LONG-TERM TRENDS IN THE GLASSEELS IMMIGRATING AT DEN OEVER, THE NETHERLANDS.

WILLEM DEKKER

Netherlands Institute for Fisheries Research, P.O. Box 68, 1970 AB IJmuiden,
The Netherlands.

ABSTRACT

Immigrating glasseels (*Anguilla anguilla* L.) have been sampled in Den Oever, the Netherlands, for numbers per dipnet haul (since 1938) and for length distribution (since 1960). The data from 1960 through 1996 were analysed to detect trends over the years. Special attention is paid to the analysis of potential artefacts caused by the sampling strategy. Mean length and numbers were positively correlated, while the timing showed independent, short-term fluctuations. From 1987 onwards, numbers of glasseels were well below the overall average, and they were significantly smaller. Since the minimum in 1991, numbers and mean lengths are both increasing, although they are still below average. It is tentatively concluded that these long-term changes are related to oceanic conditions, which have caused the prolonged and ocean-wide recruitment failure in eels, with the exclusion of suggested continental causes. Further clarification of the recruitment problem in eel is only to be expected when the reproduction problem is properly addressed, at the international level.

Key-words : *Anguilla anguilla*, glasseel, abundance, length, seasonality, trends.

LES TENDANCES PROLONGÉES D'IMMIGRATION DES CIVELLES À DEN OEVER, PAYS-BAS.

RÉSUMÉ

Les civelles (*Anguilla anguilla* L.) immigrantes à Den Oever, Pays-Bas, ont été échantillonnées depuis 1938, pour mesurer les Prises par Unité d'Effort (PUE) et, depuis 1960, la distribution des longueurs des civelles est également évaluée. Les résultats de 1960 à 1996 ont été analysés, afin de décrire les tendances durant cette période. L'analyse a été concentrée particulièrement sur les artefacts d'échantillonnage. On observe une corrélation entre la longueur des civelles et les PUE, mais la saison d'arrivée a fluctué de manière indépendante. Depuis 1987, les PUE moyennes ont baissé significativement par rapport aux années précédentes. Pendant cette période, la taille moyenne des civelles a également diminué. À partir de 1991, une augmentation de la longueur moyenne et des PUE s'est amorcée sans atteindre les niveaux précédents. Nous avons émis l'hypothèse que les fluctuations observées sont provoquées par des conditions océanographiques, et non pas par des conditions continentales. L'analyse des causes de cette baisse de recrutement devra obligatoirement prendre en compte l'étude de la reproduction de l'anguille. Cela ne peut être envisagé que par une étude menée au niveau international.

Mots-clés : *Anguilla anguilla*, civelles, abondance, longueur, saisons, tendances.

INTRODUCTION

Recruitment failure

A prolonged recruitment failure of the European eel *Anguilla anguilla* L. has been observed since the middle of the eighties all over Europe (MORIARTY, 1990). At the same time, a parallel downward trend has been found in the few records that are available for the American eel *Anguilla rostrata* (CASTONGUAY *et al.*, 1994a). For both species, potential causes have been listed (CASTONGUAY *et al.*, 1994b ; EIFAC, 1993). Since the life cycles are still largely hypothetical (TUCKER, 1959 ; DEKKER and WELLEMANN, 1989), hypotheses on the causes of the recruitment failure are still highly speculative.

The proper identification of the true causes of the historic changes in recruitment levels is hampered by two factors : the oceanic phases are by their very nature far out on the ocean and therefore difficult to study, while the continental phases are found scattered all over Europe, *i.e.* a continent wide assessment of the state of the stock is practically impossible. Experimental work can easily be implemented locally for the continental phases, but it is almost impossible to study the oceanic conditions far out at sea because of the high costs involved. This asymmetrical distribution of costs over land and sea potentially generates a bias towards identifying continental causes as the most likely ones. Although there is a need to explore the oceanic option more extensively, the current paper will analyse a set of continental data for possible information on the oceanic stages.

Eels are long lived, slowly growing animals, with broad overlap in size between cohorts from adjacent years (MORIARTY and STEINMETZ, 1979 ; VØLLESTAD and NÆSJE, 1988 ; DEKKER, 1996). Escapement to the ocean in any year comprises animals born many years apart and any continental population consists of many cohorts. Essential changes in the total population are not likely to occur in the short run. Noting the longevity and the mixing of cohorts on the continent, it seems more plausible to relate observed year to year changes (MORIARTY, 1994) to local circumstances or designate them as stochastic variation. This implies that oceanic signals in continental data are likely to be detected only in very long data series.

Glasseel sampling at Den Oever

Glasseels immigrating from the Waddensea to lake IJsselmeer have been sampled at Den Oever for scientific purposes from 1938 onwards (DEKKER, 1986). Following experimental work on the proximate causes of immigration (DEELDER, 1958), detailed measurements of the length distributions have started in 1960. Aspects of variation in the annual abundance of glasseels have been analysed before (DEKKER, 1986). In this paper, the data set on length distributions, spanning a period of 37 years now and comprising 65 584 glasseels in 438 samples, is presented and analysed for possible long-term changes ; additionally, some new aspects of the data on abundance are presented, relating to 325 104 glasseels in 11 595 dipnet hauls from 1960 onwards.

In particular, the analysis will focus on three aspects : the number of glasseels caught, the timing of their immigration season, and their length distribution. Since no *a priori* relationship between any of these aspects is suspected, each of them is analysed separately. The statistical analyses will focus on factors related to the sampling strategy in order to derive the best estimates. In particular, no effort will be made to relate immigration parameters to local circumstances. Truly oceanic effects might easily be misidentified as local circumstances through spurious correlations. Besides effects of sampling, special attention will be paid to possible confounding of each of the three time series by the two others. *A posteriori*, the resulting time series will be correlated over the years, to detect common, long-term signals that might be attributed to the oceanic phases of the life cycle.

MATERIAL

Lake IJsselmeer is a freshwater lake, reclaimed from the Waddensea in 1932 by a dike (de Afsluitdijk). The surface of the lake has stepwise declined from an original 3 450 km² by land reclamation, until in the late sixties only 1 820 km² remained. In 1976, a dike was built separating a 600 km² compartment. The discharge of the river IJssel into the lake (average 7 km³/yr, coming from the river Rhine) is sluiced through the Afsluitdijk into the Waddensea at low tide, by passive fall.

Glasseels are attracted by this flow and enter the lake by active swimming, mainly through the sluices and ship locks. In 1938, six years after the closure of the Afsluitdijk, a scientific sampling programme for glasseels was set up at the sluices in Den Oever (52°56'20"N 05°02'70"E), in co-operation between the operators of the sluices (Ministry of Water Management) and the Netherlands Institute for Fisheries Research. This sampling was carried out at night at two-hourly intervals during spring, using a 1 m² dipnet with a mesh of 1 mm², just in front of one of the closed sluices. The catch of glasseels was counted and returned to the water. The systematic sampling usually starts each year when probing indicates the actual beginning of the immigration, and ends when catches have declined to negligible quantities. The sampling procedure and the results have been described in more detail by DEKKER (1986). Additionally, since 1960, the length composition of the glasseels has been sampled. In principle, the samples used for the abundance sampling were used again for length measurements. But when catches were too low, additional dipnet hauls were made or even light devices were used to attract glasseels. In the latter case, sampling was carried out at the ship locks (52°55'90"N 05°02'80"E), not to interfere with the regular dipnet sampling. Sampling usually occurred before midnight, taking 150 animals on average. The following morning, the animals were anaesthetized in a solution of MS222 and measured to the nearest millimetre. Originally, length measurements were taken twice a week, but from 1966 onwards the programme was reduced to only once a week.

In the following analyses, these data sets will be identified as the Catch per Unit of Effort (CPUE) dataset and the Length Frequency distribution (LF) dataset respectively, naming the primary aims of the data collection. The statistical analyses presented in the subsequent paragraphs were carried out using the statistical package SAS® (SAS INSTITUTE INC., 1989), modules Genmod and Catmod. The statistical models will be detailed in the subsequent paragraphs.

NUMBER OF GLASSEELS

Statistical model

The CPUE-dataset has been analysed for the numerical strength of the annual immigration by DEKKER (1986). Year to year variation, month to month variation, hour to hour variation and variation due to the water temperature were identified as factors of substantial influence. Water temperature was found to be strongly correlated with the month and considered to be a nuisance factor and was therefore dropped. The current analysis takes the same set of explanatory variables. However, the statistical model differs in its stochastic component.

DEKKER (1986) fitted a linear model to the log-transform of the number of glasseels (y) caught per haul, taking the log of $y + 1$, *i.e.* one glasseel was added to the true observation. One glasseel normally is a negligible quantity in comparison with the true observation, but its addition cures the sparse zero observations. The log-transformation

was used (1) to normalise the residual error of the statistical model, and (2) to transform multiplicative effects of years, months and hours into additive effects. The analysis of DEKKER (1986) was based on the dataset from 1938 through 1985, and did not contain many years in which the average catch was close to 1. However, in the following years, immigration levels dropped to the order of magnitude where one glasseel is no longer a negligible quantity !

DEKKER (in prep.) re-analysed the same dataset (extended through 1995) with respect to the proper statistical distribution of the errors, taking a semi-parametric approach. The analysis showed that the statistical distribution of the residuals is indeed nearly equivalent to a normal distribution of $\log(y+1)$. However, DEKKER (in prep.) warned against the use of $\log(y+1)$ because of the effect that the transformation has on the linearity of the model at low expected values. The use of a parametric quasi-likelihood, with $\varepsilon^2 \propto \mu^2 + \mu$ was proposed as an alternative, having an error distribution comparable to $\log(y+1)$, but no distortion of the predicted values at low expectations.

Results

This suggestion of a parametric quasi-likelihood was followed in the current analysis, using the module Genmod of SAS® (SAS INSTITUTE INC., 1989), with variance $V = \mu^2 + \mu$ and a log link function. Figure 1 presents the estimated year effect conforming to the three models according to DEKKER (1986), to DEKKER (in prep.) and to the current analysis. It shows that the proposed parametric quasi-likelihood ($\varepsilon^2 \propto \mu^2 + \mu$) indeed closely resembles the statistically and computationally much more demanding semi-parametric quasi-likelihood. However, it also shows that the transformation $\log(y+1)$ does indeed differ substantially from the other two analyses in years with very low expectations due to the corrupting effect of the +1 on the multiplicativity of the model. The log-transform estimates

Figure 1

CPUE of glasseels caught at Den Oever (expressed as expected catch in April, at 10 p.m.) as a function of the year of sampling (N/haul) : comparison of estimates based on three assumptions about the statistical distribution of the observations (see text).

Figure 1

PUE des civelles capturées à Den Oever (captures attendues en Avril, à 22 heures) en fonction des années (Nb/coup) : les valeurs sont estimées à partir de trois différentes distributions statistiques des valeurs observées (voir texte).

indicate recruitment levels fell steadily from 1981 onwards, while the two others estimate a steeper decline in 1981, followed by a recovery to average values, lasting through 1987. Clearly, the choice of a statistical model is not immaterial to the interpretation of the recruitment failure. In the following, the parametric quasi-likelihood model is used, since it follows the more sophisticated results of the semi-parametric model closely, while keeping computing time and tractability of results at an acceptable level. The number of glasseels at Den Oever is shown as the year term in the log of the expected value, which means that the abundance indices are on a logarithmic scale.

The abundance of glasseels in Den Oever (figures 1 and 5a) was very high in the mid sixties, high at the end of the seventies, dropped consistently from 1979 to 1983, but did not decline below the overall mean until 1986. Finally, very low values were found from 1987 until 1993, followed by a slight increase in the most recent years. The lowest abundance on record occurred in 1991, although the changes in absolute numbers in the years following 1987 are very small indeed. The breakdown of the total variation in the numbers caught over the sources of variation is presented in table I.

Table I
Analysis of variance (ANOVA) of the number of glasseels.

Tableau I
Analyse de variance de l'évolution interannuelle du nombre de civelles.

source	deviance	%	df	mean dev.	F	P
year	8597	7	36	238.80	29.14	0.0000
month	1677	1	4	419.21	51.15	0.0000
hour	1290	1	10	128.96	15.73	0.0000
colinearity	895	1				
subtotal	12458	10	50	249.16	30.40	0.0000
MANDEL(year)*month	84	0	3	27.88	3.40	0.0169
explained	12541	10	53	236.63	28.87	0.0000
residual	94583	79	11540	8.20		
total	119666	100	11593	10.32		

Confounding by timing of the season

The above analysis of the number of glasseels is based on the assumption that the (log of the) numbers caught can be represented by three, mutually independent effects : year to year variation, month to month variation and hour to hour variation. This assumption is rather restrictive, especially since the estimated numbers of glasseels will be correlated in the following to the timing of the season. MANDEL (1959) proposed a test

for interaction effects with a low number of degrees of freedom, which is known as « MANDEL's bundle of straight lines » (MILLIKEN and JOHNSON, 1989). Instead of the full interaction of two factors, the interaction of one factor with the estimated effects of the other is modelled. Applying this test to the number of glassseels (table I) yields a statistically significant result : strong yearclasses have a higher abundance in May, and a lower in March and April. However, the magnitude of these changes is very small : a yearclass of 10 times the average abundance over the whole season (which is the maximum factor actually observed) will have 6.5 times the average in March, 7.2 times the average in April and 10.6 times the average in May. Less than 1 % of the total variance is explained by MANDEL's bundle of straight lines test. Thus, the confounding of the estimated number of glassseels by the timing of the immigration season is statistically significant, but in practice negligible.

Confounding by length of the glassseels

The influence of the average length per year cannot be estimated concurrently with the estimation of the number per year, because the one aliases the other. Since confounding of abundance estimates by length distributions seems highly unlikely, it was decided to ignore it, *i.e.* to assume changes in the average length do not influence the estimation of the number of glassseels in front of the sluices.

TIMING OF THE IMMIGRATION SEASON

Statistical model

The CPUE dataset can also be used directly to analyse the timing of the immigration. Since the sampling was conducted at (nearly) fixed intervals throughout the season, the total dataset yields a (nearly) unbiased estimate of the date of arrival. In this analysis, the date of sampling is taken as the observation, and the number caught as weighting factor for that observation. Varying sampling intensity at the very start of the season and at the very end does not have a substantial effect on the analysis, since the number of glassseels is very low during these periods.

The main season of immigration usually starts in the beginning of March, peaks at the end of April and ends in the beginning of June, although single glassseels have been observed from December through July. In figure 2, the earliest (1973) and latest (1963) patterns of immigration are shown, represented by the daily catch, corrected for the hour of sampling. This correction was based on the above analysis of the number of glassseels.

The statistical analysis of the season of immigration was based on cumulative categorical models (FAHRMEIR and TUTZ, 1994).

Dates were classified into seven-day-periods, starting on January 1st. To avoid weeks without observations, dates before March 10th were pooled (1.1 % of catches), as were dates from June 1st onwards (0.6 % of catches).

The analysis was carried out using the module Catmod of SAS®, taking each year as a separate population. The cumulative logits of the observed frequencies per week were analysed by weighted least squares. The week number was included as an explanatory variable in the model, *i.e.* a threshold intercept, to allow for the asymmetrical and non-normal distribution of the immigration over the weeks. The changes in immigration season from year to year were modelled as a shift variable.

Figure 2
Timing of the glasseel immigration season : earliest (1973) and latest (1963) season, and statistically expected season (shaded).

Figure 2
Variation interannuelle des dynamiques saisonnières de migration des civelles : saison la plus précoce (1973), la plus tardive (1963), et saison normale (en grisé).

Results

The breakdown of the variance of the model is shown in table II. The total variance is for the larger part attributable to the threshold intercept, *i.e.* the distribution of the immigrants over the dates does not conform very well to a normal distribution. The statistically expected distribution is shown in figure 2 (shaded area). Changes from year to year explain about half of the remaining variance. The evolution over the years is shown in figure 5a (timing). The season of 1963 (shown in detail in figure 2) turns out to be exceptionally late, although 1962 and 1970 were almost as late. Early seasons occurred in the mid seventies (1973 shown in detail in figure 2) and early nineties ; late seasons in the sixties and eighties. However, the long-term variation in timing hardly exceeds the short-term variation.

Table II
Analysis of variance (ANOVA) of the timing of the season.

Tableau II
Analyse de variance des dynamiques saisonnières.

source	deviance	%	df	mean dev.	F	P
threshold intercept	354431	64	11	32220.97	121.93	0.0000
year	94701	17	36	2630.60	9.95	0.0000
MANDEL(number)	155	0	1	154.53	0.58	0.4449
explained	449287	81	48	9360.14	35.42	0.0000
residual	104914	19	397	264.27		
total	553892	100	443	1250.32		

Confounding by the timing of the season and the length of the glasseels

The confounding of these estimates of the timing by the number of glasseels was again tested by MANDEL's bundle of straight lines. This test mirrors the test mentioned above on the confounding of the estimated number by the timing of the season. In this case, the parameter estimates of the yearly abundance were entered into the model as a continuous covariate. This explained less than 1 % of the total variance ($p = 0.445$). This confirms the conclusion, that the number and timing are not correlated.

As in the case of the numbers, a possible confounding of the analysis of the timing of the immigration season by factors related to the length of the glasseels cannot be tested due to aliasing with the length parameters. However, once again it seems rather unlikely that a change in average length will confound the estimation of the number caught per day, and therefore of the timing of the season.

LENGTH DISTRIBUTION OF THE GLASSEELS

Statistical model and results

The analysis of the length distribution of the glasseels was based on the LF dataset. Data were pooled per month, and also analysed by a cumulative categorical model. Explanatory variables included a threshold intercept and the year and month of sampling. Glasseels of 60 mm and shorter were pooled (0.1 %) as were glasseels of 90 mm and longer (0.0 %).

The average length of the glasseels ranged from 67 mm in 1990 to 78 mm in 1963 (figure 3). The shortest individual glasseel (length 54 mm) was observed in April 1992 ; the longest one in April 1961 (92 mm).

Figure 3

Length distribution of immigrating glasseels : distribution per month in 1990 (shortest observed), 1963 (longest observed) and statistically expected length distribution (shaded).

Figure 3

Variation interannuelle de la distribution de taille des civelles : la plus petite distribution est observée en 1990, la plus grande en 1963 et les valeurs moyennes en grisé.

During each immigration season, the average length of the glasseels decreases over the months by 2.5 mm (figure 3). But the variation from year to year is about fourfold (table III, mean deviance of 1 414 867 for year versus 349 279 for month).

Table III
Analysis of variance (ANOVA) of the length of glasseels.

Tableau III
Analyse de variance de la longueur des civelles.

source	deviance	%	df	mean dev.	F	P
threshold intercept	234435884	76	29	8083996.00	1189.15	0.0000
month	1047836	0	3	349278.65	51.38	0.0000
year	49520336	16	35	1414866.75	208.13	0.0000
explained	285004056	93	67	4253791.88	625.73	0.0000
residual	21767653	7	3202	6798.14		
total	306771712	100	3269	93842.68		

The evolution of the length distributions over the years (figure 5a) shows a gradual decline over the sixties until the mid seventies, followed by a stabilization until the mid eighties. In the mid eighties, the length of the glasseels drops sharply, with a minimum in 1991. During the last five years, the average length recovers, but it is still below former levels.

Confounding by the timing of the season and the abundance of glasseels

Confounding of these estimates on length by the numerical abundance of glasseels is not very plausible. Because of the aliasing with the year effect on length itself, this interaction could not be tested. The case of confounding of the estimation of length by the timing is much more complicated. A simple model without interaction between length and timing results in an estimated year effect of the length that is strongly correlated with the timing of the season ($r = 0.48$, $p = 0.001$), later seasons having longer glasseels. At first sight, this contrasts with the diminishing length of glasseels within each season.

The diagram shows this relationship of timing and length, both in an early and a late season. Because of the relation between month and length, late seasons will apparently have longer glasseels. Again, both aspects (length and timing) cannot be discriminated on statistical grounds. A delay of the immigration by for instance local climatic conditions seems quite plausible. On the other hand, one can hardly imagine what would cause glasseels to be longer than average, even at the start of the season, when the peak of the season still has to come. Therefore, the estimated timing was given precedence over the year to year variation in average length. The diminution of the glasseels over the months was estimated by a model including the timing of the season (MANDEL's bundle of straight lines of the parameter estimates of the timing of the season), but without a year effect. Next, the model was rerun, with the parameter of the timing held fixed, but now including a year effect. The remaining correlation of the timing with this (conditional) year effect of the average length is negligible (figure 5c, $r = 0.17$, $p = 0.158$). The most striking effect of the correction for the timing appears in 1990, an exceptionally early season in the middle of a range of years of small lengths. Without the correction for the timing, the length in 1990 is estimated to be equal to that in 1991 ; with the correction, 1990 forms the smooth transition from the low 1989 levels to the record low in 1991.

AUTO- AND CROSS-CORRELATIONS

Autocorrelation

In the above analyses, three aspects of the glasseels immigrating at Den Oever were analysed : numbers, timing and length. Each of the analyses yielded a year effect. The year of sampling was included in the analyses as a class variable. No relationship between adjacent years was enforced by the statistical models. Consequently, the years can be taken as independent realizations of the immigration. The sample autocorrelations of the number, time and length parameters over the years are shown in figure 4. The cross-relations of the three time series are presented in figure 5, in a so-called rug-plot (TUFTE, 1995). Sample correlation coefficients are given in each sub-plot.

Figure 4

Autocorrelogram of the parameter estimates of the number of glasseels, their length and timing.

Figure 4

Autocorrélogramme des différents paramètres : nombre, longueur et dynamique saisonnière des civelles.

The dataset of length measurements now contains 37 years of data, with 10 samples of 150 animals on average per year. For a consistent time series of biological data, the length of the dataset is considerable. But from the statistical standpoint, it is hardly enough to calculate autocorrelations. Consequently, only the first few terms in the autocorrelogram are statistically significant. However, the three time series of parameter estimates behave quite differently. The timing of the immigration season shows no significant autocorrelation at all, the length is positively correlated up to a time lag of 5 years and the numbers show a strong autocorrelation, fading out only very slowly over 10 years.

Given the limited length of the time series, a further formal analysis is not warranted. But the slowly fading out of the autocorrelogram for length and numbers seems to point at a non-stationary process. Long-term behaviour is dominated by trends, not by stationarity. Indeed, inspection of figure 5a shows prolonged periods of declining or rising numbers and decreasing or increasing lengths.

Figure 5
Number, length and timing of glasseels immigrating at Den Oever : correlation of trends in time series.

Figure 5
Nombre, longueur et dynamique saisonnière des civelles à Den Oever : corrélation des tendances des séries.

- a. Time series
- b. Length versus number
- c. Timing versus length
- d. Timing versus number

Crosscorrelations

The timing of the immigration is hardly correlated with the numbers and length. Concerning timing and length, this is at least partially the result of the analysis model : allowance was made for the effect of delays in the immigration season on the perceived mean length per month. This correction reduced the correlation of the timing and length from $r = 0.48$ ($p = 0.001$) to $r = 0.17$ ($p = 0.158$). The long-term variation in the timing hardly exceeds the variation from one year to the next (autocorrelation $r = 0.08$), while the length has a more gradual development (autocorrelation $r = 0.55$, or $r = 0.38$ after correction for timing). Apparently, the correlation between length and timing is spurious or caused by short-term, probably local circumstances.

The estimated average number caught per year is positively correlated over the years with the length ($r = 0.70$, $p = 0.001$). Unfortunately, no way was found to discriminate between possible confounding of one by the other in the sampling or analysis and a true correlation. However, taking in mind that there appears to be no plausible mechanism for the confounding, it is concluded that length and numbers are most likely truly correlated.

Summarizing : the length and numbers of glasseels immigrating in Den Oever exhibit long-term and synchronous changes, while the timing of the immigration season fluctuates independently, probably due to local circumstances.

DISCUSSION

Framework of the analysis

The eel is a weird animal. Despite its economical value in many rural areas of Europe (375 M. ecu, MORIARTY, 1996), there is no stock-wide management of the scattered stock. Local management of eel fisheries in restricted areas of Europe has been effective in actually steering the production, by the grace of plentiful supply of glasseels from the ocean, until the mid eighties, when a prolonged series of poor years of recruitment started. It was only then that attention focused on the collectivity of the resource, first by scientists (EIFAC, 1993 ; CASTONGUAY *et al.*, 1994a, b), later followed by the responsible management bodies at the supranational level (MORIARTY, 1996 ; MORIARTY and DEKKER, 1997).

Following the establishment of the recruitment failure of both Atlantic eel species (MORIARTY, 1990, sources cited in CASTONGUAY *et al.*, 1994a), an inventory of potential causes has been made on both sides of the ocean (CASTONGUAY *et al.*, 1994a ; EIFAC, 1993 ; BRUSLÉ, 1994), based on the scarce evidence. Furthermore, the coincidence of events on both sides of the ocean was noted (CASTONGUAY *et al.*, 1994b). It is within this framework that the analyses reported in this paper were undertaken, aiming at factual evidence contributing to the process of selection and elimination of proposed hypotheses.

Historical development

The results confirm the reported major event in the European eel population in the eighties and nineties : the number of glasseels changed dramatically over a range of years, but so does their length ! In 1991, an all time low in numbers was observed in Den Oever, even beating the prolonged recruitment failure observed in the late forties and early fifties. Following 1991, both numbers and lengths show a slight recovery, observations now corresponding to the mid eighties' level.

The observed variation in mean length of the glasseels is about 11 mm. This exceeds the differences in length reported so far throughout the geographical distribution area of the eel (TESCH, 1977, p. 136). Time series of length measurements, except for the Den Oever series analysed here, apparently are lacking, but it seems plausible that Den Oever is not the only site having variation in mean length. Other published data relate to varying ranges of years, or even unspecified periods and are therefore hardly interpretable at the stock-wide level.

During metamorphosis and immigration, the length of leptocephali and glasseels diminishes (TESCH, 1977, p. 146), apparently due to the absence of feeding. It seems quite probable to explain the observed variation in length by variation in the duration of the non-feeding phase at sea. In that case, however, one would expect shorter glasseels in the later seasons, which is contrary to the findings. Moreover, the observed changes in length (11 mm) are much larger than the reported shrinkage during metamorphosis (5 mm).

The relationship of (the onset of) the glasseel immigration to local climatic circumstances has been noted before (see DEKKER, 1986, for the Den Oever data). Indeed, the estimated parameters of the timing correlate well with the water temperature at the sluices in February and March, but much less so with April and May temperatures (figure 6). In fact, the autocorrelation of the timing of immigration over the years is of the same magnitude as the autocorrelation of the water temperatures.

Figure 6

Relation of timing of the glasseel immigration season to the water temperature at the sluices.

Figure 6

Relation entre la saison d'immigration des civelles et la température de l'eau à l'écluse.

Cause and effect in the two time series

The analyses showed a 10 % reduction in average length of the glassseels. Although no records have been kept of the weight of glassseels, it seems likely that weight will have had a parallel evolution. It has been hypothesized (EIFAC, 1993 ; CASTONGUAY *et al.*, 1994a, b) that the reduction in numbers of recruits is the direct consequence of a strong reduction in the number of adults contributing to the spawning stock. The spawning stock is then thought to have been reduced by overfishing on any of the continental life stages (reducing the numbers directly), or by habitat destruction and migration barriers reducing the profitable dispersion area of the species, or by contamination and parasitism in the adults, hindering the effective spawning migration. If indeed, the decline of the spawning stock is primary to the decline in the number of recruits, it is hard to see why the remaining progeny has attained a smaller body size concurrently with the reduction in their numbers. Density dependent processes would induce larger, not smaller body sizes.

MCCLEAVE (1987) proposed a hypothetical mechanism for the settlement of leptocephali on the continental slope, metamorphosing into glassseels. In his view, the physical contact with the ocean bottom might induce the metamorphosis of the *Leptocephalus*. CASTONGUAY *et al.* (1994a) summarise this hypothesis, and then state "The effects of the (...) oceanographic changes (...) on continental invasion of glassseels are also unknown". Apparently, they hypothesize that oceanographic changes might have induced the recruitment failure by hindering the final settlement of the leptocephali on the continent. This hypothesis, as the ones above, can indeed explain the numerical evolution. But the synchronous evolution of the length of the glassseels makes a bottleneck earlier in the life of the leptocephali more plausible. Whether this occurs in the early larval phases or even in the parental phases is an open question.

Conclusions and speculations

The analyses presented in this paper do not reveal the cause of the observed recruitment failure. But they do narrow the scope for potential explanations.

CASTONGUAY *et al.* (1994a) explicitly list four potential causes :

1. Toxicity from anthropogenic chemical contamination ;
2. Anthropogenic habitat modifications ;
3. Commercial fishing, and
4. Oceanic changes.

Crossing the reported findings with the hypotheses, it soon becomes evident that oceanic changes are the most likely cause. The other hypotheses take the reduction in spawning stock to be primary to the reduction in numbers of recruits. As stated above, this would not explain, or even contradict the observed reductions in length of the recruits. Only the first hypothesis might be reformulated in a sense that toxicity operates through the parental phases on the larval growth and survival, but in the absence of any evidence, this interpretation is rather Procrustean.

However, without actual observations of the reproduction of the eel, it will not be too difficult to find some time series of oceanographic data that correlate exactly with the glassseel observations. The floor is open for speculation. Rather than stepping into this pitfall, it is concluded that the exploitation of the eel stock, and indeed the conservation of the species, is obviously dependent on processes far beyond the current knowledge. Eels still spawn in *terra incognita*. Clarification of this unsolved mystery should be the main and foremost topic on the agenda of the scientists and managers involved in the responsible management of the Atlantic eels.

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