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Impact of yellow eel exploitation on spawner production in Lake IJsselmeer, the Netherlands

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Abstract

Exploitation of eel (*Anguilla anguilla* (L.)) may have contributed to the recruitment decline observed in the past two decades, by depletion of the spawning stock. This study assesses the impact of the relatively well-documented fisheries in Lake IJsselmeer, the Netherlands, on spawner production, using a length-structured cohort analysis model.

The yellow eel fisheries in Lake IJsselmeer overexploit the local stock of eel. Current fisheries reduce male spawner escapement to one in seven parts and reduce female spawner escapement to one in seven hundred parts of the unexploited situation.

Eel fisheries on continental life stages may have substantial impact on spawner production in all areas where a local population is dense enough to be fished. Although exploitation has not necessarily caused the currently observed recruitment decline, uncontrolled exploitation levels in major eel fisheries will impede successful recovery of stock and fisheries.

Keywords: *Anguilla anguilla*, assessment, fisheries, spawner escapement, spawning stock.

Introduction

European eel (*Anguilla anguilla* (L.)) are exploited over the entire distribution area. Exploitation reduces the local stock, resulting in reduced production of spawners. The simultaneous decline in eel stocks and recruitment* suggests that exploitation might have contributed to the decline in recruitment, by reducing the spawning stock (ICES 1999). Eel fisheries should be assumed harmful to the spawning stock, unless proven otherwise. The 'burden of proof' clearly rests with current exploitation practices (FAO 1995).

Assessments of the impact of fisheries on local eel stocks are limited in number (Sparre 1979, Dekker 1993, 1996; review in Knights, White & Naismith 1996) and do not relate spawner escapement to fishing intensity. Simulation studies (Vøllestad & Jonsson 1988, de Leo & Gatto 1995) have been tuned to field data, but these studies have focused on heavily regulated water bodies, where fishermen concentrate their effort on silver eel using fishing weirs.

Fisheries for glass eel, yellow eel or mixed yellow and silver eel dominate the European eel fisheries, by numbers and by weight (Moriarty & Dekker 1997, Dekker 2000 b). Assessment of the impact of these major classes of eel fisheries, especially with

*The word *recruitment* sometimes refers to the migration from the nursery area to the adult population, sometimes to the onset of vulnerability to fisheries. In eel, the two processes might not coincide. *Recruit* here refers to the immigrating glass eel.

regard to the consequences for spawner escapement, is a prerequisite for rational management of the entire stock.

Eel fisheries in Lake IJsselmeer, the Netherlands, constitute 2% of total yield from the European stock (Moriarty 1997). Fisheries and stock are relatively well documented by routine monitoring programmes (Moriarty & Dekker 1997), allowing for an assessment of the impact of yellow eel exploitation on spawner production. This local stock is heavily exploited (Dekker 1996) but may not be representative for other, even nearby, yellow eel fisheries in Europe (Dekker 2000a). Therefore, the current analysis will focus primarily on the processes rather than on the quantification of the impact of yellow eel exploitation on spawner production in Lake IJsselmeer. Firstly, in a retrospective analysis over the years 1989-96, the impact of existing fisheries in Lake IJsselmeer eel stock will be quantified in a length-structured assessment model. Secondly, the relation between exploitation and spawner production will be analysed, by simulation of the effect of reduced levels of exploitation, using the same model in predictive mode.

Materials & methods

Study area

Lake IJsselmeer is a shallow freshwater lake, reclaimed from the Wadden Sea in 1932 by a dike ('Afsluitdijk'). Before reclamation, it was an estuarine area known as 'Zuiderzee'. The surface of the lake has stepwise declined by land reclamation, from an original 3450 km^2, until only 1820 km^2 remained since the late sixties. The discharge of the river IJssel (average 7 km^3 per annum, from the river Rhine) is sluiced through the Afsluitdijk into the Wadden Sea at low tide, by passive fall. Glass eel immigration is facilitated by slightly opening the sluices during the season. Silver eel migrate through the sluices towards the Wadden Sea.

Fisheries

Fyke nets, eel boxes (Deelder 1974) and long lines are used to fish for eel; the former includes both summer fyke nets set in trains (90%) and larger fyke nets set on poles near the shore (10%). The larger fyke nets catch yellow and silver eel; other gears only fish for yellow eel. Fyke nets set close to the sluices catch predominantly silver eel. These fyke nets are not allowed to span the sluices themselves.

Minimum legal size is 28 cm. Since 1995, a dip net fishery for glass eel has been allowed to catch 5% of the glass eel immigrating through the sluices in the Afsluitdijk, for restocking in inland waters.

Monitoring and sampling

In conjunction with management of these fisheries, the government has kept records of landings at fish auctions. Confidential information acquired from selected fishermen indicates that auction statistics cover a stable fraction of ca. 85% of total landings; data in the current analysis have not been corrected for unrecorded landings. Samples of landings have been acquired at the auctions (Table 1). From 1989 onwards, the market sampling programme has covered all types of fisheries and has been operated consistently. In 1994, co-management by the government and an organisation of fishermen was introduced, and recording of auction statistics was taken over by the Fisheries Board ('Productschap Vis'). This has progressively affected the quality of data in a neg-

Table 1. Sample size/number of samples by year, life stage and market category. Measurements include length, weight and (externally determined) maturity. Dissection additionally includes sex and maturity (macroscopic determination of the gonads).

	Yellow eel				Silver eel			
Year	Long lines, measured	Eel boxes, measured	Fyke nets, measured	Fyke nets, dissected	'Females' >50 cm, measured	'Females' >50 cm, dissected	'Males' <50 cm, measured	'Males' <50 cm, dissected
1989	403/4	482/4	2002/15	432/9	23/1	23/1	355/5	77/5
1990	640/4	673/4	1540/11	146/3	22/1	22/1	336/5	60/5
1991	540/8	661/8	1379/118	238/8	21/1	21/1	326/4	80/4
1992	678/83	771/21	962/12	88/3	20/1	20/1	340/3	77/3
1993	570/14	488/12	1369/167	256/9	22/1	22/1	254/3	75/3
1994	517/12	781/12	1187/32	206/7	20/1	20/1	315/3	76/3
1995	565/16	500/12	1180/32	240/8	19/1	19/1	344/3	66/3
1996	611/8	533/7	1285/17	208/8	25/1	25/1	272/4	78/4

ative way. Data up until 1996 are almost complete, and will be analysed here. Eel fisheries have been sampled at least twice each spring (yellow eel) and twice each fall (yellow and silver eel). For each of the major market categories (fisheries for yellow eel by fyke nets, eel boxes, long lines and for silver eel by fyke nets), a sample of ca. 10 kg of eels was acquired. Samples were kept for one night within closed plastic bags, killing the eel. Individual length and weight were recorded during the following day. A subsample of ca. 25 eels per sample were dissected and sex and maturity recorded by macroscopic inspection of the gonads. Animals for which a definite sex could not be assigned upon macroscopic examination were marked as 'unknowns'.

Catch composition data of the samples were used to break down total landings over length classes, sex and life stages. Escapement of silver eel through the sluices in the Afsluitdijk has not been quantified. Assuming results of tagging experiments by Ask & Erichsen (1976) and Sers, Meyer & Enderlein (1993) in the Baltic are applicable in the IJsselmeer fisheries, escapement was assumed to amount to 30% of commercial catches of silver eel.

Assessment model

Dekker (1996) proposed a Markov chain matrix model structured by length as an assessment tool for yellow eel fisheries. The current analysis runs along parallel lines, but is extended to cover the process of silvering and escapement. The current model is spelled out completely in the appendix.

Using data on length composition of catches, an assumption of the population in the terminal year and an estimate of the annual growth, the model of Dekker (1996) calculates annual mortality coefficients per length class. Subtracting the natural mortality (assumed constant), an estimate of annual fisheries mortality remains. In the current extension of the model, allowance is made for several fleets fishing for the same stock and for silver eel escapement. The latter is treated as an independent fleet, 'catching' a fixed percentage of the silver eel catch of other fleets.

Following controversies over quantification of eel growth in Lake IJsselmeer (Dekker 1986), no recent estimates of growth are available. It was tentatively assumed that eel growth follows a normal distribution, with a mean growth of 3.5 cm in length per year, and a standard error of 0.35 cm.

Natural mortality in yellow eel varies considerably, ranging from negligible (Dekker 1989) to close to 100% during incidental pollution accidents (Mueller & Meng 1990) or oxygen depletion in warm summers (Rossi *et al.* 1987-1988). Moriarty & Dekker (1997, annex 3) suggest natural mortality to be in the order of 75% over the total continental life span, but Dekker (2000 b) showed this assumption to lead to incongruous results and used 75% mortality over the pre-exploited yellow eel stage instead, conforming to an instantaneous mortality rate of $M = 0.138$. This latter value will be used here for pre-exploited and exploited yellow eel.

Terminal values for population numbers were derived from catch in numbers in the terminal year 1996 and assumed fisheries mortality

$$F_{term,\,i} = 0 \qquad i \leq 26$$
$$F_{term,\,i} = 1 - (i - 35)^2/70 \qquad 26 < i < 35$$
$$F_{term,\,i} = 1 \qquad 35 \leq i$$

where *term* = terminal year and i = length class in cm.

Data for (silver) eel over 40-50 cm in length are sparse, resulting in uncertain estimates of fishing mortalities. Therefore, simulation of alternative management regimes assumed fishery mortality to be stable over lengths over 40 cm and assumed all yellow eel of over 50 cm in length to be female and to silver at a length of 65 cm.

Results

Landings of eel from the Zuiderzee/IJsselmeer area at the beginning of this century amounted to 200 to 600 tonnes per annum (0.5 to 1.5 kg/ha/a) and were slowly rising (Figure 1). After the closure of the Afsluitdijk in 1932, landings rose to over 2000 tonnes per annum (6 kg/ha/a). Directly following the Second World War, peak landings were recorded of 4750 tonnes per annum (16.4 kg/ha/a). In the following five decades, landings decreased in cycles of richer and poorer years, with peaks every 8 years. Current landings (ca. 300 tonnes per annum; 2 kg/ha/a) are in the same order of magnitude as landings a century ago.

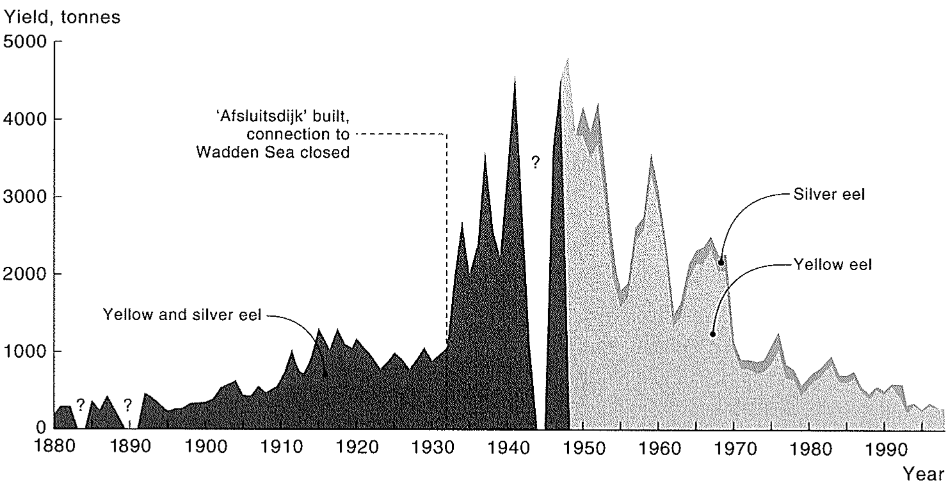

Figure 1. Yield of the Zuiderzee/IJsselmeer eel fisheries by year and life stage.

Silver eel catches declined in parallel to yellow eel catches and make up less than 10% of the total catch on average, with peak values in 1975, 1977 and 1992 of 20-25%. Large silver eel (females, length >50 cm) occurred in all years, but statistics were recorded in a few years only and comprised less than 10% of the silver eel catch in weight, 1-2% in number.

Breakdown of catches of yellow eel by length class (Figure 2) leads consistently to three distinct regions: up to 30 cm length the number caught increases with length, from 30 cm to 45 cm length the number caught decreases with 27% per cm on average and from 45 cm onwards with 9% per cm on average. Interpreting Figure 2 as a catch curve *sensu* Baranov (1918) and assuming an annual growth of 3.5 cm, annual mortality is estimated equal to 67% ($Z = 1.09$) for length classes from 30 cm to 45 cm and to 29% ($Z = 0.34$) from 45 cm length onward.

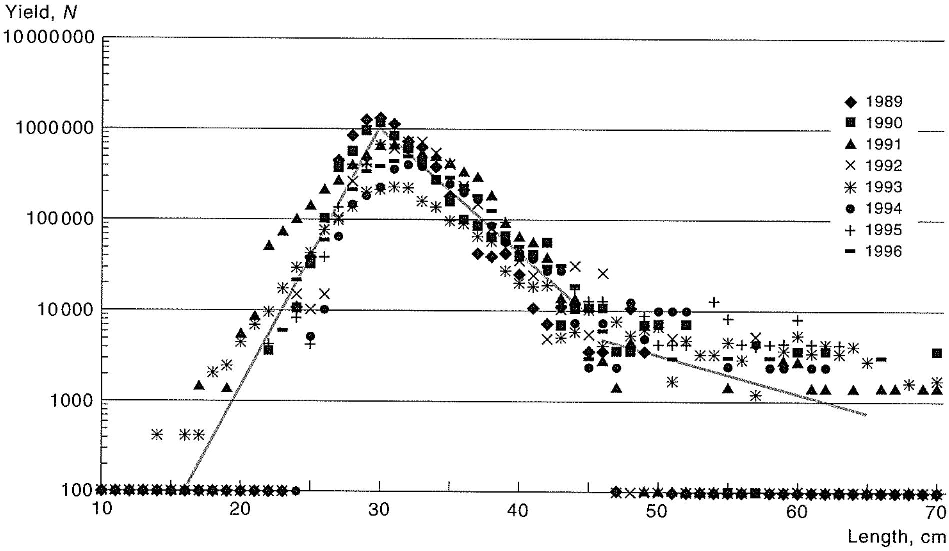

Figure 2. Length composition of the commercial catch by year. Log-linear regression lines have been fit to each of the length ranges 15-29 cm, 30-45 cm and 46-65 cm.

Males and females make up about equal shares of landings of yellow eel (Figure 3A), with a similar share for animals of unknown sex. Below 32 cm in length, the unknowns dominate; at 38 cm and above, the majority consists of females. For silver eel (Figure 3B), landings comprise only males up to 42 cm length; only females above 45 cm. In-between, only 21 animals have been observed.

Fyke net catches of yellow eel (averages 1989 through 1996) comprise 70% of total landings (Figure 4; mean length 31.7 cm); eel-box catches 15% (mean length 31.1 cm); long-line catches 10% (mean length 33.9 cm) and silver eel catches in fyke nets 5% (mean length 35.2 cm). A quarter of yellow eel landings by numbers is smaller than 30 cm in length and 80% is smaller than 35. Less than 1% by number is larger than 45 cm.

Figure 4 presents the breakdown of catches over gears averaged over the years 1989 through 1996. In the appendix, catches per year are presented for each of the fishing gears separately.

Fisheries mortalities for all three gears increase slowly from zero at about 25 cm length to a plateau level, remaining stable at greater lengths (Figure 5). For long lines, this plateau is reached at greater length (35 cm) than for the other two (30 cm). Estimated total fisheries mortality at the plateau is 1.0. Silvering occurs over a broad length range, peaking at 38 cm, at 0.25. Above 40 cm length, the rate of silvering declines to virtually zero at 45 cm length.

Population size (Figure 6) is estimated at 23 million (1100 tonnes) in 1989 and has shown a steep decline since 1991, to 8 million (450 tonnes) in 1996. Catches dropped from 9 million (450 tonnes) in 1989 to 4 million (240 tonnes) in 1996. Estimated population number per year class at the minimum legal size in 1989 amounted to 12.5 million, while in 1995 this was reduced to 5 million. Assuming a natural mortality of 75% over the pre-exploited life stage, this conforms to 20-50 million immigrating glass eel per year.

For the current fisheries (Figure 7), commercial yield per recruit was estimated at 15.8 g per immigrating glass eel, including 0.9 g silver eel catch. The annual fisheries mortality is estimated at $F \approx 1.0$ for the fully recruited length classes. The assumption that silver eel escapement amounts to 30% of silver eel production corresponds to 0.4 g male and 0.02 g female escapement per immigrating glass eel. Reduction of the yellow eel fishery to ca. 50% of the current level would optimise yield in the yellow eel fishery; reduction to ca. 33% would optimise the mixed fishery of yellow and male silver eel, which are currently the dominating market categories. Gains in commercial yield would

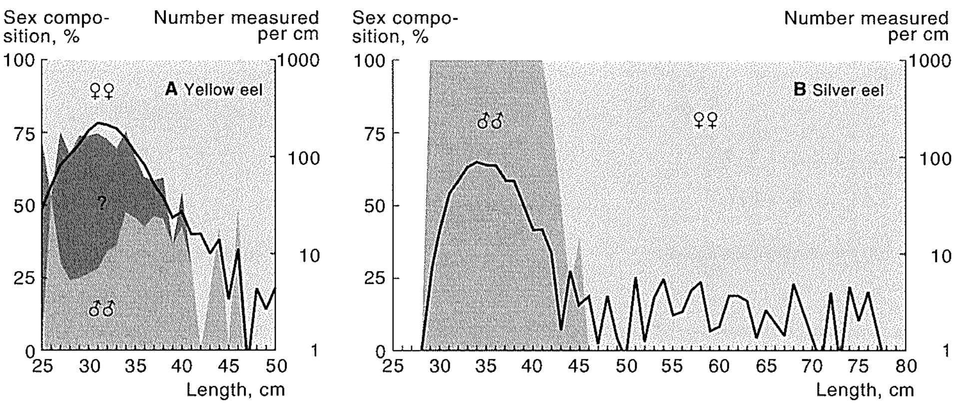

Figure 3. Sex composition of the catch (area) and number of observations (line), summed over the years 1989 through 1996.

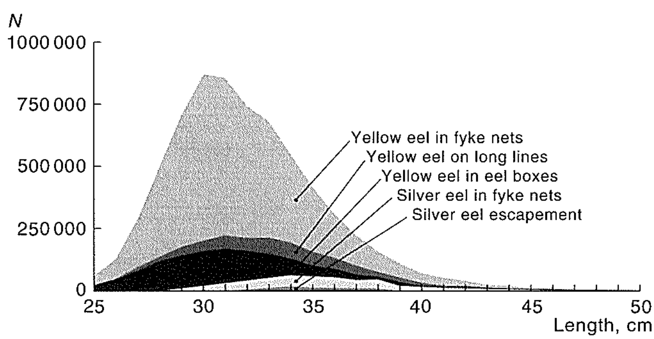

Figure 4. Composition of commercial catch, by length and gear type, averaged over the years 1989 through 1996. The assumed escapement of silver eel is presented additionally.

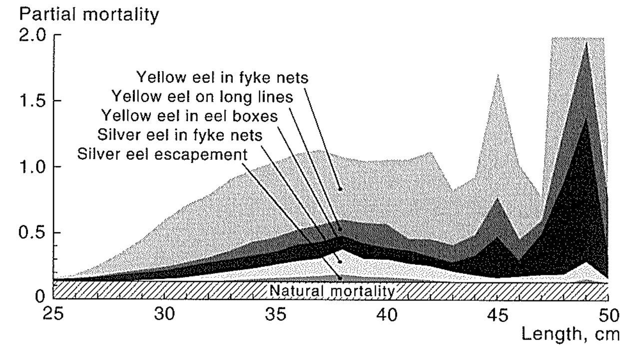

Figure 5. Estimated partial mortalities per year, averaged over the years 1989 through 1996. Silver eel escapement is presented as if it was a true mortality.

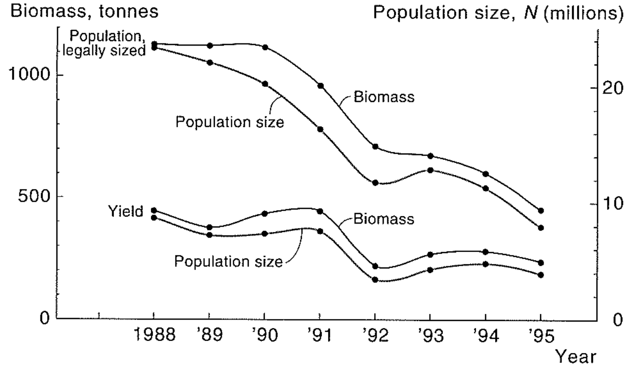

Figure 6. Total yield and estimated population size by year.

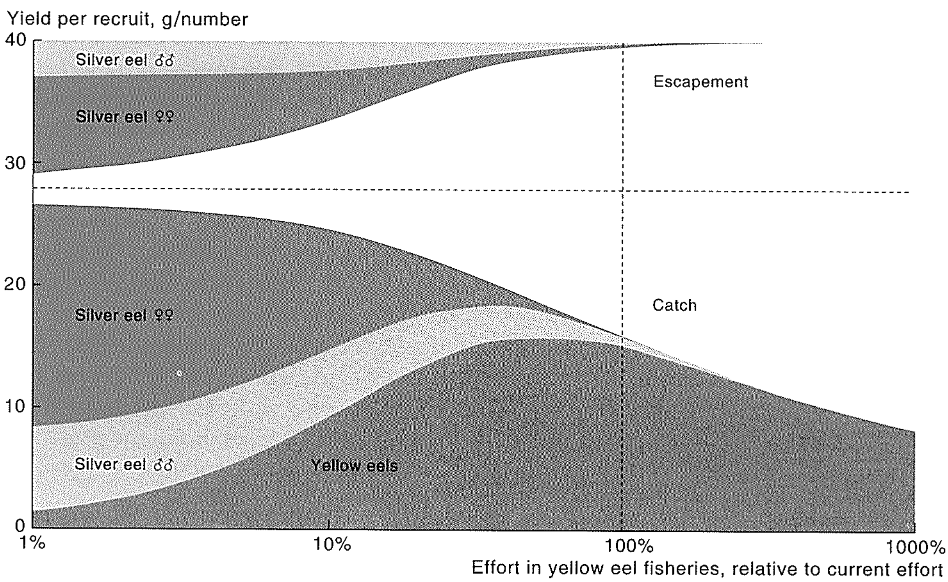

Figure 7. Predicted yield per recruit as function of effort in the fishery for yellow eel. Bottom panel presents yield to the commercial fisheries; top panel presents spawner escapement. Fishing effort is expressed in percentage of current situation, which is $F \approx 1.0$ per annum for the fully recruited length classes.

be 2.4 and 4.9 g respectively, but escapement of male silver eel would gain by 0.5 and 1.0 g respectively and escapement of female silver eel would gain by 0.2 and 1.0 g respectively. Cessation of all yellow eel fisheries while keeping silver eel fisheries at current levels would increase catch and escapement of males to 7.0 and 3.0 g respectively per glass eel and catch and escapement of females to 18.3 and 7.9 g per glass eel. The ratio of males to females by numbers would decrease from 225:1 to approximately 2:1.

Discussion

Assessment

Eel does not reproduce in Lake IJsselmeer and the local stock does not constitute a closed and self-sustaining population. Bozeman, Helfman & Richardson (1985) and Oliveira (1997) report on American eel (*Anguilla rostrata*) having restricted home ranges, but cite Bianchini *et al.* (1982), who suggest eel might have short-term home ranges in-between long-range movements. Deelder (1984) summarised literature data on migration of (European) yellow eel in the Baltic and in estuaries and rivers in northern Germany and Deelder (unpubl. reports) reports massive migrations between IJsselmeer and Wadden Sea. The present assessment assumes that the vast majority of catches in Lake IJsselmeer comprise eel from the lake itself; only recruitment of glass eel and escapement of silver eel are accounted for in the model. The local stock of yellow eel appears to contain at least two components (Figure 2): the smaller fish with a (downward) slope of the catch curve >1 and the remainder with a slope of ≈ 0.3, intersecting at 45 cm length. The intersection point at 45 cm suggests the bisection might be related to differential length and rate of silvering of the sexes. However, the absolute scarcity of females over 45 cm (Figure 2) does not match with the abundance of females in smaller length classes (Figure 3A). The steep slope of the major part of the catch tallies with the extreme overexploitation in the decades preceding the period analysed (Dekker 1991). The remainder more likely relates to migrants from stocks in neighbouring areas (up or down streams), which are less heavily exploited. This remainder constitutes less than 1% of catch in numbers. For practical purposes, the IJsselmeer stock of yellow eel up to 45 cm in length can therefore be considered to form a closed population. The close correlation between yellow and silver eel catches over the years indicates the majority of silver eels are of the same closed population. Recruitment has shown a serious decline already before the years included in the analysis (Dekker 1997, 2000), affecting the stock and yield (Figure 7). Quantitative analysis of the catch curve (Baranov 1918) (Figure 2) fails, since the stock is not in a stable state. Instead, data were analysed by a length-structured equivalent to the Virtual Population Analysis (Dekker 1996). Estimates of mortality are positively related to the assumed growth rate of 3.5 cm per year (equation 4 in the appendix gives growth and mortality only as a product) in the retrospective analysis, but possible errors in both should have cancelled out in the predictive simulation of the effect of yellow eel exploitation on silver eel production.

Biological characteristics

Dynamics of silvering have been assessed by analysis of the geographical variation in silver eel (Vøllestad 1992), by guesstimating parameters to conform with field observations (Sparre 1979) and by fitting a sparsely parameterised functional model (de Leo & Gatto 1995). In all studies, an *a priori* distinction between males and females was made. In the current analysis, male and female eel were not distinguished, although *a posteriori* sexes were assigned on the basis of length of silvered eel (Figure 8). When corrected for sex composition, which in itself varies with length (Figure 3A), current results (Figure 8) match very closely with fits of a functional model (de Leo & Gatto 1995). The close match between silvering in Italian and in Dutch waters is in agreement with the finding by Vøllestad (1992), that silver eel shows latitudinal variation in age but not in length. At 40 cm length and above, de Leo & Gatto's (1995) functional model does not match current findings, but the number of male eel in this length range is extremely low.

Local implications

Yield from Lake IJsselmeer includes 20 tonnes of male silver eels (0.3 million by number) and 2 tonnes of females. Simulation of the impact of yellow eel fisheries on the silver eel production (Figure 7) predicts a potential seven-fold rise in production of male silver eel and a seven-hundred-fold rise in female silver eel production upon cessation of yellow eel exploitation. This would imply a big increase in yellow eel density, from currently 3-5 kg/ha of eel >28 cm in length, to over 50 kg/ha. Buijse *et al.* (1993) estimated the production of the main prey species, smelt (*Osmerus eperlanus*), in Lake IJsselmeer at 130 kg/ha/a and consumption of smelt at 100 kg/ha/a of which 3.5 kg/ha/a is eaten by piscivorous eel. Consumption by eel seems not the factor limiting smelt density and consumption by eel might very well increase. Whether the predicted increase can be carried in full is questionable.

Dekker (2000 b) proposed a tentative assessment of the total European stock, and estimated fishery mortality* $F \cdot \Delta t = 0.63$ in yellow eel fisheries. Sparre (1979) assessed fisheries in the German Bight, estimating $F = 0.2$ per year, but his results do not enable

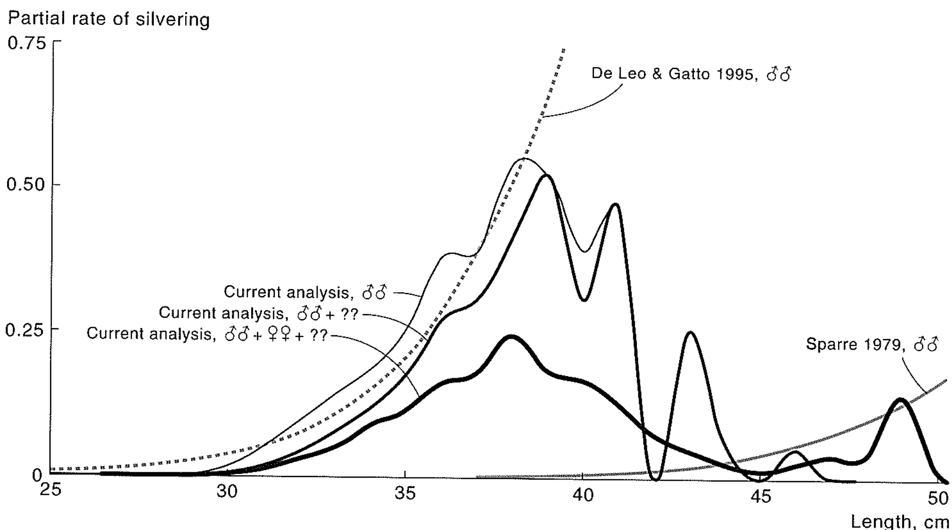

Figure 8. Rate of silvering: current analysis compared to literature data.

*Dekker (2000 b) differentiates between annual fishery mortality F and total fishery mortality over a time interval Δt, expressed as $F \cdot \Delta t$. In this text, the time span Δt always equals the duration of the life stage the estimated mortality applies to.

calculation of total mortalities over longer time spans. Current results indicate that for an average silvering eel, $F \cdot \Delta t = 3.22$ in the yellow eel fisheries of Lake IJsselmeer, which is well above the European average. The current fishery in Lake IJsselmeer is overexploiting the local stock (Dekker 1996) and a reduction to 30% of current effort would not influence yield negatively in the long run (Figure 7).

The biomass of spawners escaping from European fisheries has been tentatively estimated at 1753 tonnes (Dekker 2000 b) of unknown sex composition. According to the analysis presented, the IJsselmeer stock contributed about 10 tonnes of males and 1 tonne of females, but pristine spawner escapement is estimated at 70 and 700 tonnes respectively. Although Lake IJsselmeer fisheries constitute just one of a multitude of local eel fisheries in Europe (Dekker 2000 a), its impact on spawner escapement appears to have global dimensions.

Global implications

European eel recruitment is tentatively estimated at 2 thousand million (Dekker 2000 b). Three quarters takes place in areas surrounding the Bay of Biscay and are fished as glass eel with an estimated mortality of $F \cdot \Delta t = 3.15$ over the glass eel phase. The remaining quarter is scattered over Europe and is fished in the yellow and silver eel stages. Major yellow eel fisheries are found in the British Isles, the Netherlands, Germany and Denmark (Moriarty 1997). Moriarty & Dekker (1997) assumed these fisheries to have a low impact in comparison to glass eel fisheries. However, the current analysis suggests that yellow eel fisheries in dense (estuarine) yellow eel stocks can indeed be a match for glass eel fisheries. The impact of silver eel fisheries has only been quantified in an outer region of the distribution area (Ask & Erichsen 1976 and Sers, Meyer & Enderlein 1993) and is estimated at $F \cdot \Delta t = 1.43$. The conclusion that continental fisheries (may) substantially affect spawner escapement in all areas where the species is found in any appreciable density is inescapable.

Causes of the observed recruitment decline are unknown and might include natural or anthropogenic factors (Castonguay *et al.* 1994). Natural changes have been shown to coincide with the observed recruitment trend (Knights *et al.* 1996) and were indirectly evidenced (Dekker 1997). No trend in anthropogenic factors has been found to match the timing of the recruitment decline (Castonguay *et al.* 1994). It is unlikely that exploitation is the single cause of the observed decline, but currently uncontrolled exploitation levels in the major eel fisheries will impede successful recovery of stock and fisheries.

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Appendix

This appendix presents an integrated recapitulation of the model of Dekker (1996) and current extensions for multiple fleets and emigration of silver eel.

Representing the number of eels of length j in the stock at time t by $N_{t,j}$ and the entire stock in number at time t by a vector over length $(N_{t,j})$, growth is modelled as a transition matrix* $[G_{i,j}]$ of dimension length × length, where each cell $G_{i,j}$ quantifies the probability that an animal will grow from length class j to length class i within a time interval of one year. In the absence of mortalities and migration, the population vector at time $t+1$ is related to the population vector at time t by

$$(N_{t+1,i}) = [G_{i,j}] \times (N_{t,j}) \qquad [1]$$

Following Beverton & Holt (1957), the decline in numbers due to natural mortality, to fisheries and due to silver eel emigration is modelled in a differential equation:

$$\frac{dN_{t,j}}{dt} = -Z_{t,j} \times N_{t,j} \qquad [2]$$

Consequently, the population number at the end of the year relates to that at the beginning as**

$$(N_{t+1,i}) = (\mathrm{e}^{-Z_{t,j}}) \times (N_{t,j})^T \qquad [3]$$

Each year, new recruits $(R_{t,i})$ add to the stock. $(R_{t,i})$ is an almost completely empty vector, except for length class (6)-7-(8), which contains the number of immigrating glass eel. Combining the effects of recruitment, growth and mortality, it follows that

$$(N_{t+1,i}) = (R_{t,i}) + [G_{i,j}] \times (\mathrm{e}^{-Z_{t,j}}) \times (N_{t,j})^T \qquad [4]$$

Temporarily dropping indices of time and length,

$$Z = M + F_{fyke\,nets} + F_{eel\,boxes} + F_{long\,lines} + F_{silver\,eel\,in\,fyke\,nets} + S \qquad [5]$$

where M = instantaneous natural mortality (M_0 of Sparre 1979);
F = instantaneous mortality due to fisheries, including the combined effect of silvering and subsequent capture;
S = instantaneous rate of decline in population number due to silvering and escapement (M_1 of Sparre 1979).

The decline in numbers*** now equals

$$\begin{aligned}(D_{t,j})^T &= (1 - \mathrm{e}^{-Z_{t,j}})^T \times (N_{t,j}) \\ &= (\mathrm{e}^{-Z_{t,j}} - 1) \times [G_{i,j}]^1 \times \{(N_{t+1,i}) - (R_{t,i})\} \qquad [6]\end{aligned}$$

* The notation used mostly adheres to the standard symbols in fish cohort analysis models. Thus capital versus lowercase characters do *not* indicate matrices versus vectors, respectively. Instead, matrices and vectors are given as indexed cells, enclosed in round (vectors) or square [matrices] brackets.

** The superscript T indicates the transpose of a matrix, i.e. rows and columns interchanged.

*** In traditional fisheries assessments, the decline in numbers due to fisheries is coded as C, for Catch. In the current analysis, decline due to fisheries, due to silvering and due to other (natural) causes are all coded as D, for Decline.

Assuming independence between types of fisheries, and between fisheries and silver eel escapement, each of the components of Z contributes to the decline in numbers D, proportional to its contribution to Z, as

$$\frac{D_{fyke\,nets,\,t,\,j}}{D_{t,\,j}} = \frac{F_{fyke\,nets,\,t,\,j}}{Z_{t,\,j}} \qquad [7]$$

Substitutions and rearrangements yield equations for each type of fishery and for silver eel escapement. For example for the fykenet fishery, the catch equals

$$(D_{fyke\,nets,\,t,\,j}) = \left(\frac{F_{fyke\,nets,\,t,\,j}}{Z_{t,\,j}}\right) \times (1 - e^{-Z_{t,j}})^T \times (N_{t,j}) \qquad [8a]$$

or

$$(D_{fyke\,nets,\,t,\,j}) = \left(\frac{F_{fyke\,nets,\,t,\,j}}{Z_{t,\,j}}\right) \times (e^{-Z_{t,j}} - 1)^T \times [G_{i,j}]^{-1} \times \{(N_{t+1,i}) - (R_{t,i})\} \qquad [8b]$$

Given $[G_{i,j}]$, $(N_{t+1,i})$ or $(N_{t,j})$, M and all components of $(D_{t,j})$, equations 4 and 8 can be solved for $(N_{t,j})$ or $(N_{t+1,i})$ and the components of Z. Data for $(D_{t,j})$ are presented in Figures A.1-A.4; results for $(N_{t,j})$ and Z in Figure A.5 and A.6.

However, Dekker (1996) observed this system of equations to be numerically instable when solved backwards in time, using eq. 8.b. The population number is adequately assessed, but the distribution over length classes is not: the estimated population is concentrated in a few isolated length classes, with zeroes in between. Dekker (1996) proposed insertion of a low-pass filter in equation 8.b, resulting in

$$(D_{fyke\,nets,\,t,\,j}) = \left(\frac{F_{fyke\,nets,\,t,\,j}}{Z_{t,\,j}}\right) \times (e^{-Z_{t,j}} - 1)^T \times [LP]^a \times [G_{i,j}]^{-1} \times \{(N_{t+1,i}) - (R_{t,i})\} \qquad [9]$$

where

$$LP = 1/3 \times \begin{bmatrix} 1 & 1 & & & & & 0 \\ 1 & 1 & 1 & & & & \\ & 1 & 1 & 1 & & & \\ & & \ddots & \ddots & \ddots & & \\ & & & 1 & 1 & 1 & \\ & & & & 1 & 1 & 1 \\ 0 & & & & & 1 & 1 \end{bmatrix} \qquad [10]$$

and $a = 2$. Preliminary results of the analysis presented here, indicated $a = 2$ left some of the numerical instability intact. Therefore, $a = 3$ was chosen.

In the current analysis, eq. 9 was used in a retrospective analysis of the IJsselmeer fisheries over the period 1989 through 1996, while eq. 8.a was used for predictions of alternative management regimes.

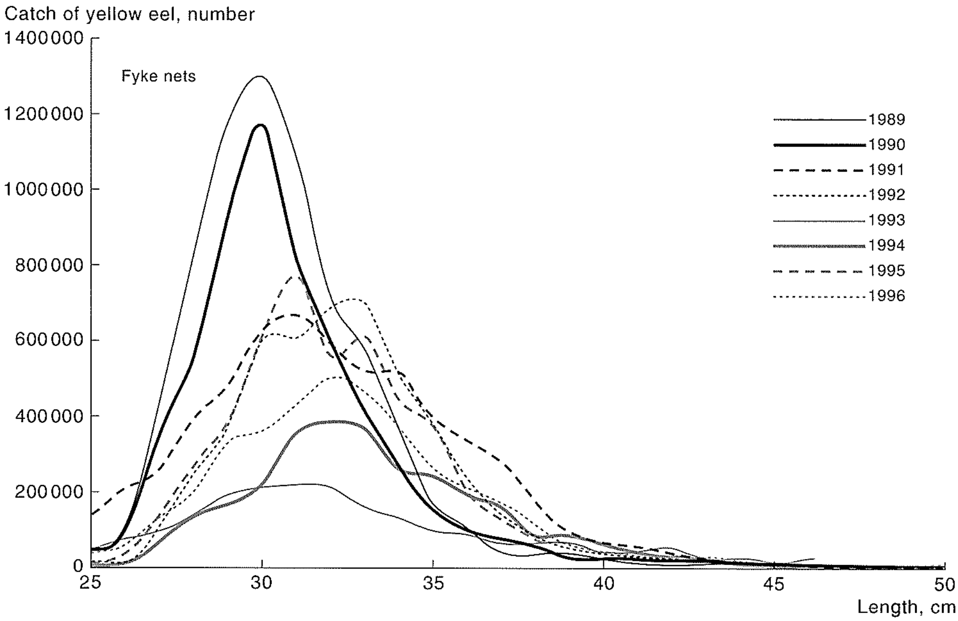

Figure A.1. Catch of yellow eel in fyke nets, in numbers per length class and year.

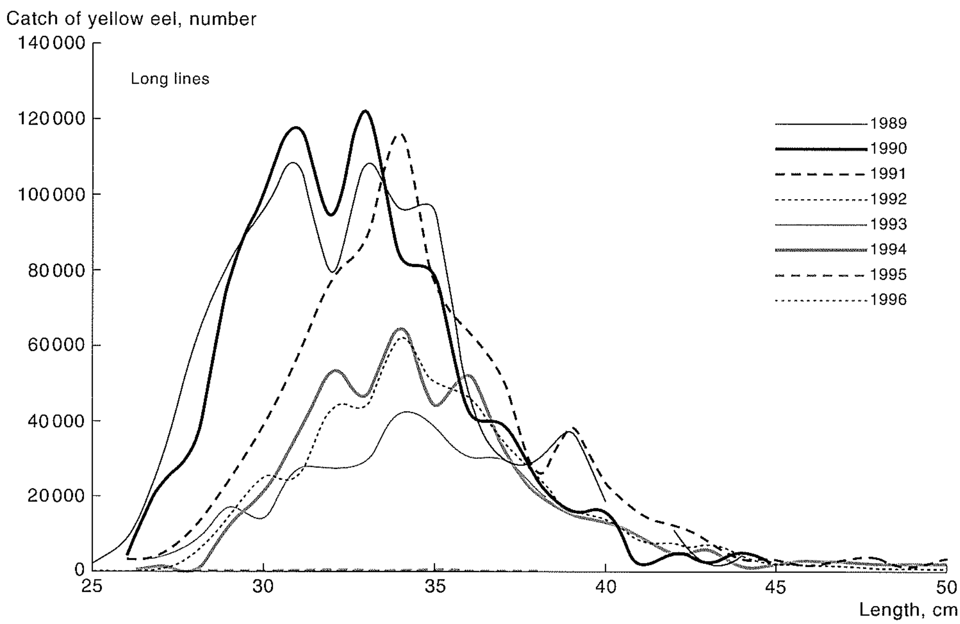

Figure A.2. Catch of yellow eel on long lines, in numbers per length class and year.

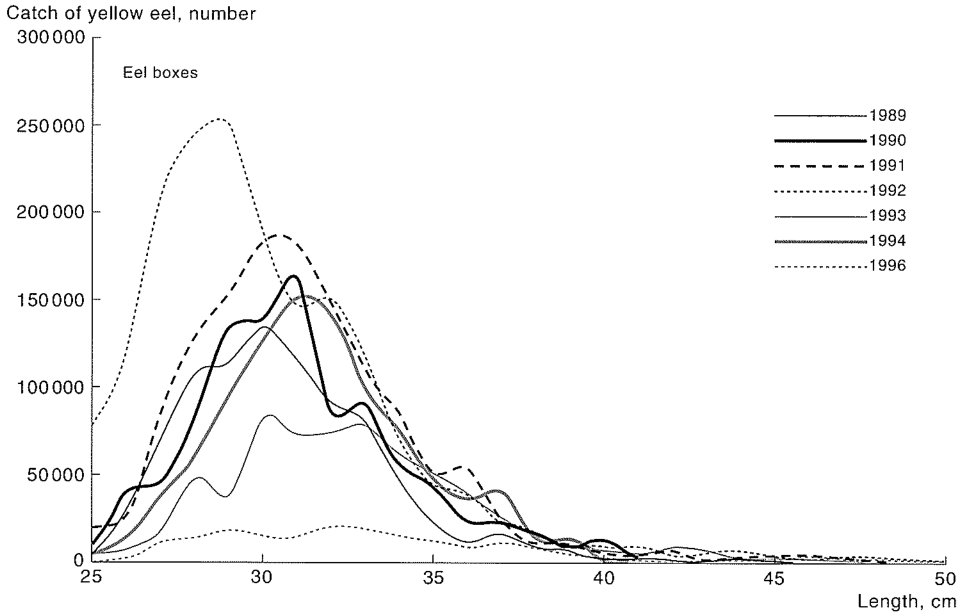

Figure A.3. Catch of yellow eel in eel boxes, in numbers per length class and year.

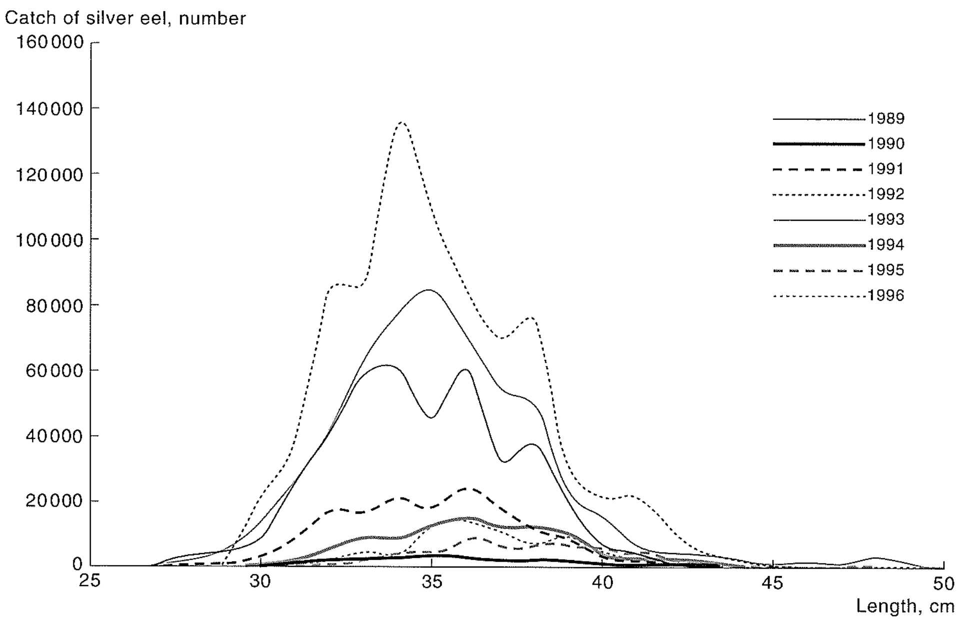

Figure A.4. Catch of silver eel, in numbers per length class and year.

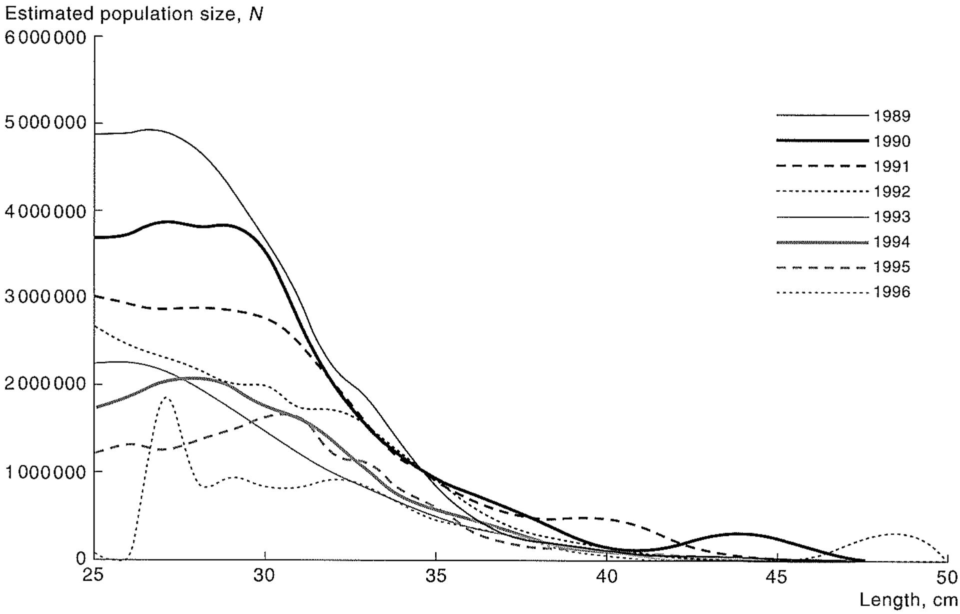

Figure A.5. Estimated population size, in numbers per length class and year.

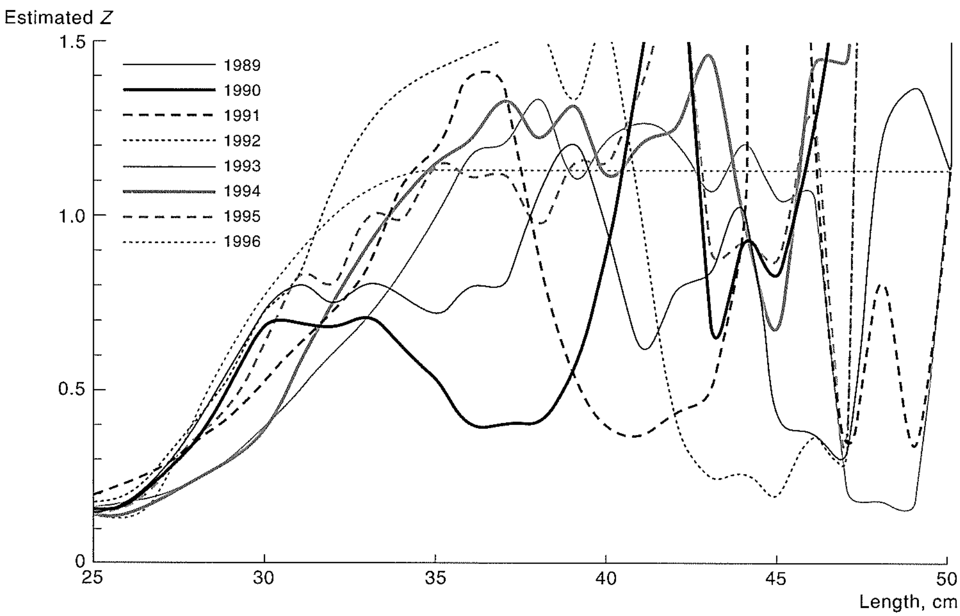

Figure A.6. Estimated rate of decline (natural and fishery mortalities, silvering, and escapement) per length class and year.