007; Maes et al. 2008). Most sampling sites (Fig. 1) are located in the basins of the rivers Scheldt, Meuse and Rhine.

In Belgium, the network is confined to Flanders (the northern region) and has been operating since 1994; data are available until 2006. It consists of 359 sites, of which 38% have been monitored more than once. In The Netherlands, the network has been running from

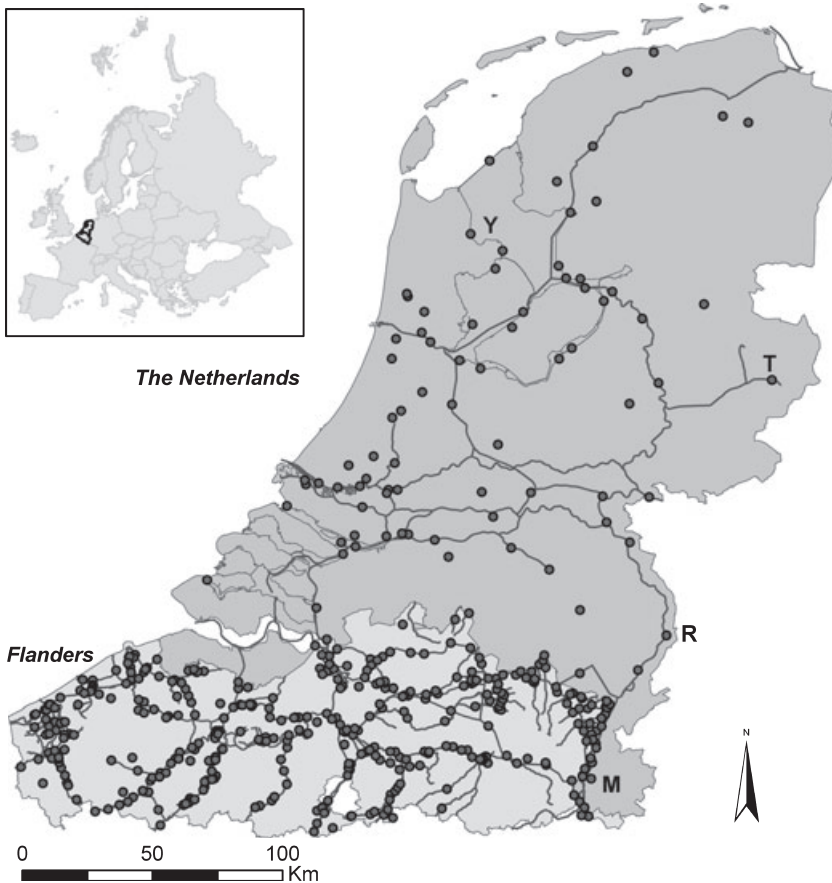


Fig. 1. Sampling locations for measuring the fat contents in yellow eel. Map of Flanders (Belgium) and The Netherlands with locations of monitoring sites in both networks. Locations Y, M, R and T refer to Lake IJsselmeer, Rivers Meuse and Roer and the Canal Twentekanaal, respectively.

1977 and annual data are available until 2004. The network consists of 92 sites; each year on average 20 sites are sampled. In both countries, eels were sampled by electro- and fyke-fishing. In Belgium, usually five eels were analysed individually from each site, and this study is based on the individual analysis of 2467 yellow eels with a selected length between 30 and 60 cm. In The Netherlands, analysis is carried out on 560 pooled yellow eel samples (25 eels per pool), eels being selected from the length class 30–40 cm. The condition factor was calculated for the Belgian eels only, following Le Cren's relative condition factor (Le Cren 1951), as recommended by Froese (2006). The relative condition factor ( $k = W/W'$ ) compares the observed ( $W$ ) and expected ( $W'$ ) weight of each individual, where expected weight is obtained using the length–weight regression ( $W = aL^b$ ) of each individual. The sex of the eels was not determined, with the exception of 1 year at four sites in The Netherlands.

Four water bodies of different typology were selected from the Dutch network (Lake IJsselmeer, Rivers Meuse and Roer and the Canal Twentekanaal) to illustrate temporal trend at specific sites (Fig. 1). The IJsselmeer is a large, shallow freshwater lake (1136 km<sup>2</sup>). The River Meuse is a major European river (total length 925 km), originating in France and flowing through Belgium and The Netherlands to the North Sea. The site at Eijsden is situated near the Belgian border at 300 km from the river mouth. The River Roer is a tributary (170 km) originating in Germany and flowing through The Netherlands into the River Meuse. It has been historically polluted by PCBs, tetrachlorobenzyltoluenes and some brominated flame retardants (de Boer & Hagel 1994). The Twentekanaal is a 65-km-long canal in the north-east of The Netherlands within the Rhine River basin.

Eels were skinned and filleted, and the same part of the muscle was used for analysis throughout the full period (mid-part of the body for Belgian eels, and dorsal part, posterior to the head for eels in The Netherlands). In Belgium, lipid was extracted from the muscle tissue and quantified using the Bligh & Dyer (1959) method. Quality was assured by participation in QUASIMEME interlaboratory proficiency testing schemes (<http://www.quasimeme.org>). Z-scores rarely exceeded 0.6 in absolute value, whereas Z-scores below 2 are satisfactory. In the Dutch eels, the fat contents were determined after Soxhlet extractions with pentane/dichloromethane (1 : 1, v/v). As the fat in eels consists of more than 95% of triglycerides, results of this Soxhlet method could easily be compared with the Bligh & Dyer results (de Boer 1988). The quality of the Soxhlet lipid determination was underpinned by analysing in-house eel reference

material with each series of samples, by an official accreditation (RvA, L097) and by successful participation, twice a year, in the QUASIMEME proficiency-testing scheme. The fat content is measured as the lipid concentration in muscle and is expressed in % of muscle wet weight (w/w).

### Statistical analysis

Both data sets were analysed using a regression model. The Belgian data (condition factor and fat content of every single eel) were averaged per site per year. To study the time (*period*) effect on the fat percentage, the following regression model was used:  $FpctA \sim period$ .  $FpctA$  is the angular transformation of the fat percentage to normalize the data (Sokal & Rohlf 1995). *Period* is a three-level factor indicating the periods divided in year groups (1994–1998, 1999–2003, 2004–2006 for the Belgian data and 1977–1981, 1982–1986, 1987–1991, 1992–1996, 1997–2001, 2002–2004 for the data from The Netherlands). Grouping was performed on a 5 years basis, but was different for both countries in order to ensure a sufficient number of data and to guarantee representativeness (sufficient variety of sites with respect to typology). To take into account that some data originate from the same location, the intercept was modelled as random. Thus, a linear mixed model was constructed (Pinheiro & Bates 2000). This regression model was validated with a residual analysis. The Tukey test was used to test if mean length and mean weight are significantly different between periods. Similarly significant differences between fat percentages and condition factor and periods were tested. Statistical analyses were performed with the statistical program S-PLUS 6.2 Professional.

### Results

Mean total length and weight of the Belgian eels over the 3-year groups are represented in Fig. 2. Mean total length over the whole data set was 41.7 cm  $\pm$  6.6 SD. There is a slight but significant variation in mean total length [1994–1998: 44.5 cm (min. 30–max. 60); 1999–2003: 41.2 cm (min. 30–max. 60); 2004–2006: 42.5 cm (min. 30.2–max. 59.6)]. Mean weight of all the eels is 137.4 g  $\pm$  80.1 SD. The weight of the eels in the first year group is larger than in the other two groups [1994–1998: 180.1 g (min. 48–max. 667.5); 1999–2003: 133.3 g (min. 33.7–max. 550.3); 2004–2006: 138.4 g (min. 36.7–max. 432.8)]. Individual lengths or weights of the eels from The Netherlands were not available, but eels over the whole period were selected within the 30–40 cm range.

Fat content in yellow eel varies considerably between sites, both in Belgium and in The

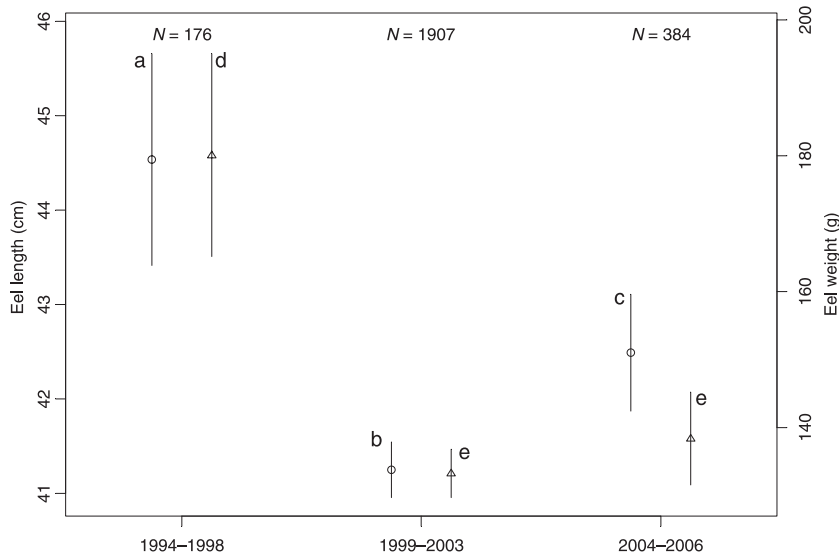


Fig. 2. Morphological parameters of the yellow eels of the 3 year groups in Belgium. Mean lengths (○) and weights (Δ) of the yellow eels from Belgium, over the 3 year groups between 1994 and 2006, analysed for muscle fat content. Bars indicate standard errors. The number of eels is indicated. Means of periods with the same letter are not significantly different from each other (Tukey test, 95% simultaneous confidence intervals).

Netherlands. In Belgium, the mean lipid content per site for 2004 varied between 2.0% and 23.4% (25 sites, mean 12.7%), while in The Netherlands analysis of pooled samples of 22 sites in 2004 varied between 4.2% and 22.6% (mean 14.1%).

Muscle lipid contents of Belgian eels from the different year groups were compared (Fig. 3a). A significant decrease in lipid content of 7.7% on a w/w basis over a 13-year period was observed in Belgian eels [1994–1998: 20.0% (min. 1.5–max. 34.6); 1999–2003: 14.8% (min. 1.7–max. 36.8); 2004–2006: 12.3% (min. 2.0–max. 27.5)]. Condition factors decreased significantly [1994–1998: 1.06 (min. 0.83–max. 1.53); 1999–2003: 1.01 (min. 0.65–max. 1.57); 2004–2006: 0.95 (min. 0.76–max. 1.19)]. *Period* was highly significant in the linear mixed model both for lipid content (ANOVA  $P < 0.0001$ ) and condition (ANOVA  $P < 0.0001$ ). All periods were significantly different from each other, indicating a monotone negative trend, both for fat ( $P < 0.0001$ ) and condition ( $P < 0.0001$ ). No systematic patterns in the residuals were found.

The time trend of the mean muscle lipid content in pooled yellow eel samples from 92 locations in The Netherlands between 1977 and 2004 is presented in Fig. 4a. Whereas before 1990, the mean fat content was generally superior to 20%, a clear and significant decrease occurred after 1990 [1977–1981: 20.8% (min. 5.3–max. 30.1); 1982–1986: 20.9% (min. 9.6–32.6); 1987–1991: 19.5% (min. 6.3–max. 34.2); 1992–1996: 16.9% (min. 6.1–max. 29.7); 1997–2001: 14.8% (min. 3.7–max. 29.2); 2002–2004: 13.1% (min. 3.5–max. 23.4)]. Statistical analysis confirmed that *Period* was highly significant in the linear mixed model for lipid content ( $P < 0.0001$ ). While the analysis indicated a monotone negative trend for lipid contents ( $P < 0.0001$ ), not all

consecutive groups were significantly different from each other. The decrease in lipid content was evident and amounts to 7.5% on a w/w basis over a 15 year period, as shown by the mean lipid content measured at sites sampled before 1991 (1977–1990: 20.6%  $\pm$  5.6 SD,  $N = 217$ ) compared with later years (2002–2004: 13.1%  $\pm$  5.7 SD,  $N = 66$ ). In Figs 3b and 4b, lipid content distribution (presented as probability densities) within consecutive year classes is given, respectively, for Belgium and The Netherlands.

The four water bodies of different typology with a long time series selected from the Dutch data illustrate this decrease at specific sites (Fig. 5). The negative trend in fat contents was consistently present in eels from different sites and different typology. All eels in The Netherlands and Belgium seem affected by this phenomenon. There is large variation in lipid contents in eels from different water bodies: eels from Lake IJsselmeer (22.6% in 2004) have a higher muscle lipid content than those from River Meuse (7.1% in 2004).

In Table 1, a hypothetical model is presented calculating the remaining energy (ER) in eels at arrival at the spawning grounds, based on different scenarios combining body weight (300, 500 and 1000 g), geographical variation in their freshwater habitat (Portugal, Belgium and Sweden) and the temporal decrease in fat (as measured in yellow eel from The Netherlands). River systems from Scandinavian countries are situated quite further from eel's spawning area than those of the west coast of the Iberian peninsula. Silver eels from the Swedish Lake Malaren have to swim at least 7500 km from Stockholm to the Sargasso Sea whereas eels from the River Tagus leaving Lisbon have to swim 5000 km to reach their spawning ground (distances calculated to Sargasso Sea at location 61°00'W and 26°30'N, the centre of the area described in van Ginneken & Maes

## Decreasing fat stores in *Anguilla anguilla* in Belgium and The Netherlands

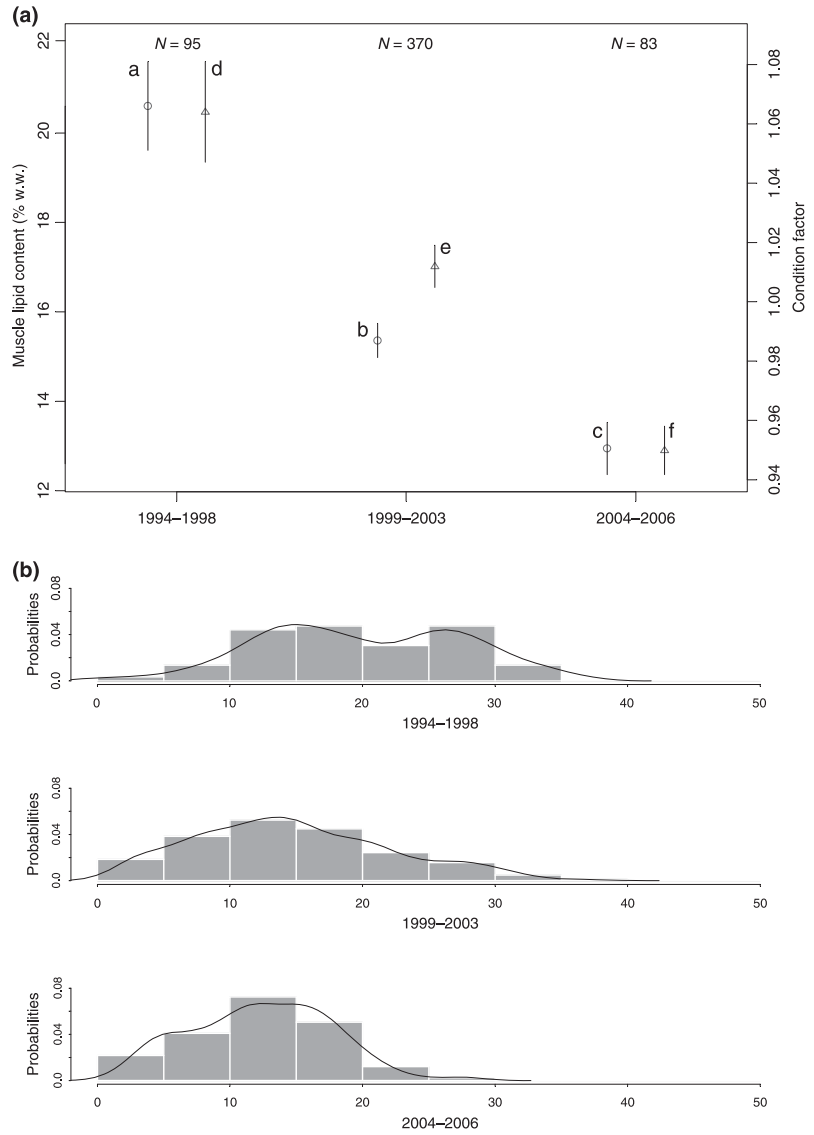


Fig. 3. Temporal trend in fat contents (% of wet muscle weight) of yellow eels in Belgium. (a) Decreasing fat contents (○) and condition factor (△) (means, bars indicating standard errors) in yellow eels in Belgium between 1994 and 2006. Secondary Y-axis is the relative condition factor. The number of sites is indicated. The means of the different periods are significantly different from each other, both for fat content and condition (Tukey test, 95% simultaneous confidence intervals). (b) Distribution (presented as probability densities) of lipid content in yellow eel in Belgium from the three periods.

(2005)). Several assumptions have been made: (1) yellow eel fat stores are representative for the silver eel energy budget, (2) silver eels with lowered fat stores do start their migration, (3) total net lipid was calculated on the basis of the muscle lipid weight (assuming lipids are predominantly stored in white muscle (Lewander et al. 1974) and assuming muscle lipid concentration is indicative for the whole body not taking account of variations of lipids in other tissues or organs), (4) a fixed value for energy requirement for migration ( $\text{g fat}\cdot\text{km}^{-1}$ ) was taken regardless of the length of the eel. This value was deduced from van Ginneken & Maes (2005) who measured the energy requirements for migration of 73-cm-long eels kept in swimming tunnels for 173 days and covering a swimming distance of 5500 km. This was carried out through two different methods (oxygen consumption

and bomb-calorimetry). Measurements of the cost of transport (COT) resulted in  $0.42 \text{ kJ}\cdot\text{km}^{-1}\cdot\text{kg}^{-1}$  for the oxygen consumption method and  $0.62 \text{ kJ}\cdot\text{km}^{-1}\cdot\text{kg}^{-1}$  for the bomb-calorimetry. If we use the mean value of both methods ( $0.51 \text{ kJ}\cdot\text{km}^{-1}\cdot\text{kg}^{-1}$ ), these eels (weighing 860 g) metabolise 66.6 g fat during a 6000 km journey to their spawning ground or  $11.1 \text{ mg fat}\cdot\text{km}^{-1}$ . COT for eels of that size to complete their journey to the Sargasso Sea can thus be estimated as 55, 67 and 83 g fat for eels originating from River Tagus (Lisbon), River IJzer (Nieuwpoort) and Lake Malaren (Stockholm), respectively. Comparing net fat quantities with COT, the ER can be deduced. From this we can conclude that in the period 2002–2004 female eels of a weight of 300 g and a muscle lipid content of 13.1% will not reach their spawning grounds, regardless of their freshwater

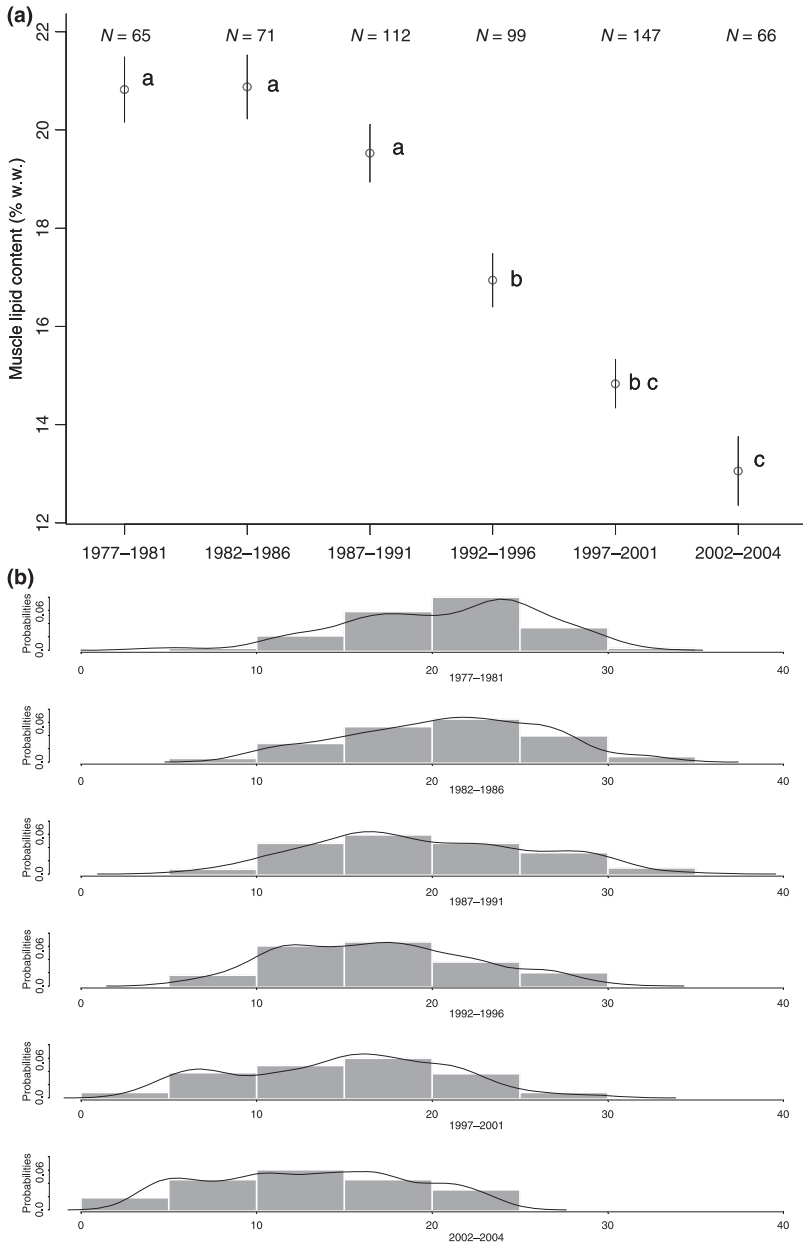


Fig. 4. Temporal trend in fat contents (% of wet muscle weight) of yellow eels in The Netherlands. (a) Decreasing fat contents (means, bars indicating standard errors) in yellow eels in The Netherlands between 1977 and 2004. The number of sites is indicated. Means of periods with the same letter are not significantly different from each other (Tukey test, 95% simultaneous confidence intervals). (b) Distribution (presented as probability densities) of lipid content in yellow eel from the Netherlands during the six periods.

origin. Northern eels of 500 g with the same muscle lipid content will probably not be able to reach the Sargasso Sea, while individuals of more southern fresh water habitats could succeed to reach their spawning site, but considering the energy left (10.5 g fat for River Tagus eels) will probably not be able to contribute to the spawning stock or only have a negligible contribution. Large females (1000 g) with this reduced muscle lipid content will be able to reach their spawning ground, and still have some energy for spawning and reproduction (48 g fat for Swedish eels and 76 g fat for River Tagus eels). However, this net ER reserve is < 50% of the amount of energy remaining in similar sized eels during 1982–1986

(126 g fat for Swedish eels and 154 g fat for River Tagus eels).

The reproductive potential (RP) was calculated as the biomass of eggs which can be produced from the ER in females, which succeeded to reach their spawning grounds. We assumed energy for activities associated to mating and spawning as zero, and all ER was converted to egg production. van Ginneken & van den Thillart (2000) used a conversion of 1.72 g eggs·g<sup>-1</sup> fat, and the same calculation was used in our model (Table 1), suggesting that (1) only large female eels (>500 g) are able to contribute to reproduction and (2) even for these large female eels the RP is very limited. Estimates of egg production for eels of 1 kg

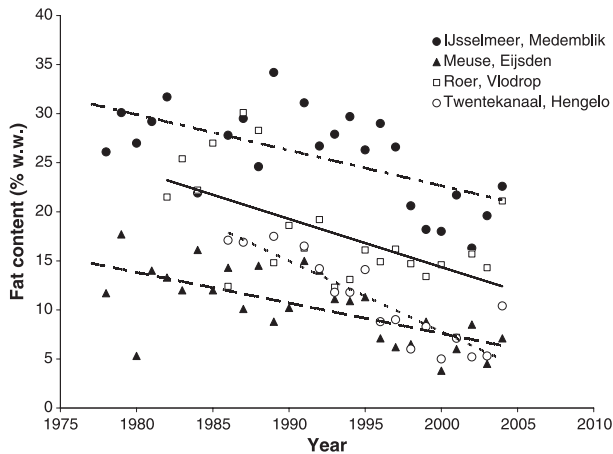


Fig. 5. Temporal trends in fat contents in yellow eels from four water bodies of different typology. Time trend of the fat content in muscle tissue (pooled samples) from yellow eels in a lake (IJsselmeer at Medemblik (Y)), a large river (Meuse at Eijsden (M)), a small river (Roer at Vlodrop (R)) and a canal (Twentekanaal at Hengelo (T)) in The Netherlands. Y, M, R and T refer to locations presented in Fig. 1. Regression curves IJsselmeer (dash-dot line):  $y = -721.24 \ln(x) + 5504$ ,  $R^2 = 0.38$ ; Twentekanaal (dotted line):  $y = -1435.4 \ln(x) + 10918$ ,  $R^2 = 0.78$ ; Roer (solid line):  $y = -979.6 \ln(x) + 7460$ ,  $R^2 = 0.34$ ; Meuse (dashed line):  $y = -619.14 \ln(x) + 4713$ ,  $R^2 = 0.43$ .

at the current mean muscle lipid level vary between 131 (Portugal), 110 (Belgium) and 83 g eggs (Sweden), dependent on the latitude.

## Discussion

The two large data sets of lipid contents in yellow eels from Belgium and The Netherlands were collected independently; monitoring design and analytic methodologies differed considerably between both countries. The number of stations and periodicity were quite different, and samples were analysed individually (Belgium) or pooled (The Netherlands). Differences in size range and the lack of individual length, weight and lipid data in the Dutch eels hinder comparability of results between both countries. Another weakness is the lack of any data about individual age or growth, and sex. Possible variations of those factors over time might to some extent correlate with our lipid data.

Large geographical variations in fat contents between yellow eels have been described earlier (Piatek 1970; Svedäng & Wickström 1997). The phenomenon might be linked to variations in environmental conditions, e.g. temperature and salinity (Andersson et al. 1991), fish assemblages, eel density (Svedäng & Wickström 1997), water typology (Piatek 1970) or trophic status (Svedäng et al. 1996). Notwithstanding the differences in both network concepts, and large variation in lipid contents of eels from

various water bodies, similar trends were obvious in Belgium and The Netherlands: a drop in lipid contents over the past 15 years by about one-third (from ca. 20% to 13%).

Muscle lipid contents in yellow eels increase with length, both under culture and natural conditions. Eels accumulate lipids during development from the elver to silver stage (Böetius & Böetius 1985). Andersson et al. (1991) reported gradually increasing fat contents in stocked yellow eels sampled in 1986 from a Swedish thermal effluent area at the Baltic from 30 to about 65 cm. Here they tended to reach an upper limit at 35–40%, whereas Larsson et al. (1990) reported a linear increase from 5% to 28% up to a weight of ca. 350 g (55 cm) in eels from an eutrophic lake in southern Scandinavia in 1988. Also in eel farms, the fat content in the eel body notably increased in relation with size (Garcia-Gallego & Akharbach 1998). Due to difficulties in sampling eels within a narrow size class, Belgian eels were selected in the 30–60 cm size range. Because mean length in the Belgian eels was 3.3 cm smaller in group 1999–2003 compared to 1994–1998 (Fig. 2), we cannot rule out that this length difference had an effect on lipid content measured. Back-calculating the data of lipid measurements in 39 yellow eels in the 70–345 g weight range presented in Larsson et al. (1990), a size difference of 3.3 cm would correspond to a decrease in 3.0% fat on a w/w basis. The recorded decrease amounts to 5.2%. In the subsequent period (2004–2006), we expected an increase in fat content, as mean eel length was again 1.3 cm larger. However, the actual fat content decreased with another 2.5%. Hence, the observed decrease in fat in the Belgian eels cannot be explained by differences in the size of the eels over the years. As eels from The Netherlands were selected from the same, narrow size class (30–40 cm) during 28 years, it seems unlikely that size differences in Dutch eels can have biased the results.

## Possible causes

Possible causes for the observed decrease in fat stores are multiple and not easy to pinpoint. Accumulation of energy through lipid storage may be affected by environmental factors such as pollution pressure (and – more specifically – endocrine disrupting substances), disease agents, changes in food availability, other global changes in the environment, changes in (density-dependent) sex ratios and even life-history characteristics, e.g. restocking.

## Pollution pressure

Evidence has been reported that contaminants may play a major role. The impact of contaminants on metabolic functions and on behaviour is broad

Table 1. Different scenarios of hypothetical calculations of the energy remaining for reproduction (ER) and reproductive potential (RP) in female eels by arrival at their spawning ground.

Eel weight (g)	Year	Mean muscle lipid content (% w w)	Net fat (g)	River Tagus, Lisbon (COT = 55 g fat)		River IJzer, Nieuwpoort (COT = 67 g fat)		Lake Malaren, Stockholm (COT = 83 g fat)	
				ER (g fat)	RP (g eggs)	ER (g fat)	RP (g eggs)	ER (g fat)	RP (g eggs)
300	1982–1986	20.9	62.7	7.7	13	†	0	†	0
300	1987–1991	19.5	58.5	3.5	6	†	0	†	0
300	1992–1996	16.9	50.7	†	0	†	0	†	0
300	1997–2001	14.8	44.4	†	0	†	0	†	0
300	2002–2004	13.1	39.3	†	0	†	0	†	0
500	1982–1986	20.9	104.5	49.5	85	37.5	65	21.5	37
500	1987–1991	19.5	97.5	42.5	73	30.5	52	14.5	25
500	1992–1996	16.9	84.5	29.5	51	17.5	30	1.5	3
500	1997–2001	14.8	74	19	33	7	12	†	0
500	2002–2004	13.1	65.5	10.5	18	†	0	†	0
1000	1982–1986	20.9	209	154	265	142	244	126	217
1000	1987–1991	19.5	195	140	241	128	220	112	193
1000	1992–1996	16.9	169	114	196	102	175	86	148
1000	1997–2001	14.8	148	93	160	81	139	65	112
1000	2002–2004	13.1	131	76	131	64	110	48	83

Calculations were made for eels from three origins in Europe, with a weight of 300, 500 and 1000 g, and with fat contents conform the means in lipid fat content measured in eels from The Netherlands over the last 25 years. The cost of transport (COT), being the energy cost (in g fat) for migration to the spawning ground, of 11.1 mg-fat-km<sup>-1</sup> was used (deduced from van Ginneken and Maes (2005) for 73-cm-long eels, see text). Assumption was made of an equal net energy requirement for migration in eels of 300 and 1000 g. Migration distance from Lisbon, Nieuwpoort or Lake Malaren to spawning location (61°W and 26°30'N) was estimated as 5000, 6000 and 7500 km, respectively. Net fat content was calculated assuming all fat is muscle fat. RP was calculated as the mass of eggs which could be produced by using all ER through a conversion factor of 1.72 g-eggs-g<sup>-1</sup> fat (as used in van Ginneken and van den Thillart 2000).

†Eels do not reach spawning grounds due to lack of energy.

(Robinet & Feunteun 2002). It may affect lipidogenesis or induce lipolysis through various mechanisms. Chemical stress induces a higher energy demand (Calow 1991). PCBs are known to disrupt thyroid hormone action in humans (Zoeller 2001). Fat accumulation may be disabled through disturbed thyroid function in fish (Leatherland & Sonstegard 1979; Singh 1989). In rainbow trout (*Oncorhynchus mykiss*) fed with PCB and mirex contaminated diets, carcass lipid content differed significantly compared to control fish, with PCBs inducing an increase in lipid content, and mirex a decrease (Leatherland & Sonstegard 1979). However Narbonne et al. (1988) found no change in carcass lipid content in mullet (*Chelon labrosus*) after feeding a PCB enriched diet. Lipid accumulation in eel was disturbed directly by inhibition of the acetylcholinesterase activity due to pesticide exposure (Ceron et al. 1996; Fernandez-Vega et al. 1999). Under laboratory conditions, eels show an increased fat consumption in the presence of cadmium (Pierron et al. 2007) or the insecticide fenitrothion (Sancho et al. 1998). Under natural conditions, Maes et al. (2005) found a strong correlation between heavy metals and a reduced condition factor in Belgian yellow eels. Also new substances, like perfluorinated compounds, are known to affect lipid metabolism, through alterations in cell membrane properties in fish (Hu et al. 2003). Indications of impact of PCBs and some pesticides on lipid content in natural eel from Belgium were reported by Geeraerts et al. (2007).

Contaminant levels in Belgium and The Netherlands are relatively high in comparison with elsewhere in Europe (de Boer & Hagel 1994). The contamination in eels from Belgium and The Netherlands is in line with these observations. Many lipophilic contaminants in wild yellow eel in both countries are very high (de Boer & Hagel 1994; Maes et al. 2008). Eels are particularly prone to the bioaccumulation of lipophilic contaminants. The PCB concentrations (measured as the sum of the seven indicators PCBs) in Belgian wild eel ( $N = 2524$ ) had an average of 605 ng-g<sup>-1</sup> wet weight (min. 3–max. 12455) (Maes et al. 2008), a 200-fold of the concentrations measured in marine fish (mean 3.1 ng g<sup>-1</sup>-wet weight (min. 0.5–max. 25) (33 individuals from five marine species from the Belgian market) (Baeyens et al. 2007). PCBs, several organochlorine pesticides and some heavy metals (e.g. lead) in yellow eels show a decreasing trend (Maes et al. 2008). However, an extensive series of emerging and less known contaminants are believed to pose new threats to our environments. BTEX (benzene, toluene, ethylene and xylene), chloroform and tetrachloroethene are present in wild yellow eel in Belgium (Roose et al. 2003). Perfluorinated compounds have been detected in high concentrations in fish from Belgium: the hepatic concentrations are among the highest concentrations ever reported for wildlife liver tissue (Hoff et al. 2005). Brominated flame retardants (BFRs), like polybrominated diphenylethers (PBDEs), hexabromocyclododecane (HBCD) and

tetrabromobisphenol-A appeared to be present in Belgian eels from industrial locations along the River Scheldt in 1999 (Morris et al. 2004). Many of these substances show increasing concentrations. Analysis in a sediment core from Norway shows an increase in PBDE concentrations in the environment since the beginning of the industrial production of PBDEs, e.g., the decabrominated diphenylethers became apparent in the late 1970s to increase gradually in the 1980s and 1990s (Zegers et al. 2003).

Indirectly, fat storage might be affected by endocrine disruption, due to specific chemicals, some of them having biological effects similar of those of the steroid hormone estrogen (Turner & Sharpe 1997). Sexual disruption and development of ovotestes have been reported in freshwater and marine fish in Europe (Jobling et al. 1998). Female yellow eels may have lower fat contents compared to males (de Boer & Hagel 1994). Therefore, endocrine disruption could be one of the indirect causes of the lower fat contents, due to a higher number of feminized eels. However, apparently there is currently no evidence for endocrine disruption in yellow eels. Plasma vitellogenin content in yellow eels are relatively low compared with other fish species exposed to high concentrations of estrogens. Research in Belgium (Versonnen et al. 2004) and in the U.K. on the River Thames (Livingstone et al. 2000; Peters et al. 2001) indicated that - despite the high exposure to and uptake of pollutants - European yellow eel under natural conditions are not sensitive to the effects of (xeno-)estrogens, as measured by the vitellogenin induction. The onset of maturation in the European eel only takes place during a period of prolonged swimming which might be a physiological stimulus necessary (van Ginneken et al. 2007). It is therefore possible that endocrine disrupting effects of pollutants become apparent during the starvation period during migration or during the spawning itself (Versonnen et al. 2004).

### *Diseases*

Another possible cause of the reduction of fat contents in eels could be infections by specific diseases. Eels are prone to new diseases (parasites, bacteria, viruses), which recently invaded the population through anthropogenic impacts. A well-known example is the parasitic nematode *Anguillicola crassus*, which invaded the European eel population in the early 1980s, that damages the swim-bladder (De Charleroy et al. 1990) and may be responsible for reduced swimming capacities (Sprengel & Luchtenberg 1991; Nimeth et al. 2000; Palstra et al. 2007). The nematode is known to induce stress in eels and to increase cortisol plasma levels (Sures et al. 2001), which leads to increases in energy metabolism and adversely affects energy accumulation (Robinet & Feunteun

2002). It was also shown (Palstra et al. 2007) that heavily infected eels and eels with a damaged swim-bladder had impaired swimming performance and spend more energy for migration, and increase overall energy consumption.

### *Global environmental changes*

Global environmental changes (such as climate change and eutrophication) and overfishing, through complex interactions on the aquatic ecosystems and their communities, might be responsible for a lower fat content, although specific mechanisms remain unknown. Factors like food availability, water temperature, sex ratio, and others may be implicated. Eels collect energy from available food and they store this as lipids in muscles and internal organs. In some species, like herring, fat stores indicate the feeding conditions experienced by the fish, being high when there is plenty of food available and low when food is scarce (Wood 1958). Significant decreases in fat levels have been reported in Baltic herring (*Clupea harengus membras*) since the late 1970s until 2000 (Ådjers et al. 2000). They were thought to be linked to large scale oceanographic changes, especially a decrease in availability of the energy-rich marine copepods. Bottom-up processes mediated via changes in mesozooplankton species composition have also induced a longer-term failure in feeding success and a decline in fat content and herring growth (Flinkman et al. 1998). Whether food availability in eel affects lipid content in eel is poorly understood: it was reported that in eels under culture conditions, lipid content can be influenced by the energy content of the food provided (Garcia-Gallego & Akharbach 1998). However male silver eels did not show any decrease in lipid content when kept for two years under starvation conditions (Böetius & Böetius 1985). In many water bodies over Belgium and The Netherlands water quality parameters have fluctuated considerably over the last 50 years. These changes in environmental conditions inevitably influenced diversity and density of food organisms. Scientific evidence is far too fragmentary to ascertain if and to what extent the decrease in lipid content could be related to suboptimal feeding conditions. In contrast, it could be argued that the low recruitment observed since the last 25 years resulting in lower eel densities and a lower level of intraspecific competition for food, and an overall gradual increase in water quality seem to indicate better feeding conditions for the eel.

Impact of global change on fat reserves might be sex driven, as the gender of an eel influences its lipid reserve, female yellow eels may have lower fat content than males (de Boer & Hagel 1994). The sex of developing gonads is labile; eel is a gonochorist where gender is determined principally by environmental

factors like population density, recruitment, and catchment characteristics. Due to the lack of sex determination in our eels we are unable to make conclusions on possible changes in sex ratios. Davey & Jellyman (2005) described sex determination in eels as primarily metagametic whereby individual growth rate during the early part of the freshwater phase is the key mechanism by which environmental conditions affect the gender of developing elvers. Causal relationships between feeding conditions and/or temperature and sex differentiation in European eel have been suggested (Lammens & Visser 1990; Holmgren 1996; Beullens et al. 1997). In the French river Frémur, Laffaille et al. (2006) observed over a nine year study (1996–2004) a gradual shift of silver eel sex ratio from male to female. They suggest a possible relationship between the observed increase in the size of silver eels and change in the sex ratio, with growth conditions resulting from an increase in the trophic status and water temperature. But also low recruitment and consequent lower densities could be a determining factor, as high densities lead to more males whereas females are predominant in low density habitats (Parsons et al. 1977).

High temperatures have been proposed to favour development as males (Beullens et al. 1997). Northern and southern eel stocks are characterised by a clear shift in sex ratio, northern regions producing mostly large females (Vøllestad 1992), where in southern stocks males greatly outnumber females (Lobón-Cervia & Carrascal 1992). If temperature is considered as one of the determining factors in sex determination, which is still under debate (Davey & Jellyman 2005), the general increase in water temperature recorded in European rivers during last century (Eisenreich et al. 2005) would result in an increasing proportion of males. However our observations do not endorse this, as in this case we would rather expect increasing fat levels.

#### *Stock management measures*

Observations of low lipid content in silver eels in a freshwater lake on the island of Gotland (Baltic Sea) have been related to stocking practices. It has been debated that in some water bodies where eels have been stocked, after silvering these eels increase motoric activity triggered by their migratory instinct, but due to a lack of imprinting they lack orientation to their spawning grounds, and thus begin to lose fat and weight (Westin 2003). Limburg et al. (2003) found a tendency towards a higher fat content in silver eels from wild versus stocked origin eels, but concluded that stocked eels nevertheless are able to migrate and show potential to contribute to the spawning stock. Our data could not support nor reject the Westin hypothesis as our lipid analysis concerns only yellow

eel. However from the Belgian data it has been deduced that lipid content in yellow eels collected from closed waters (such as lakes and oxbow lakes) are generally lower than in rivers or canals (Geeraerts et al. 2007). Considering that in Belgium eels in closed waters exclusively originate from restocking with glass eel, this could illustrate that also in yellow eels from restocking lipid content is lower than normal. However, this could also be the effect of typology or a result of high restocking rates as most Belgian closed water bodies are small and are restocked at high rates which could have led to suboptimal feeding conditions.

#### *Effects of low-energy stores*

Jonsson & Jonsson (2005) showed that especially in fish species with long distance migrations, storage of somatic reserve energy is essential in fulfilling their life cycle. As energy stores are known to be essential within the reproduction migration, effects of lowered fat content will be most acute within the silver(ing) eel, affecting migration and reproduction. The data of lipid content presented here were obtained through a monitoring study for contamination in sedentary eel with the objective to follow pollution pressure on the sampling locations. Consequently, measurements were carried out on eels in their yellow phase. So great care must be taken when extrapolating observations on yellow eel fat contents to conclusions on silver phased eels. In the absence of long time monitoring series in lipid content in silver eels, and lacking quantitative models for lipid metabolism between yellow and silver eels, we are confident that the yellow eel data can be used as a valuable proxy for the lipid status in silver eel. We believe that the decrease in lipid content as observed in yellow eels is indicative of a similar proportional decrease of energy stores in the silver eel, but data to prove this are lacking. We therefore stress, that following considerations on effect on migration and reproduction, are the outcome of a hypothetical model based on the available information. Comparative studies of lipid content and lipid metabolism in yellow versus silver eels are urgently needed.

#### *Minimum lipid content as condition for silvering*

In 1959, Thurow reported that an attainment of 'breeding livery' depends on some physiological changes, on annual increase of condition factors and on fat accumulation. He mentioned 28% fat as a critical limit. Piatek (1970) stated that the content of fat in meat tissue 'is one of the characteristics in silver eel, which stimulates it for spawning migrations'. While silver eels usually contain on average 30% of fat (Böetius & Böetius 1985), large individual variation in fat content in silver eels were reported in eels

from a lake in Norway: they contained between 12.5% and 41.9% fat (Bergersen & Klemetsen 1988). Also in Sweden, fat analysis in female silver eels from 9 different localities revealed diverging results, with means <10–28%, the proportion of eels with muscle fat content <20% was varying from 4% to 100% (Svedäng & Wickström 1997). In both countries these lower fat stores have been reported in descending silver eels, indicating that also low fat silver eels start their migration. Other authors (Larsson et al. 1990) made the assumption that silver eels only start to migrate once their fat content reached a minimal value (28%), sharing the view of Thurow (1959). It was suggested that, when fat content in the muscle reaches a level of saturation at 28%, lipid levels in the blood start to increase, triggering the production of hormones responsible for metamorphosis and sexual maturation (Larsson et al. 1990). This idea that a critical fat mass must be reached before silvering has been generally accepted as the cue to initiate silvering (Lokman et al. 2003). If the silvering process is independent on the fat content in the yellow eel prior to silvering (Svedäng & Wickström 1997), these low fat silver eels most probably will be unsuccessful as the fat contents will be too low to permit a successful migration, a normal maturation and spawning (Bergersen & Klemetsen 1988), or migration will be delayed as these low fat silver eels will try to compensate the lack of fat by eating more until they have reached the desired fat contents for their journey back to the Sargasso Sea (Svedäng & Wickström 1997). In case the silvering is dependent on a minimum fat content in their yellow stage (Larsson et al. 1990), then silvering may not even take place or only to a limited extent. Anyway, in most scenarios a negative effect of the decrease in fat on the reproduction success is to be expected.

### *Insufficient energy for migration*

Several authors described the requirements of energy for spawners to migrate and reproduce, in terms of percentage of lipids in muscle wet weight, or on body weight basis, which is commonly assumed as equal. Böetius & Böetius (1980) estimated that 18% of the energy available was used for development of the gonads, 27% was lost to routine metabolism and to metabolic activities related to maturation processes, 30% was available for migration and 25% was the residual energy after spawning. They calculated that a minimum of 20% of total lipid on body weight basis is required for successful migration and reproduction. More recently, through experiments with eels in swimming tunnels, the energy required for migration was estimated as 7.7% (van Ginneken & van den Thillart 2000), 12.6% (van den Thillart et al. 2004), 7.8% (Palstra et al. 2006a) and 6% fat (van den Thillart et al. 2007). Palstra et al. (2006b) reported

that besides 7.8% fat for migration, 5.7% is required for incorporation in oocytes, and a total of 13.5% fat is the estimated requirement for healthy migrating silver eels (Palstra et al. 2007). van den Thillart et al. (2007) concluded that with eels having around 20% fat, there is more than enough left after reaching the spawning site for gonad development and spawning behaviour. However, they further discuss that at least 13% is necessary for swimming (independently of size) and on average 7.7% is incorporated in eggs indicating that silver eels should have a fat percentage of 20.7% to be able to migrate and reproduce successfully.

If we assume 20% as the minimum limit for a normal migration and reproduction, we can compare this benchmark to our data. From Figs 3b and 4b the increase in the proportion of sites with (yellow) eels having fat contents below 20.0% is evident (Belgium 1994–1998: 54.2%, 2004–2006: 92.8% and The Netherlands 1977–1981: 41.5%, 2002–2004: 84.8%). The magnitude of the decrease in fat contents described above with a 7.7% drop over 13 years in Belgium and a 7.5% drop over 15 years in The Netherlands, with fat content dropping to 12.3% and to 13.4% respectively, is believed to be sufficient to compromise reproduction.

The study area is situated in the centre of the latitudinal distribution of the European eel and by that may be representative for the whole population. It could be argued that local environmental conditions (e.g. high pollution pressure in Belgium and The Netherlands) might be responsible for a lower fat content in eels from Belgium and The Netherlands compared to the rest of the population in other countries. Unfortunately, there are no other long time series on lipid content in yellow or silver eel available. If we make the assumption that the reported decrease extends beyond Belgium and The Netherlands and is general over the distribution area of the eel, and considering energy stores being a restrictive factor for successful migration and reproduction as debated here, there is a differentiation in reproductive success of silver eels dependent of the latitude of the river system where the eels originated (Table 1). Southern eels need less net energy for their spawning migration compared to northern ones. That would mean that at an equal lipid level, southern female silver eels could be more successful in fulfilling their migration and still have enough energy for successful reproduction. The general accepted idea that especially northern areas are the main contributors to the spawning stocks as they produce a high proportion of large highly productive females have recently been refuted by Kettle et al. (2008b) suggesting southern countries as important contributors to the spawning stock. Our observations endorse these recent observations.

In addition, it cannot be precluded, that also males may have considerable difficulties in reaching their spawning grounds. It may be assumed that male eels once arrived at their spawning ground, do not need as much ER for reproduction as females, but as male silver eels are small sized and seem to get leaner, fulfilling their migration successfully could be problematic. Male silver eels in River Frémur emigrating between 1999 and 2004 measured between 27.0 and 44.2 cm length (Laffaille et al. 2006), with a mean length of 37.2 cm. Male silver eels usually do not exceed 150 g and the decreasing trend in muscle fat content might also affect males in their successful reproduction migration. A male silver eel of 37.2 cm has an estimated weight of 91 g and with a 13.1% muscle fat content has only 11.9 g fat available. Measurements of energy requirement of eels of 43 cm swimming in tunnel trials resulted in a COT of  $0.68 \text{ kJ}\cdot\text{km}^{-1}\cdot\text{kg}^{-1}$  (van Ginneken & van den Thillart 2000). On this basis we calculated that these eels need 13.3, 16.0 and 20.0 g fat for completing their journey from Lisbon, Nieuwpoort or Stockholm to the Sargasso Sea. From these calculations it seems that currently, many male eels are not able to reach their spawning grounds. Only individuals with higher net lipid content will be able to complete their journey, but the question arises if the remaining lipid energy in these individuals is sufficient to guarantee all activities required for successful mating.

#### *Low fecundity*

Lipid energy is essential for reproduction, mobilization of lipids fuels the ovarian growth and the production of good quality eggs. Female herrings (*Clupea harengus membras*) with a higher condition factor or muscle fat content produced eggs which suffered less from early mortality and also had better total survival and hatching success (Laine & Rajasilta 1999). It has been shown that in the northern Baltic Sea, condition and fat content in herring vary seasonally and annually (Rajasilta 1992) and there are temporal differences in the diameter of spawned eggs, and in the fat content of the ovaries, which may influence the development and mortality of herring eggs and contribute to seasonal or annual variations in the production of larvae (Laine & Rajasilta 1999). In case fat reserves are low, poor fecundity is to be expected. Decreases in the lipid content of fish at the onset of the spawning season are common in many species. Lipid content in sockeye salmon (*Oncorhynchus nerka*) decreases from 9.7% to 1.8% during spawning migration from the sea to the river (Thurston & Newman 1962). In Pacific herring (*Clupea harengus pallasii*) a decrease of muscle fat content (w/w basis) of 10.8% in non-spawning herring versus 2.4% in spawning herring was reported (Huynghe et al.

2007), indicating that the amount of energy required for reproduction approaches 8.5% of muscle lipid content.

It was reported before that larger eels have more fully developed ovaries (larger oocytes) than smaller eels (Kohnenko & Bezdzenyehnykh 1973), but as a consequence of decreased lipid energy it seems that - on average - only the large female eels contribute to reproduction, and this contribution is poor (Table 1). Belgian 1 kg female silver eels with a mean lipid content of 13.1% can produce 110 g of eggs, or ca. 310,000 eggs using the conversion factor described in van den Thillart et al. (2007), which is very low compared to the quantity of eggs (0.93–2.10 millions) recorded after experimental maturation in female silver eels between 800 and 1200 g (Böetius & Böetius 1980).

In addition, these large females are rare. Size (and age) at the silver eel stage varies considerably within as well as between sampling sites (Svedäng et al. 1996). Bergersen & Klemetsen (1988) reported that descending silver eels from a Norwegian coastal lake (Skogsfjordvatn) in 1983 mostly fall in the 300–400 g weight class, and the largest eels being in the 700 g weight class. In River Frémur (France) emigrating female silver eels are between 36.6 and 111.2 cm length, but length >70 cm are scarce (Laffaille et al. 2006) and the emigrating eel population is dominated by males (Feunteun et al. 2000). In exploited habitats, like lake IJsselmeer, large sized females are even scarcer and mostly completely depleted by fisheries (Dekker 2000). In southern areas eel stocks are characterised by a dominant proportion of males (Lobón-Cervia & Carrascal 1992) and females are scarce. These data suggest that the proportion and quantity of large sized female eels over the whole stock may be limited, but emphasise the importance of these individuals as spawners and give further basis to recommend special protection measures for this part of the population.

One has to bear in mind that this assumptive approach is based on mean values of lipid content. Considering the large variation in lipid content between eels (within and between sites) (see also Figs 3b and 4b), it is clear that a much better view could be acquired when integrating frequency data of lipid content in this analysis. Several assumptions have been made which need to be assessed in more detail. Further research on the energetic requirements for migration (and reproduction) of the male and female silver eels of various size classes, combined with a better assessment of the variation in lipid content and the demographic characteristics (length, weight, sex ratio) of the silver eels over Europe will be needed to analyse RP and predict reproduction success of the migrating stock in function of latitudinal differentiation. In addition information is needed on

the status and trends of contaminants and lipid reserves in eels from coastal and estuarine habitats, as those eels may represent an important contribution to the spawning stock.

Decreasing energy stores in yellow eel and stock decline

In general fat contents in fish are considered as an indication of good health of both individual basis and stock basis. If we consider the fat content of eel populations *as such* as a general indicator for the health of the population, current observations of *poor lipid health* consolidate the view that the population is in a vulnerable shape. To our knowledge this is the first reporting of decreasing fat contents in a waning population. This health indicator is in line with other, well-known stock indicators such as low recruitment and decreasing fisheries yields. Fig. 6 compares periods of decrease in glass eel recruitment of the stock, and the period of the decrease in mean muscle lipids in yellow eels from the data of The Netherlands. Glass eel recruitment dropped at the beginning of the 1980s after the high levels of the late 1970s, and the trend kept downward since then (ICES 2007). The drop in lipid stores, as can be deduced from data from The Netherlands, seems to start some ten years later, beginning of the 1990s. Although we believe that the decrease in fat stores of the yellow eels has a negative impact on the migration and reproduction capacity in the silver eels and thus results in decreased recruitment, the timing of the decrease for both time series does not seem to endorse a causal relationship between decrease in fat content and lowered recruitment in the 1980s. However, this can not be excluded, as unfortunately, to the best of our knowledge, there are no

time series for fat content in eels dating back earlier than 1977, and still it could be possible that muscle lipid content of yellow eels prior to 1977 would have been higher than the ca 20% in the eels of The Netherlands from the end of the 1970s. Piatek (1970) found in narrow-headed eels sampled in 1961 in various habitats from Polish waters an average fat percentage of 25.1% ( $N = 25$ ). Bergersen & Klemetsen (1988) reported mean muscle fat content of 21.2% (SD 5.1,  $N = 13$ ) in yellow eels from the Norwegian coastal lake Skogsfjordvatn in 1983 which is similar to the mean values from The Netherlands in this period. Yellow eels between 70 and 350 g (~35–60 cm size range), sampled in 1988 in a southern Scandinavian eutrophic lake, had a mean fat content of ca 21.8% (SD 7.2, min. 5, max. 35,  $N = 39$ ) as deduced from a figure from Larsson et al. (1990). However, great care must be given when comparing literature data on eel fat levels between authors, as methodological and analytical issues might vary to some extent and description is often missing.

The initial decline in recruitment at the start of the 1980s and the subsequent decrease in lipid content in the 1990s could be the result of the same cause: the emergence and continuing release of toxic substances in the environment. We hypothesize the following idea as a possible key mechanism for the decline of the species: new contaminants, being produced and released into the environment during the 1970s, bioaccumulate in the fat deposits in eel with steadily increasing concentrations. These contaminants attain critical levels at the end of the 1970s, and are being metabolized (together with fat metabolism) into the migrating silver eel during starvation. Blood concentrations of the contaminants reach toxic levels and cause detrimental impact on the silver eels or the quality of their gonads. As a result recruitment levels drop at the start of the 1980s. Simultaneously, these contaminants have negative impact on lipidogenesis or can induce lipolysis, so fat contents in yellow eels start to decrease during the 1990s. Lean eels still silver and do start their migration but, due to insufficient energy stores migration and/or reproduction are not successful, and recruitment further goes down. Considering the further decrease of fat stores it is likely that also recruitment still will continue to decrease. To date, there is not enough evidence to hypothesize which specific contaminants could be responsible, either as single compounds or collectively. Endocrine disrupting chemicals may be the most important ones in this respect. There are an increasing number of studies reporting on effects of some new compounds on biota (e.g. brominated flame retardants), and their presence in aquatic organisms, and specifically in anguillid eels over the world (e.g. Ashley et al. 2007; Fromme et al. 1999; Belpaire & Goemans 2007a; for a review in

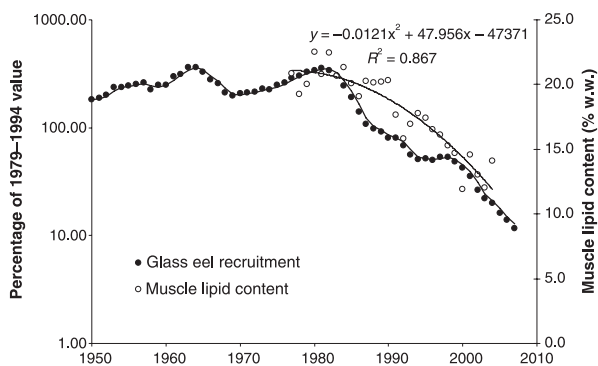


Fig. 6. Time series of glass eel recruitment in Europe (ICES 2007) and of muscle lipid contents in yellow eels from The Netherlands. Data of the time series of glass eel recruitment are geometric means of monitoring data of recruiting biomasses in 21 European rivers, each series being scaled to its 1979–1994 average. Data of muscle lipid contents are means of pooled yellow eel samples from The Netherlands between 1977 and 2004. Trend line for the lipid content:  $y = -0.0121x^2 + 47.956x - 47371$ ,  $R^2 = 0.867$ .

*A. anguilla* see Belpaire & Goemans 2007b). For some of those compounds, time series of their presence in the environment are available and their time trend coincide with the trend in stock decline. Decabrominated diphenylethers appeared in the late 1970s in Western-Europe, and increased gradually in the 1980s to peak in the 1990s (Zegers et al. 2003). But in relation to the huge number of chemical substances produced worldwide and released in the environment, ecotoxicologic information is only available for a few substances. Possibly, the decline is not caused by one contaminant, but may be the result of contaminant cocktails, combining several (newer or older) substances with synergetic effects. In this view, it is expected that the actual low quantities of recruiting glass eel could be the direct progeny of silver eels brought up in the cleaner, remote, fresh water habitats, where contaminant pressure is low. Within the national and international eel restoration plans, it makes sense to give high priority to special protection measures for eel stocks of these areas, to ensure a maximal migration of good quality spawners, including specific protection of large sized females. If pollution represents a major cause in the decline of the eel, as suggested here, it is evident that for restoring the population, the production and release of chemicals with ecotoxic properties should be stopped, and further research is needed in this field. The Water Framework Directive recently (European Commission 2006b) proposed to monitor a selection of priority substances to achieve good chemical status of European water bodies, there is however serious concern if its objective, namely the protection of aquatic life and human health, can be met, as the list of substances is very limited and monitoring strategies, measuring lipophilic compounds in water, are not adapted to avoid bioaccumulation in biota (Belpaire & Goemans 2007b). The European REACH program (European Commission 2006b), regulating the registration, evaluation and authorisation of chemicals, could be a more effective instrument to prevent the release of toxic compounds into the environment. The more or less simultaneous decreases in recruitment in the Northern-Hemisphere *Anguilla* species, such as in *A. rostrata* (Richkus & Whalen 2000; Casselman 2003) and in *A. japonica* (Tatsukawa 2003), during the last 30 years, is an additional argument endorsing the idea that some new contaminants quickly spreading over the industrialized world, are key elements in the decline. Programs to prevent these compounds to enter our aquatic ecosystems should therefore not be restricted to Europe alone.

In this paper, we suggest pollution and lipid metabolism as an important factor within the decline of the eel. Many pressures (such as oceanic changes, diseases, predation, fisheries and water quality and

habitat degradation) have been suggested or demonstrated to negatively impact the eel stock. Maybe (some of) these pressures acted in a synergetic way, resulting in the collapse of the stock. In the absence of hard evidence for one proven cause for the decline, restoration measures should take all potential causes into account.

#### Further recommendations

The EU eel recovery plan (European Commission 2007) concentrates on increasing the quantity of silver eels leaving their catchment. National eel management plans will focus on a reduction in anthropogenic mortalities within river basin districts, and aim to allow an escapement to the ocean of at least 40% of the biomass of silver eel, defined as the best estimate of the theoretical escapement if the stock had been completely free of anthropogenic influences. It was advised in 2005 (Dekker 2005) and 2006 (ICES 2006) to take into account fat content and *Anguillicola crassus* as additional parameters to be monitored within the eel restoration plans and the EC-Data Collection Regulation of the common fisheries policy. This study underlines the importance to include quality targets (such as lipid content, contamination and infection rate) within management targets and monitoring. A first step is the recent initiative taken by ICES (2007) to set up a database (the European Eel Quality Database) to compile all information on quality elements, including lipid content, in the European eel over its distribution area). Our observations of the declining fat content give new insight into the decline of the stock and raises serious concerns over the ability of the stock to recover. Therefore, we emphasize the need to include further studies on both fat contents and condition factors in eel, particularly silver eel, in the proposed stock-wide eel recovery plan. In addition, we recommend studying the relations between fat contents in yellow and silver eels and between fat and sex of individual eels, the effects of specific contaminants and parasites on fat metabolism and a possible relation between the decreasing fat contents in eel and environmental variables such as changing temperature, decreasing eutrophication, food availability and trophic status.

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